On the Origins of New Forms of Life
A New Theory

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> *By doubting we come to questioning,*
> *and by questioning we perceive the truth.*
> —PIERRE ABELARD[1]

Once again, for Rebecca, Clara, and Margaret

And such things as are not commonly known, and lie scattered here and there in other men's writings, or are found among the old monuments and archives, I shall endeavor to bring together.

—PLUTARCH, *Nicias* (1st century A.D.)

They who have presumed to dogmatize on nature, as on some well investigated subject either from self-conceit or arrogance, and in the professorial style, have inflicted the greatest injury on philosophy and learning.

—FRANCIS BACON, *Novum Organum* (1620)

The conclusion reached by a process of thought is also not infrequently the conclusion of the process of thought.

—ARTHUR O. LOVEJOY, *The Great Chain of Being* (1936).

Preface

At one time, before I had become a geneticist and an expert on hybrids, it would never have occurred to me that hybridization might play a direct and frequent role in the production of new types of organisms, one of the primary claims made in this book. In fact, until I read the *Origin of Species,* I had never given hybrids much thought at all. I knew hybridization was a technique used in plant breeding and that a mule is a hybrid of a horse and an ass. But beyond these facts, my knowledge of hybrids was minimal. And yet I still made certain general assumptions about hybrids. For example, I had always believed organisms could interbreed only if they closely resembled each other and that some rule allowed biologists to predict with certainty whether a given cross was possible. I had also assumed hybrids were always sterile.

I was surprised, then, when I first encountered Darwin's observation that "No one has been able to point out what kind, or what amount, of difference in any recognizable character is sufficient to prevent two species crossing"[2] and that "the facility of making a first cross between any two species is not always governed by their systematic affinity [that is, by how closely they are related] or degree of resemblance to one another."[3] It was difficult for me to believe biologists lacked a firm predictive rule. I also balked when Darwin pointed out that hybrids are not always sterile:

> Finally, looking to all the ascertained facts on the intercrossing of plants and animals, it may be concluded that some degree of sterility, both in first crosses and in hybrids, is an extremely general result; but that it cannot, under our present state of knowledge, be considered as absolutely universal.[4]

Darwin's comments made me wonder: How often are hybrids fertile? Do they occur naturally? What is their evolutionary significance? I decided to investigate reported accounts of hybrids. As I read, it became clear that thousands of different crosses produce fertile hybrids. Eventually, in completing a book on bird hybrids (*Handbook of Avian Hybrids of the World,* 2006), I found that the majority of avian crosses, at least the majority of those for which data on fertility is available, actually do produce hybrids that are themselves capable of having offspring. Moreover, about half (i.e., about 1,800) of the crosses listed in my book occur in a natural setting. Many of these crosses occur on an ongoing basis and have produced permanent hybrid populations. I am currently working on a survey of hybridization among mammals. There, too, I have found that many crosses produce fertile hybrids and that many such crosses occur in a natural setting. In other categories of organisms, other workers have reported similar findings. Among fish and plants, such hybrids are even more numerous than among mammals or birds. Hybrids among invertebrates seem innumerable. After looking at so much data, I began to wonder: what becomes of these myriad hybrids that, from the standpoint of geological time, are being produced in such vast numbers? If many kinds of natural hybrids can produce offspring, which is clearly the case, what is the role of hybridization in the evolutionary process?

Over the years, I have accumulated information bearing on these issues and have made a particular study of genetic mechanisms known to produce new types of organisms, many of which involve hybridization. In the process, I have come to believe that certain important flaws in standard evolutionary theory have passed unnoticed, primarily because most people are unfamiliar with the actual facts of hybridization as revealed by observation. Indeed, in comparing modern attitudes toward hybrids with the statements of naturalists of past eras, I have come to the realization that we have retained certain potent presuppositions derived from ancient systems of thought without change and without substantiation. Some of these unfounded claims are axiomatic in the modern scientific account of the natural world. In particular, a stereotypic conception of hybrids as sterile evolutionary nonentities has remained largely in force. Even many biologists think this way. In this book I have tried to replace this stereotype with a new image that better corresponds with available data. I also offer a different theory of evolution that, I am convinced, is more consistent with observation than is Darwin's. I hope the reader will be convinced as well. Of course, I expect no one to accept such a radical assertion on faith. The validity of any theory can be assessed only by sifting through the evidence, point by point, fact by fact. I have therefore done my best to construct this book with what James Boswell once described as "that diligence which alone can collect those scattered facts that genius, however acute, penetrating and luminous, cannot discover by its own force."

I want to thank the many friends and colleagues who in some way helped with this book. They are too numerous to name individually, but I would like to express my special appreciation to Stuart Katz and my wife Rebecca. Their endless enthusiasm and support for this project kept me going when I would otherwise surely have set it aside.

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Extracts

This book is concerned more with the actual characteristics of hybrids than with their reputation. However, given the theoretical nature of this work, and given that hybridization plays an important role in the theory presented, it will be worthwhile to consider not only what hybrids are, but also how they have been perceived. The peculiar, often unfounded, impressions people have had of hybrids have contributed greatly to the position allotted them in theory — perhaps as much, or even more than, the facts. The following extracts, then, are intended merely to place hybrids within the context of human opinion. From a factual standpoint, many of the statements quoted in this section are false. More is conveyed here of connotation than of fact. Indeed, those who wish merely to learn the facts about hybrids might just as well pass over this section and proceed straight to page 1. But, for the curious reader who wants to understand more of human attitudes toward hybrids, these quotations may prove informative.

> You speak words of love, but when have you been
> true? In your youth, you wed Tammuz, but then
> soon left him. Now our autumns are sodden
> with his tears. And the Allala bird, when
> he wooed you, you embraced him as your mate.
> Then you struck him, broke his wing. Now he moans
> in the forest, alone. The lion you made
> your lover, then ensnared. With wild groans
> he died writhing, dangling by a paw. You
> seduced the stallion, then harnessed him – rode
> him raw. Even Silili, his dam, knew
> the strokes of your crop …
> *The Spurning Of Ishtar* (from the *Epic of Gilgamesh*)[5]

There was a time in which there existed nothing but darkness and an abyss of waters, wherein resided most hideous beings, which were produced of a two-fold principle. There appeared men, some of whom were furnished with two wings, others with four, and with two faces. They had one body, but two heads; the one that of a man, the other of a woman; they were likewise in their several organs both male and female. Other human figures were to be seen with the legs and horns of a goat; some had horses' feet, while others united the hind quarters of a horse with the body of a man, resembling in shape the hippocentaurs. Bulls likewise were bred there with the heads of men; and dogs with fourfold bodies, terminated in their extremities with the tails of fishes; horses also with the heads of dogs; men, too, and other animals, with the heads and bodies of horses, and the tails of fishes. In short, there were creatures in which were combined the limbs of every species of animals.

The Chaldean Account of Genesis[6]

You must observe my statutes. You may not allow two different kinds of animals to mate together. You are not to plant your field with two kinds of seed, not to wear a garment woven with two kinds of yarn. *Leviticus* 19:19-21[7]

Thou shalt not sow thy vineyard with divers seeds: lest the fruit of thy seed which thou hast sown, and the fruit of thy vineyard, be defiled. Thou shalt not plough with an ox and ass yoked together. *Deuteronomy* 22:9-10[8]

The Paphlagonians were commanded by the stout-hearted Pylæmenes Enetæ, where the mules run wild in herds.

HOMER
The Illiad (8th or 9th century B.C.)[9]

It was wine that inflamed the centaur Eurytion when he was staying with Peirithous among the Lapithæ. When the wine had got into his head, he went mad and did ill deeds about the house…Henceforth, therefore there was war between mankind and the centaurs.

HOMER
The Odyssey (8th or 9th century B.C.)[10]

O Maker of the material world, thou Holy One! Which of the two wolves deserves more to be killed, the one a he-dog begets of a she-wolf, or the one a he-wolf begets of a she-dog? *The Avesta*[11]

Deep in a grotto Kallirhoë birthed a second wild monster,
Like unto neither human nor god – proud, immortal Echidna,
Half fair-faced nymph, half monstrous python,
Writhing and insatiable — deep in the secret places of the earth.

HESIOD
Theogony (c. 8th century B.C.)[12]

The Master said: "There are blades that spring up and never flower, and there are others that flower but never bear fruit."

CONFUCIUS
Analects, Book IX, XXI (5th century B.C.)

Now therefore do not marry your daughters to their sons or take their daughters for your sons; nor must you ever seek their welfare or prosperity. Only thus will you be strong and enjoy the good things of the land, and hand it on as an everlasting possession to your descendants. *Ezra* (5th century B.C.)[13]

Many creatures arose with double faces and double breasts, offspring of oxen with human faces, and again there sprang up children of men with oxen's heads; creatures, too, in which were mixed some parts from men and some of the nature of women, furnished with sterile members. EMPEDOCLES
Fragments, Book III (5th century B.C.)

Now the reason why those of the Egyptians whom I have mentioned do not sacrifice goats, female or male, is this: the Mendesians count Pan to be one of the eight gods (now these eight gods they say came into being before the twelve gods), and the painters and image-makers represent in painting and in sculpture the figure of Pan, just as the Hellenes do, with goat's face and legs, not supposing him to be really like this but to resemble the other gods; the cause however why they represent him in this form I prefer not to say. The Mendesians then reverence all goats and the males more than the females (and the goatherds too have greater honour than other herdsmen), but of the goats one especially is reverenced, and when he dies there is great mourning in all the Mendesian district: and both the goat and Pan are called in the Egyptian tongue Mendes. Moreover in my lifetime there happened in that district this marvel, that is to say a he-goat had intercourse with a woman publicly, and this was so done that all men might have evidence of it. HERODOTUS
The History (5th cen. B.C.)[14]

At last, in the twentieth month, a marvelous thing happened to Zopyrus, son of Megabyzus who was among the seven men who overthrew the Magus. One of his sumpter-mules gave birth to a foal. Zopyrus, when they told him, not thinking that it could be true went, and saw the colt with his own eyes; after which he commanded his servants to tell no one what had come to pass, while he himself pondered the matter. Calling to mind then the words of the Babylonian at the beginning of the siege, "Till mules foal ye shall not take our city" — he thought, as he reflected on this speech, that Babylon might now be taken. For it seemed to him that there was a Divine Providence in the man having used the phrase, and then his mule having foaled. Ibid.[15]

As a general rule, wild animals are at their wildest in Asia, at their boldest in Europe, and most diverse in form in Libya; in fact, there is an old saying, 'Always something fresh in Libya.' It would appear that in that country animals of diverse species meet, on account of the rainless climate, at the watering-places, and these pair together; and that such pairs will often breed if they be nearly of the same size and have periods of gestation of the same length … Elsewhere also bastard-animals are born to

heterogenous pairs; thus in Cyrene the wolf and the bitch will couple and breed; and the Laconian hound is a cross between the fox and the dog. ARISTOTLE
History of Animals (4 h century B.C.)[16]

Every living thing loves its like,
and every person his own sort.
All creatures flock together with their kind.
Ecclesiasticus (2nd century B.C.)[17]

But still 'tmust not be thought that in all ways
All things can be conjoined; for then wouldest view
Portents begot about thee every side:
Hulks of mankind half brute astarting up,
At times big branches sprouting from man's trunk,
Limbs of a sea-beast to a land-beast knit,
And Nature along the all-producing earth
Feeding those dire Chimaeras breathing flame
From hideous jaws — Of which 'tis simple fact
That none have been begot; because we see
All are from fixed seed and fixed dam
Engendered and so function as to keep
Throughout their growth their own ancestral type. LUCRETIUS
On the Nature of Things, Book II (1st century B.C.) [18]

But Centaurs ne'er have been, nor can there be
Creatures of twofold stock and double frame,
Compact of members alien in kind,
Yet formed with equal function, equal force
In every bodily part — a fact thou mayst,
However dull thy wits, well learn from this:
The horse, when his three years have rolled away,
Flowers in his prime of vigour; but the boy
Not so, for oft even then he gropes in sleep
After the milky nipples of the breasts,
An infant still. And later, when at last
The lusty powers of horses and stout limbs,
Now weak through lapsing life, do fail with age,
Lo, only then doth youth with flowering years
Begin for boys, and clothe their ruddy cheeks
With the soft down. So never deem, percase,
That from a man and from the seed of horse,
The beast of draft, can Centaurs be composed
Or e'er exist alive, nor Scyllas be —

The half-fish bodies girdled with mad dogs —
Nor others of this sort, in whom we mark
Members discordant each with each; for ne'er
At one same time they reach their flower of age
Or gain and lose full vigour of their frame,
And never burn with one same lust of love,
And never in their habits they agree,
Nor find the same foods equally delightsome —
Sooth, as one oft may see the bearded goats
Batten upon the hemlock which to man
Is violent poison. Once again, since flame
Is wont to scorch and burn the tawny bulks
Of the great lions as much as other kinds
Of flesh and blood existing in the lands,
How could it be that she, Chimaera lone,
With triple body — fore, a lion she;
And aft, a dragon; and betwixt, a goat —
Might at the mouth from out the body belch
Infuriate flame? Ibid., Book V[19]

Sulla, having marched through Thessaly and Macedon to the seacoast, prepared with twelve hundred vessels to cross over from Dyrrhachium to Brundusium. Not far from thence is Apollonia, and near it the Nymphaeum, … there they say, a satyr, such as statuaries and painters represent, was caught asleep, and brought before Sulla, where he was asked by several interpreters who he was, and, after much trouble, at last uttered nothing intelligible, but a harsh noise, something between the neighing of a horse and the crying of a goat. PLUTARCH
Life of Sulla (1st century A.D.)[20]

Hibrida or hybrida: most prob. kindred with *hubridzo, hubris* — unbridled, lawless, unnatural; hence, of animals produced from two different species, a mongrel, hybrid.
CHARLTON T. LEWIS AND CHARLES SHORT,
Oxford Latin Dictionary

So great are the provisions made in the law to ensure that men should admit no unlawful matings, that it ordains that even cattle are not to be crossed with others of a different species. No Jewish shepherd will allow a billy goat to mount a ewe or a ram a nanny, or a bull a mare, or if he does, he will be punished as an offender against the decree of Nature (which is careful to preserve the primary species without adulteration). PHILO JUDAEUS
The Special Laws (1st century A.D.) [21]

A mingled form where two strange shapes combined,
And different natures, bull and man, were joined. PLUTARCH
Life of Theseus (1st century A.D.)[22]

It has been noticed that the offspring of two different species of animals belong to a third kind and resemble neither parent, and that not all of those so born bear offspring. PLINY THE ELDER
Natural History (1st century A.D.)[23]

The Indians want hounds to be sired by tigers, and at the time of breeding they tie up bitches in the woods for this purpose. They think that the first and second litters are too fierce and they only rear the third one. Ibid.[24]

For, behold, the days are coming, in which they shall say, Blessed are the barren, and the wombs that never bare, and the paps that never gave suck. LUKE, *23:29*

And I looked and saw other flying elements of the sun, whose names are Phoenixes and Chalkydri, marvellous and wonderful, with feet and tails in the form of a lion, and a crocodile's head, their appearance is empurpled, like the rainbow; their size is nine hundred measures, their wings are like those of angels, each has twelve, and they attend and accompany the sun, bearing heat and dew, as it is ordered them from God. *The Slavonic Book of Enoch,* 12:1[25]

An eagle snatched the intestines of the victim from the hand of Galba's grandfather, who was sacrificing to Jupiter, and carried them aloft into a burgeoning oak. When he was informed this event foretold his family's ascent to the emperorship, he responded with a laugh, "Very likely — when mules foal!" Later, then, when Galba began his revolt, nothing encouraged him more than the reported foaling of a mule. Although others looked upon it as an evil and obscene portent, he himself, remembering the prediction made by the seer at the time of the sacrifice and the response of his grandfather, regarded it as the most favorable of omens. SUETONIUS
Life of Galba (2nd century A.D.)[26]

The country of Elis is noted for two marvels: Firstly, among Grecian lands, only in Elis will fine flax grow; secondly, only outside the borders of this land can an ass impregnate a mare. PAUSAUNIUS
A Description of Greece (2nd century A.D.)[27]

In India there are herds of wild horses and wild asses. Now they say that when the asses mount the mares, the latter remain passive and take pleasure in the act and produce mules of a red color and extremely swift of foot, but that these mules are impatient of the yoke and generally skittish. The people are said to catch them with foot traps and then to take them to the king of the Prasii. If they are caught as two-

year-olds they do not refuse to be broken, but when older they are just as savage as fanged and carnivorous beasts. AELIAN
On the Characteristics of Animals (3rd century A.D.)[28]

Not long thereafter, in a rock-strewn vale, he [St. Antony] espied a small man with a hooked nose, his brow crowned with sharp horns, his lower extremities ending in the feet of a goat. ST. JEROME
Life of the Hermit Paul (4th century A.D.)[29]

The griffon is so called because it is a winged quadruped. These ferocious beasts live in the Hyperborean Mountains. They have the body of a lion, and the wings and head of an eagle. They are fierce enemies of horses. When they see men, they tear them to pieces. ISIDORE OF SEVILLE
Etymologies (6th century)[30]

Indeed, we know that both the mule, which is derived from the jackass and mare, and the hinny, derived from the jenny and stallion, enjoy copulation, although they produce no offspring. VENERABLE BEDE
In Samuelem Prophetam Allegorica Expositio (8th century)[31]

Never forsake your own kind. *The Blickling Homilies* (971 A.D.)[32]

Near Wicklow, at the time when Maurice FitzGerald first gained lordship there, was seen a human prodigy, if indeed it is correct to say "human". For while he had a human body, his extremities were those of a cow. To the joints which normally connect the hands to the arms, and the feet to the calves, were instead attached the hooves of an ox.

His head was entirely bald, except for a few patches of down in place of ordinary hair.

The eyes were large, cow-like in their roundness and color.

The face beneath was flat — merely two nostrils, with no protruding nose.

Speaking no words, he could only low.

Long an attendant of Maurice's court, he came every day to meals, and what he was given to eat, he gripped in the cleft of his hooves which served him as hands, and so conveyed it to his mouth. GERALD OF WALES
Of a Man Half-Bull and a Bull Half-Man (1188)[33]

They say onocentaurs are part human and part donkey, and hippocentaurs, part human and part horse. MARTINUS LEGIONENSIS (12th century)[34]

What is the use of those absurd monstrosities displayed in the [carved decorations of the] cloisters before the reading monks? See what deformed beauty and what beautiful deformity. Why are unclean monkeys and savage lions, and monstrous centaurs, and semi-men and spotted tigers, and fighting soldiers and pipe-playing hunters represented? You may see there many bodies with one head, and one body with many heads. Here a quadruped with the tail of a serpent, there a fish with the head of a quadruped. Here a beast half horse and half goat, there another with horns and a horse's body. The variety of form is so great everywhere that marbles are more pleasant reading than manuscripts, and the whole day is spent in looking at them, instead of meditating upon the law of God.

ST BERNARD OF CLAIRVAUX (12th century)[35]

They call those of ignoble birth "hybrid." ALANUS DE INSULIS
Distinctionibus Dictionum Theologicalium (12th century)[36]

Animals of the same species naturally intermingle through copulation. In addition to these there are those that are similar, though not of the same species … And, in all the animals mixed in this way, we see that both males and females can generate and preserve the species. Yet mules generate but rarely, even if they copulate with their own or a close species. ST. ALBERTUS MAGNUS
De animalibus (13th century A.D.)[37]

Animals of new kinds sometimes arise from the intercourse of individuals belonging to different species. ST. THOMAS AQUINAS
Summa Theologica (*c.* 1265-1274)[38]

And there, beside the chasm was the Minotaur, the abomination of Crete, conceived in the wooden cow. Seeing us, he bit himself as if in rage at something within.

DANTE
The Inferno (1314)[39]

In the time that Pope Julius II brought about so many misfortunes in Italy, he made war against King Louis XII in 1512, which brought about a bloody battle near Ravenna: Shortly thereafter in the same town a monstrous child was born with a horn on its head, two wings, and a single foot like that of a bird of prey; at its knee it had an eye. AMBROISE PARÉ, *Oeuvres* (1585)[40]

Perdita: Sir, the year growing ancient,
Not yet on summer's death, nor on the birth,
Of trembling winter, the fairest flow'rs o' th' season
Are our carnations and streak'd gillyvors,
Which some call nature's bastards: of that kind
Our rustic garden's barren; and I care not
To get slips of them.
Polixenes: Wherefore gentle maiden,
Do you neglect them?

Perdita: For I have heard it said
There is an art which in their piedness shares
With great creating nature.
Polixenes: And say there be;
Yet nature is made better by no mean
But nature makes that mean: so, over that art
Which you say adds to nature, is an art
That nature makes. You see, sweet maid, we marry
A gentler scion to the wildest stock,
And make conceive a bark of baser kind
By bud of nobler race: this is an art
Which does mend nature, change it rather, but
The art itself is nature.
Perdita: So it is.
Polixenes: Then make your garden rich in gillyvors,
And do not call them bastards. *The Winter's Tale*[41]

… a knave, beggar, coward, pandar, and the son and heir of a mongrel bitch.
King Lear

In the ninth rank of prerogative instances we will place bordering instances, … They are such as exhibit those species of bodies which appear to be composed of two species, or to be the rudiments between the one and the other … from their dignity, they must be treated of and classed separately, for they point out admirably the order and constitution of things, and suggest the causes of the number and quality of the more common species in the universe, leading the understanding from that which is, to that which is possible. FRANCIS BACON
Novum Organum (1620)[42]

We find means to make commixtures and copulations of divers kinds, which have produced many new kinds, and them not barren, as the general opinion is … Neither do we this by chance, but we know beforehand of what matter and commixture, what kind of those creatures will arise. FRANCIS BACON
New Atlantis (1627)[43]

It appears, consequently, that for one egg there is one soul or vital principle. But whether is this that of the mother, or that of the father or a mixture of the two? And here the greatest difficulties are occasioned by those eggs that are produced by the concurrence of animals of different species, as, for example the common fowl and pheasant. In such an egg, I ask, is it the vital principle of the father or that of the mother, which inheres? Or is it a mixture of the two? WILLIAM HARVEY
Animal Generation (1651)[44]

Jupiter, the Heathen's great God, is said to be metamorphosed into a Dragon, whereof flyeth this tale: when he fell in love with Proserpina, he ravished her in the likenesse of a Dragon, for he came unto her and covered her with the spires of his body … so that as he begot Ceres with childe in the likenesse of a Bull, he likewise deluded her daughter Proserpina in the likenesse of a Dragon … and I think the vanity of these took first ground from the Africans, who believe that the original of Dragons took beginning from the unnatural conjunction of an Eagle and a she Wolf. And so they say that the Wolf growing great by this conception, doth not bring forth as at other times, but her belly breaketh and the Dragon cometh out, who in his beak and wings resembleth the Eagle his father, and in his feet and tail, the Wolf his mother, but in the skin neither of them both. EDWARD TOPSELL
Of the Winged Dragon (1658)[45]

This year [1637] there was a hideous monster born at Boston, in New England, of one Mrs. Mary Dyer, a copartner with the said Mrs. Hutchinson, in the aforesaid heresies; the said monster, as it was related to me, was without head, but [it had] horns like a beast, scales or a rough skin like the fish, called the thornback; it had legs and claws like a fowl, and in other respects as a woman child.
NATHANIEL MORTON
New-England's Memorial (1669)[46]

We came alongside some rocks, fearful for their height and length. On one we saw painted two monsters that at first frightened us and upon which the bravest savage would not long dare to gaze. Each was the size of a calf and had antlers like a roe deer's, a hideous expression, red eyes, and a tiger's beard. The face was almost human, the body scaled, and the tail so long it passed entirely around the body and over the head. Returning between the legs, it ended in the tail of a fish.
JACQUES MARQUETTE
Of the first Voyage made by Father Marquette toward New Mexico (1674)[47]

Those pure immortal elements, that know
No gross, no unharmonious mixture foul,
Eject him, tainted now, and purge him off. JOHN MILTON
Paradise Lost (1674)

But now why such different Species should not only mingle together, but also generate an Animal, and yet that that hybridous Production should not again generate, and so a new Race be carried on; but Nature should stop here and proceed no further, is to me a Mystery and unaccountable. JOHN RAY
The Wisdom of God Manifested in the Works of Creation (1692)

Some think, the Quince and Apple wou'd combine
In happy Union; Others fitter deem
The Sloe-Stem bearing Sylvan Plums austere.
Who knows but Both may thrive? Howe'er, what loss
To try the Pow'rs of Both, and search how far
Two different Natures may concur to mix
In close Embraces, and strange Off-spring bear? JOHN PHILIPS
Cyder (1708)

This pigeon … is also thought by some to be a bastard breed from the jack, and others assert it to be a distinct species, but 'tis very certain that a jack and another Pigeon will breed a Bird so like it, as will puzzle the authors of this assertion to distinguish it from what they call their separate species. JOHN MOORE
(commenting on the origin of the Capuchine Pigeon in *The Columbarium,* 1735)

The mules between the carp and tench partake of the nature of both fish … Whether these mules are capable of propagating their species, I cannot affirm; never having made any experiments on that subject; nor have I heard any thing said on that head with any degree of precision, or founded on experience. JOHN R. FORSTER
Philosophical Transactions of the Royal Society (1771)[48]

Hybrid: a Bastard, a monstrous Production of two Plants of different Species.
JAMES LEE
An Introduction to Botany (1788)

Hybrid: a mongrel or mule; an animal produced from the mixture of two species.
NOAH WEBSTER
An American Dictionary of the English Language (1828)

Oh, me father was the keeper of the Eddystone Light
And he slept with a mermaid one fine night.
From this union there came three;
A porpoise, and a porgy, and the other was me!
Singing, Yo ho ho, the wind blows free.
Oh, for the life on the rolling sea! *The Eddystone Light*

The commerce of the two races of whites and blacks has, by the laws of the state [of Maryland], been strictly prohibited. A free negro or mulatto intermarrying with a white woman, becomes a slave for life. A white woman having issue by any negro or mulatto, is made a servant for seven years. White men having issue by any negress or mulatto, become servants for seven years. Free negro or mulatto women, having bastard issue by white men, are subject to the same penalty. U.S. SUPREME COURT
Brewer's Lessee v. Blougher (1840)

It was by proclaiming to the labouring whites who filled the armies of rebellion that the election of Mr. Lincoln involved emancipation, equality of the negroes with themselves, and consequent amalgamation, that their jealousy was stimulated to the fighting point. Nor is this jealousy the fruit of mere ignorance and bad passion, as some suppose, or confined to the white people of the South. On the contrary, it belongs to all races, and, like all popular instincts, proceeds from the highest wisdom. It is, in fact, the instinct of self-preservation that revolts at hybridism.

EDWARD DICEY
Six Months in the Federal States (1863)[49]

That very ingenious writer, M. A. de Gobineau … has thought proper to affirm, in his *Essay on the Inequality of Human Races* (1855), that the crossing of races constantly produces disastrous effects, and that sooner or later, a physical and moral degeneration is the inevitable result thereof. It is, therefore, chiefly to this case that he attributes the decline of the Roman Republic and the downfall of liberty, which was soon followed by the decline of civilization. I am very far from sharing this opinion, and, were this the proper place, I might show that the social corruption and the intellectual degradation which prepared the ruin of the Roman power was due to quite different causes.

PAUL BROCA
On the Phenomenon of Hybridity of the Genus Homo (1864)

With forms that must be ranked as undoubted species, a perfect series exists from those which are absolutely sterile when crossed, to those which are almost or completely fertile. The degrees of sterility do not coincide strictly with the degree of difference between the parents in external structure or habits of life.

CHARLES DARWIN
The Descent of Man (1871)[50]

Bastard: Mongrel, hybrid, of inferior breed. *The Oxford English Dictionary*[51]

The *Merrow* … is not uncommon, they say, on the wilder coasts. The fishermen do not like to see them, for it always means coming gales. The male *Merrows* … have green teeth, green hair, pig's eyes, and red noses; but their women are beautiful, for all their fish tails and the little duck-like scale between their fingers. Sometimes they prefer, small blame to them, good-looking fishermen to their sea lovers. Near Bantry, in the last century, there is said to have been a woman covered all over with scales, like a fish, who was descended from such a marriage.

WILLIAM BUTLER YEATS
Fairy and Folktales of the Irish Peasantry (1888)

When Atlantis, with all her mighty cities and her cultivated fields and her great commerce and culture and riches sank into the sea long ages since, she took with her all but a handful of her colonists working the vast gold mines of Central Africa. From these and their degraded slaves and a later intermixture of the blood of the anthropoids sprang the gnarled men of Opar. EDGAR RICE BURROUGHS

Tarzan and the Jewels of Opar (1918)[52]

Surely some revelation is at hand;
Surely the Second Coming is at hand.
The Second Coming! Hardly are those words out
When a vast image out of *Spiritus Mundi*
Troubles my sight: somewhere in sands of the desert;
A shape with lion body and the head of a man,
A gaze blank and pitiless as the sun,
Is moving its slow thighs, while all about it
Reel shadows of the indignant desert birds.
The darkness drops again; but now I know
That twenty centuries of stony sleep
Were vexed to nightmare by a rocking cradle,
And what rough beast, its hour come round at last,
Slouches towards Bethlehem to be born?

WILLIAM BUTLER YEATS

The Second Coming (1919)

Introduction

I will speak of changes of form.
—OVID
Metamorphoses[105]

How does evolution occur? — That is, what natural processes bring new types of organisms into being? Expressed more technically, one might ask, what are the genetic processes that have produced the various forms scientists recognize and assign scientific names? This is the question considered in this book. Certainly, there is a great mass of literature already available on this topic. But my own, more than 20-year investigation of that literature has convinced me that *certain* widely accepted claims about the nature of evolutionary processes represent little more than unsubstantiated dogma, as unsupported by replicable experiment as the events described in Genesis.

I readily admit that *many* of the claims made by my fellow evolutionary biologists are in fact correct and entirely reasonable. But some are *inconsistent* with fact and, in my opinion, the corresponding aspects of evolutionary theory need adjustment. The theory of evolution should conform to the facts of evolution. By collecting all the relevant facts together here, I hope to lead you to the same conclusion. It remains true, as R. S. Crane liked to say, that "there is no authority but evidence." In this book I have gathered evidence of all sorts that seemed to have any direct bearing on the question at hand. Moreover, I have tried to present that evidence in such a way that a non-biologist can understand it, so long as he or she reads this book in the order it is written. For the issues considered here are of vital concern, not only to the few people who call themselves evolutionary biologists, but also to all humanity.

For the last 150 years, we biologists have been defending a fortress built by Charles Darwin. We have spent our energies hurling back the assaults of the creationist infidels and shoring up a slowly crumbling foundation that once seemed based on the hard bedrock of direct observation. But an ocean of data, accumulating since 1859, has been slowly lapping away at the rotting stone beneath Darwin’s castle, undermining its moldering walls, making it an ever more dangerous place to reside. As Darwin's most eloquent proponent, T. H. Huxley, once said, "Every great truth begins as heresy and ends as superstition." In the case of evolutionary theory, Huxley appears to have been right. Facts presented in this book do indeed suggest that certain elements of Darwin's heresy can now best be interpreted as a kind of superstition. It was Huxley, too, who warned us not to "pretend that conclusions are certain which are not demonstrated or demonstrable." I will argue that certain important tenets of modern evolutionary theory actually do fall into this category.

I want to present the facts that compelled me to abandon my former ideas of how evolution occurs. As we shall see, a different account of the evolutionary process is far easier to defend on an evidentiary basis than is the one given by most biology texts. According to this alternative view, what we may term *stabilization theory,* certain genetic processes known to disrupt the normal reproductive cycle are the typical source of new types of organisms (a variety of these *stabilization processes* are described in Chapter Four). Although stabilization theory is a new explanation as a whole, its intellectual components have a long tradition in biological thought and all the phenomena it invokes are all well known and well documented. Presenting those components, providing examples of the phenomena involved, and discussing the relevant aspects of the history of biology, will require all the chapters of this book. But, I suspect many readers will have a very different idea of the nature of evolution by the time they've reached its end.

The orthodox account of evolution is based on the ideas of Charles Darwin and the findings of Gregor Mendel. The most common name for this theory is *neo-Darwinism,* although it also is known as the *modern synthesis* (often capitalized), or the *synthetic theory.* This theory supposes that in the course of evolution the typical new form arises from a preexisting form via the gradual accumulation of distinctive traits. In other words, the new characteristics are acquired in sequence over time, not all at once. Most of these traits are assumed to be advantageous to reproduction and therefore to accumulate under the influence of natural selection. As Darwin puts it in the *Origin of Species,*

> Whatever the cause may be of each slight difference in the offspring from their parents — and a cause for each must exist — it is the steady accumulation, through natural selection, of such differences, when beneficial to the individual, that gives rise to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted to survive.[106]

In addition, modern adherents of this theory assume some of these gradually accumulating traits are neither advantageous nor disadvantageous. These "neutral" traits," too, are assumed to gradually accumulate, but at random. The process of accumulation, for both selected and neutral traits, is described as occurring in a population that does not interbreed, or does not interbreed significantly, with other, similar populations. Proponents of this view deem the latter supposition necessary, because they believe the genetic influence of interbreeding would otherwise prevent the evolving population from accumulating distinctive traits. Under this scheme, as two populations descended from a common ancestral population become increasingly distinct, they are said to "diverge." They were once the same, but depart from each other in character.

Although neo-Darwinians do assume some neutral traits can accumulate at random during the course of divergence, they also assume natural selection is the primary force driving this accumulative process. The idea of natural selection can be described as follows: (1) the individual members of natural populations differ with respect to heritable traits having a differential effect on the ability to survive and reproduce; and (2) traits favoring survival and reproduction are more likely to be passed on to the next generation. They are *naturally* selected, just as a breeder artificially selects particular traits. So, as the theory goes, traits favoring survival and successful reproduction will tend to accumulate over time and bring about changes in the affected form. This mechanism seems so obvious that it is hard at first to see any way it could be mistaken. The idea of an accumulation of differences resulting in gradual divergence (and ultimately in the production of macroevolutionary differences) is axiomatic in neo-Darwinian theory, and is therefore the orthodox account of evolution. Scientists who hold such views believe evolution is the result of ongoing change within isolated populations (which supposedly causes the divergence of those populations). Thus, two well-known evolutionary biologists, Hartl and Clark (1989: 1), assert that "fundamentally, evolution is the result of progressive change in the genetic composition of a population." But not everyone agrees with this idea.

Over the last three decades the neo-Darwinian perspective has been extensively criticized, but no one has set forward a coherent theory to replace it. In this book, I attempt to do just that. I also do my best to explain why this alternative theory is preferable to neo-Darwinian theory. The approach I have used in constructing my argument is simple. It has been to identify claims supporting neo-Darwinian theory that are widely accepted, but poorly documented, and then to examine them in the light of evidence. In his book, *The Great Chain of Being,* Arthur Lovejoy comments that there are

> implicit or incompletely explicit *assumptions,* or more or less *unconscious mental habits,* operating in the thought of an individual or a generation. It is the beliefs which are so much a matter of course that they are rather tacitly presupposed than formally expressed and argued for, the ways of thinking which seem so natural and inevitable that they are not scrutinized with the eye of logical self-consciousness, that often are most decisive of the character of a philosopher's doctrine, and still oftener of the dominant intellectual tendencies of an age.[107]

Biologists are no exception to this rule. During the course of my study of evolutionary thought, I became aware there are indeed certain tacit presuppositions made by many of my colleagues, "ways of thinking," as Lovejoy puts it, "which seem so natural and inevitable that they are not scrutinized." Indeed, for a long time I embraced many of these same assumptions myself. So long as they do escape scrutiny, these presuppositions seem clearly to demonstrate the validity of neo-Darwinian theory. But these claims cannot stand the bright light of fact. If I have properly done my work, by the end of this book each such fallacious assumption will have been spelled out and the exact nature of the errors associated with each will have been made explicit.

Let the reader be forewarned, then, that certain conclusions taken for granted within the context of neo-Darwinian theory cannot be taken for granted here. Stabilization theory posits axioms that differ from, and that are even logically inconsistent with, those of neo-Darwinism. Therefore, anyone who accepts the traditional view of evolution will have to proceed with caution. This book focuses on the validity of axioms. It attempts to show that the axioms on which stabilization theory is based are more valid, that is, are more consistent with available evidence, than are those of neo-Darwinism. Consequently, it will not be possible, nor would it be fair, for the reader to judge between neo-Darwinian theory and stabilization theory merely by considering whether the claims of stabilization theory are consistent with the claims of the standard view. Here the standard view itself is at stake. The discrimination must instead be based on whether available evidence — that is, empirical data — better supports the assumptions of one view or the other. If neo-Darwinism is flawed in its very axioms, then inferences based on that view will no longer hold water. Therefore, even when the assertions of stabilization theory radically contradict widely accepted claims concerning the nature of the evolutionary process, I ask the reader to look first to the evidence and not to dismiss such assertions simply because they conflict with the standard view.

Hybridization plays a far more important role in stabilization theory than in neo-Darwinian theory. The word *hybrid* has been defined in various ways, but a particular definition is well suited to stabilization theory. If two populations are consistently distinct with respect to one or more characters, and if a descendant of matings between those populations is discernibly mixed with respect to those characters, then that individual is a *hybrid* and any process producing such individuals is *hybridization*. (Note that *population* here simply refers to any set of organisms defined by a particular set of characteristics.) Although hybrids are often less fertile than either of their parents, many still are capable of producing offspring. Therefore, the term *partially fertile* is usually used in this book to describe hybrids that can produce progeny, since merely saying "fertile" or "sterile" under such circumstances would be misleading.[108]

Most, but not all, of the evolutionary processes posited by stabilization theory involve hybridization, a phenomenon that will be discussed in detail in the second chapter of this book. However, I would like to emphasize at the outset that this is a book about how new types of organisms come into being, not about hybridization *per se*. It is not intended to be a comprehensive review of neo-Darwinian ideas concerning the significance of hybridization. Rather it is intended to compare at a philosophical level, the relative merits of stabilization theory and neo-Darwinian theory. It does this by comparing the explanatory powers of the two hypotheses. That is, it considers a whole series of phenomena, and in the case of each of these phenomena it evaluates which of the two theories provides the better explanation of that phenomenon. Not wishing to bore the reader with extraneous considerations, I have attempted to limit discussion to those cases where such discriminations can actually be made. To discuss all the phenomena that both theories explain equally well would be both pointless and tedious. So this book, for the most, part neglects the nuances of the various neo-Darwinian debates related to hybridization. It focuses on those phenomena (and the associated explanations of those phenomena) that allow the reader to discern which of the two theories is to be preferred.

At this point the reader may wish to have some idea of what lies ahead in this book. The contents of the second and fourth chapters have already been indicated. Chapter Five discusses what is known about the prevalence of stabilization processes. Chapter Six examines the evidence of the fossil record as it bears on the relative prevalence of the processes postulated by neo-Darwinian theory and by stabilization theory. Chapters Seven and Eight explain stabilization theory in detail. These three chapters (Six, Seven, and Eight) also include historical information in order to provide intellectual context for the discussion. As an example of how stabilization theory can be applied, Chapter Nine reevaluates the origin of mammals by means of the sort of reasoning stipulated in this new perspective. Chapter Ten considers a few of the general implications of stabilization theory.

Because the evolutionary processes it emphasizes typically produce new types of organisms in a relatively rapid and abrupt manner, stabilization theory undermines a primary tenet of neo-Darwinian theory — the claim that evolution is usually a process involving the gradual accumulation of differences within an evolving population. Stabilization theory does not, however, entirely dismiss the mechanisms described in neo-Darwinian theory. It merely claims they are relevant only within a restricted domain (which will be specifically identified in Chapter Three, after certain requisite terminology has been introduced). It does, however, assert that stabilization processes are the main cause of evolution. This difference in emphasis is justified because such processes are now known to be far more widespread than was once thought. Moreover, the expected pattern of evolutionary change produced by such processes matches the pattern of change actually observed in the fossil record (Chapter Six). These processes are also far better documented than many of the evolutionary mechanisms described in neo-Darwinian theory. They therefore can justifiably claim a larger place in theory. This book, then, represents an effort to bring theory in line with currently available data. It reviews empirical evidence both from the standpoint of evolutionary phenomena requiring explanations and from the standpoint of observed phenomena that might provide those explanations.

But let's begin, in the first chapter, with a discussion of the origin and meaning of *species,* a word that lies at the center of modern biological thought.

1 On Species

It is not only what we have inherited from our fathers and mothers that exists again in us, but all sorts of old dead ideas and all kinds of old dead beliefs and things of that kind. They are not actually alive in us; but there they are dormant, all the same, and we can never be rid of them. Whenever I take up a newspaper and read it, I fancy I see ghosts creeping between the lines. There must be ghosts all over the world. —HENRIK IBSEN, *Ghosts*

For many, an evolutionary theory is an explanation of the origin of "species." But, in fact, *species* is a vague and ambiguously defined word — a fact that most biologists would readily admit — and its meaning has been endlessly debated. The ultimate purpose of this book is to make certain claims about the nature of the evolutionary process. I am convinced, however, that it would be very unwise, in beginning such a project, to pass over the fact that *species* is, in fact, an ill-defined entity. How can we expect to construct a clear explanation of the evolutionary process if a key element in our account has no clear meaning?

This first chapter, then, will examine the history, meaning, and usage of *species*. It will not gloss over, as do many works on evolutionary theory, the problems associated with this word. Such a discussion is presented here, not only to explain the fact that stabilization theory makes far less use of the word *species* than does conventiional theory, but also to make some important points about the nature of evolutionary debate. In particular, this book begins with a discussion of *species* because any clear argument, of any sort, must define its terms. Ultimately, this chapter will stipulate the exact ways in which *species* can be used within the context of stabilization theory, which are severely restricted in comparison with normal practice under conventional theory. But, before that point can be reached, a good bit of explanation will be needed to show why such restrictions are necessary.

***On the Origin of the Word* Species:** The story of the word *species* (Greek *ειδος*[109]) begins with Plato. According to St. Thomas Aquinas (*Summa Theologica*, ca. 1265–

1274 A.D.),

> the early philosophers, who inquired into the natures of things, thought there was nothing in the world save bodies. And because they observed that all bodies are movable, and considered them to be always in a state of flux, they were of opinion that we can have no certain knowledge of the truth of things. For what is in a continual state of flux cannot be grasped with certitude, for it passes away before the mind can form a judgment of it, according to the saying of Heraclitus, that "it is not possible twice to touch a drop of water in a passing torrent," as the Philosopher [i.e., Aristotle] relates.[110]
>
> After these came Plato, who, wishing to save the certitude of our knowledge of truth through the intellect, maintained that, besides these things corporeal, there is another genus of beings, separate from matter and movement, which beings he called *species* or *ideas*, by participation of which each one of these singular and sensible things is said to be either a man, or a horse, or the like. And so he said that sciences and definitions, and whatever pertains to the act of the intellect, are not referred to these sensible bodies, but to those beings immaterial and separate, so that according to this the soul does not understand these corporeal things, but the separate species of those corporeal things.[111]

As used by Aristotle, *genus* and *species* were philosophical categories. A genus was a category and a species was a subcategory of a genus. The two terms were just as often applied to inanimate things as to living ones. For example, it would have been nothing unusual to say "*house* is a species of the genus *building*." Aristotle defined a thing by specifying its "*το τι ην ειναι*," which might be rendered in English as the "what-it-is-to-be" of that thing — i.e., that which makes it what it is. (The Romans translated *το τι ην ειναι* with the word *essentia,* which gave rise to the English word *essence.*) To specify the essence of any given thing, Aristotle stated its genus and its *differentia* (pl. differentiae), the quality distinguishing the species from others in the same genus. For example, he defined *human* as "a rational animal" (*animal* is the genus and *rational,* the differentia). Aristotle's system of logic was basic to the thought of the schoolmen who laid the foundations of biology in the early modern era.

The Natural Order. Early naturalists also thought in terms of Plato's Theory of Ideas. Under this view there were two separate worlds, or "realms of being." There was this world, the one perceived by the senses, the "World of Sensible Things," and there was a second, imperceptible world, the "World of Ideas." Medieval churchmen had argued, and the schoolmen of the early scientific era still accepted, that God had created this perfect world of ideas and that it gave order to the perceptible world. The ideas, in their separate realm, were eternal and immutable.[a] In the perceptible world,

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[a] The very word *idea* was at that time more narrowly defined than today. Writing in the late eighteenth century, James Boswell comments that the great lexicographer Samuel Johnson "was particularly indignant against the almost universal use of the word *idea* in the sense of *notion* or *opinion,* when it is clear that *idea* can only signify something of which an image can be formed in the mind. We may have an *idea* or *image* of a mountain, a tree, a building; but

individuals of a given type differed in nonessential details — each was an imperfect representation, an exemplar, of an essential, eternal, perfect idea. The words used to refer to these ideas or types were those of Aristotelian logic, that is, *species* and *genus.* All of the various existing types of organisms were considered eternal and immutable, because it was believed that the various *essentiae,* which were the supposed principles by which things were made, were themselves eternal.

This notion of a parallel world inhabited by the eternal essences of a divine order will seem rather outlandish to most modern readers. But it was generally accepted by early Christian thinkers and by the schoolmen of the medieval and early modern periods. They strove to construct a hierarchy of classification that reflected the existence of a logical natural order demonstrating the existence of a rational divinity. "The best thing in creation," asserted Aquinas (*Of God and His Creatures,* XLIV), "is the perfection of the universe, which consists in the orderly variety of things."[112] In his magnum opus *De plantis* (1583), Andrea Cesalpino (1519–1603), the first great systematist of the modern era, arranged plants in a hierarchical, graded order. *De plantis* was written in emulation of Aristotle, from whom Cesalpino borrowed the method of classification by logical division, a method familiar to every educated person from the Middle Ages through the end of the eighteenth century.[113]

What many biologists fail to realize is that up to about 1800 the activity of classifying organisms remained intricately enmeshed with metaphysics. The writings of classifiers of this era are so suffused with scholastic dogma and jargon that only a specialist can now understand them.[114] The creator of the modern system of biological nomenclature, the Swedish naturalist, Carl Linnaeus (1707–1788), was no exception. Mayr (1982: 173) says the reason Linnaeus is hard to understand today

> is that many of the terms used by him, like "genus," "species," "name," to "know," and "natural system," have the very special meanings which these terms have in the system of scholastic logic. In school Linnaeus had excelled in logic, and he was evidently deeply impressed by the precision of this method. From Cesalpino on, every botanist had applied logical division with more or less consistency and it still dominated Linnaeus.

"It is principally from Aristotle," observes Daudin (1926), "that are derived the traditional notions to which natural history was to give application, beginning with the Renaissance. … Thus it was that from the end of the sixteenth to the end of the eighteenth century, the project of distributing all living beings, animal or vegetable, into a hierarchy of collective units enclosed one within another, gained such a hold upon naturalists, that it finally seemed to them the formulation of their scientific task."[115] The same sort of hierarchal system, with categories enclosing categories, is still in use today. However, unlike modern naturalists, the schoolmen thought of these categories as corresponding to the Eternal Ideas, resident in their parallel world beyond the reach of perception. As Lovejoy (1936: 227) points out, "To range

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we cannot surely have an *idea* or *image* of an *argument* or *proposition.*" (*Life of Johnson*, 23 Sept. 1777).

animals and plants in well-defined species, presumably (since the Platonic dualism of realms of being was also still influential) corresponding to the distinctness of the Eternal Ideas, was the first business of the student of the organic world." Ironically, the "well-defined species" is a subject with which many biologists are still concerned today.

Hybrids and Immutability. Although many religious people claim "species" are eternal and unchanging, no such idea is expressed in the Bible. It says only that animals and plants were created "in the Beginning," not that they remained the same thereafter. Modern religious thinkers who adhere to the notion of immutability obtained it from the schoolmen, who in their turn, took it from Aristotle, a pagan, who did make such a claim (*On the Generation of Animals,* fourth century B.C.):

> For since it is impossible that such a class of things as animals should be of an eternal nature, Therefore that which comes into being is eternal in the only way possible. Now it is impossible for it to be eternal as an individual (though of course the real essence of things is in the individual) — were it such it would be eternal — but it is possible for it as a species.[a]

The scholastic philosophers adhered to this notion of immutability, just as they did to most other things Aristotle said. Thus, in the *Summa,* Aquinas, the greatest of the schoolmen, confirms the idea of immutability:

> Therefore, since in things corruptible none is everlasting and permanent except the species, it follows that the chief purpose of nature is the good of the species, for the preservation of which natural generation is ordained.[116]

The assumption that there truly were "natural species," immutably established by the "Author of Nature," continued to hold sway on into the scientific era. Thus, in his *Essay toward a Natural History of the Earth* (1695), which is as much religious diatribe as natural history, John Woodward boasts

> I will prove … that the Animal and Vegetable Productions of the Antediluvian Earth did not in any way differ from those of the present Earth. That there were then the very same kinds of Animals and Vegetables, and the same subordinate Species under each kind that now there is. That they were of the same stature and size, as well as of the same shape; their Parts of the same Fabrick, Texture, Constitution, and Colour, as are those of the Animals and Vegetables at this day in being.[117]

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a. Book II, Ch. 1. See Hutchins (1952b: vol. II, 272). However, elsewhere (*Generation of Animals*, 747A15) Aristotle claimed animal hybrids are typically of normal fertility: “It is known that with one exception all the animals that are produced as the result of such unions copulate with each other and unite in their turn and are able to produce young of both sexes. Mules are the one exception. They are sterile and do not generate either by union with each other or with other animals.”

Often, in connection with such assertions, it was claimed that God, or a personified Nature viewed as a sentient force, had made hybrids sterile in order to prevent the various types that made up the divine creation from blending together. The marriage of these two claims — though both were unsubstantiated by observation (see Chapter 2) — is encountered again and again in the writings of a broad range of authors of the early scientific period. Thus, Oliver Goldsmith in his preface to *Brooke's Natural History* (1763: 251) writes the following:

> Happily for mankind, the most intricate enquiries are generally the most useless. Modest nature has concealed her secret operations from rash presumption; it may suffice man to be certain, that she always acts with uniformity and success. Tho' we cannot discover how animals are generated, we know that every species is still transmitted down without mixture, and that the same characteristic marks which distinguished them in the times of Aristotle and Pliny, divide them to this day. Creatures of different kinds may be brought to produce between them, indeed an animal partaking something of each, yet different from either, but here the confusion ends; for this new being, this monster of nature, is incapable of continuing the breed, and is marked with perpetual sterility.[118]

Jean-Jacques Rousseau (*Émile,* The Creed of a Savoyard Priest, 1762) gives his readers a similar account of Dame Nature's plan:

> The mere generation of living organic bodies is the despair of the human mind; the insurmountable barrier raised by nature between the various species, so that they should not mix with one another, is the clearest proof of her intention. She is not content to have established order. She has taken adequate measures to prevent the disturbance of that order.[119]

In the 1700s, many considered even plant hybrids, widely taken for granted today, unnatural. For example, *Chambers Cyclopedia of English Literature* (1727–1741) listed the following definition: "*Mules,* among gardeners, denote a sort of vegetable monsters, produced by putting the *farina fœcundans* [i.e., pollen] of one species of plant into the pistil or utricle of the other."[120] Zirkle (1935: 1) notes that

> as late as the eighteenth century hybridization was not altogether reputable and a number of the early plant breeders felt called upon to justify their attempts at crossing different species. There seems to have been a widespread belief that sexual intercourse between diverse types was an immoral perversion and that the production of new forms of life was an impious affront to the Deity, a tacit criticism of the original work of Creation.

This notion that nature proscribed hybridization to preserve the natural order is of ancient origin. The Roman poet Lucretius (*On the Nature of Things,* V, first century B.C.) gave clear expression to the idea:

> The kinds of herbage and corn and joyous trees which even now spring in plenty out of the earth yet cannot be produced with the several sorts plaited into one, but each thing goes on after its own fashion and all preserve their distinctive differences according to a fixed law of

nature.[121]

In Latin, the word *hybrida* was applied not only to hybrids, but also to anything that violated natural law. Thus, Lewis and Short (*Latin Dictionary*) give the following definition of the word from which our *hybrid* is derived: "unbridled, lawless, unnatural; hence, of animals produced from two different species, a mongrel, hybrid." In the same place, they note *hybrida* is probably kindred to *hubris* (*υβρις*), used by the ancient Greeks to designate any violation of the natural order, especially one involving sexual matters.[a] Apparently, hybrids fell under the heading of *hubris* because hybrid organisms resulted from a form of sexual contact deemed to breach that order.[122] There was a religious significance attached to such matters since the Greeks believed acts of hubris brought down the curse of the gods.

Jews, too, from an early date viewed hybridization as a desecration of a natural order laid down by God. Writing in the first century A.D., the Jewish scholar Philo Judaeus (*The Special Laws,* III, 46) asserts that

> So great are the provisions made in the law to ensure that men should admit no unlawful matings, that it ordains that even cattle are not to be crossed with others of a different species. No Jewish shepherd will allow a billy goat to mount a ewe or a ram, a nanny, or a bull, a mare, or if he does, he will be punished as an offender against the decree of Nature (which is careful to preserve the primary species without adulteration).

Many even in the modern era have expressed this idea that God abhors transgressions of natural law. For example, in his *Notes on the Miracles of Our Lord* (1846), Anglican Archbishop Richard Chevenix Trench comments that "the unnatural, the contrary to order, is of itself ungodly."[123] Such ideas are even broadened at times to encompass hybridity of a purely abstract and non-biological nature. For example, an early film critic, Victor Oscar Freeburg claimed lasting art can never result when media are mixed:

> Nature abhors a mixture of species and therefore does not allow hybrid animals to perpetuate themselves by reproduction. The history of the development of aesthetic taste shows the same abhorrence for hybrid art. Hybrid art is not pure and therefore cannot endure as art. Some of

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[a] The word *hybrida* appears in Latin in the sense of a cross-bred human being by the end of the Roman Republic (prior to 50 B.C.). Thus, Julius Caesar (*Bellum Africum,* 19.3) used *hybrida* to describe half-breed soldiers in an opposing army. A decade later, in his satires (I.7.2), Horace (30 B.C.) also uses *hybrida* in this sense. Some scholars have suggested *hybrida* was originally used in Latin in the narrow sense of hybrids between tame and feral pigs (see OED, *s.v. hybrid*), but this argument is based on usages in Pliny the Elder, and later authors dating a century or more after those just cited. The restriction in sense therefore is probably unwarranted. For a detailed discussion of this topic see Warren (1884). The Romans introduced the letter *y* during the late Republic to transliterate Greek υ into Latin (Wheelock 1963: xxxi). Apparently, the *ς* of *υβρις* became the *d* of *hybrida* because the transliteration was based on a declined form of *υβρις* such as *υβριδος* (accusative singular). The substitution of the Latin feminine ending *–a* completed the transition.

> the Greeks, for example, tried the cross-breeding of the arts by painting complexions on their statues, but the resulting hybrid, half painting and half sculpture could not endure as art and is remembered in history only as an interesting mistake.[124]

Linnaeus' Opposition to Immutability. It must be said, however, that throughout much of the history of science there have been those who rejected the claim that hybrids are unnatural and consistently sterile. In his *Histoire naturelle,* the great naturalist Comte Georges-Louis Leclerc de Buffon (1707–1788) expressed his (correct) opinion that hybrids vary in fertility depending on the cross from which they are derived: "In mixed species, that is to say in those animals that, like the mule, come from two different species, there are, as in the pure species, different degrees of fertility."[125] As early as 1825, the botanist Christian Julius Wilhelm Schiede wrote an entire book on plant hybrids occurring naturally in Germany and Italy.[126]

But Linnaeus was the first leading naturalist openly to challenge immutability. In his youth, of course, he had begun with the same views as his contemporaries. For example, in the *Fundamenta botanica* (1736) he asserted “there are as many species as the Infinite Being created in the beginning"[127] His extensive work in classification, however, exposed him to a variety of hybrids. These experiences eventually led him to change his views. The first encounter was with a plant for which he created the new genus *Peloria.*[128] In his *Dissertatio botanica de Peloria* (1744) he asserted that it was a new plant of hybrid origin. In a letter to the Swiss naturalist Albrecht von Haller, he wrote

> This new plant propagates itself by its own seed and is therefore a new species, not existing from the beginning of the world; it is a new genus never in being until now. It is a mule [i.e., hybrid] species in the vegetable kingdom.[129]

He even went so far as to propose[130] that all the various types of plants then in existence were derived from hybridization, beginning with a limited number of initial types created by divine fiat. However, his claims concerning *Peloria* and evolution through hybridization resulted both in professional embarrassment and in rebuke from the clergy.[131] For a long time thereafter he was silent on the issue, but *Peloria* had drawn his attention to hybridization. Mention of plants of hybrid origin increased in his subsequent publications.[132] In a 1751 letter to his close friend, the court physician Abraham Bäck, he said he had found hybrid plants to be "many in number," and that he believed through them he had been able to "open the door to one of nature's extensive chambers, although it is not opened without creaking."[133] In an earlier letter to the same correspondent dated September 7, 1750, he had crowed over a recently discovered plant, *Veronica spuria,* which he judged to be the product of hybridization between the genera *Verbena* and *Veronica*: "The sight of my new plant *Verbena-Veronica* delights me daily; never have botanists seen so clear an example of new species through hybridization."[134]

During ensuing years he met with a variety of other plants that seemed also to be of hybrid origin.[135,a] In *Disquisitio de sexu plantarum* (1760) he states that "it is impossible to doubt that there are new species produced by hybrid generation."[136] There he lists four "to whose origin I have been an eyewitness"[137] (*Veronica spuria, Delphinium hybridum, Hieracium taraxici,* and *Tragopogon hybridum*).[138,b] Such observations eventually led him to reject the idea of immutability. From the twelfth edition of the *Systema Naturae* (1766) he removed his long-time mantra, "*Nullae species novae*" ("No new species"), and in his own copy of the *Philosophia botanica,* he crossed out the words "*Natura non facit saltum*" ("Nature makes no leaps").[139]

Some naturalists subsequently expressed the same sort of ideas with respect to animals. Peter Simon Pallas[c] (1741–1811) proposed that domestic animals arose in much the same way that Linnaeus said new plants did. In the *Origin of Species* Darwin writes that "a doctrine which originated with Pallas has been largely accepted by modern naturalists; namely, that most of our domestic animals have descended from two or more aboriginal species, since commingled by intercrossing."[140] The idea is frequently encountered in pre-Darwinian literature. For example, Charles Howard Smith in his *Natural History of Dogs* (1839–1840)*,* argued the various modern breeds of dogs "are derived from several distinct species, which were constituted with faculties to intermix, and thus to produce the interminable varieties familiar to man."[141] Morton (1847: 276) proposed a similar idea with respect to birds, in which he asserted that certain "original species" hybridized to give rise to the diversity of forms observed today.

Ideas like Linnaeus' were also countenanced by Jean-Baptiste Lamarck (1744–

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[a] It has been argued some of the plants Linnaeus considered hybrids were probably variants not of hybrid origin (e.g., Bremekamp 1952). However, even if such were the case, it would not change the fact that Linnaeus came to view hybridization as a source of new types of organisms.

[b] In the same publication he suggests there had initially been one type of plant in each genus and that subsequent diversification within each genus arose through hybridization (Larsen 1969: 296–297). In the twelfth edition of the *Systema Naturae* (1766) he expressed his opinion that in each taxonomic order, only one kind of plant had been initially created and that all those produced subsequently had arisen through hybridization (Larson 1971: 109; see also: Eriksson 1983: 93–97; Giseke 1792: 16, 18). He eventually pushed his speculations even further, asserting only three types of plants had been initially created, each representing one of three major divisions of the plant kingdom (Acotyledons, Monocotyledons, and Dicotyledons). From these three he suggested, all of the various plants now in existence, were created through hybridization (Larson 1971: 111).

[c] Peter Simon Pallas (1741–1811), German naturalist who cataloged the flora and fauna of Russia. The German-born empress Catherine II gave him a professorship in natural history at the St. Petersburg Academy of Sciences. The following year he went on a research expedition to Siberia, which resulted in his monumental *Reise durch verschiedene Provinzen des Russischen Reichs in einem ausführlichen Auszuge* (1771–1776). His work provided a vast array of data on such subjects as botany, zoology, geology, geography, ethnography, philology, and medicine. Employing the comparative method, he laid the foundations of a new natural history that excluded metaphysics and was influential in the development of evolutionary theory.

1829), who proposed in his *Philosophie zoologique* (1809) that hybridization was a potential source of new types of organisms. In the same work, he expressed his opinion that the data on hybridization even then available spoke against the idea of immutability:

> The idea of bringing together under the name species a collection of like individuals, which perpetuate themselves unchanged by production and are as old as nature, involved the assumption that the individuals of one species could not unite in reproductive acts with individuals of a different species.
>
> Unfortunately, observation has proved and continues everyday to prove that this assumption is unwarranted; for the hybrids so common among plants, and the copulations so often observed between animals of very different species, disclose the fact that the boundaries between these allegedly constant species are not so impassable as had been imagined.
>
> It is true that often nothing results from these strange copulations, especially when the animals are very disparate; and when anything does happen the resulting individuals are usually infertile; but we also know that when there is less disparity these defects do not occur.[142]

Conservative Opposition to the Linnean Theory. Such claims of evolution through hybridization were condemned by members of the old school that embraced the notion of a divinely regulated natural order. In particular, Joseph Gottlieb Kölreuter (1733-1806) doggedly opposed Linnaeus' theory. In a shower of reports published over a twenty-eight-year period (1761-1788),[143] he set forth the results of hundreds of hybridization experiments. Mayr (1982: 645) says Kölreuter's "basic objective was to prove that hybridization of two species does not produce a third species." The ultimate motive underpinning that objective was of a religious nature. Callender (1988: 44) says Kölreuter considered Linnaeus' theory "as subversive of the doctrine of Special Creation." Kölreuter's own words show he believed in a provident Nature that always took care to prevent natural hybridization:

> Just as it is unlikely that two different kinds of animals living in natural freedom should ever produce a hybrid, so is it also improbable that a hybrid should arise amidst that most regular order Nature has established in the kingdom of plants. Nature, which always, even amidst the greatest seeming confusion, orders all in the most beautiful manner, has precluded such disarray. Amongst the animals, she has prevented it mainly by means of their natural instincts. Amongst the plants, where close proximity, wind, and insects all tend to produce unnatural mixing, will she no doubt have known how to counteract the disturbing effects of such forces by equally certain means. Probably it will be found that those means include natural instincts, just as in the case of animals.[144]

Kölreuter claimed his experiments had revealed two phenomena that refuted Linnaeus' theory.[145] First, he had noticed that some hybrids, when self-fertilized, produce progeny more similar to one or the other of their original parental forms than to the hybrid itself. On this basis he surmised (but did not directly observe) that later-generation hybrids would eventually become perfectly similar to the original forms. In subsequent literature this supposed phenomenon was called "reversion."

Modern research has shown that while some hybrids, from some crosses, do exhibit such a tendency, there is no rule of the rigid sort Kölreuter alleged. Some hybrids show such a tendency. Others don't.

Second, he had observed that when the hybrids derived from a cross are mated in each subsequent generation, not with each other, but always with one of the two parental forms originally producing them, they became more and more like that form with each succeeding generation. After many generations, they became indistinguishable. He called this the "transformation" of one parent into the other. Because he believed pollen derived from parental forms to be more potent than that derived from hybrids, he concluded that any naturally occurring hybrids would be subjected to an ongoing natural process that would transform them back into their parents. But this was merely a surmise, in no way based on the observation of natural populations and says nothing about hybrids produced in some other way. In fact, as we shall see in subsequent chapters, many stable natural hybrids are known. Kölreuter's claims were, however, accepted and widely cited by naturalists who defended the notions of immutability and Special Creation.

Gärtner. An even more sedulous member of the conservative faction was Carl Friedrich von Gärtner (1772-1850). He, too, sought to squelch Linnaeus' heresy through the assiduous hybridization of plants. As a young man he was a close family friend of Kölreuter's and like him sought experimental support for Special Creation.[146]. In 1800, he closed shop as a medical doctor and devoted the remainder of his life to botany. From about 1824 until his death he studied plant hybrids. He eventually published the results of nearly 10,000 crossing experiments, in his *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* (1849). Gärtner saw his work as a test of alternative hypotheses, Special Creation and Linnaeus' theory of evolution through hybridization (Callender 1988). He seems to have been driven by an awareness that many scientists accepted Linnaeus' views. As he notes himself in the introduction to his book,

> Hybridization is still [i.e., in 1849] considered by many botanists, to be part of nature's design and purpose, especially by those who believe that species-rich genera only could have come into being via hybridization, such as [Thomas Andrew] Knight, W. Herbert, H. Lecoq, L. Reichenbach, and many others.…Kölreuter has already disputed this hypothesis, and it will be shown here, as our investigations concerning the nature of hybridization are presented, that the essential nature of the pure species contradicts this claim.[147]

The men he mentions were all leading botanists of the era. Thomas Andrew Knight was long president of the London Horticultural Society (1811-1838) and is generally considered the most distinguished horticulturist of his time. It's no surprise he believed hybridization could produce new forms. He had developed many new types of fruit by that means himself. In the first half of the nineteenth century, William Herbert[a] (1778–1847) was the foremost English authority on plant hybridization and author of the monumental, *Amaryllidaceae* (1837). Ludwig Reichenbach[b] and Henri Lecoq[c] were both prolific authors of botanical literature and directors of important scientific institutions. Olby (1997) argues that even Gregor Mendel's "research in hybridization was in the tradition of Linnean botany which accepted that the species we know today are the children of the crossing of fewer primordial forms." Thus, Linnaeus' theory was still taken quite seriously a century after he had conceived it.

Darwin and Immutability. Darwin, of course, labored long and hard against the idea of immutability. So he did his best to undermine the idea that God specially endows hybrids with sterility. In the eighth chapter of the *Origin,* he argues that the complexity and inconsistency of the rules of hybridization speak against the idea that hybrid sterility is God's way of preventing the blending of distinct types of organisms. After discussing available data on hybridization, he writes (1859*:* 260):

> Now do these complex and singular rules indicate that species have been endowed with sterility simply to prevent their becoming confounded in nature? I think not. For why should the sterility be so extremely different in degree, when various species are crossed, all of which we must suppose it would be equally important to keep from blending together? Why should the degree of sterility be innately variable in the individuals of the same species? Why should some species cross with facility, and yet produce very sterile hybrids; and other species cross with extreme difficulty, and yet produce fairly fertile hybrids? Why should there often be so great a difference in the result of a reciprocal cross between the same two species? Why, it may even be asked, has the production of hybrids been permitted?

Like other naturalists of the time, Darwin took this issue quite seriously — elsewhere he commented that "if it could be proved or rendered highly probable that sterility in the first cross or in the hybrid offspring was a specially created endowment, it would be to us a fatal difficulty."[148] However, in his theory Darwin did not pursue the implications of the fact that many hybrids are not sterile. He merely used the known facts about hybridization, in particular the fact that different types of hybrids display different degrees of fertility, to undermine the idea of immutability. Giving scant

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[a] Darwin (1872: xv) comments that "the Hon. and Rev. W. Herbert, afterwards Dean of Manchester, … believes that single species of each genus were created in an originally highly plastic condition, and that these have produced, chiefly by intercrossing, but likewise by variation, all our existing species."

[b] Heinrich Gottlieb Ludwig Reichenbach (1793–1879). German botanist and ornithologist. The director of the Dresden Natural History Museum, founder of the Dresden botanical gardens, and joint founder of Dresden zoo. A prolific author and skilled botanical artist, his major work was the 10-volume *Iconographia Botanica seu Plantae criticae* (1823-1832).

[c] Henri Lecoq (1802-1871). French botanist. Director of the Clermont-Ferrand Botanical Gardens. His publications include *Principes élémentaires de botanique* (1828), *Étude de la géographie botanique de l'Europe* (1854), and *Botanique populaire* (1862).

attention to hybridization as a means of producing new types of organisms, he largely ignored Linnaeus' claims that evolution happened in that way. As a result, the ascendancy of his theory put such ideas in the shade. There they remained for the next forty years, although a few scientists (e.g., Kerner 1871, 1894–1895) did continue to argue that hybridization could produce new forms. Not until Hugo de Vries (1901, 1903) published his theories did such ideas again reach the forefront of evolutionary debate (see Chapter 7).

Modern neo-Darwinism has retained the scholastics' old idea of insurmountable barriers even while discarding their notion of immutability. It envisions new types of organisms arising via a process in which they gradually change. But that change is supposed to occur only in isolated populations, ones that do not interbreed. Under that view, barriers preventing interbreeding are presumed to be necessary if populations are to differentiate, by gradually accumulating differences, and not blend back together. This view ignores the great mass of evidence demonstrating that a wide variety of organisms produce hybrids in a natural setting, that such hybrids occur in large numbers, and that they often are not sterile. A very small portion of this evidence will be discussed in subsequent chapters.

Attempts to Define *Species*

Even after the task of classifying organisms had become a secular activity, the word *species* remained as prominent in scientific debate as it had been in the religious and philosophical discussions of the scholastics. Naturalists had always used the term and they continued to do so. In constructing their systems of classification, the schoolmen had wanted to be sure xiithat they were correct when they called a particular type of plant or animal a "species." Modern scientists who construct such systems (taxonomists) want to be sure of the same thing. Debate has been endless over the question of what exact criteria are appropriate for making such determinations. It sometimes seems as if nothing has changed in the several centuries since John Jewel remarked on his youth among the Oxford logicians: "What adoo was made in daily disputations for exercise of young wittes, aboute Genus and Species, and the reste of the Universals" (*A Defence of the Apologie of the Churche of Englande,* 1567[149]).

Taxonomic Treatment. For the outsider, the terminology and reasoning of a modern taxonomist can be every bit as arcane as that of the scholastics. They use Latin and Greek to name organisms, as did the scholastics. They, too, have elaborate rules they nicely follow. However, only a few points regarding modern taxonomic practice are relevant in the present context: Whatever a "species" might be, if a type or population is deemed to be a "species," standard taxonomic practice dictates that it be designated by a binomial scientific name (e.g., *Mus musculus*). This is what biologists mean when they say a population is "treated as a species." *Webster's Third*

International Dictionary defines *binomial nomenclature* as "a system of nomenclature in which each species of plant or animal receives a name of two terms of which the first identifies the genus to which it belongs and the second the species itself." On the other hand, within a population treated as a species, distinctive subpopulations are sometimes recognized. These are assigned a trinomial scientific name (e.g., *Mus musculus musculus*). A biologist says any population assigned a trinomial is "treated as a subspecies." *Webster's* defines a *trinomial* as "a name belonging to botanical or zoological nomenclature composed of a first term designating the genus, a second term designating the species, and a third term designating the subspecies or variety to which an organism belongs." When two populations or individuals are assigned the same binomial they are "treated as conspecific."

Thus, given ordinary taxonomic practice, if the process of naming an organism is to be carried out in an objective manner, biologists need a clear definition of *species.* But attempts to say which populations should be treated as species have always been, and continue to be, problematic. In the long quest to establish valid classifications, a multiplicity of definitions for *species* have been proposed.

The "Essence" Criterion. John Ray (1627–1705) seems to have been among the first to offer a definition of *species* intended for naturalists (as opposed to the ancient definition used by logicians). In his *Historia Plantarum* (1693), Ray states that

> To begin an inventory and proper classification of plants, we need to determine some criterion for distinguishing species. After long and careful consideration of this matter, nothing better has come to mind than those distinctions passed from one generation to another through seed. For whatever traits arise in an individual or in the seed of a species of plant, are accidental and not of the kind that distinguish species. … For species preserve their distinctive traits forever; one species does not arise from another, nor vice versa. [150]

Of course, there is an obvious difficulty with his definition. Such a rule would result in a huge number of types being treated as species (many cases are known of two types differing with respect to some extremely minor characteristic and yet breeding true for that trait when they are mated only with other individuals of the same type).

Ray's definition represented an effort to provide a working criterion that would allow the classification of plants and animals according to their "specific essences."[a,b] However, Ray's contemporary, John Locke, roundly rejected the idea

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[a] It was also an effort to discredit heterogony, the idea that the individuals of one "species" could occur in the progeny of another. Belief in heterogony was widespread among naturalists, and had been since ancient times (Zirkle 1959). Theophrastus (ca. 371–ca. 287 B.C.), often termed the father of botany, devoted Book II of his *Peri phyton historia,* to describing how plants "changed their species." He said this could occur when they were transplanted to a new environment and that many plants did not breed true from seed.

[b] Ray did not originate the idea that each kind of organism gives rise to progeny that are only of its own kind. For example, in his book *On Monsters and Marvels,* the sixteenth century

that systems of classification could be based on "essences" — though in doing so he constituted a distinct minority. In *An Essay Concerning Human Understanding* (1690) he tried to show the inadequacies of scholastic doctrine. There he speaks of what was then the "usual supposition, that there are certain precise essences or forms of things, whereby all the individuals existing are, by nature distinguished into species."[151] At that time, the term *species* was applied to all types of things, for example, to the various types of minerals. Locke admitted it is possible to classify things into categories on the basis of their observed characteristics. But, while his contemporaries did call those categories "species," he thought they were mistaken to suppose such categories were distinguished by, and based on, "essences" just because the word *species* was used to refer to them:

> It is very true every substance that exists has its peculiar constitution, whereon depend those sensible [i.e., perceptible] qualities and powers we observe in it; but the ranking of things into species (which is nothing but sorting them under several titles) is done by us according to the ideas that *we* have of them: which, though sufficient to distinguish them by names, so that we may be able to discourse of them when we have them not present before us; yet if we suppose it to be done by their real internal constitutions and that things existing are distinguished by nature into species, by real essences, according as we distinguish them into species by names, we shall be liable to great mistakes.[152]

In point of fact, many make the same sort of mistake even today. That is, when they see that a population is treated as a species, they are likely to assume it has the characteristics they personally associate with the name *species*. For example, they might assume the population does not interbreed with other such populations. Nevertheless, many populations treated as species do in fact interbreed, often extensively, with other populations treated as species (see Chapter 2). As Locke points out, thinking in this way can be a great mistake.

Morphological Definitions. Since the time of Locke and Ray, a wide variety of definitions for *species* have been proposed. There are, however, two main types: morphological and biological. The former places weight on resemblance, the latter, on genetic isolation. The morphology of an organism is its characteristic form, coloration, and structure. Morphological definitions, embraced primarily by researchers engaged in sorting and naming specimens, emphasize resemblance and distinctness. Under this approach, similar specimens are assigned to the same category, dissimilar ones, to different categories. Efforts to define *species* on the basis of morphology have been criticized because (1) there are many cases where morphologically similar or identical organisms are unable to interbreed; (2) large

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physician, Ambroise Paré (1982: 67) writes "For we see even in inanimate things, such as wheat coming from a grain of wheat—and not barley—and an apricot tree coming from an apricot pit—and not the apple tree—how Nature always preserves its kind and species," which is ironic given that elsewhere his book, Paré describes a variety of bizarre hybrids and monsters born of normal parents.

morphological differences sometimes exist between organisms that can and do interbreed; (3) degrees of morphological difference form a continuum and there is no objective criterion for saying how much difference between two types is required if they are to be treated as separate species.[a] Nonetheless, the vast majority of populations and specimens treated as species have been so described on the basis of morphology alone. For example, Linnaeus' plant taxonomy was based solely on the number and arrangement of the reproductive organs. Darwin was not consistent in his definition of the word *species,* but he did at times use morphological criteria. Thus, in the *Origin* (1859: 56) he tells the reader that

> the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties [of the same "species"].

But only a few pages earlier (p. 47) he states

> in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgment and wide experience seems the only guide to follow. We must, however, in many cases, decide by a majority of naturalists, for few well-marked and well-known varieties can be named which have not been ranked as species by at least some competent judges.

Such matters are still often determined by vote instead of by any objective criterion (the writer has frequently seen this method used in connection with avian taxonomy). But there is no reason why a committee lacking an objective criterion should be more correct than individuals lacking an objective criterion. Naturalists specializing in a particular group of organisms (for example, mammals) usually have a sense of the amount of difference that typically distinguishes types treated as separate species. But this is more a matter of intuition than definition. Their opinion merely reflects their personal experience regarding how much difference is typically required for two types of organisms to be treated as separate species. In point of fact, Darwin probably had it right when he said that "in order to decide whether to rank a plant as a species or a variety, we must rely on the opinions of the best & most cautious Botanists, who, however may of course be easily mistaken. [!]"[153]

Biological Definitions. Though morphological definitions of *species* have been used for centuries, and though morphology has served as the basis for distinguishing the

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[a] In recent years there have been efforts to make these discriminations using DNA sequence data, but the same three sorts of criticisms have been raised with this new approach: (1) sequence similarity does not guarantee the ability to interbreed; (2) large differences do not preclude it; (3) degrees of sequence difference again constitute a continuum (so sequence comparisons do not allow nonarbitrary discrimination of types into species). As Grant (1991: 359) notes, "Many evolutionists originally anticipated that molecular evidence in general and DNA sequence data in particular would resolve uncertainties about evolutionary relationships, but this hope has not been realized."

great majority of the various types now treated as species, throughout the latter half of twentieth century most evolutionary biologists espoused what are termed "biological" definitions of *species*. Thus, Ernst Mayr (1963: 19) noted that

> most of the definitions proposed in the last 25 years have avoided all reference to morphological distinctness. For instance I defined species (Mayr 1940) as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups."

Mayr's definition has enjoyed the broadest popularity of any definition offered for *species*, but, as we have seen, there are both practical and conceptual difficulties with its application. As Mayr himself comments, "The history of the numerous attempts to achieve a satisfactory biological species definition has been told repeatedly."[154]

Moreover, even when Mayr first proposed his definition nearly seventy years ago, biological definitions were nothing new. Mayr's teacher Erwin Stresemann (1919: 64) asserted that "forms which have reached the species level have diverged physiologically to the extent that, as proven in nature, they can come together again without interbreeding."[155] Poulton (1903, 1908) defined *species* as "an interbreeding community." In a letter to his friend Joseph Hooker dated October 22nd, 1864, Darwin himself used a biological definition: "I will fight you to the death," he writes Hooker, "that as primrose and cowslip are different in appearance (not to mention odour, habitat and range), and as I can now show that, when they cross, the intermediate offspring are sterile like ordinary hybrids, they must be called as good species as a man and a gorilla."[156] Darwin (1872: xvi) notes, too, that "Von Buch, in his excellent *Description physique des Isles canaries* (1836, p. 147), clearly expresses his belief that varieties slowly become changed into permanent species, which are no longer capable of intercrossing."[157] At about the same time, Matthew (1831) stated his belief that "the progeny of the same parents, under great differences of circumstance, might, in several generations, even become distinct species, incapable of co-reproduction."[158] Even earlier, Hunter (1787: 253) writes that

> The true distinctions between different species of animals must ultimately, as appears to me, be gathered from their incapacity of propagating with each other an offspring again capable of continuing itself by subsequent propagations; thus the Horse and Ass beget a Mule capable of copulations, but incapable of begetting or producing offspring.

In the mid-eighteenth century, Buffon explained the criteria he thought should be used in deciding what forms to treat as species:

> … the ass resembles the horse more than the barbet does the greyhound, and yet the barbet and the greyhound form but a single species, for together they produce offspring that are themselves capable of producing more offspring. But the horse and the ass are clearly different species, since together they only produce imperfect and infertile offspring. … one can always draw a line of separation between two species, that is to say, between two successions of individuals that reproduce themselves and cannot mingle, since otherwise one could, in

blending two such separate successions of individuals, reunite then into a single species.[159]

Buffon's definition of *species,* then, is very similar to Mayr's, and subject to the same sorts of difficulties. The main difference is that Mayr introduces a bit of modern jargon ("reproductive isolation" to replace Buffon's "cannot mingle").

Mayr (1982: 257) himself notes that many naturalists, from the seventeenth century through the end of the nineteenth, offered definitions of *species* that used "biological criteria to reconcile the seeming contradiction between conspicuous variation and the presence of a single essence." That is, these definitions sought to define *species* in such a way that all individuals taxonomically treated as belonging to the same species (treated as "conspecific") could be viewed as essentially the same, though they might differ morphologically from each other in many ways. The function of Mayr's own concept is similar. He said, no matter what morphological and behavioral differences distinguish two individuals, they do not differ in any essential way and should be treated as a single species if they interbreed.

Biological Definitions: Problems. The main intellectual motive for biological definitions has been the widespread belief that interbreeding populations will blend together, the very thing that Goldsmith and Rousseau said Dame Nature was so cautious to prevent (see p. 10). Darwin clearly thought reproductive isolation is important in maintaining distinct populations. For example, in the *Origin* he says "species within the same country could hardly have kept distinct had they been capable of crossing freely."[160] Elsewhere he writes "indeed it is obvious if all forms freely crossed, nature would be a chaos."[161] The idea that reproductive isolation is key in the production and maintenance of distinct new types of organisms is certainly emphasized in neo-Darwinian theory.

A theorist is free to imagine and model the evolutionary dynamics of a population satisfying the constraints of Mayr's definition. But for a taxonomist such a definition is an arduous criterion because it can be extremely difficult to determine whether two organisms are "actually or potentially interbreeding." The impracticality of such a criterion becomes evident as soon as one considers (1) how many pairs of populations might, on a purely hypothetical level, interbreed (millions); and (2) that each such population is typically composed of millions of individuals distributed over a broad geographic range. How much work, then, would be required to evaluate whether even a single such pair is "actually or potentially interbreeding?" Long ago John Locke perceived the difficulties inherent in such definitions. As he put it, "If the species of animals and plants are to be distinguished only by propagation, must I go to the Indies to see the sire and dam of the one, and the plant from which the seed is gathered that produced the other, to know this be tiger or that tea?"[162] Indeed, even if one fails to observe interbreeding in a given case, can one safely conclude that hybridization does not occur? It is always possible that hybrids may exist in some location other than those that have already been searched. Or they may occur in the same place at some other time. Surveys of natural populations are always of limited scope. As Buffon once said, regarding the possibility of natural hybridization among birds, "who knows of every tryst in the depths of the wood? Who can number the illegitimate pleasures shared by creatures of separate species?"[163]

These difficulties have led to the practice of treating morphologically distinct forms as separate species so long as they are not known to hybridize. Once hybrids have been reported between two such forms, however, their taxonomic treatment is often changed so that they are treated as subspecies of the same species. In other words, they are no longer treated as separate species. Many forms treated as distinct species are now known to hybridize that once were not known to do so. Indeed, in the writer's experience several such pairs are reported among birds every month. It can therefore be inferred that many such pairs that are not now known to hybridize will be found to do so in the future. Thus, forms are typically treated as species by default when their actual status with respect to hybridization is unknown. This practice contributes to the idea that organisms treated as separate species cannot hybridize — many people assume any form treated as a species doesn't hybridize with other such forms, even if no information is available about whether it does or not. Since the capacity to hybridize has not been investigated for the vast majority of forms treated as species, this default assumption has probably greatly distorted estimated rates of hybridization between forms treated as separate species. Obviously, if two forms can be treated as separate species only so long as hybridization between them is unknown, estimates of rates of hybridization between forms so treated will be low indeed!

The fallacy of such reasoning can be made explicit with a simple example: If it were widely supposed that an animal could not be a dog if it had fleas, then it would be hard to show that dogs often do have fleas. For suppose everyone agreed a particular animal was a dog and someone subsequently discovered that it had fleas. The discovery would be to no avail because as soon as it was announced everyone would say "That is not a dog! Dogs do not have fleas!" Since in everyone's estimation the animal would no longer be a dog, everyone would be free to go on believing dogs do not have fleas. Such would be the case even if most, or even all unexamined dogs were heavily infested with fleas. This is just the sort of "great mistake" Locke (see p. 19) was talking about. Darwin was well aware of this fallacy: "There is no way to escape from the admission that the hybrids from some species of plants are fertile, except by declaring that no form shall be considered as a species, if it produces with another species fertile offspring: *but this is begging the question*" (italics added).[164] Unfortunately, just this sort of waffling question begging is rampant among biologists today.

But questions of practical implementation aside, the greatest weakness of Mayr's definition is the vagueness of the word *interbreeding* and of the term *reproductively isolated.* A broad spectrum of observations could be described as "interbreeding." There are also various conceivable degrees of reproductive isolation. Both the observation of a single hybrid and of a million can be described as "interbreeding." Also, the production of a sterile hybrid and of a fertile one can both be called "interbreeding." How fertile and how numerous must the observed hybrids be? Is one hybrid allowed? Two? Three hundred? What is the exact criterion?

Attitudes regarding hybridization and how it should be interpreted within the context of taxonomic discussion differ from one biologist to another. Moreover, the consensus on the topic varies over time. For example, the American Ornithologists' Union's Committee on Classification and Nomenclature (*AOU Check-list* 1998: xiv) discusses hybridization in connection with avian taxonomy:

> Regarding the interpretation of hybridization [in determining whether two populations should be treated as separate species], we emphasize that a significant number of undisputed biological species of birds long retain the capacity for at least limited interbreeding with other species … Therefore, the occasional occurrence of hybridization, even between [birds] that the Committee has long recognized as species, by no means diminishes the biological reality of their *essential* reproductive isolation. In practice, interbreeding has not been the ironclad determinate of conspecificity that some would believe. Thus, essential (lack of free interbreeding) rather than complete reproductive isolation has been and continues to be the fundamental operating criterion for species status by workers adhering to the BSC [i.e., Mayr's "biological species concept"]. In particular hybridization of two forms across narrow and stable contact zones — once viewed as a sufficient criterion for treatment as one species — is now viewed as evidence for *lack* of free interbreeding. As a consequence, many pairs of [birds] that were merged [i.e, treated as a single species] in the sixth edition have been resplit [i.e., treated as two separate species] in this edition of the Check-list.

The passage just quoted illustrates some of the sticky problems associated with defining *species* in terms of interbreeding. Interbreeding is a matter of degree and the degree that constitutes "free interbreeding" has never been objectively defined. Precisely what does "essential" reproductive isolation mean? As used in the quotation, the word *essential* seems merely to indicate the Committee's opinion that in certain cases observed hybridization is not so extensive as to warrant treating the hybridizing populations as a single species. However, no exact criterion is offered by which "essentially" isolated populations can be distinguished from ones that are not "essentially" isolated. What exactly does "free interbreeding" mean? In interbreeding that is not "free" how many hybridizations can occur? How fertile can the hybrids be? If hybridization of two forms across a "narrow and stable contact zone" is to be considered a lack of free interbreeding, then exactly how narrow and how stable must the zone be? The writer knows from his own research that avian contact zones vary greatly, from one to another, in width and stability, as well as in the number of hybrids they produce, and in the fertility of those hybrids.[165] Regarding the activities of taxonomists, Ernst Mayr (1963: 499) once wrote that "an outsider would never realize how many interesting cases of evolutionary intermediacy are concealed in the seeming definiteness of the species and subspecies designations." If it were true that natural populations could be tidily sorted into two categories, those that do interbreed and those that do not, the fact that various degrees of interbreeding are conceivable would be irrelevant. However, real pairs of populations do exhibit a seemingly continuous spectrum of degrees of interbreeding.[166] This fact makes biological definitions entirely arbitrary.

Although he sporadically used biological definitions of *species*, as the occasion suited him, Darwin was clearly aware the fertility of hybrids was an impractical criterion. He reached this conclusion by comparing the results of Kölreuter (1761–1766) and Gärtner (1849), whose works were at that time the primary sources of information on hybridization in plants:

> If we followed Kölreuter's simple rule & called all plants, which were quite fertile together, varieties, it might be thought that we should at least arrive at a decided result; but this is not so, for we have seen that the two most laborious & careful experimentisers [Kölreuter and Gärtner] who ever lived, often come to a diametrically opposite conclusion on this head; and this alone suffices to show that, *practically,* fertility will not serve to distinguish varieties from species.[a]

Indeed, Darwin was well aware that the fertility of hybrids is a continuum, varying from one type of cross to another. Thus, he points out that,

> With forms that must be ranked as undoubted species, a perfect series exists from those which are absolutely sterile when crossed, to those which are almost or completely fertile. The degrees of sterility do not coincide strictly with the degree of difference between the parents in external structure or habits of life.[167]

Moreover, even those who try to use them admit biological definitions are limited in scope in comparison to morphological ones. As Grant (1981: 64) points out,

> The biological species concept applies to biparental organisms. Uniparental organisms, which do not form interbreeding groups, are not embraced by this concept. Yet uniparental reproduction is common in plants, as well as in various groups in other kingdoms.

Likewise there are difficulties associated with applying it to symbiotic forms. For example, many fungi enter into associations with photosynthetic algae to form lichens. Thousands of these lichens have been treated as species, though they are composites of two or more organisms that are themselves treated as separate species (see Chapter 4). Certainly, such composite forms have nothing to do with Mayr's *species*. Nor can biological concepts be applied to various other broad classes of organisms (e.g., fossil forms, bacteria). Such concepts also have nothing to say about the many natural populations that do not come into contact with each other (allopatric populations). So for anyone who wishes to work with real specimens and natural populations, such definitions are not at all satisfactory.

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a. In Stauffer (1987: 402). Elsewhere he says it can "be shown that neither sterility nor fertility affords any clear distinction between species and varieties; but that the evidence from this source graduates away, and is doubtful in the same degree as is the evidence derived from other constitutional and structural differences" (Darwin 1859: 248).

Thus, neither of the two primary types of definitions usually offered for *species* (neither the morphological nor the biological) succeeds in clearly stipulating how and when the word should be applied. Other types of definitions have been proposed in recent years. Most of the new proposals make allowance for molecular genetic data. But they have not led to consensus.[168] Genetic traits are not morphological traits, but defining *species* in terms of the degree to which organisms differ with respect to their genetic traits is just as problematic as defining them in terms of morphological differences. Many types of organisms that are known to hybridize continue to be treated as separate species simply because they have long been treated so and a tradition has been established. For example, sparrow expert T. R. Anderson (2006: 17) remarks that "despite their ability to interbreed successfully, I consider the Spanish sparrow (*P. hispaniolensis*) to be a separate species from the house sparrow [*P. domesticus*]." Others are treated separately by some authors because they satisfy various less restrictive definitions of *species.* When two hybridizing populations can be distinguished on the basis of certain characteristic, usually genetic, traits, they are good "phylogenetic species"[169] — this definition is a morphological wolf in genetic sheep's clothing (it's still a definition in terms of differences, although those differences may be genetic as well as morphological). When they tend more to mate with their own kind than to hybridize, they are good "recognition species."[170] This definition faces the old problem of deciding how much hybridization is allowed. Furthermore, when pre- and postmating isolating mechanisms reduce the reproductive capacity of hybrids and mixed parental pairs, hybridizing populations can even be good "biological species" according to Ehrlich and Raven's (1969) definition, which is like Mayr's but allows isolation to be a matter of degree (again the exact degree is not specified and is consequently arbitrary). Problems arise with the application of all definitions that have been proposed.[171]

Darwin. In a letter to Joseph Hooker dated December 24, 1856, Darwin wrote "I have just been comparing the definitions of species … It is really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of 'species'; in some, resemblance is everything and descent of little weight—in some, resemblance seems to go for nothing, and Creation [is] the reigning idea—in some, descent is the key—in some, sterility an unfailing test, with others it is not worth a farthing. It all comes, I believe, from trying to define the undefinable."[172] And yet Darwin certainly doesn't avoid using the word in the *Origin.* In fact, he uses it in almost in every paragraph—even in the very title of the book. Nor does he express amusement therein when commenting on the variety of its definitions: "Nor shall I here discuss the various definitions which have been given of the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species."[173] In point of fact, an examination of his own writings shows that he used at various times each of the various usual types of definitions himself.

Locke asserted that "men talk to one another and dispute in words, whose meaning is not agreed between them, out of a mistake that the significations of common words are certainly established, and the precise ideas they stand for, perfectly known."[174] The signification of *species* had not been "certainly established" in Darwin's day. It has not yet been established even today, though century and a half of thought intervenes. There is no common agreement on how it should be defined.[175] There are merely proponents of various definitions. Even the most popular of these definitions (i.e., Mayr's) has serious logical flaws making its application arbitrary. This outcome goes against Darwin's hopes. In the *Origin* (1859: 484) he asserted that his theory would allow a resolution of the problems naturalists had always had with defining *species:*

> When the views entertained in this volume on the origin of species … are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. … The endless disputes whether or not some fifty species of British brambles are true species will cease. Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and if definable, whether the differences be sufficiently important to deserve a specific name. … It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names, as with the primrose and cowslip[176] … In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.

In hoping that naturalists would cease to be "incessantly haunted by the shadowy doubt whether this or that form be in essence a species," Darwin has proved excessively sanguine. The search for the "undiscovered and undiscoverable essence of the term species" has not ceased. There has been endless debate over the meaning of the word. But its use has continued, ubiquitous not only in biology, but even in everyday conversation. Many naturalists can still be grimly serious when it comes to the issue of whether a given type of organism should be treated as a species. Different researchers use different criteria for making such decisions, just as they did in Darwin's day. For example, Mayr (1982: 171) says that when you compare the views of an ornithologist with those of an entomologist, the two will usually espouse "vastly different" definitions of *species*. Even among entomologists themselves there are differences in taxonomic practice. Thus, in a recent article in the journal *Nature,* Marris (2007: 251) observed that

> ant taxonomists have decided that anything that's worth separating should be separated at the species level, and have no truck with the subspecies at all. Butterfly taxonomists, however, like the triple-barrelled name approach and dote on subspecies. As a result, the numbers of ant species and butterfly species are not directly comparable.

Even researchers working on the same group will disagree on such points. Such the writer has certainly found to be the case for ornithologists. In deciding whether populations should be treated as species, different ornithologists emphasize different criteria. Some base their decisions on call type, others, on morphology. Many attempt to apply Mayr's definition, or some version of it. There are also many cases where morphologically identical populations are treated as separate species because they occur in separate geographic regions. For example, it is common to treat seemingly identical forms living on separate islands or separate continents as separate species. A bird could be treated, then, as a different species simply because it flew from one island to another![177,178]

These different interpretations of the word *species,* what Locke would have called the "multiplicity of its significations," produce needless misapprehension in evolutionary discussion. For example, Bullock's Oriole is often treated as a species. That is, it is assigned the binomial *Icterus bullockii.* However, this bird interbreeds very extensively with the Baltimore Oriole, which is also often treated as a species (*I. galbula*). Anyone who accepted a biological definition of *species* and saw that Bullock's Oriole is treated as a species might suppose it had the traits specified by such a definition. Such is certainly not the case. These two birds produce huge numbers of natural hybrids that are partially fertile in both sexes.[179] Conversely, there are many cases where populations treated as distinct races of the same species produce infertile or even absolutely sterile hybrids. For example, many races of the house mouse (*Mus musculus*) fit this description.[180]

Indeed, one wishes Darwin had refrained from giving a vague and ambiguous word such an important place in such an important book.

Restrictions in Usage. Given the many ambiguities and difficulties involved with the use of *species*, it might seem logical to simply drop the word from scientific debate. To speak of the "origin of a species" is to speak of the origin of a thing ill-defined, to speak of the origin of "something complicated, something that is a unity only in name" (Nietzsche, *Beyond Good and Evil,* §19).[181] As Francis Bacon said,

> There arises from a bad and unapt formation of words a wonderful obstruction to the mind. Nor can the definitions with which learned men are wont to guard and protect themselves in some instances afford a complete remedy; words still manifestly force the understanding, throw everything into confusion, and lead mankind into vain and innumerable controversies and fallacies.[182]

In the case of *species,* common practice employs a single word to refer to various entities with differing characteristics. Different people define the word in different ways. Yet, they imagine everyone is speaking of the same thing. Under such circumstances it's easy to see how "vain and innumerable controversies and fallacies" might arise.

The general usage of a word by colleagues, and by the public at large, is beyond an author's control. It is, however, possible to control usage within a single book. In this book, I restrict usage of *species,* "this manifold entity for which people have but a single name" (Nietzsche, ibid).[183] I do this in order to limit use of the word to those cases where its proper use can be clearly stipulated. Restricted, too, are occurrences of its derivatives (e.g., *speciate, subspecies, speciation, speciose, interspecific, intraspecific*, etc.), and of the various etymologically unrelated words used in place of such words (e.g., *race* replacing *subspecies*). Such words are used in only three ways:

- In referring to taxonomic treatment. For example, the phrase *treated as a species* is used to indicate that a group of organisms is referred to by a binomial scientific name (see pp. 17-18); *treated as conspecific,* is used to indicate that two populations are assigned the same binomial (such usage is reasonable because, whether or not a given treatment is correct, it is always correct to state the nature of the treatment);
- In discussing how, and under what circumstances people use words of this kind (in which case the word will be italicized or placed in quotation marks);
- In quoting other writers.

In particular, the use of such words will be avoided in all cases where their use would imply a judgment is being made as to whether the entities under discussion should or should not be referred to by the word *species.* For such implications are, indeed, often inherent in the use of certain words. For example, no one would say that a population had "speciated" if they did not think a "species" was in question. Likewise, when biologists are of the opinion that two interbreeding populations should be treated as conspecific, they often will say they “intergrade” rather than hybridize. Many reserve the term *hybridize* for interbreeding between populations they think should be treated as separate species. To refer to interbreeding between natural populations, the word *hybridization* is always used in this book in preference to *intergradation*.

Species, and its derivatives, can almost always be replaced by other words of unambiguous meaning (often they can even be deleted without change in meaning). Such a course will be followed here wherever possible. Table 1.1 gives examples of various replacements for *species,* using other words that convey the intended meaning. In addition, a few new terms will be introduced in Chapter Three to allow reference to certain distinct entities that have been lumped under the epithet *species.* In point of fact, it is the writer's opinion that we will never be able improve our understanding of the evolutionary process so long as we go on discussing "species" and concepts based upon a presumed existence of "species" (such as "speciation"), when *species* itself is a ill-defined term. Therefore, in this book, such terms and principles are viewed as fuzzy hangovers from a not entirely bygone era of thought.

Table 1.1. Examples of Converted Terminology

THE PHRASE	CAN BE REPHRASED AS:
"all the species of a genus"	*"all the members of a genus"*
"some bird species"	*"some bird"* or "*some kinds of birds"*
"a plant species"	*"a type of plant"* or *"a plant"*
"various types of species"	*"various forms"* or *"various types of organisms"*

Scientists have discarded, or restricted the usage of, many other words in the past. The same system of thought that gave us the word *species* also provided *ether.* The scholastics believed this "fifth element" filled the spaces between the celestial spheres. Later, scientists retained the notion of ether as a substance that filled outer space. Throughout the eighteenth and nineteenth centuries, there was much discussion of its physical properties, for example, its role in the propagation of light. However, explanations of physical phenomena constructed during the early twentieth century did not make use of "ether" and scientists now use the word only (1) to refer to the common solvent and general anesthetic; (2) in historical references to former scientific debate. No scientist now discusses the nature of ether or its origins. In a similar way, the writer believes that, so long as *species* has no generally accepted definition, there is no reason for scientists to discuss the nature of "species" or their origins. We can construct a more precise explanation of evolution by leaving *species*, and all of the various ill-defined notions that word has spawned, out of the picture.

In the discussions appearing in subsequent chapters it will be necessary to refer to various natural populations by their scientific names. But again, such references are not meant to imply that any judgment is being made as to proper taxonomic status. In this book, the scientific and English names used in referring to populations and specimens are based on standard taxonomies and are merely intended to designate the population in question.[184] *For this reason, the use of a binomial (or trinomial) does not, and is not meant to, imply the writer's opinion that it is correct to treat the populations in question as species (or subspecies). It merely means that the names are those used in a standard taxonomy to refer to the populations or types in question. In this book scientific names are names and nothing more.* Certainly a population or a type can be discussed as a population or a type and be referred to by a widely accepted name without any presumption being made as to whether it should be treated as a species. This is in fact the practice followed in this book. In general, stabilization theory assumes that certain types of organisms are treated as species (assigned binomial scientific names) due to human decisions and that the motives for such decisions differ (1) for different kinds of organisms; and (2) from one human decision maker to another. Some of these motives have already been explained. Others will be discussed after the necessary terminology has been introduced.

The writer is well aware that many scientists believe any population with a binomial name is a "species." But in this book the use of binomials intends no such implication—whatever the reader may infer. In fact, this entire chapter has been devoted to showing that *species* has no clear definition accepted by all scientists. Personally, I have no more opinion of what a "species" is than I do of what a "shrockbie" is. *Shrockbie* also lacks a clear definition. In fact, it has no meaning whatsoever. Of course, one can always use a word even if it lacks meaning (as I, for example, just used *shrockbie*). The ways in which the word *species* will be used in this book have already been indicated. The *use* of this word therefore is well defined even if the word itself is not.

I hope no one will consider this practice unacceptable. To be sure, in using the word *species* in the ways that I have laid down, I will be doing things any other biologist does. However, in doing them, I will not share some of my colleagues' sanguine belief that *species* is, or ever will be, well defined. When in the remainder of this book I write, "X is treated as a species," I will merely mean "X has been assigned a scientific binomial." That is, I make a statement about the behavior of my fellow biologists (they treat it as a species). But this is not convoluted or obscure. For example, the meaning of the sentence "He gave up the ghost" is clear (i.e., it means "He died.") even though *ghost* is not a well-understood or well-defined entity. One need not understand the word to fully comprehend the expression's meaning. Another example is "God knows!" When someone says "God knows!" everyone clearly understands the meaning of the sentence (i.e., it means "I certainly don't know!"), but *God* has different meanings for different people and certainly isn't a topic for scientific debate. Indeed, "God knows!" is an expression I might well use if someone asked me what a "species" is.

Conclusion. During the rise of science in the seventeenth and eighteenth centuries, the pre-scientific belief that "immutable species" actually did exist seems to have gone largely unquestioned. Naturalists transferred the word *species* (and the emphasis placed upon it) from the scholastic tradition into a new intellectual setting. Their motives were different, but they still thought some natural populations should be treated as species and others should not. The issue was never whether "species" existed, but rather what they were and how they should be defined. A system of classification, and a terminology created by followers of Aristotle and Aquinas, was taken up and extended by men of a different mind—empiricists, most of whom lacked all interest in Peripatetic philosophy.

Many modern biologists commit the same sort of error with regard to the word *species* that Locke said the scholastics did. The only difference is that, where a seventeenth century logician would speak of "essences," a biologist now would speak of "reproductive isolation." This is because many believe the essential characteristic of a "species" is captured in Mayr's (1940) definition of *species* as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." The mistake arises when they assume the typical population treated as a species is known to have this characteristic. In fact, the vast majority of all natural populations treated as species are so treated solely on the basis of the distinctive traits of specimens—it isn't known whether they are reproductively isolated. It is a mistake, then, to suppose it is known that populations so treated have this property of being isolated, or even to suppose it is known that most do. In point of fact, although there is no data bearing on isolation for most populations so treated, many such populations are known to interbreed (see Chapter 2). Anyone who assumes, then, that the typical population treated as a species does not interbreed with other such populations, is "liable to great mistakes," as Locke put it. For, from that assumption, it is easy to go further and believe neo-Darwinism's claim that new types of organisms typically come into being via the gradual accumulation of favorable variant traits in isolation. Ensuing chapters will argue that this claim is incorrect, and, in doing so, will attempt to show that the accepted conception of evolution is fundamentally at error.

2 On Hybridization

For he who is acquainted with the paths of nature, will more readily observe her deviations; and vice versa, he who has learnt her deviations, will be able more accurately to describe her paths.
—FRANCIS BACON, *Novum Organum*[185]

From the Introduction, the reader will recall that if two populations are consistently distinct with respect to one or more characters, and if a descendant of matings between those populations is discernibly mixed with respect to those characters, then that individual is a hybrid and any process producing such individuals is hybridization.

Hybrids produced by an initial cross between two parental types are known as *F_1 hybrids* (or the *F_1 generation*). Hybrids produced by matings among F_1 hybrids are known as *F_2 hybrids*, while those produced among F_2 hybrids, are *F_3 hybrids,* and so forth. *Backcross hybrids* are produced when hybrids mate with either parental type. When the resulting backcross hybrids mate again with the same parental type, the result is the second backcross generation, and so forth. Hybridization occurs in a broad range of organisms — plants, animals, and fungi.[186] Indeed, as hybridization is defined in this book, it is a well-documented phenomenon even among bacteria (see Chapter 8).

Basics of Hybridization

Gametes. Many hybrids can reproduce even without engaging in sex. For example, many can produce progeny by budding. But for those hybrids that have no means of reproduction other than sex, infertility can be an effective block to propagation. Individuals of reduced fertility produce fewer gametes than normal individuals or produce gametes that are defective. A *gamete* is a specialized cell functioning in reproduction. In sexual organisms a gamete produced by the male parent fuses with a gamete produced by the female parent to initiate formation of a new individual. This event is called *fertilization*. The male gametes produced by animals and some plants (e.g., club mosses, horsetails, ferns) are called *spermatozoa* (plural of *spermatozoon*), or simply *sperm*. Their female gametes are called *ova* (plural of *ovum*). Ova are often called *eggs*. Most plants produce male gametes called *pollen grains,* or simply *pollen*.

Gametes are generally produced in abundance. For example, a single milliliter of chimpanzee semen contains about 2.5 billion gametes.[187] A hybrid may be extremely sterile in comparison with its parents, but still produce huge numbers of viable gametes. If a chimpanzee produced a hybrid with some other animal and that hybrid had one thousandth the fertility of its chimpanzee parent, it would still produce 2.5 million spermatozoa per milliliter. Plants, too, produce gametes in mass quantities. About as many gametes are contained in a single teaspoon of pollen as in a milliliter of chimpanzee semen. The sheer quantity in which gametes are produced explains why many hybrids are partially fertile even when their gamete production is severely disrupted — a small part of a very large number can still be quite a large number. Only a single spermatozoon is required to fertilize an egg.

Reciprocal Crosses. A *reciprocal cross* is one occurring between the same two types of organisms, but with sexes reversed. For example, a jackass crossing with a mare produces the common mule. But the reciprocal cross, between stallion and jenny, yields a different animal, the hinny, seldom produced by breeders.

Reciprocal crosses are not always of equal fertility. When domestic fowl cocks (*Gallus gallus*) fertilize guineafowl hens (*Numida meleagris*), egg fertility is about 70 percent, but when guineafowl cocks inseminate domestic hens, the fertility rate is only 12 percent.[188] Some crosses are easily obtained even when the reciprocal cross is not. Chaudhuri and Mandal (1981) studied reciprocal crosses between the Stinging Catfish (*Heteropneustes fossilis*) and the Walking Catfish (*Clarias batrachus*). When stinging catfish milt was applied to walking catfish eggs, the fertilization rate was 90 percent. But when walking catfish milt was used on stinging catfish eggs, no fertilization was observed.

The fertility of the hybrid offspring (as opposed to the fertility of the cross itself in producing hybrid offspring) can also depend on the direction of the cross. Darwin (1859: 258) found it remarkable "that hybrids raised from reciprocal crosses, though of course compounded of the very same two species, the one species having first been used as the father and then as the mother, generally differ in fertility in a small, and occasionally in a high degree." For example, when Michaelis (1954) used pollen from *Epilobium hirsutum* (Hairy Willowherb) to fertilize *E. luteum* (Yellow Willowherb), the resulting F_1 hybrids were vigorous and fertile. However, when the cross was reversed, the offspring were abnormal in development and had sterile flowers. Wishart et al. (1988) investigated sperm production in hybrids between mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*). They report that an F_1 hybrid sired by an *O. virginianus* buck produced mature spermatozoa (though they were less numerous than in either pure parent and showed many abnormalities), while an F_1 individual from the reciprocal cross produced none.[189] Hybridization between these deer has produced a hybrid population that extends across the United States from Texas to Canada. Similarly, Finn (1907: 22) says F_1

hybrids produced by a wood pigeon (*Columba palumbus*) hen and domestic pigeon (*C. livia*) cock are partially fertile, but those from the reciprocal cross are not.

Studying reciprocal crosses in the salamander genus *Hynobius,* Kawamura (1953: 112–114) found that *H. nebulosus* females produce hybrids that are partially fertile in both sexes when crossed with *H. nigrescens*, but noted that "a nearly complete gametic isolation seems to be present between *nigrescens* females and *nebulosus* males." In this cross, then, reversal of the sexes has a radical effect on the outcome of the cross. In one direction it produces partially fertile hybrids of both sexes, but in the other the sperm cannot even fertilize the egg. Nonreversible reciprocal crosses of this sort constitute one of the many difficulties that arise when one concerns oneself with whether populations should be treated as conspecific (see Chapter 1). According to a biological definition of *species,* male and female individuals of *H. nigrescens* should be treated as conspecific. However, should *nebulosus* males be treated as conspecific with *nigrescens* females if the sperm of the former cannot even penetrate the egg of the latter?

Fertility in Hybrids

Variation in Fertility. The writer's surveys of published reports of avian and mammalian hybridization (McCarthy 2006; McCarthy, in prep.) have revealed a general tendency on the part of researchers to make black-and-white assessments of hybrid fertility. If an investigator doesn't observe offspring from a hybrid of a particular type, they will likely conclude all hybrids of that type are sterile. If another observer looks at a hybrid of the same type and finds it does produce some offspring, they will likely express the opinion that all such hybrids are fertile. However, the actual ability of hybrids to produce offspring varies from cross to cross, and, for a particular cross, from individual to individual. Within the context of stabilization theory, this fact is important since it opens up the possibility of natural selection among differing hybrids. Therefore, this phenomenon will be considered here at some length. Variation of this sort has long been recognized. After noting that fertility is usually lower in hybrids than in their parents, Stebbins (1969: 33) pointed out that

> the majority of interspecific hybrids, however, are not completely sterile, but are able to produce at least a small percentage of viable gametes, at least of one sex. In the F_2 or back cross progeny of such hybrids a great range of fertility exists, and in nearly all such progenies there exist some individuals which are more fertile than was the F_1. This fact was already demonstrated many years ago by Müntzing (1930) in his research on *Galeopsis tetrahit* × *bifida,* and has been found in the progeny of many other F_1 interspecific hybrids (Stebbins, 1950; Grant, 1963).

Stebbins' experience was primarily with plants, but the writer's own surveys of avian and mammalian hybrids has revealed the same variability in fertility, especially in later generations, in a wide variety of crosses. So this phenomenon appears to be characteristic of hybrids produced by a very broad range of organisms. The fact that there is variation in fertility even among hybrids derived from the same original cross is important because, as Goldman et al. (2004) point out, there is a "common perception of the reduced fitness of hybrids." Certainly, *on average,* hybrids are less able to survive and reproduce. However, there is a range of fitnesses in hybrids.[190] Those hybrids at the upper end of the range will be favored by natural selection.

Fertility often increases with backcrossing (see citations listed in Note 191). In captive crosses, this is one of the most frequently observed pathways to fertility. Thus, hybrids, known as beefaloes (or cattaloes), can be produced from the cross domestic cattle (*Bos taurus*) × American Bison (*Bison bison*). Beefalo males, produced by the first backcross are usually sterile, but when partially fertile backcross females are backcrossed again, the resulting males are frequently fertile.[192] Similarly, in the cross *Chrysolophus pictus* (Golden Pheasant) × *Lophura nycthemerus* (Silver Pheasant) the males are partially fertile, but the females are virtually always sterile. When the fertile male hybrids are backcrossed to *L. nycthemerus*, however, some of the females so produced are also partially fertile.[193] In point of fact, in many crosses the hybrids are already partially fertile in both sexes even in the first (F_1) generation.

Although most types of hybrids are less fertile than their parents, the degree of fertility varies widely according to the cross in question, from crosses producing very infertile hybrids, unknown to produce offspring, to crosses producing progeny about as fertile as either parent. Even hybrids between genera can be fertile. For example, some crosses between *Aronia* (chokeberries) and *Sorbus* (whitebeams, rowans, service trees, and Mountain Ash) produce hybrids that Christopher et al. (1991: 343) say are "completely fertile" while others result in infertile hybrids that produce fruits that contain few seeds.[194] Darwin noted long ago that hybrids

> are very generally infertile in some degree. But besides the extreme difficulty of deciding in some cases what forms to rank as species & what as varieties, we shall see that there is so insensible a gradation from utter sterility to perfect fertility that it is most difficult to draw any distinct line of demarcation between the two; — more especially as other quite independent causes often simultaneously tend to give some degree of infertility. In some very few cases it is, I think impossible to withstand the evidence that forms which are universally admitted to be good species are quite fertile together & produce quite fertile offspring.[195]

Indeed, today it is known that many thousands of crosses between organisms treated as separate species produce hybrids that are themselves capable of producing offspring.

The degree of fertility varies, too, with gender, and, as we have already seen, with the direction of the cross. It can often be improved in successive generations by selection and backcrossing. Stebbins (1959: 237) points out that "the offspring of many partly sterile hybrids are more fertile than the F_1, and this fertility often increases in later generations." Given this variability, the failure of one, or even several, individuals to produce offspring does not guarantee another hybrid produced from the same cross will also be unsuccessful. In the cross between common sunflower (*Helianthus annuus*) and Jerusalem artichoke (*H. tuberosus*), Marchenko (1962: 321) produced a large number of backcrosses to both parental plants and examined approximately 10,000 seed heads from these hybrids. Among these, only a few with a single seed were found. However, one of the plants produced by backcrossing the F_1 to *H. annuus* produced 700 seeds, thus providing Marchenko with starting material to breed rust resistance in the sunflower. Thousands of other plants from the same cross were either sterile or produced one or two seeds per plant.

As was just mentioned, the sex of a hybrid can also have a bearing on its fertility. For example, when two types of mammals cross and one sex is absent, rare, or of reduced fertility among the hybrids, it is virtually always the male. The reverse is true among birds. In other classes of organisms, however, no such bias occurs.[a] Thus, F_1 male beefaloes are virtually always sterile, but the females are partially fertile and can be backcrossed to domestic or bison bulls. However, in those classes of organisms where such biases occur there is a continuum of cases. For example, in some avian crosses, females are as common as males and lay fertile eggs. In others, they lay sterile ones. In still others no females are produced at all. Bhatnagar (1968) reported that when common pheasants (*Phasianus colchicus*) were mated with domestic fowl (*Gallus gallus*), the male-female ratio in hatched eggs was about 12:1. In a study of quail-chicken hybrids (*Coturnix japonica* × *G. gallus*), Takashima and Mizuma (1982) found that 74 percent of the surviving hybrids were male after three days of incubation, and 90 percent, after five. After hatching, all were male.

Although fertility in hybrids is a matter of degree, reports for most crosses offer no exact quantification of this characteristic.[b] Most crosses are poorly evaluated with regard to the viability of offspring. For example, in a review of avian hybridization Gray (1958) lists a single report for European Greenfinch (*Carduelis chloris*) × Yellowhammer (*Emberiza citrinella*). She describes results for a single clutch of five eggs. Three eggs were sterile, one hybrid died in the shell, and one survived to maturity. On the basis of such limited data, no firm conclusions could be reached

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[a] Haldane (1922) observed that "when in the F_1 offspring of a cross between two animal species or races, one sex is absent, rare, or sterile, that sex is always the heterozygous sex" (i.e., the sex having two different sex chromosomes). This principle is known as "Haldane's Rule." This bias is also seen in backcross progeny, not just F_1 hybrids. In mammals the *heterozygous sex* (or, as it is more commonly termed, the *heterogametic sex*) is the male. Haldane's Rule can therefore be used as a clue in certain cases. For example, if all, or even the vast majority, of available specimens on which an avian taxon is based are male, or if all of those on which a mammalian taxon is based are male, investigators should consider the possibility the taxon is of hybrid origin (i.e., whether the specimens on which the taxon is based might be hybrid). As another example, when two avian populations hybridize on an ongoing basis, but the two types of mitochondrial DNA remain spatially segregated, the female hybrids will usually be sterile (because mitochondrial DNA is maternally inherited).

[b] Ideally, studies would examine relative percentages of viable gametes, fertilization rates, and data on the viability of the hybrids in later development. But for the most part such exact information is available only for crosses involving domestic animals and plants.

concerning the general viability of offspring produced from this cross.

Even within a population treated as a single species, fertility varies from one individual to another. For example, individual human beings vary markedly in fertility. The same is true of individuals participating in hybrid crosses. Individuals sterile when mated with their own kind will likewise not produce progeny when participating in a hybrid cross. To some extent, hybrids are subject to the same constraints as other organisms. For example, they can be too young, or too old, to breed. They can also refuse to breed because it is the wrong season or because of stress induced in captivity, or because their needs have not been met in some other way.[a] How well a given cross works, then, depends in part on which individuals mate, as well as the conditions under which the mating is attempted. This fact has long been recognized. Darwin was well aware of it:

> The fertility, both of first crosses and of hybrids, is more easily affected by unfavourable conditions, than is the fertility of pure species. But the degree of fertility is likewise innately variable; for it is not always the same when the same two species are crossed under the same circumstances, but depends in part upon the constitution of the individuals which happen to have been chosen for the experiment. So it is with hybrids, for their degree of fertility is often found to differ greatly in the several individuals raised from seed out of the same capsule and exposed to exactly the same conditions.[196]

For example, Takahashi (1982) studied interfamilial hybrids (Numididae × Phasianidae) between guinea hens (*Numida meleagris*) and three different types of chicken cocks (White Leghorn, Nagoya, and Barred Plymouth Rock). He found that the number of fertile eggs was not the same from hen to hen. Instead, the hens showed a broad range of receptivity.

As Darwin notes in the passage just quoted, uniform fertility is no more the expectation in hybrids than in the crosses producing them. Many known crosses produce hybrids that are capable of producing offspring.[197] But different hybrid individuals produced by a single type of cross can differ in fertility even in the F_1 generation (which is generally much less variable than later hybrid generations). The cross Sterlet (*Acipenser ruthenus*) × Beluga (*Huso huso*), two types of sturgeon, provides an example. Kijima et al. (1988) examined the testes and ovaries of hybrids of this kind and found significant variability. In some F_1 individuals, the gonads were undifferentiated, but, in others, were fully developed and contained mature gametes. Certainly, some individuals produced by this cross are able to produce offspring; an earlier article reported F_1 hybrids mated among themselves to produce an F_2 generation.[198] Goodspeed (1915) found that most varieties of common tobacco

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a. Some evidence even suggests immunological factors affect a female's ability to conceive (Billingham et al. 1961; Haley and Abplanalp 1970; Vojtiskova 1958). Olsen (1972) found turkey hens produced fewer fertile hybrid eggs as they developed antibodies to chicken spermatozoa. McGovern (1973) says more goat × sheep hybrid embryos die when mother goats have received skin grafts from sheep and injections of ram leukocytes.

(*Nicotiana tabacum*), when crossed with the weed *N. glutinosa,* produce hybrids of relatively low fertility, only about 10 viable seeds per capsule. But Clausen and Goodspeed (1925: 279) found that when a variety of *N. tabacum* from Cuba was crossed with *N. glutinosa* the hybrids produced seed "of the same order of viability as the pure seed of the species."

Therefore, when evaluating the fertility of a given cross, it is better to reserve judgment until a variety of individuals have been tested. Even then, a degree of uncertainty remains. As Darwin (1859: 256) points out, "There are species which can be crossed very rarely, or with extreme difficulty, but the hybrids, when at last produced, are very fertile." A good example of the need for caution is the cross of barbary sheep and domestic goat. After repeated efforts to cross various types of sheep and goat, Steklenev (1972) thought it safe to write the following: "Summarizing the results of hybridization of members of the sheep and goat genera with the use of both domestic and wild forms, we can conclude the impossibility of obtaining hybrids in a single one of the tested combinations." Among the crosses discounted by Steklenev is that between barbary sheep (*Ammotragus lervia*) and domestic goat (*Capra hircus*), which various researchers attempted to cross without success.[199] Hybrid embryos were resorbed, or the fetuses, stillborn. Yet other breeders eventually succeeded in delivering a healthy, partially fertile male hybrid.[200] Moore et al. (1980) say its semen contained about 2×10^9 spermatozoa/ml, with excellent motility.

Often, the fact that a cross has not been reported merely reflects that no effort has been made to obtain it, or that the necessary technology has been lacking. Thus, with regard to lilies Rockwell et al. say that

> For centuries no attempts were made to get the natural species, the wild lilies, to cross. This was not due to the fact that members of the lily tribe were incompatible. It was, rather that the natural species come into flower over a very wide period of time — early June to late September — thus reducing the range of possible artificial crosses. Now, with modern methods of preserving pollen by cool and dry storage, almost any two species may be crossed.[201]

Crossability varies not only with the types that are crossed, but can even vary for the same individual at different times. Olsen (1972) notes that the frequency of fertile hybrid eggs decreased over a 15-week period as turkey hens developed antibodies to chicken spermatozoa. Similarly, McGovern (1973) reported an increased number of deaths in goat (*Capra hircus*) × sheep (*Ovis aries*) hybrid ("geep") embryos, when the mother goats had earlier received skin grafts from sheep and injections of ram leukocytes. A female geep was produced by a serendipitous mating of a ram and a nanny goat (Cribiu et al. 1988; Tucker et al. 1989). It birthed a healthy backcross hybrid after mating with a ram.[202] However, Tucker et al. say later attempts to breed the same geep were unsuccessful due to embryonic mortality; again suggesting antibodies had been produced.[203] Depending on the cross, then, individual fertility may be a continuum grading from the most fertile hybrid in a population to the most sterile.

Sometimes hybrids are more crossable, and thus in a sense more fertile, than their parents. For example, Rockwell et al., who were just quoted in connection with the many recent reports of new lily hybrids, say that

> This recent breakthrough in lily hybridizing, however, has also been due to the fact that, although the natural species showed marked resistance to being crossed, their hybrid offspring did not. *They crossed readily not only with one another, but also back again with the natural species.* In recent years, as a result, the floodgates to new lilies, and even to distinctly new *types* of lilies, have been opened. We now face the day when we shall have a plethora of new lilies.[204] [italics appear in original]

Nevertheless, when it comes to fertility, the writer's experience indicates that many people perceive hybrids in a stereotypic manner. They think of the common mule as soon as hybrids are mentioned. Moreover, they go on to suppose that all mules are absolutely sterile and that this supposed absolute sterility of mules is characteristic of all hybrids. In this way, a mistaken idea concerning the characteristics of a single type of hybrid (i.e., the notion that all mules are absolutely sterile) expands to become a mistaken belief about a broad class of organisms (i.e., the belief that all hybrids are sterile). As we have seen, many hybrids are partially fertile. Moreover, even the specific case of the mule is far from hopeless. While mules are typically of very low fertility in comparison with many hybrids, there have been numerous reports, some of them completely reliable, of mare mules producing offspring.[205] Here in the United States, apparently, no one even tries to breed mules, but, according to Rong et al. (1985: 821), "in China, where mules are bred intensively by artificial insemination, there has been no doubt that the animals are occasionally fertile."

Variation in the Viability of Gametes. That hybrids produce abnormal gametes has long been known.[206] Even Darwin was aware of the fact. Thus, he says that in hybrid plants "the pollen is manifestly imperfect as may be seen by everyone who has ever examined a hybrid. In like manner, with hybrid animals the spermatozoa are imperfect."[207] In a purebred individual one gamete typically looks much like the next. But in hybrids they often vary in size and shape, and many are inviable.[208] For example, although beefalo males do not usually produce sperm in the F_1 generation, when partially fertile female hybrids are backcrossed, second and third generation male backcrosses do produce sperm, and are fertile in varying degree. Their spermatozoa are abnormal, varying in shape and size even within the ejaculate of a single individual.[209] Close et al. (1996) describe many defects in the sperm of hybrid rock wallabies (*Petrogale*), which included such abnormalities as multinucleate, irregularly shaped, markedly enlarged, or multiple-tailed spermatozoa.[a] The degree

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[a] In one individual, 17.5% of the spermatozoa had twin undulipodia associated with a single head. Close et al. say that abnormalities of condensation, too, were very common in hybrid

of variability present in hybrid spermatozoa can itself vary from one hybrid individual to another. In studying the cross American bison (*Bison bison*) × domestic cattle (*Bos taurus*), Shumov and Rubtsov (1981) note that spermatozoa from ejaculates of one hybrid (3/8 bison – 5/8 domestic) were virtually all normal in structure and motility, but that the ejaculates of another (a 3/4 bison – 1/4 domestic) bull contained few spermatozoa and virtually all were structurally abnormal. According to Steklenev (1983: 62), an American Bison crossed with an F_1 hybrid from the cross yak × mithan (*Bos grunniens* × *Bos frontalis*) produced a three-way hybrid that exhibited "a comparatively normal course of spermatogenesis" with a sperm density of 4.29 million/ml, but 35 percent of its spermatozoa were abnormal.

In a plant hybrid of low fertility some of the pollen grains may be abnormally large, but most, though variable in size, will be much smaller than in a fertile plant and devoid of contents.[210] Hybrids often produce a high proportion of empty seeds.[211] Stains are widely used to detect infertile pollen because they differentially color the empty grains.[212] For example, the malachite green-acid fuchsin-orange G stain of Alexander (1969) stains fertile pollen red, and infertile pollen green.[a]

A Fallacious Assumption. Given the facts thus far presented on the fertility of hybrids, it must be clear to the reader that many hybrids of unevaluated reproductive status would turn out to be partially fertile if they were tested. Additional evidence, yet to be presented, will further tend to confirm this conclusion. However, many people, when confronted with a hybrid, will assume it is sterile unless they are provided with evidence to the contrary. This presumption that *hybrids of unknown reproductive ability are sterile,* is one of the tacit presuppositions mentioned in the Introduction. It can have a potent effect on one's theoretical outlook. Since the great majority of hybrids have not been evaluated with respect to fertility, it leads one to presume most hybrids are sterile, an assumption that, in turn, prompts the conclusion that hybrids are, in general, evolutionary dead-ends. Likewise, anyone who believes that forms should not be treated as distinct species if they produce hybrids that are not perfectly sterile, will think that any two forms producing partially fertile hybrids should be treated as belonging to the same species. This assumption that hybrids of uninvestigated reproductive status are sterile (combined with the additional widespread misconception that hybrids are rare in a natural setting) makes hybrids seem far less interesting than they otherwise might. Indeed, I am sure such presuppositions have gone far in preventing the study of hybrids. After all, from such a perspective, hybrids are freakish, sterile aberrations that can tell us little about

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sperm. In all four types of hybrids they examined, there were also elevated levels of asynapsis and XY-autosome associations during meiosis. Testicles and seminiferous tubules were usually reduced in size in hybrids in comparison with pure parental individuals, as the writer has often observed in many other types of hybrids. In a broad review of gametogenesis in plants,

[a] It stains pollen walls green and cytoplasm red. Uniformly red grains are scored as fertile; partially stained or unstained ones are scored sterile.

natural processes and the ordinary course of evolution. This preconception is self-perpetuating — since many people think hybrids are irrelevant, they lack the interest to learn more and find out that such is not the case. The curiosity is also often lacking that might otherwise prompt researchers to conduct studies that would provide additional evidence that partially fertile hybrids do occur in the wild.

Trait Variation in Hybrids

An organism descended from matings between two or more parental types will mix the characteristics of those types. As Darwin notes in the *Origin,* "when hybrids are able to breed *inter se* [i.e., among themselves], they transmit to their offspring from generation to generation the same compounded organisation."[213] The analysis of a hybrid's traits will therefore often allow the identification of its parents. The traits of parents are expressed in hybrids in two typical ways. They are either intermediate or combined. A general understanding of the nature of trait variation in hybrids is necessary if one is to understand stabilization.

Intermediacy. With respect to most traits — size, color, texture, and so on — hybrids are intermediate between their parents. For example, Hubbs (1955) evaluated a variety of fish hybrids in the family Catostomidae (suckers). In summarizing his results, he states (ibid*:* 5) that

> intermediacy is seen in such external characters as the coloration, the general body form, the size of the head, the length and protrusion of the snout, the size of the scales. … Intermediacy may involve the type of relative growth. Internal characters, such as those of the skeleton, may also be transitional. When the values for the hybrids are computed as an index, on a percentage scale grading from the value for the one parent, set at 0, to the value for the other, set at 100, the indices form a frequency distribution with the mode very close to 50, which represents ideal interjacency.

Similarly Grant and Grant (1971b) report that in Arizona natural hybrids between two cholla cactuses (*Opuntia spinosior* and *O. versicolor*) are intermediate with respect to a variety of morphological traits (e.g., stem joint diameter, tubercle height and width, color of stems, length and number of spines, fruit texture and color).

In the absence of data from captive crosses, natural hybrids are often identified as hybrids on the basis of their intermediacy. In fact, hybrids are often referred to as "intermediates." Thus, in a detailed study of a natural hybrid between two ducks, the Goldeneye (*Bucephala clangula*) and the Hooded Merganser (*Lophodytes cucullata*), Ball (1934) found the hybrid was intermediate between its parents with respect to many characteristics. These included overall length, wing and tail length, width and length of bill, degree of development of head crest, and a variety of other features. Sturgeon in the Atchafalaya River, a tributary of the upper Missouri River (western U.S.), are hybrids of the pallid (*Scaphirhynchus albus*) and shovelnose (*S.*

platorhynchus) sturgeons and are also intermediate with respect to a broad range of physical traits and in their genetics.[214] The Flame-rumped Tanager (*Ramphocelus flammigerus*) has a red rump, and the Lemon-rumped Tanager (*R. icteronotus*) has a yellow one. These birds hybridize extensively in the Andes.[215] The rumps of their hybrids are intermediate in color, in varying shades of orange.[216]

Intermediacy is seen not only in the physical characters of hybrids but also in their behavior. Evans (1966) reports that hybrids between Sharp-tailed Grouse (*Tympanuchus phasianellus*) and Greater Prairie Chicken (*T. cupido*) hold their wings further out during displays than do prairie chickens, but not so far as do Sharp-tailed Grouse. Hybrid hummingbirds often perform dive displays intermediate between their parents' displays.[217] The territorial displays of hybrid lizards (*Anolis aeneus* × *A. trinitatis*) on the island of Trinidad are intermediate too.[218] Koeppl et al. (1978) analyzed the acoustical behavior of hybrids between Richardson's Ground Squirrel (*Spermophilus richardsonii*) and the Wyoming Ground Squirrel (*S. elegans*) in southwestern Montana and found their chirps were intermediate between the two typical parental chirps. Cooper et al. (1998) note that the echolocation call frequency of hybrids between the Eastern and Large-eared horseshoe bats are also intermediate (about 40 kHz, vs. 66 kHz in *Rhinolophus megaphyllus* and 28 kHz in *R. philippinensis*). Migration routes of hybrids are often midway between those of their parents.[219] Gestation and incubation periods of hybrids are usually intermediate too. Hybrid intermediacy involves the entire organism — any trait can be affected.

Combined Traits. Although intermediacy is the rule, a given type of hybrid may not be intermediate with respect to certain traits, and instead may approach one parental type or another. For example, in birds the plumage pattern of a hybrid's head will often resemble that of one parent, while that of its body will resemble the other. Brooks (1907) collected a wild hybrid between the Blue Grouse (*Dendragapus obscurus*) and Sharp-tailed Grouse (*Tympanuchus phasianellus*). He was confused when he first saw this bird because in front it looked like a sharp-tail, but in back it looked like a blue. Kawamura (1950a) found traits of F_1 hybrid frogs between European Common Frog (*Rana temporaria*) and Japanese Brown Frog (*R. japonica*) resembled one parent with respect to some traits, but the other with respect to others. Rahman and Uehara (2004) obtained similar results with hybrids between sea urchins in the genus *Echinometra.*[a]

The vocalizations of hybrids often unite features otherwise found only separately in their parents. Marler and Tenaza (1977) say the song of a female gibbon hybrid (*Hylobates lar* × *H. muelleri*) followed this pattern. Jung et al. (1994)

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[a] Some traits in hybrids may closely approach one parent because the relevant genes, derived from that parent, are dominant over those of the other parent. Male first generation (F_1) hybrids between the Golden-winged and Blue-winged warblers (*Vermivora chrysoptera* and *V. pinus*) combine dominant traits of both parents (Nichols 1908; Parkes 1951). They have the white underparts of a Golden-winged, but the reduced facial pattern (eye-line only) of a Blue-winged (McCarthy 2006).

describe a junco × sparrow hybrid (*Junco hyemalis* × *Zonotrichia albicollis*) which, too, sang a song mixing those of its parents. Likewise, in studying natural hybrids between the Smooth Frog (*Geocrinia laevis*) and the Victorian Frog (*G. victoriana*), which occur in southeastern Australia, Littlejohn and Watson (1976a, 1976b) found that hybrid calls combine elements of the parental calls.

Traits are combined even at the molecular level, so that hybrids produce a mixture of proteins, some inherited from one parent, some from the other. Protein subunits of heterogenous origin may join in a hybrid to form a single functional unit. For example, Jiménez-Porras (1967) found that venom from natural hybrids of the Jumping Pit Viper and Picado's Pit Viper (*Atropoides nummifer* and *A. picadoi*) is electrophoretically intermediate.

Variation in Later Generations. In a natural setting, pure populations unaffected by hybridization are relatively uniform, genetically and morphologically. F_1 hybrids between such populations, too, will usually be uniform, even when the two parental forms differ rather markedly. This lack of variation results from each F_1 hybrid receiving much the same genetic complement from each parental type each time the cross occurs. However, in crosses where *later-generation hybrids* occur, a wide variety of types can arise because parental traits are variously combined in different individuals. For example, plant breeder Bernice Brilmayer notes that

> when two natural species [of begonia] are used as parents, the seedlings from one pod are all closely similar or identical, and inherit similar characteristics from each of the parents. When two hybrids are crossed — or a species is crossed with a hybrid — the seedlings will vary, often to the extent that no two are alike. These have to be grown on to maturity before the outstanding new plants can be selected with accuracy.[220]

For this same reason, high levels of morphological variability are a strong indication that a natural population is the product of hybridization (the genetic basis of this morphological variation will be explained in Chapter 3). Brainerd (1924) describes highly variable later-generation hybrids derived from crosses between various members of the violet genus *Viola.* He reproduced many of these natural hybrids with artificial crosses. In some of these later-generation hybrids leaf shape was considerably modified and some of the variants could be stabilized as new types. Figure 2.1 shows the leaves of *V. pedatifida, V. sagittata,* and various F_2 hybrids. In reference to a different violet cross giving similar results, Brainerd comments that

> In these various ways there has arisen in the numerous progeny of the hybrid under discussion a considerable diversity of foliage, such as would present insoluble difficulties to a taxonomic student who did not know that these diverse forms all came from one individual, by close-fertilized reproduction, in the short period of three or four years. The extreme differences are such as would warrant the making of several distinct species, according to the hasty methods of ordinary practice.[221]

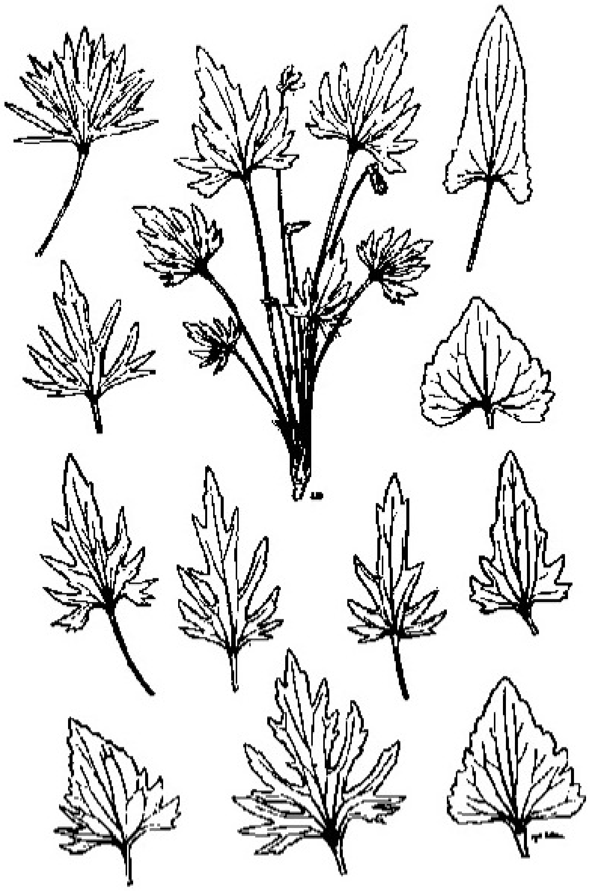

Figure 2.1: Leaf of *Viola pedatifida* (upper left), of *V. sagittata* (upper right), and of nine different F_2 hybrids. An F_1 hybrid plant is also shown (upper middle). From Brainerd (1924).

Compound hybrids. Compound hybrids are produced by successive matings between more than two different types of organisms.

For example, Sandnes (1957) first produced a hybrid between a Lady Amherst's Pheasant and a Golden Pheasant (*Chrysolophus amherstiae* × *C. pictus*), and then mated the hybrid with a Common Pheasant (*Phasianus colchicus*) to produce three-way hybrids. Compound hybrids occur also in the wild. Similarly, Harrison and Harrison (1965a) report a presumed natural three-way hybrid of Pintail Duck (*Anas acuta*) with Mallard (*A. platyrhynchos*) and Gadwall (*A. strepera*).

In western Mexico, three fish, the headwater livebearer (*Poeciliopsis monacha*), clearfin livebearer (*P. lucida*), and chubby livebearer (*P. viriosa*), produce compound hybrids on an ongoing basis.[222] Camp (1945) argued that *Vaccinium corymbosum,* the common highbush blueberry of northeastern North America, is the hybrid of four other types that he treated as separate species. Multiple hybrids are common among captive falcons (e.g., Barbary/Gyr × Peregrine/Lanner).

Hybrids with even more complex ancestry are commonly obtained, such as five-way hybrids or six-way hybrids. For example, Coimbra-Filho et al. (1993) produced a six-way hybrid between various marmosets of the genus *Callithrix.* The ability of plants to produce complex compound hybrids has long been recognized. Already, more than a century ago, Focke (1881) noted that successive intrageneric matings between types treated as separate species can result in five- and six-way hybrids (e.g., in *Begonia, Calceolaria, Pelargonium,* and *Salix*). Darwin,[223] too, was aware of compound hybrids:

> He who wishes, says Kölreuter,[224] to obtain an endless number of varieties from hybrids should cross and recross them. There is also much variability when hybrids or mongrels are reduced or absorbed by repeated crosses with either pure parent-form; and a still higher degree of variability when three distinct species, and most of all when four species, are blended together by successive crosses. Beyond this point Gärtner,[225] on whose authority the foregoing statements are made, never succeeded in effecting a union; but Max Wichura[226] united six distinct species of willows into a single hybrid.

Heterotic Traits and Synergistic Effects. With respect to some traits, a hybrid may fall well outside the range of parental variation. Such traits are said to be *heterotic*.[a] That hybrids need not be intermediate with respect to every trait has long been recognized. In his book *Evolution by Means of Hybridization* (1916), Lotsy noted hybrids in the snapdragon genus *Antirrhinum* had certain characteristics that were entirely different from those of the original parents. Thus, when he crossed *Antirrhinum glutinosum* and *A. majus,* he found individuals in the F_2 generation with flowers like those seen in the related genus *Rhinanthus* (although both parents produce flowers that are typical of the genus *Antirrhinum*).[227] In the F_4 generation he was able to stabilize a new, true-breeding type. Hagedoorn and Hagedoorn (1921)

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[a] In connection with natural stabilized hybrids, Stebbins (1959: 245) uses the term *transgressive* for traits exceeding the limits of variation found in either parent.

note that several strongly aberrant types appeared in the F_2 generation derived from the cross *Argemone mexicana* × *A. platyceras* (Mexican pricklypoppy × rough pricklypoppy). Some differed from either parent with respect to characteristics usually considered fundamental with respect to taxonomic classification (such as sepal and carpel number). The reader can see that many of the violet hybrids produced by Brainerd (Figure 2.1) have leaf shapes that are not obviously intermediate between the leaf shapes seen in their parents.

Any trait can be heterotic, but most reports of heterosis involve the overall size of the hybrids. The California redwood (*Sequoia sempervirens*), thought to be of hybrid origin,[228] is the tallest tree in the world. Therefore, with respect to height, it is certainly not intermediate between its probable parents, the giant sequoia (*Sequoiadendron giganteum*) and dawn redwood (*Metasequoia glyptostroboides*). Hybrids between the Bactrian Camel (*Camelus bactrianus*) and the Dromedary (*C. dromedarius*), which are partially fertile in both sexes, have long been bred because they are larger, more tolerant, and easier to work with than either parent.[229] According to Lakoza (1938), "in certain very important camel-breeding regions nearly the entire stock consists of hybrids of various grades." Gray (1972: 161) states that these hybrids, "show heterosis with regard to body measurements, hardiness, endurance, longevity and certain blood characters." Hybrids between Siberian Crane (*Grus leucogeranus*) and White-naped Crane (*G. vipio*) are bigger than either of their parents.[230] Similarly, the hybrid produced by a lion and a tigress (known as a "liger") is usually larger and stronger than either of its parents, whereas the reciprocal cross produces a hybrid (the "tigon") that tends to be smaller than either of its parents (Gray 1972, McCarthy, in prep.). The former cross, then, is an example of *positive heterosis,* in which the hybrid exceeds the range of variation exhibited by its parents, while the latter is an example of *negative heterosis,* in which the hybrid falls below the range of parental variation with respect to a given trait. Nevertheless, the typical hybrid, produced by the typical hybrid cross, is intermediate in size. For this reason, Stebbins (1950: 285), speaking before the advent of modern molecular techniques for the identification of natural hybrids, noted that "the detection of an existing species or subspecies as a new [i.e., as a nonintermediate] derivative of past hybridization is well-nigh impossible, since by definition such new types would not be recognizably intermediate between their parental species." This factor, then, must surely have contributed to underreporting of nonintermediate natural hybrids.

Heterosis is of evolutionary interest because it allows hybridization to produce new traits beyond the range of ordinary parental variation. For example, in Algeria *Ophrys murbeckii,* an orchid of the Atlas Mountains, is derived from hybridization between *O. fusca* and *O. lutea,* but it occurs at higher altitudes than either of its parents.[231] Johnson and Leefe (1999: 1065) report that the snail *Campeloma parthenum* (Maiden Campeloma) has a five-fold greater survival rate under stressful conditions than one of the parents that crossed to produce it, *C. geniculum* (Ovate Campeloma). Grant and Grant (1996b) showed hybrid Galapagos finches were more fit than their parents following an El Niño climatic perturbation event; the hybrids were better able to feed on the seeds of the plants present after the event. In some crosses, the hybrids produced are actually more viable and vigorous than either parental type. For example, Rockwell et al. (1961) say

> It is especially in their larger tolerances that the newer [hybrid] strains of garden lilies show their merits. Through selection of the sturdier species as seed or pollen parents, through years of testing and elimination of the weaker, or less hardy, plants, many new hybrid strains will grow and perform well where one, or sometimes both, of the parents may be grown only with the greatest difficulty, if at all … Like the mule that has more strength and endurance than either of its parents, many of the hybrid lilies show more stamina and persistence than that commonly found among their ancestors.[232]

Given the fact that evolutionary biologists so often emphasize that hybrids are inviable — as indeed many are — it is ironic that the phenomenon of hybrid vigor is so widely recognized by breeders. It is an extremely common, even typical, phenomenon.

In certain sunfish crosses (genus *Lepomis*) the hybrids are more vigorous and aggressive than their parents. Manwell et al. (1963) showed that the vigor of these fish was, at least in part, the result of an enhanced blood chemistry, combining factors from both parents.[a] Thus, *synergy,* the emergence of a new, nonintermediate trait as the result of the combination of two or more traits not previously associated in a single organism, often gives rise to nonintermediate traits in hybrids, just as the combination of two gases (e.g., hydrogen and oxygen) can produce a liquid (water). In this connection it is important to consider that the expression of any hereditary trait in any organism is the result of a complex interaction of molecules at the genetic level. In hybrids such interactions are of a novel, untried nature and can have unexpected effects. Moreover, if a hybrid derived from a cross between two parents is crossed again with a third type of parent, the compound hybrid so obtained can have traits that are not intermediate between those of the first two parents. As we saw in the previous section, both domestic and wild compound hybrids are common. There are many examples of hybrids having a trait not found in either of their parents. For example, hybrids between Audubon's Oriole (*Icterus graduacauda*) the Altamira Oriole (*I. gularis*), which occur along the eastern border of the U.S. and Mexico, have streaking on their upper backs even though both their parents lack this trait.[233]

Even as a young man, Darwin was aware that hybrids need not be intermediate. In his *Voyages of the Adventure and Beagle* (1839) he remarks that "the mule always appears to me a most surprising animal. That a hybrid should possess more reason,

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[a] Manwell et al. (1963) also analyzed hemoglobin in Bass (*Micropterus*) hybrids. They reported that hemoglobins identical to those seen in the hybrids could be produced by mixing in vitro hemoglobin subunits otherwise found only separately in the two parents. This phenomenon of hybrids assembling proteins from two subunits derived from different parents is common. For an example see Isaacs (1970).

memory, obstinacy, social affection, and powers of muscular endurance, than either of its parents, seems to indicate that art has here out-mastered nature."[234] Moreover, his later writings clearly show that he was quite familiar with the phenomenon of heterosis. For example, the following extended quotation from the first edition of *The Variation of Animals and Plants under Domestication* (1868: vol. II, 129–131) shows that he knew nonintermediate hybrids had been repeatedly reported by a wide variety of breeders and investigators. It also provides some interesting examples.

> With respect to the benefit derived from crossing distinct varieties, plenty of evidence has been published. [Augustin] Sageret[235] repeatedly speaks in strong terms of the vigour of melons raised by crossing different varieties, and adds that they are more easily fertilised than common melons, and produce numerous good seed. Here follows the evidence of an English gardener: "I have this summer met with better success in my cultivation of melons, in an unprotected state, from the seeds of hybrids (i.e., mongrels) obtained by cross impregnation, than with old varieties, The offspring of three different hybridisations (one more especially, of which the parents were the two most dissimilar varieties I could select) each yielded more ample and finer produce than any one of between twenty and thirty established varieties."[236]
>
> [Thomas] Andrew Knight believed that his seedlings from crossed varieties of the apple exhibited increased vigour and luxuriance;[237] and M. [Eugène] Chevreul[238] alludes to the extreme vigour of some of the crossed fruit-trees raised by Sageret.
>
> By crossing reciprocally the tallest and shortest peas, Knight[a] says, "I had in this experiment, a striking instance of the stimulative effects of crossing the breeds; for the smallest variety, whose height rarely exceeded two feet, was increased to six feet; whilst the height of the large and luxuriant kind was very little diminished. Mr. Laxton gave me seed-peas produced from crosses between four distinct kinds; and the plants thus raised were extraordinarily vigorous, being in each case from one to two or three feet taller than the parent-forms growing close along-side them."
>
> Wiegmann[239] made many crosses between several varieties of cabbage; and he speaks with astonishment of the vigour and height of the mongrels, which excited the amazement of all the gardeners who beheld them. Mr. Chaundy[240] raised a great number of mongrels by planting together six distinct varieties of cabbage. These mongrels displayed an infinite diversity of character; "But the most remarkable circumstance was, that, while all the other cabbages and borecoles in the nursery were destroyed by a severe winter, these hybrids were little injured, and supplied the kitchen when there was no other cabbage to be had."
>
> Mr. [Benjamin] Maund[241] exhibited before the Royal Agricultural Society specimens of crossed wheat, together with their parent varieties; and the editor states that they were intermediate in character, "united with that greater vigour of growth, which it appears, in the vegetable as in the animal world, is the result of a first cross." Knight also crossed several varieties of wheat, and he says "that in the years 1795 and 1796, when almost the whole crop of corn in the island [i.e., Britain] was blighted, the varieties thus obtained, and these only,

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[a] Darwin cites Knight (1799: 200). In the same place (p. 200) Knight says "By this process [i.e., by crossing], it is evident, that any number of new varieties may be obtained; and it is highly probable, that many of these will be found better calculated to correct the defects of different soils and situations, than any we have at present; for, I imagine that all we now possess, have in a great measure been the produce of accident; and it will rarely happen, in this or any other case, that accident has done all that art will be found able to accomplish."

escaped in this neighbourhood, though sown in several different soils and situations."[242]

Here is a remarkable case: M. Clotzsch[243] crossed *Pinus sylvestris* [Scot's pine] and *nigricans* [now *Pinus nigra,* Austrian pine[244]], *Quercus robur* and *pedunculata* [these two oaks are now usually treated as conspecific], *Alnus glutinosa* [European alder] and *incana* [gray alder], *Ulmus campestris* [English elm[245]] and *effusa* [European white elm[a]]; and the cross-fertilised seeds, as well as seeds of the pure parent-trees, were all sown at the same time and in the same place. The result was, that after an interval of eight years, the hybrids were one-third taller than the pure trees!

The facts above given refer to undoubted varieties, excepting the trees crossed by Clotzsch, which are ranked by various botanists as strongly-marked races, sub-species, or species. That true hybrids raised from entirely distinct species, though they lose in fertility, often gain in size and constitutional vigour, is certain. It would be superfluous to quote any facts; for all experimenters, Kölreuter, Gärtner, Herbert, Sageret, Lecoq, and Naudin, have been struck with the wonderful vigour, height, size, tenacity of life, precocity, and hardiness of their hybrid productions. Gärtner[246] sums up his conviction on this head in the strongest terms. Kölreuter[247] gives numerous precise measurements of the weight and height of his hybrids in comparison with measurements of both parent-forms; and speaks with astonishment of their "statura portentosa," [i.e., luxuriance] their "ambitus vastissimus ae altitude valde conspicua" [i.e., extreme height and girth]. Some exceptions to the rule in the case of very sterile hybrids have, however, been noticed by Gärtner and Herbert; but the most striking exceptions are given by Max Wichura[248] who found that hybrid willows were generally tender in constitution, dwarf, and short-lived.

Kölreuter explains the vast increase in the size of the roots, stems, &c., of his hybrids, as the result of a sort of compensation due to their sterility, in the same way as many emasculated animals are larger than the perfect males. This view seems at first sight extremely probable, and has been accepted by various authors;[249] but Gärtner[250] has well remarked that there is much difficulty in fully admitting it; for with many hybrids there is no parallelism between the degree of their sterility and their increased size and vigour. The most striking instances of luxuriant growth have been observed with hybrids which were not sterile in any extreme degree. In the genus *Mirabilis,* certain hybrids are unusually fertile, and their extra-ordinary luxuriance of growth, together with their enormous roots, have been transmitted to their progeny.[251] The increased size of the hybrids produced between the fowl and pheasant, and between distinct species of pheasants, has been already noticed. The result in all cases is probably in part due to the saving of nutriment and vital force through the sexual organs not acting, or acting imperfectly, but more especially to the general law of good being derived from a cross. For it deserves especial attention that mongrel animals and plants, which are so far from being sterile that their fertility is often actually augmented, have, as previously shown, their size, hardiness, and constitutional vigour generally increased.

However, Darwin's extensive knowledge of the effects of hybridization, and of heterosis in particular, is not reflected in the *Origin,* where he used the incorrect claim that hybrids are always intermediate to discount the idea that new types of organisms can be derived from hybridization. For example, every edition of the *Origin* published during his lifetime contained the following statement: "by crossing

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[a] Here *Ulmus campestris* probably refers to *Ulmus procera* (English elm), but the USDA Plants Database also lists *U. campestris* as a synonym of *U. glabra* (Wych elm).

we can get only forms in some degree intermediate between their parents."[252] In this way a false claim became an axiom of subsequent evolutionary thought.

Hybrid Populations

Naturally occurring populations of hybrids have characteristic traits that distinguish them from pure populations unaffected by hybridization. Certain of these traits are important in stabilization theory and will therefore be briefly discussed in this section.

Hybrid Zones. A geographic region where genetically distinct natural populations come into contact and hybridize is known as a *hybrid zone* (a hybrid zone, especially a wide hybrid zone, can also be viewed as a naturally occurring hybrid population). Hybrid zones are found in all major groups of sexual organisms.[253] The pure parental populations on opposite sides of a hybrid zone may differ with respect to almost any type of characteristic — appearance, behavior, physiology, or call. Many hybrid zones exhibit a continuum of variation, spanning the gap between parental types. Within a hybrid zone composed of partially fertile hybrids, the hybrids occupying regions closer to a particular parental type tend to be more similar to that parent. For example, a broad zone between Smith's Bush Squirrel (*Paraxerus cepapi*) and the Red Bush Squirrel (*P. palliatus*) extends from southern Tanzania through Mozambique and Malawi to northeastern South Africa (Kingdon 1974b). Hybrid squirrels occurring near the range of Smith's Bush Squirrel have almost all the traits of *P cepapi.* Those occurring near the Red Bush Squirrel have almost all those of *P. palliatus.* In intermediate regions there are squirrels of all intermediate types. Similarly in southwestern Papua New Guinea there is a hybrid zone between the Greater Bird of Paradise (*Paradisaea apoda*) and the Raggiana Bird of Paradise (*P. raggiana*). In this zone, birds vary geographically in appearance, from very similar to the Raggiana in the east to almost identical to the Greater in the west.[254] In South America (Cruzeiro do Sul, Brazil), there is a hybrid zone between two primates, the Saddle-backed and White-mantled tamarins (*Saguinus fuscicollis* and *S. melanoleucus*), in which, again, hybrids of all degrees of intermediacy occur.[255]

Intergradation. Natural hybridization is often referred to as "intergradation," especially in cases where there is clinal variation. A cline is a graded series of differences exhibited within a population (usually along a geographic line or across a region of environmental transition). In eastern North America, for example, white-tailed deer (*Odocoileus virginianus*) decline gradually in size from north to south.[256] *Intergradation* came to be applied to hybridization between populations, since the variation in such cases is commonly clinal in nature. Hybrid populations often have a very broad geographic distribution. The rate of change across such a population may be very gradual. Thus, four South American toucans often treated as species (*Ramphastos ariel, R. citreolaemus, R. culminatus,* and *R. vitellinus*) are recognizable as types within their respective ranges, but are separated by huge hybrid populations more than a thousand kilometers wide.[257] Under such circumstances use of the term *intergradation* makes sense because the populations merge gradually, one with the other, through a continuous series of intermediate individuals. However, the word is also often applied in the case of populations that interbreed regularly but maintain a sharp discontinuous boundary where they interface. Hoffmann's Woodpecker (*Melanerpes hoffmannii*) and the Red-crowned Woodpecker (*M. rubricapillus*) each have extensive ranges, but they are often said to "intergrade" in Costa Rica because they hybridize there.[258] In this case there is interbreeding without a gradual transition. The characteristics of these two birds have remained sharply distinct and the hybrid zone is quite narrow. It is misleading to use *intergrade* instead of *hybridize* to describe populations that are sharply distinct because such populations might be supposed erroneously to blend gradually via a wide hybrid zone when they don't. In this book, therefore, the word *hybridization* is used to refer to interbreeding of all kinds, whether or not it results in the production of a broad cline between the affected populations.

Compound Hybrid Zones. Compound hybrids, produced from crosses between multiple types of organisms, occur naturally in *compound hybrid zones,* contact zones where multiple forms interbreed. For example, three hummingbirds — the Purple-throated, White-throated, and Grey-tailed mountain-gems (*Lampornis calolaema, L. castaneoventris,* and *L. cinereicauda*) — have a three-way zone in southern Central America.[259,260] In eastern Australia, five other birds, sittellas of the genus *Daphoenositta*, each distinct in appearance, hybridize where they come into contact along five lines radiating from a juncture in central Queensland.[261] Near this center, hybrid birds may have ancestry involving all five different forms.[262] In eastern Africa there are compound hybrid zones between distinct types of giraffes.[263] Though these various forms are now usually treated as races of a single species (*Giraffa camelopardalis*), Dagg (1962) says they were treated as separate species until they were found to hybridize.

Mobile Zones. Many natural hybrid zones are mobile. The hybrid zone in eastern North America between the Golden-winged and Blue-winged warblers (*Vermivora chrysoptera* and *V. pinus*) moves every year, with *V. pinus* slowly taking over territory from the *V. chrysoptera*.[264] Movement has been reported in zones between even relatively sedentary animals such as fossorial insectivores and rodents. For example, Benedict (1997, 1999a, 1999b) reported on a narrow hybrid zone in southern Nebraska (central U.S.) between the Northern Short-tailed Shrew (*Blarina brevicauda*) and Elliot's Short-tailed Shrew (*B. hylophaga*). Benedict says (1999a: 135) that this hybrid zone has undergone rapid movement. For example, at one site it shifted 2.4 kilometers to the south in 22 months. Benedict says his survey showed that the zone often coincided with partial barriers to dispersal (e.g. streams, highways).[265] For example, in Adams County, it straddled West 12th Street between the towns of Hastings and Juniata. After its rapid southward shift, it stabilized thereafter on Highway 34. While surveying avian and mammalian hybrid zones, the writer (McCarthy) has noted many other cases where the zones seem to have stabilized along a dispersal barrier. For example, contact between the House Sparrow (*Passer domesticus*) and the Italian Sparrow (*P. italiae*) is blocked by the Adriatic Sea and, for the most part by the Alps, but hybrid zones do occur in those mountains in low elevation passes (see citations listed under Note 266). Gilliard (1959: 17) discusses a low pass through the otherwise high cordillera dividing northern and southern New Guinea. Mayr and Gilliard (1954: 354) named this pass "Hybrid Gap" because a variety of different types of avian hybrids had been discovered there.

Split Ranges. Since movement of a hybrid zone results from one of the hybridizing forms taking over range from the other, there is always the potential for the receding form's range to. be split. For example, the advancing zone might reach a coastline, mountain range, or river. Under such circumstances, the distribution of the receding form would become discontinuous, splitting on either side of the range of the advancing one. This process probably accounts for many situations where one organism has two ranges separated by the range of another. Examples are such hybridizing pairs as the Turquoise and Collared jays (*Cyanolyca turcosa* and *C. viridicyana*) of the Peruvian Andes, or the Hooded and Carrion crows (*Corvus cornix* and *C. corone*) of Eurasia.[267] In the latter case, the one of crow hybridization, there are two hybrid zones some 4,000 kilometers apart, one in western Europe, the other in Asia. The range of the Hooded Crow lies in between.

Extinction. Hybridization in some cases can lead to the extinction of one of the hybridizing forms. Extinction by this means is most often observed when interbreeding is extensive and one hybridizing type is far outnumbered by the other.[268] The Rusty Grebe (*Tachybaptus rufolavatus*) was confined to Lake Alaotra on Madagascar, where it hybridized so intensely with the invading Little Grebe (*T. ruficollis*) that it seems already to have ceased to exist as a separate genetic entity.[269] Two other birds, the Yellow-throated Miner (*Manorina flavigula*), and Black-eared Miner (*M. melanotis*) hybridize extensively in southeastern Australia. Contact occurs just east of Adelaide. Backcrossing results in a continuum of hybrids, with the darkest almost indistinguishable from the Black-eared Miner, and the palest almost like the Yellow-throated. *M. flavigula* ranges over most of Australia, while *M. melanotis* has a restricted range. Virtually no pure flocks of the latter remain. [270,a]

Expansion of a new type of organism of hybrid origin that is fitter than its parents can also lead to local extinction of its progenitors.[271] An increasing number of well-documented examples are becoming available of natural hybrids that are adaptively superior to their parents (in addition to the cases already discussed see

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a. A more speculative possibility is that extinction may occur via movement of hybrid zones. For example, an advancing hybrid zone, might reach an uninhabitable region such as an ocean, desert or mountain range, leaving no remaining habitat for the receding type.

citations listed in note 272). Thus, after the rusty crayfish (*Orconectes rusticus*) was introduced to Wisconsin and Michigan (northern United States), it hybridized with the native *O. propinquus* (northern clearwater crayfish). Perry et al. (2001) found that the hybrids were superior to both parents in competing for limited food resources and that hybridization consequently poses a threat to *O. propinquus*. A similar case is that of the hybrid between the Mallard (*Anas platyrhynchos*) and the Pacific Black Duck (*A. superciliosa*), which is displacing its parents from New Zealand. This case is discussed in Chapter Four (p. 112). Hegde et al. (2006) recently showed that extensive hybridization between two radishes that have become naturalized in California, *Raphanus sativus* (cultivated radish) and *R. raphanistrum* (jointed charlock), have produced hybrids that are so fit that they have brought on the local extinction of the parents.

Wide Zones and Hybrid Populations. When hybrids occur only at low frequency, parental populations can overlap broadly without significant genetic consequence. For example, the Mourning Warbler (*Oporornis philadelphia*) and Canada Warbler (*Wilsonia canadensis*) have almost identical breeding ranges in Canada and the northeastern United States. But, because there are only a few reports of hybridization between them, the situation appears stable.[273] Levels of hybridization in this case do not appear to be high enough to significantly affect either population. On the other hand, if mixed matings produce progeny at higher rates, and those offspring are more fertile and viable, extensive hybrid populations can arise. Kingdon (1974a: 41, 42–43, 45) discusses a large hybrid population (or broad hybrid zone) in southern Tanzania and northern Mozambique between the Checkered Elephant-Shrew (*Rhynchocyon cirnei*) and the Black-and-rufous Elephant-Shrew (*R. petersi*). This zone is so wide that pure parental individuals almost never come into contact to produce F_1 hybrids. In such cases virtually all individuals within the zone are later-generation hybrids. Such is the case with two avian hybrid zones, between Bullock's Oriole (*Icterus bullockii*) and the Baltimore Oriole (*I. galbula*), and between the Rose-breasted and Black-headed grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*) on the Great Plains of North America.[274] Thulin et al. (2006) report similar findings regarding hybrids between the European Hare (*Lepus europaeus*) and Mountain Hare (*L. timidus*) in Sweden. Hybrid zones composed solely of later-generation hybrids (where F_1 hybrids are rare or absent) occur in a broad range of organisms.[275]

The width of a hybrid zone depends in part on the viability and fertility of the hybrids. When they are relatively infertile and inviable, the zone will be narrower, all other factors being equal. When they are more fertile/viable, it will be wider. This makes sense — if a hybrid zone is thought of as a population, it would be expected to grow (i.e., get wider) if the hybrids were fitter. Even in crosses where the hybrids are quite fit, a hybrid zone may act to isolate the parental types from each other — the zone is so wide that they are isolated by distance. The extremely wide hybrid zones between *Ramphastos* toucans (pp. 52-53) are an example.

Hybrid Taxa. There are many hybrid populations and hybrid specimens have been treated as species or subspecies (see citations listed under Note 276). Indeed, among botanists such practice is standard, since it is now well accepted that many plants treated as species had hybrid origins."[277] For example, it is now well known that *Helianthus anomalus* (western sunflower) and *H. paradoxus* (paradox sunflower) are both natural hybrids derived from the cross *H. annuus* × *H. petiolaris*.[278] A long-recognized case of a hybrid population being treated as a "subspecies," is the population *hanseni* treated as a subspecies of *Potentilla glandulosa* (sticky cinquefoil).[279] This population was derived from crossing between two other populations treated as races of *P. glandulosa* (*nevadensis* and *reflexa*) and occurs in a middle altitude mountain meadow environment intermediate between those of its two parents. Hybrids between *Rhododendron caucasicum* and *R. ponticum* are another example of a hybrid population being treated as a species (*R. sochadzeae*). Milne et al. (1999) say these hybrids are abundant in Turkey. There have even been attempts to treat practically every distinct hybrid variant produced by a cross as a separate species. For example, Viosca (1935) and other researchers[280] showed that 81 irises, treated as 81 distinct species by Small and Alexander (1931), were various later-generation hybrids descended from a three parents, *Iris brevicaulis* (zigzag iris), *I. fulva* (copper iris), and *I. hexagona* (dixie iris).

However, many biologists do not think hybrid animal populations should be treated as named taxa. For this reason, such populations are often stripped of their scientific names as soon as their hybrid origin becomes known. And yet among animals, fertile, or partially fertile, hybrids are innumerable (many examples have already been mentioned in this book, but see also the citations listed under note 281). Thousands of natural hybrid populations have been documented in the Animal Kingdom. In addition to those already listed, many other existing populations of sexual animals are derived from hybridization but have been, or are currently, treated as species or subspecies (see citations listed in Note 282). For example, Kingdon (1974a) notes that populations produced from hybridization between the two elephant-shrews mentioned in the previous (*Rhynchocyon cirnei* and *R. petersi*) have been named as "subspecies" (*macrurus, shirensis*).

My book *Handbook of Avian Hybrids of the World* (McCarthy 2006) lists many birds of hybrid origin that have been, or are currently, treated as species (Table 2.1). Some of these are merely based on rare hybrid specimens, for which no corresponding natural population is known. But some hybrids treated as species are common birds. The Italian Sparrow, *Passer italiae* is derived from the cross *P. domesticus* × *P. hispaniolensis* (House Sparrow × Spanish Sparrow).[a] *P. italiae* is locally abundant, and occurs in Italy and other localities in the Mediterranean Basin including Crete, Malta, Corsica, and northern Africa. A famous example of a hybrid being treated as a species, actually of two distinct types of hybrids being treated as

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[a] Due to the fact that it is now recognized as being of hybrid origin, *italiae* is sometimes treated as a race of *P. domesticus.*

two distinct species, is that of Brewster's Warbler (*Vermivora leucobronchialis*) and Lawrence's Warbler (*V. lawrencei*), both of which are derived from the warbler cross *Vermivora chrysoptera* × *V. pinus*.[283] Due to their hybrid origin they are no longer treated as species by the American Ornithologist's Union. The dispute over whether they were hybrids lasted more than half a century and they were treated as species for many years.

Hybridization between the Slate-colored Junco (*Junco hyemalis*) and the Oregon Junco (*J. oreganus*) has generated a stabilized hybrid population that has been treated as a "subspecies," *cismontanus,* of *J. hyemalis*.[284] Similarly, Short and Horne (2001: 423) note that a population in northern Bolivia that appears to be a semi-stabilized hybrid population derived from the cross *Ramphastos cuvieri* (Cuvier's Toucan) × *R. tucanus* (Red-billed Toucan) has been treated as a "subspecies," *inca,* of *R. tucanus*.[a] Sibley and Monroe (1990) say the Uganda Paradise Flycatcher (*Terpsiphone emini*) is a stabilized hybrid population derived from the cross *T. rufiventer* (Black-headed Paradise Flycatcher) × *T. viridis* (African Paradise Flycatcher). Wolters (1975–1982) says *T. rufiventer* itself is probably a stabilized population derived from the cross *T. tricolor* (Ashy-tailed Paradise Flycatcher) × *T. viridis*.

Animal populations treated as species occur all over the world.[285] Brandon-Jones et al. (2004: 121) say a population of monkeys on Malenge Island, Indonesia is probably derived from hybridization between the Moor Macaque (*Macaca maura*) and Tonkean Macaque **(***M. tonkeana*). This population has been treated as a species, the Togean Macaque (*M. togeana* or *Cynopithecus togeanus*). Tosi et al. (2003) say genetic evidence shows the Stump-tailed Macaque (*M. arctoides*) is derived from ancient hybridization between the Long-tailed Macaque (*M. fascicularis*) and the Toque Macaque (*M. sinica*). An avian population of this type occurs in equatorial Africa. It has been treated as a "subspecies," *crossensis,* of the Green-throated Sunbird, *Nectarinia rubescens,* but is now thought to be a hybrid population produced by crossing between *N. rubescens* and the Buff-throated Sunbird (*N. adelberti*).[286] A population in Minnesota is treated as a "subspecies," *thamnos,* of the coyote, *C. latrans*. Regarding *thamnos* and another, highly variable hybrid population in New England, Lawrence and Bossert (1969: 8) say that

> *thamnos* is intermediate between [*Canis*] *latrans* and the New England population and while it overlaps strongly with the former, it overlaps almost equally strongly with the latter … The

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[a] Due to the hybrid nature of the connecting populations, Short and Horne recently treated *cuvieri* and *tucanus* as conspecific.

Table 2.1 Some birds that have been treated as species, but which are known to be, or evidence suggests them to be, of hybrid origin (McCarthy 2006).

Crax estudilloi	*Hylocharis pyropygia*	*Pseudastrapia lobata*
Crax viridirostris	*Lesbia eucharis*	*Rhipidornis gulielmi*
Francolinus ochropectus	*Lesbia ortoni*	*Oriolus percivali*
Francolinus schlegelii	*Leucochloris malvina*	*Psaltriparus lloydi*
Perdix labatici	*Neolesbia nehrkorni*	*Dicrurus andamanensis*
Pternistes cooperi	*Ptochoptera iolaima*	*Myadestes coloratus*
Tetrao medius	*Selasphorus floresii*	*Cossypha albigularis*
Tetrao hybridus	*Selasphorus underwoodi*	*Ficedula semitorquata*
Tetrao lagopoides	*Thalurania lerchi*	*Muscicapa lendu*
Lophura imperialis	*Trochilus violajugulum*	*Terpsiphone emini*
Lophura hatinhensis	*Zodalia glyceria*	*Parus pleskei*
Callipepla leucoproson	*Zodalia thaumasta*	*Pycnonotus nieuwenhuisii*
Anas breweri	*Caprimulgus ruwenzorii*	*Zosterops tephropleurus*
Anas maxima	*Grus nigricollis*	*Acrocephalus cinnamomeus*
Anas meroïdes	*Ardea wurdemannii*	*Turdoides hindei*
Anas oustaleti	*Calidris cooperi*	*Nectarinia moreaui*
Clangula angustirostris	*Calidris paramelanotos*	*Nectarinia ousteleti*
Columba chiriquensis	*Platycercus adelaidae*	*Nectarinia prigoginei*
Fuligula ferinoides	*Platycercus erythropterus*	*Passer italiae*
Fuligula homeyeri	*Platycercus macgillivrayi*	*Motacilla subpersonata*
Fuligula marloides	*Tyrannus apolites*	*Ploceus intermedius*
Mergus anatarius	*Manacus cerritus*	*Ploceus ruweti*
Pteroglossus ollalae	*Pipra anomala*	*Ploceus victoriae*
Todirhamphus miyakoensis	*Pipra heterocerca*	*Estrilda rufibarba*
Celeus roosevelti	*Anabacerthia temporalis*	*Lonchura pallidiventer*
Colaptes ayresi	*Phlegopsis barringeri*	*Carduelis ambigua*
Colaptes hybridus	*Ptilonorhynchus rawnsleyi*	*Serinus citrinipectus*
Acestrura decorata	*Xiphorhynchus insignis*	*Serinus flavigula*
Acestrura harterti	*Xiphorhynchus juruanus*	*Oryzoborus atrirostris*
Amazilia cyaneotincta	*Pardalotus ornatus*	*Oryzoborus nuttingi*
Amazilia distans	*Lanius bogdanowi*	*Spizella taverni*
Amazilia neglecta	*Lanius dichourus*	*Sporophila insulata*
Archilochus violajugulum	*Lanius darwinii*	*Sporophila zelichi*
Calliphlox iridescens	*Vireo propinquus*	*Helminthophaga cincinnatiensis*
Chalcostigma purpureicauda	*Corvus edithae*	*Vermivora lawrencei*
Chrysolampis chlorolaemus	*Cicinnurus goodfellowi*	*Vermivora leucobronchialis*
Coeligena lawrencei	*Cicinnurus lyogyrus*	*Camarhynchus conjunctus*
Coeligena purpurea	*Craspedophora bruyni*	*Chlorophanes purpurascens*
Coeligena travesii	*Dypyllodes gulielmi*	*Chlorospringus tacarcunae*
Eriocnemis isaacsonii	*Heteroptilorhis mantoui*	*Diglossa gloriosa*
Eucephala hypocyanea	*Janthothorax bensbachi*	*Euphonia vittata*
Eucephala scapulata	*Janthothorax mirabilis*	*Geospiza darwini*
Eucephala smaragdocaerulea	*Loborhampus nobilis*	*Ramphocelus chrysonotus*
Heliangelus luminosus	*Loborhampus ptilorhis*	*Ramphocelus dunstalli*
Heliangelus rothschildi	*Neoparadisaea ruysi*	*Ramphocelus inexspectata*
Heliangelus speciosus	*Paradisaea bloodi*	*Ramphocelus festae*
Heliangelus squamigularis	*Paradisaea mirabilis*	*Spiza townsendii*
Heliangelus zusii	*Paradisaea mixta*	*Tangara arnaulti*
Heliotrypha barralli	*Parotia duivenbodei*	*Tangara gouldi*
Heliotrypha speciosa	*Paryphephorus duivenbodei*	*Quiscalus stonei*

> trend away from the typical coyote and towards both [*C.*] *lupus* [i.e., wolf], and [*C.*] *familiaris* [i.e., domestic dog], already apparent in Minnesota *thamnos,* has progressed considerably farther in the New England population. … These comparisons suggest the possibility that the divergence from the typical coyote pattern, culminating in the New England population, is, in part at least, caused by some mixing with wolf as well as with dog stocks.

Short and Horne (2001: 413) say three populations (*osculans, pintoi,* and *theresae*), formerly treated as "subspecies" of the Channel-billed Toucan (*Ramphastos vitellinus*), are now considered to be of hybrid origin. Moreau's Sunbird (*Nectarinia moreaui*) is thought to be a stabilized hybrid population produced by crossing between Loveridge's Sunbird (*N. loveridgei*) and the Eastern Double-collared Sunbird (*N. mediocris*). The Adelaide Rosella (*Platycercus adelaidae*), a parrot of southeastern Australia, another hybrid treated as a species is the natural hybrid of the Crimson Rosella (*P. elegans*) and the Yellow Rosella (*P. flaveolus*).[287] It is abundant within its limited range (which could also be viewed as a hybrid zone). Manwell et al. (1963) showed that two fish, the Red-eye Bass (*Micropterus coosae*) and the Spotted Bass (*M. punctulatus*), are both almost certainly derived from hybridization between the Smallmouth Bass (*M. dolomieu*) and the Largemouth Bass (*M. salmoides*).

Many taxa have also been described on the basis of one or a few hybrid specimens. For example, Frith (2006: 53) comments that

> Rawnsley's Bowerbird *Ptilonorhynchus rawnsleyi* was originally described and illustrated … by Diggles [1867] … The unique specimen of Rawnsley's Bowerbird has to date been regarded by various authors to have represented: (a) a valid bowerbird species *P. rawnsleyi,* (b) an adult hybrid individual resulting from the natural crossing of a Regent Bowerbird *Sericulus chrysocephalus* with a Satin Bowerbird *P. violaceous* or (c) an aberrant or "sport" of the Satin Bowerbird.

The original specimen of Rawnsley's Bowerbird was lost, but another such bird was recently observed and photographed near Brisbane, Australia. Frith (2006), an expert on bowerbirds, concluded both birds were almost certainly hybrids from matings between Regent and Satin bowerbirds. A bear shot in 1864 at Rendezvous Lake, Barren Grounds (northern Canada), is a probable hybrid between polar and brown bears (*Thalarctos maritimus* and *Ursus arctos*). Now in the Smithsonian, it was treated as a new species and genus (*Vetularctos inopinatus*) by Merriam (1918). Brown bear-polar bear hybrids are common in captivity.[288] On the basis of five specimens, a hummingbird of northeast Brazil was described as a species, the Flame-rumped Sapphire (*Hylocharis pyropygia*). It is now thought to be a hybrid of two other birds, the Glittering-bellied Emerald (*Chlorostilbon aureoventris*) and the White-chinned Sapphire (*Hylocharis cyanus*).[289] Sibley and Monroe (1990: 121) list the Intermediate Parakeet (*Psittacula intermedia*) and say it is likely a "good species." But as late as the early seventies, Forshaw (1973: 338) noted that only five specimens were known. This bird of northern India has long been treated as a species, but was recently recognized as a hybrid derived from crossing between the Plum-headed and Slaty-headed parakeets (*Psittacula cyanocephala* × *P. himalayana*).[290]

Reasons for Treating Hybrids as Species or Subspecies. The practice of treating hybrids as species is understandable:

(1) a hybrid zone has a specific geographic distribution (as is the case in a non-hybrid population), the individuals within the zone have characteristic traits (as is the case in a non-hybrid population);

(2) in broad hybrid zones, the hybrids are often relatively fertile and viable (as is the case in a non-hybrid population);

(3) a hybrid is easily recognizable as a hybrid only in comparison with its parents. When no such comparison is made, a hybrid seems simply to be a distinct type that should be treated as a species. It's easy to see how a researcher concerned only with sorting and classifying specimens might overlook the hybrid nature of individuals being classified: hybridization produces individuals and populations different from either parent (i.e., they are different *types* of organisms); and

(4) Many populations composed of two or more distinct forms connected by clinally varying intermediate populations (which could be viewed as wide hybrid zones) are treated, or have been treated, as species or subspecies.

A case in point is a population of firs treated by Mattfeld (1930) as a separate species (*Abies borisii-regis*), but which Stebbins (1950: 281) claimed should be treated as a single species together with its parents *A. alba* (European Silver Fir) and *A. cephalonica* (Greek Fir), since they all interbreed. *A. alba* occurs from the northwestern Balkan Peninsula to northern Greece. *A. cephalonica* is found in central and southern Greece. Interbreeding between the two has produced the clinally varying hybrid population that Mattfeld described as *A. borisii-regis*.[291] It occurs in intermediate regions such as the Athos Peninsula of northeastern Greece, parts of Macedonia, and in Bulgaria's Rhodope Mountains. Another investigator might have described this same population as a hybrid zone. A similar case is that of the Californian oak *Quercus alvordiana,* which also is a clinally varying population of hybrids, between the blue oak (*Q. douglasii*) and the Sonoran scrub oak *Q. turbinella*.[292]

Since this practice of treating hybrid populations as named "species" and "subspecies" is common, not only among botanists, but also, in the writer's experience (McCarthy 2006; McCarthy in prep.), among ornithologists and mammalogists, it seems to be a widespread practice among biologists in general.

Once such populations are recognized as clinal hybrid populations, there are many who would argue that they should be stripped of their taxonomic status. But since many populations formerly treated as species or subspecies have proven to be of this nature, many currently so treated are surely of the same kind, although they may not yet be recognized as such.

Hybrid Animals and Artificial Selection. Breeders commonly use artificial selection to produce new breeds from the variable offspring of hybrid crosses. In particular, they have long used a process, known as the backcross breeding method,[293] to obtain new types of organisms. The approach is to identify a type possessing some desirable trait[a] and then to hybridize it with a "target stock" lacking the trait. If hybrids are obtained, the next step is to backcross them to the target stock in order to “introduce" the trait. Basically, the process is the following:

(1) individuals from the target stock are crossed with some other stock having the trait;

(2) hybrids with the trait are backcrossed to the target stock;

(3) backcross progeny exhibiting the trait are selected for further backcrossing or bred among themselves;[b]

(4) selection over ensuing generations stabilizes the trait and eliminates other, undesirable traits that may be present (low fertility prominent among them);

(5) the new breed becomes stable when hybrid individuals of both sexes are sufficiently fertile to maintain the breed without further backcrossing.

The process is commonly used in producing new types of cage birds.[294] As Renzo Esuperanzi, the great breeder of fringillid finches, points out,

> Many [finch] hybrids, if they did not in some cases give us an indication of the genetic affinity of two species, would serve only as exhibition specimens and little more. However, when the hybrids are fertile, it is an entirely different matter. For one can then use them to produce a new, intermediate form or to carry a trait over from one species to another.[295]

A famous example is Duncker's introduction of red coloration into canary stocks by crossing canary hens with the South American Red Siskin (*Carduelis cucullata*).[296] Partially fertile male hybrid progeny were then backcrossed to canaries to introduce the trait. The same method has been used to transfer traits *to* the Red Siskin from the

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[a] Usually called the "donor parent."

[b] The parental type to which backcrosses are repeatedly made is often called the "recurrent parent."

Eurasian Siskin (*C. spinus*) and from the Hooded Siskin (*C. magellanica*).[297] These events are relatively recent, but the history of canary breeding stretches back to the sixteenth century, when they first became available in Europe. Thus, of canaries, an early naturalist Johann Matthäus Bechstein (1757-1822) noted that

> Their original grey colour [i.e., that of the Island Canary, *Serinus canaria*], which merges into green beneath, almost resembling the colours of the Linnet [*Carduelis cannabina*], has by means of domestication, climate, and intermixture with other birds (in Italy with the Citril [*Serinus citrinella*] and Serin [*S. serinus*], in Germany with the Linnet, Greenfinch [*Carduelis chloris*], and Siskin [*C. spinus*]), become so multifarious, that Canaries may now be met with of almost every colour; but grey, yellow white, blackish, and red brown continue the chief colours, but which are individually seen in every degree of shade or combination, and thus presenting innumerable differences.[298]

Were it not for such early records, one might suppose that the bewildering array of modern canary breeds had been produced simply by long applied selection without the use of hybridization to produce variation on which that selection could act. Similarly, the domestic chicken was recently shown to be of hybrid origin.[299]

A variety of cattle breeds are derived from hybridization of European domestic cattle (*Bos taurus*) with the Zebu (*B. indicus*). In the U.S., several new breeds have been produced from this cross, important ones including the Beefmaster (Zebu × Shorthorn and Hereford), Brangus (Zebu × Angus), Charbray (Zebu × Charolais), and Santa Gertrudis (Zebu × Shorthorn). In Africa, too, the Sanga breed, which is tolerant of the tsetse-fly-transmitted trypanosomes responsible for nagana, a disease deadly to non-African cattle, is derived from this cross.[300]

The Bengal, a popular cat breed was produced in the 1980's by hybridizing the domestic cat (*Felis catus*) to the Asiatic leopard cat (*F. bengalensis*). This work was carried out primarily by Jean S. Mill of Millwood Bengals cattery in Covina, California. She began with partially fertile female backcross hybrids to domestic cat. After further backcrossing these hybrids to domestic, she obtained partially fertile males. The hybrids were then bred among themselves. Subsequent selection produced a cat with both the exotic coat of a leopard cat with the amiable disposition of a domestic.[301]

The Arkhar-Merino breed of sheep was produced between 1934 and 1950 at Kurmektinski experiment station of the Academy of Sciences of what was then the Kazakh SSR. It is derived from hybridization of domestic sheep (*Ovis aries*) with the Argali (*O. ammon*), which occurs in the mountains of western and central Asia. The intent was to develop a new breed that would combine the valuable qualities of the Merino with the Argali's tolerance of high altitudes. The breeding process began domestic when 212 Merino ewes were inseminated with *O. ammon* semen (Rumjancev et al. 1935). Forty-three F_1 lambs were obtained. Isenžulov (1938) says 400 domestic ewes were then inseminated with sperm from F_1 rams. About 400 offspring were obtained in the following year (1937). In 1938, about 500 more second generation backcross offspring and later-generation hybrids were obtained.

According to Isenžulov (1938), "the vast majority of the hybrids combine the desired characters of both parental forms. When transferred to a high altitude (2500-3000 m), they throve and showed good increase in body weight and in weight and length of fleece." Kushner and Kitaeva (1938a) found that the hybrids blood profile was superior to that of the domestic sheep parent with respect to suitability for breeding at high altitudes. Subsequent selection for desirable characteristics produced the stable new breed.[302]

Hybrid Plants and Artificial Selection. Plant breeders, too, commonly start with variable hybrid plants and then apply artificial selection to produce new crops, trees, and flowers with desirable properties. Soliman (1992: 199) claims no other factor has had a greater impact on agricultural production. New breeds produced by hybridization vary widely in the proportion of their genetic composition (Carver and Taliaferro 1992). Some varieties so produced are very close to one parent, but have only one or a few traits from the other (this is similar to a natural process that has been called "introgression." See Note 303). At the other end of the spectrum are breeds that derive their traits in equal number from both parents. In the former case, one can think of the new hybrid as a slightly altered version of one of the original parental forms, in the latter as a distinct, new composite.

A complete list of all the new crop plants produced by hybridization followed by artificial selection would be both tedious and beyond the scope of this book, but the curious reader is referred to a summary paper on this topic by Kalloo (1992). An inventory of the cultivated flowers derived from hybridization would probably be even lengthier. Here we will only mention a few examples of new breeds of plants derived from hybridization.

Thus, a rubber-producing plant from Mexico, guayule (*Parthenium argentatum*), was crossed with northern relatives to transfer cold tolerance to guayule.[304] A new variety of okra (*Abelmoschus esculentus*) resistant to Yellow vein mosaic disease, the most serious disease of that plant, was developed by crossing *A. esculentus* with *A. manihot* (edible hibiscus). The modern strawberry is derived from hybridization of the Virginia strawberry (*Fragaria virginiana*) and the beach strawberry (*F. chiloensis*).[305] Rockwell et al. (1961: 32) say

> It should be remembered that, nowadays, few of our popular garden flowers are still the original species. Run down the list — roses, iris, peonies, phlox, delphinium, poppies, gladiolus, marigolds, petunias, zinnias, tulips, daffodils, and shrubs such as lilacs and azaleas — in the forms which we use in our gardens, are the results of man-made crosses, hybrids bearing little resemblance to the original wild species from which they have been developed. This hybridizing process goes back, in most cases, through hundreds of years; in some, as with the rose, so far as to be lost in antiquity.

A great deal of the history of rose breeding, however, is known. Most early European roses did not have the characteristic of continuous, or repeat, bloom as do most roses today (damask roses were an exception). But by the early 1800s, four

Chinese rose cultivars, which did bloom repeatedly, had become available to European breeders — a pink and a red China Rose, as well as a blush and a yellow Tea Rose. These were crossed with European roses to produce new repeat-blooming varieties. The first of these new repeat-blooming roses to appear in Europe, the Bourbons, resulted when French breeders crossed China Roses with various Old Roses.[306] The Hybrid Teas are the most important of the Modern Roses. They are "the result of hybridising the Hybrid Perpetuals with the Tea Roses in the 1840s. The Hybrid Teas are an entirely new type of rose bearing so little resemblance to those of the past that they might almost be regarded as a new plant. For most of the twentieth century they dominated the rose scene and are still the most popular roses today."[307] Austin notes (2005: 15) that "strong yellow became available [in the Hybrid Teas] only when the French rose breeder Joseph Pernet-Ducher hybridised the Austrian briar [*Rosa foetida*] with the Hybrid Teas sometime around the year 1900."

Early Use of Hybridization. It is certainly true that the "hybridizing process goes back, in most cases, through hundreds of years." A detailed history of this process for all domestic breeds and varieties would fill many volumes. But a few examples will serve to illustrate how long breeders have been using hybridization to produce new plants and animals. Thus, John Moore (1735) lists various pigeon breeds produced by hybridization. In the first volume of his *Histoire Naturelle des Oiseaux* (1770), Buffon comments that certain finches[a] (such as the European Goldfinch, *Carduelis carduelis*, and the Eurasian Siskin, *C. spinus*) easily cross and that "the hybrids they engender can, in uniting with each other, produce more individuals like themselves and so form new intermediate species."[308]

In addition to such early reports, modern technology has documented examples of breeders' use of hybridization even in ancient times. The Madura breed of cattle, widespread in Indonesia, has been shown by multiple molecular genetic criteria to be derived from hybridization between Zebu and Banteng (*B. javanicus*). Ward et al. (1999) concluded that these animals were crossed on the island of Madura some 1500 years ago.

As for plants, sometime prior to 1717 Thomas Fairchild (1667–1729) produced a new variety of pink (*Dianthus*) by crossing a carnation (*D. caryophyllus*) with a sweetwilliam (*D. barbatus*).[309] In that same year Richard Bradley (d. 1732) wrote of obtaining numerous new varieties from hybridization in the auriculas of the genus *Primula* (*New Improvements of Planting and Gardening,* London, 1717):

> 'Tis from this accidental Coupling that proceeds the Numberless Varieties of Fruits and Flowers which are raised every Day from Seed. The yellow and black Auriculas, which were the first we had in England, coupling with one another, produced Seed which gave us other varieties, which again mixing their Qualities in like manner, has afforded us little by little, the

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a. He mentions the European Goldfinch (*Carduelis carduelis*), Eurasian Siskin (*C. spinus*), and the "le serin" which probably refers to the domestic canary, not the European Serin (*Serinus serinus*).

> numberless Variations which we see at this Day in every curious Flower-Garden; for I have saved the Seeds of near a hundred plain Auriculas whose Flowers were of one Colour, and stood remote from others, and that Seed I remember to have produced no Variety; but on the other hand, where I have saved the Seed of such plain Auriculas, as we have stood together, and were differing in their Colours, that Seed has furnish'd me with great Varieties, different from the Mother Plants.[310]

The French botanist Henri-Louis DuHamel du Monceau (1728) asserted "almost all the fruits that gardeners call *new* are only composites of other older ones which can be recognized easily."[311] Zirkle (1935) discusses the work of a variety of eighteenth century hybridizers who produced by that means a wide variety of new vegetables, fruits, and flowers. By end of the eighteenth century Thomas Knight[a] was using hybridization on a large scale to breed a wide array of improved cultivated plants.[312] Linnaeus himself (*De sexu plantarum,* 1760) enthused about the potential of hybridization to produce new crop plants:

> Here is a new employment for botanists, to attempt the production of new species of vegetables by scattering the pollen of various plants over various widowed females. And if these [foregoing] remarks [on hybridization] should meet with a favorable reception, I shall be the more induced to dedicate what remains of my life to such experiments, which recommend themselves by being at the same time agreeable and useful. I am persuaded by many considerations that those most numerous and most valuable varieties of plants which are used for culinary purposes, have been produced in this manner, as the several kinds of cabbages, lettuces, etc.[313]

The Number of Hybrid Pairings is a Triangular Number. The math of triangular numbers shows that hybrids are probably viable more often than otherwise might be supposed. Attempts at hybridization often end in failure because the hybrids from many crosses turn out to be too infertile or inviable. Nevertheless, many such efforts are successful. Here is why: The number of possible combinations from a set of n types is n(n-1)/2. That is, it is a triangular number (the sum of the n integers from 1 to n). For example, one hundred types of organisms can be paired in 100(99)/2 = 4,950 different ways. Thus, even if viable hybrids could be obtained in only one percent of the potential combinations of 100 different types of organisms, there would be 50 successful combinations. This figure does not even take into consideration the additional possibilities introduced by reciprocal crosses, backcrosses, and later generation crosses. This reasoning suggests hybridization may well be effective in producing viable organisms in far more cases than might otherwise be expected. Therefore the fact that most crosses produce either inviable hybrids, or no hybrids at all, should not be used — as it often is — to discount the

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[a] Thomas Andrew Knight (1759–1838). President of the London Horticultural Society (1811-1838). Considered to be the most distinguished horticulturist of his time, he developed many new breeds of fruit via hybridization.

significance of hybridization of hybridization in evolution.[a] Instead of making blanket claims of hybrid inviability and "hybrid breakdown," evolutionary biologists should consider the many well-documented cases of hybrid viability and vigor.

Conclusion. Long ago Darwin (1859: 254) pointed out that hybrids are not always sterile: "Finally, looking to all the ascertained facts on the intercrossing of plants and animals, it may be concluded that some degree of sterility, both in first crosses and in hybrids, is an extremely general result; but that it cannot, under our present state of knowledge, be considered as absolutely universal." Even today, many biologists pay little heed to this fact, although a vast number or reports have since accumulated demonstrating that many hybrids are partially fertile. Indeed, there are probably far more cases of this sort known today than Darwin would ever have anticipated.

This chapter has provided a wide variety of examples demonstrating that the fertility of hybrids varies from cross to cross, and individually, depending on the sex, age, and genetic constitution of the individual in question. It has also shown that hybridization is a widespread natural phenomenon and that many hybrids have even been treated as species or subspecies. A huge number of natural hybrid zones are known.

We have seen that many kinds of hybrids are partially fertile, and that they vary greatly not only in their fertility, but with respect to many other traits. These facts have fundamental implications for biological thought. If many types of natural hybrids have the ability to conceive offspring, the opportunity exists for natural selection to act to increase fertility with each passing hybrid generation. Fertility responds to artificial selection by breeders, much like any other heritable trait that varies from one individual to another. Certainly, fertility varies from one hybrid individual to another (and from one type of cross to another as well). The potential evolutionary significance of hybridization becomes especially apparent if we consider the fact that hybrid vigor is characteristic of a wide variety of crosses.

If we leave stereotypes behind and view hybrids as varing individual organisms, then they can be seen in another light — as unshapen clay awaiting the hands of natural selection.

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[a] Moreover, certain laboratory techniques can be used to overcome sterility in F_1 hybrids. For example, the cereal triticale was derived from a cross between wheat and rye. The F_1 hybrid in this case is quite sterile. But breeders were able to use the cell division inhibitor colchicine to obtain fertile offspring. They used the colchicine to double the number of chromosomes and obtain a fertile stable hybrid (organisms with unpaired chromosomes usually exhibit reduced fertility). There are also natural processes that can double the number of chromosomes and produce fertile hybrids (see Chapter Four). Colchicine inhibits mitosis (Eigsti 1938, Blakeslee and Avery 1937). A mitosis that takes place after treatment with colchicine is called a *C-mitosis*. During the prolonged metaphase of a C-mitosis, the chromatids repel each other, but are still connected at the centromere (the chromosomes form an X-shaped structure). Presently, the chromatids part, but do not segregate. They then become enclosed by a new nuclear membrane and interphase begins. In this way a diploid nucleus becomes tetraploid.

3 Karyotypes: Variation, and Stasis

No one supposes that all the individuals of the same species are cast in the very same mould. These individual differences are highly important for us, as they afford materials for natural selection to accumulate, in the same manner as man can accumulate in any given direction individual differences in his domesticated productions. —CHARLES DARWIN
On the Origin of Species (1859)[314]

An organism with a distinctive karyotype (i.e., with a distinctive set of chromosomes) will often be treated as a distinct species. Another characteristic that commonly results in two populations being treated as separate species (or separate subspecies for that matter) is morphological distinctness (physical differences that can be detected among specimens), a fact already mentioned in Chapter One. Any set of physical traits may be involved, but most commonly such traits are ones detectable by visual inspection. Populations distinguished on the basis of morphological traits are so common, and are mentioned so often in the remainder of this book that they will be designated by a special name: *somasets.* Types distinguished on such a basis will be termed *somatypes.* We will also have a special name for populations and types distinguished on the basis of karyotypes, but first a few technicalities.

Cells and Chromosomes. The cell is to biology what the atom is to chemistry. All living things other than viruses are composed of cells. A *cell* is a membrane-bounded compartment, usually microscopic, filled with a complex liquid called cytoplasm. Within the cytoplasm are various structures with specific functions. Broadly speaking, all cellular organisms can be divided into two categories, bacteria and *eukaryotes* (viruses, which are not cellular, constitute an additional major category). Many eukaryotes are multicellular (animals, plants, and most fungi). That is, they are organisms composed of multiple cells. There are also many single-celled eukaryotes. Each eukaryotic cell has a set of linear chromosomes enclosed in a nuclear membrane. A bacterial chromosome is single, circular, and not so enclosed. A *chromosome* is a complex structure with two main components: (1) a chain of millions of purine and pyrimidine molecules known as *deoxyribonucleic acid* (DNA) and (2) an intricate structural framework that supports and manipulates that chain.[315] It is the DNA that contains the hereditary information directing the development of an organism. Along the DNA chain present in each chromosome are distinct, relatively small, regions, known as *genes,* which govern the various traits of an organism. They are actual segments of the chain. Each gene occurs at a particular location on a chromosome, known as the gene's *locus* (pl. *loci*). A single human chromosome may contain thousands of loci affecting thousands of different traits.

Karyotypes. The chromosomes of a eukaryote can usually be sorted into types on the basis of length and other physical characteristics, as well as their genetic content. For example, the largest human chromosome is known as Chromosome 1. Each human being has two copies of this chromosome, and two copies of each other type of human chromosome, except for the sex chromosomes. A man has a single copy of each sex chromosome, one X chromosome and one Y chromosome. A woman has two X chromosomes, but no Y chromosome.

Although the same set of chromosomes is normally present in an each cell of an individual multicellular organism, eukaryotes treated as different species, even closely related ones, often have different sets.[316] Often, when a chromosome from one such form is aligned with an otherwise identical chromosome from another, certain loci do not match. For example, a locus present in one chromosome may be absent or inverted in the other. Likewise, two otherwise identical sets of loci may occupy two different positions on the two chromosomes. Commonly, too, the loci present in a single chromosome will be shared out in blocks into two or more separate chromosomes in another organism. There may also be differences in the number of chromosomes present. Disparities of all these kinds, where the chromosomes have been restructured relative to each other, are called *structural differences.*

When viewed from this structural perspective, the set of chromosomes characteristic of a particular type of organism is called its karyotype, an important term in stabilization theory. As defined under stabilization theory, a *karyotype* is a set of chromosomes in which a particular set of loci is distributed onto particular chromosomes in a particular order and relative orientation (the DNA segments between the loci also are distributed in a particular order and orientation). Similarly, a *chromosome pair* is here defined as two chromosomes in the same cell that have the same set of loci, distributed in the same order and relative orientation (again, the regions between the loci are assumed to be distributed in the same particular order and orientation). With respect to the genetic information that it contains, the same locus can differ between the two members of a chromosome pair. For example, a locus for eye color on one chromosome of a pair might contain a gene for blue eyes, but contain a gene for brown eyes on the other. Such variant genes, segments of DNA differing in molecular composition but occurring at the same locus on different chromosomes, are known as *alleles*.

The sorts of structural differences just described distinguish, for example, the human karyotype from that of a chimpanzee (*Pan troglodytes*). Humans and chimpanzees do not have the same number of chromosomes and there are also differences in the structure of the individual chromosomes. The Y chromosome differs markedly in size in humans and chimpanzees. An obvious structural difference is that the equivalent of human Chromosome 2 exists as two separate chromosomes (2A and 2B) in the chimpanzee. Moreover, various other human chromosomes cannot be aligned intact with those of a chimpanzee. For example, there are regions on human chromosomes 1 and 18 that are inverted relative to the same regions on the equivalent chimpanzee chromosome.[317] Two large inversions also distinguish a human Y chromosome from that of a chimpanzee.[318] There are many other structural differences differentiating these karyotypes.[319] In general, the karyotypes of more distantly related organisms are more extensively rearranged relative to each other.[320]

Chromotypes and Chromosets. Since many populations treated as separate species differ with respect to karyotype, many hybrids have chromosomes that do not exactly match in pairs. This mismatching is a result of the normal process of sexual reproduction, where a parent typically passes only one chromosome of each of the types present in its karyotype to its offspring. Since the other parent does the same, an F_1 hybrid receives a pair of a given type only when that same type is found in both its parents. Any type of chromosome found in only one parent will have no match in the hybrid.

Individuals with such unmatched chromosomes, ones not occurring in pairs, are known as *structural heterozygotes*. Such mismatches disrupt the production of gametes and reduce the fertility of the affected individual.[321] Because of this reduction in fertility, populations with distinct karyotypes have often been treated as separate species — their hybrids are relatively infertile, sometimes markedly so. A second characteristic, then, the presence of two distinct karyotypes, often causes two populations to be treated as separate species. As White (1973: 338) clearly states:

> In most groups of animals that have been studied by cytogeneticists in detail, it has been found that even the most closely related species differ cytologically, i.e., their karyotypes can be distinguished by a difference in chromosome number, shape, size or other features. In groups such as *Drosophila, Chronomus,* grasshoppers, beetles, mammals and many others, [such] cytotaxonomic differences seem to be almost invariably present.

In this book, a set of individuals sharing the same karyotype will be termed a *chromoset;* a type of organism having a particular karyotype will be called a *chromotype*. Although it is true many populations treated as separate species are distinct chromosets, many treated as different subspecies are too. In a broad range of eukaryotes, populations of both these kinds are known (see Table 3.1). Such differences often are so small that they are not easily observed, and yet they are

Table 3.1 References Documenting that Taxa Differ in Karyotype

Group	Reference (many additional relevant publications are not cited)
Plants	Avery 1938; Bowers et al. 2003; Darlington 1937, 1939; Hauber and Bloom 1983; Grant 1981, 1985; Levin 2002; Stebbins 1950, 1971.
Fungi	Caten and Newton 2000; Howlett 1996; Maniotis 1980.
Invertebrates	Dobzhansky et al. 1977; Goldschmidt 1982; Insua et al. 1994; John et al. 1983; Sobti and Obe 1991; Wesley and Emmel 1975; White 1973a, 1973b, 1978; Zhou et al. 2005.
Fish	Azevedo et al. 2007; Dorofeyeva 2001; Ferreira et al. 2005; Gustavo and Molina 2005; Marescalchi 2005; Matthey 1949; Nirchio et al. 2002; Ojima et al. 1986; Pazza et al. 2006; Ross 1973.; Rossi et al. 2005; Shimabukuro et al. 2004; Swarca et al. 2005; Thorgaard 1983; Voelker et al. 2005.
Amphibians	Anderson and Moler 1986; Aprea et al. 2007; Bogart 1969, 1972, 1973; Cuny and Malacinski 1985; Green 1985; Green and Delisle 1985; Haertel et al. 1974; Makino 1934, 1939; Moritz 1987; Mancino et al. 1976; Matthey 1949; Wasserman et al. 1968.
Reptiles	Arevalo et al. 1993, 1994; Dosselman et al. 1998; Gorman 1965a, 1965b, 1968, 1969; Gorman and Atkins 1966, 1967, 1968; Gorman and Dessauer 1965; Gorman et al. 1967, 1968, 1971; Gorman and Lynch 1969; Lamborot 2001; Lamborot and Eaton 1992; Lowe et al. 1970; Matthey 1949; Sites et al. 1993, 1995; Strasburg and Kearney 2005.
Birds	Bed'Hom et al. 2003; Belterman and Boer 1984; Bulatova 1973; Bulatova and Panov 1973; Bulatova et al. 1972; Brumback 1974; Bush et al. 1977; Castro et al. 2002; Christidis 1983, 1986a, 1986b; 1987; Crew and Koller 1936; Francisco and Galetti 2001; Harada and Buss 1981; Jeon et al. 1997; Lucca 1974; Lucca and Rocha 1992; Lucca and Waldrigues 1985; Makino et al. 1956; Matthey 1949; Radjabli et al. 1970; Roslik and Kryukov 2001; Schmutz and Oliphant 1987; Shields 1982; Shoffner et al. 1979; Slizynsky 1964; Sokolovskaja 1935; Steklenev and Kozikova 1989; Swan and Christidis 1987; Sultana and Bhunya 1981; Takahashi et al. 1975; Valverde de Oliveira et al. 2001; Yamashina 1941a, 1941b, 1942, 1943.
Mammals	Baker et al. 1975, 1981; Baker and Bickham 1986; Banaszek et al. 2000a, 2000b, 2002, 2003; Bengtsson 1980; Borodin et al. 1998; Bowers et al. 1973; Brünner and Hausser 1997; Capanna 1973; Chiarelli 1975; Cothran and Honeycutt 1984; Cribiu et al. 1988; Dowler 1989; Eldridge 1991; Eldridge and Close 1992; Eldridge et al. 1988, 1990, 2001; Fedyk et al. 1991, 1993; Fredga and Narain 2000; Gardner and Patton 1972); Gava and de Freitas 2002, 2004; Gordon 1978; Hayman 1989; Hauffe and Piálek 1997; Hoffmann et al. 2003; Hogan et al. 1993; Honeycutt and Schmidly 1979; Jones and Searle 2003; Jones et al. 1973; Khudr et al. 1973; King 1993; Lay and Nadler 1969; Lay et al. 1975. Lee et al. 1972; Lyapunova and Yakimenko 1986; Lyapunova et al. 1980, 1990; Macey and Dixon 1987; Markov and Dobrianov 1985; Mascarello 1978; Matthey 1949, 1963; Mazurok et al. 2001; Moska 2003; Narain and Fredga 1996, 1997, 1998; Pembleton and Baker 1978; Piálek et al. 2001; Polyakov et al. 2002, 2003; Poorman 1982; Qumsiyeh et al. 1988; Ratkiewicz et al. 2000, 2003; Reig and Kiblisky 1969; Ribeiro et al. 2003; Robinson and Skinner 1983; Robinson et al. 1981, 1983, 1984; Rumpler and Albignac 1975; Sawatzki and Cooper 2007; Searle 1984, 1988, 1991, 1993; Sharman et al. 1990; Sobti and Obe 1991; Spotorno et al. 1994; Stangl 1986; Sudman et al. 1987; Thaeler 1974, 1980; Tucker and Schmidly 1981; Wahrman and Goitein 1972; Wahrman and Gourevitz 1973; Wahrman et al. 1969; Walker 1983: 584, 585, 626; Winking et al. 1988; Wojcik et al. 2002; Wyttenbach et al. 1999; Zahavi and Wahrman 1956.

present.[322] Many such minor deletions, duplications, and inversions differentiate the karyotypes of humans and chimpanzees.[323] Therefore, to the many pairs of chromotypes exhibiting obvious structural differences, we must add many more pairs that differ with respect to such "cryptic" structural rearrangements, ones that are not immediately apparent under the microscope, but that are detectable by other, more discriminating techniques. Even small differences of this sort can have a marked adverse effect on the fertility of hybrids.[324]

While such karyotypic differences between closely related forms are indeed very common, it should be mentioned that there are examples of closely related fruit flies in the genus *Drosophila* that differ morphologically, but that appear not to differ with respect to karyotype.[325] This fact receives much attention because geneticists so often use fruit flies in their experiments. There are also cases of the same kind known among mosquitoes.[a] As Sumner (2003: 197) points out, the existence of such exceptions does not change the fact that "karyotypes usually differ between organisms, even closely related ones."

The individuals composing a single somaset can often be broken down into two or more distinct chromosets (recall that a somaset is a population distinguished on the basis of morphological traits). For example, *Mus musculus* (house mouse), though treated as a single species, has distinct chromosets (with distinct geographic ranges), each with its own particular karyotype.[326] Each of the chromosets within the single somaset *Mus musculus* constitutes a reproductively stable population because all members of a particular chromoset have the same karyotype. But when the members of different chromosets come into contact and interbreed, they produce structurally heterozygous offspring of reduced fertility.[327] This phenomenon is seen not only in mice, but also in a broad range of organisms.[328] So in this case the group of organisms treated as a species (*M. musculus*) is equivalent to the somaset. Here, taxonomists do not treat the chromosets as separate species.

On the other hand, chromosets of the same somaset are often treated as different species because their karyotypes differ, especially when the structural differences in question severely affect the fertility of hybrids. Reeves' Muntjac (*Muntiacus reevesi*) and the Indian Muntjac (*M. muntjac*) look the same, and so form a single somaset. Nonetheless, they are usually classified as different species (here, the two chromosets are treated as a separate species). Matings between these two types of muntjacs produce hybrids of low fertility.[329] Chromosets of a single somaset typically have distinct geographic ranges that come into contact only along their margins, if they come into contact at all.[330]

Note that distinct karyotypes defining distinct chromotypes need not differ at the genetic level. Each can contain the same genes in a rearranged state. For this reason, the genes in two different karyotypes may specify the development of the same

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[a] Ayala and Coluzzi (2005). Studies of homosequentiality in fruit flies and mosquitoes used low-resolution methods depended on the fact that these forms have polytene chromosomes. Cryptic structural differences might well be detectable using the high resolution methods available today.

somatype. For example, various distinct chromosets of *Mus musculus* are genetically indistinguishable.[331] The same is true of the distinct chromosets composing the *Rattus sordidus* complex.[332]

In the upcoming discussion of stabilization theory, the vagueness of the word *species* and the consequent difficulties of its application in a theoretical context (see Chapter 1) are avoided through the use of *chromoset, chromotype, somaset,* and *somatype,* words more specific than *species.* These names allow populations to be discussed as groups with a particular characteristic — say, by a particular morphology, without any implication being made that they have some other characteristic, such as reproductive isolation. Table 3.2 provides some examples of how these terms can be applied. With this approach, interbreeding is no longer the major issue it is within the context of neo-Darwinian theory because it is of interest only in itself as a phenomenon, not as a criterion used in defining categories. A somaset is a somaset whether it interbreeds with other somasets or not. Likewise, a chromoset is a chromoset whether or not it interbreeds with other chromosets. This change in terminology also overcomes various practical difficulties. For example, the most common definition of the word *species* (i.e., Mayr's biological species concept) cannot be applied in the case of the many types of organisms not engaging in sex, but the names *chromoset, chromotype, somaset,* and *somatype* can. Populations that have been treated as species have often been either sets of individual organisms having the same karyotype (i.e., chromosets), or sets of such sets having the same somatic form.

Table 3.2

REPLACE:	WITH:
"chromosomal race"	"chromoset"
"species with a distinct karyotype"	"chromoset"
"a type of organism defined by its karyotype"	"chromotype"
"morphologically distinct race"	"somaset"
"morphologically distinct species"	"somaset"
"a type of organism defined by its morphology"	"somatype"

Sources of Variation

Natural selection cannot act without variation. If all individuals are the same, there are no individual differences among which to select.[a] So evaluation of a mechanism's potential to produce variation is essential in assessing its evolutionary significance. In this book all genetic variation is assigned to three broad categories according to the source from which the variation is derived: (1) *point mutations;* (2) *meiotic recombination;* (3) *chromosomal mutations*. The nature of each of these three

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[a] Indeed, according to the fundamental theorem of natural selection, a basic rule of population genetics, "the rate of increase of mean fitness is equal to the genetic variance in fitness" (Hartl and Clark 1989: 164).

sources of variation will be explained in the next three sections.

Point Mutation. The word *mutation* is used to refer both (1) to a heritable change in an organism and (2) to a change in the genetic material (DNA). Although its meaning is usually a little more specific, *point mutation* will here be defined as any local change in DNA that does not produce a new karyotype.[a] Point mutations usually have no discernible effect on the development of an organism (that is, they alter the DNA, but the alteration does not change the organism's traits). When they do, most affect a single trait. For example, in the fruit fly *Drosophila melanogaster,* white-eye mutants that are otherwise normal result from a point mutation affecting a single gene.

Alternation of Generations. In eukaryotes that reproduce sexually there is an alternation of generations, involving two cyclic stages, *haploid* and *diploid,* each of which produces the other. In the haploid stage each cell of the organism contains one autosome of each type (an autosome is any chromosome other than a sex chromosome). In diploid cells the autosomes are present in pairs. For example, in the human life cycle, a multicellular diploid organism alternates with single-celled, haploid gametes (i.e., sperm and egg). In organisms having a single pair of sex chromosomes, each haploid cell contains one sex chromosome, but each diploid cell contains two. In humans, and many other types of animals, the diploid stage is the one producing a multicellular organism visible to the naked eye. But in many plants the haploid phase is more prominent. Many other eukaryotes are unicellular and microscopic throughout both phases (e.g., yeast).

Meiotic Recombination. In organisms that undergo this alternating cycle, the process of cell division producing the haploid stage from the diploid is called *meiosis.* During meiosis the two members of each chromosome pair come into direct contact, exchange DNA, separate from each other, and pass into separate cells. During meiosis, when two chromosomes belonging to the same pair exchange DNA, they trade alleles at some loci. For example, at the eye-color locus there might be an exchange of blue- and brown-eye alleles. As a result, the chromosome that originally specified blue eyes would be altered to specify brown eyes. The offspring individual receiving this chromosome, then, would have a different combination of traits than if the exchange had not occurred. For example, she would have brown eyes and, say, brown hair (instead of blue eyes and brown hair). For this reason, variation of this sort is called *recombination*. There is a recombination of traits (in this case, brown eyes with brown hair, instead of blue eyes with brown hair). Once these exchanges

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[a] Strictly speaking a point mutation is a change in a single base pair in the DNA chain. Here I intend it to mean any mutation not resulting in karyotypic changes. So the term would include not only point mutations *sensu strictu,* but also any mutations affecting the function of a single a single gene (e.g., the insertion of a transposable element).

have occurred during the initial stage of meiosis, the two members of each chromosome pair break away from each other and pass into separate gametes without undergoing any further alteration.

In exchanges of this sort, between the two members of a chromosome pair, no new loci are added or deleted. Nor is the relative order or orientation of the loci altered in any way. Such exchanges only trade alleles between equivalent loci. All the variation is allelic. No structural variation (additions and deletions of loci, or rearrangements of loci) is produced. There is only variation of preexisting alleles at preexisting loci that occur in a preexisting order on preexisting chromosomes.

Therefore, if the variation at a particular locus is considered for a particular diploid chromoset with a karyotype in which all autosomes are paired, only a certain finite number of different variants can be produced by meiosis. For example, if variation at the eye color locus were considered for the chromoset as a whole, there might be an allele for blue eyes present at the eye-color locus on some chromosomes of some individuals in the chromoset, an allele for brown eyes present on other chromosomes, and one for green eyes on still others, but there might be none for yellow or orange eyes. Under such circumstances, no matter how many exchanges occurred, meiosis would never produce an individual with orange or yellow eyes. The *only* ways those colors could arise would be either

(1) through the creation of a new allele on some chromosome within the population by some process other than meiotic recombination (i.e., through the occurrence of a point mutation), or
(2) through the introduction of a preexisting allele from outside the chromoset.

Similarly simple reasoning leads to the conclusion that meiotic recombination can have only limited effect on a trait controlled by genes at multiple loci (see Appendix A). This idea is nothing new, but it has been glossed over in neo-Darwinian theory. Long ago, even before the nature of point mutation was known, geneticist E. B. Babcock (1918: 120) commented that

> A factor mutation [i.e., a mutation in gene] probably involves some sort of change within the group of similar molecules occupying a particular locus in a particular chromosome [such is indeed the case]. Obviously the number and direction of the changes possible in such an entity are limited and the sum of the limits of change in all the loci in the chromosome group [i.e., karyotype] of a given species would define the limits of factor mutations for that species.

So Babcock is saying that a karyotype imposes a limit on variation. This fact is clear. In defining a particular set of loci, a karyotype constitutes a stable domain within which point mutations and exchanges of alleles can occur. Such changes at the various loci of a karyotype can occur without changing the structure of the karyotype. But viewed within the context of the chromoset it defines, a karyotype is normally stable. A karyotype, and its corresponding chromoset, can therefore be thought of as a genetic context. Under stabilization theory

(1) chromosets are the context within which the Mendelian processes described in neo-Darwinian theory occur;

(2) new karyotypes are created by other, non-Mendelian processes.

Since a chromoset is a population of fully intrafertile individuals, interbreeding is unhindered and there is selection for favorable alleles at each locus. The karyotype defines the population in which such allelic (Mendelian) selection can occur. Mendel's Laws[a] form the basis for virtually all the evolutionary mechanisms normally discussed in neo-Darwinian theory. But they apply only to meiosis involving chromosome pairs. They say nothing about the meiotic behavior of unpaired chromosomes. Nor do they tell us anything about the production of new types of organisms by means of non-Mendelian processes (such as most of the stabilization processes to be discussed in Chapter 4). They do not explain how new chromosets arise.

Chromosomal Mutations. Suppose two hybridizing somasets belong to the same chromoset. Then in their hybrids the sort of genetic variation resulting from meiosis will be limited to the kind just described (meiotic recombination). For, when individuals with the same karyotype mate, the structure of the karyotype remains stable. There is little or no tendency for the number of chromosomes to change from one generation to the next. Chromosomes are not subjected to forces that rip them apart, rearrange them, and reassort them into new karyotypes.

In hybridization between chromosets, however, an additional type of genetic variation occurs due to *chromosomal mutations.*[333] When individuals from distinct chromosets mate, some or all of the chromosomes of the resulting (F_1) hybrid will be either unpaired or inexactly paired. Two chromosomes are perfectly paired if and only if they have the same loci in the same order and orientation (the regions between those loci must also lie in the same order and orientation). Chromosomes entirely lacking a match do not undergo a regular distribution into gametes as paired chromosomes do. No cellular mechanism exists to deal with unpaired chromosomes.[334] So they pass into gametes at random.[335] In consequence, different gametes end up with different chromosome complements. Some contain one chromosome of a given type; others contain none of that type. When chromosomes are partially matched, the affected chromosomes undergo breakage and rearrangment during meiosis. Such partially paired chromosomes (i.e., ones in which some subregions match, but others do not) exchange nonequivalent loci during meiosis so

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[a] Gregor Mendel (1822–1884), Austrian monk noted for his experimental work on heredity. His three laws may be stated as follows: 1) during the production of gametes two copies of each hereditary factor segregate so that offspring receive one factor from each parent; 2) the laws of chance govern which particular characteristics of the parental pairs will occur in each individual offspring; 3) one factor in a pair of traits dominates the other in inheritance.

that both their genetic content and their overall structure are altered.[a] In some cases, where partial matches exist between three or more chromosomes, they join together to form a chain, an event that can also lead to erratic assortment, breakage, and restructuring. Even attempts on the part of the cell to repair the damage can lead to alterations when broken fragments are attached to new chromosomes (translocations). Note that Mendel's Laws, which apply to the meiotic behavior of paired chromosomes, do not apply to the sorts of processes producing chromosomal mutations.

There are additional types of chromosomal mutations, yet to be discussed, that do not result from hybridization. However, chromosomal mutations are more common when hybridization does occur. Whereas point mutations affect individual genes without changing the structure of the chromosome on which the affected gene resides, *chromosomal mutations involve restructuring, deletion, and/or duplication of chromosomes, as well as their reassortment into new sets. They also involve the deletion, duplication, and/or reordering of loci (and/or segments of DNA between loci) within a chromosome or set of chromosomes*. In short, as defined here, a chromosomal mutation is any mutation producing a new karyotype.

Chromosomal mutations are of three general types, all of which are commonly induced by hybridization between distinct chromosets:

- Alteration of the structure of individual chromosomes (*chromosomal rearrangement*), which may involve reversal in the orientation of a portion of a chromosome (*inversion*) or a transfer of part of chromosome to another location on the same chromosome or on some other chromosome (*translocation*); It can also involve the deletion or duplication of a portion of a chromosome.

- Deletion or duplication of entire chromosomes (*aneuploidy*), or duplication of entire sets of chromosomes (*polyploidy*);

- The combination, in a single organism, of chromosomes previously found only separately in two distinct chromosets (*chromosomal reassortment*).[b]

Chromosomal mutations are sometimes called "gross" mutations because, by affecting entire chromosomes, sets of chromosomes, or large blocks of genes within chromosomes, they recombine and/or duplicate and/or delete hundreds, or even thousands, of genes at a time. On the other hand, the effect of a point mutation, even when detectable, is typically limited to a particular trait or, at most, to a set of related

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a. Shaw et al. (1983) showed such mutations are nonrandom in the sense that certain rearrangements are repeatedly produced by F_1 individuals from the same hybrid cross.

b. The term *chromosomal mutation,* is usually used only in connection with changes that affect the structure of a chromosome, as opposed to deleting or duplicating an entire chromosome. However, in this book the term will encompass any change to the karyotype, including those involving addition and deletion of entire chromosomes.

traits. A chromosomal mutation typically affects many traits because it involves many loci. Admittedly, some point mutations have more obvious effects than others. Likewise the effects of some chromosomal mutations are more limited than those of others. However, in general, chromosomal mutations have effects so large that they are qualitatively distinct from those of point mutation. The effect is of a different order of magnitude.

Even in the absence of point mutation, the reassortment, duplication, and deletion of multiple large blocks of genetic material occurring with chromosomal mutations can have major developmental effects. The simplest demonstration of this fact is seen in F_1 hybrids, which are often markedly different from their parents even though the individual chromosomes are passed unaltered from parent to offspring. Consider how different the common mule is from either of its parents. Here the change is brought about simply by combining in a single organism (i.e., the mule) the unaltered chromosomes of two different organisms (i.e., horse and ass). It results solely from interactions of genes present in new combinations or in different dosages. Thus, even by itself, the reassortment of unaltered chromosomes into new karyotypes — without point mutation and chromosomal restructuring — can be sufficient to bring about the production of new somatypes. In interchromoset crosses producing partially fertile hybrids, the numerous additional chromosomal mutations that occur in later hybrid generations can produce a broad spectrum of morphological variability.

Due to the great amplification of chromosomal mutations in interchromoset hybridization, meiosis in such hybrids (structural heterozygotes) is often severely disrupted. For this reason, interchromoset hybrids produce many more inviable gametes than do organisms with fully paired karyotypes. Many of the gametes do not contain the necessary genetic information to make them viable. Obviously, the production of fewer viable gametes will result in reduced fertility. *However, the viable gametes they do produce are far more variable in genetic content than are those produced by ordinary meiosis in an individual with a fully paired karyotype.* The chromosomes present in the two parents are present in the gametes in various combinations that could not occur in either parental type. In fact, in later-generation hybrids new chromosomes, not present in either of the parents participating in the initial cross, are often present. These have been built up out of blocks of genes present only on separate chromosomes in the parents (or present on the same chromosome in different relative order). Therefore, in later generations, karyotypes vary greatly from one hybrid individual to another with respect to genetic content and level of chromosome pairing. Thus, interchromoset hybridization produces individuals with combinations of genes, and with restructured chromosomes, that could never arise from intrachromoset matings. Traits therefore vary far more among such individuals than among individuals produced by intrachromoset matings. Under such circumstances, meiosis becomes a far more potent source of variation.

On the other hand, in the case of intrachromoset matings, point mutation is the only well-characterized source of variation other than meiotic recombination. But point mutations are extremely rare because the process that duplicates DNA, the hereditary material, is remarkably reliable.[336] Among eukaryotes, point mutation rates are very low. Consider, for example, the number of gametes that bear a mutation in a particular gene. The frequency of such gametes varies from one type of organism, and from one type of gene, to another, but the highest rate given by Dobzhansky et al. (1977: 69) was one gamete in ten thousand. The low end of the range given by the same authors was about one in a billion. Moreover, a point mutation, by definition, affects a very local region of a particular chromosome.

For example, the DNA polymer chain contained in a single chromosome might contain on the order of 100,000,000 linked units, known as *base pairs* (each is a purine molecule paired with a pyrimidine). Gregory et al. (2006) say human Chromosome 1 contains around 286 million base pairs and 3,141 genes A single point mutation in Chromosome 1 would typically affect only one or a few of those 286 million pairs and no more than one gene.

What is more, most point mutations have no effect on development unless they happen to occur in a gene (the apparently functionless regions between genes make up the majority of the DNA in the typical eukaryotic chromosome). Even mutations that do occur in genes often have no effect on development. When they do, they are very rarely advantageous and only one or a few traits are affected. Many point mutations that do have an effect are detrimental, or even lethal, a fact long recognized.[337,a] For all these reasons, point mutations are not a plausible source of rapid, evolutionary change. Thus, when all matings are within a single chromoset, stabilization theory assumes that point mutations are a relatively insignificant source of new variation.

Certain types of chromosomal mutations (e.g., aneuploidy, polyploidy), though they occur at increased rates in hybrids, can also arise in the progeny of non-hybrid individuals. Individuals with Down's syndrome, a form of aneuploidy, are a familiar example. People exhibiting this syndrome have a normal human karyotype except that they have three copies of chromosome 21, a condition known as "trisomy 21." Note that, as was the case with the common mule, no chromosomes are rearranged in the case of Down's syndrome, but numerous traits are nevertheless affected. The multiple changes result from an increased dosage of the many different genes on Chromosome 21.

Because of the mechanisms just discussed (and because of certain additional mechanisms to be discussed in Chapter 4), variability is a characteristic trait of later-generation hybrids. High levels of variability within a natural population therefore are usually an indication the population is of hybrid origin.[b] Variability is also an

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a. Even those point mutations typically having the largest effect, i.e., stop mutations and ones affecting regulation, usually only a single gene.

b. Of course, observed variation may also reflect inherent variation within a population rather than hybridization. But if (1) the variation occurs primarily in the vicinity of the range of another closely related organism, and (2) individuals in that vicinity tend also to be more similar to that other organism, hybridization is the more tenable explanation.

indication of fertility (McCarthy 2006), since (1) F_1 hybrids must be at least partially fertile if later generations are to occur, and (2) variation produced by hybridization is typically seen only in later generations.[a] Thus, variability itself is a factor that can aid not only in identifying hybrid populations, but also in predicting the fertility of hybrids themselves.

Stasis

Even in cultures preceding the advent of science it was believed hybridization would cause distinct populations to blend and become homogeneous (see Chapter 1). This idea is widespread even today. Experience with actual hybrid zones, however, has shown that hybridizing somasets usually remain distinct. Typically each has a broad geographic range in which there is relatively little morphological variation, but the region between the hybridizing forms contains a variable population of morphologically transitional hybrids. In this section we will look at some examples of stable hybrid zones and then consider the genetic basis of this stability.

Stability of Hybrid Zones. There are many well-documented examples of hybridizing populations remaining stably distinct. For example, Collar (1997: 421) notes that Buffon's Macaw (*Ara ambigua*) and the Military Macaw (*A. militaris*) are "sometimes treated as conspecific, but in spite of evidence of interbreeding the characters of the two forms are consistently different over their respective ranges."

Indeed, differences between hybridizing somasets can remain stable over long periods of time — many such hybridizing pairs have shown no significant tendency to blend, even after decades of observation. For example, a stable hybrid zone exists in southeastern Queensland, Australia, between two mammalian somasets, Herbert's Rock Wallaby (*Petrogale herberti*) and the Brush-tailed Rock Wallaby (*P. penicillata*). These are also distinct chromosets. Structural heterozygotes are present within the zone, but not elsewhere.[338] And yet, the two are not blending and losing their distinctive morphologies. In the United States the sunflowers *Helianthus annuus* and *H. petiolaris* form hybrid populations (i.e., large variable hybrid populations) in many areas, but remain distinct outside regions of hybridization.[339] Also in the United States, the butterflies *Collias eurytheme* and *C. philodice* produce

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[a] In the *Origin* Darwin (1859: 273) claimed that mongrels were more variable than hybrids (*mongrel* was the term used by Darwin for the products of matings between types that he considered to be "conspecific"). However, this assertion is only partially true. In general, any cross will produce variability, so long as later-generation hybrids can be produced. However, later generations can only be produced if the hybrids are partially fertile. Hybrids between closely related organisms, what Darwin would call "mongrels," are more likely to produce later generations, and hence variability, since they are more likely to be fertile. But hybrids between more distantly related organisms are actually *more* variable in those cases where later generations can actually be produced, especially in the case of later-generation compound hybrids.

a full range of hybrids in some localities, but show no evidence of fusing elsewhere.[340] Fooden (1997: 228) evaluated monkeys in a hybrid zone between *Macaca mulatta* (Rhesus Macaque) and *M. fascicularis* (Long-tailed Macaque) in southeast Asia. Across the zone a rapid morphological transition occurs from one somatype to the other. And yet outside the zone they remain uniform and pure.

Some zones are surprisingly stable. Perhaps, the best-known hybrid zone involving a pair of North American birds is between two woodpeckers, the Yellow-shafted Flicker (*Colaptes auratus*) and the Red-shafted Flicker (*C. cafer*). It extends some 3,000 km from New Mexico and Texas to southeastern Alaska and contains huge numbers of hybrids partially fertile in both sexes.[341] Every conceivable variant between *C. auratus* and *C. cafer* exists within the zone. Nevertheless, hybrids very rarely occur outside the zone. There is no indication the parents are going to blend and lose their distinctive traits. The two have remained distinct in all geographic regions outside the zone of contact. An expert on this zone, W. S. Moore (1995: 5) says this it is "at least 4000–7000" years old. Obviously, then, this means the situation is extremely stable — No merging of the two parental populations has occurred, though intense hybridization has been taking place at least since the time when the pyramids were built at Giza.

Two wood warblers were once treated as separate species, Audubon's Warbler (*Dendroica auduboni*) and the Myrtle Warbler (*D. coronata*). They are quite different in appearance. However, when these two small songbirds were found to hybridize, the American Ornithologists' Union decided they should both be called "Yellow-rumped Warbler" and said the single binomial *Dendroica coronata* should apply to both.[342] Intense hybridization occurs between these birds from southern Alaska to southwestern Alberta. Throughout this large region virtually all birds are hybrid.[343] Nevertheless, ornithologist Robert Zink (1995: 703) estimates at current rates of hybridization it would take at least "3,200,000 generations (likely over 6,000,000 years) for the fusion of these two taxa to include 3,000 km (only a part of the total range [of these two birds])." This is an underestimate, he says, and yet it "greatly exceeds the estimated time for the duration of a passerine [i.e., songbird] species in the fossil record (0.5 to 1.0 million years; Brodkorb 1971)." We can therefore condense Zink's comments to a single sentence: These two somasets will always remain distinct.

Mayr (1982: 284) refers to “a case of two species of California oaks (*Quercus*), hybrids of which are known from the Pliocene to the present, and yet where the two species have retained their essential integrity.” The Pliocene Epoch ended some 1.6 million years ago. Surely, if Mayr’s oaks were going to merge, they would have done so by now. He goes on to say, “the genetics of such situations is not understood at all, for it seems as if some part of the genotype of the two species is not affected by the hybridization. The two species, in such a case, seem to remain ‘reproductively isolated,’ in the sense that they do not fuse into a single population.”[a]

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a. Here Mayr is referring to hybrids between *Q. douglasii* and *Q. turbinella* (see Tucker 1952; Stebbins 1969).

Why are Hybrid Zones Stable? Thus, observation shows hybridizing populations usually remain distinct despite extensive interbreeding. When Mayr was writing, twenty-five years ago, it is true "the genetics of such situations" was not understood. But various factors have since been identified that keep hybridizing somasets from blending over time. Two types of explanations are generally offered. One is cast in terms of environmental factors, while the other is in terms of dispersal and selection against hybrids. The usual formulation of explanations of the former type is the environmental gradient model. This attributes the maintenance of hybrid zones to the differing habitat requirements of the two parental somatypes.[344] For example, Good et al. (2000) argue that adaptation to distinct environments maintains differences between Glaucous-winged and Western gulls (*Larus glaucescens* and *L. occidentalis*).[a] Fritsche and Kaltz (2000) make a similar case for the hybrid zone between two plants commonly used in herbal medicine, *Prunella grandiflora* (Large Self-heal) and *P. vulgaris* (Common Self-heal).

Nevertheless, the location of a hybrid zone often seems not to depend on environmental conditions. For example, in the northeast corner of the Sinai Peninsula is a narrow hybrid zone between two chromosets usually treated as races of *Acomys cahirinus* (Cairo Spiny Mouse). Wahrman and Goitein (1972: 235) say it seems "little correlation exists between the chromosome forms and the present environmental conditions of their respective areas of distribution." A hybrid zone between two birds, the Black and Painted francolins (*Francolinus francolinus* and *F. pictus*), extends across India from the Arabian Sea to the Bay of Bengal.[345] That between the Rock Pigeon (*Columba livia*) and Hill Pigeon (*C. rupestris*) begins in northern India and ends in southern Siberia.[346] Each of these avian zones passes through such a wide variety of environments it seems unlikely zone maintenance is related to habitat. In point of fact, hybrid zones often occur where there seems to be no significant change in the environment. For example, regarding the shrew hybrid zone mentioned above (pp. 53-54), Benedict (1999a: 135) notes that it follows an irregular course and is not associated with any particular type of soil or vegetation. Indeed, the region of Nebraska in question is monotonously uniform with respect to most environmental factors.

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[a] A special case of the environmental gradient model is the environmental mosaic model (Harrison and Rand 1989; Rand and Harrison 1989). It describes situations where the differing habitats are patchily distributed. Hybridization occurs where the two environments meet. For example, in the U.S. the forest-dwelling American Toad (*Bufo americanus*) and Fowler's Toad (*B. fowleri*), which occurs in open habitats, hybridize in transitional environments where they come into contact. Their distributions are patchy wherever their preferred environments are patchy (Blair 1941; Jones 1973; Volpe 1952, 1955). Another special case of the environmental gradient model is the bounded hybrid superiority model (Moore 1977; Moore and Buchanan 1985; Moore and Price 1993; Pierotti and Annett 1993), which assumes hybrids are fitter than the parental somatypes in the transitional portion of the environmental gradient, but less fit elsewhere.

Such situations, where the role of the environment is at best obscure, are explained as *tension zones*.[347] Tension zones occur when dispersal of hybrids from the zone is balanced by influx of parental individuals. The mechanism is simple. When parental types have a reproductive advantage versus the hybrids, they keep the zone narrow by moving into it at higher rates than hybrids move out. This bias in dispersal keeps the genetic influence of hybrids from spreading outside the zone. In general, the larger the selective disadvantage against hybrids, the narrower a tension zone will be. The more mobile the participating organisms, the wider it will be.[348] One probable example of a tension zone is that between the Black-capped Chickadee (*Parus atricapillus*) and the Carolina Chickadee (*P. carolinensis*). It extends across the eastern United States from New Jersey to Kansas through a variety of environments. Bronson et al. (2003) monitored the reproductive success of mated pairs within this zone. Unmixed parental pairs of either parental type produced more than twice as many fledglings per nest as did hybrid pairs.

Much debate has focused on whether environmetal gradients or tension zones are more important in maintaining zone stability. The two, however, are not mutually exclusive. A tension zone can exist in a region of transitional habitat. Thus, Delport et al. (2004) argue both habitat characteristics and a balance of dispersal and selection seem to play a role in maintaining a hybrid zone between two large south African birds, the Damaraland and Red-billed hornbills (*Tockus damarensis* and *T. erythrorhynchus*). Regarding a hybrid zone between the Cherry Stone Clam (*Mercenaria mercenaria*) and Southern Quahog (*M. campechiensis*), Bert and Arnold (1995) came to similar conclusions. "The structure and genetic architecture of this hybrid zone," they say, "appear to be products of a complicated interaction between both types of selective forces cited in the two competing models."

Karyotypes and the Maintenance of Hybrid Zones. Distinct chromosets break up spatially into separate populations that hybridize where they come into contact.[349] Spatial segregation on either side of such zones occurs because (1) karyotypically mixed populations produce many infertile offspring, and so tend to shrink; and (2) karyotypically pure chromosets produce fertile offspring and tend to expand. Expansion brings the chromosets into contact, but infertility of structural heterozygotes resulting from that contact limits overlap of the chromosets. With time, hybrid populations come to occupy relatively narrow interface regions (hybrid zones) between more extensive regions occupied by pure, karyotypically uniform, fully fertile parental chromosets. The population dynamics of such situations fit the tension zone model, but presumably, each of the parental chromosets would tend to occupy those regions where they had a reproductive advantage (as in environmental gradient models). In fact, examples are known of chromosets breaking up along an environmental gradient.[350]

Thus, in those situations where hybridizing populations differ karyotypically, chromosomal models provide an explicit explanation of how populations remain morphologically distinct despite ongoing interbreeding. The chromosets on either side of such zones can, and often do, have different genes. The distinct genetic content of their karyotypes programs the development of different organisms with different morphologies. The *genetic* uniformity (and hence morphological uniformity) within each of the two hybridizing chromosets is maintained by selection for *karyotypic* uniformity within each of the two chromosets. For in an otherwise uniform population, there is selection against any aberrant individual with a differing karyotype. In matings with karyotypically normal individuals any such individual produces structurally heterozygous offspring of low fertility (see p. 68).

Hybrid zones are widely viewed as sources of "gene flow" (i.e., as causing genetic mixture of the participating populations). However, as we have just seen, a tension zone between chromosets may serve as a buffer, actually preventing gene flow. There is gene flow into the zone, but not between the two parental populations. Although the two are interbreeding, they are, in a real sense, reproductively isolated. In spatial computer simulations, hybridizing chromosets can remain distinct indefinitely (McCarthy et al. 1995). In narrow hybrid zones, gene flow is prevented by the reduced ability of hybrids to survive and reproduce, and in wide ones it is prevented by distance itself.

Conclusion. Hybridization is associated with two seemingly contradictory phenomena, variation and stasis. However, this contradiction is illusory. In fact, the variation produced by hybridization is limited to the hybrid populations produced by such interbreeding. Morphological stasis is a feature of the interbreeding parental forms, which retain their distinctive characteristics outside the zone of contact. Cases are known where hybridizing populations have remained distinct for thousands or even millions of years. True, hybrid zones are highly stable in the sense that they can continue to exist for eons of time. Yet, in general, within most such zones, the hybrids themselves are extremely variable.

Stabilization theory distinguishes three types of variation. At one level, there is the slow accumulation of point mutations. This process is ongoing and is not a result of meiosis. It produces new alleles. At another level there is intrachromoset variation resulting from meiotic recombination involving paired chromosomes. Allelic variation of this type is described and predicted by the rules of Mendelian genetics. Intrachromoset meiosis can produce numerous changes in a single generation. But change from this source is inherently limited because it involves the recombination of preexisting traits and alleles. At a third level there are chromosomal mutations. These are often, but not exclusively the result of meiotic reassortment and restructuring in structural heterozygotes produced by interchromoset matings. Chromosomal mutations bring about radical, rapid changes in morphology. They create new sets of loci and new karyotypes. They can be duplicate, delete, and recombine thousands of genes in a single generation. Chromosomal mutations brought about by interchromoset matings not only produce new karyotypes, but also combine, in a single organism, traits that were previously found only separately in one or the other parents. Moreover, they produce a wide variety of different hybrid individuals with different combinations of such traits. Variation of this type is non-Mendelian.

It is the first two of these three levels of variation that are emphasized in modern evolutionary discussion (neo-Darwinian theory). The third level, which is the focus of stabilization theory, receives relatively little attention, apparently because the theoretical framework underpinning contemporary evolutionary discussion is based on Mendel's Laws, which apply only to intrachromoset matings. Such rules say nothing about processes that bring about karyotypic change. Such changes fall outside their scope. In the next chapter we will consider in more detail how new types of organisms arise via stabilization processes and the chromosomal mutations associated with them. This discussion will be illustrated by numerous examples.

4 Stabilization Processes: Examples

> *Any advance in our knowledge depends on the possibility of seeing species originate.*
> —HUGO DE VRIES
> *The Origin of Species by Mutation* (1902)[351]

This chapter will list and explain various kinds of stabilization processes and give examples of each. Stabilization processes differ from many of the processes described in the evolutionary scenarios of neo-Darwinian theory, in that they are far better documented—For each kind of stabilization process, there are definite, well-known examples of new types of organisms being so produced. Before listing these processes, it will be necessary to introduce some additional terminology.

Apomixis. *Apomixis* is a very common form of reproduction. It stands in contrast to the life cycle of sexual forms undergoing alternation of generations (see p. 72). In apomixis fertilization does not occur. There are two main types of apomixis, *agamospermy* and *vegetative reproduction* (Figure 4.1). In agamospermy the embryo develops from specialized reproductive tissues, but without fertilization. Although agamospermy is a term not usually applied to animals, many animals do reproduce by means that in a plant would be called agamospermy. So in this book, the term will be used not only in referring to plants, but also in a general way to refer to all forms reproducing this way. Animal agamosperms are usually called *parthenogens*.[a] In both plants and animals, parthenogenesis involves development of the embryo from an unfertilized egg. However, in plants, additional types of agamospermy are

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a. There are various forms of parthenogenesis. For example, in animals *gynogenesis* is a special type of parthenogenesis in which the sperm activates development of the egg, but makes no genetic contribution to the embryo, which develops from the egg alone. The equivalent process in plants is called *pseudogamy* by some authors (e.g., Grant 1981). The most common form of parthenogenesis in animals is *thyletoky*, the development of unfertilized eggs to produce female clones. There are also *arrhenotoky,* development of unfertilized eggs into males and fertilized eggs into females (occurs in haplodiploid hymenoptera and spider mites) and *amphitoky* (or *deuterotoky*), development of unfertilized eggs into either sex. Pichot et al. (2000, 2001) report that Saharan Cypress, *Cupressus dupreziana*, produces seeds derived entirely from pollen with no genetic contribution from a female gamete.

recognized in which the embryo develops from reproductive tissues other than the egg cell. In the upcoming discussion there will be no need to refer to those types specifically so they need not be enumerated here.

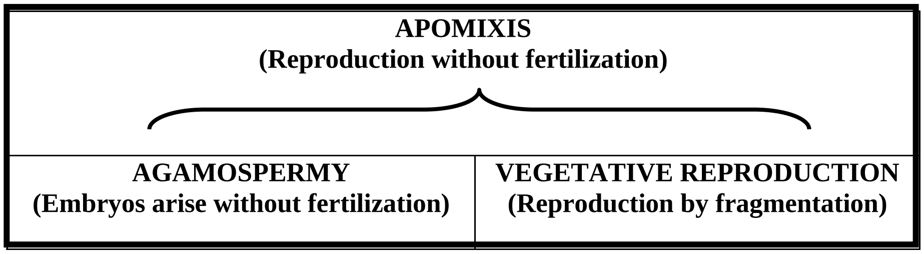

Figure 4.1: The two types of apomixis.

Vegetative Reproduction. In vegetative reproduction no embryo is produced. Reproduction instead proceeds by fragmentation. The growing organism breaks, or is broken, into two or more pieces, each of which lives on as an individual.[a] Separation can be caused by forces external to the organism (e.g., a gardener taking a cutting from a plant). It can also involve the genetically programmed production of a process that detaches itself to live and mature separately. For example, a strawberry plant can send out a runner that then sprouts separate plants. Sea anemones, and many other types of organisms, reproduce by budding, a process in which a new individual grows out of the original organism. In animals fragmentation can be voluntary. Thus, in some starfishes (e.g., *Linckia multifora* and *Echinaster luzonicus*) intentional amputation (autotomy) occurs. One of the arms pulls itself away, regenerates, and forms a new animal. In others (e.g., *Allostichaster polyplax* and *Coscinasterias calamaria*) the body breaks itself into more equal parts. The missing parts then regenerate. The various modes of apomixis should not be confused with *hermaphroditism,* where a single individual has both male and female sex organs, and where fertilization does in fact occur. Nor should it be equated with *self-fertilization,* which is a process undertaken by some types of hermaphrodites (for example, barnacles and many flowering plants).

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a. In speaking of vegetative reproduction, many authors emphasize a variety of processes that may occur prior to fragmentation of an individual to form two or more individuals. For example, Grant (1981: 6–7) notes that plants produce surface stolons and runners, underground rhizomes and tubers, offset buds on corms and bulbs, adventitious buds on cut stems or fallen leaves, and vegetative propagules arising within a flower or inflorescence. But prior to fragmentation, none of these processes produce a new individual. They only add various appendages to a single individual. In vegetative reproduction, fragmentation is always the essential step in creating offspring.

Clones. When organisms reproduce agamospermously or vegetatively, they produce offspring genetically identical to themselves. Both an individual produced in this manner and the entire line of individuals produced in this way are called *clones.* Any process producing a new type of clone capable of self-replication produces an extremely stable new form, so stable that different individuals are in fact genetically identical, or at least very nearly so. The only genetic differences are those that arise through rare mutations during, or subsequent to, the initial production of the clone. Any form that reproduces clonally (i.e., any apomict), once produced, would therefore be expected to show little or no variation over time. However, as we shall see, most clonal organisms of known origin and treated as species are derived from hybridization, and genetically distinct clones can be produced from hybrid crosses between the same two parent forms when different, genetically distinct, parental individuals are used. For example, different matings among hybrids in later generations, and backcrosses involving different later-generation hybrids, can produce distinct types of clones. In many cases, such clones differ among themselves, though each is a genetically invariant, stable, morphologically distinct lineage. Such naturally occurring arrays of clones ("clonal complexes") arising from later-generation hybridization may span much of the range of possible intermediate forms between the parents that originally crossed to produce the array. In contradistinction to a clone, breeders often call a hybrid line a *strain* when it is maintained by sexual, as opposed to apomictic, reproduction.[352]

Alternative Life Cycles: A single type of organism may be capable of producing progeny in more than one way. Many organisms with a sexual life cycle can also reproduce vegetatively. For example, many seed plants can propagate from a detached twig or leaf. Hybrids treated as various species of the European blackberry genus *Rubus* are seed-sterile, but can reproduce both agamospermously and vegetatively.[353] The Yellow-spotted Goanna (*Varanus panoptes*) is a varanid lizard that usually reproduces by means of sex. But Lenk et al. (2005) report that *V. panoptes* females are also capable of parthenogenetic reproduction. Many organisms combine all three modes of reproduction (sexual, agamospermous, and vegetative). For example, many members of the genus *Rubus,* just mentioned, not only can produce seed both sexually and agamospermously, but also can produce offspring by rooting of stem tips. Different types of organisms reproduce by these modes at different rates. How often a given type of organism exploits one or the other of these three modes depends on the form in question. For example, Yellow-spotted Goannas rarely reproduce parthenogenetically. Sexuality is their normal mode. An agamosperm reproduces primarily by agamospermous means. But most agamosperms are also capable of sexual reproduction, at least at low levels.[354] As Grant (1981: 11) points out,

> In some plant groups agamospermy replaces sexual reproduction completely (obligate agamospermy). In other plants some seeds form by agamospermous processes and some by sexual processes (facultative agamospermy). As with vegetative propagation, no sharp line can

be drawn between sexual and asexual reproduction, but instead the two modes are bridged by transitional conditions.

Some organisms (e.g., many parasitic worms, aphids, gall wasps) actually alternate parthenogenesis and sexual reproduction seasonally, or in response to various environmental factors.[355] Earthworms are hermaphrodites and reproduce sexually in pairs, but can also regenerate an entire body from a severed piece. Potentially, hermaphroditic organisms can self-fertilize, but many types either regularly mate, or can alternatively mate, with other individuals (i.e., they can *outcross*). Relative rates of selfing and outcrossing vary widely from one type of organism to another. Some types of hermaphrodites virtually always outcross, while others nearly always self. Earthworms, just mentioned, are an example of the former. An example of the latter is suckling clover (*Trifolium dubium*).[356]

Haberer's Groundpine, *Lycopodium habereri,* a plant of hybrid origin (from the cross *L. digitatum* × *L. tristachyum*), can reproduce both through spores and vegetatively.[357] The ability to reproduce by alternative means can allow hybrids of very low fertility to produce later-generation hybrids even by the sexual route. For example, Stebbins (1959: 236–237) describes work he carried out on hybrids between *Leymus triticoides* (beardless wildrye) and *L. condensatus* (giant wildrye). These two very distinct types of grasses hybridize easily. The F_1 hybrids are vigorous and intermediate in appearance, but extremely infertile.[358] Stebbins (1959: 236) states that

> they form from 1 to 5 per cent of stainable [i.e., fertile] pollen, but in spite of having cultivated them for several years in the presence of abundant normal pollen derived from their parents, we have never been able to find a single seed on them. In addition to artificial hybrids made from controlled pollinations, we have observed numerous wild plants which resemble closely the known hybrids, and which like them have a low degree of pollen fertility combined with almost complete failure of seed production. We must, however infer that they occasionally produce seed, since intermediate clones are found which include a whole spectrum of variability from *E. triticoides* to *E. condensatus* [note: in 1959 the official name of the genus *Leymus* was *Elymus*], and these have likewise various grades of fertility.

Stebbins goes on to say that this array of intermediate types was no doubt produced by rare sexual propagation on the part of the F_1 hybrid, which usually engages only in vegetative reproduction. He points out that each year a single such hybrid clone can produce 1000 flowering stems, each with about 200 florets, a total of 200,000 florets. Stebbins calculates that even if the hybrid's fertility were extremely low (one fertile seed per 100,000 florets), it would still produce two seeds annually, which would amount to 200 seeds over a 100-year lifetime. So a single such hybrid plant could produce 200 later-generation hybrids. These would maintain themselves by vegetative reproduction or, in the case of those showing a higher grade of fertility, by sexual reproduction as well. His own investigations led Stebbins to believe such situations, where highly sterile hybrids occasionally produce offspring by sexual means, are not uncommon among grasses and a wide variety of other plants.[a]

The various epithets used to pigeonhole organisms, such as *parthenogen, apomict, sexual, outcrosser, selfer, agamosperm,* etc., are generalizations. Relatively few organisms reproduce by one and only one of these modes. An organism may be called a "parthenogen," but still at times reproduce sexually. The name *parthenogen* usually means only that parthenogenesis is an organism's usual, not its exclusive, mode of reproduction. A predominantly sexual plant may be called "sexual," but still at times reproduce apomictically. A plant that usually self-fertilizes may be called a "selfer" and still outcross on occasion. In order to understand various statements in the upcoming discussion, it will be important to keep these facts in mind. For example, it might seem contradictory to speak of "agamosperms hybridizing" if one did not realize many organisms that reproduce primarily by agamospermous means are also capable of occasional sexual reproduction.

Stabilization Processes

A *stabilization process* is any series of events in which selection for a stable reproductive cycle results in the production of one or more new, stable forms of life. Such processes usually involve some type of chromosomal mutation, although certain exceptions to this rule will be discussed.

Because (1) most stabilization processes require the occurrence of chromosomal mutations and (2) chromosomal mutations are ordinarily very rare events, one might suppose stabilization processes would be too rare to have any evolutionary significance. However, stabilization theory maintains that they are, if measured in terms of the number of new forms they produce, in no way exceptional. In fact, it will be claimed that the *typical* new form is the product of such a process. It will be argued that stabilization processes are rare events only in the sense that the vast majority of individuals composing any given natural population do not participate in a stabilization process that ends up producing a new type of organism. But this sort of rareness does not detract from the significance of such processes — when they do occur, stabilization processes produce a new stable form with a new stable reproductive cycle. In other words, a rare, brief series of genetic events produces a permanent change.

Ordinary experience affords examples of events analogous to stabilization processes. For example, a man throwing a ball for a dog might complete ten thousand cycles of throwing and fetching, but on the ten-thousand-and-first throw the ball might lodge in the crotch of a tree. The dog would then be unable to return it. This single, extremely rare event breaks the cycle of throwing and fetching. It produces a permanent new state of affairs. In the same way, the cycle of meiosis and fertilization stably reproduces a particular karyotype until some rare disruptive event,

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[a] Stebbins (1959: 236). Herbert (1837: 342-343) discusses a *Crinum* hybrid that was absolutely sterile for many years, but then produced a single fertile seed in each of two successive years.

such as a doubling of the chromosome number or the introduction of new chromosomes via hybridization, breaks the cycle and produces something new.

Each time meiosis produces a gamete, a chromosomal mutation can occur. Every time two gametes produced by two distinct chromotypes unite in fertilization, a chromosomal mutation does in fact occur. Each such chromosomal mutation can initiate the production of a new form via a stabilization process. But the number of such fertilizations taking place in a single year is vast. Likewise, the number of gametes produced on this planet even in a single day is astronomic. Either of these numbers must far and away exceed the number of forms of life that have existed in all the past eons of geological time. Therefore anyone wishing to assess the evolutionary significance of stabilization processes should ignore the fact that only a tiny fraction of meioses and fertilizations would be expected to initiate a stabilization process. Rather, they should consider whether that tiny fraction of such an enormous number might represent a significant number of forms. But first let's consider what different sorts of stabilization processes are known and look at some examples of each.

Polyploid Production. Polyploid organisms have three or more complete sets of chromosomes. Polyploids are produced by processes that duplicate chromosome sets. Diploid organisms have two sets of chromosomes. Haploid organisms have only one. Polyploids with a particular number of chromosome sets are designated by names that reflect their level of ploidy (triploids have three sets, tetraploids have four, pentaploids have five, and so forth). Each type of polyploid organism is a distinct chromotype and each corresponding population is a distinct chromoset. Polyploids arise from preexisting organisms via the addition of one or more entire extra sets of chromosomes. Any process giving rise to polyploids is known as *polyploidization*. As has already been mentioned (p. 76), polyploidization is a kind of chromosomal mutation. Polyploids are of two basic types. *Allopolyploids* arise through hybridization, while an *autopolyploid* arises from a single parental form. Beetleweed (*Galax urceolata*) is an example of a natural autopolyploid.[359] Actually, beetleweed has both a diploid and tetraploid form, which are treated as conspecific. The two are similar except that the tetraploid is substantially larger, and a bit sturdier, with thicker leaves. Their distribution in eastern North America is also similar, with the tetraploid ranging somewhat wider.[360]

In the case of an allopolyploid, chromosome doubling stabilizes the reproductive cycle because it confers fertility. Hybrids produced by interbreeding between two diploid organisms normally receive one haploid set of chromosomes from each of their parents. Thus, as has already been mentioned, hybrids derived from matings between distinct chromotypes will have some or all of their chromosomes unpaired. The result is structural heterozygosity, which, recall, has a severe adverse effect on the fertility of the hybrids (see Chapter 3). However, when all of a hybrid's chromosomes are doubled, something that commonly occurs, all are paired once again. The resulting allopolyploid is fully fertile.[361] An allopolyploid that has achieved fertility by such means is known as an *amphiploid.* Amphiploids are of interest in an evolutionary context because they often have adaptively superior combinations of parental characters.[362]

The simplest case is the situation just described of an amphiploid derived from matings between two diploid parents. However, in any type of hybrid, chromosome doubling eliminates any sterility due to mismatched chromosomes. For example, a tetraploid might hybridize with a diploid. The offspring would therefore normally be triploid. Chromosome pairing is always poor in triploids (or in any odd-number polyploid) so fertility is correspondingly low. However, in the example just given, if chromosome doubling occurred, the resulting fertile hexaploid would have all chromosomes paired. Obviously, doubling the chromosomes will always produce a fully paired karyotype, no matter what kind of hybrid is in question.

Common bread wheat (*Triticum aestivum*) is an example of a common amphiploid. This hexaploid came into being about 7,000 years ago from hybridization between rivet wheat (*T. turgidum*), a tetraploid, and Tausch's goatgrass (*Aegilops tauschii*), a diploid.[363] In fact, Talbert et al. (1998) say it arose repeatedly as the result of multiple hybridization events. Rivet wheat itself is a much older, natural amphiploid derived from hybridization between two diploid grasses. One was the goatgrass *Aegilops speltoides*.[364] The other was either wild einkorn (*Triticum boeoticum*) or another wild wheat, *T. urartu*, more likely the former.[365] Another natural amphiploid is *Plagiomnium medium* (medium plagiomnium moss), shown by Wyatt et al. (1988) to be derived from hybridization between *P. ellipticum* (elliptic plagiomnium moss) and *P. insigne* (plagiomnium moss).

Specific Modes of Polyploid Production. Polyploids arise in various ways. Here we will consider two such processes that are actually known to occur (others have been proposed, but appear to be poorly documented):

(1) unreduced gametes;

(2) somatic multiplication.

The latter of these two modes of polyploidization seems to be the more common, but for those readers who are interested the relative prevalence of these two main ways in which polyploids arise is discussed in Appendix B. Relevant evidence is discussed at some length in that appendix, but in short, well-established facts indicate that polyploid production via unreduced gametes is extremely common in a natural setting. Somatic doubling may also be a common natural occurrence, but more research is needed to establish this. A third type, zygotic doubling (see Appendix C), has been observed many times under experimental conditions, but it is unclear how often it occurs under natural circumstances.

Unreduced Gametes. The terms *haploid, diploid, triploid,* and so forth, are applied also to gametes (and not only to the organisms that produce those gametes). Thus, a gamete that contains one set of chromosomes is haploid. One that contains two is diploid, and so forth. Therefore, when a haploid gamete (with one set of chromosomes) fertilizes a diploid gamete (with two sets of chromosomes), the resulting organism is triploid (it has three sets of chromosomes). A second hypothetical example would be the fertilization of a triploid egg by a diploid sperm, which would produce a pentaploid offspring.

The usual product of meiosis is a gamete containing half as many chromosome sets as do the cells of the organism producing the gamete. For example, a diploid organism normally produces haploid sperm. Such gametes are called "reduced" because the number of chromosome sets they contain has been reduced relative to the number present in the organism producing them. Therefore, when two such haploid gametes fuse during fertilization, a diploid offspring with two sets of chromosomes is produced (Figure 4.2a). This process produces a stable life cycle where parents produce offspring with the same number of chromosomes as themselves: The diploid phase of the organism produces haploid gametes; haploid gametes fuse to produce diploid phase, and so forth.

However, diploid organisms also produce some diploid gametes along with their normal, haploid gametes.[366] Such gametes are called "unreduced" (there has been no reduction in chromosome number versus the producing organism). Diploid organisms produce unreduced gametes that are diploid, but polyploids can produce unreduced gametes that contain more than two sets of chromosomes. When unreduced gametes fuse, or when an unreduced gamete fuses with a haploid gamete, a polyploid offspring results (Figure 4.2b). This process produces organisms with chromosome counts differing from their parents'. For example, hybrids between maize (*Zea mays*) and eastern gamagrass (*Tripsacum dactyloides*) are male sterile, but female fertile.[367] In the hybrids, reproductively functional eggs are diploid.[368] In backcrosses these eggs fuse with haploid pollen from either parent to produce triploid offspring.[369]

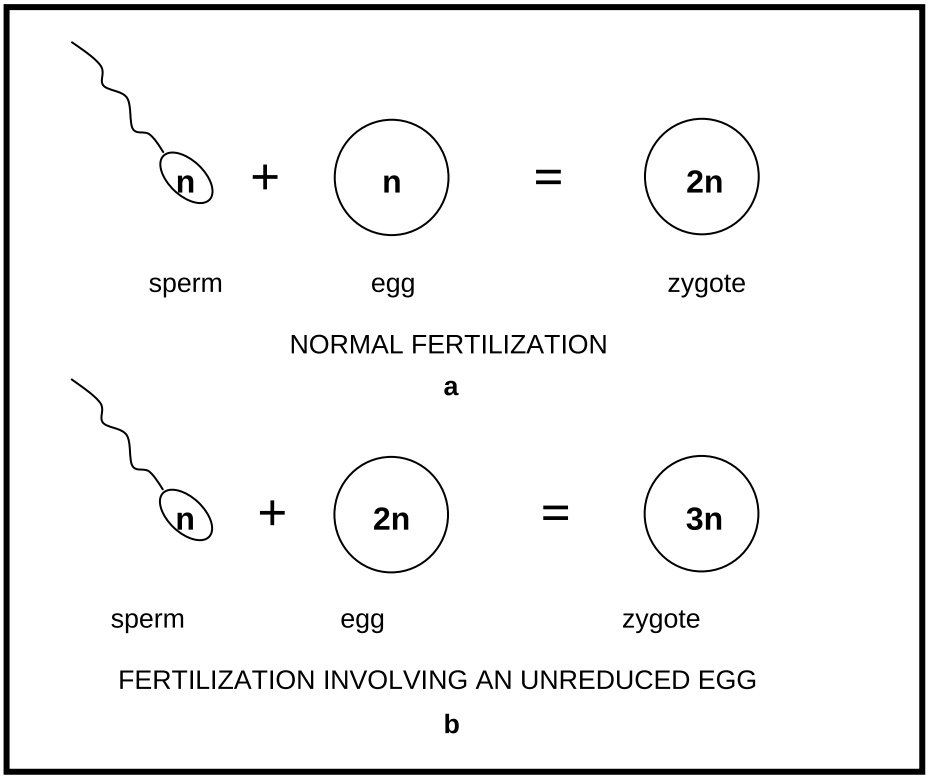

Figure 4.2: (a) Two haploid gametes fuse to produce a diploid zygote; (b) A haploid gamete and a diploid gamete fuse to produce a triploid zygote.

Polyploid organisms regularly produce gametes that would be considered unreduced if they were produced by a diploid organism.[370] For example, a tetraploid normally produces diploid gametes. Chourrout et al. (1986) exploited this fact to produce a triploid breed of rainbow trout (*Oncorhynchus mykiss*) by crossing diploid and tetraploid forms. The haploid gametes of the former united with the diploid gametes of the latter to produce triploid offspring. A triploid form of the loach *Misgurnus anguillicaudatus* (oriental weatherfish) spawns eggs containing one, two, or three sets of chromosomes.[371] Matsubara et al. (1995) fertilized triploid eggs from this source with haploid sperm to produce tetraploid offspring.

Müntzing (1930, 1932) proved the tetraploid annual herb *Galeopsis tetrahit* (brittlestem hempnettle) is derived from hybridization. *G. tetrahit* has been treated as a species since the time of Linnaeus. Müntzing synthesized it via a three-step process (diagrammed in Figure 4.3). He first crossed *Galeopsis pubescens* (Downy Hempnettle) and *G. speciosa* (Large-flowered Hempnettle). The resultant hybrids were quite infertile and exhibited irregular meiosis. They had only about eight percent viable pollen. The F_2 generation was composed mostly of diploids, but there was one triploid that arose from the union of a haploid gamete and a diploid gamete.[372] When Müntzing backcrossed this triploid individual to *G. pubescens,* it produced a single seed, which grew into a tetraploid plant. This tetraploid individual arose when a triploid egg was fertilized by a normal haploid gamete from *G. pubescens.*[373] It produced 70 percent viable pollen and yielded fertile progeny via self-fertilization. These artificial allopolyploids matched *G. tetrahit* in morphology and karyotype. Moreover, they produced fertile progeny when crossed with *G. tetrahit,* but were reproductively incompatible with *G. pubescens* and *G. speciosa*. Therefore, naturally occurring *G. tetrahit* almost certainly arose via a similar process.

Another case of a new stable type produced by the union of unreduced gametes is the tetraploid hybrid Karpechenko (1927, 1928) obtained by crossing cabbage and radish (*Brassica oleracea* × *Raphanus sativus*). In this cross, the F_1 hybrid is quite sterile due to a nearly complete lack of chromosome pairing. However, it does produce some viable diploid gametes. Fusion of such gametes gave rise to Karpechenko's tetraploid, the "rabbage" known as radicole (*Raphanobrassica*)*,* in the F_2 generation. These F_2 plants exhibited regular meiosis and were fertile. Moreover, they were reproductively stable, yielding later generations morphologically similar to the F_2.[a]

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a. Karpechenko wanted to develop a hybrid with the leaves of a cabbage and the root of a radish, but *Raphanobrassica* turned out to agriculturally useless because it has the root of a cabbage and the leaves of a radish. A much more successful related allopolyploid is the raparadish, an allopolyploid hybrid between *Raphanus sativus* and *Brassica rapa* (field mustard), which is widely grown as a fodder crop (Lange et al. 1989).

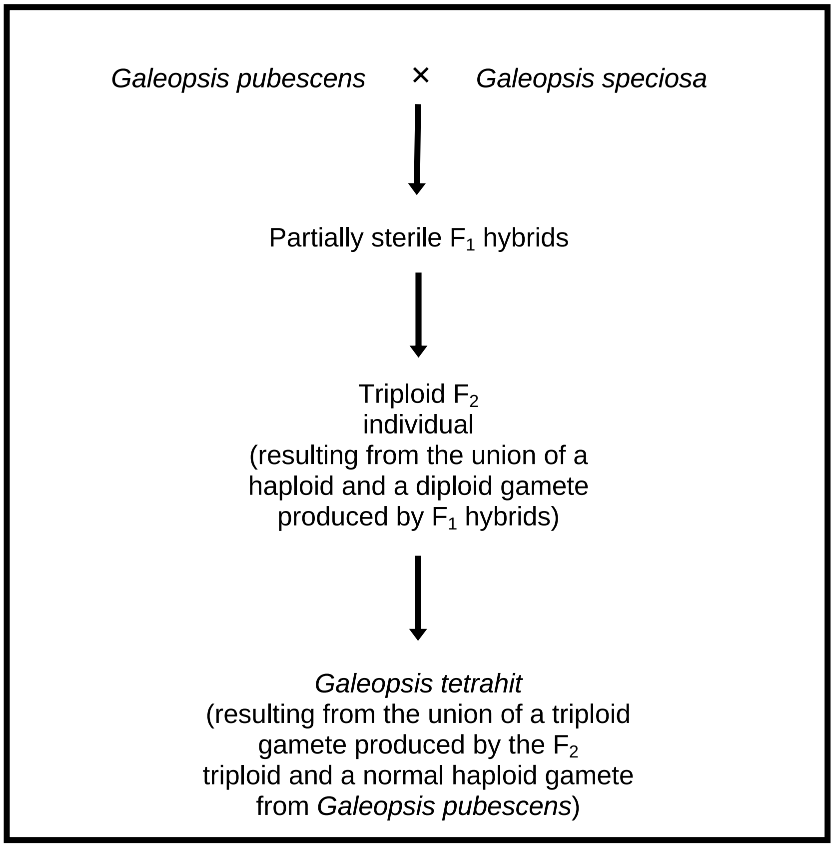

Figure 4.3: The three-step stabilization process producing brittlestem hempnettle (*Galeopsis tetrahit*).

Pinkava et al. (1985: 473) say that a diploid chromotype of the cactus *Cylindropuntia fulgida* (jumping cholla) provided both a diploid and a haploid gamete that joined to produce an autotriploid chromoset (treated as conspecific with *C. fulgida*). Like most triploids, these autotriploids are quite sterile. However, they propagate themselves clonally via efficient vegetative reproduction (through easily detached stem segments). Uzzell (1963, 1964) reported that two North American salamanders, *Ambystoma platineum* (Silvery Salamander) and *A. tremblayi* (Tremblay's salamander), are triploid parthenogens. Sessions (1982) showed they had both been produced via a two-step stabilization process: (1) an *A. laterale* (Blue-spotted Salamander) male crossed with an *A. jeffersonianum* (Jefferson Salamander) female to produce a female hybrid; (2) this female hybrid produced diploid eggs that were fertilized by *A. jeffersonianum* males, which produced *A. platineum.* Fertilization of the same eggs by *A. laterale* males produces *A. tremblayi*. Both of these salamanders are parthenogens.

When multiple spermatozoa fertilize a single egg, the effect on the chromosome number of the fertilized egg (i.e., on the *zygote*) can be the same as fertilization by a single unreduced spermatozoon. However, while the production of polyploids by this method has in fact been observed,[374] it seems much rarer than polyploidy induced by unreduced gametes, presumably because the eggs of most organisms have a mechanism that efficiently prevents the entry of multiple spermatozoa.

Somatic Multiplication. A new polyploid form can also be produced when (1) a chromosomal mutation increasing the number of chromosome sets occurs in a somatic cell (i.e., a cell that is not, and is not destined to become, a gamete); and (2) that cell goes on to form by cell division an entire polyploid segment within an organism that otherwise remains diploid; (3) that segment, or a portion of that segment, separates from the parent organism and/or produces offspring to found a new polyploid line. For example, the Kew Primrose (*Primula kewensis*) was produced via a stabilization process of this kind. Its origin was well documented.[375] First, an F_1 hybrid was produced between the primroses *P. floribunda* and *P. verticillata.* It was diploid and highly sterile, but was propagated via cuttings. Later, in three separate years, this otherwise sterile clone produced fertile tetraploid shoots that gave rise immediately to the fertile, constant tetraploid now known as *P. kewensis* (these shoots each developed on the diploid hybrid from single cells in which chromosome doubling had occurred). In this way, the Kew Primrose emerged as a new type of plant with a stable sexual reproductive cycle.[a]

Processes producing polyploids, such as those just described can generate whole assemblages of related polyploids ("polyploid complexes"). For example, a diploid with the chromosome set A, could cross with a second diploid having the complement B, to produce a tetraploid with the set AB. The second of the diploids

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[a] Hiesey et al. (1971) report a similar case in monkey flowers (*Mimulus*), where a diploid F_1 hybrid produced a tetraploid shoot.

could cross with a third, having the set C, to produce the tetraploid BC. Another cross (A × BC) could produce a hexaploid with the complement ABC. The continued production of polyploids in this manner can produce an array of forms with even higher levels of ploidy. Grant (1981) gives many examples of naturally occurring polyploid complexes.

Aneuploidy. Aneuploidy is produced by multiplication or deletion of individual chromosomes. For example, a diploid organism with a chromosome count of 2n might produce an aneuploid offspring with an extra copy of one chromosome (so the total chromosome count would be 2n + 1). It might also produce an offspring that lacked a copy (so the count would be 2n - 1).[a] The addition or subtraction of a single chromosome often has an affect on multiple characters. Torrey's willowherb (*Epilobium torreyi*[376]) is an example of a form derived from aneuploidization.[377] It is thought to be an aneuploid derivative of largeflower spike-primrose (*E. pallidum*[378]).

One example of aneuploidization, Down's syndrome, has already been mentioned. Down's syndrome arises when a gamete containing an extra copy of chromosome 21, usually an egg from an older mother, combines with a gamete containing the normal complement of human chromosomes. The result is an individual with three copies of Chromosome 21. Such gametes result from a mistake in meiosis ("nondisjunction") in which a gamete receives both members of a chromosome pair instead of only one as usually occurs. Males with Down's syndrome are in general far less fertile than individuals with a normal human karyotype, but they do produce some viable gametes.[379] Females are quite fertile, 50 percent of their eggs carry two copies of Chromosome 21. There is the potential, then, for such an aneuploid egg to combine on rare occasion with a similarly aneuploid spermatozoon from a male Down's individual to produce a reproductively stable type with a fully paired karyotype. In this way, if this new type were viable, a stabilization process could at least hypothetically, produce a new, fertile type with a chromosome count of 2n = 48 (instead of the normal 46). It is hard to assess just how often new forms arise via the addition or deletion of individual chromosomes, but this issue is discussed briefly in Appendix D.

Production of Permanent Translocation Heterozygotes. Permanent translocation heterozygotes represent an additional type of organism produced by rapid stabilization processes. A *translocation* occurs when a portion of a chromosome is transferred to another location, either on the same chromosome or on some recipient chromosome not belonging to the same chromosome pair as the donor chromosome. Two chromosomes that belong to the same chromosome pair, that is, that contain the same set of loci in the same order, are called *homologous.* The two members of a chromosome pair are *homologs.* A *reciprocal translocation,* the most common kind

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[a] Reductions and increases in chromosome numbers due to chromosome breakages and fusions are also often described under the heading of aneuploidization (e.g., Grant 1982: 359–361), but here will be placed under the heading of chromosomal rearrangements.

of translocation, is an exact interchange of chromosomal segments between two chromosomes not belonging to the same chromosome pair (nonhomologs).

In a *translocation heterozygote* two pairs of homologous chromosomes have reciprocally exchanged nonhomologous segments between one member of each pair. As a result each of the affected chromosome pairs contains both homologous and nonhomologous segments. Put another way, each such pair has one translocated chromosome, and one normal (untranslocated) chromosome. More than two chromosome pairs can be altered in this way so that some or all of the chromosome pairs are composed of a translocated and an untranslocated member.

Organisms having chromosomes rearranged in this way are known as *permanent translocation heterozygotes*.[380] Due to the way reciprocal translocations are processed during meiosis, all the translocated chromosomes pass to one gamete and all the normal chromosomes pass to the other.[381,a] As a result, only two types of gametes are produced. One has all the translocated chromosomes and the other has all the normal ones (here "translocated" and "normal" are relative terms since in naturally occurring organisms it is usually unknown which of the two types was original). These two sets of chromosomes ("normal" and "translocated") are known as *Renner complexes.* In well-studied organisms of this type, the various Renner complexes have been assigned formal names. In one of the best-known permanent translocation heterozygotes, the evening primrose *Oenothera lamarckiana,*[b] the two Renner complexes are called *velans* and *gaudens.* So the karyotype of *O. lamarckiana* is designated as "*velans/gaudens*." Genetic interchange (crossing-over) between Renner complexes is very rare, so that chromosomes in distinct complexes differ genetically in many respects.

Aneuploidization is a common stabilization process among permanent translocation heterozygotes because there is an enhanced tendency to produce aneuploid gametes.[382] The result is the production of numerous trisomic forms (forms having three copies of a chromosome instead of the usual two). But the most common stabilization process seen in organisms of this type occurs when forms with distinct Renner complexes hybridize to produce new forms.[383] For example, hybridization of *O. lamarckiana* with another evening primrose, *O. strigosa*, which has the Renner complexes *deprimens* and *strigens*, yields four different types, *velans/deprimens, velans/strigens*, *gaudens/deprimens,* and *gaudens/strigens*.[384] Some hybrids produced by such recombinations of Renner complexes are reproductively stable and others are not.[385] By this means new stable types can be

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[a] In translocation heterozygotes, the translocated chromosomes form quadrivalent associations during pachytene. Segregation can then occur in two ways: (1) *adjacent disjunction,* in which each daughter cell receives a translocated and a normal chromosome. The resulting gametes are then inviable because they are deficient in some genes and duplicate in others (2) *alternative disjunction,* in which both translocated chromosomes go to one daughter cell and both normals go to the other. The gametes then contain all necessary genetic material and are viable. See King and Stansfield (1985).

[b] The scientific names used in this section follow Grant (1981).

produced in a single generation. *O. lamarckiana* itself arose by such a process via hybridization between *O. biennis* and *O. hookeri*.[386] This event occurred within the last two or three centuries in Europe where the two parental forms, both native to North America, were introduced.[387] *O. lamarckiana* spread across Europe and later to North America. In fact, most of about 18 forms of European *Oenothera* that Renner (1942) treated as species arose in this way.[388]

Production of New Agamosperms. Recall that (1) agamospermy is a mode of reproduction in which the embryo develops without fertilization; and (2) parthenogenesis is a special form of agamospermy in which such development proceeds from an unfertilized egg (and not from other types of reproductive tissues). Most, but not all, agamosperms are polyploid.[389] However, the stabilization processes producing them differ from those producing sexual polyploids in that they do not require a recovery of pairing via chromosome doubling. The karyotype of an agamosperm can be completely unpaired. In the great majority of cases, distinct agamospermous somasets are also chromosomally distinct either in ploidy or with respect to chromosomal rearrangements.[390] That is, they are distinct chromosets. Since many agamosperms are the products of hybridization between chromosets, the process that produces them is a kind of chromosomal mutation.

The population of Australian lizards designated by the name *Heteronotia binoei* contains various chromosets. Moritz (1984) reports that one of them, a triploid parthenogen, arose through a two-stage stabilization process: (1) hybridization between two diploid chromosets produced diploid hybrids; (2) the hybrids backcrossed with parental males to produce triploid female parthenogens. Since the production of unreduced gametes is greatly enhanced in hybrids,[391] the backcrossing female hybrids probably supplied diploid eggs that united with haploid sperm from the male parents to produce the triploid females. Because these females were able to reproduce without fertilization, they each founded a separate clonal line of descendants. Note that the production of each parthenogenetic founding female required a chromosomal mutation.

The triploid parthenogenetic snail *Campeloma parthenum* (Maiden Campeloma) formed via a similar two-step stabilization process.[392] The steps were: (1) a *C. geniculum* (Ovate Campeloma) male crossed with *C. limum* (File Campeloma) female to produce a parthenogenetic diploid; (2) this diploid then backcrossed to a *C. geniculum* male to produce a triploid parthenogenetic female which founded a clonal line (*C. parthenum*). Again, the genetic events producing this clone were chromosomal mutations. Scali et al. (2003) studied stick insects of the genus *Bacillus.* They report the parthenogen *Bacillus atticus* hybridizes with the sexual *B. grandii* to produce sexual diploids and a parthenogenetic triploid. The diploids are treated as a species (*B. whitei*), as is the triploid clone (*B. lynceorum*).

The origins of the parthenogens just mentioned were inferred from analysis of their karyotypes and genetic constitution. In many cases, however, parthenogenetic forms have actually been synthesized by hybridizing their parents under controlled conditions. For example, two Australian morabine grasshopper chromosets are treated as a single species, *Warramba virgo*.[393] Chromosome studies showed that these two parthenogenetic chromosets arose through hybridization between two other grasshoppers, known as *P169* and *P196*,[394] both of which are sexual. One of these parthenogenetic chromosets, composed of the two western clones, "Boulder" and "Zanthus," has been synthesized in the laboratory by crossing the parents, *P169* and *P196*.[395] Another grasshopper, the naturally occurring parthenogenetic delphacid leafhopper *Muellerianella 2-fairmairei-brevipennis,* was produced by hybridization between *M. brevipennis* and *M. fairmairei*.[396] It, too, has been artificially replicated by crossing its parents.

Agamic Complexes. An assemblage of multiple polyploid and agamospermous chromosets can be formed en masse via repeated hybridization. Such assemblages are known as *agamic complexes.* Coyne and Orr (2004: 18–19) note that agamic complexes

> harbor a core of diploid species with obligate sexual reproduction. The sexual species hybridize to form polyploids that may themselves reproduce sexually but more often reproduce through agamospermy. Repeated bouts of interspecific hybridization, polyploid formation, and occasional sexual reproduction of the agamospermous forms can produce a continuum of variation between the sexual forms.

Grant (1981: 442–444) gives the dandelion genus *Taraxacum* as an example of an agamic complex. It contains 28 sexual diploid populations treated as species, all of which can be crossed to produce hybrids. Such hybridization produces a huge variety of polyploids, most of which are agamosperms. These typically produce either bad pollen or no pollen at all, but some are capable of sexual reproduction as well. Together with the 28 core diploids, they have been treated as nearly 2,000 (!) separate species.[397] Other extensive agamic complexes occur in such plant genera as *Alchemilla, Crataegus, Hieracium,* and *Rubus*.[398] The *Alchemilla* (lady's mantle) complex, for example, contains about 1,000 forms that have been treated as species.[399] As examples of animal groups in which agamic complexes occur, White (1973: 700) mentions earthworms, weevils, simuliid flies, and brine shrimp.

Production of New Vegetative Forms. Although hybridization often has an adverse effect on fertility, new forms of hybrid origin capable of vegetative reproduction can propagate and persist even when absolutely sterile. Modes of vegetative reproduction include sprouting and fragmentation in plants. In animals, equivalent processes are known as splitting and regeneration. Budding occurs in both animals and plants. Vegetative reproduction also occurs in most fungi.

One example of this type of stabilization process has already been given, the vegetatively-reproducing natural hybrids between the ryes *Leymus triticoides* and *L. condensatus* (see p. 88). These hybrids, which are treated as a species (*L. multiflorus*), occur in southern California. Though seed sterile, they have spread vegetatively throughout much of the vast San Joaquin Valley. Walter (1977) gives another example of a highly sterile grass (*Holcus mollis*) of probable hybrid origin propagating itself by vegetative reproduction. The widely cultivated edible banana *Musa paradisiaca* is a sterile seedless hybrid from the cross *M. acuminata* × *M. balbisiana*.[400] Although incapable of sexual reproduction, it is propagated vegetatively by offshoots.

Bartley's Clubmoss (*Huperzia bartleyi*), a natural hybrid, was produced by the cross *H. lucidula* × *H. porophila* (Shining Clubmoss × Rock Clubmoss).[401] It is sexually sterile but widespread in the eastern United States. It reproduces by means of wind-dispersed shoots.[402] Werth and Wagner (1990: 701) note that among the horsetails (Equisetaceae) there are a number of examples of sterile somatypes treated as species that are of hybrid origin. They are rendered reproductively competent by vegetative reproduction from stem fragments. Werth and Wagner give the example of Ferris' Horsetail (*Equisetum ferrissii*), a hybrid derived from the cross Common Horsetail × Smooth Horsetail (*E. hyemale* × *E. laevigatum*). They say it "occurs well beyond the range of one of its parents, demonstrating that vegetative reproduction by fragmentation can be effective in accomplishing long distance dispersal of the hybrid, especially along lake shores and rivers.[403] Although it is a sexually sterile hybrid, it is common enough to be reckoned with over an extensive area of North America."

The bittercress *Caramine insueta* is a natural triploid hybrid derived from *C. rivularis* and *C. amara*. It arose in the vicinity of Urnerboden, Switzerland, sometime during the twentieth century through the fertilization of a diploid *C. rivularis* egg cell by haploid *C. amara* pollen.[a] These hybrids are highly sterile, producing only 2–3 percent good pollen. Yet Grant (1981: 409) says "they reproduce well and have spread locally over a 16-hectare area, where they predominate over the parental species. Reproduction is partly by vegetative and partly by sexual means."

An agamospermous life cycle, because it does not ordinarily involve meiosis,[404] does not produce genetic variability. However, since many organisms having such a life cycle also have a sexual life cycle, the same sources of variation are available to them as to organisms that are strictly sexual. Sexual reproduction may be impaired in such organisms, but still occur at low rates. When vegetative reproduction is combined with low levels of sexual reproduction, whole complexes of new forms can arise. In the southwestern United States, walkingstick cactus (*Cylindropuntia spinosior*) and jumping cholla (*C. fulgida*) produce F_1 hybrids that are highly seed-sterile but have a great capacity for vegetative reproduction via fallen stem joints.[405] Vegetative reproduction by these hybrids has produced a stable somaset of clonal descendants identical to the F_1 founders. Over evolutionary time, rare sexual reproduction by members of this F_1-identical somaset occasionally produces later-

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a. Franzke and Mummenhoff (1999); Urbanska et al. (1997); Urbanska-Worytkiewicz (1977a, 1977b). *Caramine insueta* has since produced a fertile allopolyploid derivative by doubling of its genome (Franzke and Mummenhoff 1999; Urbanska et al. 1997). This derivative is now treated as a species, *Cardamine schulzii* (ibid).

generation hybrids, each of which founds a morphologically distinct clonal somaset propagated by vegetative reproduction (recall that, although F_1 hybrids are generally uniform, their gametes are highly variable, see Chapter 2). Many of these later-generation hybrids are morphologically distinct (as is usual with variable later-generation hybrids produced by interbreeding between distinct parental somasets). Each distinct somatype among the later-generation hybrids produces via vegetative reproduction a distinct clonal somaset of invariant descendants (Figure 4.4). In addition, each of these clones, if sexually fertile in any degree whatsoever, can on rare occasion, found additional types of clones via sexual reproduction (as is the case with the F_1 clones). This process has produced an abundant population of hybrids in the Gila Valley in southwestern Arizona. Grant (1981: 465) notes that one of the clonal somasets in that hybrid population "covers an area 20 miles long by 26 miles wide in the desert." He also says (ibid) that because the hybrid population forms "a distinctive element in the Arizona flora" it is treated as a species, *C. kelvinensis.*[406] Pinkava et al. (1985: 472–473) note that the predominant somatype within the polytypic *C. kelvinensis* is a triploid and that evidence strongly suggests that *C. fulgida* provided the unreduced gamete producing this new chromotype. Hence, the primary somaset of *C. kelvinensis* was produced by a chromosomal mutation.

Contingent Stability. In some cases, a form can be both temporally and morphologically stable even when it is incapable of reproduction. For example, even absolutely sterile hybrids, incapable of apomictic reproduction, can be produced on an ongoing basis by hybridization between their parents. Such forms are often treated as species. Bogart et al. (1987) showed that a sterile triploid salamander, which had been treated as a species (*Ambystoma nothagenes,* Kraus 1985)*,* is recreated in each generation as a hybrid of *A. texanum* and *A. laterale.* In northern Australia, the Chestnut-breasted Munia (*Lonchura castaneothorax*) and the Scaly-breasted Munia (*L. punctulata*) interbreed on an ongoing basis. These birds, then, have produced a natural population of hybrids, but captive breeding shows that the resulting hybrid is quite sterile.[407] Consequently, although there may conceivably be occasional hybrids of this type that are in some degree fertile, in a state of nature all, or at least the vast majority, of the birds produced by this cross are invariant F_1 hybrids. These hybrids represent a distinct, naturally occurring stable type that has existed for as long as its parents have been hybridizing (potentially thousands or even millions of years). Clinally varying populations produced by hybridization, too, are contingently stable. They are not morphologically stable, but they are temporally stable because they continue to exist for as long as the hybridization that produces them continues to occur. As has already been noted, such clinal populations have often been treated as species or subspecies.

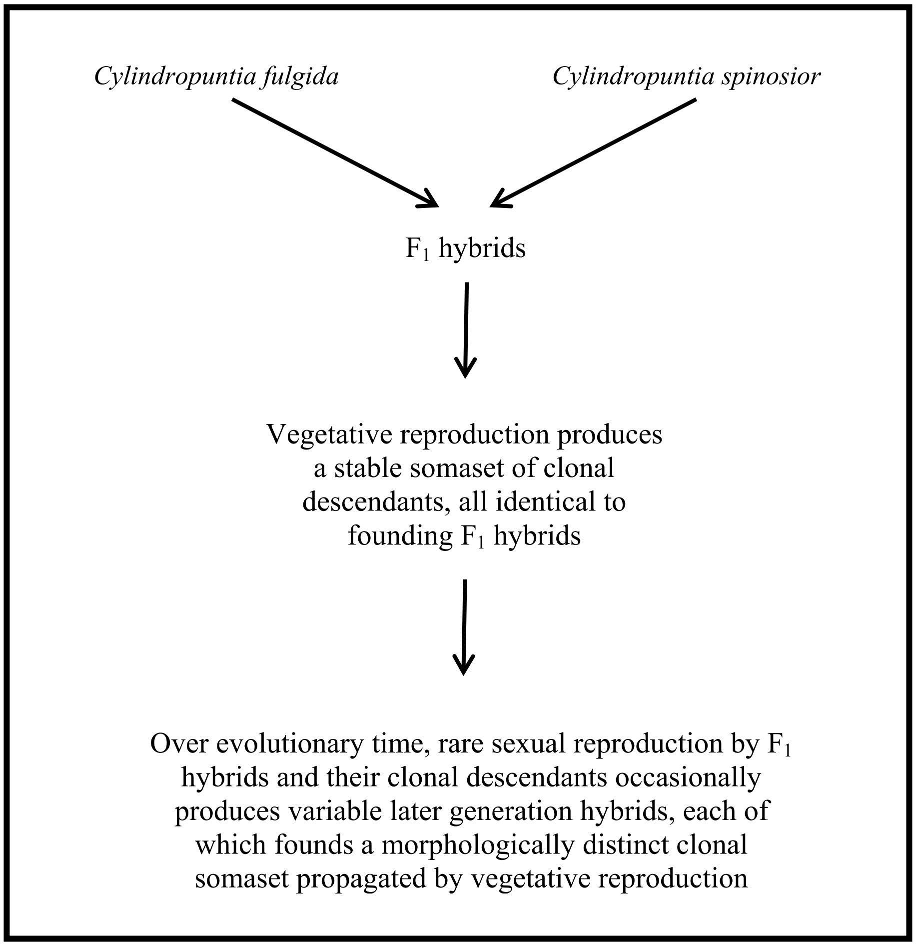

Figure 4.4: Stabilization processes producing the various somasets of the cactus *Cylindropuntia kelvinensis.*

Some types of organisms are only capable of reproduction with the aid of some other type of organism. Therefore their continued existence is contingent upon the existence of that other form. Fishes in the genus *Poeciliopsis* inhabit the rivers of western Mexico. Multiple hybridizations between females of *P. monacha* (headwater livebearer) and males of several other members of *Poeciliopsis* have produced various diploid and triploid forms. For example, hybridization with *P. lucida* (clearfin livebearer) has produced the all-female form *P. monacha-lucida*.[408] All the diploid forms are populations composed solely of females that can produce offspring only when their eggs are fertilized by the male of some other form.[409] For example, since *P. monacha-lucida* is composed only of females, fertilization by *P. lucida* males is required to produce progeny.[410] Thus, *P. monacha-lucida* is a stable form found under natural circumstances, but it could not continue to exist in the absence of *P. lucida.* By first crossing the Gila topminnow (*P. occidentalis*) with *P. monacha* and then crossing the F_1 hybrids with *P. lucida,* Whetherington et al. (1987) found a variety of clones could be produced differing significantly with respect to their abilities to survive and reproduce. This production of multiple clones with distinct properties from the F_1 of a single cross is like the production of multiple clones by the F_1 in the *Cylindropuntia* cactus cross described by Grant (see p. 101), except that in the present case the hybrid reproduce parthenogenetically instead of vegetatively.

Sometimes a form capable of reproduction is also produced by other forms on an ongoing basis. For example, parthenogenetic *Cnemidophorus* lizards can reproduce clonally, but they are also repeatedly produced by hybridizations between their parental forms.[411] Remarkably, a form produced by another form can sometimes produce its own parent. An example of this type of system is seen in the complex of fishes produced by matings between female finescale dace (*Phoxinus neogaeus*) and male northern redbelly dace (*P. eos*). Along the U.S.–Canada border these fish hybridize to produce an all-female population that includes diploids, triploids, and single individuals having both diploid and triploid cells ("mosaics").[412] Some of the eggs produced by diploids and by diploid-triploid mosaics develop clonally; others (nearly half) are fertilized by one of the parents to produce triploids. Triploid hybrids are capable of producing haploid eggs that can then be fertilized by either parent or by other hybrids. When fertilized by *P. eos,* the resulting hybrid is virtually indistinguishable from *P. eos.*[413] All of the various forms in this complex arise via chromosomal mutations. In the case of some organisms only marginally capable of reproduction, their repeated production by their parents may be essential for the prevention of extinction.

Production of Symbiotic Associations. Many organisms form permanent relationships known as symbiotic associations. Many such associated pairs are treated as species. Thus, Margulis and Schwartz (1998: 364) say at least one-quarter of all fungi treated as species enter into associations with photosynthetic microbes to form lichens and that some 13,500 of these lichens have been treated as species distinct from the two forms that compose them. This practice is common because a lichen usually looks entirely different from the fungus and alga that unite to produce it.[414] Though such composite forms are not the products of chromosomal mutations the production of a symbiotic association is a type of stabilization process because it produces a new stable type of organism with a stable reproductive cycle. (Note that the process producing such forms is analogous to hybridization even if it is not, strictly speaking, hybridization itself, inasmuch as it involves the melding of two distinct forms. Moreover, such organisms commonly exhibit emergent or synergistic traits, as do ordinary hybrids.)

A special form of symbiotic association can exist between cells, in which one type of cell lives inside another.[415] Many biologists believe the complex cells characteristic of eukaryotes first arose when non-nucleated bacteria engulfed other bacteria to create compound organisms that thenceforward existed as single, symbiotically cooperative organisms. This fusion of bacteria is known as *symbiogenesis* or *endosymbiosis*. Indeed, Margulis and Schwartz (1998: 111) go so far as to say that "All protoctists [i.e., simple eukaryotes] evolved from symbioses between at least two different kinds of bacteria — in some cases, between many more than two."

Recombinational Stabilization. In another type of stabilization process, *recombinational stabilization,* a variable hybrid population produces a new stable form without the addition of chromosome sets. As we have seen, many natural hybrid populations are composed of partially fertile individuals. In such sexual populations, due to the production of a broad spectrum of later-generation hybrids, genetic variation is quite high. Because such populations contain variable individuals capable of producing offspring, they are subject to natural selection just as are populations unaffected by hybridization. The only difference is that hybrid populations are far more variable. So most of the natural selection processes described in conventional population genetics also apply to hybrid populations, even though such processes are typically thought of as occurring in pure, reproductively isolated populations. Indeed, they are more applicable; for the rate of genetic change resulting from selection is proportional to the genetic variance of the population (Fundamental Theorem of Population Genetics). Hybrid populations almost always have higher genetic variances than pure parental populations, usually far higher. So the potential rate of evolutionary change in hybrid populations is extremely high. In particular, fertility is variable in hybrid populations.

In general, as has already been stated in Chapter Two, sexually produced progeny of F_1 hybrids are usually highly variable, whether they are produced by matings among the F_1 hybrids themselves or from backcrosses to the parents. The same is true of the progeny of hybrids in subsequent generations. But breeders often report that hybrid stocks maintained for many generations become less variable over time. For example, Brilmayer (1960: 188) notes that the ricinifolia begonia (*Begonia ricinifolia*) which is derived from a hybrid cross (*B. heracleifolia* × *B. peponifolia*), yields fairly uniform progeny when self-fertilized because its "characteristics have become established over a long period of time."

Selection among the highly variable progeny descended from a hybrid cross allows breeders to combine traits previously found only separately in the two parents from which the hybrids were derived. As Rockwell et al. (1961) point out,

> Hybridization, the breeding of new lilies, then, is not an idle pastime of the curious gardener or of the grower who wants to cross two lilies and raise the seed to the flowering stage just to see what will happen. It is a deliberate attempt to raise hardier lilies, more able to endure adverse conditions, more adapted to the garden; flowers which should retain many of the virtues of both parents, but lack most of the bad qualities. The ideal solution, that of combining *all* of the good qualities and eliminating all the faults, shall probably never be attained. In many of the new lilies, however, so much improvement has been made that the value of hybrid lily strains, as compared to the true species, has been proved to the satisfaction of all experts and gardeners.[416]

Recall that breeders use the word *strain* to distinguish hybrid derivatives that are sufficiently fertile to maintain themselves by sexual reproduction. Obviously, within such strains, individuals that are more fertile will tend to produce more progeny. Therefore, within such strains fertility will tend to improve over time since it is itself a heritable trait. The fact that fertility tends to improve under the influence of artificial selection without the production of polyploids in later-generation hybrids has long been known. This phenomenon has been repeatedly reported by a variety of authors.[417] Even Darwin (1868: vol. II, 110) mentions what may have been a case

> given by M. Groenland,[418] namely, that plants, known from their intermediate character and sterility to be hybrids between *Ægilops* and wheat, have perpetuated themselves under culture since 1857, *with a rapid but varying increase of fertility in each generation*. In the fourth generation the plants, still retaining their intermediate character, had become as fertile as common cultivated wheat. [italics are Darwin's]

Five pages later, he states, in connection with "the influence of free intercrossing" of plants and animals under domestication, that "if additional vigour and fertility be thus gained, the crossed offspring will multiply and prevail."[419]

In *Variation* (1868: vol. II, 109) he says the idea that selective breeding under domestication eliminates sterility in domestic breeds derived from hybridization "was first propounded by Pallas," the eighteenth century naturalist. In the *Origin* Darwin expressed his belief that not only plant hybrids could recover their fertility under domestication, but also those of animals:

> The various races of each kind of domesticated animal are quite fertile when crossed together; yet in many cases they are descended from two or more wild species. From this fact we must conclude either that the aboriginal parent-species produced at first perfectly fertile hybrids, or that the hybrids subsequently reared under domestication became quite fertile. This latter alternative, which was first propounded by Pallas,[420] seems the most probable, and can, indeed, hardly be doubted. … According to this view of the origin of many domestic animals,

> we must either give up the belief of the almost universal sterility of distinct species of animals when crossed; or we must look at sterility, not as an indelible characteristic, but as one capable of being removed by domestication.[421]

Elsewhere he comments in a similar vein:

> But as with our domesticated animals, a cross-breed can certainly be fixed and made uniform by careful selection in the course of a few generations, we may infer that the free intercrossing of a heterogeneous mixture [i.e., a hybrid population] during a long descent would supply the place of selection, and overcome any tendency to reversion;[a] so that the crossed race would ultimately become homogeneous, though it might not partake in an equal degree of the characters of the two parent races.[422]

Natural selection would be expected to act in a similar manner within the context of natural hybrid populations to favor the emergence of fit, fertile strains as new, reproductively stable somatypes. And various natural somatypes are in fact known to have had such an origin. Studies with plants (Gallez and Gottlieb 1982; Grant 1966a, 1966b; Rieseberg 1991; Rieseberg et al. 1990; Stebbins 1957; 1958: 183) have shown that such fertile derivatives can even be reproductively isolated when backcrossed to the parental types from which they are derived (backcross hybrids of low fertility are produced), a finding that has led some to refer to these derivatives as a "species."

Such ideas are anything but new. Long ago Lotsy (1916) pointed out that the complex variation resulting from wide crosses could potentially provide an extraordinarily rich genetic variability on which selection might act. Although it has not been widely accepted among evolutionists, the production of new forms by this method is commonplace among breeders. It should be said, though, that the notion has had a few major proponents over the years, even among evolutionists themselves. For example, in considering possible sources for the high degree of genetic variability required for rapid evolutionary change, Stebbins (1959: 248) asserted that:

> because of the slow rates at which it occurs, mutation can never provide by itself enough variability at any one time to fulfill such conditions. Genetic recombination must therefore, be the major source of such variability so that the evolutionary lines most likely to take advantage of a changing environment are those in which recombination is raised to a maximum. This is accomplished most effectively by mass hybridization between populations having different adaptive norms.

Similarly, Lewontin and Birch (1966) asserted that "the introduction of genes from another species can serve as the raw material for an adaptive evolutionary advance."

Nevertheless, this notion has never gained wide acceptance among biologists. In

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[a] Reversion is an ancient notion. Thus, Aristotle (*Generation of Animals,* Bk. I, Ch. 18) states that "resemblances recur at an interval of many generations."

the writer's opinion, biologists have not rejected the idea because they are unaware that many hybrids can produce offspring or that hybrid populations are typically more variable than populations unaffected by hybridization. On the contrary, most seem to be conscious of these facts. Rather it seems they have failed to embrace Stebbin's view because it conflicts with a core tenet of neo-Darwinism: the consensus belief that forms treated as species typically arise as gradual change occurs in groups of interbreeding individuals reproductively isolated from other such groups. Recall that neo-Darwinian theory says evolutionary change occurs through selection of traits existing *within* each isolated population. To accept Stebbin's suggestion would be to reject neo-Darwinism's conception of evolution at a fundamental level *because he is asserting evolution is more likely to occur rapidly in hybrid populations than in isolated ones*. Therefore, when a biologist who accepts neo-Darwinian theory hears hybrids of a certain type produce offspring in a natural setting, she must assume those offspring lack potential. Not to do so would be to begin to think in a whole different way. Perceiving the world through neo-Darwinian glasses, she does not think in terms of how natural selection might affect the hybrid population over time. Instead, merely by assuming reproductive isolation of the parental populations is as yet imperfect, she dismisses the fact that hybridization is producing fertile individuals. She knows quite well that orthodox theory says evolution occurs within parental populations, not hybrid populations. So even though it is known that a broad array of hybrids are partially fertile and that a huge number of such populations occur in a natural setting, she pays little attention to these facts and goes on thinking as before. Neo-Darwinists assume any fertility seen in hybrids is residual and that it is in the process of elimination because, in their view, the parents have not yet become perfectly isolated. And, of course, there are many uninformed people who hold the stereotypic view of a hybrid as something absolutely sterile and not occurring in a natural setting. These, too, will easily dismiss Stebbin's assertion.

Nevertheless, it is now well known that a new form can emerge, without the addition of chromosome sets (i.e., without the production of polyploids), as a stable population of interbreeding individuals within the context of a variable, interbreeding hybrid population. These new derivatives are selected artificially by the breeder for fitness and fertility; in the wild they are naturally selected. In a formal biological setting the process producing such stable derivatives goes under a variety of names: "recombinational speciation,"[423] "allohomoploid nothospeciation,"[424] or "stabilization of segregates."[425] Here we will call such products *recombinant derivatives,* because they recombine portions of the genetic material found separately in their parents. The process that produces such derivatives is recombinational stabilization. Breeders seem to lump all types of fertile hybrid derivatives indiscriminately under the name *strain,* so they would use that name for a recombinant derivative. However, breeders, who are more interested in the fact of fertility, are often less exact in their choice of terms, than biologists who are interested in the underlying genetic mechanisms that produce the fertility. In particular, any fertile polyploid line would almost certainly also be called a strain. Breeders have produced innumerable recombinant derivatives (for practical purposes these recombinant strains can be distinguished from polyploid strains by the fact that their stabilization requires multiple generations, whereas polyploids stabilize almost immediately). Many natural recombinant derivatives have been treated as species. Indeed, among mammals and birds where cases of polyploidy and parthenogenesis induced by hybridization are virtually unknown, nearly all stabilized populations of hybrid origin must be of this type.

In general, any natural population will here be assumed to be a recombinant derivative when it (1) reproduces sexually; (2) is known to be of hybrid origin; and (3) is clearly not a polyploid. In subsequent discussion, two kinds of recombinant derivatives will be recognized: (1) those produced when distinct somasets of a single chromoset hybridize; and (2) those produced when distinct chromosets hybridize. In the case of such derivatives of intrachromoset matings, two somatypes cross to produce a variable population of hybrids. Under such circumstances, the hybrids are usually fully fertile even in the initial hybrid generations (since they are not structural heterozygotes). Once the hybrid population has been produced, individuals with certain genes can be artificially or naturally selected to stabilize a new somaset. In a natural setting, a degree of genetic isolation from the parental forms would be required for this process to lead to a new, uniform stable population. This partial isolation could be provided by any of the "prezygotic" mechanisms specified by standard evolutionary models — isolation by distance, behavior, ecological preferences, etc. Otherwise interbreeding with the parents would continue to influence the derivative hybrid population. For example, one could suppose two types of birds came into contact only on a particular island and formed a hybrid population there. Under such circumstances interbreeding might proceed to such an extent that eventually all individuals on the island would be hybrid. Natural selection could then proceed in the same way described in neo-Darwinism's account of evolution in a variable population. Even Darwin seems to have recognized that a degree of isolation assists the stabilization of new hybrid populations. In a letter to Fritz Muller dated January 1st, 1874, Darwin refers to "the fact of hybrids becoming more fertile when grown in number in nursery gardens." The footnote Darwin attached to this comment explains that "When many hybrids are grown together the pollination by near relatives is minimised."

Potentially any factor that prevented, or at least sufficiently reduced, matings between the hybrid and parental population would serve the same purpose. Meise (1936a) notes that in central and eastern Algeria there are huge, extremely variable populations derived from hybridization between the House and Spanish sparrows (*Passer domesticus* and *P. hispaniolensis*). However, he points out that in several isolated oases in southern Algeria and southwestern Tunisia only a stabilized derivative, *flückigeri,* of this hybridization is found. The isolation would not have to be of a geographic nature, such as in the example just given. It could also be based on behavioral tendencies or on habitat preferences — any factor that prevented ongoing backcrossing.[a] Potentially, it could even result from the unlimited expansion of a hybrid zone until the pure parental individuals were entirely eliminated by interbreeding with hybrids — which would be the most extreme form of isolation conceivable. In such a case the remaining variable hybrid population could then undergo stabilization through selection. In the absence of such isolating factors, the hybrid population would continue to mate extensively with its parents and would continue to vary clinally, as in the typical hybrid zone, instead of becoming a uniform population.[b]

A special case involves recombinant derivatives of interchromoset hybridization without the production of polyploids.[c] Derivatives of this process have chromosome numbers having no simple relationship to the chromosome numbers of their parents, as is the case with polyploids. For example, Winge (1940) crossed two mustards, *confertifolia* and *violacea-petiolata*, usually treated as conspecific types under *Erophila verna* (spring draba). These types exhibit a large difference in chromosome number. The former has 15 chromosomes, while the latter has 32. Meiosis was disrupted in the F_1 hybrids because many chromosomes were unpaired. As a result seed fertility was severely reduced (only about 3% of normal). The F_2 generation was variable in morphology, fertility, and chromosome number. However, by the F_9 generation, in some cases sooner, Winge was able to extract, reproductively stable, fertile, morphologically uniform recombinant derivatives each with one of six distinct chromosome numbers ($n = 22, 23, 25, 29, 31, 34$). Although, Winge did not carry out the experiments, if any of these derivatives were backcrossed to either parent, hybrids of reduced fertility would almost surely have resulted (due to reduced chromosome pairing).

Many biologists consider the stabilization of recombinant derivatives from interchromoset matings, to be of especial interest, because under such circumstances new forms can emerge that have all the characteristics usually expected of "species" — the emergent populations can have a new karyotype and be morphologically distinct, uniform, and be reproductively isolated. Referring to such derivatives, Stebbins (1958: 183) pointed out long ago that "the establishment [i.e., the production] of fertile, true-breeding lines from the progeny of partly sterile interspecific hybrids without change in the chromosome number [i.e., without the

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[a] Again, any of the "pre-zygotic" isolating mechanisms posited by neo-Darwinian theory would serve the purpose.

[b] Under such circumstances the range of somatic variation within a single chromoset would be limited by the range of genic variation found among its individual members. To go beyond the range of genetic variation defined by the karyotype, hybridization with some other chromoset would be required.

[c] Stable derivatives of this type are often called *homoploid derivatives*. Grant (1981) called the process producing such derivatives "recombinational speciation." But following the conclusions reached in Chapter One, we will avoid use of any terms that based on the word *species*. Stebbins (e.g., 1959) referred to the process that produced such stabilized derivatives as "stabilization of segregates."

production of polyploids] has been accomplished in several genera of plants, and there is every reason to believe that it has occurred repeatedly as a natural phenomenon in plant evolution."[426] Naturally occurring chromosets have since been genetically verified as recombinant derivatives of hybridization between other chromosets or even artificially re-created by crossing their parental chromotypes.[427] Artificial recombinant derivatives produced in this way (perhaps not corresponding to any naturally occurring form) have also been extracted from interchromoset hybrids both by evolutionary biologists in a formal setting[428] and by a wide variety of breeders. Moreover, computer simulations of natural hybridization between chromosets corroborate this inference and confirm the feasibility of stabilizing recombinant derivatives of interchromoset matings under natural conditions[429]

When a recombinant derivative is produced from interchromoset matings, chromosomal mutations occur. The first chromosomal mutation that occurs during such a process is the combination of parental chromosomes in F_1 hybrids. Because the parents are distinct chromotypes, their F_1 hybrids are structural heterozygotes. As a result, meiosis in F_1 individuals is disrupted and additional chromosomal mutations occur. Chromosomes are broken up and reconnected in new configurations as well as reassorted into new sets composed of chromosomes and genes previously present only in separate organisms. Such is the effect of structural heterozygosity on meiosis.[430] Similar mutational events occur during meiosis in later-generation hybrids descended from such matings. Repeated crossing-over, breakage, repair, and reassortment (more chromosomal mutations) create restructured chromosomes and a reassorted karyotype in which genes from both parents are mingled (for example, see the analysis of *Helianthus paradoxus* carried out by Rieseberg et al. 1996). The newly combined genes in this new karyotype interact to specify the development of a new type of organism with a new combination of traits. The emergent chromoset can differ from its parental chromosets with respect to the structure of a single chromosome, or with respect to many. Recombinant derivatives produced from interchromoset matings do not require the assistance of prezygotic isolation factors to get established.[431]

The Red Wolf (*Canus rufus*) of eastern North America is a recombinant derivative derived from hybridization between the Coyote (*C. latrans*) and Grey Wolf (*C. lupus*).[432] The cyprinid fish *Gila seminuda* (Virgin Chub) also had such an origin. It is derived from the cross *G. elegans* × *G. robusta* (Bonytail × Roundtail Chub).[433] *Pinus densata,* a pine native to the Tibetan Plateau, is also a recombinant derivative, derived from hybridization between two other Asian pines: *P. tabuliformis* and *P. yunnanensis*.[434] Another example is the perennial herb *Penstemon clevelandii* (Cleveland Penstemon), which occurs in southern California. It comes from hybridization between *P. centranthifolius* (Scarlet Bugler) and *P. spectabilis* (Showy Penstemon).[435] The parents in this case differ markedly in their floral characters. *P. centranthifolius* has red trumpet-shaped flowers and *P. spectabilis* has broad tubular, bluish flowers).

Werth and Wagner (1990: 701) discuss Haberer's Groundpine, *Lycopodium habereri,* which is a recombinant derivative of the cross *L. digitatum* × *L. tristachyum* (Fan Clubmoss × Deeproot Clubmoss).[436] This plant has spread over much of eastern North America. Wagner (1992) mentions two other clubmoss recombinant derivatives: (1) *Lycopodium zeilleri* (Zeiller's Groundpine), from the cross *L. tristachyum* × *L. complanatum* (Groundcedar); and (2) *Lycopodium sabinifolium* (Savinleaf Groundpine), from the cross *L. tristachyum* × *L. sitchense* (Sitka Clubmoss).

Two more examples are *Argyranthemum lemsii* and *A. sundingii.* These two shrubs have been described from the Anaga Peninsula, Tenerife, Canary Islands.[437] Both are derived from hybridization between the same pair of parents, the coastal *A. frutescens* and the montane *A. broussonetii.* The parents differ markedly in morphology.[438] This case is of interest because these two distinct stable recombinant derivatives treated as two separate species arose in separate valleys from the same parental combination (one parent being the pollen donor in the case of one derivative, but the other parent being the donor in the case of the other).

An example of a currently emerging animal recombinant derivative appears to be the hybrid population produced in New Zealand by interbreeding of the Mallard (*Anas platyrhynchos*) and the Pacific Black Duck (*A. superciliosa*). These hybrids are quite fertile[439] and are increasing at the expense of their parents, which both seem headed for extinction in New Zealand.[440] Hybrids are now more common there than is either pure parent. Gillespie (1985: 466) says that in the Otago region the proportion of pure black ducks "has declined from 100% prior to the introduction of the Mallard in 1867 to less than 5% in 1981."[441] He also says the proportion of pure Mallards has been rapidly decreasing "in response to increasing hybrid levels." The hybrids are now in the majority in New Zealand and it seems likely they will soon swamp both their parents out of existence there and stabilize as a new type. Indeed, on the basis of specimens taken in the Marianas Islands, where hybridization of this kind also occurs, hybrids of this type have already been treated as a species, Oustalet's Duck (*Anas ousteleti*).[442]

Such situations, where hybridization occurs in a geographically isolated region, probably assist the stabilization of new hybrid forms.[a] Once the variable hybrid population fills the island environment to the exclusion of both parental types, selection within the population leads to the emergence of a new type just as in the models of genetically variable, reproductively isolated populations described in orthodox theory. There is little ongoing hybridization with the parents to maintain variation within the hybrid population. Isolation of such incipient forms can be ecological rather than geographic. Thus, Stebbins (1969: 30) says that "if the opening up of new habitats provides strong selective pressures in new directions, and if this condition is reinforced by any of a number of possible isolating mechanisms, the progeny of hybrids can respond to these new conditions by evolving in new

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[a] Following Stebbins (e.g., 1959), Gross and Rieseberg (2005) argued isolation, and the resultant protection of a new derivative, can result from ecological factors. See Appendix F.

directions more easily than can their parents."[a]

Note however, that although recombinational stabilization occurs within the context of a hybrid zone, there is no reason to suppose that it must convert the entire hybrid zone into a new stable form. In general, a new form can emerge within the context of a hybrid zone even while the zone itself continues to exist (for example, polyploids often emerge within hybrid zones that continue to exist on an ongoing basis). Thus, recombinational derivatives can emerge as a cluster of individuals in one part of a hybrid zone and yet leave the remainder of zone unaffected (McCarthy et al. 1995).

On the other hand, many clinally varying wide hybrid zones have been treated as species or races. McCarthy (2006) lists many avian taxa of this kind. Grant (1981: 270) gives an example of a plant population of this type, the phlox *Gilia achilleifolia* (California gilia)*,* which he says

> is believed to be of hybrid origin between some ancient members of the diploid *G. capitata* [bluehead gilia] and *G. angelensis* [chaparral gilia] groups … *Gilia achilleifolia* is intermediate morphologically between the putative parental species in every plant part. It is also extraordinarily variable in its morphological characters. This variability is expressed in the form of local racial differentiation. Some races of *G. achilleifolia* approach *G. capitata* in morphology, while other races approach *G. angelensis.* Indeed, the former races have been confused taxonomically with *G. capitata* and the latter with *G. angelensis.*

Though such populations have often been assigned scientific names, they do not have certain of the characteristics many biologists expect of a "species." For example, they are not morphologically uniform, and their members typically interbreed extensively with members of the parental populations. They may also lack stable karyotypic differences distinguishing them from other related groups. However, they do have some of the expected characteristics, so they are likely to be treated as distinct taxonomic entities: They are morphologically distinct from other types, have a separate geographic range (between the ranges of the parents), and such populations are stable in the sense that they continue to exist for long periods of time (i.e., they are temporally stable, although they are morphologically variable). Variable hybrid populations are temporally stable because the parental populations that interbreed to produce them are temporally stable. The stabilization process producing them is simply: (1) the initial contact of the parental populations; (2) subsequent interbreeding to produce a population of hybrids. Depending on the population in question, different degrees of stability and uniformity are reported. Presumably some of these populations, which are isolated by distance from their parents, have undergone selection. How often such populations will be treated as

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[a] Stebbins attributes this idea to Wiegand (1935). See also: Anderson and Stebbins (1954), who proposed novel traits in hybrids would facilitate the invasion of habitats not exploitable by either parent, and that such novel capabilities probably facilitate the formation of new stabilized hybrid forms. More recent authors have expressed similar notions (e.g. Gross and Rieseberg 2005). See Appendix F.

species depends on how stable, extensive, and distinctive they may be. It also depends, to a certain extent on the type of organism involved. For example, a botanist would probably be more likely to treat a known hybrid population as a species than would a zoologist.

New types of organisms produced by the stabilization of hybrid populations are known from both captivity and the wild. For example, Restall (1997: 83) notes that although hybrids between the Bengalese (*Lonchura domestica*) and the Black Munia (*L. stygia*), two estrildine finches, were initially variable and of low fertility, they have been stabilized as various types that now breed true. Some of these recombinant derivatives have been officially accepted as new breeds of Bengalese.[a] The South American butterfly *Heliconius heurippa* is a stable recombinant derivative of hybridization between *H. melpomene* and *H. cydno*.[443] Mavárez et al. (2006: 870) say that two other butterflies, *H. pachinus* and *H. timareta* may also be derivatives of this cross. Gompert et al. found that the alpine butterflies in the Sierra Nevada of western North America (genus *Lycaeides*) were also hybrid recombinant derivatives. Pinoche Creek larkspur (*Delphinium gypsophilum*), which occurs in the valleys and foothills of California, is another recombinant derivative, from hybridization between foothill larkspur (*D. hesperium*) and Byron larkspur (*D. recurvatum*).[444,b]

Recombinant derivatives produced from interchromoset hybridization have all the qualities usually expected of "species" because they represent chromotypes that are distinct from either of the parental chromotypes. Hybrids between the recombinant derivative chromotype and either of the two parental chromotypes are of reduced fertility because they are structurally heterozygous (see p. 68). Stebbins (1957) produced a stable recombinant derivative from interchromoset matings involving a strong sterility barrier. The cross was between *Elymus glaucus* (blue wildrye) and *Elymus multisetus* (big squirreltail).[445] F_1 hybrids between these grasses are highly sterile (less than 1% good pollen and only about 1 seed per 1,000 florets). The plants were backcrossed to *E. glaucus* and 173,000 florets from the resulting backcross hybrids produced 15 seeds, which yielded 11 mature plants. One of these eleven was partially fertile and had characteristics of both *glaucus* and *multisetus*. It was self-fertilized and yielded among its progeny vigorous, fully fertile individuals that yielded hybrids of low fertility when crossed with either of the original parents.

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[a] Indeed, although its true origin is unknown, it is widely believed the Bengalese itself is a fertile hybrid produced centuries ago by the Chinese (McCarthy 2006).

[b] Permanent translocation heterozygotes constitute a probable additional general category of recombinant derivatives. In groups containing such forms as well as forms with ordinary, fully paired karyotypes, it is thought that the heterozygote forms arise from the ordinary ones via hybridization (Grant 1981: 389, 392). The production of new reciprocal translocations has been shown to occur within the context of interchromoset hybrid zones (Hauber and Bloom 1983). For example, permanent translocation heterozygotes among the evening primroses (*Oenothera*) probably initially arose this way (Cleland 1964, 1972). Presumably, the translocations are initially produced during meiosis in structural heterozygotes resulting from interchromoset matings, but this point is not very well established.

In such cases a tremendous amount of human labor is required to extract a stable derivative. But the natural process requires no human effort. In a natural setting such plants are produced on a regular basis, year after year, generation after generation, wherever appropriate parental forms come into contact and produce hybrids.

Grant (1966a, 1966b, 1966c) also obtained such a derivative. The original cross was between the phloxes *Gilia malior* (scrub gilia) and *G. modocensis* (modoc gilia), which produce F_1 hybrids with less than 2% pollen fertility due to structural differences between the parental karyotypes. Grant extracted stable, fertile recombinant derivatives from later-generation hybrids by selecting for fertility and vigor. The entire extraction process took about ten generations. All chromosomes were paired in the extracted forms, but some were derived from one of the original parents, and some from the other. As a result, hybrids from backcrosses of the derivative to either parent had karyotypes with some unpaired chromosomes. Therefore they were structurally heterozygous and quite infertile (see p. 68). For example, when one of the derivatives was backcrossed with *G. malior,* the resulting hybrids had 4 to 18 percent viable pollen and seed fertility of less than 1%. So the extracted form was reproductively isolated, to some degree, from both of its parents. This is why recombinant derivatives of interchromoset hybridization are more like what is usually thought of as a "species" than are derivatives of intrachromoset hybridization, where the derivative and the parents are usually completely interfertile.

Conclusion. This chapter has listed several different types of well-documented stabilization processes:

(1) *Production of a Polyploid.* In this process, an offspring form is produced that has more chromosome sets than its parental form(s). For example, a hybrid derived from two forms has all the chromosomes of both its parent forms so that it has two full sets of chromosomes one derived from each of its parents. Another example would be an offspring form that had three full sets of chromosomes, whereas its parent form had only two.

(2) *Production of an Aneuploid.* One or more chromosomes are added to or deleted from the chromosome set of the parental form.

(3) *Production of a Recombinant Derivative (Recombinational Stabilization).* In this process, which depends on hybridization, the chromosome set of the offspring form is composed of chromosomes derived from two different parents. The chromosomes may be inherited intact, or some or all of them may be rearranged. Some or all may also be of mixed origin (composed of blocks derived from both parents).

(4) *Production of a Permanent Translocation Heterozygote.* In this process, a new permanent translocation heterozygote is produced by hybridization between two pre-

existing permanent translocation heterozygotes. For a definition of permanent translocation heterozygote, click here.

(5) *Production of an Agamosperm.* The production of a form capable of reproduction in which the embryo develops without fertilization. Such organisms are usually the products of hybridization between two or more pre-existing forms.

(6) *Production of a Vegetative Form.* Production of a form capable of reproduction via budding or segmentation.

(7) *Production of a Contingently Stable Form.* Production on an ongoing basis of individuals that are incapable of reproduction themselves, but that continue to occur so long as their parental forms continue to exist. Such forms are often treated as species.

(8) *Production of a Symbiotic Association.* Two or more forms join together to exist as a single entity that ends up being treated as a taxonomic category.

These various types of stabilization processes are all well-known, well-understood ways of producing new types of organisms. This chapter also pointed out that many such forms have been, or are currently being, treated as species. Most, but not all, of these processes depend upon hybridization. It was also explained how such processes, through their repeated occurrence can generate entire complexes of related forms (e.g., agamic complexes, polyploid complexes). Concrete examples were given of each of these various types of stabilization processes. So stabilization processes are observed facts, not theoretical mechanisms. They provide proof of evolutionary change.

5 Stabilization Processes: Prevalence

If it be asked, what is the improper expectation which it is dangerous to indulge, experience will quickly answer, that it is such expectation as is dictated not by reason, but by desire; expectation raised, not by common occurrences of life, but by the wants of the expectant; an expectation that requires the common course of things to be changed, and the general rules of action to be broken. —JAMES BOSWELL, *Life of Johnson*

Neo-Darwinian theory and stabilization theory posit distinct explanatory mechanisms for the phenomenon of evolution as observed in the fossil record. In this chapter and the two that follow, we will attempt to assess how much of evolution is accounted for by each of these two theories.

According to neo-Darwinian theory, (1) reproductive isolation is an essential factor in the process that gives rise to differentiated populations; and (2) genetically distinct populations typically can arise only when a previously existing population is broken up into two or more reproductively isolated sub-populations.[446] This idea is frequently encountered in evolutionary discussion. For example, in a recent article in *Scientific American,* Wong (2001) avers that

> in order for one species to diverge into two, a population must be divided into two groups that cannot interbreed. Usually this reproductive isolation stems from genetic incompatibility, which can arise when a geographical barrier separates the groups, allowing them to drift apart genetically.

A mountain range rises up, continents drift apart, a river changes course — an endless variety of factors have been proposed as contributing to such break ups. But whether it be geographical, temporal, behavioral, or ecological, some isolation mechanism is generally posited that supposedly allows two populations, descended from a common ancestral population, to build up a distinctive set of traits by gradually accumulating favorable mutations over time. The theoretical outcome of this process is two new populations *intrinsically* isolated from each other. The isolation is based not upon external factors that prevent mating, but upon physiological incompatibilities preventing fertilization, or resulting in inviability or sterility of hybrids produced by the cross. Various authors have put forward mechanisms to explain how intrinsic isolation arises, but all these explanations are flawed (see p. 191 *et seq*.). It is well to remember, however, that it is a *theoretical* notion that populations have to be intrinsically isolated if they are to become and remain genetically distinct. In this book, we have already encountered evidence demonstrating that many populations treated as species are not intrinsically isolated in any strict sense. A wide variety of crosses between such populations are known to produce fertile, or at least partially fertile, hybrids in the wild (see Chapter 2). As we have repeatedly seen, many natural populations treated as species or subspecies are known to be of hybrid origin.

Prevalence of Polyploidy. In connection with stabilization theory, it's important to realize that polyploid organisms are extremely common. An initial point to consider in assessing the prevalence of polyploidy is that biologists tend to assume any organism of unknown status is diploid. For example, Wu et al. (2001) comment that "in recent years, comparative mapping studies using molecular markers have revealed that several crop species traditionally considered diploids, such as maize and various members of the genus *Brassica,* are actually polyploids." Here "traditionally considered" means "considered in the absence of evidence to the contrary." This particular assumption therefore has the odd effect of leading one to suppose that most organisms are diploid (since the ploidy level of most organisms has not been investigated). In fact, however, it is unknown whether the typical organism is diploid.

Despite this traditional default assumption, it is now well established that the production of new forms through polyploidy is extremely common in plants.[447] Masterson (1994) estimated that the rate of polyploidy among plants is between 30 and 80 percent. More than half a century ago, Stebbins (1950: 299) said it was already known that important crop plants such as wheat, oats, cotton, tobacco, potato, banana, coffee, and sugar cane were polyploids and that the actual parentage of wheat (*Triticum aestivum*), cotton (*Gossypium hirsutum*), and tobacco (*Nicotiana tabacum*) had already been determined.[448] More recently, Hilu (1993) estimated that about 75 percent of domesticated plants are polyploid.

One of the most surprising findings of recent genetic research is the ubiquity of polyploidy — even in taxonomic categories where no one expected to find it. Over the last decade certain organisms have been singled out for intense genetic analysis with modern automated techniques. Detailed examination of an array of these so-called "model organisms" has shown that most are in fact polyploid.[449] For example, rice (*Oryza sativa*) was recently demonstrated to be an ancient polyploid.[450,a] The

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a. Ancient polyploids are often difficult to recognize, but new technology has made their identification easier in recent years. In general the approach used to identify natural polyploids has been to measure the amount of DNA and number of chromosomes present in the genome of each of the various types of organisms of a related group of taxa in order to see whether same is probably true for yeast (*Saccharomyces cerevisiae*).[451] Indeed, Soltis (2005: 5) reports it now appears *all* angiosperms (flowering plants) are either polyploid or descended from polyploids. This means the vast majority of extant plants are polyploid — some 240,000 angiosperms are treated as species (among gymnosperms, the second largest plant category, only about 720 are so treated[452]). Even more surprising is the finding that all vertebrates are probably also ancient polyploids (see citations listed in Note 453).[a] In other words, a doubling of chromosome number appears to have occurred during the evolution of the vertebrates at an early stage prior to their diversification. These findings represent quite a change in perspective. Writing only a generation ago, Schultz (1980: 314) remarked that a majority of biologists were still unaware that polyploid vertebrates even existed. Ancient polyploids are often difficult to recognize because chromosomes fuse or break over time, hampering analyses based on chromosome counts. Also, mutations subsequent to the original event initially producing a polyploid may obscure an organism's true status. As a result, with the passing generations the chromosomes of a polyploid start to look more like those of a diploid as such changes accumulate, making chromosomes that were originally duplicates become more distinct from each other.[454,b] Hence, even many types of organisms that now appear to be diploid must have been polyploid in origin.

The idea that polyploidy is rare among animals was once widely accepted. The arguments most often offered to support this claim were (1) that the extensive gene duplication seen in polyploids would dilute the effects of new mutations and so make significant adaptive changes unlikely;[455] and (2) that animals are somehow too "complex" to tolerate the dramatic genetic changes associated with polyploidy.[456] Neither idea is accepted today. The former has been dismissed because gene duplication is now seen as actually opening an opportunity for genic evolution since one gene copy can go on performing its accustomed function while other copies are freed to mutate and adapt to new functions.[457] The latter objection, as Orr (1990) points out, has been invalidated by the fact that many animals are now actually *known* to be polyploid. Gregory and Mable (2005: 478), who recently surveyed known animal polyploids, note that polyploidy is

> relatively common among the vertebrates and … also occurs widely among invertebrates. In

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polyploidization events have likely occurred. In some cases this approach is straightforward. For example, when one type of organism exhibits (1) a chromosome count equal to the sum of the counts of two other related forms and (2) the amount of DNA in its genome is equal to the sum of the amounts present in the genomes of the other two, then that organism is very probably an allopolyploid derived from hybridization between the other two. The more refined techniques of recent studies count the number of gene homologs present in the putztive polyploid.

[a] Thus, Spring (1997) found three paralogs exist, on average, in the human genome for each of 52 *Drosophila* genes and proposed that the extra human genes were produced by two allopolyploidization events early in vertebrate evolution.

[b] This process is called *diploidization.*

> fact, examples of naturally occurring polyploidy can be found in nearly all of the major invertebrate phyla, and cases may yet be discovered in the remaining taxa (e.g., Cnidaria, Echinodermata) if interest could be stimulated in such a survey.

Among vertebrates, polyploidy is especially extensive among fishes, but there are numerous known examples, too, among amphibians and reptiles.[458] In particular, it now appears that a doubling in chromosome number preceded the diversification of teleost fishes (superorder Teleostei), which means it is likely this entire group is polyploid.[459] The vast majority of all fishes are teleosts. In fact, Teleostei is by far the most diverse vertebrate group, containing roughly half of all vertebrate taxa treated as species. The vast majority of all extant fishes are teleosts. We can therefore no longer speak of "the scarcity of polyploidy in the animal kingdom as a whole," as Stebbins (1950: 368) once did. Certain large families within Teleostei (e.g., Salmonidae,[460] Catostomidae[461]) are now known without doubt to be polyploid.[462] Others (e.g., Cyprinidae[463]) are known to contain many polyploid forms of recent origin. Even among the non-teleosts (a distinct minority of fishes fall into this category), many polyploids are known.[464] Gregory and Mable (2005: 477) say an ancient doubling of chromosome number in

> the vertebrate lineage has been followed by many more recent polyploidization events (including in the teleosts at large). Although recent polyploidy is rare among mammals and birds,[465] this is clearly not true of groups like fishes and amphibians.[466] In reptiles, too, there are numerous known instances.[a] … As in plants, there are signs of repeated polyploid formation in certain lineages, and there may in fact be complex networks of hybridization among some related species.[b]

Elsewhere Mable (2004: 453) notes,

> Although polyploidy has been involved in speciation in both animals and plants, the general perception is often that it is too rare to have been a significant factor in animal evolution and its role in plant diversification has been questioned. These views have resulted in a bias towards explanations for what deters polyploidy, rather than the somewhat more interesting question of the mechanisms by which polyploidy arises and becomes established in both plants and animals.

Here Mable refers to the assertions of H. J. Muller (1925), whose views concerning

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[a] Among reptiles, known polyploids are, apparently without exception, unisexuals (Gregory and Mable 2005). Most are of known hybrid origin (Bickham 1984; Bogart 1980; Darevsky 1992; Olmo 1986).

[b] It has long been realized that certain types of animals produce polyploid offspring at high rates. For example, Fankhausen (1945: 20) notes that "among the larvae of salamanders the frequency of spontaneous changes in chromosome number appears to be higher than in most diploid species of plants, and the percentage of polyploid individuals produced by treatments with cold or heat is considerably greater than that obtained by similar experiments with plants."

the rarity of polyploidy in animals were long influential (Appendix E spells out the shortcomings of the arguments offered by Muller to support his mistaken idea that animal polyploids must, for genetic reasons, be rare). Also, says Mable (ibid: 453), proponents of the idea that animals are less often polyploid than are plants have focused

> largely on a limited number of taxa where it [i.e., polyploidy] is particularly rare (predominantly mammals and *Drosophila*) and which are unlikely to reflect the full diversity of animal reproductive strategies. This approach has tended to curtail studies of polyploid evolution in animals, especially in groups like mammals where the first reports of polyploid species have been made only recently.

These first reports to which Mable refers were made by Gallardo et al. (1999, 2004), who discovered that the Plains Viscacha-Rat, *Tympanoctomys barrerae,* is tetraploid. They say (2004: 443) evidence "strongly suggests a hybrid derivation" for this rat. Gallardo et al. (ibid) also say the recently described Golden Viscacha-Rat (*Pipanacoctomys aureus*) appears to be a tetraploid of hybrid origin.

Thus, polyploidy is nearly ubiquitous in plants. Among animals, it appears the typical vertebrate has a set of chromosomes that is the product of one or more ancient polyploidization events partially masked by subsequent point and chromosomal mutations. Moreover, many animal forms treated as species are known to be derived from more recent polyploidization events, as are many invertebrate forms. It would be tedious to list here all known cases of animal polyploids, but the curious reader is referred to Gregory and Mable's (2005) excellent review.

Polyploidy and Hybridization. Because of the strong association between polyploidy and hybridization (see Chapter 4), the wide prevalence of polyploidy indicates natural hybridization, too, is widely prevalent. Allopolyploidy (which, recall, is polyploidy resulting from hybridization) has long been thought to be important in plant evolution because of the large number of known natural plant amphiploids treated as species,[467] and, more recently, because it is thought to open opportunities for new gene regulation mechanisms.[468] Many natural allopolyploids have been recreated artificially by crossing their parents.[469]

Hybridization produces polyploids not only in plant crosses, as has long been realized, but also in crosses between animals.[470] For example, Kobayasi and Hashida (1977) report triploid males in the F_1 progeny produced by crossing two diploids, Goldfish (*Carassius auratus*) and Cruscian Carp (*C. carassius*).[471] Polyploidy in the *Bulinus truncatus/tropicalis* complex of African snails is the result of hybridization,[472] and in the European freshwater limpet, *Ancylus fluviatilis*.[473] Some evidence suggests that polyploids are produced more frequently when the hybridizing parents are more disparate. In his research on toad hybrids in family Bufonidae, Bogart found that

> polyploid tadpoles appear occasionally in control crosses, and in low frequencies if the parents

are considered to be included in the same species group. The frequency of polyploids increases substantially if the parents are from different species groupings and, in some crosses involving very distantly related species, only polyploids are found.[474,a]

Many supposed autopolyploids are actually derived from hybridization, but are not recognized as such due to the official taxonomic treatment of the hybridizing forms. That is, they are products of hybridization between forms that are distinct, but treated as conspecific. Suomalainen et al. (1987: 100) state that polyploid vertebrates of known origin have generally "proven either to be species hybrids or hybrids between different cytological races [i.e., different chromosets] of a single species." Among plants many cases reported as examples of natural autopolyploidy involve hybrids between populations treated as distinct races.[475] There can be large numbers of structural differences between related chromosets. There can also be only a few, or even one. All degrees of difference exist.[476] This is one reason why it is generally hard to distinguish allopolyploids derived from hybridization between chromosets with very similar karyotypes from autopolyploids derived from multiplication of a single chromosome set. Therefore, many polyploids that look like they are the result of doubling or multiplying one and the same chromosome set (autopolyploids) may actually be allopolyploids. As Grant (1981: 306) points out, even among the few accepted case of natural autopolyploidy

> at least some are interracial autoploids [i.e., they are polyploids derived from hybridization between types treated as distinct races of the same species] as, for example, *Biscutella laevigata* [Buckler Mustard] and *Solanum tuberosum* [Irish potato]. Hybridity of one sort or another is thus usually present in polyploids in plants.

Although breeders using artificial techniques do often produce autopolyploids, they seem even more often to produce allopolyploids.[477] It has long been known that natural polyploids among plants are most often produced by the latter of these two methods, that is, as hybrids.[478] Nearly fifty years ago Stebbins (1959: 237–238) stated that "the production of stable, true-breeding new species through doubling the chromosome number of a sterile interspecific hybrid, is now generally recognized as one of the commonest ways in which plant species arise." For example, Brochmann et al. (2005) found that, among 47 plant polyploids from Svalbard Island, all were of hybrid origin. Today it is realized most natural polyploids, not just among plants but polyploids of any kind, are derived from hybridization (i.e., they are *allo*polyploids).[479] Ancient polyploids are thought, like recent polyploids, to have been mostly produced by allopolyploidy rather than autopolyploidy.[480]

Not only is there good reason, then, to suppose hybridization is widespread

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[a] Another reason to suppose allopolyploidy is more common than autopolyploidy is that closely-related forms usually show an arithmetic progression in chromosome number, not a geometric one. As Winge (1917) pointed out long ago, the former is consistent with hybridization followed by chromosome doubling, whereas the latter is expected when chromosome numbers are repeatedly doubled without hybridization.

among plants, but there is also strong evidence the typical vertebrate is derived anciently and/or recently from hybridization. This conclusion seems inevitable given facts already mentioned: (1) polyploidy is usually triggered by hybridization; (2) vertebrates in general are now thought to be ancient polyploids; (3) many extant vertebrate taxa are known to have had their origins recently as polyploids (produced by hybridization); and (4) even many non-polyploid vertebrates treated as species are known to have had a hybrid origin. This conclusion is in direct opposition to the traditional view that the great majority of vertebrates are diploid and rarely of hybrid origin.

Agamospermy. Recall that agamosperms are organisms in which the embryo develops without fertilization from specialized reproductive tissues. Agamospermy is widespread in plants.[481] Among animals, it is limited to parthenogenesis (agamospermy in which embryos develop from unfertilized eggs). Animal groups in which parthenogens occur include ribbon worms,[482] rotifers,[483] tardigrades,[484] reptiles,[485] amphibians,[486] sea anemones,[487] flatworms,[488] polychaete worms,[489] starfishes,[490] and insects. Suomalainen et al. (1987: 175) say parthenogenesis is known from all major insect groups except dragonflies. White (1973: 700) notes that only about one in a thousand animal forms treated as species are actually known to be capable of parthenogenetic reproduction. However, it is not possible to infer the true number capable of parthenogenesis on the basis of the number currently known. After all, every year more different kinds of animals are found to have this capability. For example, the Yellow-spotted Goanna, the varanid lizard mentioned in the previous chapter (p. 87), has long been treated as a species but was only recently (2005) found to be capable of parthenogenetic reproduction. The tendency to assume organisms are sexual and not agamospermous until they are proved to be agamospermous is widespread (this is another of the unsubstantiated default assumptions that tend to shore up neo-Darwinian theory). But in the present context, it is less important to determine the number of existing agamosperms than to note that (1) agamosperms are organisms whose origins are easily determined and (2) their origins, when known, are consistently through hybridization.

Chapter Four gave examples of agamosperms, known to be derived from stabilization processes triggered by hybridization. Since natural polyploids most often arise through hybridization (i.e., most are *allo*polyploids), and since agamospermy is strongly associated with polyploidy (Christopher et al. 1991: 333; Gregory and Mable 2005: 442),[491] one would expect agamospermy, too, to be closely associated with hybridization and very often to result from it. Such is the case. One of the most obvious facts indicating agamosperms are often of hybrid origin is the finding that many are of low sexual fertility and produce many bad gametes (a characteristic typical of hybrids). For example, many plant agamosperms are sexually sterile, or have reduced fertility, due to disrupted meiosis.[492] There is no reason to expect low fertility to be a common characteristic of organisms capable of agamospermous reproduction if they are not commonly of hybrid origin.[a]

Another clear indication of their hybrid origin is the observation that when agamosperms do reproduce sexually, they usually produce highly variable offspring, but not when they reproduce agamospermously. This hypervariability seen in the sexual reproductive mode is exactly like that seen in later-generation hybrids and therefore suggests that the parental plants are themselves hybrids. As Grant (1981: 424) notes, "Wide segregation of this sort as observed in [the agamosperms of] *Potentilla, Rubus, Sorbus,* and *Citrus* reveals the hybrid constitution of the agamospermous mother plant. The breeding behavior of the agamospermous plant, in short, is like that of an interspecific hybrid." Variation of this type in the F_1 generation of hybrids produced by crossing the lemon (*Citrus limon*) and grapefruit (*C. paradisi*),[493] which are both agamosperms, suggests that one or both of these common citruses are themselves of hybrid origin (recall that an F_1 generation derived from hybridization between pure types normally is not variable).

The fact that agamosperms are very frequently the products of hybridization has long been recognized.[494,495] Those of known origin are typically allopolyploids. Thus, Asker and Jerling (1992: 112–113) point out that many agamosperms "are of hybrid origin and have arisen as allopolyploids from sexual parents."[b] For example, agamospermy has been shown to arise in hybrids involving the genera *Hordeum* and *Triticum*.[496] For example, Mujeeb-Kazi (1981) produced hybrids between *Hordeum vulgare* (barley) and *Triticum turgidum* (rivet wheat) and between *H. vulgare* and *T. aestivum* (common wheat). He then backcrossed each of these two types of F_1 hybrids to their respective wheat parents. Both backcrosses produced agamospermous plants, although none of the parents are agamosperms. Agamosperms are also known to have been produced by hybridization in the genera *Antennaria*,[497] *Calamagrostis*,[498] *Crepis*,[499] *Parthenium*,[500] *Potentilla*,[501] and *Rubus*.[502] Naturally occurring agamosperms in some of these genera (*Antennaria, Potentilla,* and *Rubus*) have been resynthesized by crossing their parents.[503] Nogler (1984) says a cross between two sexual grasses, *Schedonorus pratensis* × *S. phoenix* (meadow fescue × tall fescue), produces agamospermous hybrids. Nearly all the agamospermous ferns studied by Manton (1950, ch. 11) were shown to be of hybrid

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[a] Grant (1981: 424) notes that Gustafsson (1946–1947), following Darlington (1937, ch. 11) argued stabilizing selection for male fertility is relaxed in apomicts, and that consequently the absence of good pollen does not necessarily signify hybridity. But as Grant (ibid) points out in "pseudogamous apomicts like *Potentilla,* … where some good pollen is necessary for seed formation, the production of much bad pollen after irregular meiosis is surely a strong indication of hybridity." Moreover, a relaxation of the stringency of selection would not mean that the production of bad pollen would somehow become reproductively advantageous. Hence, there is no reason to expect the many different types of apomicts *characteristically* to develop this trait.

[b] Gustafsson (1946–1947) argued against the idea that hybridization causes agamospermy. His claims were influential, but were based on counterexample crosses. That is, he pointed out that most crosses do not produce agamosperms. However, the crucial point is that *most* agamosperms of *known* origin seem to be derived from hybridization.

origin. We have already encountered a specific example of agamospermy arising through hybridization: The fertile hybrid between cabbage and radish, radicole (*Raphanobrassica*), whose mode of origin has already been described (p. 94), can reproduce both sexually, vegetatively, and agamospermously. It is not only sexually fertile like its parents, but also produces seed without fertilization.[504] So the cross producing this hybrid gave rise to a new stable form capable of agamospermous reproduction, whereas its parents are capable only of sexual and vegetative reproduction. The Maiden Campeloma (*Campeloma parthenum*), which, recall (p. 99), is an allopolyploid parthenogenetic snail*,* is a population composed of multiple clones, each separately produced by separate hybridizations between its sexual parents.[505]

Christopher et al. (1991: 344–345) state that "in the Maloideae [a subfamily of the rose family Rosaceae] interspecific hybridization provides a pathway for the generation of new taxonomically recognizable entities. Even in *Pyrus,* which is mostly diploid and sexual, hybridization is 'undoubtedly involved in the evolution of the genus' (Bell and Hough 1986). Polyploidy, apomixis, and self-compatibility may arise after hybridization and help isolate hybrids from parental species." They go on to give the genus *Sorbus* as an example (Christopher et al. use *apomixis* in the narrow sense of agamospermy, as do many other authors):

> In Europe, the center of diversity of the genus, the primary species are sexual diploids (Challice and Kovanda 1978). Three of these species — *S. aria, S. aucuparia* L., and *S. torminalis* (L.) Crantz … hybridize to produce polyploid apomicts (Gustafsson 1946–1947). In the United Kingdom, in addition to these primary species there are 17 species, all of which are presumed apomicts combining [genes] of two or more of the primary species (Richards 1975).

For example, they say,[506] *Sorbus aucuparia* (European mountain ash) presumably crossed with *S. rupicola* (rock whitebeam), a tetraploid, to yield triploid *S. arranensis* (Arran whitebeam), which then crossed with *S. torminalis* (checkertree) to produce the tetraploid *S. intermedia* (Swedish Whitebeam). They also say, *S. aucuparia* and *S. rupicola,* the same pair that yielded *S. arranensis* on the Isle of Arran in Scotland, crossed to produce two other forms treated as species (*S. minima* in Wales and *S. tamamsjanae* in Armenia). These three hybrid forms, derived from the same cross, differ in morphology.[507]

Vertebrate parthenogens of known origin are apparently all of hybrid origin.[508] By chromosomal, molecular genetic, and morphological criteria, seemingly all types of parthenogenetic lizards thus far investigated have been shown to be of hybrid origin.[509] For example, five lizards of the genus *Lacerta* are known to be of hybrid origin: *L. armeniaca, L. dahli, L. rostombekovi, L. unisexualis,* and *L. uzzelli*.[510] They are all parthenogens derived from various crosses between sexual congeners.[511] In point of fact, no matter the category of organism, virtually all agamosperms of known origin, whether animal, plant, or fungal, are derived from hybridization (see citations listed in Note 512). The only exceptions that the writer has been able to identify are new forms produced by artificial techniques such as application of chemicals or heat shock. Some cases of this sort are discussed in Appendix C.[a]

The origins of so many agamosperms are known because hybridity is easier to detect in these organisms than in the case of nonpolyploid sexual organisms derived from hybridization (i.e., recombinant derivatives). This is because in agamosperms meiotic recombination generally does not occur.[513] The karyotype is therefore usually a stable combination of unaltered chromosomes anciently derived from the initial cross. This lack of alteration makes it easy to identify the parents involved in the original cross. Agamosperms, then, constitute a class of organisms that are (1) commonly treated as species; (2) often of known origin; and (3) are typically derived from hybridization. Clearly, it is not usual for agamosperms to come into being through gradual divergence under the influence of natural selection. Those few that are of known, but not hybrid, origin all seem to be the products of artificial stabilization processes such as the case of the parthenogenetic silkworm described in Appendix C.

However, the reader should not suppose the foregoing facts imply hybridization typically produces agamosperms. The only claim made is that agamosperms are typically the products of hybridization. As we have repeatedly seen, hybridization can also produce non-agamospermous forms. Indeed, various crosses between plants capable of agamospermous reproduction give rise to sexual progeny.[514] For example, Gustafsson (1946–1947: 145–146) says that the crosses *Potentilla recta* × *P. adscharica* and *P. canescens* × *P. verna,* which are both between agamosperms, yield F_1 generations that are wholly or predominantly sexual. So hybridization can produce agamosperms from sexual parents and produce sexual progeny from agamospermous parents. The transition can proceed in either direction. The important point is that agamosperms are a separate category of organism (in addition to polyploids) in which new types of organisms are typically produced by stabilization processes associated with hybridization.

Prevalence of Vegetative Reproduction. Most plants can reproduce vegetatively. Many cultivated plants are seed-sterile and must be propagated vegetatively.[515] These range from the Irish potato and sweet potato to flowers such as tiger lilies and some roses.[516] Vegetative reproduction is widespread in flowering plants (angiosperms).[517] Gustafsson (1946–1947: 272) notes that in Scandinavia about 80% of all angiosperms are capable of vegetative propagation and that about 50% can

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[a] The fact that agamosperms are commonly derived from hybridization is well established, but it has been proposed that agamosperms may arise by other means (see Koltunow and Grossniklaus 2003), for example mutation and epigenetic gene regulation. These proposals lack empirical support. Agamospermous individuals do occur at low frequency in some sexual populations, e.g., laboratory populations of *Drosophila* (Templeton 1983). Such populations have been subjected to artificial selection to increase the frequency at which such individuals are produced. For example, turkeys (*Meleagris gallopavo*) have been subjected to selection to increase the frequency of parthenogens (Olsen 1957, 1965). However, there appears to be no conclusive evidence that any natural agamospermous population arose in this way.

actually spread rapidly by this means. Vegetative reproduction is also common among ferns, liverworts, and club mosses.

A very small minority of animal forms treated as species reproduce exclusively by vegetative means, but a much larger number are capable of both sexual and vegetative reproduction (the same could be said of flowering plants).[518] According to White (1973: 744), vegetative reproduction, is a common occurrence among cnidarians, polyzoans, tunicates and other invertebrate groups. Hughes (1987) states that, "generally, soft-bodied animals with powerful regenerative capabilities clone by somatic division" (i.e., by vegetative reproduction). The tunicates of the genus *Doliolum* are an example (tunicates are tough-skinned marine animals related to vertebrates). Adults of this genus bud hundreds of offspring in a chain.[519] These individuals eventually separate as sexual adults. Sipunculid worms of the genus *Aspidosiphon* can reproduce by simply constricting and separating the rear end of the trunk to form a new individual.[520] Margulis and Schwartz (1998: 361) say vegetative reproduction via budding is "almost universal in ascomycotes" a fungal phylum containing some 30,000 forms treated as species. Many ascomycotes are incapable of sexual reproduction (ibid). Table 5.1 lists phyla in which vegetatively-reproducing forms are common (most such forms are also capable of sexual reproduction). Thus, the great majority of plants and fungi — and a broad range of invertebrate animals as well — are capable of vegetative reproduction. Inasmuch as 98 percent of all animal forms treated as species are invertebrates,[521] these facts indicate that this reproductive mode is extremely common across a broad range of organisms.

Vegetative Reproduction and Hybridization. When a new form of hybrid origin is capable of vegetative propagation, it can propagate itself even when it is absolutely sterile and totally incapable of agamospermous reproduction. Even Darwin was aware of this fact. In a letter to his cousin Francis Galton dated December 18, 1875, he wrote

> If two plants are crossed, it often, or rather generally, happens that every part of stem, leaf, even to the hairs, and flowers of the hybrid are intermediate in character; and this hybrid will produce by buds millions on millions of other buds all exactly reproducing the intermediate character. … Here we have nothing to do with the reproductive organs. There can hardly be a doubt from what we know that the same thing would occur with all those animals which are capable of budding, and some of these (as the compound Ascidians) are sufficiently complex and highly organised.[522]

Table 5.1: Some phyla in which both vegetative and sexual reproduction are common.

Phylum[a]	Number of taxa treated as species[b]	Examples	Reference[c]
Anthophyta	230,000	angiosperms (flowering plants)	1, 3
Filicinophyta	12,000	Ferns	2
Hepatophyta	6,000	Liverworts	2
Lycophyta	1,000	club mosses	2
Ascomycota	30,000	yeasts, blue-green molds, morels, truffles, lichens	2
Bryozoa	4,000	moss animals	1, 2
Ctenophora	100	comb jellies	2
Rotifera	2,000	Rotifers	2
Nemertina	900	ribbon worms	2
Cnidara	9,400	hydras, jellyfishes, corals, sea anemones, sea wasps	1, 2,
Annelida	15,000	annelid worms	2
Sipuncula	150	peanut worms	2
Phoronida	?	phoronid worms	2
Platyhelminthes	20,000	Flatworms	2
Porifera	5,000–10,000	Sponges	2
Echinodermata	7,000	starfishes, seastars, urchins	2, 4
Urochordata	1,400	tunicates, sea squirts, ascidians, larvaceans, salps	1, 2

a. Names of phyla follow Margulis and Schwartz (1998).

b. Counts are taken from Margulis and Schwartz (1998).

c. Key to references cited: (1) White (1973); (2) Margulis and Schwartz (1998); (3) Grant (1981); (4) Campbell (1987).

Vegetative reproduction can, in fact, be a more viable option than sexual reproduction even in non-sterile individuals. In a forest, for example, a solid canopy of foliage might shade out sprouting seeds, while shoots attached to the mother plant might attain sufficient height to reach sunlight. Even Darwin (1859: 43), who in the *Origin* largely discounted the significance of hybridization in the production of new types of organisms, asserted that in plants "propagated by cuttings, buds, &c., the importance of the crossing [i.e., the hybridization] both of distinct species and of varieties is immense."[523] But Darwin neglected to mention (or perhaps did not know) that a vast variety (indeed, judging from the previous section, the vast majority) of organisms are in fact capable of propagating themselves vegetatively without the aid of human beings. Therefore, by Darwin's own reasoning, if not his assertions, hybridization must play a huge role in the production of a broad range of forms. Among vegetatively reproducing forms, the natural production of new types of organisms through hybridization, followed by vegetative reproduction, is limited only by the number of different viable forms hybridization can produce (whether sterile or not). Stabilization processes of this type, hybridization producing new forms capable of vegetative reproduction, must therefore be extremely common in a natural setting.

Prevalence of Natural Recombinant Derivatives. Biologists tend to assume any organism of unknown origin is not of hybrid origin. Since the vast majority of forms treated as species are of unknown origin, this tendency poses a difficulty for anyone who attempts to argue that stabilization processes are probably far more prevalent than has been heretofore supposed. From a technical standpoint, it is far more difficult to determine the origin of a recombinant derivative than to determine that of a polyploid or agamosperm, which have complete sets of unaltered chromosomes that can easily be matched with those of putative parental organisms. Typically, in a derivative of interchromoset matings, only some of the chromosomes are present that were found in its parents. It is also more difficult to reproduce a natural recombinant derivative by artificially crossing its parents, than to reproduce a polyploid or an agamosperm by similar means. Stabilizing such a derivative may take many generations. Moreover, in a hybrid population derived from interchromoset matings, meiotic recombination breaks up and recombines any mismatched chromosomes in hybrids. Such breakups and recombinations occur repeatedly in every generation until the derivative is stabilized. As has already been mentioned, this extensive recombination makes it far more difficult to equate the chromosomes of a recombinant derivative's karyotype with the chromosomes of its parents. In many cases, only pieces of chromosomes can be identified as equivalent. In contrast, the chromosomes of organisms that reproduce vegetatively and/or agamospermously are easily equated with those of any potential parental organism; in such organisms the structure of the chromosomes normally remains unaltered because the stabilization processes producing such forms do not ordinarily involve meiotic recombination. Nor do the processes producing new polyploids. The stabilization processes creating such forms therefore do not restructure the chromosomes. Due to the difficulties involved with documenting forms derived from recombinational stabilization, one expects the number of verified cases to be smaller than in the case of polyploids and agamosperms. And such is in fact the case. As Coyne and Orr (2004: 351) note, this may mean only that this mode of producing new forms "is difficult to detect and document." But well-documented examples do exist. Such forms have been treated as species or subspecies (see citations listed in Note 524).

On the other hand, if one estimated the prevalence of the gradualistic processes described in orthodox theory on such a basis, one would be forced to conclude that such processes were either extremely rare or that they did not occur at all. There seem to be no documented cases in which an existing form treated as a species arose gradually from a preexisting one under natural circumstances. It is widely believed that many types of organisms of unknown origin are the result the gradual accumulation of favorable mutations in isolation as neo-Darwinian theory claims. Such may indeed be the case. But well-documented examples are sparse. Certainly, even in the case of recombinant derivatives, the evidence is far more substantial than even the best-documented case of a natural somaset treated as species arising from a preexisting one by the gradual accumulation of favorable mutations in isolation. The question of the relative prevalence of stabilization processes versus the processes posited by neo-Darwinian theory must be evaluated by other criteria. The most reliable criterion is the fossil record, which will be discussed in the next chapter.

One thing, however, does suggest interchromoset recombinational stabilization occurs frequently — many closely related forms differ not only with respect to karyotype, but also with respect to the structure of individual chromosomes. Most of the stabilization processes described in Chapter Four merely take intact chromosomes and recombine them into a new karyotype. They do not change the structure of individual chromosomes. For example, polyploidization multiplies the number of sets of chromosomes. Aneuploidization adds and subtracts chromosomes. But in both cases the chromosomes remain intact. However, as we have seen, interchromoset recombinational stabilization can rip chromosomes apart and reassemble the severed blocks into new, restructured chromosomes. Genes retain their relative order within those blocks, but the blocks themselves are rearranged into a new order. They may also be broken up and joined to blocks from other chromosomes.

Over the last three decades, studies comparing the chromosomes of a broad range of organisms have clearly demonstrated that such chromosomal blocks commonly occur in a rearranged order in different types of organisms (or broken up onto separate chromosomes).[525] Such blocks are known as "syntenic groups." They are chromosome segments in which the same genes occur in the same order in different organisms. Typically, closely related organisms differ with respect to fewer such rearrangements. Those more distantly related differ with respect to more.[526] For example, Ruvinsky and Graves (2005: 352) say that when human, mouse, cat, and cattle are compared, the chromosomes are "scrambled almost beyond recognition," but the same authors say the chromosomes of cattle differ from those of sheep with respect to only a few rearrangements. If many new types of organisms come into being via recombinational stabilization, one expects to find such pattern. Closely related organisms would differ with respect to fewer rearrangements (they would be separated by only one or a few recombinational stabilization events). On the other hand, distantly related organisms would differ with respect to more (they would be separated by many such events). If relatively few forms came into being via interchromoset recombinational stabilization, one would not expect the phenomenon of chromosomal rearrangement to be so prevalent; there is no other well-characterized mechanism that would allow new chromosomal rearrangements to get established (since they are deleterious when rare and unlikely to spread in a non-hybridizing population).

Verne Grant was one of the primary proponents of the idea that recombinant derivatives of interchromoset mating can get established in a natural setting. He called this process "recombinational speciation" and called such strains "homoploid derivatives" to distinguish them from polyploid derivatives of hybridization. At one time, Grant thought the production of such derivatives was a common process in a natural setting. However, the large amount of work involved in his artificial extraction of a recombinant derivative from the cross *Gilia malior* × *G. modocensis* convinced him otherwise.[527] The experiment was successful, but difficult. He concluded that the production of stable recombinant derivatives from interchromoset matings "is a far less common mode of speciation in plants than is amphiploidy" (Grant 1981: 270). But Grant reached this conclusion before reports of naturally occurring derivatives of this type became available. The necessary technology for positively identifying such forms was lacking at that time. Nor was there the widespread interest in identifying such populations there is today. Moreover, plants do not labor. If the same series of matings occurred in the wild that Grant carried out in the greenhouse, then a new stable form would appear. The amount of human labor required to reproduce such an event is irrelevant. Speaking of the production of fertile breeds derived from avian crosses, Buffon said long ago that "all that we can do by art, Nature, too, can do, and has done, thousands and thousands of times over."[528] Computer simulations indicate the production of such recombinant derivatives is entirely feasible process. Indeed, judging from the simulations, the process seems almost inexorable when some of the potential derivatives of a cross are fitter than their parents (McCarthy et al. 1995). Both of the two most cited theoretical papers on the topic (Buerkle 2000; McCarthy et al. 1995) predict the production of new forms by this means is an entirely workable process (see Appendix F). Indeed, it is well known that the products of a wide variety of crosses exhibit hybrid vigor. So it is not at all surprising some hybrid forms are able to get established as new types since many are also partially fertile. It is for this reason, for example, that Slack (1979: 79) says hybrid carnivorous plants "are generally relatively easily grown as compared with their parents."

Vegetative Reproduction and Triangular Numbers. A capacity for vegetative reproduction aids new types of organisms in getting established. Stebbins (1969: 29) correctly noted that the deleterious effect of hybridization on fertility would prevent many natural hybrids from getting established as new types of organisms: "In many hybrids, the complete sterility of the F_1 individuals effectively negates any possible influence of hybridization, and in many others a high degree of sterility is a serious barrier to its later influence." He also notes that "because of the integrated nature of adaptive genotypes … most of the segregants from wide crosses will be less adaptive than the parental genotypes, particularly in the original parental environments."

But when they are capable of vegetative reproduction (or agamospermous reproduction), even extremely sterile hybrids can get established as new types of organisms. In fact, the possession of such alternative reproductive capacities would with time often permit the production by sexual means of a variety of later-generation hybrids, some of which might have an enhanced level of fertility. Such fertile types would be favored by natural selection and therefore would likely get established as new types. As Asker and Jerling (1992: 113–114) note, certain agamosperms of hybrid origin "would be unable to reproduce sexually. Some are male sterile, even if the sterility might depend on other factors than hybridity. To acquire the capacity for apomictic seed formation, in a sterile hybrid capable only of vegetative reproduction, would mean an enormous increase in fitness."[529] Hence, a capability for agamospermous and vegetative reproduction would facilitate the production of new sexual forms.

Moreover, as has already been shown, it is not important that hybrids from *most* crosses will be maladaptive. The number of combinations that can be made from a set of n types is a triangular number, n(n-1)/2. So the number of potential hybrid pairings that can be produced from a given set of related forms is usually far in excess of the number of forms in that set. Thus, in the example given earlier, 100 different types of organisms could be paired in 100(99)/2 = 4,950 different ways. And, in point of fact, the number of hybrids known for a given group of related forms often does exceed the number of forms in the group.

For example, there are about 130 types of waterfowl treated as species. But there are about 500 different known types of waterfowl hybrids.[530] About 18,000 orchids are treated as species. More than 35,000 types of orchid hybrids are on record, and the number is ever increasing.[531] Rienikka notes that by 1960, "hundreds of new orchid crosses were being registered each month."[532] Obviously, then, it makes little difference if the vast majority of hybrid pairings fail; for if even a small percentage of the total possible combinations *are* successful, then it will be possible for many types of hybrids to get established as new types of organisms. For example, in the case of orchids there are 18,000(17,999)/2 = 161,991,000 combinations. If only one in a thousand of these combinations were successful, 161,991 new viable forms would come into being.

In addition, there are many reasons to suppose that natural hybridization is far more common than available reports suggest. This underreporting of hybridization is the result of several different factors (for a discussion of underreporting see Appendix G).

Prevalence of Animal Hybrids. Hybridization has long been considered a major evolutionary force among plants.[533] However, it is widely supposed that animal hybrids are less common, or are more sterile than those produced by plants. Among evolutionary biologists studying animals, the main interest of hybridization seems to have been with regard to processes that produce reproductive barriers *preventing* hybridization, not ones producing new types of organisms directly from hybridization.[534] Interest in processes of the latter type has been much more in evidence among botanists.[535] If hybridization actually were rarer among animals, then stabilization processes, due to their strong connection to hybridization, would be less significant among animals than among plants. But there does not seem to be any great difference between the two categories with respect to rates of hybridization

Those who claim hybridization does not play an important evolutionary role among animals list sterile or inviable animal hybrids as evidence that interbreeding does not occur. But it is also possible to compile long lists of plant hybrids that are sterile and/or inviable. The fact that many plant hybrids are sterile was established by formal scientific studies as early as the eighteenth century.[536] It is sometimes claimed that animal hybrids should somehow be more frequently sterile than plant hybrids simply because X-Y (or W-Z) sex determination characterizes animals but not plants. But this assertion can be dismissed for two reasons. First, in certain categories of animals sex chromosomes are not well differentiated.[537] Such is the case, for example, among lizards[538] as well as a wide variety of invertebrates.[539] In fact, it is now recognized that the "dominant Y" system of sex determination characteristic of mammals is only one among a wide variety of sex-determining mechanisms in animals.[540] Even among mammals, not all have the dominant Y system. Second, the data refute it: Many hybrids between animal forms treated as species are, in fact, known to be partially fertile (see Chapter 2). Indeed, such hybrids are common among birds and mammals (McCarthy 2006; McCarthy, in prep.).

Knowledge of animal hybrids is certainly less advanced than in plants, probably, at least in part, because plants are far easier than animals to cultivate and breed.[541] With the exception of certain invertebrates and fish, fertilization by artificial means is far more difficult in animals, which means that hybridization experiments are usually much harder to carry out. However, this relative deficit in our knowledge concerning the fertility of animal hybrids should not lead us to the conclusion that they are more sterile than plant hybrids. Indeed, available information suggests the majority of animal hybrids are partially fertile. In my own survey of hybridization in birds (McCarthy 2006), I found that, for those avian crosses for which information on fertility is available, the ratio of crosses producing partially fertile hybrids to those producing highly sterile ones is about six to one. In the survey of mammalian hybrids I am currently conducting, I also find partially fertile hybrids are common.

Another objection, sometimes raised, is that animals are less likely than plants to cross with individuals not of their own kind, because they consciously choose a mate. Let it first be said this objection often is not even relevant since many animals — in particular many fishes, amphibians, and invertebrates — release their gametes into water, where they can easily mix with the gametes of other types of organisms. An abundant array of animal forms reproduce in this way and a wide variety of naturally occurring freshwater and marine animal hybrids are known.[542] Moreover, it is well known that animals may become confused when it comes to choice of mate. Early in life many types of animals, particularly those providing parental care to their young, such as mammals and birds, pass through a brief receptive period during which external stimuli determine their future choice of mate.[543] For example, when nanny goats raise lambs, or ewes, kids, the cross-fostered males prefer to mate with females of the same type as their foster mother.[544] The psychological process creating this sexual preference is known as *imprinting*. Certain characteristics become established at that time that will later elicit courting and mating in the adult. Most birds will readily imprint on whatever bird raises them. In fact, early exposure can cause a nestling to imprint even on a non-bird or an inanimate object. Thus, Ardrey (1969) describes a case of a peacock raised in a reptile house at the Vienna Zoo imprinting on a giant tortoise. It followed the tortoise everywhere. "And," as Ardrey says (ibid: 125),

> when time came for such matters, the maturing white peacock fell in love with the tortoise. The bird refused to eat if removed from the reptile house. Neither would he give eye or least affection to the most attractive peahen the keeper could find. He had pledged his troth as birds will do, and monogamous instincts kept his heart unwavering. Through quite a long life the white peacock never left the reptile house, or ceased to follow his tortoise about.

Konrad Lorenz (1952, 1972: vol. I) studied this phenomenon in a variety of birds. One of his jackdaws treated him as if he were its mate. Lorenz also had a goose and rooster that were attracted to each other and not to individuals of their own kind. He had ducklings that followed him wherever he went. By exposing newly hatched geese to a beach ball, he convinced them forever afterward that the ball was their mother.

In captivity, animals commonly adopt young not of their own kind, which usually results in the young imprinting on the fostering type. However, some types of animals are much more willing to play the role of foster parent than are others. Breeders regularly resort to fostering in the case of certain hybrid crosses in which the biological parents tend to abandon their young. Birds commonly used for this purpose are the Bengalese (*Lonchura domesticus*) and the domestic canary (*Serinus domesticus*). Such adoptions are apparently fairly common, too, in a natural setting. A variety of reports are on record. For example, Briehagen (1984) reports a Dunlin (*Calidris alpina*) adopting the brood of a Temminck's Stint (*C. temminckii*). Beardslee and Mitchell (1965) report a case of a Prothonotary Warbler (*Protonotaria citrea*) singing the song of the Yellow Warbler (*Dendroica petechia*) and tending

Yellow Warbler young. Mixed broods often occur, too, when one bird lays eggs in the nest of another.[545] Some reports are surprising. For example, the writer knows of a case in which a puma-leopard hybrid (*Felis concolor* × *Panthera pardus*) was fostered on a Fox Terrier, and another in which a female Dobermann Pinscher raised a pig. When adult, the pig spent all its time with dogs instead of other pigs, and behaved in many ways like a dog. It would leap up on visitors and attempt to bark at strangers. Also bizarre is an account that appeared in *The Ibis,* a prominent ornithological journal, in which a captive female Golden Eagle (*Aquila chrysaetos*) hatched and reared three chickens![546]

Direct fostering is not necessary for imprinting. A male bird may learn an "incorrect" song by hearing it from a bird singing near the nest and later sing that song and attract a mate not of his own kind. For example, Lemaire (1977) showed that hybridization resulted when an accident of early learning had led a Reed Warbler (*Acrocephalus scirpaeus*) as an adult to sing a song combining elements of Reed Warbler song with those of the Marsh Warbler (*A. palustris*). Female birds tend to choose mates that sing the songs they were exposed to early in life.[547]

In captivity, animals may be kept without access to mates of their own kind. If some other type of animal is present in the cage, hybridization will often result. Mating can occur even between the most disparate partners. For example, Morris (1970: 502) says a male squirrel monkey (*Saimiri sciureus*) caged with a female spring-hare (*Pedetes capensis*), a rodent, repeatedly attempted copulation. With regard to captive doves, long-time aviculturist Arthur Butler (1906: 346) comments that

> In the case of the more excitable and vicious of the *Columbæ* [i.e., pigeons and doves] I have had abundant evidence that they are not only desirous of breeding with those of another species, but with any other bird in the enclosure with them, though in no respect related and perchance not more than an eighth or tenth their bulk. A Passerine dove which I still have so persecuted a hen Zebra-finch with its attentions that I had to remove it to another cage, while three Steel-barred or Picui-doves which I had for some years would coo and bow to any other dove however large it was: but it is not only among the *Columbæ* that one notices these depraved traits, for in my 'Foreign Finches' 1st ed. p. 78 I have recorded the fact of a Rosella parrakeet trying its utmost to induce a Red-crested Cardinal to accept it as a husband.

"Yet," says Butler (ibid), "there are still men so inattentive to what is constantly going on around them, that they persist in dogmatically asserting that no bird or beast willingly intermarries with an alien species." Mating between forms highly disparate in size are not limited to birds. Male Steller sea-lions (*Eumetopias jubatus*) are about 10 times as large as female California sea-lions (*Zalophus californianus*). Yet natural hybrids occur. Most *Z. californianus* females participating in such matings die of suffocation or of wounds sustained during copulation.[548] The same *Eumetopias* male killed 12 *Zalophus* females by lying on them until they died. In such cases, the urge to mate apparently overcomes any tendency that an animal may have to restrict its attention to mates presenting normal cues. Similarly, in a natural setting, when an animal is on the edge of, or outside, its normal range, it may not meet a mate of its own kind. If some other type of animal is present, hybridization may result. In the case of those types of animals that consciously choose a mate, imprinting and a scarcity of appropriate mates are probably the two main factors giving rise to hybrid populations.

In light of such evidence, from both captivity and the wild — in particular, in light of the large number of natural animal populations documented as having had a hybrid origin — there is certainly no reason to believe animals always refuse to mate with individuals not of their own kind.

The Scala Naturae. What, then, is the motivation for the many, apparently unsubstantiated assertions that animal hybrids and evolution of animals are somehow fundamentally different from those of plants? Is it perhaps the self-flattering notion that animals are somehow special, higher, nobler? In particular, is such reasoning simply a manifestation of the ancient tendency to place *Homo sapiens* above other, supposedly baser, organisms? This bias is indeed long-standing. When zoology was emerging as a science in the eighteenth century, its practitioners arranged their taxonomies in accordance with an age-old ordering principle handed down from medieval times, the *scala naturae* (literally, "the ladder of nature"). Also known as "The Great Chain of Being," this system had religious roots and pictured beings rising in a linear order of perfection, starting with inanimate minerals and rising through fossils (which were considered something between the mineral and the living), to plants, animals, humans, celestial beings, and, ultimately, God. As St. Albertus Magnus (*De animalibus,* thirteenth century A.D.) put it, "Nature does not make [animal] kinds separate without making something intermediate between them; for nature does not pass from extreme to extreme without an intermediate."[549] This is the so-called Law of Continuity ("*Natura non facit saltum"*), often cited by Darwin. In his *De docta ignorantia* (1440), the schoolman Nicolas of Cusa makes similar claims:

> All things, however different, are linked together. There is in the genera of things such a connection between the higher and the lower that they meet in a common point; such an order obtains among species that the highest species of one genus coincides with the lowest of the next higher genus, in order that the universe may be one, perfect, continuous.[550]

The *scala naturae* was the dominant worldview of European thinkers for centuries.[551] It was strongly associated with the ideas of divine order, perfection, continuity, and gradualism. To a great extent, the view of evolution expressed in the *Origin of Species* is a temporalization of a previously static *scala naturae*,[552] which is to say that it used the same sort of terminology and made many of the same assumptions, but placed the discussion in a temporal context. Thus, in describing the *scala*, the seventeenth century philosopher Gottfried Wilhelm Leibniz used many of the same terms ("chains," "missing links," "gradation," …) later used in the context of neo-Darwinian theory:

> All the different classes of beings which taken together make up the universe are, in the ideas of God who knows distinctly their essential gradations, only so many ordinates of a single curve so closely united that it would be impossible to place others between any two of them, since that would imply disorder and imperfection. Thus men are linked with the animals, these with the plants and these with the fossils, which in turn merge with those bodies which our senses and our imagination represent to us as the absolutely inanimate. And, since the law of continuity [i.e., "*Natura non facit saltum*"] requires that when the essential attributes of one being approximate those of another all the properties of the one must likewise gradually approximate those of the other, it is necessary that all the orders of natural beings form but a single chain, in which the various classes, like so many rings, are so closely linked one to another that it is impossible for the senses or the imagination to determine precisely the point at which one ends and the next begins.[553]

Having never seen among plants a progression in perfection from "base" to "noble," botanists rejected the *scala* as a basis of classification at an early date.[554] But the concept of a linear chain of order held sway among zoologists until Georges Cuvier published his authoritative classification of animals, *Le Règne Animal,* in 1817, in which he divided the Animal Kingdom on the basis of anatomy into four phyla of equal rank (vertebrates, mollusks, radiates, and articulates). After Cuvier, no biologist would again assert an ordering principle of "growing perfection" constitutes an appropriate basis for constructing systems of classification. But the tendency lingers, even today, to think of a mammal as somehow more advanced than a bird, or of a reptile as more complex than a fish, and certainly, of an animal as more advanced than a plant. This predisposition to place animals and, in particular, human beings "above" other organisms seems still to foster a mindset that discounts the extensive evidence demonstrating the significance of stabilization processes in animal evolution, since most such processes directly depend on the occurrence of hybridization.

Predicted Phylogenies Disagree. A separate line of reasoning, in terms of the differing predictions of evolutionary relationships, suggests stabilization processes are far more common than has generally been realized. It relates to the fact that distinct data sets often suggest different arrangements of classification. Darwin thought the system of taxonomic classification could and should reflect evolutionary history. He considered this a practical and laudable goal because

(1) the existing system of classification was treelike in its structure (as are most filing systems) and

(2) he believed evolution itself had also been treelike (strictly divergent) in its pattern.

The idea that taxonomic classification can, does, and should reflect evolutionary history is widely considered to be one of Darwin’s most important insights and constitutes what is known as the “cladistic” approach to systematics (a clade is a hypothesized group consisting of a single common ancestral type and its descendant forms, supposedly produced by divergence). Cladists assert that, for any given set of taxa, it is possible to construct accurate trees of descent ("phylogenetic trees”) indicating mutual relationships in terms of the time since any given pair in the set shared a common ancestor.

However, such predicted phylogenies are always hypothetical. They are constructed under the assumption that organisms sharing more traits are more closely related. Conversely, the time since the common ancestor is assumed to be greater for organisms that hold fewer traits in common. Before the advent of modern biotechnology, the traits compared in such studies were ordinary physical features (tooth shape, presence/absence of hooves, number of vertebrae, etc.) and sometimes, also, behavioral traits.

But in recent years the comparison of genetic traits has become more common. For example, the chemical structure of the gene for the enzyme amylase might be compared in various types of organisms. Those in which the gene structure (as measured by various biochemical techniques) is more similar would be assigned to closer branches of the resulting tree. On the basis of a second gene, for example the gene for elastin, a second tree of relationships could be constructed, which might, or might not, be the same as the tree based on amylase structure.

Many biologists believe concordance is generally observed between independent gene trees. In their minds, this supposed fact lends strong support to the idea that evolutionary history should be represented as a strictly diverging tree.[a] But, in reality, nothing is more common than disputes over who has published the right tree.[b] As Whitfield (2007: 248) comments, "different genes from the same set of organisms often predict different trees." Admittedly, in the case of such disputes there is usually the expectation (given enough time and research, and given the right assumptions and the correct set of traits) that the “correct” tree will eventually be revealed. But in reality, more data does not seem to resolve such disputes. As Milner (1993: 84) points out,

> many cladistic classifications that are supposed to be repeatable by other cladists have turned out to be controversial. When results don’t jibe, cladists accuse each other of not following proper procedure or of selecting the wrong characters for comparison — a problem older than Linnaeus.

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[a] The mere fact that all the various known types of organisms can be arranged into a treelike classificatory hierarchy reflects nothing about their mode of origin. After all, the distinct elements of *any* set (e.g., a set of business documents, the set of known minerals, the objects in your grandmother’s attic) can be arranged on the basis of their distinctive traits into a treelike system of classification. In fact, as Panchen (1992: 8) notes, “there is no extrinsic method of establishing that the natural order of organisms is a divergent hierarchy,” as opposed, say, to a reticulate network.

[b] In fact, since one researcher will often use a variety of methods to construct trees from the same set of data, a single study will often present several distinct trees.

Such discrepancies affect classification even at the highest level — distinct gene trees for archaebacteria, bacteria, and eukaryotes are not concordant.[555] Another example is Hedges' (1999) complete rearrangement, based on more recent molecular data, of the previously accepted phylogeny for Class Reptilia. In studies of a wide variety of other taxonomic groups, a similar lack of concordance has been found (see citations listed in Note 556).[a] Minelli (1993) cites a profusion of cases in which ongoing controversies are fueled by non-concordant data. Some researchers have simply given up. After an extensive inquiry, in which she attempted to place the various major invertebrate groups into a treelike scheme of relationships, Willmer (1990) reached the conclusion that it would be impossible to specify any single tree in any way consistent with all the data (recall that 98 percent of all animal forms treated as species are invertebrates). It is well known that the same is true of angiosperms (flowering plants). The vast majority of living plants are angiosperms. As Syvanen (1994: 252) points out, the problem has always been that "characters upon which [phylogenetic] trees could be constructed give conflicting trees, depending upon how the characters are weighted. Thus botanists have never been able to reach agreement upon the shape of a species tree [for angiosperms]." It would be impossible to list and consider every existing category of organism, but it may be worth mentioning that Class Pisces (fish), a large, heavily researched, and diverse category, is also in taxonomic disarray. Thus, in the introduction to their *Encyclopedia of Aquatic Life* (1997),[557] Banister and Campbell acknowledge

> There is no universally accepted classification for fishes. In some circumstances detailed studies have produced a classification for one level of hierarchy based on one philosophy whereas in other areas different philosophies have been used as the basis for the classification of a different category. … Within the world of fish classification these are exciting times, but producing more problems than solutions. Yet these have caused all professional ichthyologists to think deeply about the nature of classification and to try and produce a scheme that reflects the true genealogical relationships of fishes. Rather than produce a misleading classification that might be assumed to be definitive, our text stresses many of the problems. We felt it better to admit the current state of uncertainty and confusion, to admit that there are profound disagreements between different schools of ichthyological thought and to admit that there is much about which we are ignorant. Even the four living and two extinct classes of "fishes" mentioned in this volume cannot be arranged in a way that would not produce criticism from one group of researchers or another. There is no really satisfactory solution at the moment. Consequently the classification (arrangement might be a better word) adopted here is a neutral one, and is meant to be a convenient map to guide people around the many unfamiliar groups of fishes.

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a. As Panchen (1992: 238) notes, "in the case of the animal phyla, it has been regarded, probably throughout this century, as difficult to produce a hierarchical clustering of high ranks, although various patterns of sub-kingdoms and super-phyla have been suggested." See also: Inglis (1985).

If the goal were merely to bore the reader, such cases could be listed almost *ad infinitum.* It seems sufficient, however, to say that a vast amount of research has failed to demonstrate the existence of a single treelike hierarchy. Such findings prompted Panchen (1992: 243) to assert that the very "existence of a hierarchy embracing all living things is in doubt."[a] Charles Heiser (1966: 31) put the problem in humorous allegorical form:

> Once upon a time there was a large family who lived deep in the woods in a far off place. They were taxonomists and they were very, very poor. … the oldest boy of the family decided that he would have to go out into the world to make his fortune. As was customary and proper, his father had a talk with him before he left. There was, he said, in a kingdom some distance away a great castle in which were imprisoned three beautiful princesses whose names it was rumored were the True Species, the True Classification, and the True Phylogeny.

The father goes on to tell his son that the fearsome castle is fraught with many perils. But, he says, he who rescues the fair princesses will not only have them as his wives, but also possess their kingdom and all its riches. The son sets forth, and one by one his brothers follow. They take various tools — compound microscopes, scalpels, computers, and pipettes — to aid them in their quests. But, sadly, not one ever returns.

Heiser, who was writing more than forty years ago, says the old taxonomist had one last son, Daniel Niell Alonozo, who "has also left home, and there are some it is said who expect D. N. A., as he is called, to conquer all." However, we see today that data derived from the study of this much-vaunted DNA has failed to broach the dreaded castle's ramparts. Indeed, in recent years automated robots and computers, which analyze DNA without human aid, have produced mass quantities of genetic data. This data has put the need for doubt beyond doubt. Thus, Doolittle (2000: 95) commiserates with his fellow biologists on the shortcomings of a discredited hypothesis — the idea of a tree of life:

> It is as if we have failed at the task that Darwin set for us: delineating the unique structure of the tree of life. But in fact, our science is working just as it should. An attractive hypothesis or model (the single tree) suggested experiments, in this case the collection of gene sequences and their analysis with the methods of molecular phylogeny. The data show the model to be too simple. Now new hypotheses, having final forms we cannot guess, are called for.

One obvious hypothesis accounting for this observed lack of concordance, documented so laboriously by so many studies, is that natural hybridization and the production of new types of organisms through stabilization processes is rampant. If the production of new types of organisms through such processes is a widespread

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[a] It's easy to see how systematists would be attracted to the idea of classifications reflecting evolutionary history. Such an assumption makes their task, which would otherwise be a mere dry sorting into categories, a matter of sleuth work in which the researcher seeks to reconstruct the history of life.

phenomenon, as stabilization theory predicts, then the topology of evolutionary relationships would be expected to be largely reticulate (weblike, not treelike) and distinct genes (or distinct sets of traits) would be expected often to yield different trees because, under such circumstances many types of organisms would receive their traits from two different parental forms. In other words, there would be a lack of concordance among trees based on different data sets. And, as we have seen, this is exactly the state of affairs that has been observed. In fact, in many cases we should expect non-concordance. For example, in the case of angiosperms we have long known hybridization is an everyday occurrence.[558]

Proof of Evolution. We have proof of evolution occurring via stabilization processes. A wide variety of forms treated as species are known to be derived from stabilization processes. Many have actually been reproduced from their natural progenitors. Their origins are *known,* and not a matter of mere theoretical conjecture. Moreover, there is reason to suppose forms derived from such processes are underreported because hybridization itself is underreported (see Appendix G). In contrast, claims that new types of organisms come into being gradually in isolation are weakly supported by observation. Since scientists cannot hope to observe gradual evolutionary processes in the direct way stabilization processes can be observed, it may well be asked: Has reproductive isolation brought about the gradual emergence of even a single type of organism treated as a species? Many biologists would say that the typical organism comes into being in isolation in a gradual manner. But does this belief reflect empirical findings? Or is it a mere habit of thought, prompted by theory, but unsupported by evidence?

Given the briefness of human existence, proof concerning the gradual emergence of new types can only be based on fossil evidence. But the fossil record does not support the claim that new types of organisms typically arise gradually (see Chapter 6). Of course, scientists look to nature and claim that certain natural populations seem to represent the various stages that might be expected to occur during gradual "speciation" in the past. Various authors offer plausible examples of this type.[559] But the evidence they offer never seems actually to prove that the case in question is one of gradual origin. *In other words, forms alleged to be of gradual origin, never seem to be of known origin.* Certainly their origins are not known in the same sense that the origins of forms derived from stabilization processes are known. In point of fact, it seems that whenever a claim is made that a particular type of organism is of gradual origin it is always possible to construct some other, equally plausible scenario accounting for its origin in terms of some stabilization process.

The Guam Rail. For example, a colleague once claimed that the Guam Rail (*Gallirallus owstoni*) must be of gradual origin. His argument was that *G. owstoni* is flightless, occurs only on Guam, and that there are no other rails on that island, even in the fossil record, that might have hybridized to produce *G. owstoni*. Moreover, polyploidy is very rare among birds and vegetative reproduction unknown. On this basis he concluded that this bird *must* be of gradual origin.

However, his explanation of the origin of *G. owstoni* is merely hypothetical and it's possible to construct alternative (equally hypothetical) scenarios that are just as plausible as his: First note that (1) other rails exist on other western Pacific islands;[560] (2) all rails can swim;[561] and (3) chains of small islands connect these islands to Guam. Given these facts, we can equally well suppose, again, entirely hypothetically, that (1) hybridization producing a new type of rail could have occurred on some other island and produced a bird like the Guam Rail; (2) birds of that type reached Guam by swimming from island to island; and (3) such birds became extinct elsewhere.

It would be possible to continue fabricating such unsubstantiated histories indefinitely. For example, a second scenario consistent with stabilization theory might suppose multiple types of rail once existed on Guam and hybridized to produce the Guam Rail, and that these parental types were not preserved, or have not been detected, in the fossil record there. The mere construction of these two scenarios, of course, proves nothing. *The important point is that the scenario constructed by my colleague doesn't prove anything either*.

Evolution of Horses. The evolution of horses is the example of gradualistic evolution that springs to many people's minds. They usually picture a series of fossil horses assembled in the 1870's by paleontologist Othniel C. Marsh. But even this well-known case is no longer considered valid. Milner (1993: 222) notes that

> Marsh's classic unilineal (straight-line) development of the horse became enshrined in every biology textbook and in a famous exhibit at the American Museum of Natural History. It showed a sequence of mounted skeletons, each one larger and with a more well-developed hoof than the last. (The exhibit is now hidden from public view as an outdated embarrassment.) [parenthetic comment is Milner's]

These fossils were held up as a shining example of gradualism until Simpson (1951) finally showed Marsh's specimens were not even successive members of a single line of descent, let alone stages in an unbroken, gradually evolving lineage. Indeed, for all that is known, they might have been the products of a series of complex hybrid crosses. There is not enough information to decide.

At least Marsh tried to provide actual evidence of gradual evolution. In the writer's experience it seems biologists rarely even try to document claims that forms are of gradual origin (at least not in the rigorous sense that forms derived from stabilization processes have been documented). Instead the tendency is to offer unsubstantiated claims, such as my colleague's concerning the Guam Rail, as "proven" examples. Certainly, no one has documented the gradual origin of any type of organism in the absolutely unambiguous way that Rieseberg and his co-workers have demonstrated the hybrid origin of the sunflowers *Helianthus anomalus* and *H. paradoxus* (Rieseberg 1991; Rieseberg et al. 1990, 1991, 1993, 1995, 1996; Ungerer et al. 1998). There seems to be a double standard in the evidentiary requirements.

When they think about the origin of new types of organisms, especially of new animal forms, most biologists still do not think of stabilization processes as typical. This attitude is counter-inductive: knowledge of the better researched cases should be applied in inferring the origins of those forms whose histories are more poorly known. At the very least, since those organisms whose origins are well-known to us typically do arise via stabilization processes, there is absolutely no reason to suppose that those of unknown origin *typically* arise via a different and poorly documented process (the gradual accumulation of favorable mutations in reproductive isolation). Likewise, since most organisms of known origin are derived from processes involving hybridization, there is no reason to suppose ones of unknown origin are mostly derived from processes not involving hybridization.

Conclusion. Three main conclusions were reached in this chapter, each conflicting with neo-Darwinian theory's assumption that new forms treated as species typically come into being as populations that gradually diverge in isolation:

(1) There seem to be no cases of natural populations treated as a species that are actually known to have come into existence via the gradual accumulation of favorable mutations in isolation. Certainly, available data indicates this type of evolution is not typical (this fact will be driven home in chapters 6 and 7);

(2) In general, forms treated as species and of known derivation are derived from stabilization processes (which often involve hybridization);

(3) Very often, biologists construct different evolutionary trees for the same set of organisms, when they base their inferences on different data sets. This fact suggests that the production of new forms via stabilization processes involving hybridization is a frequent occurrence over evolutionary time.

Neo-Darwinism has claimed hybridization is unlikely to lead directly to the production of new stable forms, because hybrids, supposedly, are always too inviable and sterile to accomplish this.[562] From the viewpoint of neo-Darwinism, hybrids are seen merely as entities selected against (because they are deemed less likely to survive and reproduce).[563] This perception is peculiar, given that it is well known that many types of hybrids exhibit a vigor significantly in excess of their parents' (see Chapter 2). Moreover, as we have repeatedly seen, many hybrids are quite capable of producing offspring. It must be remembered, too, for any given category of organisms, the number of hybrid combinations often far exceeds the number of forms treated as species within that category. Therefore, even if most types of hybrids are inviable, there are so many different crosses and kinds of hybrids that a sufficient number of viable hybrids will be produced even if the hybrids produced by the great majority of crosses are inviable.

Among the conclusions reached in this chapter a single fact is key: A broad survey of available evidence indicates forms of *known* origin are typically the products of stabilization processes. This fact is patently inconsistent with neo-Darwinism's claim that new types of organisms usually come into being gradually in isolation. Although it would be impossible to prove stable forms never come into existence via the gradual accumulation of favorable mutations in isolation, there certainly seems to be a dearth of evidence that they *typically* do. Scientific thought should be guided by observation. As Francis Bacon, the great proponent of induction, once said (*The Advancement of Learning,* 1605),

> The wit and mind of man, if it work upon matter, which is the contemplation of the creatures of God, worketh according to the stuff, and is limited thereby; But if it work upon itself, as the spider worketh his web, then it is endless, and brings forth indeed cobwebs of learning, admirable for the fineness of thread and work, but of no substance of profit.[564]

According to Bacon, then, our theories about how evolution typically occurs should be guided by what we have actually observed and *know* about the origins of new types of organisms. Therefore, to the extent we can explain such origins without reference to reproductively isolated, gradual change, he would say that we should do so, since origins through such gradual changes are far more poorly documented than those occurring through stabilization processes.

Bacon's advice is consistent with the most basic philosophical rules used in judging theories. For example, Ockham's razor ("Vain to do with more what can be done with less") implies the best theory is the simplest one, that superfluous assumptions should be eliminated. Isaac Newton echoes this dictum in his First Rule of Reasoning in Philosophy, which says that "we are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances." Stabilization processes are "true" in the sense that Newton intended because they are known to occur. We have already seen that many existing forms are known beyond doubt to be the products of particular, well-characterized stabilization processes. On the other hand, the origin of new forms through the gradual accumulation of differences in reproductive isolation is a poorly documented phenomenon. Moreover, stabilization processes are a sufficient explanation of how new types of organisms typically come into being because, as we shall see in the next chapter, we know new types of organisms typically do arise abruptly. Therefore, in accounting for the origins of the vast majority of forms, the scenarios posited by neo-Darwinian theory are both insufficient and superfluous — stabilization theory provides a clearer, better-documented, and sufficient explanation.

6 The Fossil Record

Experiments show, that after repeated failures, the union of two recognized species may at last, under very favourable circumstances, give birth to fertile progeny. Such circumstances, therefore, the naturalist may conceive to have occurred again and again, in the course of a great lapse of ages. —CHARLES LYELL, *Principles of Geology* (1832)[565]

The fossil record provides the best and most convincing evidence for the prevalence of stabilization processes. Obviously, the origin of a new type of organism through a stabilization process would have two expected features: (1) *abruptness,* the new form would come into being suddenly; and (2) *stability,* subsequent to its initial appearance it would remain stable with respect to its characteristic traits indefinitely. For example, a new polyploid comes into being very rapidly, in one or two generations usually, and is stable thereafter. And, in fact, as this chapter will show, the typical fossil form does conform to the pattern expected for stabilization processes — and, in so doing, fails to conform to the sort of pattern predicted by neo-Darwinian theory. Usually, when a given fossil form is traced down through the geological strata, it remains the same, all the way to the lowermost stratum in which it occurs; the strata below contain different, similarly stable types. Looking at fossils, then, leads to the conclusion that there is typically a discontinuity in the origin of new types of organisms. For the origin of a fossil form usually seems quite abrupt and there is little change thereafter. This sudden appearance of new forms is called *saltation*. Stabilization theory offers a simple genetic explanation of saltation: *Fossil forms that appear to have a saltational origin are assumed to be the products of stabilization processes.* In the past, however, saltation has never been accounted for in terms of well-understood genetic processes. Instead, it has merely been set forward as an observation inconsistent with the gradualistic processes posited by neo-Darwinian theory. Many paleontologists have emphasized saltation is the dominant pattern seen in fossils. Georges Cuvier was the first.

Cuvier. Baron Georges Cuvier (1769–1832) established the science of vertebrate paleontology. According to Mayr (1982: 109), his "contributions to science are almost too extensive to be listed." Cuvier often entertained crowds with his prodigious knowledge of comparative anatomy, identifying animals from a single bone. His *Le Règne Animal* was the earliest taxonomic classification to include descriptions of fossil forms (many of which he himself had discovered) alongside those of living organisms. Although he never tried to explain *how* new fossil types might come into being, no one in the pre-Darwinian period produced more new evidence demonstrating that evolution actually does occur than did Georges Cuvier. His *Récherches sur les Ossemens fossiles des Quadrupèdes* (1812) provided irrefutable proof of the occurrence of evolution. Cuvier's demonstration was clear: The lower the stratum, the more distinct its fauna from that of the present (viz., the lower the percentage of modern types and the higher that of extinct ones). Cuvier documented the fact of evolution theorists would later try to explain.[a] He popularized the idea that fossils tell the story of past life on earth.[b] Thus, in *Essay on the Theory of the Earth* (1827: 3), he writes:

> We admire the power by which the human mind has measured the motions of the celestial bodies, which nature seemed to have concealed forever from our view. Genius and science have burst the limits of space; and observations, explained by just reasoning, have unveiled the mechanism of the universe. Would it not also be glorious for man to burst the limits of time, and, by means of observations, to ascertain the history of this world, and the succession of events that preceded the birth of the human race?

And yet, Cuvier saw no evidence that one fossil form gradually changes into another. In looking at any given form, he saw long-term stability; in looking from one form to the next, he saw sharp morphological distinctions.[c] When Lamarck

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[a] Rejecting the then-accepted idea that the number of existing types of organisms had been constant ever since they were "created in the Beginning," Cuvier actively advocated the idea of extinction. In his *Mémoires sur les espèces d'éléphants vivants et fossiles* (1800) he compared the skeletons of Indian and African elephants with the fossil remains of mammoths, and with those of what was then known as the 'Ohio animal' (which he later named mastodon). This paper showed, for the first time, that the extant elephants were distinct from the fossil forms and that the latter must therefore be extinct. As Cuvier pointed out, such animals would be too large to escape notice if they still existed.

[b] Xenophanes of Colophon (570–480 B.C.) has been credited with being the first to recognize that fossils were evidence of former life (Osborn 1894: 36).

[c] Cuvier's claim that new forms appear abruptly in the geological record and then continue without alteration was used by later thinkers to support creationism (Gillispie 1996: 103). The abruptness seemed consistent with special creation by God (although Cuvier's finding that different types made their paleontological debuts in different geological strata clearly did not). The lack of change was consistent with the supposed sacred immutability of "species," but, again, the idea of extinction obviously was not. Many writers have unjustly accused Cuvier of obstinately maintaining that fossil human beings could never be found. In his *Essay on the Theory of the Earth*, he did say that "no human bones have yet been found among fossil

proposed that the transmutation of one type into another is gradual, Cuvier claimed to see nothing in the fossil record contradicting the idea that the typical form is static once it comes into existence. In response he wrote:

> If the species have changed by degrees, we ought to find traces of these gradual modifications. Thus, between the palaeotheria and our present species, we should be able to discover some intermediate forms; and yet no such discovery has ever been made.[566]

Cuvier, however, rarely speculated on the observations he reported.[a] He seems to have been more interested in documenting the fact of evolution than in identifying the underlying biological forces that brought it about. His attitude seems to have been the same as that of modern paleontologist Stephen Jay Gould, who once told the writer that saltational change had to be accepted with or without explanation since it is an empirical fact documented in the fossil record. However, I have long thought it unlikely that other scientists would accept the phenomenon of saltation in the absence of a clear genetic explanation. The supposition that new types of organisms are typically produced by stabilization processes provides such an explanation.

Darwin's Emphasis on Gradualism. From youth, apparently, Darwin believed gradualism is inherently more rational and scientific than saltational accounts of evolution. Thus, Mayr (1982: 509) asserts that

> As a result of studying the writings of the theologian Sumner (1824: 20), Darwin had come to

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remains," but he made it clear exactly what he meant: "When I assert that human bones have not been hitherto found among extraneous fossils, I must be understood to speak of fossils, or petrifactions, properly so called" (Cuvier 1818: 130). Petrified bones, which have had time to mineralize and turn to stone, are typically far older than ordinary bones. Cuvier's point was that all human fossils that he knew of were of relatively recent age because they 1) had not been petrified and 2) had been found only in superficial strata (Cuvier 1818: 133–134; 1827: 121). But he was not dogmatic in this claim. When new evidence came to light, he included in a later edition an appendix describing a skeleton that he freely admitted was an "instance of a fossil human petrifaction" (Cuvier 1827: 407).

[a] In particular, he nowhere refers to the Bible in scientific argument. In fact, his claims concerning past history often conflicted with Scripture (Coleman 1962; Russell 1982). A creationist would say that the various types of organisms existing today are not only constant in form over time, but also that they have been constant since "the Beginning." Cuvier consistently argued the contrary (i.e., that new types regularly replace older types in the fossil record). Cuvier explained the abrupt appearance of new fossil forms in terms of immigration, not creation: "I only say that they did not originally inhabit the places where we find them at present, and that they must have come from some other part of the globe" (Cuvier 1827: 113; Russell 1982: 41–44). Nowhere did he advance the hypothesis of successive new creations (Russell 1982: 43). Moreover, since he consistently promoted the idea that there has been a temporal succession of forms in the geological record (*ibid*), he could not have believed the various types of organisms that exist today were specially created "in the Beginning."

the conclusion that all *natural* things evolve gradually from their precursors, while discontinuities, such as sudden saltations, are indicative of a *supernatural* origin, that is, indicative of intervention by the creator. All of his life Darwin took great pains to reconstruct a gradual evolution of phenomena that at first sight seemed clearly the result of sudden origins.

"In other words," says Gruber (1974: 126), "sometime in his Cambridge years, 1827–30, Darwin took cognizance of the proposition that in order to show something is of natural origin it must be shown that it evolved gradually from its precursors, otherwise its origins are supernatural. This formulation of the choices open to rational men remained a leitmotif throughout his life."

In Darwin's day many people considered rapid change unnatural. Many, especially those of the conservative upper crust to which Darwin belonged, felt any abrupt alteration was a threat to the social order. The French Revolution had recently strengthened acceptance in England of the idea that any sudden alteration was an inherent violation of the natural order. But the notion goes far back, to days when aristocracies strove to maintain the status quo. For example, in a Middle English translation of de Deguilleville's *Le Pèlerinage de la Vie Humaine*, Nature (personified) describes herself:

That that j do j do bi leysure,
For j am not hastyf,
And al mutacioun that is doon in haste j hate.[567]

(That that I do I do by leisure, for I am not hasty, and all mutation that is done in haste I hate). Anyone who opposed such views was branded a radical. Darwin seems to have harbored just such a traditional prejudice against sudden change, or at least to have been aware that many of his readers would hold such views.

It's no surprise, then, that Darwin's account of evolution does little to explain saltation, the abrupt production of new types of organisms. Certainly, his theory is lacking in this respect. Natural selection can have effect only if traits show variation. Virtually the only type of variation considered in the *Origin* is the minor sort seen in intrachromoset matings, not the major sort resulting from chromosomal mutations — the sort of variation, as Darwin describes it, seen in "a bird born with a beak 1/100th of an inch longer."[a] However, it is now generally recognized that saltation — if one thinks of stabilization processes as examples of saltation — is in fact a natural process, not a supernatural one. But the production of new types of organisms, through stabilization processes, was largely unrecognized in Darwin's day.

Darwin's emphasis on the claim that breeding was a process of accumulating

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[a] In a letter to Sir Charles Lyell dated January 22, 1865, Darwin used this example to illustrate the sort of variation that he thought natural selection worked on. In the next sentence he went on to say that "The more I work, the more I feel convinced that it is by the accumulation of such extremely slight variations that new species arise" (Darwin 1887: vol. III, 33).

tiny differences is puzzling since he admitted he could not observe such differences himself. In the *Origin* he states this inability explicitly:

> If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice; but its importance consists in the great effect produced by the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye — differences which I for one have vainly attempted to appreciate. Not one man in a thousand has accuracy of eye and judgment sufficient to become an eminent breeder.[568]

Presumably, then, not one person in a thousand had ever observed the sort of variation on which Darwin's theory is based, nor had he observed it himself!

Paleontologists' Objections. Mayr (1982: 508) notes that after the publication of the *Origin*, paleontologists objected to Darwin's claim that evolution is a gradual process and "insisted on the sudden origin of new types in the fossil record and on the total absence of intermediate types."[a] Adam Sedgwick and Louis Agassiz[b] were among the most prominent of these opponents. These scientists claimed fossil evidence for gradualistic evolution was entirely lacking. Today these knowledgeable naysayers are often dismissed as religious fuddy-duddies. But even the agnostic[569] Thomas Henry Huxley, Darwin's foremost advocate, saw inconsistencies in the geological record[570] and warned Darwin that any absolute claim that new types always arise gradually would be an unnecessary burden to the theory.[571]

Remarkably, even Darwin's close friend Sir Charles Lyell, the great proponent of the efficacy of gradual processes in geology, eschewed gradualism in the biological realm.[c] In his influential *Principles of Geology*, Lyell used Cuvier's arguments to reject the idea that evolution is gradual.[572] Lyell emphasized that the

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a. Elsewhere Mayr (1982: 617) comments that all the great leaders of paleontology during the late nineteenth and early twentieth centuries—Cope, Marsh, Dollo, Abel, Osborn, and Matthew—all explained the origins of new forms in terms of saltation.

b. Swiss-born American zoologist, paleontologist, and glaciologist Louis Agassiz (1807–1873) studied under Cuvier and became the leading American naturalist in Darwin's day and the world's foremost authority on fossil fish. Agassiz and Lyell were longtime friends and each admired the geological work of the other (Gould 1979). As Winsor (1979: 111) points out "an idea of descent with modification, though far from Darwin's, modeled on embryological development, was attractive to many of Agassiz's contemporaries. He [Agassiz] could perfectly well imagine such a process of transformation, but he saw no evidence of it actually having taken place." In his assessment of the evidence, new forms typically came into being abruptly, and then persisted without appreciable change, right up to the time of their extinction.

c. Although, in his explanations of evolution, Darwin seems to have been a strict gradualist, Lyell described how sudden huge catastrophes could occur through ordinary agencies, for example, an earthquake causing the Mediterranean to suddenly inundate the Caspian basin. See Lyell (1835: vol. III, 130).

typical fossil form does not change with time.[a] Much to Darwin's chagrin, his friend never accepted the idea of gradual natural selection.[573,b] Although he had been open-minded enough to help Darwin get the *Origin* published, Lyell himself seems to have been a saltationist. He asserted the geological record shows each fossil form has a date of first appearance and a date of extinction[574] and that it typically changes very little during the interim.[575] He said these "births and deaths" are spread fairly evenly over time,[576] so that the number of types surviving is smaller when the amount of elapsed time is greater.[577,c] Some types, he said (and such is in fact the case), survive for long ages unchanged. Thus, he writes (Lyell 1835: vol. III, 395), that "the Eocene testacea which still flourish may be said to have outlived several successive generations of the organic world, just as Nestor survived three generations of men."

This portrayal of evolution is fundamentally different from Darwin's, who emphasized the ongoing mutability of types, not their stability. According to Darwin, a hypothetical human population about to produce a new, nonhuman type would be initially homogeneous, but would, with time, break up into sub-populations. Due to a lack of interbreeding, these once-human sub-populations would gradually become more and more distinct as they took on differing traits (perhaps long ears in one group and hairy skin in another). Each sub-population would then divide into sub-sub-populations, each of which would gradually diverge in character from other sub-sub-populations, becoming less and less like humans (and less and less like each other). This process of division and divergence continues indefinitely. There is no sudden appearance of new types, as in Lyell's description. Instead, gradual change occurs along each separate line of descent. This is the basic account of evolution still

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[a] Because Lyell offered no explanation of how new fossil forms could appear suddenly, some authors have suggested he was a creationist. Lyell's actual outlook, however, seems to have been more complex. He believed God was the "First Cause" of every event, but that God had laid down natural laws that were the "intermediate" or "secondary" causes of events here on earth. In his view, scientific explanation was a matter of seeking out these secondary causes or natural laws (see Lyell 1835: Vol. II, 426). Lyell's true attitude can be judged from his response to comments on the topic made by his friend astronomer Sir John Herschel. In a letter Herschel asserted that the process producing new organisms, "could it ever come under our cognizance, would be found to be a natural in contradistinction to a miraculous process—although we perceive no indications of any process actually in progress which is likely to issue in such a result" (Wilson 1972: 439). In response, Lyell said he had left this point "to be inferred" in his book because he didn't think "it worthwhile to offend a certain class of persons by embodying in words what would only be speculation" (*ibid:* 439). Thus, it seems clear that Lyell believed new types of organisms actually are created by natural means, but that he didn't know what those means might be and didn't wish to offend anyone by speculating. Being circumspect is hardly the same as being a creationist.

[b] Even in his book, *The Antiquity of Man* (1863), in which he attempted to accommodate Darwin, Lyell refused to exceed the simple admission that the human race is "old" and nowhere said a fossil type gradually changes with time (Desmond and Moore 1991: 515).

[c] Lyell knew the proportion of extinct to extant forms in a given stratum progressively rises with a stratum's age and used this insight to establish the relative ages of geological formations located in different parts of the world (Lyell 1835: vol. III, 395).

given in modern neo-Darwinian theory (the notion of divergence long predates Darwin and can be traced back as far as the seventeenth century; see p. 227).

Darwin's ideas of intermediacy contrast starkly with those of Lyell. When Lyell spoke of intermediacy, he referred to the status of an assemblage of types of organisms making up the flora and fauna as a whole (any given form within such an assemblage was, however, unchanging from “birth” to extinction). Thus, he would have said that the faunal assemblage that existed in North America 10 million years ago was generally intermediate between the assemblage that existed there 20 million years ago and the one that exists today. But Darwin used the word *intermediate* to refer to a link in a single, gradually evolving lineage. He said that a new forms typically arise via a process where one form gradually changes until it becomes a new form.

Darwin's Gaps. The expectation under Darwin’s assumption of strict gradualism is to see each fossil form slowly transforming into descendant forms in a more or less continuous evolutionary sequence. But 27 years after Cuvier's death, Darwin himself admitted the paleontologists of his day had still not found intermediates between fossil types. Thus, in the *Origin* he writes:

> Geological research, though it has added numerous species to existing and extinct genera, and has made the intervals between some few groups less wide than they otherwise would have been, yet has done scarcely anything in breaking down the distinction between [fossil] species, by connecting them together by numerous, fine, intermediate varieties; and this not having been effected, is probably the gravest and most obvious of all the many objections which may be urged against my views.[578]

Darwin explained away this absence of "numerous, fine, intermediate varieties" by asserting that the geological record was "extremely imperfect." He claimed this imperfection (which was supposedly so extreme that gradual evolution would not be observed in the fossil record even if it had occurred) was the reason "why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduating steps."[579]

This argument ran counter to the opinions of Adam Sedgwick.[a] Sedgwick was

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a. According to Milner (1993), Adam Sedgwick (1785–1873) had an "essentially generous and placid nature" and was "much beloved by many generations of geology students." Modern writers have often condemned Sedgwick because he was, in his youth, a proponent of the claim that geological evidence demonstrated the past occurrence of the biblical flood. But such was the view of many, perhaps most geologists of his time. In 1831, after reading Lyell’s *Principles of Geology,* he publicly recanted his former position: “Having once been myself a believer and, to the best of my power a propagator of what I now regard as a philosophic heresy … I think it right, as one of my last acts before I quit this Chair [as president of the Geological Society], thus publicly to read my recantation. We ought, indeed, to have paused before we first adopted the diluvian theory, and referred all our old superficial gravel to the action of the Mosaic Flood. For of man, and the works of his hands, we have not yet found a one of the foremost geologists of the day. The namer of the Cambrian Period, he served as president and vice-president of the Geological Society of London. Just before Darwin embarked for his voyage aboard the *Beagle*, Sedgwick had given him a crash course on geology and the techniques of fossil collection. Although he remained on cordial terms with Darwin in later life, Sedgwick rejected the idea of the gradual origin of new types of organisms through divergence and natural selection, and he rebuffed Darwin's assertion that the fossil record is excessively fragmentary.[580] In a review (Sedgwick 1860) of the newly published *Origin*, he asserts that "in the great stages of the Palaeozoic series (through Cambrian, Silurian, Devonian, and Carboniferous rocks) we have in each a characteristic fauna; we have no wavering of species … and they preserve their typical forms till they disappear."[a] He goes on to state his exact objection to an argument based on gaps in the fossil evidence: "if you deny my conclusion grounded on positive evidence, I toss back your conclusions, derived from negative evidence — the inflated cushion on which you try to bolster up the defects of your hypothesis … I see no proofs of enormous gaps in geological time … Where do the intervening and connecting types exist, which are to mark the work of natural selection? We do not find them."

The Missing Links are Still Missing. Nevertheless, Darwin continued to express faith that his "gaps" would eventually be filled by the work of future generations of paleontologists. Several of those future generations are now past, but the evidence gathered during the interim has only strengthened the view that the pattern seen by Cuvier is indeed typical, and that cases are rare in which one fossil type changes gradually into another. Milner (1993: 199) summarizes the glaring problem with Darwin's argument: "Another century of fossil discoveries, he believed, would fill in the picture. In fact, many transitional forms have since come to light, but they are still comparatively rare." More specifically, there seem to be very few examples of gradual evolution as Darwin described it. That is, of a single type gradually changing over evolutionary time until it becomes a new, morphologically distinct type. If there

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single trace among the remnants of a former world entombed in these deposits" (see Sedgwick 1831).

[a] Darwin sent a copy of the *Origin* to Sedgwick on its publication. In a letter dated 24 Nov. 1859 (see and Smith 1991), Sedgwick gave Darwin his assessment: "If I did not think you a good tempered & truth loving man I should not tell you that (spite of the great knowledge; store of facts; capital views of the correlations of the various parts of organic nature; admirable hints about the diffusions, thro' wide regions, of nearly related organic beings; &c &c) I have read your book with more pain than pleasure. Parts of it I admired greatly; parts I laughed at till my sides were almost sore; other parts I read with absolute sorrow; because I think them utterly false & grievously mischievous — You have deserted—after a start in that tram-road of all solid physical truth — the true method of induction — & started up a machinery as wild I think as Bishop Wilkin's locomotive that was to sail with us to the Moon. Many of your wide conclusions are based upon assumptions which can neither be proved nor disproved. Why then express them in the language & arrangements of philosophical induction?"

are *any* such cases, then they are at best very rare. Indeed, paleontologists Stephen Stanley and Derek Ager (1979) state that "the known fossil record fails to document a single example." Instead, Stanley (1981) says, there is a very marked tendency for each fossil form to appear abruptly, remain stable in form for long periods of time thereafter, and then to go extinct:

> The record now reveals that species typically survive for a hundred thousand generations, or even a million or more, without evolving very much. We seem forced to conclude that most evolution takes place rapidly … After their origins, most species undergo little evolution before becoming extinct.

Moreover, major portions of the fossil record are now very well known and lack the gaps upon which Darwin's argument depends. For example, for any widespread marine organism, the fossil record is virtually continuous from the Cambrian, which ended almost 500 million years ago, to the present. The question then must be asked: Is it reasonable to base a general theory on what appears to be a rare phenomenon? Aristotle weighed in on this point. Thus, he writes (*History of Animals,* I, 6),

> We must not accept a general principle from logic only, but must prove its application to each fact. For it is in facts that we must seek general principles, and these must always accord with facts. Experience furnishes the particular facts from which induction is the pathway to general laws.[581]

It is not enough to say, as did Ernst Mayr (1963: 436), one of the most eloquent proponents of gradualism, that "the 'missing links' between most of the major categories of vertebrates have been found in the 100 years since Darwin." These are not the "missing links" that pose a difficulty for neo-Darwinian theory. The problem is not to show there are distinct stable types, intermediate in form between other distinct stable types (such types would be expected to occur even if evolution were strictly saltational). The challenge, for anyone who claims that gradualistic evolution is the norm, is to document cases in which a single fossil form gradually changes into a distinct fossil form. Moreover, it would not be enough merely to show such transformations have occurred. It would in fact be necessary to show such transformations are *typical* of fossil forms. But it seems clearly documented cases are scarce at best.[a] Certainly, then, there is no reason to suppose it is typical to observe

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a. Kucera and Malmgren (1998) say even those few studies purporting to demonstrate phyletic gradualism often suffer from a serious logical flaw. When a new form arises suddenly and the form it arose from then gradually dies out, they say (*ibid:* 60) sample means for the morphological characters distinguishing the new form will seem to show a gradual shift over time. However, as they point out, this is a mere artifact caused by calculating means using samples that include both the new type and a declining old type. For example, in their own study those authors evaluated two foraminiferans, the conical *Contusotrucana contusa,* and its flat ancestor *C. fornicata*. What at first seemed to be a gradual increase in conicity from *C. fornicata* to *C. contusa,* turned out to be a gradual increase of the *mean value* for "conicity" one fossil type gradually changing into another. Moreover, given that gradual evolution is by definition a very slow process, we have no hope of observing it anywhere if not in the fossil record. Therefore, the idea that new types of organisms typically arise gradually, in reproductive isolation, remains a belief without definitive empirical support. Whereas the origins of many forms produced by stabilization processes are now known evolutionary fact.

Saltation versus Gradualism. During the eighty years following the publication of the *Origin,* many naturalists had saltationist views. Mayr comments that "Among those who accepted evolution after 1859 were not a few who were far more impressed by the occurrence of sudden mutations than was Darwin. Botanists and horticulturalists, in particular, cited numerous cases … where a strongly deviant type suddenly originated. … By the end of the 1880s this apparently had become the prevailing opinion."[582] Prior to Darwin virtually all evolutionists had been saltationists.[583] Étienne Geoffroy Saint-Hilaire (1772–1844), for example, thought birds must have arisen from dinosaurs by saltation.[584] If anything, Cuvier was a more extreme saltationist than Geoffroy. Geoffroy said that new organs always arise by modification of ones preexisting in ancestral forms. "Cuvier, on the other hand," says Russell, "was always ready to admit Nature's power to form entirely new organs in response to new functional requirements."[585] Karl Ernst von Baer (1792–1876), the founder of embryology, was a saltationist.[586] In a series of essays[587] he criticized Darwin's theory and instead explained evolution in terms of saltations guided by a vaguely defined "tendency to perfection." Richard Owen (1804–1892), the English comparative anatomist and paleontologist, "conceived change to have taken place by abrupt variation, independent of environment and habit."[588] In his *Anatomy of Vertebrates* (1866–1868), he says this change takes place through "departures from parental type, probably sudden and seemingly monstrous, but adapting the progeny inheriting such modifications to higher purposes."[589] William Bateson (1861–1926), coiner of the word *genetics,* wrote, "Species are discontinuous: May not the variation by which species are produced be discontinuous too?"[590]

Some had more balanced views. For example, Albert von Kölliker (1817–1905), the Swiss zoologist and histologist, entertained notions of evolution through

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subsequent to the abrupt appearance of the *fully* conical *C. fornicata.* The mean shifted gradually because the flat *C. fornicata* specimens gradually declined in number over time as they died out (not because the conic *C. contusa* form gradually arose by slow alterations from the flat *C. fornicata* type). Studies claiming to demonstrate phyletic gradualism appearing to suffer from this sort of logical deficiency include Arnold (1983), Hunter et al. (1988), and Malmgren and Kennett (1981). To demonstrate phyletic gradualism one must show one fossil form gradually changes into another. To do this, one must first show (1) that each of a series of temporal samples is internally invariate with respect to the traits defining the form in question (that is, the possibility should be eliminated that the samples might contain individuals of two distinct stable types that are merely changing in relative frequency over time); and (2) that the members of the series gradually change over time so that they connect the ancestral and descendant forms.

saltation, but thought evolutionary change could also occur gradually. In his critique of Darwin's theory (*Über die Darwin'sche Schöpfungstheorie,* 1864), he maintained that "no transitional forms between existing species are known"[591] and proposed his own theory of heterogeneous generation. "The fundamental idea of this hypothesis," he said, "is that under the influence of a general law of evolution creatures produce from their germs others which differ from them."[592] But Kölliker did not stress saltation. In fact, he wrote that a "difference between the Darwinian hypothesis and mine is that I postulate many saltatory changes, but I will not and indeed cannot lay the chief stress upon this point, for I have not intended to maintain that the general law of evolution which I hold to be the cause of the creation of organisms, and which alone manifests itself in the activity of generation, cannot also so act that from one form others quite gradually arise."[593,a] Darwin's friend Thomas Henry Huxley, too, felt that evolution could be either gradual or saltatory. In his review of the *Origin*, he wrote that

> Mr. Darwin's position might, we think, have been even stronger than it is if he had not embarrassed himself with the aphorism, "Natura non facit saltum," which turns up so often in his pages. We believe, as we have said above, that Nature does make jumps now and then, and a recognition of the fact is of no small importance in disposing of many minor objections to the doctrine of transmutation [i.e., Darwin's theory].[594]

Bateson (1894: 15) also bemoaned the "gratuitous difficulties which have been introduced by this assumption." Indeed, Darwin here adopted the exact expression (*"natura non facit saltum"*) the Scholastics had employed for centuries to express the idea that the "natural order" exhibited a continuous range of variation, their so-called "Law of Continuity" (see p. 136).[595]

Others, however, thought Darwin's emphasis on minor change had not gone far enough in eschewing saltation. In 1867, a Scottish engineer, Fleeming Jenkin, attacked Darwin's theory in the June issue of the *North British Review.* Though Darwin had given saltational changes (which he called "single variations") short shrift in the first four editions of *Origin,* Jenkin's article convinced him that he had not been stringent enough. In a letter to Alfred Russel Wallace, Darwin wrote,

> F. Jenkin argued in the 'North British Review' against single variations ever being perpetuated, and has convinced me … I always thought individual differences more important; but I was blind and thought that single variations might be preserved much oftener than I now see is possible or probable.[596]

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a. Saltationists often referred to vaguely defined laws governing evolution and they were frequently associated with the orthothogenetic, or vitalistic movement. Proponents of orthogenetic evolution claim that evolution is purposeful and directed. Vitalism is a doctrine claiming that the processes of life are not explicable by the laws of physics and chemistry alone. These thinkers made the error of attempting to explain a real, observed phenomenon (saltation) in terms of unobserved, undocumented phenomena (e.g., "vital impulse").

In the fifth edition of the *Origin* (1869) Darwin added a section further emphasizing his belief that selection of small individual differences was the paramount evolutionary force. After discussing a hypothetical case involving selection between slim and stocky wolves, he wrote the following:

> It should be observed that, in the above illustration, I speak of the slimmest individual wolves, and not of any single strongly-marked variation having been preserved. In former editions of this work I sometimes spoke as if this latter alternative had frequently occurred. I saw the great importance of individual differences, and this led me fully to discuss the results of unconscious selection by man, which depends on the preservation of the better adapted or more valuable individuals, and on the destruction of the worst. I saw, also, that the preservation in a state of nature of any occasional deviation of structure, such as a monstrosity, would be a rare event; and that, if preserved, it would generally be lost by subsequent intercrossing with ordinary individuals. Nevertheless, until reading an able and valuable article in the 'North British Review' (1867), I did not appreciate how rarely single variations, whether slight or strongly-marked, could be perpetuated.[597]

Saltation and Stasis. The battle between the gradualists and the saltationists, which is further discussed in Chapter Seven, continued until the 1940s, when a strong intellectual shift occurred. Gradualism then became the ascendant perspective among biologists. But in the early 1970s paleontologists Niles Eldredge and Stephen Jay Gould raised the flag of saltation once again.[598] Their 1972 article caused an evolutionary uproar that has not subsided to this day. As had many of their saltationist colleagues in years gone by, they emphasized that a wide variety of fossil types 1) arise suddenly and 2) are static thereafter. Gould (1980a: 182) later expressed the problem succinctly:

> The history of most fossil species includes two features particularly inconsistent with gradualism: (1) *Stasis.* Most species exhibit no directional change during their tenure on earth. They appear in the fossil record looking much the same as when they disappear; morphological change is usually limited and directionless. (2) *Sudden appearance.* In any local area, a species does not arise gradually by the steady transformation of its ancestors; it appears all at once and "fully formed."

For years Eldredge had sifted through fossils trying to document examples of slow, steady directional change. Instead he found that "once species appear in the fossil record, they tend not to change very much at all. Species remain imperturbably, implacably resistant to change as a matter of course — often for millions of years."[599] For example, over an eight-million-year period, the only detectable alteration in one of the trilobites Eldredge had been studying was a slight change in the structure of its compound eyes, the number of lens-rows dropped from eighteen to seventeen.[600] Eldredge (1995: 68) asserts paleontologists have hesitated to emphasize the observed pattern of stasis in the fossil record because it is inconsistent with neo-Darwinian theory: “For the most part it has been paleontological reluctance to cross swords with Darwinian tradition that accounts for the failure to inject the empirical reality of stasis into the evolutionary picture."

But exacting studies like Eldredge's really serve only to emphasize the existence of a phenomenon that most people could infer on the basis of ordinary experience. Look at any guide to the identification of fossils. Each of the listed types must be relatively stable — otherwise the pictures and descriptions provided by the guide would be useless. For each type, a guide specifies a particular time range during which that form existed. Outside that range, the type in question is not known to exist. Each type remains identifiable by its description and/or picture over the entire period of its existence, from its first appearance to extinction. The very fact that such guides can be used to identify fossils, then, shows that fossil forms are stable. If the typical fossil form changed gradually over time until it became a new form, then a picture in a guidebook would allow identification of only a particular stage in such a transitional process. Other stages would not match the picture. But, typically, a single picture does in fact suffice to identify a fossil form during any period of its existence. Each particular fossil form is not only recognizably distinct, but also stable in form over the entire period in which it is known to exist. That is, each has a characteristic set of traits retained largely unchanged. Each such form appears in the fossil record at a certain lowermost stratum with its peculiar set of traits that remains stable up to the time of the form's extinction. This is the typical pattern seen in fossils.

Many types of organisms existing today have persisted unaltered for vast ages. This fact has long been known. Even Huxley, Darwin's most ardent supporter, was aware of it. In the *Origin*'s year of publication (1859) he gave a lecture entitled *On the Persistent Types of Animal Life.* In it he noted that

> certain well marked forms of living beings have existed through enormous epochs, surviving not only the changes of physical conditions, but persisting comparatively unaltered, while other forms of life have appeared and disappeared. Such forms may be termed "persistent types" of life; and examples of them are abundant enough in both the animal and the vegetable worlds. Among plants, for instance, ferns, club mosses, and *Coniferæ,* some of them apparently generically identical with those now living, are met with as far back as the Carboniferous epoch [which ended nearly 300 million years ago]; the cone of the oolitic [i.e., 135–152 million years ago[a]] *Arancaria* is hardly distinguishable from that of existing species; a species of *Pinus* has been discovered in the Purbecks [which date to about 144 million years ago[b]], and a walnut (*Juglans*) in the cretaceous rocks [the Cretaceous Period ended about 65 million years ago]. All these are types of vegetable structure, abounding at the present day; and surely it is a most remarkable fact to find them persisting with so little change through such vast epochs. Every subkingdom of animals yields instances of the same kind.[601]

The cassowary (*Casuarius casuarius*), the second-largest extant bird, is known from 24-million-year-old deposits.[602] Fossil insects, preserved in amber for long eons of

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[a] The Yorkshire Oolite Rocks date to Upper Jurassic about 135–152 mya.

[b] The Purbeck Formation of Durlston Bay, Dorset, brackets the Jurassic/Cretaceous boundary (~144 mya).

time are often indistinguishable from living ones.[603] In an article describing his experience examining ancient insects in Harvard's Museum of Comparative Zoology, Paul Zahl (1978: 237) makes the following comment on fifty-million-year-old amber-preserved specimens in the museum's collection:

> In each was a fly, ant, grasshopper, beetle, or spider, all perfectly lifelike as though some magic wand had cast the spell of frozen sleep upon them. [They looked] singularly like the fly, ant, grasshopper, beetle, or spider in my own garden. Had evolution overlooked such genera during the intervening fifty thousand millennia?

Many of the crocodilians (alligators, crocodiles, caimans, gharials) have apparently persisted without change for some 200 million years (2000 times the "lifetime" of *Homo sapiens*). Stokes (1982: 510) states that the inarticulate brachiopod *Lingula anatina* "appeared first in the Cambrian and has persisted without change through a life history of innumerable generations spread over at least 500 million years." Extant animals such as the horseshoe crab once dodged the tread of dinosaurs.[a] The Dawn Redwood (*Metasequoia glyptostropoides*) was once known only from fossils. This tree, dating back to at least the Upper Cretaceous (about 70 million years ago), was discovered alive in China in 1941. Modern specimens are nearly identical to the ancient fossils.[604] Unchanged from the time of the dinosaurs, it is now popular with landscapers here in the United States. Schindewolf (1993: 190) notes that in the ideally preserved remains of 220-million-year-old (Triassic) triopsid crustaceans from the Keuper formation in Franconian region of southwest Germany,

> Every detail of the structure of the body and its most delicate appendages can be made out — the eyes, the antennae, the mandibles, with their serrated masticatory surfaces, the maxillae, with their rows of fine bristles, the filmy swimmerets (exopodites and endopodites) set with bristles, the brood chamber filled with eggs, and much more. As a consequence, a very detailed comparison with the Recent species *Triops cancriformis* could be made, and the author stresses that even the most minor characters were identical.

Romer (1966: 129) says *Homoeosaurus*, a contemporary of early dinosaurs (Jurassic Period), “appears to have been almost identical in structure” with a modern lizard, the tuatara (*Sphenodon punctatus*), now confined to islands off the coast of New Zealand. The fossils of the modern ocean-dwelling mollusc *Neopilina galatheae* can be found alongside extinct 350-million-year-old trilobites.[605] The ostracod *Sylthere vonhachi* is known from the Upper Ordovician (i.e., prior to 490 mya) and still exists today.[606]

How do living forms persist so long without change? The cases cited are glaring. But the typical organism in the fossil record shows the very same pattern on a more modest time scale. The only difference is that, in the usual case, a fossil form exists

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[a] The extant horseshoe crab (*Limulus*) actually predates the dinosaurs. The history of this trilobite-like animal began in the time of the trilobites, more than 300 million years ago, in the Paleozoic Era. It looked the same then as it does today.

unchanged for millions, rather than hundreds of millions, of years. Neo-Darwinian theory would say this stability is imposed by functional restrictions on form dictated by the environment. But are environmental constraints really so demanding? Over such long time periods, it seems radical changes in the environment must have occurred. Is it plausible that the environment, especially an environment altered greatly with time, should be able rigidly to control and stabilize the form of every part of an organism?

As Bowler (1989: 337) notes, by the 1970s many paleontologists had become dissatisfied with gradualistic explanations of evolution

> because many of the classic examples of gradual change had not withstood the test of modern techniques. If there were no genuine cases of gradualism in the record, then the argument for treating all cases of sudden change as the result of imperfect [fossil] evidence was undermined. It might be better to reexamine the evidence in a new light, putting aside the traditional Darwinian assumption of gradualism and opting instead for a model of evolution that would allow for the sudden appearance of new forms as indicated by the fossil record.

The abruptness of the paleontological data is still clearly at odds with gradualistic explanations of evolution, just as it was in Cuvier's day. As Winsor (1979: 112) notes

> Even species that resemble one another in all but the most trivial details are seen to maintain their particular distinctness generation after generation, often for millions of years. It takes a very determined and sympathetic searcher to find any transformations in nature comparable to the appearance of domestic breeds, and such forms are not regarded as species.

If anyone, could be described as a "very determined and sympathetic searcher," it was Ernst Mayr. He, too, admits saltation is the typical pattern: Although he maintains that a "certain proportion" of fossil forms undergo gradual change into subsequent forms,[a] "far more frequently," he says, "the extant species are supplemented by — or the extinct species are replaced by — new species that turn up in the fossil record. In the classical literature this sudden introduction of new species was usually ascribed to instantaneous saltations."[607] As Gould (1980a: 189) puts it, "All paleontologists know that the fossil record contains precious little in the way of intermediate forms."

Peripheral Isolates. It is a key assumption of neo-Darwinian theory that mutations occur at random so that they are spread fairly evenly over time. An even pattern of mutation such as this does little or nothing to explain the abrupt appearance of new forms seen in the fossil record. If evolutionary change is to be abrupt, mutation must

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[a] Mayr cites a single paper Gingerich (1976) for this claim that a "certain proportion of lineages" undergo gradual evolution. Gingerich's study covered only four fossil mammal forms from the Paleocene and Eocene. So it seems — even if one granted that Gingerich's claims of gradual evolution were supported by his data — that "minuscule proportion" would have been more appropriate than "certain proportion."

be concentrated in a single, brief interval of time. But conventional theory does offer explanations, however unsatisfactory they might be. One commonly proposed mechanism supposes that rapid change can occur in "peripheral isolates."[608] Here, a small sub-population of individuals is pictured as breeding in isolation from others of their own kind. Due to the small size of population, some variants (i.e., alleles) of certain genes are lost from the reproductive process by chance. The supposed result is the production of a new type of organism with a new set of traits distinguishing it from the old one. These new traits are generally imagined to be advantageous, permitting the new type to compete with and rapidly supplant preexisting types. Speaking of himself in the third person, Ernst Mayr (1982: 617), who first proposed the peripheral isolates scenario (Mayr 1963), comments that his explanation

> was ignored by paleontologists until used by Eldredge and Gould (1972) [who, Mayr says …] accepted Mayr's interpretation that such new species had originated somewhere in an isolate (peripheral or not) and were able to spread far and wide if they were successful.[609] This interpretation of the 'introduction of new species' (as Lyell called it 150 years earlier) agrees well with the fossil record.

But no population treated as a species is actually known to have had its origin via peripheral isolation. Or, at the very least, if any such populations are known, they are far less numerous than the many forms treated as species now known to have been produced by stabilization processes. Alleged examples of populations produced in peripheral isolation are typically anecdotal. Alternative hypotheses accounting for their origins are not excluded on any logical basis. For example, the distinctive traits of an equatorial penguin might plausibly be explained as a matter of peripheral isolation. Nevertheless, other origin stories (e.g., migration, hybridization, environmental effects on phenotypic plasticity) might seem equally plausible. It seems that in all such cases the actual mode of origin is attributed to peripheral isolation, but is actually unknown and seems never to have been documented.

Moreover, logically speaking, we have no reason to suppose that peripheral isolation should be able to produce organisms that are genuinely new — Alleles may be lost from a population under such circumstances, but no new ones will be introduced because the only genetic changes that can occur are due to ordinary meiotic recombination within a chromoset (see Chapter 3). Even with artificial or natural selection, no new alleles would appear (because selection is an eliminative process, not a creative one). Unless a point mutation occurs in a gene — an exceedingly rare event — no new alleles can be introduced into a closed population. In particular, in the case of the peripheral isolates scenario, it is safe to assume no mutations whatsoever occur (since this process is supposed to be rapid, there is no time). If alleles are selected against and lost, the only possible result is a decrease in genetic variability: Any new set of alleles present in a supposedly new type of organism generated by such a process, then, would be a mere subset of those alleles already seen in the preexisting population. As Mayr himself says (1963: 393) "Many of the peripheral populations, particularly the more isolated ones, are established by a single fertilized female or a small group of founders which carry only a fraction of the total genetic variability of the species." Therefore, there seems to be no real potential for the evolution of any new traits under such circumstances. Even if genetic divergence and significant morphological novelty could be produced in such peripheral populations, any organisms thus produced would almost certainly still be able to mate freely with individuals of the preexisting type. What, then, would prevent the preexisting population from simply reabsorbing the new population as soon as the two came back into contact? Moreover, the process described in the peripheral isolates scenario is an extreme form of inbreeding (the mating of closely related organisms). It is well known that inbreeding tends to bring out deleterious, or even lethal, traits. So it seems unlikely such a process would be likely to produce a superior new type of organism capable of displacing preexisting types.

Consideration of a concrete example suggests the shortcomings of the peripheral isolates scenario. Suppose ten caged tigers were allowed to breed. Suppose the number of tigers was kept small in every generation. How long would it be before those tigers suddenly became something other than tigers? How long would it be before they became physiologically incompatible in matings with normal tigers, so that interbreeding of the two types produced hybrids of low fertility? If, after its sudden appearance, this supposedly new type of organism were released from its cage, would it be likely to spread and quickly replace normal tigers? At the very least, it is fair to say that we have no reason to suppose the typical form treated as a species comes into being in such a manner.

Speedy Gradualism. Another attempt to resolve the contradiction between neo-Darwinian theory and the fossils is the "speedy-gradualism" argument: If change occurs rapidly during a single time period, but not for millions of years thereafter, the pattern might seem saltational. But what if this "short" period of change lasted 20,000 years? Wouldn't it be reasonable to simply change the meaning of "gradual" and say that while 20,000 years is not a million years, it's still a very long time, plenty of time for gradual selection and everyday genetic phenomena to take their course and create a new type of organism? This argument was proposed as an explanation of one of the best-documented cases of saltation, the Turkana mollusks described by P. G. Williamson (1981). The speedy gradualists say some shift in the environment forced Williamson's mollusks to change, that the changes occurred "gradually" during a relatively brief (20,000-year) transition period, with the environment stabilizing thereafter, maintaining the new types unchanged for millions of years.[a] But this is not the picture painted in the *Origin.* There, Darwin explicitly states his views: “natural selection can act only by taking advantage of slight successive variations; she [i.e., Nature] can never take a leap, but must advance by

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a. Williamson, himself, does not accept this explanation. Instead he suggests, following Gould, that some form of “developmental constraint” (or “homoeostasis”) holds fossil forms constant. But the genetic basis of developmental constraint is, as Williamson himself admits (1981: 215) “obscure.” In Chapter 7 of this book an explicit genetic explanation of stability is presented.

the shortest and slowest steps."[610] In this kind of evolution, variation arises randomly over time, and is not concentrated in a single, brief interval. But the fact that fossil types appear to come into being abruptly is not the most serious difficulty confronting neo-Darwinism. As Williamson (1981) points out,

> The principal problem [with the available paleontological data] is morphological stasis. A theory is only as good as its predictions, and conventional neo-Darwinism, which claims to be a comprehensive explanation of the evolutionary process, has failed to predict the widespread long-term morphological stasis now recognized as one of the most striking aspects of the fossil record.

Moreover, Williamson says the appearance of new types of mollusks was "initially accompanied by a major increase in phenotypic variance." But orthodox theory says individual variation does not increase in response to changes in the environment. On the other hand, an initial increase in variation actually can be the expectation under stabilization theory. In particular, in the case of recombinational stabilization, such variability is expected. The more distant the cross initiating the process, the higher the expected level of variation, as long as later-generation hybrids can be produced (Soliman 1992: 199). Later stages of the process are characterized by increasing uniformity because many of the variants produced are too infertile and/or inviable to meet the challenge of continued existence. They are displaced by the few that do.

Conclusion. It seems fair to say the foregoing facts indicate that the burden of proof is now on the proponents of neo-Darwinian theory. Typically, forms of known origin are derived from stabilization processes (see chapters 4 and 5). The single potential source of evidence demonstrating the occurrence of the gradual processes described in orthodox theory, the fossil record, fails to provide evidence that new types of organisms normally arise in a gradual manner. Far from it! The typical fossil form has an abrupt origin and persists largely unchanged thereafter. There may be some few cases where the changes observed in a fossil form are consistent with gradualistic scenarios. But cases consistent with stabilization theory are far and away more typical. Neo-Darwinism, then, which claims evolution is mainly a matter of the gradual accumulation of differences between diverging populations over time, is inconsistent with the usual pattern of change documented by paleontological data (punctuated equilibrium).

Someone unfamiliar with the dogmas of evolutionary biology might say facts should outweigh theory. But faith in any accepted theory can cast doubt upon the reliability of conflicting evidence. If a piece of data seems to overturn a widely accepted rule, then that datum is scrutinized and scrutinized again. This kind of prejudice is as old as science itself. With his telescope, Galileo found evidence contradicting the long-accepted view that the earth stood at the center of the universe. Nevertheless, scholars of his time were so steeped in tradition that they either refused to look through his telescope or, when they did, doubted the evidence of their own eyes. They were convinced Galileo was somehow tricking them. Instead they relied on tradition and authority. As one of these men put it: “I have as witnesses most excellent men and noble doctors … and all have admitted the instrument [Galileo’s telescope] to deceive.”[611]

Some of my colleagues have even told me they are convinced there would be more evidence for gradualistic evolution if only fossils provided more information about soft anatomy. The right kind of evidence just hasn't been preserved, they say. But ideally preserved fossils *do* provide a great deal of very detailed evidence on soft anatomy (any reader who doubts this should reread Schindewolf's description of the triopsid crustacean *Triops cancriformis* on p. 158) and that evidence, too, is strongly consistent with the idea that saltational evolution is typical. I, for one, cannot accept the idea that we should assume gradual evolution is widespread when there is so little observational data to support it. Are we to be free to imagine any phenomenon unsupported by observation exists even though we are unable to observe it? Everyone knows that such a perspective is altogether antithetic to normal scientific practice. It paves the way for unicorns, supernatural beings, and any number of other phantasms.

Attempts to reconcile fossil data with gradualistic evolutionary theory have led to implausible scenarios (peripheral isolates, speedy gradualism). However, the data is in fact consistent with the idea that stabilization processes frequently produce new types of organisms. Why does theory ignore the fact that saltation is the normal mode of evolution seen in the fossil record? Hasn't the time come for us to take our paleontologist colleagues' findings fully into account? According to the apostle Paul, "faith is the substance of things hoped for, the evidence of things not seen."[612] But the evidence of science, the accepted criterion of the empirical tradition, is the evidence of things that actually *are* seen. Is gradualism the religion of biology?

7 The Unknown Force

There may be an unknown factor that will cause quite as great a surprise as Darwin's.
—HENRY FAIRFIELD OSBORN
The Hereditary Mechanism and the Search
for the Unknown Factors of Evolution (1895)

The distinction between the saltationist and gradualist perspectives is more than a question of temporal pattern. It is also more than a simple disagreement over the size of the steps in evolution. After all, "big" and "small" are always relative. Gradualists say evolutionary changes are "minor" and "continuous." Saltationists say they are "major" and "discontinuous." But what do these words really mean? At some level, evolution has to be discontinuous because genes themselves are particulate. An organism either receives a given gene from its parents or it doesn't. It can't receive 32.4 percent of a gene. Thus, in a diploid organism, the offspring receive one copy of a particular version (allele) of a gene, or two copies, or no copy at all. There are no other possibilities. So, even with simple intrachromoset meiotic recombination, there is a jump: zero to one, one to two, two to one, …

At the heart of the gradualist perspective is the idea that the forces creating new types of organisms are “ordinary." The genetic processes that acted in the past to create new types of organisms are supposed to be the same as those acting at the present day in the ordinary production of offspring. The same process acts not only in the short run to produce offspring, but also in the long run to produce types quite distinct. As Gould (1980b: xiii) remarks, this gradualist evolutionary perspective, which has dominated biological thought since the 1940s, has "its central emphasis upon continuity in process and cause for all evolutionary events from the spread of alleles in local populations to major trends in the history of life." In short, gradualistic accounts of evolution are strongly associated with the uniformitarian perspective. Darwin himself was a uniformitarian, an outlook he took from Lyell. This uniformitarian argument is eminently reasonable when properly applied, but it is often misinterpreted.

Scientists often shy away from admitting that some natural forces are still unknown or that forces active in the past are no longer in operation. So long as known forces can reasonably explain the phenomenon in question, this attitude is entirely justifiable. But sometimes the previous existence of a force can be inferred from its effects, even though the nature of the force itself is unknown. Cuvier believed the house-sized boulders scattered over Europe proved vast, violent floods had overwhelmed the land in bygone eras.[613] Because he could not fathom the cause of these catastrophes, he vaguely attributed them to "the operation of problematical causes."[614] The nature of the force that could wreak such devastation was, for Cuvier, a burning question. Thus, regarding his own attempts to resolve this issue, he confessed that "these ideas have haunted, I may almost say have tormented me."[615]

Although he knew nothing of past ice ages, Cuvier had been right in assuming some unknown, "problematical cause" had been at work; for he had never realized such great stones ("glacial erratics") could be carried from the place of origin to their current positions by glaciers or that much of Europe had once been buried beneath a massive layer of ice. This fact remained unknown during his lifetime. His student, Louis Agassiz, first proposed the radical idea that periodic ice ages had occurred in prehistoric times and that glaciers had carried erratics to their present positions. As a good uniformitarian geologist, the usually astute Lyell opposed Agassiz's ice age theory.[616] No such forces are active today, Lyell reasoned; therefore we should deny they were active in the past. Of course, he was mistaken. What known force did Lyell think it was that had moved boulders weighing thousands of tons, many miles from their known origins? Not gradual sedimentation, surely.

The reader might suppose the ideas expressed in stabilization theory represent a radical rejection of traditional biological thought. But this alternative explanation of how evolution occurs can in fact be interpreted as a modern manifestation of an alternative scientific tradition in which many naturalists have claimed evolutionary change is saltatory. Therefore stabilization theory is neither radical, nor indeed is it even novel with respect to many of its tenets. It merely supplies an explicit explanation for the discontinuities long emphasized by saltationists. In the past, adherents of this intellectual faction were at a disadvantage because they lacked well-documented examples of processes producing saltatory change. Scientists of this school believed evolution was saltatory, but they knew of no force that might produce such change. And yet, they were convinced some such force *must* exist; for in their view, forms treated as species seemed to be discrete, stable types unconnected by morphological intermediates.

A recurrent theme in saltationist thought was the idea that the forces involved in ordinary reproduction are distinct from those producing forms sufficiently distinct to be treated as a species. Saltationists were not satisfied with the idea that the production of new types of organisms is simply a matter of the gradual accumulation of minor variation over time. Like Cuvier with his glacial erratics, they sought an unknown force. As Sedgwick put it: "a new phenomenon unaccounted for by the operation of any *known* law of Nature" (italics are Sedgwick's).[617] In his *Address to the British Association* (1858), Richard Owen pointed out that "it may be well to bear in mind that by the word 'creation' the zoologist means 'a process he knows not what.'"[618]

This attitude is exemplified in the writings of Henri Milne-Edwards (1800–1885). As did virtually all French naturalists of the nineteenth and early twentieth centuries,[619] Milne-Edwards rejected Darwin's theory altogether because he saw no connection between everyday individual variation and the production of forms treated as distinct species. He thought the action of the environment would never be able to generate new types of organisms sufficiently distinct to warrant treatment as distinct species. Instead, he believed they were "created"—but not by God. Milne-Edwards emphasized that, when a saltationist speaks of the "creation" of a new type of organism, there is no intention to imply it

> has arisen from the dust, rather than from a pre-existing animal whose mode of organization was different; he merely means that the *known* properties of matter, whether inert or organic, are insufficient to bring about such a result, and that the intervention of a *hidden cause,* of a *power of some higher order,* seems to him necessary.[620] [italics added]

De Vries. Perhaps the most successful post-Darwinian saltationist was Hugo de Vries (1848–1935). De Vries dominated evolutionary thought during the first decade of the twentieth century. His theories, which "achieved an enormous popularity,"[621] grew out of his own experimentation.

In 1886, beginning with nine evening primroses (*Oenothera lamarckiana*), he began a long-term study in which he sought to identify individuals with new traits.[622] Among 15,000 offspring of these nine plants he found two new types, five plants of each type. On the basis of their distinctive morphology, he later decided these two types should be treated as new species. He named them *O. lata* and *O. nanella.* In the next generation, among 10,000 plants produced from *O. lamarckiana* parents, he found three more of each of these types and one of a third type, which he named *O. rubrinervis.* Having found these new types, he was prompted to very carefully examine the next generation of 14,000 plants. He found 63 *O. lata,* 60 *O. nanella,* and eight *O. rubrinervis* individuals. He also found three additional new forms, which he named *O. albida* (15 plants), *O. oblonga* (176 plants), and *O. scintillans* (a single plant).[623] In the same generation he raised 41 plants by self-fertilizing a single individual that had arisen from *O. lamarckiana* in a previous generation. This type he later named *O. gigas.*

All these new types arose under culture, but he also found *O. lata* and *O. nanella* growing wild. Most of these types appeared repeatedly among the progeny of *O. lamarckiana* in successive generations. Most, too, were reproductively stable.[a] De

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[a] The *O. lata* plants were an exception. They made no pollen, and could produce seed only when fertilized by the pollen from other types of plants. *O. scintillans* also was exceptional. Only a percentage of its offspring were again of the *scintillans* type. The rest were like *O.*

Vries thought he had discovered the real way that new types of organisms came into being and that it was not the way Darwin had described. As de Vries put it,

> Once formed, the new species are as a rule at once constant. No series of generations, no selection, no struggle for existence are needed. Each time a new form has made its appearance in my garden, I have fertilized the flowers with their own pollen and have collected and sown the seed separately. The dwarf forms produce nothing but dwarves (*O. nanella*), the white ones nothing but white ones (*O. albida*), the *O. gigas* nothing but *O. gigas,* the red-nerved ones [i.e., *O. rubrinervis*] nothing but the corresponding specimens.[624]

He was impressed by the fact that these new types appeared repeatedly, in different generations, *de novo* among the offspring of *O. lamarckiana* (except *O. gigas,* which made its appearance only once as a single individual from which all subsequent *O. gigas* plants were derived). "A species therefore is not born only a single time," said de Vries, "but repeatedly, in a large number of individuals and during a series of consecutive years."[625] "In fact," he says elsewhere, "one can study the birth of a species as readily as that of any individual, be it plant or animal."[626]

De Vries' experience with these new forms, and others obtained in subsequent experimentation, led him to believe, as Milne-Edwards had, that the type of variation giving rise to new types of organisms was different from ordinary ongoing variation. He therefore assigned variation to two distinct categories. In English translations of his works, the first type is termed "fluctuating variability" or "individual variability." The second type is called "discontinuous variability." To refer to individual changes falling under the heading of this latter type of variation, de Vries used one of the same terms, *single variations,* Darwin had used to refer to sudden changes producing new forms.[a] Thus, says de Vries,

> There is, so to speak, always plenty of material for selection in every species, and in every character. But individual variability is, as far as it goes, by no means unlimited … Single variations are chance phenomena into whose essential nature we have as yet no insight. We know that they occur and that they occur seldom; but not too seldom. As to how they come about, scarcely anything is known, but it is generally assumed that they appear suddenly (by far the majority of observations that have been adduced as instances come under the heading of hybridization) … They suddenly change a species into a new form; or, from a variety, they make a new one absolutely different … Single variations seem to be presented by all

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lamarckiana. But the other five new forms did make pollen and produced exclusively offspring of their own kind when self-fertilized.

[a] In addition to single variation, Darwin used the terms, *sport, spontaneous variation, sudden variation,* and *bud-variation* to refer to a saltation. Indeed, he used *single variation* only once in each of the first four editions of the *Origin,* where the more common term was *sport.* Thus, in the first edition, he says (1859: 32), "No one supposes that our choicest productions have been produced by a single variation from the aboriginal stock," where he seems literally to mean "a single large change." In *Variation of Animals and Plants under Domestication,* the usual terms used for the same phenomenon were *spontaneous variation, sudden variation,* and *bud-variation*. Darwin used the word *mutation* only in the old, general sense of "change."

> characters, to proceed in every direction, and to be, apparently, without limit. To sum up, individual differences are always present, occur in every direction and in every character, but are limited and conform to definite laws. Single variations, on the other hand, are sporadic phenomena, appearing only from time to time, and suddenly changing the forms of life.[627]

De Vries was right in asserting that his single variations had a different genetic basis. Later research by other workers showed his "fluctuating variability" corresponds to variation resulting from ordinary meiotic recombination (see Chapter 3). His single variations, we now know, resulted, for the most part, from stabilization processes such as those described in Chapter Four, in particular those associated with permanent translocation heterozygotes (of which *O. lamarckiana* is an example).[628] His *O. gigas,* for example, is a polyploid derived from *O. lamarckiana*.[629] His *O. albida, O. lata, O. oblonga,* and *O. scintillans* were trisomics produced by aneuploidization.[630]

However, *O. rubrinervis* and *O. nanella* were products of ordinary crossing-over, not chromosomal mutations.[a] De Vries probably included these two cases among his list of single variations because (1) the affected traits were obvious: size (*O. nanella*) and flower color (*O. rubrinervis*); and (2) meiotic recombination in permanent translocation heterozygotes is very rare,[b] so when such recombination does occur, it can bring about what appears to be a permanent change (there is prominent change that remains stable in subsequent generations). Thus, in the special case of translocation heterozygotes, ordinary meiotic recombination can produce effects suggesting the discontinuity of stabilization processes. So it is not surprising de Vries classed both of these mutations as single variations, since they both resulted in the abrupt production of a permanent new form. But, in general, his single variations were brought about by chromosomal mutations. The line he drew between "individual variability" and "discontinuous variability" roughly corresponded to a line between ordinary (intrachromoset) meiotic recombination (see Chapter 3) and stabilization processes involving chromosomal mutations (see Chapters 4).

De Vries eventually presented his results and ideas in *The Mutation Theory* (1901–1903) and in *Species and Varieties: Their Origin through Mutation* (1905). In these books he specifically rejects the idea that forms treated as species arise gradually in isolation through natural selection. Instead, he proposes that the production of such forms is typically an abrupt event producing a new and subsequently stable type. Although he thought Darwin had been right in asserting a parallel exists between natural and artificial selection, de Vries was convinced Darwin had misunderstood the methods actually used by breeders. As de Vries put it: "selection is a conservative agency. It fixes new characters that have already arisen,

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[a] Emerson (1935). These resulted from what Muller (quoted in Babcock 1918: 117) called "the emergence in a state of homozygosis, through crossing over, of recessive factors constantly present in the heterozygous stock."

[b] That is, meiotic crossing-over between the Renner complexes in permanent translocation heterozygotes is rare (Grant 1981: 386).

but it cannot of itself produce new forms."[631] He saw "single variations" as the main source of new types of organisms. In his estimation, "individual variability" was "of very subordinate importance," both in nature and in the greenhouse.[632] Moreover, he realized his single variations were closely associated with hybridization (the connection between hybridization and stabilization processes has been repeatedly noted in this book). For example, de Vries claimed

> It is impossible to insist too much that the much talked of progress in cultivation is a delusion if the part played by crossing [i.e., hybridization] is left out of account or if the results of this crossing are regarded as the effect of selection. And this happens only too often. Hybridization is so much more certain and easy a way than selection of getting something new that breeders would nearly always be working against their own interests if they did not expose their plants as freely as possible to natural cross-fertilization.[633]

Darwin and Saltation. De Vries was wrong, however, in asserting that Darwin was ignorant of ordinary breeding techniques. Darwin carried on an extensive correspondence with breeders and was well aware that sudden change occurred in domestic stocks. In particular, he made a special study of what he called "bud-variation," in which a plant produces a bud that grows into an offspring individual with highly distinctive characteristics. But variation of this sort receives little attention in the *Origin.* Darwin gave it significant treatment only in *Variation of Animals and Plants under Domestication* (1868). For example, in *Variation* he writes

> In the early half of this chapter I have given a long list of plants in which through bud-variation, that is, independently of reproduction by seed, the fruit has suddenly become modified in size, colour, flavour, hairiness, shape, and time of maturity; flowers have similarly changed in shape, colour, and doubleness, and greatly in the character of the calyx; young branches or shoots have changed in colour, in bearing spines, and in habit of growth, as in climbing and weeping; leaves have changed in colour, variegation, shape, period of unfolding, and in their arrangement on the axis. Buds of all kinds, whether produced on ordinary branches or on subterranean stems, whether simple or, as in tubers and bulbs, much modified and supplied with a stock of nutriment, are all liable to sudden variations of the same general nature.[634]

In addition to using the term single variation, Darwin referred to such variation by a variety of other names ("sports," "spontaneous variations," "sudden variations"). The following passage from *Variation* (1868: vol. I, 213) shows that Darwin's notions of breeding were not always so far from those of de Vries:

> From what we now see occasionally taking place in our aviaries, we may conclude that sudden variations or sports, such as the appearance of a crest of feathers on the head, of feathered feet, of a new shade of colour, of an additional feather in the tail or wing, would occur at rare intervals during the many centuries which have elapsed since the pigeon was first domesticated. At the present day such "sports" are generally rejected as blemishes; and there is so much mystery in the breeding of pigeons that, if a valuable sport did occur, its history would often be concealed. Before the last hundred and fifty years, there is hardly a chance of

> the history of any such sport having been recorded. But it by no means follows from this that such sports in former times, when the pigeon had undergone much less variation, would have been rejected. We are profoundly ignorant of the cause of each sudden and apparently spontaneous variation.

Elsewhere in the same book he states his opinion that pigeon "fanciers can act by selection on excessively slight individual differences, as well as on those greater differences which are called sports."[635] He also says "it is probable that some breeds, such as the semimonstrous niata cattle, and some peculiarities, such as being hornless, &c., have appeared suddenly from what we may call a spontaneous variation."[636] But he rarely expressed such opinions in the far more widely read *Origin*. What seems to be the only affirmative reference to saltation in that book comes in the first chapter on variation under domestication

> One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. Some variations useful to him have probably arisen suddenly, or by one step; many botanists, for instance, believe that the fuller's teazle, with its hooks, which cannot be rivalled by any mechanical contrivance, is only a variety of the wild Dipsacus; and this amount of change may have suddenly arisen in a seedling. So it has probably been with the turnspit dog; and this is known to have been the case with the ancon sheep.[637]

Certainly, elsewhere in the *Origin*, Darwin consistently emphasizes gradual change, not saltation, especially in connection with natural, as opposed to domestic, variation. As has already been noted (p. 156), Darwin placed an increasing emphasis on the importance of continuous variation in later editions of the *Origin.* Certainly, de Vries is correct in saying that Darwin, at least Darwin as he expressed himself in the *Origin,* “left out of account” the part played by hybridization in the origin of new types of organisms. In the *Origin* he stressed gradual divergence. Hybridization's role in breeding is almost entirely dismissed.

For example, in the *Origin* Darwin expresses his belief that all the various breeds of domestic pigeons are descended by divergence from a single ancestral stock. There he claims "it is impossible to make the present domestic breeds by the crossing of any lesser number: how, for instance could a pouter be produced by crossing two breeds unless one of the parent-stocks possessed the characteristic enormous crop?"[638] In a letter to the American naturalist Asa Gray, Darwin went so far as to assert that "whatever holds good in the formation of a pouter pigeon holds good in the formation of a natural species of pigeon."[639] But, in fact, Darwin apparently didn't know anything about how the pouter had been bred. Such knowledge was available. If he had searched English libraries, he might have found John Moore's *Columbarium* (1735), in which Moore explicitly reports the pouter was first obtained by hybridizing the “Dutch Cropper” pigeon with a breed known as the “Horseman."[a,640] De Vries would certainly have been right if he had merely said

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[a] Buffon (*Histoire Naturelle,* XVI, 547–548) expressed the opinion that most of the various

Darwin had had little personal experience with breeding prior to the publication of the *Origin,* Before that book appeared in 1859 Darwin seems to have bred only pigeons. He did not become interested even in these until the summer of 1855.[641] Moreover, within three years, he dropped pigeon breeding entirely.[642] During this period, from 1855 to 1858, he kept a wide variety of breeds. Many of these unfortunate birds he poisoned and boiled in order to compare their skeletons.[643] Indeed, his actual breeding experience even during this period must have been quite meager. Three years is hardly enough time to accomplish much in the way of pigeon breeding. And comparing skeletons could not have done much to educate him about breeding techniques. According to his biographers, Desmond and Moore (ibid: 428), his description in the *Origin* of pigeon breeding had a specific motivation:

> Darwin wanted to show nature composed of myriad tiny variations invisible to all but experienced fanciers. These enthusiasts could judge to one-sixteenth of an inch. And the differences that only they could spot formed the raw material to be accentuated through generations of selective breeding. From such minute aberrations, enormous sculpted changes had been wrought by fanciers leading to today's pouters, fantails, runts and tumblers … Darwin believed that similar imperceptible variations held the key to Nature's own Malthusian selection.

And yet, it should be said that outside the pages of the *Origin,* Darwin actually embraced hybridization as a source of saltatory change, especially in *Variation* and in his later correspondence, where he made saltatory claims rather similar to those of de Vries (see Appendix H).

However, de Vries' views were clearly in conflict with those Darwin expressed in the *Origin,* the views most people identified with the name Darwin. When de Vries' theory first appeared, many biologists of the day considered it more consistent with observation than Darwin's. As Provine (1986: 220) notes, "by the turn of the century a growing number [of biologists] were supporting the idea that natural selection could not be the primary mechanism of speciation because too many differences between closely related species were apparently nonadaptive." Thus, the American geneticist T. H. Morgan (1903) remarked, "It is well known that the differences between related species consist largely in differences of unimportant organs, and this is in harmony with the mutation theory [of de Vries], but one of the real difficulties of the selection theory [of Darwin]."[644] Independently of de Vries, the Russian botanist Korschinsky (1899, 1901), a disciple of Kölliker, brought

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breeds of domestic pigeons were derived from intercrossing of three naturally occurring forms. Thus, he says: "It is therefore quite possible, as we have already suggested, that the Rock Dove [*Columba livia*], the Wood Pigeon [*Columba palumbus*], and the Turtle Dove [*Streptopelia turtur*], species that appear to keep themselves separate in a natural state, may nevertheless unite frequently in captivity and that from their union may be produced the majority of our domestic pigeon breeds, of which some are of the size of the Wood Pigeon, and others resemble the Turtle Dove in their smallness, their shape, etc., and others resemble the Rock Pigeon, or show affinity to all three."

together a vast mass of data demonstrating that saltational change had been widely reported. Darwin's claims of gradual evolution were also opposed by taxonomists, many of whom felt that any process creating new types of organisms by gradual selection would never work because their experience had, in their opinion, shown populations treated as species have insufficient individual variability to support such a process.[645] Taxonomic method was based on the fact that characters are typically constant among specimens treated as conspecific and that such characters are reproduced in every generation. Darwin claimed that traits show significant individual variation within populations treated as species and that gradual change is ongoing in such populations. Taxonomists called a population a "good species" when it showed little or no variability. Not surprisingly, such conflicting views were hard to reconcile. Others pointed to the absence of intermediates. They believed it should be possible, if preexisting types of organisms gradually evolve into new ones through intermediate forms, to find "numerous, fine, intermediate varieties" (Darwin's words) connecting them, both in the fossil record and in nature. When this prediction did not fit observation, many scientists questioned Darwin's theory.

From De Vries to the Modern Synthesis. But as the twentieth century unfolded, de Vries' theory gradually fell into disrepute. De Vries knew the sudden "single variations" he had witnessed were connected with hybridization, but genetics was still in its infancy. He had no clear notion of the nature of the actual genetic processes underlying his observations. He was unable to predict when his single variations would occur. In the years after the publication of his books, far more progress was made in understanding the genetic basis of trait inheritance than in elucidating the nature of single variations. As a result, the mechanisms of intrachromoset meiotic recombination (see Chapter 3) were worked out very early in the history of genetics, before 1920, primarily by T. H. Morgan's group at Columbia University. It was realized concurrently that Mendel's Laws accurately described the sort of variation arising from ordinary meiotic recombination, the sort occurring in intrachromoset matings. Thus, at the time, Babcock (1918: 117) commented that

> During the decade following de Vries's announcement of his theory, biological interest shifted from the general problem of evolution to the more specific problem of heredity. The rediscovery of Mendel's law at once focused attention upon the inheritance of particular characters. Then began the era of experimental evolution in which, under the leadership of Morgan, most remarkable progress has already been made. The traditional problem of heredity, its mechanism, has been solved. We know, not only that the ultimate hereditary units are germinal, but also that they are located in that particular portion of the germ cell called the chromatin [the complex of DNA, RNA, and protein making up the chromosomes], and there is an ever-growing body of evidence proving that each hereditary unit occupies a particular locus in a particular chromosome. These hereditary units have been designated by various terms, but are most commonly referred to as genes, genetic factors, unit factors or simply factors.

Morgan's work, elucidating the effects of meiotic recombination, examined the inheritance of point mutations in *Drosophila* (Morgan 1911, 1915), but it soon became apparent that genetic factors following Mendelian inheritance exist in a wide array of sexual organisms.[646] On the other hand, progress in understanding the stabilization processes producing chromosomal mutations went more slowly. Since meiotic recombination had been elucidated and chromosomal mutations had not, many felt that de Vries' theory was too vague, or even unscientific. Moreover, at that time it was still widely thought that hybridization, an important factor in de Vries' theory, was rare or nonexistent in a natural setting.

A new faction of biologists rose up, who placed great emphasis on the evolutionary potential of meiotic recombination and point mutation. Like Darwin, this new faction assumed the origin of new types of organisms could be explained in terms of traits that (1) showed variation *within* a population, and (2) could be imagined as gradually becoming more or less common in a population under the influence of natural selection. Atop Darwin's theory they erected a mathematical superstructure based on Mendel's Laws. The only sort of change described was the sort that could occur in intrachromoset matings, because Mendel's Laws could describe nothing else. This new way of explaining evolution, combining Mendel and Darwin, became known as the "modern synthesis," and the theory associated with this movement became known as "neo-Darwinism."[a] This new theory had a tremendous impact on future biological research. The pioneers of this approach (e.g., Dobzhansky 1937a; Fisher 1930; Haldane 1932; and Wright 1931) took simple formulas—which Mendel had used to predict the outcome of a generation or two of peas—and extended them to describe long-term evolutionary processes. Their basic approach was to use these rules to quantify certain mating procedures employed by agricultural breeders ("assortative mating," "inbreeding," "mixed mating," etc.).[647]

This agricultural influence is especially apparent in the case of the American geneticist Sewall Wright, who contributed more models to population genetics than anyone else. Wright was trained in genetics at Harvard's Bussey Institution, which emphasized biological sciences related to agriculture and horticulture.[648] He went on to spend the first decade of his post-graduate career (1915–1925) working for the U.S. Department of Agriculture. During this time, one of his major responsibilities was the analysis of data from a long-term experiment on inbreeding in guinea pigs, an experience that was greatly to influence his later work in evolutionary theory.[649] Provine (1986: 142) notes that "from very early in his career, Wright saw evolution as deeply related to what he knew of evolution in domestic populations."

However, it is now apparent that many genetic processes bringing about abrupt, major evolutionary change (such as the various types of stabilization processes listed

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a. The name *neo-Darwinism* predates the modern synthesis by several decades. The term was already in use by the early 1890s (Ward 1891). But it has become the epithet usually used to refer to the theory of evolution developed during the modern synthesis, which describes evolution as a process of statistical change in isolated populations. Originally it merely referred to a faction of biologists that placed great emphasis on natural selection as opposed to the inheritance of acquired traits.

in Chapter 4) were left out of account by Wright and his contemporaries. This omission is understandable since at that time such processes were poorly understood and little known. Indeed, it must have seemed, and it actually was, a great scientific advance to understand intrachromoset meiotic recombination, which Mendel's Laws describe. It must also have been satisfying to use those laws to construct concise, seemingly valid, analytical models of evolutionary processes. But it now seems those early evolutionists rushed too soon to consensus. Simply identifying a process that can hypothetically produce change is not the same as showing it is the typical source of new types of organisms. As Francis Bacon (*Novum Organum,* 1620) said

> Even when men build any science and theory on experiment, yet they almost always turn with premature and hasty zeal to practice, not merely on account of the advantage and benefit to be derived from it, but in order to seize upon some security in a new undertaking of their not employing the remainder of their labor unprofitably and by making themselves conspicuous to acquire a greater name for their pursuit. Hence, like Atalanta, they leave the course to pick up the golden apple, interrupting their speed and giving up the victory.[650]

Scientists of this new school, who called themselves “population geneticists,” thought of evolution in terms of an entire population gradually changing and taking on new traits. They equated the word *species* with "reproductively isolated population." The production of new types of organisms via hybridization between such populations, then, did not enter their picture of evolution. They tended to focus on the gene and to ignore the chromosome. In short, they thought in terms of Mendelian models that described variation resulting from intrachromoset mating (see Chapter 3). This approach allowed them to construct tidy mathematical models predicting how evolution would occur, *given their assumptions.* Such models were attractive because they seemed to prove the feasibility of evolution under the influence of natural selection. Even more, they lent the field an air of scientific rigor, something previously lacking. No one in this ascendant school thought in terms of chromosomal mutations. Or, if they did, they thought of them as aberrations. So the new models of evolutionary change left out this potent source of variation. By the 1930s, people who constructed such models were the leaders of evolutionary biology. More and more, de Vries' observations in *Oenothera* were dismissed as the result of "chromosomal irregularities."[651] By the time de Vries died in 1935, he had seen his theories fall into neglect. Nevertheless, his direct observation—that new types of organisms can come suddenly and repeatedly into being and remain stable thereafter—is fundamentally at odds with the basic tenets of orthodox theory and should not be forgotten.

A Tradition Becomes a Heresy. Though neo-Darwinism eventually gained wide acceptance, not everyone was satisfied that all aspects of evolution could be explained by models based on point mutation and the long-term effects of meiotic recombination. For example, E. B. Babcock (1918: 120–121) pointed out that many closely related forms differ with respect to karyotype and that the mere reassortment of alleles occurring in intrachromoset meiotic recombination would not be expected to produce a new karyotype:

> Yet, chromosomes are genetic units of a higher order than factors [i.e., genes], each chromosome containing many factors and in general behaving as a continuous entity . . . It seems to be necessary, therefore, to postulate some process by which these major entities [i.e, chromosomes] become altered in number or recombined in entirely new systems. We are dealing here with phenomena of a different sort [from] factor mutations [i.e., gene mutations], and the latter appear, therefore, to be of slight significance in the origin of species having unlike chromosome numbers [i.e., different karyotypes]. Alterations in chromosome number may be brought about either by the unique or irregular behavior of one or more members of a chromosome group or by hybridization between species.

By "unique or irregular behavior of one or more members of a chromosome group," Babcock seems to have meant "processes producing chromosomal mutations."

Others insisted the fossil record was inconsistent with the gradualistic paradigms of the modern synthesis. Otto Schindewolf (1896–1971) was an adamant saltationist and, from the 1930s on, maintained that neo-Darwinism was an inadequate explanation of the abrupt changes seen in the fossil record. He summarized his position in his magnum opus *Grundfragen der Paläontologie* (1950). Schindewolf was perhaps the most prominent German paleontologist of the twentieth century. Reif (2004) comments that all German paleontology coalesced in Schindewolf's evolutionary theory, known as "typostrophism," and that this "theory dominated German paleontology for decades after the war [i.e., World War II] and only recently has the synthetic theory [i.e., neo-Darwinian theory] been seriously considered." But Schindewolf's ideas have had little impact in the United States and England since *Grundfragen* was only recently translated (1993) into English. Moreover, even a sympathetic reading of that translation (by this writer) could discover no trace of a genetic explanation for the saltational phenomena Schindewolf describes. He simply argued that gradual genetic processes posited by neo-Darwinism failed to explain the saltational pattern observed in the fossil record and that some other mechanism must therefore be at work. Noting that Darwin had explained the discontinuities between extant forms by supposing that intermediate types had died out, Schindewolf (1993: 333) wrote,

> For the modern plant and animal world, such an explanation might, in a pinch, appear conceivable; but it is no longer tenable once we take the fossil material into account. We would have to find there all the transitional forms and links that are missing in modern classes, orders, and families; but this is not the case. Even in groups that are entirely extinct, we always see, even when material evidence is extremely abundant, the same picture *of a sharp separation and discontinuity between the individual typal categories.* [italics are Schindewolf's]

According to Schindewolf, "Paleontology will have fulfilled its mission when the evolutionary processes it has deduced" are successfully attributed to genetic processes that are observed in extant organisms.[652] This attribution, he asserted, "must be left to experimental genetics to answer."[653] If, instead of leaving the job to geneticists, he had made some attempt himself to specify the mechanisms involved, he might have made a more convincing case. But he really seems to have had no idea what mechanisms might be involved: "In biological fields," he wrote, "we must take the basic phenomena of life into account and use them in our deductions, even though for the time being we cannot determine their nature more precisely or explain their mechanics."[654] He put his faith in an unknown force.

Harvard paleontologist George Gaylord Simpson (1902–1984) proposed the idea of "quantum evolution" to account for the saltational fossil data. For example, in one publication (Simpson 1944), he comments that

> the term “quantum evolution” is here applied to the relatively rapid shift of a biotic population in disequilibrium to an equilibrium distinctly unlike an ancestral condition.[655]

Later he claimed that gradual transitions between fossil forms "are not recorded because they did not exist," and "that the changes were not by transition but by sudden leaps in evolution. There is much diversity of opinion as to just how such leaps are supposed to happen." (Simpson 1949: 231).

The botanist J. C. Willis (1868–1958), a fellow of the Royal Society, was also a saltationist. He noted, as others had before him,[656] that the features used by taxonomists to classify organisms are typically nonadaptive, and that these diagnostic traits of particular types of organisms are nevertheless found in all individual specimens of a form. On this basis, he argued gradual natural selection could play no significant role in shaping such forms.[657] Such a process could not explain, he said, why all the members of each form each have all the useless traits characteristic of that form. Willis' view of evolution relied largely on the occurrence of major mutations. Thus, he asserted "a single mutation, usually very divergent from the parent form, may give rise, at one step (not gradually as under Darwinism) to a new form, of family, generic, specific, or varietal rank." (Willis 1949: 14). In his opinion, "chromosome alterations" were the causes of these mutations.[658,659] Sewell Wright (1941: 345) commented that the view to which Willis was "most systematically opposed is that of evolution by gradual statistical transformation of populations." Wright himself was perhaps the greatest exponent of such statistical explanations of evolution.

But it is Richard Goldschmidt (1878–1958) who remains the best remembered of twentieth century saltationists, at least in the United States. When Goldschmidt fled Hitler's Germany to become a professor at Berkeley, he was a geneticist of international standing. But his saltationist claims soon brought him lasting censure. Goldschmidt dismissed the evolutionary significance of point mutation and instead proposed that the "decisive change in the genetic material" actually causing abrupt, macroevolutionary changes is a "change in chromosomal pattern." The saltational shift producing forms treated as distinct species occurs, he said, when the structure of the chromosomes is reshuffled and scrambled.[660]

In his book, *The Material Basis of Evolution*[661] (1940), Goldschmidt explores these ideas. There he also points out, as Babcock and other biologists had before him, that organisms treated as distinct species very often have distinct karyotypes, a fact that has been firmly established by subsequent studies (see citations in Table 3.1). Across a broad range of organisms, closely related forms very often differ in chromosome number and/or with respect to the structure of individual chromosomes (this fact was emphasized in Chapter 3), so that a chromosomal mutation would be required to convert one's karyotype into the other's. Even members of the same genus with identical chromosome counts commonly differ with respect to the structure of one or more individual chromosomes. Such is the case for example with the chimpanzee (*Pan troglodytes*) and the pygmy chimpanzee, or bonobo (*P. paniscus*).[662] Goldschmidt was convinced the process producing new sets of chromosomes — whatever it might be — was the same process producing the sort of morphological and physiological differences that prompt biologists to treat forms as distinct species.[663] "We have long been seeking a different type of evolutionary process," he wrote in the best saltationist spirit, "and have now found one; namely, the change within the pattern of chromosomes [viz., changes in karyotype]."[664]

Goldschmidt also emphasized the discontinuous nature of the paleontological data. Thus, he says, Schindewolf (1936) "shows by examples from fossil material that the major evolutionary advances must have taken place in single large steps, which affected early embryonic stages with the automatic consequence of reconstruction of all the later phases of development. He shows that the many missing links in the paleontological record are sought for in vain because they never existed."[665]

But Goldschmidt gave no clear account of what the process might be that produced changes in karyotype. Nor did he specifically explain mechanisms whereby such changes could affect the development of an organism once they had occurred. He simply suggested that a "systemic mutation" can suddenly arise and produce a new organism with a new set of chromosomes.[a] Such a mutation, he said, would rearrange many, or even all, of the chromosomes. Goldschmidt called gradual evolution (statistical changes in the frequency of allelic variants) "microevolution,"[b] and point mutations affecting individual genes, "micromutations." He dismissed the evolutionary significance of both. "Microevolution within the species," he said,

> proceeds by accumulation of micromutations and occupation of the available ecological niches by the preadapted mutants. Microevolution, especially geographic variation, adapts the species to the different conditions existing in the available range of distribution. Microevolution does not lead beyond the confines of the species, and the typical products of microevolution, the

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[a] An alternative possibility, the cumulative fixation of structural rearrangements arising in a uniform, non-hybridizing population ("stasipatric speciation") is thought to be unworkable due to the adverse effect of structural heterozygosity on fertility (Key 1968).

[b] Yuri Filipchenko introduced the words *microevolution* and *macroevolution* in his book *Variabilität und Variation* (1927).

> geographic races, are not incipient species. There is no such category as incipient species. Species and higher categories originate in single macroevolutionary steps as completely new genetic systems. The genetical process which is involved consists of a repatterning of the chromosomes, which results in a new genetic system. The theory of the genes and of the accumulation of micromutants by selection has to be ruled out of this picture.[666]

As Goldschmidt conceived them, systemic mutations were chance events that suddenly produced "a huge effect upon a series of developmental processes leading at once to a new and stable form, widely diverging from the former."[667] He emphasized his belief that (1) no intermediates fill what he called "the bridgeless gaps" between forms treated as species; (2) systemic mutations allowed evolution to leap these gaps and create discretely distinct new forms.

He was one of the most prominent geneticists of his era. His claim was correct that many somatypes treated as distinct species are distinct chromotypes. And yet he was ridiculed when he suggested that a systemic mutation could both arise de novo in a single individual and nevertheless get established as a new type. He had failed to explain how a solitary, radically altered organism, created by a single, random, massive mutation, would find a mate of its own kind. Nor did he explain how a set of chromosomes could be rearranged so abruptly. How did the chromosomes get shortened and lengthened? How did the structure of the chromosomes get rearranged? Goldschmidt said only that the observed existence of such chromosomal rearrangements distinguishing closely related forms implied the existence of some unknown mechanism of rearrangement — *an unknown force.* The observation was correct. Therefore, his conclusion that such a mechanism exists was also correct. The only known mechanisms with such an effect are stabilization processes producing chromosomal mutations.

Goldschmidt's radical and largely unelucidated claims came at a time when nearly all of his colleagues had already embraced the new models of population genetics. This field seemed to offer an unprecedented numerical exactitude comparable to that of mathematics or physics. Adherents of this new discipline believed Mendel's Laws sufficiently described the genetic events underlying evolution and that evolution occurred gradually, not abruptly by way of the mysterious systemic mutations Goldschmidt was proposing. In particular, a major proponent of the new movement, Fisher (1930), had argued that large mutations would almost surely be maladaptive: "for greater changes the chance of improvement diminishes progressively, becoming zero, or at least negligible, for changes of a sufficiently pronounced character." This view was widely accepted. To most biologists,[668] Goldschmidt's ideas seemed to hark back to the abandoned theories of Hugo de Vries. Not surprisingly, Goldschmidt was roundly rejected by most of his colleagues.

Nevertheless, it is now well known that large-scale changes in the genetic material do occur and that they can indeed be beneficial. Take polyploidy. Otto and Whitton (2000) note that while it is easy to speak of hypothetical adverse effects,

> changes that polyploidization does produce can be enormously important for the evolutionary success of newly formed polyploid lineages. Changes in features such as metabolism, developmental rates, gene regulation, and physiological tolerances can alter biotic interactions, ecological tolerances, and facets of reproductive isolation such as mating behavior and breeding system.

There's no reason to suppose a mutation has to be bad just because it's big. All the various types of chromosomal mutations described in Chapter Four do occur and can be beneficial.

Actually, some of Goldschmidt's notions were not that radical. In a paper read at a general meeting of the American Association for the Advancement of Science, Goldschmidt (1933: 547) emphasized

> the importance of rare but extremely consequential mutations affecting rates of decisive embryonic processes which might give rise to what one might term hopeful monsters, monsters which would start a new evolutionary line if fitting into some empty environmental niche.

Later workers such as Stebbins (1959), Gilliard (1959), and Rieseberg (1997) expressed the opinion that a markedly new type would be more likely to get established if an empty niche were available. Others later emphasized the idea that mutations in genes affecting early developmental processes could have a major effect. This idea is essentially the same as that set forward by Alan Wilson and his co-workers fifty years later.[669]

But, in general, Goldschmidt's speculations were not well received. As Milner (1993: 222) notes, "There is a grotesque humor about the unfortunate phrase 'hopeful monster' that lent itself to caricatures of Goldschmidt's ideas and obscured the theoretical issues." The mechanisms he offered were vague, undocumented, and, as a result, unconvincing. Moreover, one can detect in Goldschmidt's tone a sweeping unapologetic condescension that probably rubbed many of his colleagues the wrong way. He expressed himself in absolutes as if he could somehow know that a systemic mutation is involved in the production of every form treated as a species. He insisted a mystery process no one had observed was the key to evolution. In the end, largely due to Goldschmidt, saltation became anathema to an entire generation of evolutionary biologists. For many it remains a heresy even today.

Some later evolutionists have embraced a watered-down formulation of Goldschmidt's theories. For example, Lewis and Raven (1958) supposed that chromosomal rearrangements that were less massive would not have such a severe adverse effect on fertility and viability. Such changes, they suggested, might become established through some unknown mechanism, perhaps "mutator genes" (Lewis 1962; Lewis and Raven 1958) or possibly extreme inbreeding.[670] Grant (1981: 173–175) notes there has been a school of thought that argues the establishment of new structural rearrangements can be driven by the ability of such arrangements to lock up favorable gene combinations from recombination. However, this ability would not be expected to offset the extremely deleterious effect of structural heterozygosity on fertility.[671] All the offspring of an individual such as Goldschmidt had described would, perforce, be structurally heterozygous (since the new individual would have to mate with an individual of the preexisting type). But the fact remains—forms treated as distinct species very often do have distinct karyotypes.

From One Karyotype to Another. Any acceptable theory of evolution should account for the genesis of the karyotypic differences that so often distinguish distinct types of organisms. But neo-Darwinian theory falls short in this respect. Most biologists, population geneticists in particular, weren't convinced by Goldschmidt's explanation of the fact that distinct chromosets are often treated as distinct species. They dismissed the data on karyotypic differences along with Goldschmidt's explanation of that data, and chose instead to focus on mutations in genes and the long-term effects of meiotic recombination. Attributing all evolutionary change to such phenomena, they neglected stabilization processes and chromosomal mutations. To this very day, karyotypic differences tend to be disregarded by many evolutionary biologists, as is the fact that stabilization processes can disrupt karyotypes and restabilize them in new forms.

Stabilization theory provides a clear and simple explanation of this phenomenon. It *assumes* new stable forms are typically produced by stabilization processes. Therefore, under stabilization theory it is to be *expected* that distinct related forms would commonly have distinct karyotypes. New types of organisms produced by such processes would usually have new karyotypes because such processes typically do reassort and rearrange chromosomes. As we have seen, the effect of stabilization processes on karyotypes is known from direct observation. By definition, new polyploids always have different karyotypes from their parents. In general, new agamosperms do too. In those cases where their parents' karyotypes differ, so do forms that stabilize as new recombinant derivatives. The same is often true of a vegetatively-reproducing form produced by hybridization. As we have seen (Chapter 6), the geological record indicates new somatypes typically arise abruptly and remain recognizably the same for many millions of years. Such observations would be expected whenever a somatype arose via a chromosomal mutation producing a new chromoset. Under such circumstances, the members of a chromoset would be expected to be relatively homogeneous in form and comparatively distinct from those of other, preexisting chromosets because the new karyotype defining the chromoset would lock in a particular set of loci. A particular gene might vary from one individual to another (in other words, at a given locus there would be allelic variation of genes), but the set of loci present in the karyotype would not, which in such cases would place a limit on genetic variation. By defining these limits, it would therefore, to a great extent, stabilize the morphology of the new form.

The new karyotype would also restrict the scope of morphological variation over time because the karyotype of parent and offspring would contain the same set of loci, generation after generation. Any variation present in the population subsequent to stabilization would be restricted to allelic variation at the various stable loci. Such allelic variation would be the result of intrachromoset meiotic recombination or point mutation. Recall from Chapter Three that any ongoing production of variation from either of these two sources would be minor in comparison with the initial leap that occurs when a new type of organism is produced by a chromosomal mutation. For those organisms that reproduce sexually, the stability of meiosis in large groups of individuals with identical, fully paired karyotypes would permit new chromosets to maintain themselves largely unchanged, indefinitely (the exact genetic basis of the stability of sexual chromosets is spelled out in Appendix I). Organisms whose life cycles do not involve meiosis reproduce clonally. So they, too, would be expected to vary little with time. Even those exceptional organisms whose peculiar meiotic mechanisms permit a certain amount of karyotypic variation (e.g., the fruit flies of the genus *Drosophila*) are constrained to a degree by the adverse affects of structural heterozygosity. So that they, too, are bounded with respect to morphological variability by karyotypic stability.[a]

These considerations provide a mechanistic explanation for the long-term evolutionary stasis that paleontologists have observed in fossil forms. It would be a simple consequence of the fact that the typical form treated as a species has a stable reproductive cycle.[b] *Once a stabilization process produces a new form with a particular karyotype and that form establishes a stable reproductive cycle, a particular set of chromosomes is repeatedly passed, unaltered, from parent to offspring in the same way, generation after generation. Any ongoing minor variation observed between major chromosomal mutational events producing new types of organisms can be attributed to ongoing intrachromoset recombination and*

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[a] The karyotypes of the fruit flies of the genus *Drosophila* are often highly variable even within a single population and thus constitute an exception to the general rule of karyotypic uniformity within populations. Geneticists often use these insects as model organisms in investigations of evolutionary processes because the reproduce much more rapidly than most other types of organisms and have certain features that facilitate genetic analysis. For this reason, there is a tendency for geneticists to think in terms of drosophilids when they generalize concerning the effects of karyotypes. *But fruit flies are not representative of the typical eukaryote with respect to the effects of chromosome structure on fertility;* they are distinct from the vast majority of sexual organisms in having special meiotic mechanisms that better tolerate a common type of chromosomal rearrangement (paracentric inversions). In this respect, they are not at all typical of eukaryotes in general. However, only paracentric heterozygotes are widespread in natural drosophilid populations (White 1973a: 745, 1978: 175). Even in *Drosophila,* chromosomal sterility is a common phenomenon. For example, structural heterozygosity for *peri*centric inversions has a strong adverse effect on fertility (Ashburner 1989; White 1978: 174). Likewise X-autosomal translocations result in sterility in drosophilids (Ashburner 1989: 566). These cytological constraints place bounds on karyotypic variability that in turn place constraints on morphological variability in these flies.

[b] Under this view, such forms might be described as stable, discontinuous states of matter, one of the possibilities suggested by Maynard-Smith and Szathmáry (1995).

occasional point mutation.[a]

Stabilization theory assumes that stabilization processes are the main source of new forms. It also assumes that ordinary reproductive processes are very accurate and that each form persists largely unchanged until some stabilization process, usually triggered by hybridization, disrupts the ordinary life cycle and gives rise to a new form. These assumptions account for, and are consistent with, the observed stasis of fossil forms. Stabilization theory says the morphological stability seen in most fossil forms is simply the result of having a stable reproductive cycle. It also holds that ordinary interchromoset recombination produces ongoing minor variation, but that it does not usually accumulate to such a degree that a new form is taxonomically recognized. Instead, it equates the differences arising from such processes with what has been variously called accidental, individual, or fluctuating variation.

Point mutations, under stabilization theory, can accumulate over time within a single non-hybridizing population. Nevertheless, the theory claims that this process does not usually produce the sort of new forms normally treated as species. That role is assigned to chromosomal mutations, which, according to stabilization theory, cause the large abrupt steps seen in the fossil record. The theory portrays point mutations as significant only in the production of new traits. These claims are made because *most fossil forms, especially those treated as distinct species, arise abruptly with numerous distinctive traits from the outset. The slow accumulation of point mutations cannot produce this effect. Therefore, it would simply be illogical to claim such a process does produce such forms.*[b]

Just as Cuvier could not conceive that huge boulders had been transported far from their origins by the glaciers of past ice ages, Goldschmidt failed to consider the possibility that new types of organisms might be produced by stabilization processes, in which the new karyotype is frequently derived from not one, but two parents. In fact, such processes were poorly known when he presented his theories. He rejected gradualism, but retained a basic component of the gradualistic paradigm: the notion that a new form must be descended from one and only one form immediately ancestral to itself. In speaking of how new chromosomal patterns arise, he clearly stated his assumption that "one pattern is evolved from another one, which can

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[a] Under stabilization theory most of the various models of evolutionary change described in conventional neo-Darwinism would apply only to variation of this latter sort. Since they apply only to Mendelian processes. They have no relevance with regard to chromosomal mutations.

[b] Of course, one can conceive of a stable fossil form (1) differing from its predecessors with respect to a minor trait that could plausibly arise via a point mutation; (2) arising abruptly; (3) being stable thereafter; and (4) being treated as a species. And stabilization theory, in fact, would explain any such organism as the product of a single point mutation. However, there appear to be few fossil forms fitting these requirements. In fact, the origin of the multiple morphological traits used to distinguish the typical fossil form seems best explained by chromosomal mutation (the accumulation of point mutations is excluded as a candidate process because the production of new fossil forms is typically abrupt).

hardly be doubted."[672] With such an assumption, it is difficult to see how one karyotype could be changed into another, even with time, let alone abruptly as Goldschmidt suggested. Such changes would not be expected to spread through a population under the influence of natural selection — Neo-Darwinian theory says structural changes are unlikely to accumulate over time, because structural heterozygosity is usually associated with reduced fertility.[673]

On the other hand, stabilization processes are known typically to result in the establishment of new chromosets, as has already been explained. It isn't necessary to suppose such processes produce viable organisms. It is a well-known, documented fact that they can. Indeed, many different hybrid crosses produce not only viable, but even partially fertile offspring. Such processes can combine the previously tested genes of two existing, viable types. There is no need to posit a lonely "hopeful monster" looking for a mate — such processes normally produce multiple individuals on an ongoing basis (as de Vries said long ago), which can mate among themselves or can backcross. In fact, in many cases, no partner is required to establish a new stable type (e.g., a new type of agamosperm, or an organism capable of self-fertilization or effective vegetative reproduction).

In organisms derived from stabilization processes, chromosomes are not simply rearranged, as Goldschmidt supposed. Such organisms are genuinely new: they have a new complement of genes. These genes can interact in new ways during the course of development and produce novel effects. The extreme variation generated by such processes would allow natural selection rapidly to create new types. As we have repeatedly seen (Chapter 4), new, stable forms can come into being via stabilization processes in as little as a single generation. Even the few generations required to generate a new stable recombinant derivative are an instantaneous blip in the context of geologic time.

On the basis of available evidence it does indeed seem probable that such processes are frequently, or even typically, the source of new types of organisms. If such is the case, the saltationist tradition, which has long sought an unknown force, will finally be vindicated — the mechanisms underlying the origin of the typical form treated as a distinct species would, in fact, be distinct. They would be qualitatively different from those involved in ordinary reproduction. When a population geneticist asserts that the mechanisms of inheritance underlying "speciation" are the same as those involved in everyday reproduction, she means that they are governed by the same rules — those formulated by Gregor Mendel. But Mendel's Laws do not apply to the sorts of chromosomal processes typical of stabilization processes.

A Caveat: Although stabilization theory posits that saltation is generally the result of chromosomal mutations, it does include the supposition that some point mutations have a more or less marked effect, producing what amounts to an abrupt, permanent change. Thus, a mutation in a single gene will sometimes affect a prominent trait, such as flower color. However, a point mutation typically affects only a single character, or a set of related characters. For example, a mutation in a single pigmentation gene might affect one trait (e.g., fur color) or several different traits that all depend on that same gene (e.g., fur, skin, and eye color). Indeed, the decision to treat two forms as separate species is occasionally based on a distinction involving a single trait. Thus, Heiser (1966: 32) notes that when systematists make this decision, "Sometimes a single character is used; this may admittedly result in quite artificial groups but can sometimes be defended on the grounds of convenience." However, most biologists frown on such practice.

Suppose, then, that such a point mutation affected a prominent characteristic recognizable in a fossil specimen. If such a mutation occurred in some ancient population, then the mutated and unmutated types would today be observed as distinct fossil forms. Such would be the case even if the two types interbred on an ongoing basis. Under such circumstances a point mutation would have produced a change that would be perceived today as saltational. Likewise, even ordinary meiotic recombination without point mutation, when it involves genes affecting prominent characters, can produce a change that seems saltational. De Vries' *O. rubrinervis* and *O. nanella* are examples already discussed. But, again, under such circumstances multiple traits are not usually affected. Moreover, such recombination produces a permanent, stable change, only in the case of certain special genetic systems, such as de Vries' permanent translocation heterozygotes. In permanent translocation heterozygotes, trait changes due to recombination are stable because they occur so rarely that they do not fluctuate from one generation to the next. In most types of genetic systems, however, meiotic recombination results only in ongoing, fluctuating change.

Moreover, most point mutations do not produce obvious changes in the traits of organisms. And those that do produce such changes typically affect only one, or a few related, traits. There seem to be no examples of a point mutation affecting a wide variety of traits, as is typically the case with a chromosomal mutation. Chromosomal mutations, though, are indeed expected to affect many different traits because they typically involve many different genes. Indeed, a single chromosomal mutation often encompasses thousands of genes. And most cases of saltation do involve changes in many traits, and not an isolated change in a single salient character. So for these typical cases of saltation, point mutation is not a satisfactory explanation.

According to one proposed scenario, point mutation can account for saltations involving multiple character changes. This explanation supposes that a point mutation occurs in a gene affecting early development and that as a result many traits are altered by a change in a single gene. However, this explanation has several shortcomings. First, there is the fact that such a developmental mutation would not produce a change in karyotype. Organisms differing with respect to many traits and treated as distinct species commonly differ also with respect to karyotype. The idea of a point mutation in a gene governing development does nothing to explain the origin of such karyotypic differences. Second, many organisms treated as distinct species produce hybrids of reduced fertility. There is no reason to expect that a mutation in a gene affecting early development would result in the production of a new type producing infertile hybrids in matings with the preexisting type. Third, and most important, there seem to be no documented examples of such a developmental mutation producing a new type treated distinct species, while there are many documented examples of such forms being produced by chromosomal mutations.

It should also be noted that minor chromosomal mutations involving small blocks of DNA would be expected to affect far fewer traits than major ones involving multiple entire chromosomes. Because they would change fewer traits, lesser chromosomal mutations would have effects that would be expected to be more like those of a point mutation. However, despite this contingence of the lower end of the chromosomal mutation continuum with the upper end of the point mutation continuum, the effects of point mutations and chromosomal mutations are for the most part qualitatively distinct. Most chromosomal mutations involve whole chromosomes or large portions of chromosomes and affect many different traits. They are therefore on a different scale. Point mutations affect a single gene if they affect any gene at all. So they can be expected to have major effects only if they are allowed to accumulate. But most fossil forms arise abruptly with numerous distinctive traits. Therefore, even though it is true that some few forms have been treated as species on the basis of traits that could plausibly arise via a single point mutation, we certainly have no reason to suppose most forms so treated had such an origin, or even that many did.

Types. Modern biology texts emphasize the word *species* should be defined in terms of populations of individuals. However, Cuvier, and his paleontologist successors, in recent years most prominently Stephen J. Gould and Niles Eldredge, have provided extensive empirical support for the idea that the entities biologists typically treat as species are, morphologically, 1) separated from each other by sharp discontinuities; 2) constant over time; and 3) each composed of individuals that differ relatively little from one to the next. These are some of the very features creationists emphasize in arguing that evolution does not occur. In fact, although they are all biological notions and have an easily interpreted meaning, they come close to summarizing the ancient essentialist conception of *species*. Essentialism posited the existence of a parallel world of ideas occupied by "essences" that determined the forms of all the various types of organisms in the visible world (see Chapter 1). The essentialist outlook, then, was typological. Individual variation was irrelevant under that view.

Many present-day biologists disapprove of thinking in terms of types. They emphasize that individual variation is the *sine qua non* of natural selection. And yet, there was an element of truth in the essentialist outlook: Despite individual variation, a tiger can be distinguished from a lion, a sand dollar, from a sea urchin. A particular type of bird can be identified from a single picture of an individual representing the type. There are types. But what is the essence of each type? Obviously, the essence of a type is the set of traits distinguishing it from other types. The thing each lion has in common with every other lion is a particular set of traits differentiating it from other related types of animals. The idea that each type of organism has an essence, in the sense of a characteristic set of traits, is not, however, necessarily inconsistent with the gradualist outlook. An evolving population, as described in the typical gradualistic scenario, actually is composed of individuals sharing a characteristic set of traits. It is the idea of constancy that does not, and *a priori* cannot, find a place in gradualistic accounts of evolution. Mayr (1982: 38–39) states this clearly:

> Constancy and discontinuity are the points of special emphasis for the essentialists. Variation is attributed to the imperfect manifestation of the underlying essences … Genuine change, according to essentialism, is possible only through the saltational origin of new essences. Because evolution as explained by Darwin is by necessity gradual, it is quite incompatible with essentialism.

Certainly, constancy and saltation are inconsistent with gradual change. But, as we have seen, one fossil form does not usually change gradually into another. Darwin's explanation of evolution is largely inconsistent with observation.

Stability of Form. It is often asserted that a given type of organism has a particular form and particular habits because it is constrained by the demands of its habitat. Many biologists consider natural selection to be a force that shapes every aspect of an organism to fit its environment. But this idea seems only to be a retention from an older system of thought. In early nineteenth century England the conventional idea was that "species" had been designed by God, each unique and perfect for the circumstances under which it lived.[674] Darwin's contemporaries saw "species" as "complex mechanisms from the divine workshop, and exquisitely fitted to their places in the world," so obviously designed that their very existence seemed to imply the existence of a Designer.[675] This doctrine ("*physico-theology*") had a major proponent in English philosopher and theologian William Paley, whose arguments were, at one time, accepted by all "gentlemen of respectability." As a young man, Darwin himself seems to have embraced this perspective. While studying at Cambridge, Darwin had been required to read Paley. Late in life (1876), Darwin recalled his college experiences in his autobiography. There he writes

> In order to pass the B.A. examination, it was also necessary to get up Paley's 'Evidences of Christianity,' and his 'Moral Philosophy.' This was done in a thorough manner, and I am convinced that I could have written out the whole of the 'Evidences' with perfect correctness, but not of course in the clear language of Paley. The logic of this book and, as I may add, of his 'Natural Theology,' gave me as much delight as did Euclid. The careful study of these works, without attempting to learn any part by rote, was the only part of the academical course which, as I then felt and as I still believe, was of the least use to me in the education of my mind.[676]

From the study of Paley's works, Darwin retained in later life the idea that "species" are wondrously suited to "their places in the world." Thus, as an old man, he said that he had wanted his theory to "account for the innumerable cases in which organisms are beautifully adapted to their habits of life — for instance a woodpecker or a tree-frog to climb trees, or a seed for dispersal by hooks or plumes."[677] Paley believed a sentient deity accommodated the structure of organic beings to particular ends. Darwin's faith was in an unconscious god, natural selection, which he believed to be omnipotent when allowed to act over geologic time. It, too, shaped organisms to particular ends. A tendency to describe the attributes of "species" with quasi-religious awe persists even today in biology. But it seems fair to say that the decision to describe animals as "wonderfully suited" or "exquisitely fitted" or "beautifully adapted" is a subjective judgment. On the objective level, one can say only that any type of organism not as yet extinct is "adequately suited" to the circumstances under which it finds itself.

Only when the traits in question can be construed as useful does neo-Darwinian theory satisfactorily explain why all individuals of assigned to a particular taxonomic category are characterized by certain attributes. It is perhaps for this reason Darwin wished to see utility in every aspect of every organism. But even his allies often disagreed with him on this point. According to Desmond and Moore (1991: 246), "His relentless utilitarianism — his demand that every curlicue and hue of the oddest orchid must function in order to be selected — made Huxley wince." For example, Darwin claimed in the *Origin* (1859: 200) that

> *every* detail of structure in *every* living creature (making some little allowance for the direct action of physical conditions) may be viewed, either as having been of special use to some ancestral form, or as being now of special use to the descendants of this form either directly, or indirectly through the complex laws of growth. [italics added]

In fact, the traits that consistently distinguish one form treated as a species from another often seem to lack any utility, and yet remain unchanged, generation after generation. As Bateson puts it,

> more often they are just those features which seem to us useless and trivial, such as the patterns of scales, the details of sculpture on chitin or shells, differences in number of hairs or spines, differences between the sexual prehensile organs, and so forth. These differences are often complex and are strikingly constant; but their utility is in almost every case problematical.[678]

Many physical, chemical, and mathematical systems tend toward particular states. When perturbed, a pendulum will eventually return to a stationary, plumb position. When the square root of any positive number is repeatedly taken, the series of results will converge on 1. When hydrogen and oxygen are combined, they burn to form water. These stable states towards which processes tend are called *absorptive.* Thus, if a group of mating organisms is thought of as a process, what would constitute an absorptive state of that process? Clearly, one such state would be that in which all individuals in the group share an identical fully paired karyotype because any individual that deviates from this state either will be of reduced fertility or produce progeny of reduced fertility.[a] Typically, in an unstable hybrid population, most individuals have karyotypes that are not fully paired and, consequently, are of low fertility. If a fully paired karyotype does appear in any generation, in any small group of individuals engaging in sexual reproduction, then that group will have a tremendous reproductive advantage over the other hybrids in the population. If members of that group are well enough suited to the environment in which they happen to find themselves, they will rapidly increase and become a stable chromoset (McCarthy 1995; McCarthy et al. 1995). The process producing such a recombinant derivative leads to a new stable genetic state.

Note that stabilization processes are not only stabilizing, but also formative. For example, in the case of the production of a recombinant derivative from interchromoset matings, a given hybrid variant with poor pairing might be extremely well suited to the environment in which it found itself, but be at an extreme disadvantage relative to a fully paired type when it came to producing gametes. Thus, if the paired type were even reasonably suited to its environment, it would win out. The process is formative because the genes contained in the winning, fully paired karyotype specify a particular genetic program and, thus, determine the development of a new type of organism.

More broadly, any stabilization process involving chromosomal mutation leads to an absorptive state when it gives rise to a new life cycle in which a particular karyotype regularly gives rise to an identical offspring karyotype. For example, when two lizards hybridize to create a female parthenogen, they create a new type of organism with a stable life cycle in which the karyotype is regularly replicated. Likewise a new type of grass produced by the crossing of two other grasses might be sterile but be capable of stable vegetative reproduction. In this case, too, the karyotype is stably replicated. The life cycles of such forms are perfect examples of an absorptive state — both reproduce clonally and do not change thereafter. The only possibility for change in such clonal lineages is point mutation. But point mutations are very rare, so rare in fact that distinct clones produced anciently by separate occurrences of the same type of hybrid cross are usually morphologically identical and extremely similar at the genetic level even today.

Thus, it isn't surprising that related forms treated as distinct species often differ with respect to useless traits. Under stabilization theory such traits can be viewed as by-products of the karyotypic restructuring characteristic of stabilization processes. This is true especially if such processes are assumed to be the typical source of new types of organisms (as is the case under stabilization theory). Not all genes contained in the stable karyotype of a new form produced by such a process would be advantageous. Some genes would be present only because they happened to be on a

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a. When individuals with identical, fully paired karyotypes mate, they reliably produce offspring with the same karyotype as themselves. But when individuals mate that have identical, karyotypes that are not fully paired, they do not produce offspring with the same karyotype as themselves. It is for this reason that a fully paired karyotype represents an absorptive state.

chromosome that happened to be present when the new karyotype first stabilized and the new chromoset became established. The total complement of genetic material defined by the stabilized karyotype would program the development of a particular stable somatype.[a] Therefore, traits would tend to persist even if they were not beneficial, and would come to characterize the chromoset. Even detrimental traits, such as hereditary diseases, might persist for many generations if the genes specifying them were present in the initial karyotype that originally conferred reproductive stability (and no alternative, more favorable alleles existed in the chromoset).

Enhanced Effect of Point Mutations. Even if consideration is limited to random point mutations not directly caused by stabilization processes, stabilization theory paints a more plausible picture of evolution than does orthodox theory. Under that view of evolution, the presumed prevalence of hybridization, makes it common for any given type of organism to have two distinct types of parents. Parental forms, too, would often be derived from two distinct parental forms of their own, and so forth, back through time. With this repeated doubling, the number of ancestral forms for any given modern form would be huge.[b] The descendant form could inherit a point mutation occurring in any one of these ancestors. On the other hand, under neo-Darwinian theory, the number of ancestral forms is far smaller (see Figure 7.1). Therefore the number of inheritable point mutations is also far smaller. Thus, under stabilization theory, it is much easier to understand how the accumulation of point mutations might play a significant role in evolution (the chance that such a mutation would occur would greatly increase if the number of ancestral individuals were so much larger). The accumulation would not, however, occur within a single isolated lineage. Instead, it would occur within multiple, hybridizing lineages. So this assumption inverts the topology of descent (see Figure 7.1).

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[a] These karyotypic rearrangements may also alter gene expression by altering the distribution of euchromatin and heterochromatin.

[b] If the parental forms of an extant type of organism are viewed as the previous generation and the "grandparental forms" as the generation before that, then going back in time the number of ancestral forms of an extant organism doubles under stabilization theory with each generation. Therefore, in terms of "generations of forms," the number of ancestral forms of an extant form that have existed within the last n generations (assuming a doubling in every generation) is

$$\sum_{i=1}^{n} 2^{n}$$

The same number under neo-Darwinian theory is merely n. That is, in the former the increase is the summation of an exponential, but in the latter it is only linear.

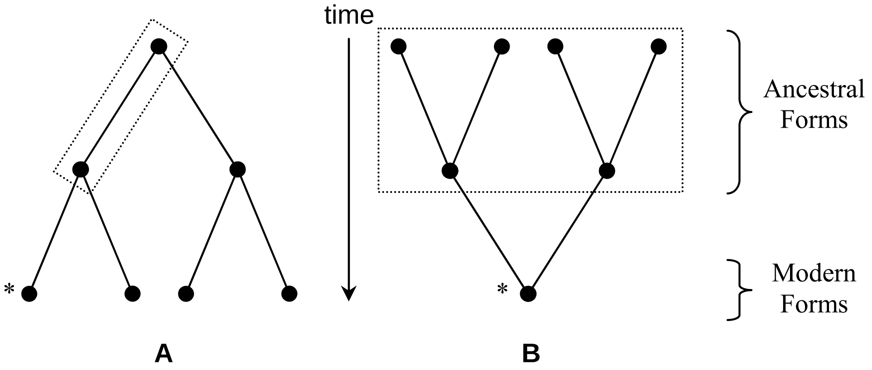

Figure 7.1. Stabilization theory inverts the topology of descent. A: Topology under neo-Darwinian theory. B: Topology under stabilization theory. Note that in tree A, the modern form (marked with an asterisk) can inherit from only two ancestral forms (the two enclosed in the box). In tree B, the modern form (again marked with an asterisk) can inherit from six different ancestral forms. Topology B, then, clearly implies more ancestral forms for any given modern form, especially when the implications of the topology are considered within the context of geological time.

However, under stabilization theory, point mutations play no direct role in the production of new stable forms, as do chromosomal mutations. The evolution of genes is decoupled from the production of new forms. Alteration of genes through point mutation is viewed as an ongoing process occurring within populations composed of individuals that are largely uniform and stable over time. Gradual statistical changes are therefore assumed to occur in genes. But the typical form is assumed to come into being abruptly and change little thereafter. The theory says it is only as one form succeeds another over geological time that point mutations, which occasionally produce new traits, begin to have major effect as they accumulate within a *lineage of forms* (see Chapter 8). In contrast, neo-Darwinian theory assumes point mutations typically do have a major effect (by accumulating within a *lineage of individuals* in the successive generations of a single isolated population). Stabilization theory claims the accumulation of point mutations does not usually lead gradually to the production of new forms. Instead such a mutations are conceived of as arising within populations of individuals that already share a particular karyotype and a particular stable set of characteristic traits. Typically they do not alter the essential features that characterize form. Only when that form goes on to produce an offspring form, can that mutation become part of the genome of a new form. Even then, it is the genetic events that occur during the stabilization process producing that new form that determine the new form's characteristic features.

A Basis for Hybrid Infertility. Various theories have been offered to explain why hybrids are commonly less viable and/or fertile than their parents. One explanation, which makes sense with regard to the production of inviability, as opposed to infertility, is that hybridization combines at random two distinct genetic programs, which may interact in an inharmonious way. Here the causative factors are clear enough — production of organisms by a trial-and-error approach of this sort would be expected often to lead to bad results. The combination in a single organism of two genomes that are separately functional will frequently (but not always) result in adverse interactions because each of the genes in one genome must be compatible with all the genes in the other. Stabilization theory concurs neo-Darwinian theory in explaining hybrid inviability in this way. Therefore, if one is attempting to judge the two theories on the basis of their explanatory powers, one cannot discriminate on this basis. However, as we shall see, the phenomenon of hybrid *sterility* is a different matter. In this latter case, stabilization theory provides a much more satisfactory explanation than does neo-Darwinian theory.

A frequently encountered explanation of the infertility of hybrids suggests that natural selection acts directly to increase reproductive isolation. In this scenario, two distinct somasets are derived from a single ancestral somaset by divergence in geographic isolation. This process, known as "reinforcement", supposedly occurs when the two somasets come back into contact (“secondary contact”). At this stage, natural selection is said to favor those individuals that mate with their own kind. Thus, it is said, reproductive isolation eventually becomes complete, as hybrids become less viable and fertile. Reinforcement, however, is controversial.[679] Even those who accept the idea of reinforcement, would admit many biologists do not accept it. Selection for infertile, inviable offspring is, in fact, a contradiction in terms — natural selection is a process favoring traits that help, not hinder, the production of offspring. Indeed, no explanation, accounting in terms of natural selection, for the general finding that hybrids are typically of reduced fertility is accepted by all biologists.

But many do accept an explanation not based on selection, the Dobzhansky-Muller (D–M) model.[680] This explanation, however, is seriously flawed. An explicit presentation of the D–M model would require the introduction of a number of technical concepts. But non-geneticists can simply ignore such technicalities and consider the D–M model as a simple black-box process. For those who wish it, Coyne and Orr (1997) give a concise description of this model, quoted in the footnote below.[a] The process there described produces two genetically distinct populations. Coyne and Orr say it is "entirely possible," if individuals from those two populations interbred, that the resulting hybrids "could be sterile" (this is the sort of hypothetical language typically used in connection with the D–M model).

However, there is really no reason for us to *expect* such hybrids to be sterile. Since the D–M model is supposed to explain a general phenomenon (hybrid sterility), it should identify a general causative mechanism. An analogy will clarify: If we wished to take a boat out for a cruise, it would be "entirely possible" that it would sink. But in the absence of known causative mechanisms making such an event likely or inevitable (e.g., enemy gunboats on patrol, gale warnings, an incompetent captain), we would have no reason to *expect* it to occur. If shipwreck is not the expected outcome under such circumstances in even one case, then, certainly, we would have no reason to *expect* shipwreck to a regular outcome of going for a boat ride.

The same reasoning applies to the D–M model. True. It describes a process that *could* produce sterile hybrids. But its proponents fail to explain why we should *expect* it to do so. If it were somehow true that two distinct types gained an advantage by producing sterile offspring together, then we would expect natural selection to favor the production of sterile hybrids. We would therefore expect sterility generally to be a trait of hybrids. However, the D–M model eschews selection and it specifies no other causative mechanism. If, in the case of any particular cross, hybrid sterility is shipwreck, where is the gunboat that will make such cases likely? For, given that most crosses produce hybrids of reduced fertility, there must be some factor that makes it likely for crosses to have this characteristic. Under stabilization theory the gunboat is the widespread occurrence of karyotypic differences distinguishing even closely-related forms (see Chapter 3). Under such circumstances hybrids are expected to be structural heterozygotes, which are typically less fertile than their homozygous parents. Structural heterozygosity is known to disrupt meiosis and interfere with the production of gametes.[681] Here the causative mechanism is clear. Hybrids commonly have impaired fertility because they are often structural heterozygotes.

But in the case of the D–M model the *causative* mechanism (i.e., the mechanism making the production of such crosses not merely possible, but *likely*) is not at all

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a. Coyne and Orr (1997) give the following, typical account of the D–M model: "If postzygotic isolation is based on incompatibilities between two or more genes, hybrid sterility and inviability can evolve unimpeded by natural selection. If, for example, the ancestral species had genotype aabb, a new mutation at one locus (allele A) could be fixed by selection or drift in one isolated population because the Aabb and AAbb genotypes are perfectly fit. Similarly, a new allele (B) at the other locus could be fixed in a different population since aaBb and aaBB genotypes are also fit. But it is entirely possible that when the AAbb and aaBB populations come into contact, the resulting AaBb hybrids could be sterile or inviable. The A and B alleles have never been 'tested' together within a [single individual], and so may not function properly in hybrids."

clear. Proponents of the model claim a sufficient degree of genetic difference will prevent two individuals from producing fertile offspring together. But this is merely an assumption, not an explanation. It is not immediately clear why infertility should be produced by the combination of two genetically distinct individuals. After all, if any two individuals are not a pair of clones, they will differ genetically. So virtually all individuals that mate to produce fertile offspring do differ genetically. Since this is the case, why should we suppose additional randomly accumulated differences in genes would result in a pair producing sterile offspring? Neo-Darwinians fail to explain *how* these additional genetic differences would cause the production of sterile offspring with disrupted meiosis and few viable gametes. They also fail to explain why we should expect genetically distinct populations to produce infertile hybrids. Really, this seems to be littler more than a vague, old idea that even predates any precise science of genetics. For example, according to Darwin (1872), the German botanist Max Ernst Wichura (1817-1866) maintained the "view of the sterility of hybrids being caused by two constitutions being compounded into one." This sounds well enough. But what exactly does it mean?

Proponents of the D–M model seem to confuse cause with correlation. True, a hybrid between parents highly distinct at the genetic level is—all other things being equal—more likely to be sterile than one whose parents are genetically alike. But this is only correlation. Karyotypic differences, too, are usually greater when parents are more distinct at the genetic level.[682] Under such circumstances, one needs to decide which of the two phenomena is causal. Is it genetic difference? Or is it karyotypic difference? Night correlates with day because it always follows day. But day does not *cause* night. The rotation of the earth causes both day and night. In the case of karyotypic differences, the causative mechanism is clear, well known, and well documented: recombination of rearranged homologs during meiosis in structural heterozygotes disrupts the process that produces gametes.[683] It therefore reduces the fertility of structurally heterozygous hybrids.

On the other hand, while there *may* be adverse effects of purely genetic differences on fertility, there seem to be few, if any, well-documented cases. Studies purporting to demonstrate this phenomenon rarely control for the possibility that karyotypic differences are causing the sterility attributed to genetic differences. No one knows how genetic differences between the parents of hybrids might produce a disruption of meiosis in the hybrids themselves. Certainly, the idea that genetic difference in parents leads, in itself, to a disruption of meiosis in their hybrids has not been shown empirically to be a general phenomenon. Rather, the existence of such a general phenomenon is a mere inference drawn by neo-Darwinians on the basis of theory. How this happens, they cannot say. So there is no reason to suppose parental genetic differences should regularly cause sterility in hybrids. The D–M model therefore provides no real explanation of the fact that the typical hybrid is of reduced fertility.

Nineteenth century naturalists used the term "physiological species" to refer to forms that were unable to interbreed due to physiological incompatibility. Darwin's inability to account for such forms was a point of concern even to his supporters. When Darwin first proposed his theory, Huxley adopted it only "subject to the production of proof that physiological species may be produced by selective breeding."[684] Three decades later he was still of the same opinion: In a letter dated May 17, 1891, Huxley writes, "I insisted on the necessity of obtaining experimental proof of the possibility of obtaining virtually infertile breeds from a common stock in 1860 … From the first I told Darwin this was the weak point of his case from the point of view of scientific logic. But, in this matter, we are just where we were thirty years ago."[685] Even today, this proof has not been forthcoming.

Darwin himself concluded "after mature reflection"[686] that natural selection could not account for the evolution of the "physiological species." Thus, in the sixth edition of the *Origin* (1872) he states that "the sterility [characteristic] of first crosses and of their hybrid progeny has not been acquired through natural selection."[687] Nor did he believe selection could cause forms to develop an inability to produce F_1 hybrids. Thus, in a letter to Alfred Russel Wallace dated April 6, 1868, he writes:

> The difficulty of increasing the sterility through Natural Selection of two already sterile species seems to me best brought home by considering an actual case. The cowslip and primrose are moderately sterile, yet occasionally produce hybrids. Now these hybrids, two or three or a dozen in a whole parish, occupy ground which might have been occupied by either pure species, and no doubt the latter suffer to this small extent. But can you conceive that any individual plants of the primrose and cowslip which happened to be mutually rather more sterile (i.e., which, when crossed, yielded a few less seed) than usual, would profit to such a degree as to increase in number to the ultimate exclusion of the present primrose and cowslip? I cannot.[688]

In response, Wallace wrote "I will say no more, but leave the problem as insoluble, only fearing that it will become a formidable weapon in the hands of the enemies of Natural Selection."[689] And yet Darwin did, in fact, think the generality of the phenomenon indicated "the cause, whatever it may be, is the same or nearly the same in all cases."[690,a] In this regard, even Darwin posited an unknown force. He also refers to this mystery factor in *The Descent of Man* (1871):

> the sterility of crossed species has not been acquired through natural selection: we can see that when two forms have already been rendered very sterile, it is scarcely possible that their sterility should be augmented by the preservation or survival of the more and more sterile individuals; for, as the sterility increases, fewer and fewer offspring will be produced from which to breed, and at last only single individuals will be produced at the rarest intervals. But there is even a higher grade of sterility than this. … in genera of plants including numerous

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a. Elsewhere Darwin (1872: 248) writes "Take the case of any two species which, when crossed, produced few and sterile offspring; now, what is there which could favour the survival of those individuals which happened to be endowed in a slightly higher degree with mutual infertility, and which thus approached by one small step towards absolute sterility? Yet an advance of this kind, if the theory of natural selection be brought to bear, must have incessantly occurred with many species, for a multitude are mutually quite barren."

> species, a series can be formed from species which, when crossed, yield fewer and fewer seeds, to species which never produce a single seed, but yet are affected by the pollen of the other species, as shewn by the swelling of the germen. It is here manifestly impossible to select the more sterile individuals, which have already ceased to yield seeds; so that the acme of sterility, when the germen alone is affected, cannot be gained through selection. This acme, and no doubt the other grades of sterility, are the incidental results of certain unknown differences in the constitution of the reproductive system of the species which are crossed.[691]

Thus, among those who think in terms of the neo-Darwinian paradigm, there has been longstanding controversy over the causative factors underlying the general phenomenon of hybrid sterility. Neo-Darwinian explanations of this phenomenon are convoluted, logically flawed, and disputed. To those biologists weary of the intricacies of this debate, stabilization theory offers a clear, brief explanation of the general phenomenon of hybrid infertility: *Populations treated as distinct species often belong to distinct chromosets.* When individuals with different karyotypes mate, the resulting hybrids are structurally heterozygous (see p. 68). Structural heterozygosity commonly has an adverse effect on fertility.[692] It is for this reason that populations tend to break up spatially into karyotypically pure chromosets. Being like other members of the population pays a large reproductive dividend (any immigrant or mutant individual with an aberrant karyotype will not find a mate of its own kind and so will produce structurally heterozygous progeny of low fertility). Karyotypic differences, then, can be used to explain why hybrid infertility is such a widely observed phenomenon—so long as it is assumed new types of organisms commonly come into being via stabilization processes involving chromosomal mutations. The evidence presented thus far in this book strongly suggests that the origin of types of organisms by this means is indeed typical.

Origin of karyotypic differences. And why do such karyotypic differences between populations arise in the first place? It is because the karyotype of each population arises *independently* of the karyotypes of other populations. Within a given sexual chromoset there is selection for a single uniform karyotype because variation of karyotypes results in the production of structural heterozygotes of low fertility. However, within a second chromoset there can be selection for uniformity with respect to some other karyotype. Thus, the karyotype of one population can evolve independently of the karyotype of another. As a result, natural selection for uniformity *within* each group stabilizes two different karyotypes. So there is nothing to coordinate the structures of the two resulting karyotypes, and they will likely differ in some, or many, respects.

Hybrids between such populations, then, are typically structural heterozygotes. Therefore, their fertility is expected to be reduced. Their sterility is not selected for in any direct way; rather it is incidental to the selection for the fertility associated with karyotypic uniformity within populations. Since populations treated as distinct species often have distinct karyotypes, matings between such populations often produce relatively infertile hybrids. It is unknown how many hybridizing taxa differ in this way. But there are certainly more than enough cases for sterility of this type to be perceived as a general phenomenon. Thus, the basis of the general phenomenon of hybrid sterility is clear under stabilization theory, but nebulous under orthodox theory. It can be stated concisely: Many, though by no means all, sexual somasets treated as separate species are distinct chromosets, so hybrids between such somasets are often structural heterozygotes of reduced fertility. Their sterility is an incidental result of selection for fertility (karyotypic uniformity) within populations.

The Nature of Natural Selection. Under stabilization theory, the primary factor governing the emergence of new types is natural selection for a stable reproductive cycle. Among the many different types of hybrids produced in a hybrid zone, a variety of types might survive to reproductive age and thrive as individuals. But no single type could emerge and establish itself as a new stable form if it were incapable of stable reproduction. In sexual organisms, the major determinant of reproductive ability is chromosome pairing.[a] If the karyotype of a sexual organism is fully paired so that meiosis can proceed normally, then that organism will be much more fertile than one having a karyotype that is not fully paired. Thus, during the early stages of its emergence as a new form, a recombinant derivative derived from interchromoset matings would be subject to at least one strict constraint. It would need to stabilize its reproductive cycle via the reestablishment of chromosome pairing. For a recombinant derivative of *intra*chromoset mating, the factors contributing to stabilization would be the same as those acting to stabilize populations in neo-Darwinian theory (isolation, selection, random loss of alleles, etc.). Of course, stabilization processes can equally as well produce types of organisms that *lack* fully paired karyotypes. For example, many agamosperms are triploid, but have stable, clonal reproductive cycles. Forms that reproduce vegetatively, too, have no need of a fully paired karyotype. Nevertheless, any form lacking a stable reproductive cycle of some kind, resulting in the stable reproduction of a particular karyotype, will be ephemeral. It cannot persist as a stable type. Obviously, in order to get established, even a form with a stable reproductive cycle would need access to a suitable environment. Once established, the form could spread to a new environment only if that environment suited its nature.

But in most cases some degree of allelic variability would remain after the karyotype had stabilized. The exact range of that variability would be determined by the range of allelic variation occurring in the set of loci defined by the karyotype. This variation might be quite high in the case of a new recombinant derivative. Advantageous allelic variants would tend to persist, and deleterious ones, to die out. Under such circumstances, the long-term effect of selection would be the gradual

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[a] Of course, other factors (e.g., viral and bacterial infection) can affect fertility, but such factors affect only certain types of organisms or individuals. In contrast, the effect of improper chromosome pairing on meiosis is a general phenomenon affecting the fertility of hybrids produced by a broad range of eukaryotes.

diminution of variability.[a] Nevertheless, in some cases even detrimental traits might linger for many generations (for example, if they were recessive, or if no more favorable allele existed). Thus, the sort of selection that occurs after karyotypic stabilization would be similar to that described in standard neo-Darwinian models (individual selection among variant alleles).

But the kind of selection that creates a new chromoset would, obviously, choose between karyotypes—it would select a reproductively stable karyotype. That karyotype would contain a particular set of genes (and hence specify a particular set of traits). Those genes might vary to some degree between different members of the chromoset (there might be allelic variants at any given locus). But from the moment of its inception, the chromoset defined by the karyotype would have to (1) have a sufficiently stable reproductive cycle to get established, and (2) specify the development of an organism that was sufficiently suited to the environment in which it first found itself (otherwise it would not survive). Thus, under stabilization theory there is a broad brushstroke that initially creates a chromoset. It chooses not between individuals, but between karyotypes, and, consequently, between the somatypes corresponding to those karyotypes.

Under this view, phenomena are easily explained that are hard to understand under neo-Darwinism's perspective. For example, there has been much discussion of the question of why agamospermy is not more widespread.[693] Such a trait would appear to be highly advantageous to any individual that possessed it. So orthodox theory predicts that far more types of organisms should have it than the number that actually do. However, stabilization theory assumes the typical form arises via a stabilization process and that most such processes involve hybridization. Hence, since hybridization requires the parents be capable of sexual reproduction, and since agamospermy only arises *de novo* from purely sexual parents in a small minority of crosses, most types of organisms produced by stabilization processes will not be agamospermous.

Similarly, neo-Darwinian theory fails to adequately account for the existence of altruism, since everything is there explained by the selfish needs of the individual. For example, at the approach of a predator some birds will give a warning call, even though that call endangers the individual making it. If the typical form were shaped by selection for traits advantageous for the *individual* that possessed them, as neo-Darwinian theory claims, then the trait of being unselfish would be selected against. An identical difficulty pertains to the existence of social insects with distinct neuter forms. How do such forms arise gradually under the influence of selection if they do not produce offspring? Such phenomena have been explained in terms of "kin selection," in which the benefit of a trait to genetic relatives supposedly outweighs the detriment to the individual that possesses it. But kin selection is a notion many biologists don't accept. However, according to stabilization theory, the typical form treated as a species already has all of its characteristic traits at the time it first arises.

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[a] Therefore high levels of variability in an extant population would suggest a recent origin, and low levels, an ancient one.

Individual competition is not an important factor in stabilization theory. Therefore, such forms can be successful and yet be composed of individuals that cooperate and make sacrifices for each other or for the benefit of the whole (e.g., bees, baboons, humans) or they can be composed of selfish individuals that do not cooperate and make few sacrifices of any kind (e.g., sharks). Likewise, a particular form can be composed of several distinct types from the time of its inception. For example, a stabilization process could give rise to a karyotype capable of reproducing itself via a cycle that also produced alternative karyotypes corresponding to neuter forms incapable of reproduction.

Critics of neo-Darwinian theory have objected that certain traits are useless except when perfectly formed. They say this fact proves natural selection could not form such traits in a gradual manner. But, as we have seen, gradual natural selection is not the only theoretical option. Every day, millions of highly variable gametes are randomly produced in the gonads of millions of hybrids in thousands of different hybrid zones worldwide. These gametes, and the offspring produced by them, are constantly winnowed because, if they are to continue to exist, they must have the necessary characteristics for survival. Extended over geological time, this process would generate an astronomical number of karyotypic variants and, thus, seems easily capable of creating a vast array of complex organic structures corresponding to those variants. Moreover, the number of ancestral point mutations would be far higher with hybrid evolution (see p. 190). Also, the various stabilization processes not connected with hybridization (e.g., autopolyploidy) can produce forms with novel traits. Finally, it should be considered that under stabilization theory a trait need not be useful to be characteristic of an organism. So there is no need to assume an imperfectly formed trait has to be useful. For example, a form incapable of flight might have rudimentary wings and yet give rise to an offspring form with better developed wings and capable of flight. All these factors greatly increase the probability of the production of viable complex variants.

Gradualists Are Not True Uniformitarians. Charles Lyell, the father of uniformitarianism, limited his explanations of geological change to “the known or possible operations of existing causes” because he believed the history of science showed this method has always put scientists “on the road to truth—suggesting views which, although imperfect at first, have been found capable of improvement, until at last adopted by universal consent.”[694] He also felt theories based on unobserved forces “relieve men of the painful necessity of renouncing preconceived notions.”[695] The production of new types of organisms via stabilization processes is a “known operation of an existing cause”—an existing phenomenon having a known effect. In contrast, the gradual evolution of one form into another via "numerous, fine, intermediate varieties" is supported by little, if any, observational data. Therefore, in denying the efficacy of known forces (stabilization processes) to produce new stable forms, and in embracing an unobserved, theoretical force (gradual "speciation" in reproductive isolation), gradualists have actually abandoned their own professed faith in the explanatory sufficiency of ordinary, known phenomena.

Similarly, gradualists claim evolution can be entirely understood as the gradual accumulation of mutations in genes. Supposedly, as soon as two populations (descended from a common, ancestral population) differ with respect to a sufficient number of genes, they become distinct "species" and are no longer able to interbreed. But this process has never been observed. Only the origin of new types of organisms through stabilization processes has actually been seen. Of course, gradual changes in populations have in fact been observed under conditions of artificial selection. But, so far as we know, physiologically isolated populations, producing hybrids of low fertility, have not been produced by this means. Nor have we seen forms treated as species arise in such a manner. So far as we know, they have been produced only via stabilization processes. Nor do the mechanisms of inheritance discussed in neo-Darwinian theory explain the origin of new chromosets. They do not apply to karyotypic evolution. True, in a population of individuals sharing the same karyotype, various versions (alleles) of a gene might occur at a particular locus. With the passage of generations, these alleles might become more or less common in the population. But at no time would these statistical shifts in allele frequency bring about a change in the karyotype. Moreover, point mutations are excessively rare. Even those that do occur are either detrimental or without effect in the vast majority of cases. So the production of new forms by the gradual accumulation of such mutations would be such a slow process that it could never be directly observed. It could only be observed, even potentially, in the fossil record. But, as we have seen (Chapter 6), it has not been observed even there (or, if it has been observed, it is at best an extremely rare phenomenon). *For all these reasons, the gradualists' claim, that the typical new form arises gradually from an ancestral form, is inconsistent with true uniformitarian doctrine.*

Position Effects. Other than the speedy gradualism scenario, the peripheral isolates scenario, and the idea of developmental mutations, the only commonly discussed model (within the context of neo-Darwinian theory) offering an explanation of how new stable somasets might suddenly appear is the idea of *position effects*. In this scenario, rearranging the position of genes on a chromosome is supposed to have an effect on their function, and thus, on the development of the affected organism. But, while position effects could perhaps play a role in the production of new forms, they are certainly inadequate as a comprehensive explanation of saltational change. This limitation can be inferred from several facts:

- Chromosomal rearrangement is unnecessary for the production of new somatypes. For example, the mule differs markedly from its parents, the horse and the ass. But the position of genes cannot come into question in this case because the individual chromosomes of a mule are identical to those found in its parents and have not been rearranged in any way. All the developmental effects of hybridization in this case (and in the case of all other F_1 hybrids produced by interbreeding between distinct chromosets) are due solely to the chromosomes of the parents being reassorted into a new, combined karyotype. Polyploids are another example of new stable forms being produced without chromosomal rearrangement.

- The amount of DNA found in each cell of a given organism (cellular DNA content) varies from one form treated as a species to another, even in the case of closely related ones such as human and chimpanzee.[696] But cellular DNA content usually varies relatively little between different members of a single somaset. Together, these two facts suggest the process creating new somasets changes the quantity of DNA present. Stabilization processes add and delete DNA, but simple rearrangement of the chromosomes doesn't.

- The existence of distinct chromosets within a seemingly uniform somaset shows even extensive rearrangement of the karyotype can fail to bring about any significant alteration in the form of an organism. For example, the previously mentioned Indian muntjac (*Muntiacus muntjak*) and Reeves' muntjac (*M. reevesi*) are somatically identical and yet have markedly different karyotypes. The former has 46 chromosomes, but the latter, only seven.[697] In the well-studied fruit flies of the genus *Drosophila,* too, there is often wide variation of chromosome structure within morphologically uniform somasets.[698]

- Other than stabilization processes no forces are known that would create a new karyotype (a position effect presupposes a new karyotype).

- Developmental changes resulting from stabilization processes are far better documented than ones resulting from position effects.

Thus, position effects fail to account for all the data and are poorly documented. But stabilization processes are well documented. Moreover, they can in fact rearrange chromosomes without additions or deletions (possibly producing position effects). But these are not the only sorts of mutations they produce. They can also generate deletions and duplications (creating dosage effects). Moreover, the combination, in a single organism, of genes previously found only in two separate types of organisms, can produce novel genetic interactions, heterosis, synergistic effects, and new combinations of traits. Since the genes are packaged in chromosomes, such changes introduce and/or duplicate and/or delete hundreds, or even thousands, of genes at a time. Genes do not function in isolation. They are affected by the function of other genes. For example, some genes turn on (i.e., become "transcriptionally active") only when certain other genes are active. So even in the absence of position effects (i.e., in situations where no structural rearrangement of any chromosome has occurred), the introduction, deletion, and duplication of large blocks of genetic material (chromosomes and pieces of chromosomes) would affect this complex interaction between genes and therefore alter the development of the organism. Thus, stabilization theory provides a more plausible, better documented, and more comprehensive explanation of the phenomenon of saltation, than does any theory based on position effects alone.

Hybrids in the Fossil Record. If the fossil remains of any longstanding, stable hybrid zone were examined, together with the fossils of the parent populations crossing to produce it, neither would change much with time. The fossils of the parents would stay the same, right up through the strata (recall the example in Chapter 3 of two types of hybridizing flickers that have remained distinct since Egyptian times; see p. 80). The fossils of the hybrids would vary from one individual to another within any particular stratum sampled, but they would typically show no progressive change over time in successive strata (as would be the case with the hybrid flickers).[a] The non-progressive, spatially localized variation typical of a hybrid zone does not imply the existence of change in the participating parental forms in the fossil record. In fact, it implies stability of those forms over time.

Moreover, there is good reason to suppose hybrids will be rare in fossil samples even in cases where hybridization has been longstanding and intense. For suppose specimens were randomly sampled from any single stratum, corresponding to some particular time in the past, over all geographic regions where the two parents and their hybrids at that time existed. In most cases, since parental ranges are typically much larger than hybrid zones, the samples would come from areas occupied by parental individuals. Hybrid fossils would be common only within the relatively small region corresponding to the hybrid zone. But recall from Chapter Two that hybrid zones move from one place to another, even on the short timescale of human observation (see p. 53-54). This means a hybrid zone would be expected to move extremely extensively over geological time so that the remains of hybrids would be spread widely hither and thither across the landscape. So hybrid remains would be spread thinly over regions occupied the great majority of the time by parental individuals. Therefore among fossil remains there would be a large percentage of pure individuals and only a smattering of hybrids. To a paleontologist looking at fossils, the parental types would seem morphologically discrete despite the former occurrence of ongoing hybridization.

Hybrids versus Stable Types. New types of organisms arising as polyploids, agamosperms, or vegetatively reproducing organisms are stable and uniform as soon as they come into existence. Although many of these are of hybrid origin, they do not have the characteristics often associated with the name *hybrid* (inviability, infertility, variability). However, all recombinant derivatives, in getting established, pass through a stage where they are at least variable. In the case of those produced by

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[a] Of course, the delicate bones of birds are rarely found as fossils. Therefore, other types of organisms, more abundant as fossils, would be more appropriate as subjects for the study of fossil hybrids.

interchromoset hybridization, there are generations in which many individuals are infertile and/or inviable as well. These unstable hybrid populations from which recombinant derivatives emerge are typeless because they are composed of a broad variety of genetically distinct individuals. They tend to be infertile and inviable, and to have a localized occurrence that's typically limited to the geographic region intervening between their parents' ranges. All these traits mean that these variable hybrids are relatively rarely seen in comparison with the fully fertile, viable, and widespread parental forms that produce them. They are the rare inhabitants of Goldschmidt's bridgeless gaps. The parents are numerous because they are chromosets composed of fully fertile and viable individuals sharing the same fully paired karyotype, which confers a stable reproductive cycle.

If we assume the typical form treated as a species arises by one of the various known types of stabilization processes, it becomes much easier to understand the observed discreteness between, and uniformity within, most populations treated as species. The karyotype corresponding to a particular chromoset specifies a particular invariant set of loci. Allelic variation can occur at each of these loci (and indeed, new alleles can arise through mutation at each those loci), but the set of loci present is stable. The fact that all individuals with the same karyotype share the same set of loci limits their development within a certain scope. In other words, the fact that a chromoset's members share a single karyotype makes them relatively uniform in morphology, as well as in other respects. For the same reason, distinct chromosets are morphologically discrete (so long as the distinct karyotypes defining them are distinct with regard to the genetic information they contain). There is no existing intermediate form between a polyploid and its parents because the process that produces a polyploid does not produce intermediate individuals with intermediate karyotypes. A single new karyotype is produced. Nor are there such intermediates in the case of new forms that reproduce agamospermously or vegetatively. Even in the case of new recombinant derivatives, where intermediates do exist, they are relatively rare compared to the stabilized derivative or its parental forms—the casual observer might not notice intermediates at all. So even here, the perception is one of discreteness. Only certain karyotypes both (1) program the development of a viable organism and (2) are reproductively stable. These are stable points in the universe of all conceivable chromosome sets. They expand and preponderate. Karyotypic intermediates between such points correspond to forms that are either entirely inviable, and so that do not exist, or that are so inviable that they are rarely seen. Thus, the prediction of stabilization theory is, in fact, the morphological discreteness ordinarily observed between forms treated as distinct species.

The idea of the production of new forms as a process of rapid transition between points of long-term stability fits better with the saltationist ideas of Darwin's cousin, Francis Galton, than with those of Darwin himself. Galton (1869) compared the evolution of new types of organisms to a stone with many flat sides ("Galton's Polyhedron"). When such a stone is rolled across a table, it is unstable until it comes to rest on one of its facets. Once at rest, it becomes stable once more and requires considerable force to set it rolling again. Galton did not base this analogy on any known genetic mechanism—the science of genetics did not yet exist—but the analogy does extend to mechanisms known today. Each flat side can be seen as analogous to a stable karyotype with its corresponding chromoset and somaset. The rolling, unstable state is hybridization (with its disruption of stable reproductive cycles and resulting chromosomal reassortment and recombination). The force that pulls the unstable polyhedron down to rest on a new facet is selection for a new form that is both reproductively stable and adequately suited to its environment.

Goldschmidt's observation that populations treated as distinct species commonly have distinct karyotypes, separated by karyotypic gaps (intermediate karyotypes that do not actually occur), can also be explained by considering the implications of observed hybrid variation in light of what Cuvier called the Principle of the Conditions of Existence. Consider the innumerable different karyotypes produced by chromosomal mutations. Some will contain the necessary information to produce a viable individual and some will not. Only those with all of the genes necessary for survival will be reproduced and continue to exist. As Cuvier observed long ago,

> Since nothing can exist that does not fulfill the conditions that render its existence possible, the different parts of each being must be coordinated in such a way as to render possible the existence of the being as a whole, not only in itself, but also in relation to its environment.[699]

Seen in this light, the ability to survive under a given set of conditions is not a consequence of environmental influences. It is a necessary attribute, demanded of each form from the moment of its inception. This idea is by no means new. In speaking of the origin of the functional traits of organisms, Aristotle (*Physics,* Book II, Ch. 8) said it had probably been a matter of trial and error:

> Why should not nature work, not for the sake of something, nor because it is better so, but just as the sky rains, not in order to make the corn grow, but of necessity? What is drawn up must cool, and what has been cooled must become water and descend, the result being that the corn grows. Similarly if a man's crop is spoiled on the threshing-floor, the rain did not fall for the sake of this—in order that the crop might be spoiled—but that result just followed. Why then should it not be the same with the parts [of the body] in nature, e.g., that our teeth should come up *of necessity*—the front teeth sharp, fitted for tearing, the molars broad and useful for grinding down the food—since they did not arise for this end, but it was merely a coincident result; and so with all the other parts in which we suppose that there is purpose? Wherever then all the parts came about just what they would have been if they had come to be for an end, such things survived, being organized spontaneously in a fitting way; whereas those which grew otherwise perished and continue to perish.[700]

Long ago, Lucretius observed that "if the first beginnings of things could in any way be vanquished and changed, it would then be uncertain too what could and what could not rise into being."[701] When a stabilization process creates a new stable chromotype, "the first beginnings" are in the initial cell in which a chromosomal mutation occurs. Often, that founding cell is a fertilized egg (i.e., a zygote). It may also be an unfertilized egg in which chromosome doubling occurs, or a single mutated somatic cell that amplifies by cell division and separates from the parent organism to live on as a new type of organism. In all such cases a new karyotype arises. The organisms specified by such karyotypes may or may not survive to reproduce because, when such changes occur, it is uncertain what can and what cannot "rise into being." Many will fail to meet the conditions of existence.

Some of these new forms are immediately stable. They reproduce clonally, by self-fertilization, or arise repeatedly in sufficient initial numbers to allow sexual reproduction. Other forms, derived from hybridization, are not immediately stable. They require more than a single generation to establish themselves and are initially far more variable than the parents that crossed to produce them. In these sexual hybrids, meiosis gives rise to a hypervariable array of gametes. Even one such hybrid may produce vast myriads of gametes, each with a distinct genetic content. Some of these germ cells may contain the proper genetic information to permit fertilization, the first step in the cycle of life. Those gametes lacking the requisite genes will degenerate and cease to exist. They do not fulfill the necessary conditions of existence. Again, the union of those gametes that do survive will form a variety of zygotes. Some of these will go on to develop into mature organisms. Those that do not are, again, those that fail to the meet the conditions of existence. They die as embryos, fetuses, infants, or juveniles—and their karyotypes pass out of existence with them. They are among the myriad non-occupants of the bridgeless gaps. Of all the populations produced by hybridization, only a few will have reproductive traits permitting continued existence in the absence of ongoing hybridization. Among these, those derived from hybridization among somatypes of the same chromoset will be maintained by the same sorts of forces described in neo-Darwinian theory. Those derived from hybridization between chromosets will maintain themselves only if they have a stable reproductive cycle. Each such population of the latter type will have a specific, new, stable karyotype common to all its members—it will be a new chromoset. With the passing generations, each such novel sexual chromoset will become increasingly stable and uniform as selection increases fertility and eliminates unfavorable variants. Of all these stabilized chromosets, some will continue to deal effectively with environmental demands. Those that do not will decline in number and cease to exist.

8 On Diversification

Something there is that doesn't love a wall,
That sends the frozen-ground-swell under it,
And spills the upper boulders in the sun;
And makes gaps even two can pass abreast.
—ROBERT FROST, *Mending Wall*

If stabilization theory is accepted as a working hypothesis, then the intellectual structure based on Darwin's description of evolution will have to be reevaluated. In particular, if the production of new types of organisms via stabilization processes is assumed typical, then a question arises—How do stabilization processes produce distinct groups of related forms (e.g., vertebrates, molluscs, mammals, insects, etc.)? Thus far, we have spoken of organismal types treated as subspecies or species, but we have not considered *higher categories* (i.e., genera, families, orders, classes, etc.). But a higher category is a type of organism, too. For example, a mammal is a type of organism. Mammalia, the order to which mammals belong, is also a category of the taxonomic hierarchy. Thus, in the language of stabilization theory, the present chapter discusses the questions of how forms treated as higher categories arise and how they become distinct from each other.

The answer to this question would be simpler if it were necessary only to describe an explanatory evolutionary mechanism. But there is some question whether such "higher categories" have any real existence, or, if they do, whether biologists have defined them correctly. When we observe nature, we don't see higher categories. We see individual organisms. Taxonomists and tradition have created the categories into which organisms are sorted. The validity of many, perhaps even most, higher categories is, or has been, a point of dispute among taxonomists themselves.[702] Systems of classification fall in and out of favor. In the 1960s there were two accepted kingdoms (plant and animal). Then a five-kingdom system became popular (animals, plants, fungi, protoctists, and bacteria). More recently, this number has been reduced from five to three (Archaea, Bacteria, and Eukarya).[703] Who knows how long this latest arrangement will hold sway?

Thus, explaining evolution is more than a simple matter of accounting for the origin of a particular set of categories through some sort of natural process. A full explanation has to consider not only evolutionary mechanisms, but also the predilections and prejudices of biologists themselves. We have to distinguish between the artificial and natural aspects of the phenomenon of higher categories. We also need to consider how, under stabilization theory, the simple, microscopic organisms found in the earliest known terrestrial strata could have evolved into the wide array of complex organisms inhabiting the earth today.

The Indiscretion of Discreteness. In the old, two-kingdom system of classification, bacteria were classified as plants. More recently, however, many biologists have claimed that the filing status of bacteria should be changed. In particular, in a system first proposed by Whittaker in 1959, cellular organisms were divided into five kingdoms, one for bacteria (Monera) and four eukaryotic ones (Protoctista, Fungi, Plantae, Animalia).[704] Recall from Chapter Three that (1) eukaryotes are organisms with cells having a set of linear chromosomes enclosed in a nuclear membrane; and (2) bacteria are single-celled organisms in which the chromosome is single, circular, and not so enclosed. Under the five kingdom system, Kingdom Protoctista comprised unicellular eukaryotes and their immediate multicellular descendants.[705] In general, Protoctista has been used as a catchall category for any simple eukaryote that doesn't fit well in one of the other three eukaryotic categories (animals, plants, and fungi).

The five-kingdom system of classification made it seem as if all bacteria shared a more recent ancestor than does any bacterium with any eukaryote. But it is certainly questionable whether such a belief is justified. For example, cyanobacteria employ chlorophyll *a* in photosynthesis, as do plants and a wide variety of protoctists. It seems improbable this same, complex molecule evolved independently in three unrelated groups (Monera, Protoctista, and Plantae), especially when it is known that various other types of chlorophyll are capable of carrying out the job of photosynthesis. Those bacteria, protoctists, and plants that contain this molecule must therefore have inherited chlorophyll *a* from some common ancestor, and so must be more closely related than this system of classification suggests. The simple photosynthetic organs of cyanobacteria (thylakoids) are similar in structure to those in the more complex photosynthetic organs (chloroplasts) of eukaryotes.[706] As Minelli (1993: 134) points out, some biologists regard cyanobacteria as true plants, while others regard them as true bacteria. Some bacteria have traits that link them with fungi and funguslike protoctists. Thus, Golubic and Knoll (1992: 55) note that

> Myxobacteria exhibit the most elaborate behavior and life cycle among prokaryotes [i.e., bacteria]. The rod-shaped, gliding cells of myxobacteria aggregate in a coordinated fashion to build large, 0.1–0.2 mm high, often strikingly colored fruiting bodies filled with millions of spores. Actinomycetes form mycelia, extensive networks, and fungus-like filaments (hyphae). They reproduce by spores or conidia borne on specially differentiated structures.

These organisms have numerous traits characteristic of fungi. Is it a good idea to assign them to a kingdom entirely separate from fungi? Whether such a classification is reasonable or not, it is clearly plausible to suppose early simple eukaryotes with funguslike traits first evolved from bacteria with funguslike traits.

Since biologists generally accept the assertion (based on fossil evidence) that bacteria existed long before any eukaryote, they also accept the idea that simple eukaryotes (protoctists) first evolved from bacteria. But protoctists cannot have evolved from *all* the different bacterial types that preceded them in time. Presumably, they evolved from some subset. Therefore, types of bacteria that are also descended from this subset share more recent common ancestors with protoctists than with other bacteria not descended from that subset. So Monera, the category in which all bacteria have often been lumped, does not constitute what many biologist term a "natural" taxonomic category (that is, its composition is not based on degree of evolutionary relationship).

Likewise, the more complex eukaryotes (fungi, plants, and animals) are widely assumed to be the descendants of early protoctists. But, again, they cannot be the descendants of *all* early protoctists. Some protoctists (e.g., *Myxomycota, Acrasiomycota*) are more similar to fungi than to plants or animals. Others resemble plants (e.g., they engage in photosynthesis). Still others have animal traits (e.g., eyespots, motility, jaws). It is thus reasonable to suppose some protoctists share more recent ancestors with fungi than do other protoctists (and others, with plants; still others, with animals). It seems, then, that Protoctista is no more a "natural" category than is Monera. This logical inconsistency has prompted many biologists to embrace contradictory claims. In particular, many accept both (1) that bacteria are "profoundly" different from eukaryotes, an opinion that suggests the two types should be placed in highly distinct categories (i.e., in separate kingdoms), and (2) that eukaryotes are the descendants of bacteria. Which is it? Are they profoundly different or are they direct descendants? Clearly, the latter of these two ideas is the more plausible: the characteristics distinguishing each of the various major types of protoctists probably arose from bacterial types with such characteristics. Similarly, one might expect that the various types of protoctists gave rise to more complex eukaryotes with corresponding traits. For example, it seems likely that funguslike protoctists arose from bacteria with funguslike traits, and fungi arose from funguslike protoctists (and, in fact, most botanists do think certain members of one large and varied protoctist group, Chlorophyta, must be similar to the ancestors of plants).[707]

Efforts have been made to partition Protoctista and allot its contents to the three categories of fungus, plant, and animal. But many organisms seem to fall between the types deemed typical of these three categories. The various euglenids engage in photosynthesis, but they also have eyespots and feed like animals.[708] Cryptomonads also combine the characteristics of plants and animals,[709] as does the chlorophyte *Chlamydomonas.*[710] Water molds (Oomycota) have many characteristics in common with fungi, but have cell walls composed of cellulose (as do plants) instead of chitin (as do ordinary fungi).[711] They also have undulipodia, another trait not usually considered characteristic of fungi (an undulipodium is a long, threadlike appendage used in cell locomotion as seen, for example, in spermatozoa).[712]

In truth, it appears the long-standing desire to have a strictly discrete system of classification has imposed artificial boundaries between many taxa. The system that taxonomists employ is a hierarchical bucket sort, the same system used by the scholastics centuries ago. There are various kingdoms, containing various states, containing various cities, containing various houses, containing various rooms, containing various buckets. We have placed each organism's name on a strip of paper and have decided each strip of paper should be placed in one and only one bucket. We have agreed that no strip can be left out on the floor between buckets or on the frontier between kingdoms.

But nature isn't listening. Anyone who is willing to take the time can find innumerable examples of organisms that don't fit into any particular bucket, city, or kingdom (see Table 8.1). Biologists often disagree on the category to which a given form should be assigned. Indeed, Pearse et al. (1987: 454) note "Animals with characters resembling those of two or more otherwise discrete groups exist at every taxonomic level and present difficulties in classification." There are, of course, distinct types. The typical bacterium is, in fact, radically different from the typical eukaryote. But typical types are more than typical—they are stereotypical. They represent a category in the naturalist's mind. In biology, as in any other realm, stereotypic thinking saves trouble in the short run, but in the long run it leads to trouble. In the present case, the prominence of the stereotype obscures a fact of basic evolutionary significance: many types of organisms don't fit the category to which they have been assigned (thus, even Darwin said, "intermediate and troublesome forms often destroy our definitions"[713]) Anyone who thinks in terms of stereotypes will tend to overlook these types sitting on the edge of the bucket, those that might just as well be placed in a different category. This kind of mindset makes the accepted taxonomic topology (a dichotomously branching tree) seem more plausible and concurrently makes the accepted evolutionary topology (also a dichotomously branching tree) seem valid. The existence of intermediate forms therefore tends to undermine these orthodox views. Such forms are gaps in the intellectual walls we place around types. Often they go unrecognized because there is a human tendency to think in terms of rules instead of exceptions. Moreover, ordinary taxonomic practice tends to conceal them since it is usual to classify specimens as being of one type or the other, and not to leave them unclassified somewhere in between. However, a careful examination of nature reveals many such organisms do exist. As Robert Frost said of the gaps that each winter appeared in the wall dividing his own property from his neighbor's,

> No one has seen them made or heard them made,
> But at spring mending-time we find them there.[714]

Table 8.1: Just a few of the abundant counterexamples to the idea that taxonomic categories are discrete. Most of the intermediates listed here are extant. Some are extinct. The intermediate nature of these forms may in some cases intimate a hybrid origin. However, they are listed here only because they are morphologically intermediate between the types indicated in the left-hand column, not because they are thought to be hybrid.

CONNECTED CATEGORIES	INTERMEDIATE FORMS
Snakes-Annelids[715]	Caecilian amphibians, blind worm snakes (Typhlopidae), amphisbaenids
Annelids-Arthropods[716]	Velvet worms (onychophorids), polychaete annelids
Annelids-Molluscs[717]	Monoplacophorans
Annelids-Lophophorates[718]	Polychaete worms, phoronid worms
Chordates-Arthropods[719]	*Nectocaris,* placoderms
Mammals-Reptiles	Synapsids, pterosaurs, loricates (see Chapter 9)
Reptiles-Amphibians[a]	Caecilians, Paleozoic reptiles (e.g., *Seymouria, Diadectes*)
Insects-Crustaceans[720]	Rotifers; half-insects (*Protura*); doubletails (*Diplura),* bristletails (*Archaeognatha*)
Rotifers-Echinoderms (Crinoids)[721]	Ectoprocts
Bivalved molluscs-Phoronids[722]	Brachiopods
Birds-Mammals[b]	Platypus
Platypus-Otter[723]	Otter Civet (*Cynogale*)
Cats-Weasels[c]	Jaguarundi (*Felis yaguarundi*)
Cats-Mongooses[d]	Fossa (*Cryptoprocta ferox*)
Carnivores-Primates[e]	Kinkajou (*Potos flavus*)
Carnivores-Insectivores	Giant Otter Shrew (*Potamogale*)[724]
Rodents-Insectivores[725]	Shrew mice (*Blarinomys, Coelomys*); shrewlike rats (*Rhynchomys*); mouse shrews (*Myosorex*); shrew rats (*Archboldomys, Echiothrix, Melasmothrix, Tateomys*); mole-voles (*Ellobius, Prometheomys*); mole rats (*Bathyergus*, *Cryptomys*, *Georychus*, *Heliophobius*, *Heterocephalus*, *Myospalax*, *Nannospalax, Spalax, Tachyoryctes*)
Moles-Shrews	Mole shrews (*Anurosorex, Solisorex*); shrew moles (*Neurotrichus, Uropsilus, Urotrichus*)

a. Romer (1966: 102) states that "Primitive Paleozoic reptiles and some of the earliest amphibians were so similar in their skeletons that (as was the case with *Seymouria* and *Diadectes*) it is almost impossible to tell when we have crossed the boundary between the two classes."

b. Calder (1978: 142). Grützner et al. (2004) showed that the platypus (*Ornithorhynchus anatinus*) genome shares genes with the bird Z and mammal X chromosomes. There are two obvious hypotheses that might account for this finding: (1) both bird Z and mammal X genes primitively existed in a single genome, but bird Z genes were later lost in mammals and mammal X genes were later lost in birds; or (2) these two distinct gene complexes came into being separately, one in birds and one in mammals, but were united by an exceptionally distant hybridization producing viable, fertile offspring.

c. Although classified as a cat, the jaguarundi is intermediate in appearance between mustelids and cats. Known in Central America as the "otter cat" or "weasel cat," it is like a mustelid in having short legs, a slender elongate body, a very long tail, and small and flattened head, particularly the nasal region (members.aol.com/cattrust/jagundi.htm).

d. Although the fossa is usually grouped with the mongooses in family Herpestidae, Nowak (1999: 785) notes that it has sometimes been placed in the cat family (Felidae).

e. Though treated taxonomically as a carnivore, the kinkajou is more primate-like than many primates. Judging by its arboreal habits, its rounded head, its short face, its long, fully prehensile tail, its large, forward-facing eyes, and its largely frugivorous diet, taxonomists once classified it as a primate, calling it *Lemur flavus* (Kays 2001, 2003; Kaysand Gittleman 1995: 300).

Murids-Porcupines[726]	Long-tailed Porcupine (*Trichys*); echimyids (esp. *Chaetomys*); Maned Rat (*Lophiomys*)
Porcupines-Insectivores[727]	Hedgehogs (Erinaceidae); tenrecs (Tenrecidae)
Rats-Hamsters[728]	Ratlike hamsters (esp. *Tscherskia triton*)
Murids-Jerboas[729]	Kangaroo rats (*Dipodomys*); and kangaroo mice (*Microdipodops*); jumping mice (Zapodidae); pocket mice (*Heteromys, Liomys, Perognathus*)
Murids-Squirrels	Rat-squirrel *Laonastes* (Diatomyidae)
Hystrichognathids-Sciurognathids[730]	Gundis (Ctenodactylidae)
Amphibians-Fish[731]	Crested newts (*Triturus*); eel-newts (*Amphiuma*); Paleozoic tetrapods (e.g., *Acanthostega; Ichthyostega*)
Teleosts-Elasmobranchs[a]	Ratfish (*Hydrolagus colliei*)
Bryozoans-Brachiopods[732]	Phoronid worms
Snakes-Lizards[733,b]	*Ophiognomon*, *Chamaesaura*, *Panasepsis*,. *Acontias*, *Acontophiops*, *Typhlosaurus*, *Procelotes*, *Scelotes*, *Typhlacontias, Tetradactylus, Chalcides*, Leptophylophidae, *Bipes*, *Pachyrhachis*
Bees-Moths[734]	Clear-winged moths (Sesiidae), bee hawk-moths (*Hemaris*)
Bees-Flies (Hymenoptera-Diptera)	Hover flies (Syrphidae); social wasps (Vespidae)
Nerve-winged insects-Mantids[735]	Mantispids; e.g., Styrian Praying Lacewing (*Mantispa styriaca*)
Birds-Reptiles[736]	Archaeopterygids, avimimids, ornithomimids, garudimimids
Sphenisciforms-Procellariforms[c]	Eudyptulid penguins (*Eudyptula*)
Hawks/Eagles-Storks/Herons[d]	Secretary Bird
Ratites-Carinates[737]	Tinamous (Tinamiformes), lithornithids
Galliforms-Anseriforms[e]	Screamers, Magpie Goose

a. Ohno et al. (1969) remark that "the ratfish [*Hydrolagus colliei*] is an evolutionary oddity. It has a cartilaginous skeleton and fertilizes internally as do sharks and rays of the class Elasmobranchii, yet it wears gill covers (opercula) like bony fish (Osteichthyes), and it belongs to a class of its own, Bradyodonti."

b. If the difference between a lizard and a snake is measured in terms of the presence/absence of legs, then various intermediate taxa represent a continuum of variation between the extreme of having four legs and having no legs. For example, all modern pythons have rudimentary rear limbs, small claws at the base of the tail. *Bipes* has two small front limbs. Indeed, some organisms classed as lizards lack legs.

c. According to Martinez (1992: 140) the penguin genus *Eudyptula* "apparently links penguins and Procellariformes." An Internet site (neaq.org/penguins/littleblue.html) states that Little Blue Penguins (*Eudyptula minor*) are "Far more reminiscent of their flying cousins the Procellariformes, shearwaters, petrels and albatross.

d. Kemp (1994) notes that the secretary bird is always placed in its own monotypic family and often in its own suborder (Sagittarii), sometimes even in its own order (Sagittariformes). It shares anatomy of skull and head (except long upper lashes) with eagles (which belong to order Falconiformes), but aspects of its breeding behavior are most similar to storks (Ciconiiformes). DNA-DNA studies indicate close affinity to storks *and* birds of prey.than the other 16 penguin species."

e. Screamers (Family Anhimidae) have been described as links between Galliformes and Anseriformes (Carboneras 1992a: 528). Also Marchant and Higgins (1990: 1114) say many osteological features of the Magpie Goose (*Anseranas semipalmata*), of New Guinea and northern Australia, "resemble screamers rather than Anatidae."

Tyrant Flycatchers-Manakins	Cinnamon Tyrant-manakin (*Neopipo cinnamomea*)[a]
Tyrant Flycatchers-Cotingas[b]	Tytyras (*Tytyra*), becards (*Pachyramphus*)
Todies-Motmots	Tody motmot (*Hylomanes momotula*)[c]
Owls-Nightjars[738]	Oilbird (*Steatornis caripensis*)
Owls-Hawks	Hawk Owl (*Surnia ulula*)[d]
Hawks-Cuckoos	Hawk-cuckoos (*Hierococcyx*)[e]
Songbirds-Nonpasserines[f]	Sunbirds, Shrikes
Crows-New World Blackbirds	Tamaulipas Crow (*Corvus imperatus*)[g]
Crows-Starlings[h]	Stresemann's Bush-Crow (*Zavattariornis stresemanni*); Piapiac (*Ptilostomus afer*)
Plovers-Sandpipers	Diademed Sandpiper-plover (*Phegornis mitchellii*)[i]
Vultures-Eagles	Palm-nut Vulture (*Gypohierax angolensis*)[j]

a. Genus *Neopipo* contains a single aberrant "manakin" *N. cinnamomea* found in Amazonia. According to Ridgely and Tudor (1994: 697), it resembles the Ruddy-tailed Flycatcher (*Terenotriccus*) to a remarkable degree, though it has long been considered a manakin. They propose this bird be called the Cinnamon Tyrant-Manakin and say "this species so resembles Ruddy-tailed Flycatcher that it could easily be passed over in the field."

b. Fitzpatrick (2004: 449, 453) says various authors treat two South American genera, *Tytyra* (tytyras) and *Pachyramphus* (becards), either as tyrant flycatchers (Tyrannidae) or as cotingas (Cotingidae), or as a separate family (Tityridae). They share many characters with both tyrant flycatchers and cotingas.

c. The Tody Motmot (*Hylomanes momotula*) looks intermediate between todies (Todidae) and motmots (Momotidae) and differs from other birds assigned to Momotidae in its small size, facial pattern, lack of racquet tips on the tail and of serrated bill edges (Snow 2001: 279 and Plate 23).

d. Classified as an owl this bird is similar to falconiforms in its long tail, wing shape, and diurnal habits. Harrison and Greensmith (1993: 327); Perrins and Middleton (1998: 396).

e. Payne (2005: 470) says hawk-cuckoos (*Hierococcyx*) look much like Eurasian Sparrowhawks (*Accipiter nisus*), for example, the Large Hawk-Cuckoo (*Hierococcyx sparverioides*), is like *A. nisus* in wing and tail shape, broad body plumage pattern, and color, and flight pattern. Small birds respond to it as they do to sparrowhawks.

f. Classified as passerines, shrikes have the weak feet of a songbird, but they are birds of prey with the keen eyesight and sharp beak of a hawk, which are nonpasserines (Harris 2000; Lefranc 1997; Perrins and Middleton 1998). The Old World sunbirds are similar in appearance to New World hummingbirds. Like hummingbirds they have iridescent plumage and hovering flight on rapidly vibrating wings. Both are small to very small birds. Both probe flower tubes for nectar with long beaks. Both supplement their diets with insects and use spiders' webs in constructing their nests. Sunbirds, however, are classified as passerines and hummingbirds as nonpasserines. Cheke and Mann (2001); Perrins and Middleton (1998); Williamson (2001).

g. In his section on the Tamaulipas Crow (*Corvus imparatus*), Goodwin (1986: 66) notes that this "species, with its relatively small bill, small size, slender appearance and the rich gloss on its silky plumage, shows a remarkable convergence towards some of the American blackbirds in the family Icteridae."

h. Of the Piapiac (*Ptilostomus afer*), Madge and Burn (1994: 135) say "this long-tailed black African corvid recalls both magpies and *Corvus* crows in outward appearance … It might well be that like *Zavattariornis* of Ethiopia it is perhaps a surviving relic of a long extinct group of crows that have no close link to the present-day corvids; indeed both of these African aberrant crows share a remarkable superficial resemblance to quite different groups of starlings." Elsewhere, they say (ibid: 123) Stresemann's Bush-Crow (*Zavattariornis stresemanni*)recalls "a starling rather than a crow."

i. Regarding *Phegornis mitchellii* (Diademed Sandpiper-plover), Meyer de Schauensee (1966) noted that "whether this bird is a sandpiper or a plover is still uncertain."

j. Thiollay (1994) says the Palmnut Vulture (*Gypohierax angolensis*) is intermediate between fish-eagles and vultures. Most similar to *Neophron percnopterus* (Egyptian Vulture), it also recalls juvenile *Haliaeetus vocifer* (African Fish Eagle), which is sympatric with *N. percnopterus* in North Africa (*G. angolensis* occupies an intermediate range).

Bats-primates[739]	Flying Lemurs (Dermoptera)
Molluscs-Annelids-Chordates[740]	Chaetognaths, caecilians, *Pikaia*
Gastropods-Bivalves[741]	Bivalved gastropods (Juliidae)
Animals-Protoctists[742]	Zoomastigota, Acrasiomycota, mesozoans (*Dicyema*, *Dicyemmerea*, *Conocyema*)
Plants-Animals	Euglenoids,[743] cryptomonads,[744] chlorophytes (e.g., *Chlamydomonas*),[745] zoomastigotes[746]
Plants-Fungi[747]	Water molds (Oomycota)
Fungi-Protoctists[748,a]	Acrasiomycota, Chitridiomycota, Labyrinthulata, Myxomycota, Plasmodiophora, Hyphochytriomycota
Bacteria-Eukaryotes[749,b]	Myxobacteria, cyanobacteria, pelobiontids, dinoflagellates, rhodophytes, archaebacteria, microsporans
Ferns/mosses-Seedplants[750]	Cycads, seed ferns, ginkoaleans, progymnosperms
Gymnosperms-Angiosperms[751]	Gnetophytes
Plants-Protoctists[752]	Chlorophyta, Acrasiomycota

a. Campbell (1987: 550) states that "Even with five kingdoms instead of only two, the slime molds are a taxonomic enigma. They resemble fungi in appearance and life style, but the similarities are beileved to be the result of convergence. In their cellular organization, reproduction, and life cycles, slime molds depart from the true fungi and probably have their closest relatives among the protoctists."

b. Doolittle (1999, 2000); Margulis and Schwartz (1982: 42, 62, 72, 74; 1998: 117-118); Martin (1999); Minelli (1993: 131, 134); Reichenbach (1984); Xiong et al. (1998). Because of their peculiar nuclear organization, dinoflagellates have been called *mesokaryotic,* that is, "between prokaryotic and eukaryotic" (see Margulis and Schwartz 1982: 74). According to Minelli (1993: 136), rhodophytes (Aconta) are recognized as eukaryotes "lacking both flagella and centrioles and possessing plastidia similar to the cyanobacteria, and pigments intermediate to those of the cyanobacteria and the green plants."

Dubious Assumptions. As we have seen (p. 137 *et seq.*), when different traits are used to construct phylogenetic trees for the same set of organisms, different trees are implied. There is very often a lack of concordance in the results based on different datasets. Some traits may suggest the relationships of the organisms should be described by one tree, while other traits may suggest the nature of their relationships are quite different. Under such circumstances, the tree that "best" fits the data is selected. But this procedure presupposes that some "real" tree of descent actually exists. If the production of new forms via stabilization processes is common over evolutionary time, then there will be no *real* tree, let alone a best one. The reason: such processes so often involve hybridization that they would give rise to a weblike network of descent, not a tree. Under such circumstances, "best" would merely mean "best, given a particular set of assumptions about how the data should be weighted." But the supposition that "best" means "real," the usual assumption under orthodox theory, causes discordant data to be treated as statistical noise and ignored.

It is important to realize that the results of this categorization process depend on initial assumptions that are arbitrary and subject to bias. Any given organism has an essentially infinite number of traits. From this infinite set, the investigator must choose some particular, finite subset of traits if the classification process is to be carried out. A geneticist might consider genetic traits more significant and limit her attention to genes. A paleontologist has no genetic information and instead bases classifications on morphological traits, as do many naturalists. If a different set of traits, whether genetic, morphological, or a combination thereof, is chosen to serve as the basis for categorizing a given set of organisms, a different taxonomic classification often results. Nevertheless, there is no proven, objective criterion that allows one category of traits to be excluded in favor of another.

Even after a subset of traits has been chosen, subjective decisions remain. Rules for evaluating the selected set of traits must also be chosen. Certain traits might be considered more significant or reliable and be given greater weight in the analysis. Sometimes, this weighting is done almost unconsciously. For example, existing opinion concerning the way taxa are related to one another can limit the mental scope of the investigator. Thus, if two taxa have traditionally been considered distantly related, then traits they hold in common (and that therefore would seem to contradict tradition) are likely to be discounted. For example, although pterosaurs (winged creatures, formerly known as pterodactyls, that lived concurrently with dinosaurs) are now known to have been furry and are generally believed to have been warm-blooded (see p. 252), they remain classified as reptiles. In other words, there is a conservative tendency to dismiss what seems to undermine accepted ideas concerning the natural order. The result of this circular mode of reasoning is that ideas of the natural order become bogged in dogma.

This logic is reflected in the wide acceptance of the concepts of *homology* and *analogy.* Biologists call the existence of similar features in organisms they consider to be unrelated “analogy.” They say analogy is found when organisms live under similar conditions or have similar habits. The same needs in each case are supposed to cause structures serving similar functions to evolve over time. When a given situation is viewed in this light, it is said that the organisms in question have undergone “convergent” evolution. Here, use of the word *convergent* indicates the speaker believes the organisms are actually distantly related, but have approached each other in form. The nature of the correspondence between the two organs or structures is presumed to be one of mere similarity, not genetic relationship. Therefore, when attempting to arrange a set of organisms into a phylogenetic tree reflecting their mutual relationships, anyone holding such views can justify omitting traits from analysis by claiming they are analogous. By definition, if a trait is analogous, it has no bearing on questions of genetic kinship. For example, it could be claimed that the fur seen in fossil pterosaurs, mentioned in the previous paragraph, does not indicate a relationship between these animals and mammals. Indeed, one could argue that pterosaurs were reptiles, entirely unrelated to mammals, and that fur arose in these creatures independently of the evolution of fur in mammals. To justify this claim, one might assert flight placed on pterosaurs metabolic constraints requiring the evolution of a more efficient form of insulation than ordinary reptilian scales. Such is the typical line of reasoning of those who think habitually in terms of analogy and convergence.

In contrast, when biologists believe two organisms are related, they often claim dissimilar structures are essentially the same, in the sense that both are descended with modification from a corresponding structure in a common ancestor. In this case, the word *homology* is employed. Thus, if a researcher believed a theory asserting the swim bladder of fishes evolved into the lung of land animals, she would say lungs and swim bladders are *homologous*. Claims of homology allow a researcher to make claims of relationship even when organisms have dissimilar traits.

Rarely, then, is a scientist stating a known fact when he makes an assertion about whether two structures are analogous or homologous. Rather, he is indicating something about his own beliefs concerning the nature of the relationship between the two organisms in question (i.e., whether their relationship is close or distant). He is also saying something about whether he believes the trait to be useful from the standpoint of constructing phylogenetic trees (i.e., whether it is "phylogenetically informative"). The concepts of homology and analogy therefore have a potentially insidious effect. Once a widely accepted hierarchy of relationships has been established by tradition, claims of analogy allow a researcher to discount the presence of similar traits in organisms that have traditionally been considered unrelated, and to ignore dissimilarities in those considered related. This approach to evolutionary analysis gives *carte blanche* to those who wish to ignore new data and maintain the status quo. Also, to those who wish to claim conflicting gene trees are rare, it provides a simple means of homogenizing the data. Faced with such inconsistencies, they can simply say similar genes are the result of convergence in organisms they consider unrelated.

Biologists are apparently motivated to unwittingly shape their experiments and, under the influence of the concepts of analogy and homology, inadvertently even to selectively winnow their data to obtain concordant results. For example, the writer has seen cases where professors encouraged their graduate students to limit the number of taxa and traits in phylogenetic studies in order to obtain "clean" results (i.e., results where all the data implied the same tree of relationships). The object of this approach seems to be to eliminate unnecessary complications that stand in the way of presenting clearly resolved trees. But its effect is to prevent evidence of nonconcordance from emerging. Those who engage in such practices clearly believe the true history of evolution has been a matter of branching divergence. "Clean" results consistent with this view are therefore seen as correct. However, as we have already seen in Chapter Five (p. 137 *et seq.*), phylogenetic trees are often, even typically, non-concordant despite such biases that tend to tidy the results. Naturalists have long believed that a supposedly treelike pattern of evolutionary history was reflected in the treelike configuration of their chosen system of classification. But this notion may be entirely illusory. The two patterns may well be—indeed much evidence suggests they are—entirely distinct. Perhaps then we should look for another evolutionary topology.

Similarity chains and Similarity Sets. Intermediate forms can be used to unite disparate types into *similarity chains* in which those types that form adjacent links in the chain are relatively similar. Although those types at the two ends of the chain might be quite different, types of organisms constituting adjacent links in such a chain might plausibly produce new types by stabilization processes involving hybridization. For example, most people would think that a mallard duck (*Anas platyrhynchos*) would be unable to hybridize with a mute swan (*Cygnus olor*). Indeed, no such hybrids seem to have been reported. However, both of these birds do hybridize with the Canada Goose (*Branta canadensis*) and hybrids of both types have been reported from a natural setting.[753] Among birds as a whole, the author has found that such chains of hybridizing forms can be much longer.[754] For example, Figure 8.1, which summarizes reports of hybridization among waterfowl, clearly shows that a wide variety of similarity chains could be constructed among such birds.

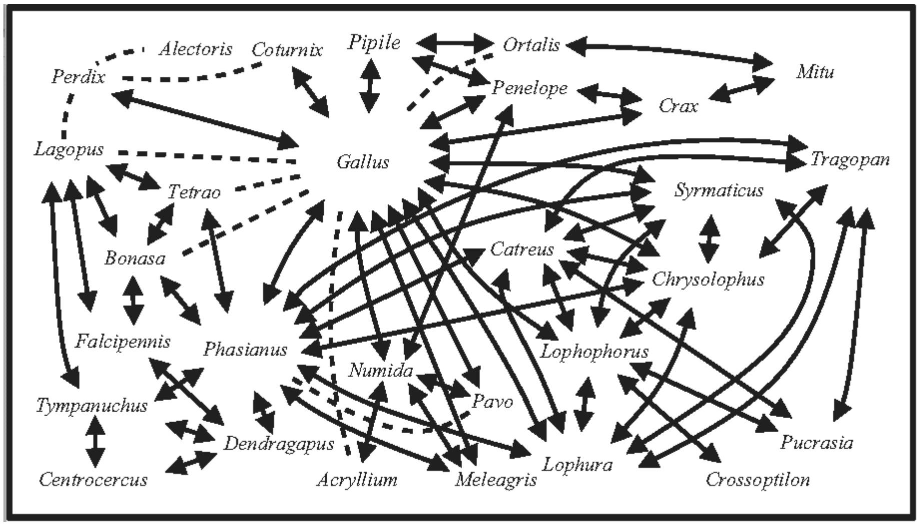

Figure 8.1: Diagrammatic representation of reported hybridization among waterfowl genera (arrows connecting genus names indicate hybridization has been reported between the two connected genera; dotted lines indicate that available reports need further verification).

This idea of chains of hybridizing forms is a fundamental principle in stabilization theory. Over evolutionary time, the composition of such chains would change as (1) new types of organisms occasionally came into being; and (2) older forms occasionally died out. A trait initially present in only a single type of organism in an ancient chain might therefore spread with time until it was present in many or all forms in a modern chain. The trait might spread merely at random, but it would spread more rapidly if those types of organisms having it could better avoid extinction. For example, early plants lacked vascular systems. But suppose some form in an early similarity chain (ancestral to modern vascular plants) obtained this trait (or an approximation of it). Such a trait would be advantageous and would permit its possessor to exploit drier environments inaccessible to other types of organisms in the same similarity chain. In successive chains more and more new vascular forms would appear because vascular forms would be fitter than nonvascular forms. They would thus exist for a longer time and produce more offspring forms than nonvascular forms. When new forms are produced via stabilization processes involving hybridization between adjacent forms in the chain, vascular forms would come to predominate, as is the case with modern plants. Thinking in terms of similarity chains, then, one can see how an increasing number of forms with a particular trait can come into being even when the trait itself originally came into being only once in a single type of organism. The general nature of this process is diagrammed in Figure 8.2.

One can also see why the potential power of point mutation is greatly amplified under stabilization theory. For by spreading in successive chains from the form that initially obtained it, such a mutation can affect a much broader range of organisms. Moreover, each individual organism has far more ancestors in which such a point mutation can occur (see Figure 7.1). Under this view, similarity chains succeed each other in a manner parallel to the succession of generations in an ordinary population.[a] Note that the parent forms and offspring forms in this process are analogous to the parent individuals and offspring individuals of neo-Darwinian theory. Those parent forms with traits favored by natural selection produce more offspring forms (whereas under neo-Darwinian theory, those parent individuals with advantageous traits produce more offspring individuals). *The selection is between types of organisms, not individuals.* There is no slow change of one form into another. There is only production of new stable forms by pre-existing stable forms. In some cases,

Similarity chains are really an oversimplification. Normally the ability to hybridize is not limited to a set of organisms that can be arranged in a simple linear chain. Many forms treated as species have the ability to hybridize with numerous partner forms. For example, the mallard duck (*Anas platyrhynchos*) has been reported to hybridize with about 60 other waterfowl treated as species. More realistically, then, one can posit a *similarity set,* a set of forms in which all members are connected to at least one other member by the potential to hybridize. In such a set, a favorable trait would be able to spread to an increasing number of set members over time. The situation would then be analogous to neo-Darwinism's description of the spread of a favorable trait within an ordinary population (the set of individuals making up a population is analogous to the set of forms making up a similarity set)

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[a] Specifically, it would be analogous to a population model with successive nondiscrete generations, since some forms would survive from one generation to another.

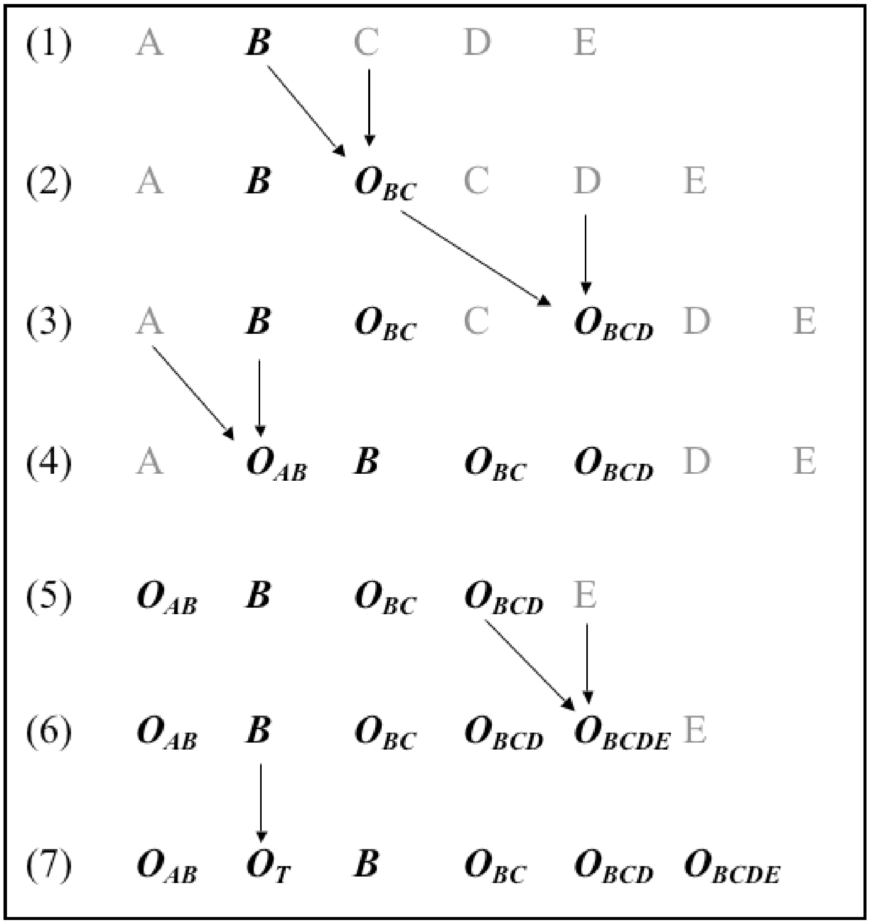

Figure 8.2. A series of similarity chains showing the spread over time of an advantageous trait (forms with this trait are shown in bold italic); (1) Initial similarity chain. A series of five life forms, A, B, C, D, E (adjacent forms in the series are assumed to be more similar and hence more hybridizable). Initially, the only form with the advantageous trait is B; (2) B has hybridized with C to produce offspring life form O_{BC} (in the figure "O" stands for "offspring form"); (3) O_{BC} has hybridized with D to produce offspring life form O_{BCD}; (4) A has hybridized with B to produce offspring life form O_{AB}; C has become extinct; (5) A and D have become extinct; (6) O_{BCD} has hybridized with E to produce offspring life form O_{BCDE}; (7) B has produced a tetraploid O_T; E has gone extinct. From the set of life forms in the original chain only B has survived; all life forms in the similarity chain now have the trait.

The reader might correctly suppose the large differences between some types of organisms prevent the production of hybrids. This is indeed the case. However, such gaps may have been bridged in former times by extinct (stable and discrete) intermediate forms, so that hybridizing forms would be less disparate. It is also possible hybridization could in some cases occur despite our perception of a large disparity between the taxa involved. Indeed, broad surveys of hybridization in birds and mammals (McCarthy 2006; McCarthy, in prep.) indicate similarity, whether genetic or morphological, is an imperfect predictor of crossability. Moreover, intermediate forms often connect taxonomic categories supposed to be entirely distinct.

In the previous section, it was pointed out that intermediate forms connect even the broadest categories (plants, animals, fungi, bacteria). It is not surprising, then, that lesser categories are connected as well. For example, among mammals, flying lemurs (genus *Cynocephalus*) are often placed in a separate order of their own (Dermoptera), but various authors have also classified them on various occasions as bats (Order Chiroptera), primates (Order Primates), and insectivores (Order Insectivora). For example, Duff and Lawson (2004), the taxonomic standard used for mammals discussed in this book, classify them as primates. The Raccoon Dog (*Nyctereutes procyonoides*) is placed in the same family as dogs (Canidae), but it is obviously similar to raccoons, which belong to a different family (Procyonidae). Scientists have long argued over whether tree shrews (Tupaiidae) are primates or insectivores. Classified as a cat (Family Felidae), the Jaguarundi (*Felis yagouaroundi*) resembles a weasel or otter (Family Mustelidae), while the Fossa (*Cryptoprocta ferox*) seems to connect the cat family with the civets and genets (Family Viverridae). Classified as a carnivore (Order Carnivora), the kinkajou (*Potos flavus*) is very similar to a primate. The clear-winged moths, classified as Family Sesiidae of Order Lepidoptera, have a variety of features that are hornet- or beelike. Both bees and hornets are classified as belonging to a separate order (*Hymenoptera*). Bivalved gastropods (Family Juliidae) are intermediate between snails and bivalved molluscs, normally treated as separate classes (Gastropoda and Bivalvia) of the phylum Mollusca. In other words, juliids bridge the gap between categories that, from a taxonomic standpoint, are as distinct as a bird and a fish. Considered even more distinct (different phyla), annelid worms and arthropods are connected by onychophorans, which have traits characteristic of both. One could go on and on. Such forms seem innumerable. Once again, Table 8.1 gives a (by no means complete) sampling of such organisms. The existence of such intermediates suggests similarity chains may stretch, or formerly stretched, further than one might at first suppose.

Under stabilization theory intermediate organisms are expected. But under neo-Darwinian theory they constitute a problem. For only some of these intermediates can be explained. One of the most common explanations offered under that view is that the form in question belongs to one category but gains an advantage by mimicking another. For example, one might suppose clear-winged moths gain protection from predators by imitating bees and hornets, which also have clear wings. But in many cases explanations in terms of mimicry are subject to obvious objections. Bivalved gastropods have a small, coiled structure like a snail shell attached to the apex of a bivalved shell. They also have heads like those of snails (not found in ordinary bivalves). What is the advantage of a snail mimicking a bivalve, or a bivalve mimicking a snail?

Admittedly, some taxonomic categories seem entirely discrete. They do not seem to be connected by any intermediate forms of any kind. But stabilization theory interprets these well-defined categories in a different way. Under this view, two discretely different but related extant categories are seen as two similarity sets descended from a single ancient similarity set that did contain intermediate forms now extinct. And, in fact, extinct fossil forms do connect many similarity sets that seem to be unconnected today (see Table 8.1). A well-known example is the reptilelike fossil bird *Archaeopteryx.*

Note that this process of breaking similarity sets into isolated subsets is analogous to the process of divergence described in neo-Darwinian theory. But this sort of divergence involves the extinction of intermediate *forms* (Figure 8.3), whereas neo-Darwinian divergence involves a dying out of intermediate *individuals.* Note also that the natural selection among the various forms within an isolated similarity set is analogous to the selection the neo-Darwinian paradigm describes as occurring in a reproductively isolated lineage composed of interbreeding individuals. Note also that the various forms within a similarity set need not correspond to types treated as species. They could just as well be forms treated as genera or families (and in fact, many intergeneric and interfamilial hybrids are known).

Within this context, one can clearly see the significance of the contrasting phenomena of hybrid vigor and hybrid inviability (neo-Darwinists often discuss the latter of these two phenomena under the heading of "hybrid breakdown"). As we have already seen (chapters 2, 3, and 4), breeders often observe that the products of particular crosses are more vigorous than, and have characteristics superior to those of, their parents. Nevertheless, evolutionary biologists often discount the creative powers of hybridization by noting that hybrids are frequently inviable, and that inviable hybrids are unlikely to produce a new, successful form. However, crosses of both types do exist, those that produce viable hybrids and those that produce inviable ones. From the perspective of stabilization theory, the implication of this fact is that some crosses will give rise to forms that can outcompete forms produced by other crosses. *The propagation of new forms via hybridization, then, is blocked only in the case of those crosses producing inviable hybrids, not those that produce vigorous hybrids with advantageous characteristics.* In other words, there is natural selection for certain hybrid forms and against others.

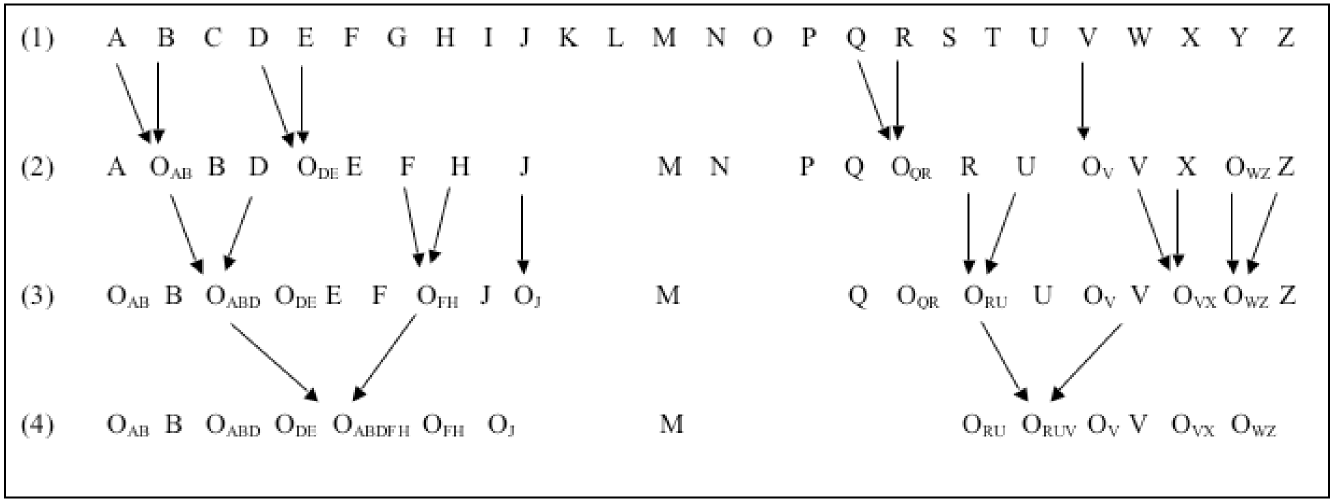

Figure 8.3. A series of similarity chains illustrating the concept of divergence under stabilization theory; (1) Initial status of the similarity chain. A series of 26 life forms, A, B, C, …, Y, Z (adjacent forms in the series are assumed to be more similar and hence more hybridizable); (2) Several life forms (C, G, I, K, L, O, S, T, W, and Y) have become extinct. New life forms (O_{AB}, O_{DE}, O_{QR}, and O_{WZ}) have been produced via hybridization and V has produced the autopolyploid O_V; (3) Addional life forms (A, D, H, N, P, R, and X) have become extinct. New life forms (O_{ABD}, O_{FH}, O_{RU}, O_{VX}, and O_{WZ}) have been produced via hybridization and J has produced the O_J via aneuploid increase; (4) More life forms (E, F, J, Q, O_{QR}, U, and Z) have become extinct. New life forms (O_{ABDFH}, and O_{RUV}) have been produced via hybridization. The originally connected chain has now diverged into two separated groups. Only the relict intermediate form M still connects the two isolated similarity chains.

It is well known that many types of organisms today represented by one or a few forms were anciently represented by a diverse array of forms. For example, shelled cephalopods were abundant in the time of the dinosaurs and occurred in a diverse array of forms. But today the Chambered Nautilus (*Nautilus pompilius*) and a few closely related forms are the sole survivors. The surviving representatives of such groups are often much smaller than some members of the ancient group. A nautilus is about the size of a dinner plate, but some ancient shelled cephalopods were the size of airplane tires. Modern lycopods (clubmosses) are tiny, but in the Palaeozoic many lycopods were the size of trees. This *residual dwarfism* is apparent when various modern taxa are compared to their forebears. It may often be an artifact of preservation or simply a result of impression. For example, if forms in a particular category varied widely in size, the largest forms might be preserved as fossils with higher probability or make a greater impression on the observer than the smallest. Under such circumstances a surviving intermediate-sized form might seem like a dwarf, even though smaller forms once existed. Under stabilization theory this sort of reduction in diversity, whether the single remaining form is dwarf or not, is an evolutionary dead-end. The residual form has become isolated. There are no similar types with which it can interact genetically via hybridization. This situation results in an inability, or at least a marked reduction in the capacity, of the isolated form to produce new forms. This type of reproductive isolation would prevent any further evolution from occurring (neo-Darwinian theory describes an analogous situation in which a population can lose much of its ability to evolve due a loss of genetic diversity).

Note that under the view of evolution just described the standard system of taxonomic classification becomes an artificial construct. Its dichotomously branching topology would no longer correspond to a topology of historical events. From the standpoint of stabilization theory, there is really no reason even to have a formal hierarchy of categories. In fact, the niggling assiduity lavished on the classification of each and every type of organism under the present system becomes absurd (e.g., "Kingdom: Animalia; Phylum: Chordata; Class: Mammalia; Order Primates; Family: Hominidae; Subfamily: Homininae; Tribe: Hominini; Genus: Homo; Species: sapiens"). Surely we will be able to find a less cumbersome way of designating a particular sort of organism. For my own part, I would be satisfied to refer to organisms by their common names and to have an identification number that could be added in those cases where any doubts might arise concerning the exact identity of the organism in question. For example, one might write "Bengal Tiger (AGK-345-821)." This format would be compact, unambiguous, and much easier to pronounce and spell than the Latin and Greek epithets currently in use. The mental tyranny of the scholastics would then, at last, be at an end.

No doubt there will be those who will reject the implications of the facts discussed in this section. They will say our taxonomic system is the result of centuries of labor by thousands of naturalists and should not be lightly discounted.

Tradition carries weight, they will say. But I simply find puzzling those of my colleagues who think this way and want to go on and on rearranging and patching taxonomies. I see them much as Frost saw his neighbor who insisted on mending walls every spring:

> He is all pine and I am apple orchard.
> My apple trees will never get across
> And eat the cones under his pines, I tell him.
> He only says "Good fences make good neighbours."
> Spring is the mischief in me, and I wonder
> If I could put a notion in his head:
> "*Why* do they make good neighbours? Isn't it
> Where there are cows? But here there are no cows.
> Before I built a wall I'd ask to know
> What I was walling in or walling out,
> And whom I was likely to give offence.
> Something there is that doesn't love a wall,
> That wants it down." I could say "Elves" to him,
> But it's not elves exactly, and I'd rather
> He said it for himself. I see him there
> Bringing a stone grasped firmly by the top
> In each hand, like an old-stone savage armed.
> He moves in darkness as it seems to me,
> Not of woods only and the shade of trees.
> He will not go behind his father's saying,
> And he likes having thought of it so well
> He says again, "Good fences make good neighbours."[755]

From Simple to Complex. An evolutionary theory should account, on a genetic basis, for the successive changes observed in the fossil record. That is, it should explain mechanisms that would allow ancient fossil forms to give rise to those of the present day. As we have seen in the previous chapter, stabilization theory in many respects provides a superior explanation of this process. But, one fact might seem to limit its applicability: In the very early stages of the fossil record bacteria are the only forms present. Stabilization processes are strongly linked with hybridization. In bacteria ordinary hybridization cannot occur because individuals of separate sexes do not exist. Bacteria reproduce by binary fission, a process in which the parent bacterial cell splits transversely into two daughter cells of equal size. So one might suppose hybridization could have played no role in the first stage of evolution. However, binary fission is not the only genetic mechanism in the bacterial repertoire. Though they lack sexes, bacteria do have a form of sex, a process known as *conjugation.* During conjugation, one bacterium injects DNA into a second, recipient bacterium.[a] The amount of DNA transferred varies from one conjugation event to

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[a] Other processes can produce a bacterium with genes from more than one source. For

another. Conjugation occurs not only between individuals belonging to the same bacterial type, but also between types treated as separate species.[756] Bacteria can therefore produce new offspring types via matings between two or more distinct types.

Conjugation is a form of hybridization (see p. 34). When one bacterium injects its DNA into some other type of bacterium, the recipient individual is altered genetically so that it differs from the parent bacterium that produced it by binary fission. It also differs from the bacterium that injected the DNA, which can be viewed as a second parent via conjugation. Because the resulting hybrid bacterium differs genetically from the types that produced it, it will usually differ also with respect to its traits. If it goes on to reproduce itself through binary fission, a distinct new type differing from both parental types will result. For instance, in a study of naturally occurring hybridization between two bacteria, *Bacillus licheniformis* and *B. subtilis*, Duncan et al. (1989: 1606) found that in such hybrids an average of 89 traits out 1,000 were altered from the original condition of the recipient, and that, on average, 56 of these 89 remained stable in the new line descended by binary fission from the initial hybrid individual. Presumably, such hybrid types will survive and stably reproduce if the new combination of traits specified by the new combination of genes is sufficiently favorable. Conjugation between even very distinct types of bacteria is a commonplace, well-documented phenomenon. For example, such exchanges have been repeatedly observed between *Escherichia coli* and *Synechocystis* PCC6803, a cyanobacterium.[757]

A new gene arising through mutation in a single bacterium can be passed, then, not only to the descendants of that bacterium produced by binary fission, but also to ones produced via conjugation. Thus, under stabilization theory, binary fission plays the same role in the bacterial realm as does ordinary reproduction among multicellular organisms. It reproduces the parental type. Therefore, under that view, the stability over time of a bacterial type reflects the stability of reproduction inherent in binary fission, just as the temporal stability of a eukaryotic form reflects the stability of a genetically stable reproductive cycle (see pp. 186-189). But conjugation between distinct types is equivalent to the disruptive processes associated with sexual hybridization. As with sexual hybridization, the offspring of conjugation will be of varying types. Some will be more viable than others. Those that are sufficiently viable to survive and stably reproduce will become new stable types. Among unicellular organisms reproducing by cell division, conjugation between distinct types produces new stable types. It is therefore a form of stabilization process. The word *karyotype* is not usually used in connection with bacteria. Note, however, that as it is defined under stabilization theory (see p. 68), *karyotype* can be applied even in the case of these non-eukaryotic microorganisms.

The ability to conjugate is widespread in bacteria today.[758] In fact, it seems no bacterium is known to be incapable of it. Since conjugation has been observed in a

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example, bacteria excrete DNA, which can then be taken up by another bacterium; viruses (bacteriophages) can carry genes from one bacterium to another.

wide variety of modern bacteria, it is likely even very early bacteria had this capability. Even in the very earliest fossil-bearing strata of the fossil record, dating back to the early Archaean (~3.5 billion years ago), multiple bacterial types are present.[759,a] It is reasonable, then, to suppose conjugation between distinct types was a common way of producing new types of organisms even at the earliest known stages of the evolutionary process. The early earth can thus be pictured as a bacterial playground, devoid, perhaps, of more complex types of organisms. This state apparently lasted some two billion years. These simple organisms have since elaborated into the wide variety of organisms seen today. If conjugation between distinct bacterial types was prevalent even during this very early period, then the production of new types of organisms via this means was probably widespread as well. Such a mechanism could bring about large amounts of subsequent evolutionary change. This seems especially likely given that conjugation also occurs in a broad range of simple eukaryotes.[760]

As has already been explained, hybridization of two types of organisms is not a process analogous to the averaging of two points on a geometric line. Although many traits in a hybrid will be intermediate to those seen in the parental types, other traits will not be (they will be heterotic or synergistic). In consequence, a new hybrid type produced from two interbreeding parental types is not bounded by the traits of the founding pair. Backcrossing, matings among the hybrids themselves, and interbreeding with additional parental types can produce an ever-increasing variety of types. Descendant types can become increasingly distinct. But they would not do so in a treelike fashion. A different topology applies in the case of hybridization and conjugation (see Figure 8.2). Since conjugation combines, in a single bacterium, the DNA of two different types, it is entirely plausible to suppose novel, synergistic traits would arise from time to time as a result of the interaction of genes newly combined in a single individual. In particular, such characteristics as true sexual reproduction, multicellularity, multiple chromosomes, and many other features typical of more complex organisms might well have arisen first as synergistic traits. This is the assumption under stabilization theory.

The theory also assumes (1) that various characteristic traits of eukaryotes evolved separately in different types of early bacteria; and (2) that these traits were later combined in single organisms via the sort of process outlined in Figure 8.2. For example, one can suppose that at some point hybridization among ancient bacteria produced forms with a membrane-bound nucleus. Such a process might also have

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[a] The production of a new form via hybridization requires the preexistence of at least two distinct parental forms. Current scientific debate gives serious consideration to only two hypotheses concerning the origin of life on earth, exogenesis and primordial abiogenesis. The latter of these two hypotheses claims life arose spontaneously from non-living matter early in earth's history, more than 3.5 billion years ago. The former says life did not originate on earth, but instead came from elsewhere. No attempt will be made here to determine which of these two hypotheses is correct, but in either case one can suppose life began on earth with multiple types of bacteria, either arising spontaneously or introduced from elsewhere.

yielded types with the ability to package genetic material into individual, linear chromosomes. Certain extant microsporan bacteria undergo meiosis during their life cycle, a characteristic usually seen only in eukaryotes.[761] Thus, this trait, too, might have been present in early bacteria. The rudiments of multicellularity are seen in various types of extant bacteria with ancient origins, for example, in cyanobacteria, organisms as old as any in the fossil record.[762] Again, this trait was probably present in some bacteria at a very early stage of evolution. Some types of cyanobacteria are simple unicells, but others are among the most elaborate of bacteria. The most complex are multicellular mosslike forms visible to the naked eye.[763] In both unicellular and multicellular cyanobacteria structural and functional differentiation occurs in which different cells perform specialized functions.[764]

Hybridization within an early bacterial similarity set containing separate forms in which these basic features of eukaryotes were separately present, then, could produce descendant sets, in which single forms combined these traits. As this process of assembling eukaryotic traits continued, presumably symbiogenesis also would play a role. Recall (see pp. 104-105) that certain of the tiny organs ("organelles") of eukaryotic cells (e.g., mitochondria, chloroplasts) are now believed to be the descendants of ancient bacteria engulfed by single-celled precursors of eukaryotes (this is a form of symbiogenesis). With the occurrence of such events, and with further conjugation, larger and increasingly complex forms could make their debuts. Later, various similarity sets composed of relatively complex protoctists with plant, animal, or fungal characteristics would give rise to sets of simple plants, animals, and fungi, respectively. As one similarity set succeeded another over evolutionary time, this process would eventually produce the structurally complex organisms characteristic of the more recent stages of evolution.

Note that at no point in this process is it necessary to suppose new forms arise via the gradual accumulation of distinctive traits in isolation. A colleague once claimed that the extensive hybridization posited by stabilization theory would prevent living forms from increasing in number. This, he said, was the case because any pair of hybridizing populations would merge so that two preexisting forms would become one. An ongoing reduction in the number of existing forms would supposedly result. To make up for this deficit, he said, it would be necessary to assume that the sorts of processes described under neo-Darwinian theory also commonly produced new types of organisms. Otherwise the number of existing forms would steadily dwindle. This, however, is interpreting stabilization theory with a neo-Darwinian eye. In fact, such an argument is little more than a resuscitation of the medieval idea that hybridization must inevitably lead to a blending and confusion of forms (see Chapter 1). We have seen that people often suppose hybridization causes populations to merge, when in fact observation tells us that hybridizing populations usually remain morphologically and geographically discrete even when an active hybrid zone has long connected them.

Nothing in stabilization theory is inconsistent with the proliferation of living forms. We have just seen how, under the theory, simple organisms would have produced a wide array of more complex ones via conjugation and symbiogenesis. With the advent of eukaryotic sexual reproduction all the various stabilization processes discussed in previous chapters would also come into play (some, such as the production of an autopolyploid via somatic chromosome multiplication, probably predated sex). These would only accelerate the production of new types of organisms. Thus, with the sorts of processes posited in the theory, there is an unlimited potential to increase the number of stable forms. For example, two forms might hybridize to produce a third stable form, say an allopolyploid. Thousands of examples of this are known. This new, third type might go on to hybridize with some fourth form to produce a fifth form via recombinational stabilization. The fifth might produce on its own, a sixth, autopolyploid form. Obviously, such mechanisms can go on creating an ever-increasing number of forms, ad infinitum. So there is no need whatsoever to posit the sorts of gradual processes described in neo-Darwinian theory.

The Concept of Radiation. Neo-Darwinian theory requires that descriptions of evolution be in terms of trees of descent, with limbs strictly diverging. Such explanations of evolution in terms of divergence are certainly nothing new. They long predate Darwin, as he himself was well aware. In the *Origin* Darwin quotes Constantine Samuel Rafinesque (*New Flora of North America,* 1836: 6) as saying that "all species might have been varieties once, and many varieties are gradually becoming species by assuming constant and peculiar characters."[765] In 1796, Étienne Geoffroy Saint-Hilaire noted a "unity of plan" among related organisms that suggested common descent.[766] Indeed, in *The Critique of Judgment* (1790),[767] even Immanuel Kant expresses the idea:

> When we consider the agreement of so many genera of animals in a certain common schema, which apparently underlies not only the structure of their bones, but also the disposition of their remaining parts, and when we find here the wonderful simplicity of the original plan which has been able to produce such an immense variety of species by the shortening of one member and the lengthening of another, by the involution of this part and the evolution of that, there gleams upon the mind a ray of hope, however faint, that the principle of the mechanism of nature, apart from which there can be no natural science at all, may yet enable us to arrive at some explanation in the case of organic life. This analogy of forms, which in all their differences seem to be produced in accordance with a common type, strengthens the suspicion that they have an actual kinship due to descent from a common parent.[a]

By 1766, Buffon was convinced new forms could arise by divergence from a common ancestor.[768] The idea can be traced back at least as far as the German philosopher Gottfried Leibnitz (1646–1716), who thought the various types of cats might be descended from a common ancestor.[769]

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a. In his *Zoonomia* (1794), Darwin's grandfather, Erasmus Darwin, spoke of "the essential unity of plan in all warm-blooded animals" (Osborn 1894: 145), which again suggests belief in their descent from a common ancestor.

Large groups of related forms are often described as arising via a process of divergent specialization called *radiation*, in which a single, ancestral form gives rise to numerous descendant “specialized” types. Thinking in terms of radiation gives rise to a particular way of talking about the evolutionary process. The ancestral form that founds a radiation is typically described as "small, primitive, and generalized" and, often (when terrestrial animals are in question) as an "insectivore." The various types of organisms descended from it are "adapted" to particular "niches." In other words, they are supposed to be "specialized" for a particular way of life. They may be large carnivores, flying frugivores, small herbivores, or marine creatures living on plankton. In speaking of this process, evolutionary biologists talk of "lineages radiating into adaptive niches" or "post-extinction divergence." Always it is supposed that a radiation begins after a mass extinction has eliminated most of the forms that came into being during the previous radiation. Always, a "primitive, small, generalized" type initiates the new radiation. The various forms produced by any given radiation are always "more progressive" than those produced by the preceding one. At the end of a radiation, all the various specialized types it produces are wiped out again. All that remains is a "small, primitive, generalized" type (which founds a new radiation) and a few other types (whose descendants eventually go extinct). This viewpoint is the standard line expressed in educational texts introducing students to geology, paleontology, and evolutionary biology.[770] For instance, Kemp (1982: 321) lists features of a typical adaptive radiation:

> The radiation commences after a sudden mass-extinction has removed most of the lineages of the previous radiation … the radiation commences from a single lineage of small carnivore-insectivore which was part of the previous radiation and survived the mass extinction … the members of the radiation are more progressive … the termination of the radiation is marked by the simultaneous loss of all the species composing it. A few lineages survive, as manifested by the appearance of new species of these lineages at the commencement of the next radiation. The surviving lineages consist mainly of small animals.

In portraying the geneses of groups of related forms, biologists tell the same sort of story again and again. Such accounts are widespread because, for many biologists, the very word *related* means "descended from a single common ancestor" (here *single* should be emphasized). Key words such as *generalized* and *non-specialized* reflect the theoretical assumption that evolution is a matter of refining a general category into a variety of advanced forms suited to "specialized niches."

Living in the Industrial Age, when specialization of labor was seen as the key to efficient production, Darwin seized on the factory metaphor and asserted that any generalized form (i.e., one that lacked a specialty) would be outcompeted and driven to extinction by specialized ones: "the modified descendants of [i.e., the various types descended from] any one species will succeed by so much the better as they become more diversified in structure, and are thus enabled to encroach on places occupied by other beings."[771] Thus, evolution, as conceived by Darwin, moves from the generalized type to the specialized type. Darwin made the world a workhouse.

Progress and efficiency are important themes running throughout the Darwinian paradigm. It is for this reason that modern biologists use the adjective *primitive* rather than *old* in referring to early fossil forms; *primitive* suggests a sense of progress, when used in conjunction with words like *modern* or *advanced*, that the words *old* and *young* do not. Insectivorous diet and small size are commonly presumed because such traits are traditionally considered "non-specialized" and "primitive." But it is hard to see why. A small insectivore seems about as well suited to insect prey as is a lion to the consumption of larger victims.

In the early nineteenth century naturalists were fascinated with embryology. They saw a parallel between the course of embryonic development and the supposed progression from simple, “lower” forms to more complex, “higher” ones (i.e., invertebrate, to fish, to reptile, to mammal, and finally to human). Thus, in his best-selling book, *Vestiges of the Natural History of Creation* (1844), Robert Chambers based his rather peculiar account of evolution on this “law” of parallelism. As Bowler puts it, Chambers claimed that

> a species with a particular grade of organization has a natural period of gestation during which its embryos advance to the appropriate point on the scale of development. If something could *extend* the growth process for a short period, the embryo would develop a little further on the scale and at birth would appear as a member of the next highest species. The process of evolution thus consists of a long series of small extensions in the period of gestation, each allowing life to advance one step further along the hierarchy of complexity.[772]

This so-called law of parallelism was, at least initially, a linear concept in which each new form could be ranked along a single line of progress. But the idea of a divergence from a “generalized” common ancestor gained support from studies of embryological development. In his *Über Entwicklungsgeschichte der Thiere* (1828), the German embryologist Karl Ernst von Baer (1792–1876) asserted there is no real resemblance, at any stage in its development, between the embryo of an organism in a “higher” category (e.g., Mammalia) and adult forms in “lower” categories (e.g., Pisces or Reptilia). Rejecting the notion that development was a matter of a straightforward climb up the *scala naturae*, he maintained that the development of an embryo into a mature organism is a process of specialization.[773] Because the early embryo generally looks the same, even in the case of very distinct types of organisms (e.g., bird and mammal), he said it was “generalized.” According to von Baer, from this generalized embryo, various, branching developmental pathways led to various types of mature organisms, each with its own particular specialty. The process of development became a matter of acquiring organs having specialized functions.

Von Baer’s ideas were influential and had effects even outside the field of embryology. In particular, the most prominent British paleontologist of Darwin’s day, Richard Owen, thought von Baer’s picture of branching specialization could be adapted to the fossil record. He attempted to show that the earliest members of a given taxonomic group to appear in the record lack specialized traits.[774] The subsequent history of a group, Owen said, was an outward radiation of various lines leading to distinct specialties. Thus, according to Desmond and Moore (1991: 433),

> Owen imagined fossil animals as less specialized than today's. Trace each lineage back and the more general the animals become. Eventually we must arrive at the original archetype—the ideal mould from which they are all forged.

But the meaning of "general" in the context of fossils cannot be the same as in the context of embryology. The fossil organisms to which Owen referred were mature organisms. So it would make no sense to say that an early mammal fossil was identical to that of an early bird (in the same way that a mammalian embryo is indistinguishable, at an early stage, from that of a bird). In general, early embryos are much the same in different vertebrate classes. But mature organisms most definitely are not. Thus, in the fossil context, Owen seems to have converted the meaning of the word *general* from "common to a variety of categories" to "lacking specialized traits."

Despite this seeming fallacy, Darwin incorporated into his theory of natural selection the idea of a generalized type gradually evolving into a variety of specialized types. In a letter to Huxley dated April 23, 1854, he wrote that "The discovery of the type … of each great class, I cannot doubt, is one of the very highest ends of Natural History."[775] In the *Origin,* he refers to Owen's "most interesting work" *On the Nature of Limbs* (1849), in which Owen adapts von Baer's ideas to fossils.[776] Darwin was also familiar with Milne-Edwards' claim that specialized organs make for a more efficient organism (Milne-Edwards compared specialized organs with specialized workers on an assembly line). In particular, Darwin seems to have been convinced by his friend William Carpenter that evolution is a matter of continuous change from the generalized to the specialized (Boorstin 1983: 321, 394).[777]

Along with many other naturalists in the mid-1800s, Darwin believed all organisms in a category were constructed according to a basic plan, an "archetype," that epitomized the category.[778] Although most naturalists saw archetypes as ideal or abstract forms, models on which all organisms of a given group (e.g., vertebrates) are constructed, Darwin saw more. As he himself noted in the margin of Owen's book (*On the Nature of Limbs*):

> I look at Owen's Archetypes as more than ideal, as a real representation as far as the most consummate skill & loftiest generalization can represent the parent form of the Vertebrata—I follow him that there is a created archetype, the parent of its class.[779]

In Darwin's mind, the archetype, an abstract form, became a living, breathing ancestor. He visualized an ancient, generalized progenitor giving rise, by means of gradual radiation, to a plethora of specialized descendants. Thus, in the *Origin,* he claims that, in the gradual adaptation of limbs to various functions (e.g., burrowing, swimming, flying),

> the bones of a limb might be shortened and widened to any extent, and become gradually enveloped in thick membrane, so as to serve as a fin; or a webbed foot might have all its bones, or certain bones, lengthened to any extent, and the membrane connecting them increased to any extent, so as to serve as a wing: yet in all this great amount of modification there will be no tendency to alter the framework of bones or the relative connexion of the several parts. If we suppose that the ancient progenitor, the archetype as it may be called, of all mammals, had its limbs constructed on the existing general pattern, *for whatever purpose they served*, we can at once perceive the plain signification of the homologous construction of the limbs throughout the whole class.[780] [italics added]

Note that even Darwin admits (italics) that the limbs of this "ancient progenitor" must have served *some* purpose (walking? pouncing? climbing?). Therefore, even if one chose to suppose evolution did proceed in a strictly divergent, treelike fashion, there would be no reason to believe that the progenitor (from which the others are descended with modification) was unspecialized. Why, then, should we suppose it was a "generalized" archetype? Surely, it would have had its own way of living and, thus, would have been specialized in its own way.

The idea of specialization in evolution is strangely attractive, but it really doesn't make sense. The analogy doesn't work. In the world of economics, specialization confers an advantage in accomplishing some overall task. Specialized workers band together to assemble a car or construct a house and so obtain an advantage over any individual who would attempt to do the same on her own. Here, a complex task is carried out more efficiently with specialized workers. The same analogy holds, as Milne-Edwards points out, with respect to the various specialized organs that make up a living being. There, the various specialized organs perform together the overall task of maintaining the organism in existence. But even if we grant that some types of organisms specialize and that some do not, it is still clear that distinct specialized forms do not cooperate like factory workers to accomplish a common goal. From the standpoint of the factory metaphor, a form of organism is an individual. If there is no overall task, then there is no particular advantage in specialization. It therefore seems that Darwin based an important claim of his theory on an inappropriate analogy.

Conclusion. Since even bacteria are known to engage in a form of hybridization, we may reasonably suppose new types of organisms were arising by stabilization processes, even in times as old as the earliest strata in the fossil record. There therefore seems to be no need to posit gradual divergence in isolation, even at the very earliest stage of evolution on earth. The processes posited by stabilization theory appear to be sufficient to explain everything we know from fossils about evolution.

Indeed, we have no clear evidence that the various higher taxonomic categories are "natural" (i.e., that they can and should be delineated in terms of descent from a single common ancestor). Biologists have long disputed the correctness of their phylogenetic trees and the allotment of organisms into taxonomic categories (see

Chapter 5), in what Thompson (1992: 3) called the "endless search after the blood-relationships of things living and the pedigrees of things dead and gone." There is certainly no reason to take such quarrels as evidence that the history of evolution has been treelike in form. In fact, the very existence and prevalence of such disputes constitutes evidence to the contrary. Still less can we assume that diverse arrays of related forms arise via a process of “radiation”—an idea based on a flawed analogy. It appears biologists have needlessly attempted to force all of the various forms of life on Earth into a tidy, strictly branching, artificial system of classification that fails to reflect the true nature of their origins. In point of fact, all that we truly know is that this poorly substantiated hierarchal topology originated in the arcane metaphysical dogmas of the scholastics (see Chapter 1). Given the facts thus far presented in this book it seems far more plausible to suppose a different topology applies. We can picture similarity sets evolving over time into new similarity sets, networks replacing networks. Stabilization processes can be envisioned as starting with a few simple organisms during the first stages of life on earth and then, with time, producing a wide array of complex forms.

9 On the Origin of Mammals

Whatever we see could be other than it is.
Whatever we can describe could be other than it is.
There is no a priori order of things.
—LUDWIG WITTGENSTEIN
Tractatus Logico-Philosophicus[781]

This chapter is intended to illustrate how the alternative intellectual perspective provided by stabilization theory can enhance understanding of the evolutionary process. The case considered will be the origin of mammals. The typical biology text gives the following account of the origin of the various mammalian orders (usually referred to as the "mammalian radiation"): 1) A "small, primitive, generalized" mammal living in the early Cretaceous was the common ancestor of marsupial mammals (in which the young are born at an early stage of development) and of placental mammals (in which the young are born at a later stage of development);[782] 2) By the end of the Cretaceous, some 60 million years later (approximately 70 million years ago), small, "primitive," "generalized" marsupials and placentals existed; 3) With the demise of the dinosaurs, placental mammals quickly "radiated" into the "adaptive niches" vacated by their former reptile overlords; 4) Ever since, the various major categories of mammals (hoofed herbivores, insectivores, whales, bats, carnivores, edentates, monkeys, rodents, seals, etc.) have remained relatively stable.

Such is the usual account given of the genesis of mammals. But another story can be told, which is, in many ways, more consistent with available data. This chapter reevaluates the origin of mammals from the standpoint of stabilization theory, and in so doing, reaches some radically different conclusions. Stabilization theory presumes the origin of new types of organisms through stabilization processes is a typical, widespread phenomenon. There is therefore no reason to propose or to seek to identify a common ancestor of all mammals. Instead, the basic approach will be to seek similarity sets (see Chapter 8) of precursor organisms that could give rise to each of the various major types of mammals.

The Mesozoic Era. In geology texts, the Mesozoic Era, which began some 250 million years ago (mya), is usually called the "Age of Reptiles." It is divided into three periods, the Triassic, Jurassic, and Cretaceous (see Table 9.1). In the typical description, encountered in texts on geology, paleontology, and evolutionary biology, it is "the era during which reptiles dominated life on earth until their extinction at the end of the Cretaceous Period, 65 million years ago." The idea that reptiles "ruled" the Mesozoic dates back to Cuvier, who in the early nineteenth century asserted there had once been a time when reptiles were dominant.[a] It also comes from the popular misconception that dinosaurs were all large. Such was not the case—while some dinosaurs weighed 80 tons, others were as small as chickens.[783] It comes, also, in part, from the common belief that the category "dinosaur" contains more different kinds of animals than it actually does. Only two orders of Mesozoic reptiles are classed as dinosaurs, the saurischians (such as *Tyrannosaurus* or *Apatosaurus*[b]) and the ornithischians, which included armored and horned dinosaurs (e.g., *Ankylosaurus*, *Stegosaurus* and *Triceratops*[c]), and various other forms, among which *Iguanodon* is perhaps the best known.

Table 9.1: Periods of the Mesozoic and Cenozoic Eras[784]

Era	**Period**	**Years since period began (approximate)**
Cenozoic	Quaternary	1,600,000
	Tertiary	65,000,000
Mesozoic	Cretaceous	144,000,000
	Jurassic	206,000,000
	Triassic	248,000,000

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[a] In 1808 he identified as a giant marine reptile a fossil from a mine near Maastricht in the Netherlands. He named it *Mosasaurus*. He also identified as a large flying reptile a fossil found in Bavaria, which he named pterodactyl (*Pterodactyle* Cuvier, 1809). These finds led him to propose there had been a time when reptiles had been predominant (Rudwick 1997). His diagnoses of these animals as reptiles are called into question later in this chapter.

[b] *Apatosaurus* is the name now assigned to the form once known as *Brontosaurus*.

[c] The writer would like to raise a question for further investigation: Were the ceratopids (*Triceratops* and similar extinct organisms) actually giant chameleons? The peculiar head structure of extant chameleons, in particular the casque characteristic of these animals, is similar to that of ceratopids. Many chameleons also bear facial horns reminisent of those of ceratopids. For example, Jackson's Chameleon (*Chamaeleo jacksonii*) has horns recalling those of *Triceratops* in number, placement, and shape. Under this hypothesis, chameleons would be an example of residual dwarfism (see p. 222).

Other ancient creatures, traditionally categorized as reptiles and popularly included with dinosaurs, were not dinosaurs at all: pterosaurs (flying, batlike creatures, formerly known as pterodactyls), mosasaurs (whalelike marine predators), and plesiosaurs (includes two general categories, one a long-necked, paddle-flippered type, the other seallike). Moreover, many extant reptile forms (e.g., crocodilians, turtles, lizards) date back at least as far as the earliest dinosaurs and have been widespread ever since. Many other types of animals, far too numerous even to mention, were also the dinosaurs' contemporaries.

Another tendency contributing to the belief that the Mesozoic Era was "ruled by reptiles" is the inclination to believe that animals, known only from fossils, had the full suite of characters defining modern reptiles. For instance, most people think of pterosaurs as egg-laying, cold-blooded, flying reptiles with naked, scaly skin. In fact, however, in some cases, where the texture of a pelt has been preserved in fossils, pterosaurs can be seen to have been fur-bearing animals.[785] According to Wellnhofer (1991: 164), this "direct proof of a hairlike body covering seems to have confirmed the warm-bloodedness of pterosaurs once and for all, as only mammals, i.e., warm-blooded creatures, have hair today." Various researchers have pointed out that, besides fur, the elevated metabolism characteristic of flying animals, and the fact (known from fossils) that pterosaurs could live in a chilly habitat, make it highly likely that pterosaurs were warm-blooded.[786] There is no fossil evidence that pterosaurs laid eggs.[787] Studies of their bones have shown that pterosaurs grew rapidly, as do mammals and birds, not slowly like reptiles.[788] Warm-blooded young usually require parental care to prevent death by exposure.[789] So pterosaurs, which were abundant during the Mesozoic, may not have even been reptiles, let alone "ruling" reptiles.

No single person has seen all the fossils found over the years—or even most of them—but fossils are nevertheless widely assumed to substantiate the basic tenets of evolutionary biology. The stories told about fossils are familiar to most biologists, but the fossils themselves are not. The reason for this discrepancy is straightforward. It is much easier to read and assimilate a story about the fossil data than to evaluate the evidence itself. Part of the story told about fossils is the claim that mammalian fossils from the Mesozoic are rare. Romer (1966: 197) emphasizes this point:

> Mammals presumably came into existence toward the end of the Triassic [248-206 mya], but we know extremely little about their history during almost the entire span of the Mesozoic [248-65 mya]. The oldest known mammals appear in the "Rhaetic" beds at the Triassic-Jurassic boundary [_206 mya]. In the Jurassic [206-144 mya], almost all known mammalian remains come from two English localities … and one small bone pocket at Como Bluff, Wyoming. In the early Cretaceous [~130 mya], … our knowledge is confined to fragments from the Trinity sands of Texas and the Wealden of Southern England. Further, almost all the earlier Mesozoic remains consist of isolated teeth, or, at the most, jaws; prior to the Upper Cretaceous [~75 mya] we have not one satisfactory skeleton and very little skull material.

> Even in the Upper Cretaceous, mammal remains are rare, mostly fragmentary, and are found only in a few areas in North America and Mongolia. In consequence we are still in the dark about much of the history of Mesozoic mammals. We know little about the dental anatomy of most of the forms which have been found; and the sparseness of the record suggests that groups which have escaped detection may well have existed.

During the forty years since Romer wrote these words, the fossils of more Mesozoic mammals have been found, but they are still considered rare. This rarity has been explained in various ways. Thus, it is said that in the early days of fossil hunting, when the great museum collections were being assembled, the emphasis was largely on dinosaurs, and that mammals were supposedly neglected. Being warm-blooded, mammals are also thought to have been more common inland, at higher elevations—conditions under which fossils are rarely preserved because erosion tends to destroy them.[a]

Table 9.2: Epochs of the Cenozoic Era

Period	**Epoch**	**Years since epoch began (approximate)**
Quaternary	Holocene	10,000
	Pleistocene	1,600,000
Tertiary	Pliocene	5,000,000
	Miocene	24,000,000
	Oligocene	34,000,000
	Eocene	54,000,000
	Paleocene	65,000,000

One fact, however, is particularly salient. Mesozoic terrestrial fossils of *all* kinds are extremely sparse.[790] Even in the Paleocene, the first epoch of the Cenozoic Era ("Age of Mammals"), such deposits are well known only in western North America (Table 9.2 provides the names of the various periods and epochs of the Cenozoic era, together with their approximate dates).[791] During the preceding, vast period of time that geologists call the Mesozoic Era, which lasted some 180 million years, terrestrial deposits are sparse indeed. Our knowledge of Mesozoic land animals has been obtained almost exclusively from three regions of the world (southern England, Mongolia, and western North America). Moreover, the fossils from these three sites

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[a] Since the bones of large mammals tend to be more cancellous than those large reptiles (de Buffrénil and Mazin 1990), those of reptiles are more likely to be preserved as fossils.

cover a very small percentage of the time interval in question. As Clemens, et al. (1979: 8) note,

> It is emphasized that for the present, negative evidence has little value for Mesozoic mammals. That is, the absence of a group of mammals at a particular time and place [in the fossil record] generally cannot be taken as an indication that it did not in fact occur then and there. The only areas in which negative evidence may be given some, but not conclusive weight [i.e., because the samples are not so inadequate as elsewhere] are those for the Rhaeto-Liassic (Late Triassic or Early Jurassic) of southwestern Britain, the Late Jurassic of southern England and western United States, the Late Cretaceous of Mongolia and the Late Cretaceous of the Rocky Mountain and High Plains of North America.

Outside southern England, Mongolia, and western North America, animals unknown today may well have been abundant throughout the Mesozoic and Paleocene. During this entire time, continental Europe, Africa, Asia (except Mongolia), Australia, South America, Antarctica, and eastern North America are largely a blank, either very poorly known, or not known at all. Given such huge gaps in the data, claims of the rareness of early mammals largely lack empirical verification.

But a review of the literature prompts the suspicion that the most significant reason for the reported preponderance of reptile remains in Mesozoic fossils lies not so much in the actual rarity of mammalian fossils, but rather in a strong tendency of paleontologists to classify fossils as "reptile" if from the Mesozoic, and as "mammal" if they date from a later time. For instance, in referring to an early collector, a modern paleontologist wrote the following: "He [i.e., the collector] *knew* that the teeth were from the 'secondary' (Mesozoic) and therefore really ought to be reptilian" (Norman 1985: 10). This bias seems to be especially pronounced when it comes to large animals.

The reasons for this bias are subtle, complex, and sheltered by tradition. One obvious explanation, however, is stereotypic thinking. Consider the distinction between fossil mammals and fossil reptiles, already alluded to in the case of pterosaurs. When we hear that an animal is a "mammal," a number of traits spring to mind. Many of these features (warm-bloodedness, four-chambered heart, mammary glands, parental care, diaphragm, raised external ear, viviparity, hair, etc.) are not, or are only very rarely, preserved in fossils. “As a result,” notes dinosaur expert David Norman, “the first true mammals are recognised as fossils almost by weight of opinion, rather than anything more scientific.”[792]

Even in the case of living animals, some of these traits are not valid criteria for distinguishing reptiles from mammals. Crocodiles have hearts with four chambers and care for their young. Even various kinds of frogs exhibit parental care.[793] Certain mammals are cold-blooded, including manatees, hyraxes, sloths, tenrecs, naked mole-rats, platypuses, and some bats.[794,a] Scales are usually considered diagnostic of

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[a] Constantine (1961: 95) found that when *Euderma maculatum* (Spotted Bat) was cooled it became torpid and its body temperature sank to 9˚C.

reptiles, but these features are seen also in certain mammals. In some, scales are limited to certain regions of the body, for example, scaly-tailed squirrels (Anomaluridae), pichichiegos (*Chalmyphorus*), Asiatic shrew-moles (*Uropsilus*), echimyids (Echimyidae), and some porcupines (*Atherurus, Trichys*).[795] In others, most of the body is covered. Examples include the Javan rhinoceros,[796] armadillos, and pangolins. On the other hand, pterosaurs, traditionally pictured as naked and scaly, are now known to have been furry. The modern leatherback turtle (*Dermochelys*), classed as a reptile, is warm-blooded,[797,a] lacks a bony shell, and has leathery, scaleless skin.[798] Many reptiles, including about half of the extant snakes and lizards, give live birth.[799,b] But it is usually unknown whether a given extinct animal was viviparous or laid eggs. Moreover, in those exceptional cases where the mode of birth can be determined for a fossil form, the findings are sometimes contrary to stereotype. Ichthyosaurs are traditionally classified as reptiles, but fossils show they gave live birth to their young in the sea as dolphins do. Nevertheless, when a paleontologist finds in a fossil two or three bony features that usually distinguish modern mammals from modern reptiles, the conclusion is often that all the other features stereotypically associated with a mammal were also present in the corresponding extinct animal.

The same is true of artists' renderings of extinct animals. Let an artist draw a gray or brown animal with fur and ears that stand up from the head and the viewer will have the strongest tendency to think of the pictured animal as a mammal, with all the traits characteristic of mammals. Let her base an illustration on the same set of bones and draw a green animal with naked skin and no ears, and the viewer will think "reptile." It is important always to keep in mind that drawings purporting to represent the outward appearance of Mesozoic animals often reflect the theoretical biases of the artist and are frequently based on scant fossil evidence. Although pictured as complete and intact, the animals illustrated are in many, perhaps even most, cases actually known only from a fragment of a jawbone or a few teeth.

This chapter examines each of the major categories of modern mammals (and even some of the minor ones). For each type of modern mammal (e.g., rodents, carnivores, armadillos, whales, etc.), we will see that a similar category of Mesozoic precursors is known from the fossil record. These precursors have been largely ignored, perhaps because their existence does not fit with the accepted claim of orthodox theory that the many different types of extant mammals are derived from a single “generalized” Cretaceous form. The existence of such precursors does fit, however, with stabilization theory. If new types of organisms typically arise through stabilization processes, we are not looking for a common ancestor of mammals, or a

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[a] In cold water (7˚ C) *Dermochelys* can maintain a body core temperature 32˚ F (18˚ C) above that of its environment (Frair et al. 1972).

[b] Viviparity occurs in a diverse array of organisms including rotifers (Margulis and Schwartz 1998: 249), molluscs (ibid: 291), onychophorans (ibid: 330), echinoderms (ibid: 321), fish (Schultz 1989; Smith et al. 1975; Wourms et al. 1991), and arthropods (Campbell 1987: 627). All scorpions give live birth (Rubio 2000).

common ancestor of whales. Instead, our expectation is that ancestral similarity sets would produce descendant similarity sets of a comparable nature. Thus, various early rodentlike forms would give rise to various more modern rodent forms. The accepted view is not that modern forms might be expected to arise from precursor forms similar to themselves (e.g., marine mammals from earlier marine mammals), though this idea may seem straightforward and plausible to the uninitiated reader. For example, widely accepted theory claims that whales are descended from a tiny, shrewlike animal, and that the whole transformation required only 10 or 20 million years.

Synapsids. Synapsids were creatures that are often described as "mammallike reptiles." They could just as reasonably be called "reptilelike mammals" because they exhibit both reptilian and mammalian traits. The synapsids had their heyday in the Permian Period (286–248 mya), right before the Mesozoic Era.[a] They derive their name from the fact that they had a single temporal opening on each side of the skull, as is the case in mammals. Among paleontologists, the tendency is to call animals with a single such opening "synapsids" if they are older than the Jurassic (before about 206 mya) and to call them "mammals" if they are younger. For this reason, the "origin of mammals" is more a verbal convention than a precisely dated historical event. As Nowak (1999: 1) points out,

> There has been intensive debate regarding the morphological and temporal boundary between reptiles and the first mammals. Recent fossil studies have revealed some specimens that do not clearly fall into either group and have challenged the significance of the direct articulation of the lower jaw and skull as the key indicator of mammalian origin.

Many synapsids had features considered characteristic of mammals, not reptiles, such as the presence of two occipital condyles (bony knobs forming a joint between the head and neck) and well-differentiated teeth.[800] But the synapsids have traditionally been classified as reptiles, apparently, for theoretical reasons since standard accounts of the history of life say 1) that mammals evolved from the synapsids and 2) that mammals evolved from reptiles.[801] If both of these assertions are assumed to be true, then synapsids have to be classified as reptiles.

But were synapsids conventional reptiles? Or were they a distinct type of animal that arose concurrently with reptiles? The earliest known synapsid fossils are as old as the earliest known reptile fossils. As Romer notes, "Primitive synapsids were already present in the Pennsylvanian—perhaps even the early Pennsylvanian." The Pennsylvanian began more than 300 million years ago, which means the synapsids long antedate dinosaurs, pterosaurs, ichthyosaurs, and all the other "saurs" that have come to characterize the Mesozoic Era.

Certainly, many different kinds of synapsids are known. There were herbivorous, insectivorous, and carnivorous forms, some fairly large. The early

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[a] Early synapsids are usually called *pelycosaurs*; later ones, *therapsids*.

Triassic (approx. 230 mya) herbivore *Kannemeyeria* was the size of an ox.[802] Another, earlier herbivore, *Moschops* of the late Permian (approx. 260 mya), was even bigger—16 feet long.[803] Contemporary with *Moschops* were smaller, doglike, carnivorous synapsids (*Lycaenops*) with long canine teeth and running legs. These animals are believed to have hunted the large herbivores in packs, like wolves.[804] *Lystrosaurus* was a hippolike aquatic creature with a widespread distribution.[805] The molelike insectivore *Cistecephalus* lived underground, where it probably dug for bugs and worms.[806] *Estemmenosuchus* was a late Permian carnivore whose skull had strange bony protuberances, which may have borne horns in life.[807] The tritylodonts of the late Triassic and early Jurassic[a] were small herbivores with rodentlike teeth.[808] An important evolutionary question, then, arises: Did all these varied types simply die out, as modern dogma would have it? Or are the various extant kinds of mammals descended from similar synapsid types?

The Problem of Diversity. Neo-Darwinian theory holds that all the functional diversity, evident in the various synapsid types, was in fact wiped out as Mesozoic reptiles usurped the synapsids' "adaptive niches." Typically, the claim is made that only the "basic structural plan" of mammals was derived from the synapsids. This view is somewhat peculiar because, in terms of bony remains—the only basis on which the basic structure of an extinct animal can be reconstructed—few traits consistently distinguish mammals from reptiles. In fragmentary fossils, even these traits are largely undetectable. But even when they can be discerned, we have already seen there is no reason to immediately conclude that such traits were associated in life with the various non-fossilizable traits defining mammals and reptiles. What, then, exactly is the "basic structural plan" of a mammal?

The notion of a basic structural plan seems to reflect only an attempt on the part of paleontologists to accommodate a constraint imposed by theory, which demands a common ancestor. In the minds of many biologists, the common ancestor is a pliable entity representing a general taxonomic category in its "primitive," incipient state (this is the "archetype" discussed in Chapter 8). Neo-Darwinian theory says that with the passage of time natural selection shapes this general entity (which has, at the outset, the full set of traits that define its corresponding category) into a variety of specialized forms suited to various niches (but still belonging to that category). This pattern of shared descent from a single common stem form, the key evolutionary topology of neo-Darwinian theory, is termed *monophylety*. In contrast, when new types arise from similar old types (i.e., new carnivores from earlier carnivores, new herbivores, from earlier ones), the pattern is "polyphyletic"—there is no common stem form. If stabilization processes involving hybridization are common modes of evolution, then polyphylety is a widespread pattern.

Orthodox theory usually says the first mammal came into existence about 220 million years ago. Most commonly, the morganucodonts are accorded this honor.

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[a] For example, *Beinotherium* and *Oligokyphus*.

They are typically described as "small, primitive, generalized" animals. It is thought they were insectivores. All later mammalian orders, both extant and extinct, are supposedly derived from this common ancestor (monophylety). Only one line of descent, passing through the pantotheres of the late Jurassic (approx. 150 mya), is supposed to lead from these "first mammals" to modern marsupial and placental mammals. Theory says all other Mesozoic animals categorized as mammals, and not in this line, died out without issue—and that any special traits they might have had (horns, gnawing teeth, hooves, and so forth) disappeared with them.[a] The diversity of form present in these other types, and their presumptive suitability for a variety of ways of life, are generally ignored because it is assumed their lines ended in oblivion. But such conclusions are in no way necessary, nor, after careful consideration, are they even plausible. An evaluation of the probable origins of two extant mammals, the armadillo and the pangolin, will begin to reveal the fallacy of this mode of thought.

Armadillos and Pangolins. A taxonomic category containing a variety of forms is often named for a particular form within that category. Thus, among dinosaurs, the iguanodontids are named for *Iguanodon*, the tyrannosaurids for *Tyrannosaurus*, the stegosaurids for *Stegosaurus*. Likewise, the ankylosaurs are named for the four-ton *Ankylosaurus*, which lived in the latest Cretaceous.[809] Numerous other ankylosaurs existed, ranging down *Struthiosaurus,* about the size of a human being.[810] Ankylosaurs were among the most common large animals of the Cretaceous, but fragmentary remains indicate that similar forms existed already at least as early as the lower Jurassic, for example, *Sarcolestes*.[811] Known from every continent except Antarctica,[812] all ankylosaurs were armor-clad. In addition, some had a tail tipped with a heavy mass of bone that could be whipped from side to side with potentially lethal effect. Paleontologists have classified ankylosaurs as dinosaurs, and assert that they died out at the end of the Cretaceous. But is this so?

The extant giant armadillo (*Priodontes maximus*) is widespread in South America.[813] Compare *Priodontes* (Figure 9.1a) with a typical reconstruction of the Cretaceous ankylosaur, *Nodosaurus* (Figure 9.1b). Allowing for the vagaries of reconstructing the appearance of an organism from fossils, *Nodosaurus* appears quite similar to *Priodontes*. However, accepted theory would, almost certainly, account for the observed similarity between ankylosaurs and the giant armadillo, not in terms of genetic relationship, but by referring to "gradual adaptation to similar environments." But, if armadillos started evolving from a "small, primitive, generalized" placental mammal after ankylosaurs died out, this process of "adaptation" must have been rapid indeed. The ancestors of *Priodontes* can be traced through the fossil record all the way back to the Paleocene,[814] immediately after the ankylosaurs are said to have gone extinct.

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[a] Under the neo-Darwinian view, the only generally recognized exception to this claim is a separate line leading to the extant monotremes (the echidnas and duck-billed platypus).

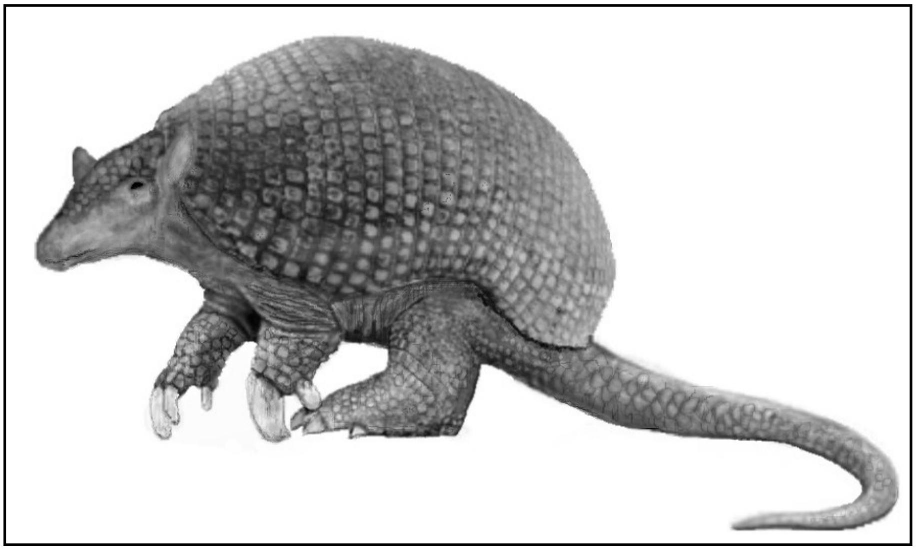

Figure 9.1a: South American Giant Armadillo (*Priodontes maximus*).

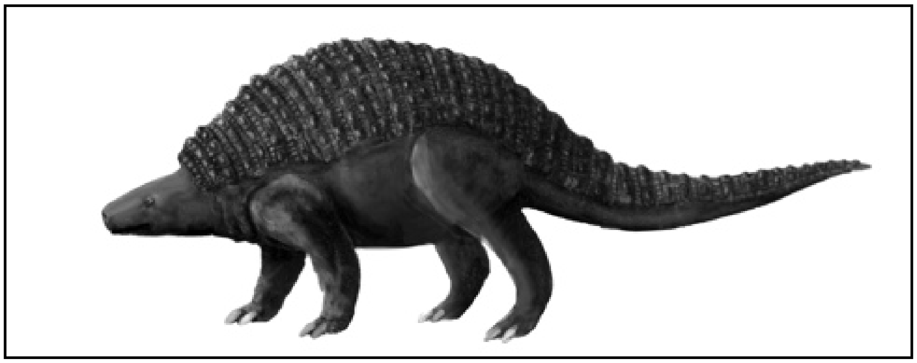

Figure 9.1b: A reconstruction of *Nodosaurus*.

A "giant" armadillo (*Priodontes*) is not even quite as large as the smallest known ankylosaur (*Struthiosaurus*). But much larger armadillos (*glyptodonts*), now extinct, survived long enough to be hunted by the pre-Columbian peoples of South America only a few thousand years ago.[815] Glyptodonts the size of a small car survived into the late Pleistocene (e.g., *Glyptodon*). Such animals were about the size of *Ankylosaurus* itself, the largest of the ankylosaurs (the Pleistocene ended only about 10,000 years ago). Like certain ankylosaurs, some of these giant armadillos had tail clubs. In both ankylosaurs and armadillos, these clubs could be armed with long, bony spikes.[816] These observations suggest that paleontologists have created an artificial distinction by classifying Mesozoic "ankylosaurs" as reptiles and post-Mesozoic armadillos as mammals. Given available evidence, and given stabilization theory's assumption that descendant forms typically arise from precursor forms similar to themselves, the obvious conclusion seems to be that the various forms described as armadillos of the "Age of Mammals" (the Cenozoic Era) are descended from the various forms described as ankylosaurs of the "Age of Reptiles" (the Mesozoic Era).

The wide acceptance of the notion that ankylosaurs are reptiles can be attributed to two factors: (1) most paleontologists specializing in dinosaurs are unlikely to be familiar with the specifics of armadillo anatomy (which is, in fact, poorly known compared to that of most mammals); and (2) the categorization of armadillos as mammals is based on soft anatomy (armadillos give live birth, nurse their young, are warm-blooded, and have hair to a greater or lesser degree in addition to their scales). Such traits are rarely or never seen in fossils. But the reasoning of stabilization theory suggests the various forms described as ankylosaurs, too, had the soft traits of a mammal, since their hard anatomy is so similar to that of armadillos. But, if such is the case, what about other Mesozoic "reptiles" similar to ankylosaurs (members of Order Ornithischia)? Are some of these, too, mammals on masquerade?

Incredibly, this seems likely to be the case with one of the most famous "dinosaurs," *Stegosaurus*, an animal usually considered closely related to the ankylosaurs. According to Bakker (1986: 187), "*Stegosaurus* and its close kin were the only common large, beaked dinosaurs in the late Jurassic." Stegosaurids became rarer through the Cretaceous as the ankylosaurs became more numerous, but are known even from the end of that period.[817,a] The familiar image of *Stegosaurus* shows a creature with spikes tipping its tail and upright angular plates sheltering its spine. The small inset in Figure 9.2 depicts a typical museum reconstruction of this animal (no doubt familiar to many readers). But this reconstruction of the living animal is uncertain—articulated stegosaurid remains have never been found.[818] As Dixon et al. (1988: 156) point out,

> No one is certain exactly how the bony plates were arranged on the back of *Stegosaurus*. Although many well preserved specimens have been found … the plates have never been found actually attached to the skeleton. Some paleontologists maintain that they lay flat in or on the skin, and formed a defensive armor over the back and upper flanks.

This alternative viewpoint has interesting implications. Suppose (1) the plates actually did lie flat on the skin in an overlapping fashion (which would certainly seem to afford better protection against predators); and (2) the “tail” spikes were not on the tail, but instead were huge claws on the feet. How would such an animal look? Clearly, it would closely resemble extant pangolins (see Figure 9.2).

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a. For example, *Dravidosaurus.*

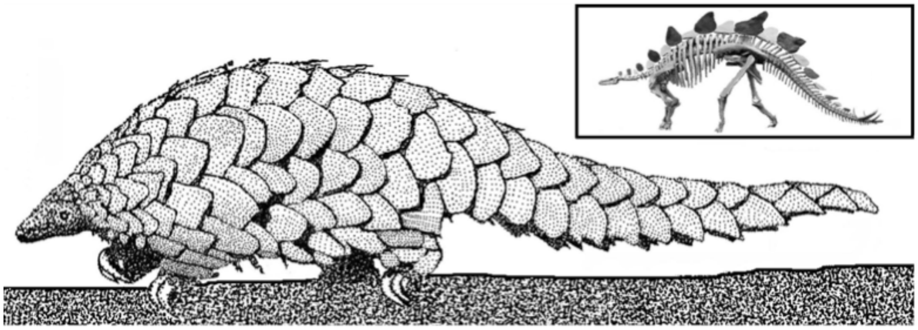

Figure 9.2: Main figure: Giant Pangolin (*Smutsia gigantes*). Inset: A typical reconstruction of the familiar *Stegosaurus*. Note that the shape of the pangolin's scales, and their size in proportion to body size, are similar to those of the animal shown in the inset (in a pangolin's armor about half of each scale is hidden by overlap). Note, too, on the pangolin's feet, the presence of large claws, which, in the reconstruction of supposed stegosaurids, have perhaps been misinterpreted as tail spikes (see text).

The pangolins, or scaly anteaters, are classified as mammals (Order Pholidota). Nevertheless, the back, upper flanks, and the outer surfaces of a pangolin's legs are covered with large scales similar in shape to the armor plates of a stegosaurid. Several different kinds of pangolins are extant. A Giant Pangolin (*Smutsia gigantes*) is pictured in Figure 9.2. In the figure, note that although only a portion of each scale shows (because each is mostly covered by the ones that overlap it), the scales of a pangolin are actually about as large in proportion to body size as are a stegosaurid's armor plates. A pangolin's scales are attached to the skin, not the skeleton and can bristle because they are attached only at one end. For this reason, one would not expect them to remain in place in a fossilized animal. They would detach after death as the skin decomposed. Known stegosaurid remains are so severely disarticulated that it is not even certain how many scales they had. The supposed tail spikes of stegosaurids are about as large in proportion to body size as are the huge claws of a pangolin (see Figure 9.2). In stegosaurids, also, these spikes (claws?) may well have been attached to the feet, and not the tail.

The overall form of a pangolin, too, is similar to that of a stegosaurid—a long thick tail, highest point at hips, nose to ground. The proportion of the limbs is also similar. A pangolin's skull, which bears little resemblance to that of other living mammals, is quite similar to that of a stegosaurid.[819] Pangolins have no teeth.[820] Even in large stegosaurids, the jaws are weak and the teeth are tiny and ineffectual.[821] Stegosaurids apparently used gizzards to grind their food.[822] The presence of a gizzard is not usually considered a mammalian trait, but pangolins do possess this organ.[823] Giant armadillos and most types of pangolins share a similar lifestyle. Most are nocturnal, burrowing forms. According to Walker (1983), the diet of the giant armadillo "consists primarily of termites, but ants, other insects, spiders, worms, larvae, snakes and carrion are also consumed." Pangolins also feast on such fare. Both armadillos and pangolins use their heavy claws to rip into termite mounds, anthills, and carcasses and then, with their long, protrusible tongues, lap up their dinners.[824]

Various types of pangolins exist, distributed over much of the tropical world, from West Africa to Borneo.[825] Fossil forms are known, too, from North America.[826] Fossils recognized as pangolins date to as early as the Paleocene,[827] just after stegosaurids supposedly went extinct.[a] The largest living pangolin is about two meters long,[828] the smallest known stegosaurid (*Kentrosaurus*), measures about two and a half meters.[829,b] Similarly, the length of the largest extant armadillo is about two meters,[830] while the smallest ankylosaur known (*Struthiosaurus*) measured two meters.[831] As has already been mentioned, huge armadillos, probably exterminated by humans, survived in South America until a few thousand years ago.

The modern giant armadillo is so similar to the ancient ankylosaurs that it is only reasonable to suppose it is descended from them. The same is true for pangolins and stegosaurids (although the case is somewhat weaker because the exact external form of stegosaurids is a point in dispute). These similarities strongly suggest that two of the most common "dinosaurs" of the so-called Age of Reptiles—ankylosaurs and stegosaurids—were in fact mammals, and, even more remarkably, that their direct descendants exist even today. So in their cases, it seems, there was no "extinction of the dinosaurs"—there was merely a reconceptualization and reclassification (both may be cases of residual dwarfism; see p. 221). If so, then the diet of stegosaurs and ankylosaurs was probably not herbaceous, as has been conjectured. The diets of their modern counterparts would suggest that they were primarily insectivores that also ate small vertebrates and carrion. Their jaws completely lack the grinding teeth needed to process tough plant material. They probably used darting tongues to feed on insects and small vertebrates then ground them in a gizzard.

The apparent mammalian status of stegosaurs and ankylosaurs seems also to contradict the idea that Cretaceous mammals were small (since many forms in these two categories were huge animals). Moreover, if the ankylosaurs and stegosaurids were placental mammals, as are their apparent modern counterparts, then the

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[a] Norman (1985: 152) notes that stegosaurids have been found in latest Cretaceous strata.

[b] Perhaps most of the giant stegosaurid/pangolins died out at the end of the Cretaceous, while the smaller forms lingered on. Burrowing, which is a trait associated with small body size (Auffenberg 1962; Auffenberg and Weaver 1969; McNab 1980), may have helped the smaller stegosaurid/pangolins to survive the catastrophic effects of the K-T asteroid impact. Fossil evidence proves the former existence of larger (8-foot) pangolins (*Manis paleojavanicus*) from Borneo and Java. These appear to have died out in the late Pleistocene, which ended only about 10,000 years ago (Flannery 1995). Unconfirmed reports say a horse-sized pangolinlike animal, the "veo," still exists on the Indonesian island of Rintja (Pfeiffer 1963; Shuker 2003: 264–265). Cryptozoologists suggest the veo may be a relict population of *M. paleojavanicus.*

placental mode of reproduction must date to a far earlier date (at least to the early Jurassic) than that generally proposed in the mammalian radiation dogma, according to which the first placentals appeared in the late Cretaceous (about a hundred million years later). Such findings raise the suspicion that at least some of the other members of Ornithischia, the "reptilian" order containing ankylosaurs and pangolins, may turn out to be mammals, too, since the bony structure of other ornithischians is similar to that of ankylosaurs and stegosaurids. Nevertheless, accepted theory says simply that armadillos and pangolins evolved from "small, primitive, generalized" placental mammals living late in the Cretaceous, and that they have nothing whatever to do with dinosaurs. Presumably a neo-Darwinian would account for the near identical appearance of modern giant armadillos and ancient ankylosaurs by ascribing it to "adaptation to similar niches." This is implausible—armadillos appear in the fossil record right after “ankylosaurs” supposedly went extinct. The only clear distinction between the two is that the fossil animals we call ankylosaurs lived in the “Age of Reptiles,” while the ones we call armadillos lived in the “Age of Mammals.”

It may be this tendency to categorize on the basis of time simply reflects a lingering bias among biologists. Some attention has already been given (see p. 136) to the influence of the *scala naturae* on biological thought. In its classical conception, the *scala* was simply a static ordering of beings, from "lowest" to "highest." Early evolutionary thinkers temporalized this concept by asserting that "lower" biological forms arose at an earlier date, and "higher" ones arose at a later date. Thus, the relative positions of the various animal forms in the old, static hierarchy gave rise to a particular temporal ordering of the story told about evolution. Briefly, this story said the order of appearance was (1) invertebrates, (2) fish, (3) amphibians, (4) reptiles, (5) birds, and (6) mammals.

Even today, this viewpoint seems to contribute to habits of thought that tend to bias the way scientists talk about fossils. In particular, the idea that mammals are "higher" and that they came after reptiles seems to dispose paleontologists to call very similar animals (e.g., ankylosaurs and giant armadillos) by different names and to make very different claims about their natures (i.e., that one is a reptile and the other a mammal). Another example is seen in the ease with which biologists accept the idea that synapsids were reptiles. If synapsids were classified as early mammals (as might seem reasonable on the basis of their hard anatomy), the earliest known mammals would then be the contemporaries of the earliest known reptiles.

Primates and the Origin of Placental Mammals. Only rarely can we look at a fossil and directly determine mode of birth. We can, however, with a high degree of certainty assign many fossils to particular taxonomic categories. Moreover, studies of plate tectonics have generated detailed information that has now been synthesized into a fairly exact picture of the relative positions of the continents in past geologic ages. When past continental contacts are considered in conjunction with fossil data, clear conclusions can be reached concerning the antiquity of placental mammals. For example, consider the primates, members of the mammalian order to which we ourselves belong. The very earliest known primate fossils date back no further than the late Cretaceous (approx. 70 mya). But the absence of earlier primate fossils does not mean primates themselves were absent at an earlier date. For *all* terrestrial organisms the fossil record is next to nonexistent in the early and middle Cretaceous, a period of about sixty million years (beginning at about 144 mya). Moreover, because their tropical forest habitat is not conducive to the formation of fossils, primates are rarely preserved even in much more recent strata.[832] Primates therefore could easily have existed long before the date corresponding to the earliest known primate fossils.

Those fossils that actually are known strongly suggest primates—and placental mammals—are much older than is generally believed. The first fact to consider in this connection is that monkey (cercopithecoid) fossils are known from the mid-Tertiary both of Africa and South America.[833] At that time, South America had long been isolated from Africa by an ocean barrier, since about 105 mya.[834] Primates are not aquatic animals. With few exceptions (*Nasalis*, *Haplalemur*, *Homo*), they are, in fact, notorious for their complete inability to swim. Even a narrow moat will efficiently contain these animals in zoos. How, then, did monkeys reach both of these continents? It seems utterly implausible to suppose they came into being on one of the two landmasses and then swam across open ocean to colonize the other. Apparently, the data can be explained only by assuming that monkeys arose prior to the separation of South America and Africa. Monkeys are not the only primates with this sort of paleogeographic distribution — Lemurs are also known from the early Miocene of Africa[835] and the Eocene of South America.[836] Since monkeys, lemurs, and all other primates are placental mammals, these facts imply that placental mammals arose before 105 mya. The same inference concerning the antiquity of the placental mode of reproduction can be drawn on the basis of the distribution of fossil ungulates (see p. 253) and elephants (see p. 265). The fact that stegosaurid/pangolins are known from Jurassic strata is also consistent with this conclusion. Some writers have suggested monkeys and lemurs "rafted" across the Atlantic Ocean on dead trees and debris. But this is implausible. Drifting at random, without provisions on an open ocean, a primate would face almost inevitable death. Death by thirst or drowning would be the two most likely dooms, but starvation and fatal exposure to the elements would also be high on the list of probable fates. Other writers speak of "waif dispersal," but this term seems to be little more than an erudite way of saying "they got there somehow."

But primates may have arisen much earlier. Fossil lemurs are common in the early Tertiary of North America and Eurasia.[837] Together these two modern continents composed the proto-continent "Laurasia.″ The earliest known specimen is a lemur molar from the late Cretaceous (or early Paleocene) of Montana.[838] Extant lemurs are limited to Madagascar, an island that, according to Rabinowitz et al. (1983) has been isolated by an ocean barrier since at least 150 mya, that is, the late

Jurassic.[a] About latest time that a lemur could have walked from Madagascar to Laurasia was in the early Cretaceous—at about 170 mya.[839] These facts suggest that primates predate 170 mya and, consequently, that placental mammals arose in (or prior to) the early Jurassic—a time when it is generally agreed that the latest synapsids were still in existence.[b]

Similar conclusions can be reached by considering the paleogeographic distribution of other placental mammals. For instance, until recently it had been thought the lesser anteater (*Tamandua*), which is a placental, evolved in South America subsequent to the isolation of that continent. But a well-preserved specimen of *Tamandua*, recently discovered in the Messel oil shales of Germany, dates to the middle Eocene.[840] Again, the most recent time prior to the Eocene that an anteater could have walked from Germany to South America was before the formation of the Tethys Sea (~170 mya), which long separated the northern and southern continents. Tamanduas, also, must predate 170 mya. The age and paleogeographic distribution of stegosaurid/pangolins and ankylosaur/armadillos suggest these creatures, also, came into existence prior to the middle Jurassic. This conclusion again suggests placental mammals date back to the time of the synapsids. But if placentals actually are as ancient as the synapsids, then the story cannot be correct that orthodox theory tells about mammals evolving from a generalized Cretaceous precursor. Moreover, as the next section shows, if we conclude that placental mammals arose far earlier (i.e., at least 100 million years earlier) than generally supposed, it becomes possible to explain things that orthodox theory can't.

Rodents and Lagomorphs (Gliriforms). Nowak (1999: 1) says there are 4,809 mammalian forms treated as species that are either extant or that have existed within historical time (within the last 5,000 years). Of these, he says, 2,052 are rodents (Order Rodentia),[841] and that an additional 81 are lagomorphs (rabbits, hares, or pikas).[842] Under orthodox theory, the origin of these animals is a complete mystery. The earliest fossils generally acknowledged as rodent date from the late Paleocene, the first epoch of the "Age of Mammals" (approx. 60 mya). These first rodents were already fully developed, according to Romer—that is, they already had all the skeletal and dental traits that distinguish their kind today.[843] No earlier fossils have been accepted as rodent ancestors because (recall once again) *all* placental mammals, including rodents, are assumed to be descended from "small, primitive, generalized" placental mammals living in the late Cretaceous, whose descendants "radiated" into various "niches" left vacant by extinct dinosaurs.

There were, however, rodentlike animals that greatly predate the late

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[a] According to the same authors, Madagascar attained its current position relative to Africa in the early Cretaceous.

[b] The absence of monkeys from Madagascar may mean that they came into existence sometime after that island became isolated, which occurred at least as early as 150 mya (Rabinowitz et al. 1983). But their presence in South America suggests that they existed prior to the separation of that continent from Africa (at about 105 mya).

Cretaceous. These creatures existed long before, and survived to overlap the earliest acknowledged rodents. These animals were the multituberculates, whose name refers to the multiple tubercles on their rodentlike molars. They are well known from their common fossils. Paleontologist T. S. Kemp (1982: 287) says multituberculates were "rodent-like, and this comparison extends not only to their anatomy, but also to the large number of individuals and of species that occurred on a world-wide basis." The fossil record is replete with their remains. Multituberculates had already existed for some 100 million years when they were supposedly replaced by the first rodents.[844] Most were the size of rats or mice—although some were as large as beavers—and many had incisors suitable for gnawing that were separated from masticatory molars by a gap, as in modern rodents.[a] For example, *Taeniolabis*, is a large multituberculate known from the late Cretaceous to late Paleocene. Its skull and teeth are very similar to those of recent squirrels.[845] Clemens and Kielan-Jaworowska (1979: 143) state that *Taeniolabis*' "massive skull, gliriform incisors, reduced premolar dentition, and large complex molars strongly suggest that this multituberculate was a rodent-like herbivore." *Fossils of this organism lie on the same level with, or immediately below, strata containing the earliest fossils that have been called rodent.*

Over the years a variety of investigators[846] have suggested multituberculates are the ancestors of rodents, and of the related lagomorphs. Animals in these two groups are jointly known as *gliriforms*. But this proposal has never been accepted. Orthodox theory assumes multituberculates "branched off" from the "line" leading to modern mammals long before the accepted date for the first appearance of placental mammals (viz., it is assumed they were "prototherians").[847] In other words, conventional thinking asserts rodents and lagomorphs, which are placental mammals, could not possibly be derived from multituberculates, because 1) the first multituberculates are known to predate the conventionally accepted date for the advent of the first placental mammal by many millions of years; and 2) it is generally assumed the placental mode of reproduction did not arise among later multituberculates, but rather in a separate line of mammals. The fact that such reasoning is widely accepted has an ironic sting. For while there is no clear fossil evidence to show early mammals were not placental, there are thousands of fossils showing multituberculates were similar to gliriforms. The extreme similarity between multituberculate teeth and those of rodents would be "superficial," as some authors suggest,[848] rather than real only if we could be sure the multituberculates were not ancestral to acknowledged rodents and lagomorphs.[b] But the superficiality

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[a] For a description of the dentition of a typical rodent see Hillson (2005: 73 *et seq.*).

[b] It is sometimes objected that some multituberculates have a non-rodent trait: extra incisors. Thus, although Romer (1966: 200) does say the teeth of multituberculates were rodentlike in having a pair of large incisors above and below. He also says smaller lateral upper incisors were present in some forms. But this observation is actually consistent with the idea that multituberculates are transitional between early mammals, on the one hand, and later lagomorphs and rodents on the other. In fact, extant lagomorphs normally do have extra

of the similarity seems itself to be a phantasm when viewed in light of (1) the observed similarity of multituberculate hard anatomy to that of recognized gliriforms; (2) the absence of any other candidates for "gliriform ancestor"; (3) the implausibly abrupt advent of the earliest creatures officially designated as gliriforms (they already had at their earliest appearance all the traits characteristic of modern gliriforms); and (4) the fact that the last fossils designated as "multituberculate" immediately precede and even somewhat overlap the first fossils designated as gliriform. The numerous multituberculate forms known from fossils are easily pictured as giving rise to a wide variety of descendant gliriform types.

The claim that multituberculates independently evolved gliriform traits becomes even more suspect if we consider that a separate, but similar, claim has been made with respect to the notoungulates of South America. Biologists have long puzzled over the supposedly sudden appearance of rodents in South America (lower Oligocene of Patagonia). It is most peculiar, they say, that whole families of distinctively South American rodents should appear out of nowhere, on a previously rodentless continent that had at that time been isolated from other landmasses by ocean barriers for many millions of years. The controversy centers on whether these rodents “island hopped” from North America or “rafted” over from Africa. If these ideas were correct, then the advent of South American rodents would indeed be a puzzling matter. But when the writer found paleontologists had ignored multituberculates as obvious rodent ancestors on other continents, he came to suspect that pre-Oligocene South American forms ancestral to modern rodents, too, might have been given a different name in order to make fossils fit accepted theory. An examination of South American fossils soon revealed earlier formations, of Paleocene and Eocene age (e.g., the Riochican, Casamayoran, and Mustersan), did contain types similar to rodents.[849] But, again, paleontologists usually do not *call* them rodents. To call them rodents would be to assert they shared common ancestry with rodents of other continents. Any such assertion would carry with it the conclusion that the ancestors of South American rodents had already been present on that continent when it separated from Africa (prior to 105 mya). This conclusion would, as in the case of multituberculates, in turn imply rodentlike forms ancestral to modern rodents were already in existence at a date far too early to be consistent with accepted theory. Nevertheless, certain “notoungulate” families dating from earlier South American strata do contain gliriformlike animals, for instance forms in the family Interatheriidae. Dixon et al. (1988: 252) say that “most interatheriids were quite small, rodent-like mammals. They were a long-lived group, with fossil representatives dating from the late Paleocene [i.e., the Riochican] to the late Miocene.” In the same place they state that “*Notostylops* [one of the members of the family Notosytlopidae] was a rather rabbitlike animal which lived in the

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incisors; they have three pairs of upper incisors at birth, two as adults (Walker 1983: 473). Rodents normally have but a single pair, but in many genera the upper incisors bear a single vertical median groove (Walker 1983), probably marking the line of fusion between incisors separate in ancestral forms.

undergrowth, eating herbaceous plants and other low growing vegetation … *Notostylops* would have had a short, deep face to accommodate the unusual rodentlike dentition characteristic of this family." [a,b] In general, members of the notoungulate families Notostylopidae and Interatheriidae were rodentlike and those belonging to family Hegetotheriidae were rabbitlike. These forms are often called as "ungulates," [850] but it appears that they for the most part had claws, not hooves.

The idea that multituberculates and certain notoungulates were actually early gliriforms is, again, consistent with the conclusion that placental mammals date back at least as far as the early Jurassic. Moreover, even if we consider only fossils officially accepted as gliriform (and ignore multituberculate and notoungulate fossils altogether), we would reach much the same conclusion—the temporal and geographic distribution of such fossils largely parallels that of the fossils discussed in previous sections (of primates, tamanduas, ankylosaur/armadillos, and stegosaurid/pangolins), and thus provides yet another line of evidence corroborating the early origin of placental mammals.[851] True, many gliriforms can indeed swim and would therefore be able to pass narrow water barriers, unlike primates. But the idea of an ocean-going porcupine or rabbit closely approaches the realm of the impossible. Thus, with rodents and lagomorphs we seem to be reaching far back into the latter days of the synapsid era.[c,a]

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a. In writing of *Typotherium*, the representative genus of the South American family Typotheriidae, Scott (1962: 510) says that "at first the skull of this animal might easily be mistaken for that of a rodent and was, at one time, actually referred to that order. Indeed a superficial likeness to the Rodentia characterizes most of the Typotheria." As in rodents, *Typotherium* has ever-growing (rootless) chisel-shaped incisors, separated from large rootless molars by a gap (Scott 1962: 510). The only significant difference between the dentition of *Typotherium* and that of a modern rodent seems to be its nonfused lower incisors. It is beyond the scope of this book to give a detailed analysis of the numerous fossil genera included in the various South American families containing rodentlike animals, but the following supposedly "non-rodent" categories are suspect and should be searched for early gliriforms: Interatheriidae; Notioprogonia (Hericosborniidae, Notostylopidae); Typotheriidae (Mesotheriidae).

b. If the remains of rodentlike animals seem scarce in South America, it should be remembered that the fossiliferous deposits themselves are rare. As Scott (1962: 511) notes, "It must always be borne in mind that in South America those mammal-bearing formations which are more ancient than the Pliocene are almost all confined to the far south and that the absence of many groups, which might reasonably be expected to occur there [i.e., in South America], was probably occasioned by climatic factors." It certainly seems more reasonable to seek the origin of South American rodents among earlier rodentlike South American animals than to imagine several distinct families of rodent genera swimming (or "rafting," or "island-hopping") across the open ocean to colonize a new continent. Moreover, the assumption simply isn't plausible that gliriform traits evolved independently in three supposedly unrelated categories of organisms (i.e., in notoungulates, multituberculates, and modern gliriforms).

c. In fact, if haramayids are multituberculates, as some authors have suggested (see Clemens and Kielan-Jaworowska 1979), then the date would move back even further, to the late Triassic (approx. 220 mya).

Bats. Among mammals, more forms treated as species are included in the order Chiroptera (bats) than in any other, with the exception of Order Rodentia. Nowak (1999: 259) says there are 977 such forms. Like that of rodents, the origin of bats is a mystery. As is the case with birds, their fossils are rarely preserved due to their delicate bone structure. In the entire fossil record, complete bat fossils are known from only two locations, both of Eocene age, the Messel shales of Germany and the Green River Formation of southwestern Wyoming (U.S.).[852] These ancient bats, which are relatively common within these two fifty-million-year-old formations, are very similar to modern bats.[853] From earlier deposits only teeth are known. Fruit bats, which are largely restricted to tropical environments unconducive to fossil formation, are known from just two partial skeletons (of Oligocene and Miocene age).[854] The rapid and early amplification of bats has long perplexed biologists; no ancestral forms are recognized. Habersetzer et al. (1992) assert that the finding that the earliest known bat fossils are fully evolved suggests the actual origin of bats took place at a far earlier date.

Bats puzzled Darwin, too. He could not think what lifestyle would bring about gradual selection for wings. In referring to "half-winged bats," Darwin said, "It is not possible to imagine what habits an animal could have had with such a structure."[855] The most widely accepted theory of bat origins says bats are descended, once again, from a "small, primitive, generalized" insectivore living late in the Cretaceous Period. This insectivore supposedly spent its time searching for insects in trees. When done with one tree, it would descend and go to another. Wings, it is said, evolved to aid these animals in getting from tree to tree, first by gliding, then by flapping. Ultimately, as the story goes, early bats stopped searching for bugs in trees and came to feed on airborne insects.[856] Their descendants then supposedly went on to diversify into a variety of forms, most feeding on insects, but others eating fruit, nectar, blood, flesh, fish, or even pollen.[857]

But fossil evidence substantiating this story is lacking. The earliest recognized bats are not "half-bats." They are fully developed. The accepted explanation of bat origins also ignores the fact that a type of animal much more similar to bats than the typical terrestrial or arboreal insectivore is known to have existed throughout much of the Mesozoic, prior to the advent of bats. A large variety of forms existed in this category. Some had the wingspan of a sparrow; others, that of a small airplane.[858] These animals had naked wings, and some forms, at least, are known to have had hairy bodies. In many, the flight membranes not only connected with the sides of the body, but also incorporated the hind legs and tail—again, as in bats. Analysis of the hind limb anatomy suggests these animals hung upside down when not in flight.[859] We know they varied in lifestyle as well, because the teeth of different forms were suited to the consumption of different types of foods. The idea that they were warm-blooded is now generally accepted.

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a. Also, among the Triassic synapsids, were other small creatures with rodentlike teeth such as the tritylodonts (Dixon et al. 1988: 193; Romer 1966: 185).

As the reader may have guessed, the type of creature in question is the pterosaur. But pterosaurs (long known as pterodactyls) have not been proposed as bat ancestors, perhaps because the idea that they are something other than reptiles has not been widely considered until recent years. Nevertheless—however pterosaurs have been classified—certain of these animals, (such as the small, insectivorous, short-headed, hairy, warm-blooded *Sordes pilosus,* were quite batlike.[860] Indeed, fossil remains clearly show that *Sordes* had thick fur and, on this basis, Wellnhofer (1991: 102) draws a general conclusion about so-called flying reptiles: "This is undeniable proof that pterosaurs were not naked or covered with reptilian scales, but that they were hairy." Also similar were such forms such as *Anurognathus*, *Batrachognathus* and *Scaphognathus*.[861] These three latter types are known only from the late Jurassic and thus long predate the first acknowledged fossil bats.[862] But the fossils of some small forms described as pterosaurs are known from the late Cretaceous.[863] Even in late Jurassic strata, the remains of small pterosaurs are relatively rare, perhaps because the small, delicate bones of these animals were rarely preserved.[864] The 50- or 60-million year period intervening between the late Jurassic and late Cretaceous is a gap in the terrestrial fossil record in which even large, durable bones have not been preserved, let alone those of bats and pterosaurs. It is more reasonable to suppose modern bats are descended from these similar precursor forms than from a generalized shrew. This is true despite the fact that, unlike bats, most pterosaurs supported the wing with a single finger. In bats, typically, all digits but one are involved in supporting the wing. A relatively minor difference such as this, however, seems much easier to overcome than that between bats and the entirely wingless, shrewlike ancestor proposed for bats by orthodox theory. In fact, mutations resulting in digital fusion by means of soft tissue webbing are fairly common. They affect aberrant individuals in a variety of mammals, including humans.[865] Perhaps, too, there was variation in pterosaurs with respect to this trait so that some types supported the wing with more digits than did others.

In addition to bats and ancient pterosaurs, various types of living mammals have skin flaps running between the fore and hind limbs and are capable of gliding, although they lack the skeletal characteristics of bats. Included in this category are the flying squirrels (*Aeromys*, *Glaucomys*, *Hylopetes*, *Petaurista*, *Petinomys*, *Pteromys*, and the anomalurids), the flying lemurs (Dermoptera), and the gliding possums (*Acrobates*, *Petaurus*, and *Shoinobates*). All of these animals are nocturnal and, like bats, hide away in dark hollows and crevices by day. Typically, they consume fruits, nuts, nectar, insects, and small vertebrates. Flying lemurs, however, seem to restrict themselves to fruits and vegetable matter. They are not known to consume insects or vertebrates.[866] Unlike flying squirrels, flying lemurs hang upside-down from branches when not in flight. They are quite large and their forebears might plausibly be connected with the ancestors of the large Old World fruit bats (Megachiroptera). Gliding mammals are known from the Paleocene, the very earliest epoch of the "Age of Mammals."[867] Inasmuch as their skeletal remains are like those of other wingless mammals, even earlier fossils, such as those of certain multituberculate/rodents, could easily represent such animals. The forebears of animals of this type then may have anciently participated in a similarity chain connected to pterosaurs that eventually gave rise to the similarity chain composed of modern bats.

Ungulates. The most characteristic feature of ungulates is the hoof. In addition, many ungulates bear either horns (cattle, deer, rhinoceroses) or tusks (hippos, chevrotains, musk deer, pigs). A few have both (guemals, muntjacs). Many others, such as horses and camels, have neither. All living ungulates are included in one of two categories, perissodactyls (even-toed ungulates) and artiodactyls (odd-toed ungulates). In the traditional account of evolution, perissodactyls and artiodactyls first appear in the Eocene. Perhaps for this reason, paleontologists tend to place the fossils of earlier hoofed animals into other "extinct" orders to indicate they are somehow basically different from, and not ancestral to, taxa included in the two extant ungulate orders Perissodactyla and Artiodactyla. This practice tends, in turn, to reinforce the story told about ungulates “first appearing” in the Eocene. Moreover, as we have seen, fossiliferous terrestrial deposits of Eocene age are far more common and widespread than those dating from the preceding epoch (i.e., the Paleocene). This discrepancy might easily lead a paleontologist interested in ungulates alone to suppose ungulates suddenly appeared or became abundant in the Eocene.

Nevertheless, earlier animals with hooves are known from the Paleocene, some of them with tusks and/or horns. These forms seem to constitute reasonable ancestors for ungulates of later date. Several ancient mammalian orders that supposedly left no descendants include fossil forms that seem to qualify as ungulates: Order Condylartha[868] (e.g., Arctocyonidae and Phenocodontidae; Order Litopterna[869] (e.g., the horselike Proterotheriidae and Notohippidae, as well as the camellike Macraucheniidae); orders Notoungulata (e.g., rhinoceroslike toxodontids and tapirlike isotemnids); and Amblypoda[870] (e.g., Xenungulata, the rhinoceroslike Dinocerata,[a] and the members of Family Coryphodontidae). The small, horselike *Hyracotherium* is known from the Paleocene of North America.[871] Van Valen (1988) describes early South American ungulates that were the contemporaries of dinosaurs. In the late Cretaceous of North America, there existed *Protungulatum*, an ungulate that is abundant in the Montanan Hell Creek formation, where it is found alongside *Tyrannosaurus rex*.[872] Thus, the idea seems plausible enough that the various early ungulates could have been the ancestors of the various ungulates of later times.[b]

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a. Compare the 6 stubby horns of the uintathere *Eobasileus* (Dixon 1988: 234), with the 6 stubby horns of *Protoceras* (Dixon et al. 1988: 270), which existed much later, in the late Oligocene and early Miocene.

b. There are also the late Cretaceous hadrosaurs, also ornithischians, which had a variety of strange, often hornlike growths atop their heads. In artists' renderings, these large (30-foot-long) animals have been portrayed as typical dinosaurs, but they had large nostrils, suggesting a well-developed sense of smell; a tooth pattern reminiscent of that seen in many modern

Of course, many of the early ungulates just listed are considered to be unrelated forms that evolved "in parallel" in response to similar "environmental demands." The similarity is, again, supposed to be due to convergence (see p. 213 *et seq*.). In defense of this viewpoint, it should be said that until the 1960s it must have seemed much more reasonable to suppose highly similar types of terrestrial animals could come into being on different continents in a completely independent fashion. Up to that time, convincing evidence (in particular, paleomagnetic evidence of sea-floor spreading) documenting continental drift was unavailable. Moreover, religionist attacks on evolutionary theory claimed only special creation could explain the presence of similar terrestrial animals on widely separated, fixed landmasses. Proponents of evolution perhaps felt compelled to address these objections with any argument they could bring to bear, however implausible it might seem today.

If we still believed continents were immobile, it would be easier to believe that the rhinoceroslike "leontinids" and "toxodontids",[a] and the elephantlike "pyrotheres" (see p. 265) of ancient South America might have nothing to do with the rhinoceroses and elephants of Africa and Eurasia.[b] The paleontologists and taxonomists who created our system for classifying fossils had no idea that the oft-noted similarities of these animals could actually be the result of a common descent from precursors living at the time that Africa was still in contact with South

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ungulates; they also cared for their young in a nest or den. As in ungulates, two or three digits were relatively enlarged on each foot and bore hooves. These animals are often drawn in a semi-bipedal stance, but the presence of hooves on the forefeet seems inconsistent with such a posture.

[a] Although they are not formally recognized as the remains of rhinoceroses, certain South American fossils suggest rhinoceroses date to sometime prior to the mid-Cretaceous separation of Africa and South America. Among the huge, extinct "notoungulates" of Patagonia are large horned creatures, ostensibly similar to present-day rhinoceroses. The presence of these rhinoceroslike animals in geographically isolated South America is usually explained in terms of convergent evolution. Inasmuch as these animals were discovered at a time long before the idea of continental drift was accepted, such an explanation must have seemed reasonable at the time. In light of modern knowledge such an explanation seems implausible and should be reevaulated. Here space for discussion of this topic is limited, but the curious reader is invited to compare modern rhinoceroses with the Oligocene (Deseadan) notoungulate *Leotinia gaudryi,* described and pictured by Scott (1962: 505–506). Note: Scott classifies *Leotinia* as a toxodont, but more recent authors (e.g., Savage and Russell 1983: 168) have treated leontinids and toxodonts as distinct types of notoungulate. Other South American toxodonts (many of which bear median horns on the forehead or nose) that are worthy of further investigation in connection with rhinoceroses are: *Abothrodon*, *Adinotherium*, *Alitoxodon*, *Chapalmalalodon*, *Dinotoxodon*, *Eutomodus*, *Eutrigodon*, *Gallardodon*, *Gyrinodon*, *Haplodontherium*, *Mixotoxodon*, *Neoadinotherium*, *Neotrigodon*, *Nesodon*, *Nesodonopsis*, *Nonotherium*, *Ocnerotherium*, *Palaeotoxodon*, *Palyeidodon*, *Paratrigodon*, *Phobereotherium*, *Posnanskytherium*, *Proadinotherium*, *Prototrigodon*, *Stenotyphanos*, *Stereotoxodon*, *Toxodon*, *Toxodontherium*, *Trigodon*, *Trigodonops*.

[b] Similarly, Dixon et al. (1988: 253) suggest the South American *Homalodotherium* is "highly reminiscent" of the North American and Old World chalicotheres.

America. They could not picture horses swimming from North to South America, which in their minds had always been immobile and distantly removed continents. So horselike prototheriids could have nothing to do with horses. With our knowledge of plate tectonics, however, we can imagine prototheriids evolving from various earlier forms with horselike traits whose descendants later became isolated by water barriers. But we are burdened with a system of classification tainted by the biases of a less-informed era. It's time to re-examine the fossils and reconsider traditional mammalian taxonomy in light of modern knowledge concerning the former positions of the continents.

Under stabilization theory's assumption that similar organisms should share similar ancestors, knowledge of the geographic distribution of extant (or, at least, relatively recent fossil) flora and fauna can be used to patch up gaps in the fossil record. For example, in the present case, the worldwide distribution of fossil ungulates suggests an origin at least as early as the lower Cretaceous, even though a vast gap exists in the terrestrial fossil record (on the order of 60 million years) prior to the late Cretaceous. Continental Cretaceous deposits are abundant only late in the period and even these are severely limited in geographic extent (Mongolia and western North America). Angiosperms were not widespread until the middle Cretaceous. The oldest reliable grass fossils apparently are pollen grains of the grass *Monoporites annulatus,* dated to the uppermost Cretaceous[873] (although grasses might have begun to proliferate somewhat earlier[874]). Ungulates, which feed largely on grasses, would be relatively rare until the vegetation favoring their expansion became common. The ready availability of grass (which can much better withstand the effects of continual grazing than can most other plants) then, may explain the rapid expansion of ungulate populations in the early Tertiary. For all these reasons, we might expect it to be difficult to trace the earlier course of Cretaceous ungulate evolution through fossils alone. But the presence of a variety of ungulates in the Tertiary of both South and North America prior to the unification of those two continents (at about 5 mya) suggests ungulate evolution may eventually be traced back at least to the early Cretaceous.

Moreover, it may be worthwhile to reconsider the reptile status of certain ornithischian "dinosaurs" of the Jurassic and early Cretaceous with ungulatelike traits (such as the *heterodontosaurids* and *hypsilophodontids*). Potential precursors of ungulates existed even in synapsid times, in the late Paleozoic/early Mesozoic.[875] In the shape of its skull, and in the general appearance of its skeleton, the large synapsid herbivore *Kannemeyeria* (early Triassic) was reminiscent of the much later rhinoceroses (as were the Permian herbivores *Pareiasaurus* and *Scutasaurus*). The skull of their contemporary, *Estemmenosuchus,* resembles that of the much younger uintathere ungulates.[876] Only theory excludes these alleged reptiles from consideration as ungulate ancestors.

Even if these earlier "reptiles" are excluded from consideration, there is certainly no reason to suppose the earliest fossils officially accepted as ungulates are indeed the earliest ungulates. There is absolutely no evidence that the ungulates of the late Cretaceous and Paleocene evolved gradually from the "small, primitive, generalized" Cretaceous placental mammal embraced by orthodox biology. These earliest “officially approved” ungulates are by no means identical to the ungulates of more recent strata. But hybridization among such forms (and of these forms with other ungulate forms as yet unknown from fossils) may well have given rise to the various and numerous ungulates of later times. Presumably the production of such forms would in many cases be as straightforward as was the production of the various modern breeds derived from hybridization of the Zebu (*Bos indicus*) with European domestic cattle (*Bos taurus*), a cross that produces partially fertile hybrids of both sexes.

Cetaceans. Biologists use the word *whale* to refer not only to the large marine mammals commonly designated by that name, but also to other, smaller members of the order Cetacea such as dolphins, porpoises, belugas, and narwhals. In this book the word *whales* is used in this broader sense. Under orthodox theory, the origin of whales is obscure. Relatively few marine fossils of any kind are known from the Paleocene, the first epoch of the Cenozoic Era, the so-called Age of Mammals.[877] It isn't surprising, then, that no fossils of whales or whalelike animals are known from the Paleocene. The earliest fossil forms usually classified as whales date from the ensuing epoch, the Eocene (~54–34 mya).[878]

Traditional theory, once again, asserts that whales, like the other placental mammals discussed in this chapter, evolved from a "small, primitive, generalized" terrestrial placental mammal living in the late (approx. 70 mya) Cretaceous Period. Many even take it for granted that whale ancestors first evolved into ungulates and only later became whales.[879] The creatures usually proposed as whale precursors are the mesonychid ungulates of the middle and lower Paleocene. But writers who assert this radical transformation actually occurred rarely mention that late Paleocene fossils documenting the transition between mesonychids and the earliest recognized whales are entirely lacking.[a] As paleontologist Robert L. Carroll (1997: 329) notes,

> It is not possible to identify a sequence of mesonychids leading directly to whales, although some teeth now recognized as belonging to primitive whales were originally described as from mesonychids. All adequately known mesonychids were terrestrial in most aspects of the skeleton, and some show specializations for cursorial [i.e., running] locomotion.

Carroll (1997: fig. 12.19) pictures the skull of the upper Paleocene mesonychid *Sinonyx* beside that of *Pakicetus* (lower Eocene), a supposedly transitional form between mesonychids and early whales. The teeth of *Sinonyx,* as figured there, are more similar to those of a modern dog than to those of an whale. Recent finds have

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[a] Known fossils are from the Eocene and are already quite whalelike. *Ambulocetus* (Thewissen and Aria 1994; Thewissen et al. 1996) cannot be counted as a transitional form because it is actually younger than the oldest rcognized cetacean *Himalayacetus* (Bajpa and Gingerich 1998).

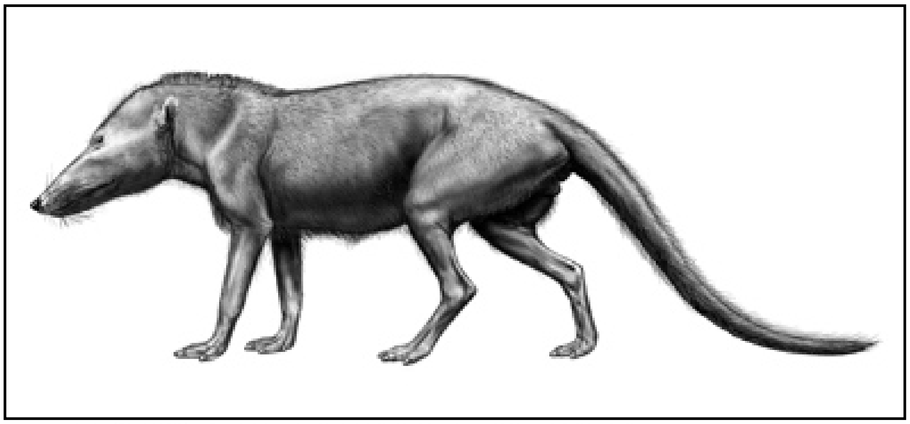

Figure 9.3: A recent reconstruction of *Pakicetus*, which appears on the website of the laboratory of Hans Thewissen (J. G. M. Thewissen), one of the most widely recognized authorities on early fossil whales. Although the information accompanying this figure on the website states that "pakicetids were the first cetaceans," and in the literature *Pakicetus* is usually described as a primitive whale, this animal has all the appearance of a primitive, doglike, terrestrial carnivore. Illustration by Carl Buell, and taken from http://www.neoucom.edu/Depts/Anat/Pakicetid.html.

shown *Pakicetus* itself was a terrestrial animal with fully developed legs. Apparently, the main reason for classifying it as a cetacean is that its ear structure is in some ways similar to that of a whale. But an examination of the currently accepted reconstruction of *Pakicetus* (Figure 9.3) will convince most readers that *Pakicetus,* as a whole, is more like a dog than a whale. On the same web page,[880] maintained by the laboratory of Hans Thewissen, a widely recognized authority on early fossil cetaceans, where Figure 9.3 originally appeared, another illustration shows the skulls of two pakicetids (*Ichthyolestes* and *Pakicetus*) are comparable to that of a modern coyote (*Canis latrans*).

But those who make such claims also embrace the notion that whales (and all other placental mammals) evolved from a tiny late Cretaceous shrewlike insectivore. They fail to mention, or perhaps do not realize, that whalelike, whale-sized creatures existed already in the Cretaceous, prior to the Paleocene.[881] These animals, called mosasaurs, were air-breathing marine animals.[a] They were abundant and existed in a wide variety of forms, ranging in size up to 20 m (~65 ft)—slightly longer than a bull sperm whale.[b] As Lingham-Soliar (1995: 178) notes, "From a handful of

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[a] Since baleen, characteristic of certain modern whales, does not fossilize (Dixon et al. 1988: 233), some of these ancient whalelike animals may have had it.

[b] Rothschild and Martin (2005: 341) say a mounted specimen of a mosasaur at the University of Kansas is 20 meters long.

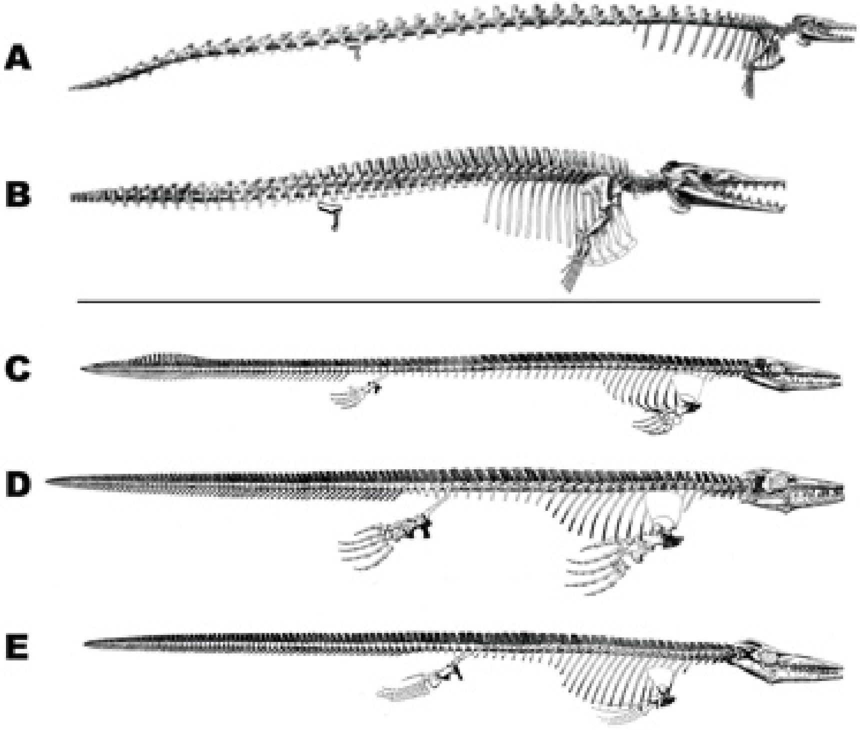

Figure 9.4: The two skeletons (from Kellogg 1936, not shown to scale) above the line are those of two animals generally recognized as early whales, A: *Basilosaurus cetoides* (~18m/60ft), also known as *Zeuglodon*, and B: *Zygorhiza kochii* (~6m/20ft). Both are from late Eocene strata. The three skeletons below the line (figures from Williston 1898, Plate LXXII), all of late Cretaceous age (~30 million years older than *Basilosaurus* and *Zygorhiza*), belong to animals normally classified as marine reptiles of the family Mosasauridae (mosasaurs). C: *Clidastes propython*, D: *Platecarpus tympaniticus*, E: *Tylosaurus proriger*. Although these three animals are shown about the same size in the drawing, in life, *Clidastes* was the smallest (~4 m/13 ft), *Platecarpus*, the next largest (~7 m/24 ft), and *Tylosaurus*, the largest of all (~30 ft/ 9m). Note that while the hind limbs are more developed in the older forms (C, D, E), they are also present, in a reduced state, in the younger ones (A and B). Thus, forms A and B are intermediate between the Cretaceous forms and modern whales.

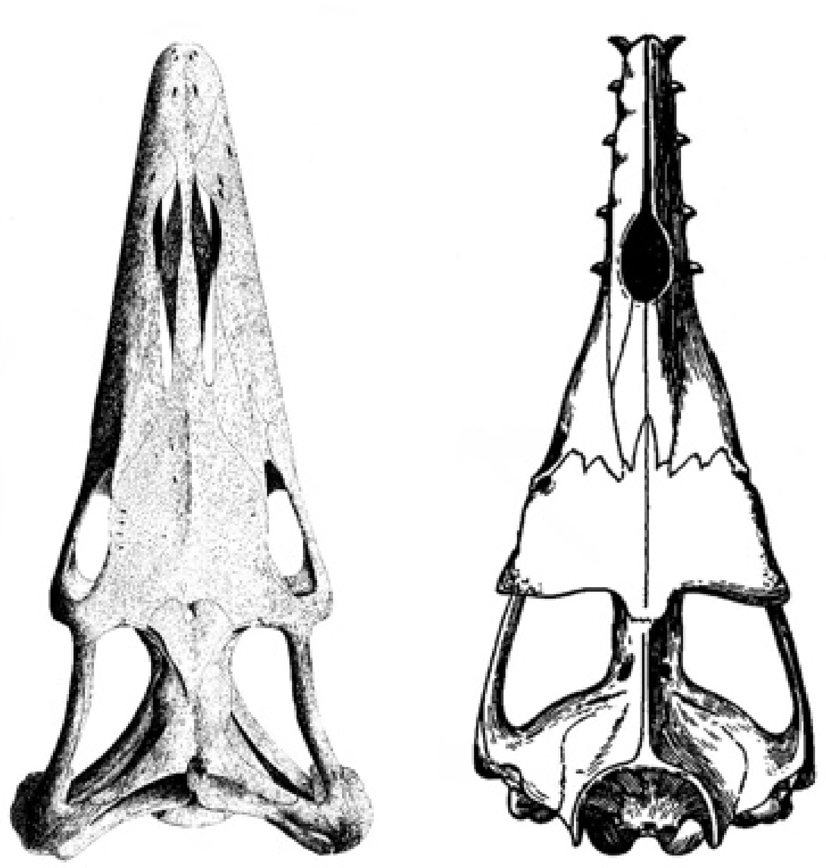

Figure 9.5: Comparison of the skulls of a mosasaur and an early whale (dorsal views). A: The late Cretaceous mosasaur *Platecarpus coryphaeus* (from Williston 1898: Pl. XIV). B: The middle Eocene whale *Dorudon atrox* (from Fraas 1904). Note that the while the nasal openings are in approximately the same position in both skulls, there is a single, fused opening in the more recent *Dorudon.*

species in the Turonian [~94-89 mya] they expanded to a total of approximately seventy species worldwide during the course of their evolution." The conventional account of that evolution says, however, that mosasaurs were reptiles and that they became extinct, along with the dinosaurs, at the end of the Cretaceous (~65 mya).

Nevertheless, the skeletons and skulls of mosasaurs and early whales are similar (figures 9.4 and 9.5). As Lindgren et al. (2007: 158-159) point out, "the dorsal and caudal vertebrae in the backbone of" the late Cretaceous mosasaur

> *Plotosaurus* have similar dimensions … and are arranged in functional units (tail stock, displacement unit and propulsive surface) comparable to those of living, pelagic vertebrates, such as whales, dolphins and porpoises.

The teeth of *Mosasaurus hoffmanni,* as pictured by Lingham-Soliar (1995: 160) are quite similar to those of late Miocene *Zygophyseter varolai,* an early sperm whale (Bianucci and Landini 2006). The teeth of mosasaurs such as *Mosasaurus*[882] and *Hainosaurus*[883] are similar, also*,* in both size, and in crown and root morphology, to those of large, living toothed whales, such as those of *Orcinus, Physeter,* and *Pseudorca* (Hillson 2005: 72, fig. 1.47).[a, b]

Like modern whales, mosasaurs were deep divers — their remains show signs of avascular necrosis (Rothschild and Martin 1988, 2005; Martin and Rothschild 1989), a condition resulting when nitrogen forms bubbles in body tissues after a dive. A recent study has shown deep-diving sperm whales are also affected by this condition (Moore and Early 2004). Moreover, the remains of giant squid, prey taken by large extant toothed whales during deep dives, have been found in the gut contents of ancient mosasaurs (Rothschild and Martin 2005: 343).

Some have claimed mosasaurs are related to snakes (Lee 1997; Lee and Caldwell 2000), an idea first proposed more than a century ago by paleontologist Edward Drinker Cope (Cope 1869).[c] (Animals currently classified as early whales, such as *Basilosaurus* or *Zygorhiza,* are also often described as snakelike. For example, Wong (2002) discusses "the probable progenitors of the snakelike basilosaurines and modern whales."[d]) The other commonly received theory is that

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[a] They also resemble in morphology, if not in size, the teeth of such medium-sized whales and dolphins as *Delphinapterus, Feresa, Globicephala, Lagenorhynchus, Peponocephala, Steno,* and *Tursiops* (Hillson 2005: 72, fig. 1.47).

[b] Sperm whales' lack of upper teeth has been the basis of a longstanding objection to the idea that mosasaurs are the ancestral to whales. However, functional upper teeth are present not only in early sperm whales such as the middle Miocene *Scaldicetus* (Hirota and Barnes 1995; See also p. 9 of: http://collections.nhm.org/newsletters/pdfs/2006-01.pdf), but also in all of the extant genera of toothed whales just mentioned, other than the sperm whale genera (*Kogia, Physeter*).

[c] Lee (1997) went so far as to define the taxon Pythonomorpha as the most recent common ancestor of mosasauroids and snakes, together with all its descendants.

[d] Mosasaurs are usually described, too, as moving like snakes, with a sinuous motion, through the water. The writer finds this claim implausible—the pygal and caudal vertebrae of

mosasaurs are related to varanid lizards, such as the Komodo Dragon (Lingham-Soliar 1995; Pellegrini 2007). This idea was popularized by Cuvier in the early nineteenth century (though he was not the originator of the notion).

But it should be mentioned that, even earlier, a widely respected comparative anatomist asserted that mosasaurs were whales. The first mosasaur jaws were found in 1766 in St. Pieter's Mountain in the Dutch city of Maastricht.[884] But a second specimen, a huge partial skull discovered nearby in 1780, received far more attention. It was 1.6 m (5.2 ft) long. Most contemporary investigators thought it belonged to a huge crocodile. But in a paper published in the *Philosophical Transactions of the Royal Society,* Pieter Camper (1786) pointed out that the teeth and vertebrae of the incognitum were similar to those of living toothed whales. Camper (1722-1789) was professor of medicine, surgery, anatomy, and botany at the University of Groningen, and an authority on medical illustration, he was perhaps the most eminent comparative anatomist of his day (Bell 1949). Camper pointed out that the teeth of the unknown animal were embedded in deep sockets within the bone of the jaw, a fact confirmed by modern investigators (Lingham-Soliar 1995: 169). Such a condition is characteristic of neither snakes nor of varanid lizards (King and Green 1998). Indeed, such ("thecodont") teeth are generally characteristic of mammals (Smith 1958: 223).[a] In particular, the form of the Maastricht animal's teeth, as Camper pointed out, and has already been mentioned, are like those of large extant toothed whales.

Camper died, however, soon after publishing his paper. His extensive fossil collection, which contained some of the best mosasaur specimens then known, passed into the hands of his son, Adriaan Gilles Camper. It was this son who first concocted the notion that mosasaurs were varanid lizards. Cuvier, who originated the idea that the Mesozoic was dominated by reptiles, readily embraced the idea that mosasaurs were huge lizards (though mosasaur fossils are always found in association with fossils of known marine origin). With the weight of his great reputation, he established the younger Camper's theory as one of the standard hypotheses usually considered in discussions of mosasaur origins.[885]

The varanid theory was based on Adriaan Gilles' assertion that certain skeletal characters found in mosasaurs are not found in modern whales.[886] However, a glance at figures 9.4 and 9.5, will convince most readers that mosasaurs have much in common with early whales. Certainly, they have far more in common with whales than does the late Cretaceous terrestrial insectivore traditional theory posits as the common ancestor of whales and all other placental mammals (it should be emphasized that all of the various forms classified as mosasaurs, too, are of late

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mosasaurs have long transverse processes (Lindgren 2005: 1162, fig. 4; Williston 1898, Plates XLII & LIV) that would limit any bending in the horizontal plane. The caudal vertebrae of whales also have long transverse processes — whales progress by flexing the body in the *vertical* plane.

[a] With the exception of crocodilians, thecodont teeth are not characteristic of extant reptiles (Jacobson 2007: 6).

Cretaceous age). They are also far more similar to whales than is *Pakicetus*. One would not expect the ancient ancestors of whales to have every characteristic of modern whales. Their dissimilarity with respect to a few minor bony traits should not be allowed to obscure the well established fact that mosasaurs were huge, whalelike, air-breathing animals with whalelike teeth and that they had the same sort of prey as modern whales.[a]

Lingham-Soliar (1995: 178) says the disappearance of mosasaurs at the end of the Cretaceous "is an enigma," "sudden and unexpected." "Remarkably," he says," like the dinosaurs, they were replaced by the mammals." But for anyone who supposes mosasaurs are the ancestors of whales, there is nothing remarkable. There is only another case of the now familiar tendency of paleontologists to identify as reptiles forms of Mesozoic age—even when those forms are highly similar to younger forms known to be mammals. Here, once again, biologists have continued to embrace the "small, primitive, generalized" terrestrial, placental mammal of the late Cretaceous, despite the credulity required for such a view and despite the obvious similarity of cetaceans to mosasaurs, creatures tradition calls "reptile."

Terrestrial Predators. When a biologist thinks of mammalian terrestrial predators, the tendency is to think of the members of Order Carnivora. Nevertheless, animals that regularly kill and eat other animals occur in several other mammalian orders. Although various writers suggest insectivores are more "generalized" than other mammals, they are nevertheless predators of a sort, and thus are suited to a certain way of life. It seems likely that many insectivores feed on insects only because they themselves are small. Young crocodiles catch and eat insects, but prey on antelope when they are older. Small carnivores such as coyotes, foxes, mongooses, civets, and kinkajous eat both insects and small vertebrates. Insects can be a staple even in the diet of large “carnivores.” Termites and other insects are the primary food of the sloth bear (*Ursus ursinus*), an animal that sometimes weighs more than 300 pounds.[887] In the present discussion the insectivores of Order Insectivora will therefore be grouped together with the carnivores of Order Carnivora as predators.

Insects and meat are important not only for the predators just mentioned, but also for most primates. Many primates actually are predators. While it is true that

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[a] A few small fossils interpreted as the impressions of scaly skin have been recovered in connection with mosasaur remains (Geist et al. 2002; Snow 1878). On this basis it has been claimed that these animals were reptiles. But the patterns seen in these fossils may merely represent the texture of the skin itself, not that of scales covering the skin. The conclusion that they represent scales seems to have been prompted by the preconception that these animals were reptiles. Mammalian skin is known to exist in a vast variety of textures (Montagna 1971, 1974). In some cases it can have a texture that in a fossil would be nearly indistinguishable from reptile scales. For example, the naked tail of a beaver (*Castor canadensis*) bears such a pattern (Nowak 1999: 1308). There seems therefore to be no reason whatsoever to suppose on the basis of few fossils of dubious interpretation that mosasaurs were scaly when their skeletal anatomy so clearly implies a relationship with early whales.

there are certain largely herbivorous and/or frugivorous primates (e.g., gorillas, many of the lemurs), meat and insects are important in the diet of many primates. On the other hand, certain forms categorized as carnivores seem unworthy of the name. The panda is so classified, yet it consumes bamboo almost exclusively. Vegetable matter makes up 96 percent of diet of the South American spectacled bear (*Tremarctos*), another member of order Carnivora.[888] The diet of Blanford's fox (*Vulpes cana*) consists largely of fruit.[889] Like most bears, the chimpanzee subsists primarily on vegetable matter, but will eat meat whenever possible. Many other primates rely heavily on both meat and insects.[890] Moreover, certain primates are physically similar to certain procyonid carnivores. For example, the night monkeys (genus *Aotus*) are similar to the Kinkajou (*Potos flavus*) and the olingos (genus *Bassaricyon*).[891] Like most mammalian predators, primates have bifocal vision that allows a fine judgment to be made of the distance to the prey, and large canines with which to bite it. It seems reasonable, then, to think of the typical primate as an arboreal variation on the general predator theme.

We have every reason to think mammalian terrestrial predators are much older than orthodox theory suggests. Viverrid carnivores, for example, must have existed quite early because viverrids, such as civets and mongooses, exist today in Madagascar,[892] and also existed elsewhere—viverrids are also known from the Eocene of Europe.[893] Since Madagascar has been isolated from other landmasses at least since the late Jurassic[894] (about 150 mya), these facts suggest forms similar to modern viverrids existed already in early Jurassic times. Likewise, the presence in modern Madagascar of a peculiar nocturnal, catlike predator with retractable claws, the Fossa (*Cryptoprocta*),[a] suggests that cats had already begun to evolve by the early Jurassic (otherwise the cats known from other landmasses than Madagascar, would have come into being independently of, and be unrelated to, the fossa). Among mammalian types, the predators are among the easiest to link with the synapsids. In fact, orthodox theory derives not only carnivores, but also all other mammals from a particular group of predatory synapsids, the cynodonts, known from Permian and Triassic fossils. While it seems implausible to derive such types as whales, bats, and ungulates from the dog- or bearlike cynodonts ("cynodont" means "dogtooth"), it does appear many of the later predators accepted as mammals (e.g., *Morganucodon* and *Sinoconodon* of late Triassic and Jurassic; *Amphilestes* and the triconodonts of the Jurassic and Cretaceous; the numerous known predators of the Tertiary) can reasonably trace their roots to the cynodonts. Although the cynodonts are considered "mammallike reptiles" (synapsids), their bones and teeth are more like those of modern mammals (in particular those of modern predatory mammals) than are those of any modern reptile.[895,b]

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a. Various taxonomists have classified the Fossa as either a true cat or a viverrid. Its appearance certainly seems to reflect a closer connection with the former (although its skull is more elongated than that of the typical cat). See: Gregory (1951: vol. II, Fig. 20.18); Walker (1983: 1054).

b. In the Jiulongshan Formation of Inner Mongolia, Chinese paleontologists (Qiang Ji 2006)

Pinnipeds. In addition to the terrestrial carnivores there are the pinnipeds (seals, sea lions, and walruses). In recent taxonomies, pinnipeds are often categorized as a family of the Order Carnivora. But in past years they were usually placed separately in Order Pinnipedia. This indecision reflects the fact that seals do not seem to fit very well with the largely terrestrial (with the exception of otters) members of Order Carnivora. Nevertheless, they show certain similarities to land carnivores in their anatomy and behavior. Accepted theory says pinnipeds, also, are descended from a "small, primitive, generalized" placental mammal living in the late Cretaceous by way of a terrestrial carnivore intermediate. But once again, this seems to be an unnecessary assumption inasmuch as seallike animals were already in existence in the late Cretaceous. These animals are to be found among the smaller, supposedly reptile, Mesozoic marine predators, the plesiosaurs. Their build was seallike and they fed on fish. In particular, the remains of such creatures as *Plesiosaurus* (Figure 9.6) and *Peloneustes* are reminiscent of modern pinnipeds. Plesiosaurs are known even from early Mesozoic formations. The nothosaurids, creatures somewhat less suited to an aquatic environment and widely considered to be ancestral to the plesiosaurs, date back to the early Triassic.[896] Why, then, should we embrace the “primitive placental” of the late Cretaceous?

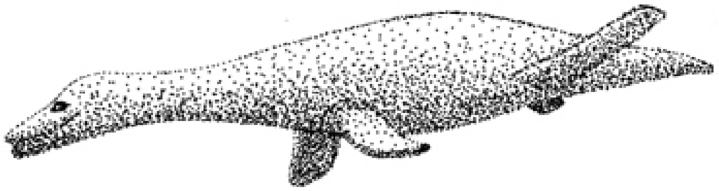

Figure 9.6: Typical reconstruction of *Plesiosaurus* (Jurassic).

Proboscideans (Elephants): During the late 1800s Florentino and Carlos Ameghino discovered in South America the remains of a huge extinct mammal. They named it *Pyrotherium* or “fire beast,“ a reference to the volcanic ash in which the first specimens were found. *Pyrotherium* and related forms (“*pyrotheriids*”) were a long-lived group prominent in South American deposits from the late Paleocene to Upper Miocene.[897] The Ameghinos believed that *Pyrotherium* was an early proboscidean.[898] Amherst professor Frederic B. Loomis (1914) discovered an intact skull of *Pyrotherium*, which seemed to him clearly to demonstrate its proboscidean affinity.[899] Romer (1966: 246) points out that *Pyrotherium* was not only

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recently discovered *Castorocauda lutrasimilis,* a beaver-tailed aquatic predator with otterlike teeth, in middle Jurassic strata (dated to 164 mya).

> the size of an elephant but anatomically had paralleled the proboscideans to a very remarkable degree. The dorsal nasal openings indicate the presence of a proboscis … The many similarities in body, skull, and dentition all suggest that *Pyrotherium* was really related to proboscideans, then developing to the east in Africa.

But for many biologists similarity—or, seemingly, even identity—is not enough. In the same place, Romer goes on to express his belief that these resemblances between pyrotheres and the early proboscideans of Africa "are surely a case of exceedingly close parallelism." In Romer's defense, it can be said that he was writing at a time when continental drift was not yet an established geophysical phenomenon. He thought in terms of fixed continents and believed elephants (and all other placental mammals) had rapidly evolved from small, generalized late Cretaceous insectivores. As such, his perspective excluded the idea that pyrotheres might be connected with elephants in other parts of the globe (but even some early writers thought the similarity of *Pyrotherium* and *Barytherium* indicated a "land bridge" had once existed between Africa and South America[900]). Such similarities extend to the various features of the skeleton. For example, Salas et al. (2006: 765) point out

> The remarkably similar morphology of the proboscidean and pyrothere femur (i.e., long, flat, and compressed anteroposteriorly, a head that faces nearly upward and is clearly higher that the greater trochanter, both condyles subequal in size) and some other hind limb elements … imply that the general mechanics of support and movement in both groups are comparable.

Dixon et al. (1988: 249) also note the extreme similarity between pyrotheres and elephants: "In life, *Pyrotherium* probably looked like the early elephant *Barytherium*, its African contemporary. *Pyrotherium* had a massive body supported on pillarlike legs, short broad toes, short thick neck, and a head equipped with a trunk and incisors enlarged to form tusks." But these authors, like Romer, attribute the similarity not to genetic relationship, but to convergent evolution.

Barytherium is known from the late Eocene and early Oligocene of North Africa.[901] Dixon and his colleagues appear to be correct in asserting that *Barytherium* and *Pyrotherium* were similar. A comparison of dentitions reveals their teeth are virtually identical.[902] These two animals both had bilophodont teeth (both premolars and molars) of the same size and shape. In both, the second upper, and first lower incisors formed chisel-shaped tusks bearing enamel only on the outer surface of the tooth. The claim that "convergent evolution" could produce such extreme similarity is implausible.

Evidence discussed thus far in this chapter indicates a much earlier origin for placental mammals than is commonly received. This conclusion, together with our now-firm knowledge that Africa and South America were in direct contact in the early Cretaceous, suggests pyrotheriids and barytheriids are not just forms that evolved in "parallel." It is more plausible to suppose that *Pyrotherium,* and related South American forms, were descended the same ancestral proboscidean similarity set giving rise to *Barytherium* in Africa (and that that set existed prior to the separation of those two continents). In other words, it seems likely proboscideans were already in existence in Gondwanaland in the early Cretaceous. Thus, proboscideans would be many millions of years older than biologists generally believe. In fact, it is even conceivable further analysis of fossils will show *Pyrotherium* and *Barytherium*. are merely distinct names applied to a single form that predated and long survived the separation of Africa and South America.[a]

Marsupials. If the bones of a fossil animal are the same as those of an extant form classified as a marsupial, then one can confidently classify the fossil type as a marsupial. But such is not the case when a fossil form is now extinct. R. A. Barbour, an expert on marsupial anatomy, says "the marsupial skeleton is essentially mammalian and has few unique features present in all species."[903] Even among living mammals, traits typical of marsupials are not found in every kind of marsupial. For example, the angle of the lower jaw is not always inflected in marsupials,[904] nor do all marsupials have epipubic bones.[905,b] Therefore, when we look at the fossil remains of an extinct animal, we cannot be certain the bones in question are those of a marsupial. Even on the basis of soft anatomy, Marsupialia is a rather poorly defined category. For example, many forms classified as marsupials lack a pouch (see comments in Note c). And yet, when remains of extinct mammals

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[a] Another form worthy of investigation with regard to proboscideans is *Diprotodon* of the Australian Pleistocene. This large animal has sometimes been described as a marsupial elephant. However, its soft anatomy is unknown, and its skeleton bears little if any resemblance to those of extant marsupials (the discussion of marsupials in this chapter explains why extinct forms cannot be diagnosed as marsupials).

[b] Moreover, many early mammals (and not just those that have been posited as early marsupials) had epipubic bones (von Koenigswald and Storch 1992: 155). No marsupial has a baculum, but many placental mammals also lack this feature (e.g., *Homo sapiens*). True, a post-orbital bar is absent from the skull of most (perhaps all) marsupials, but the same is also true for a wide variety of placental mammals (e.g., it is typically absent in rodents, as well as in many edentates, carnivores, seals, sirenians, cetaceans, bats, perissodactyls, and even in some artiodactyls (e.g., wart hogs).

[c] Even on the basis of soft anatomy, Marsupialia is a rather poorly defined category. The usual dictionary definition says marsupials are "pouched mammals." But, in some forms classified as marsupials, the pouch consists merely of small folds of skin near the teats, for example, certain didelphids and dasyurids (Walker 1983: 10). Other marsupials possess a pouch for only part of the year (some dasyurids); and at least one-third of all forms treated as marsupial species lack a pouch entirely (Kirsch 1977b; Walker 1983). According to Walker (1983) and Kirsch (1977a) these include the caenolestids, certain dasyurids, marmosids, monodelphids, and such genera as *Caluromysiops, Caluromys*, *Glironia, Lutreolina, Metachirus, Myrmecobius,* and *Philander*. In particular, the vast majority of American marsupial species lack this feature. Some marsupials even have longer gestation periods than those of some placentals. For example, rabbit (*Oryctolagus*): 28–33 days; rat (*Rattus*): 21–26 days; mouse (*Mus*): 19–21 days (Nowak 1999). The kowari (*Dasyuroides byrnei*), a marsupial mouse, has a gestation period of 30–36 days (Lee and Carrick 1989; Nowak 1999). A North American chipmunk, *Tamias striatus,* is the same size as a kowari, and its gestation period of

are discovered in regions where marsupials predominate today (e.g., Australia and New Guinea), or are assumed to have predominated in times past (South America), it is often assumed the fossils in question are those of marsupials. Mammalian specimens found outside those regions are typically categorized as placental.[a] In previous sections of this chapter, we have sought plausible ancestors for each of the various mammalian types. In the present section, however, since the marsupial type is itself poorly defined, there will be no effort to identify such forms. We will merely attempt to gain some idea of when and where marsupial traits first began proliferating.

Some authors[906] have suggested the marsupials first arose in Laurasia, which recall is the ancient precursor landmass that gave rise to North America and Eurasia. But this position seems untenable because: (1) outside the southern continent complex (Australian Region, Antarctica, South America), the only extant marsupials not introduced by human agency are the seven didelphid genera that invaded North America over the Isthmus of Panama within the last five million years; (2) in strata predating the collision of North and South America, the fossils of extant marsupials are known only from the southern complex; (3) extinct marsupials cannot be reliably identified as marsupials from their bony remains even when those remains are intact; (4) fossils from outside the southern complex, which are supposed to represent the earliest known marsupials (known almost exclusively from the late Cretaceous[907,b])

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31 days (Nowak 1999) is comparable a kowari's . Another trait generally considered characteristic of marsupials, tenacious attachment of the young to the mother's nipples, is known to occur in a wide variety of (placental) rodent genera (Gilbert 1995). In addition to the genera listed by Gilbert, Walker (1983) lists the following genera as having this trait: Conilurus (p. 707), *Leporillus* (p. 709), *Zysomys* (p. 709), sand *Mastacomys* (p. 716). Some sources say marsupials develop no placenta during the course of reproduction. But, as marsupial experts Hugh Tyndale-Biscoe and Marilyn Renfree (1987: 310) point out, "There has been much debate over whether marsupials possess a true placenta." (Ramsey 1982; Walker 1983: 39). The current consensus of opinion on this point seems to be that 1) early in the development of the embryo, a yolk-sac placenta forms in both placental mammals and marsupials, and 2) a chorio-allantoic placenta develops thereafter, not only in the typical placental mammal, but also in certain marsupials, for example, Peramelidae, Thylacomyidae, and *Phascolarctos* (Ramsey 1982: 19, 75; Walker 1983: 45; Strahan 1995: 167; Tyndale-Biscoe and Renfree (1987: 311). Additional marsupials may also have a chorio-allantoic placenta since little information—or even none at all—is available on the reproductive anatomy of most marsupials (Tyndale-Biscoe and Renfree 1987: 14).

a. Traditional mammalian classification has treated marsupials and placental mammals as two separate major categories within Order Mammalia, but the difficulties of definition just mentioned have led some recent workers (e.g., Nowak 1999) to drop the category Marsupialia altogether, to break up the forms traditionally assigned to that category into various orders, and simply to list them along with the various placental orders.

b. It is true, however, that a few alleged marsupials dating to the early Tertiary have been found in the Old World (Crochet 1986; Gabunia et al. 1985; von Koenigswald 1982). With the exception of those described by von Koenigswald (1982), these are tiny, isolated teeth, about the size of a large grain of sand. On the other hand, von Koenigswald's "opossums" from the are so extremely fragmentary we can in no way feel assured of their marsupial status. As Clemens (1979: 192) points out,

> The fossil record of Mesozoic marsupials [of which the Cretaceous is the third period] is an odontologist's [i.e., a tooth expert's] delight. Almost all the known specimens are isolated teeth or, at most, dentulous [i.e., toothed] fragments of maxillae and dentaries [i.e., jaws]. … Small fragments of *Eodelphis* and *Didephodon* have been discovered and described, but they are not extensive enough to serve as the basis of a restoration of the entire skull. Likewise, elements of postcranial skeletons have been tentatively identified, but, to the best of my knowledge, restoration of an entire skeleton or even a limb has yet to be attempted.

And yet debate has centered, not upon whether these rudimentary specimens actually were marsupials, but rather upon the question of how the alleged descendants of these supposed early marsupials reached the southern continents.

Thus, the only firm evidence—that is, the geographic distribution of known (extant) marsupials and their fossils—is strongly consistent with the idea that marsupials never existed outside the southern continent complex until South and North America came into contact a few million years ago. That is, the only evidence carrying any weight suggests extant marsupial forms represent the remnants of a similarity set that was until recently restricted to the southern complex of formerly connected continents, and that appeared much later than did the earliest placental mammals (probably after Africa separated from South America and the rest of the southern continent complex in the middle Cretaceous). It was within this southern similarity set that the traits characteristic of marsupials first proliferated. Our line of reasoning thus far has strongly suggested placental mammals date back at least to the early Jurassic. In other words, the placental type appears to be ancient, while the marsupial type seems to be a relatively recent innovation.

Conclusion. The example (Class Mammalia) discussed in this chapter suggests that numerous widely accepted notions should be discarded (such as "radiation" and "primitive" "generalized" forms). In particular, if the conclusions reached in this chapter are, in the main, correct, there is no reason to think reptiles predated mammals or that they "dominated" them during the Mesozoic. Numerous synapsids, many of them large, existed during the early Mesozoic—and even as early as the Permian—and these we may reasonably consider to be early mammals. Other forms, many of them large and "dominant," existed far back into the "reptile" age, and yet can be interpreted as ancestors of the various modern mammalian orders (e.g.,

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Messel oil shale are largely complete, but have apparently only been identified as marsupial because they have an incisor count of 5/4 (von Koenigswald and Storch 1992: 155). Incisor counts are a shaky basis of diagnosis for two reasons: 1) Many, perhaps even most, modern marsupials do not have such a count (for example, the Virginia Opossum, *Didelphis virginiana,* has a incisor count of 3/3); 2). As Ziegler (1971) has emphasized, 5/4 was a common incisor count not just in early marsupials, but in *all* early mammals (on this basis he has suggested 5/4 was the primitive state). See also Barbour (1977: 242).

mosasaurs, plesiosaurs, multituberculates, pterosaurs). Evidence (offered in the sections of this chapter on ungulates and proboscideans) suggests that early elephants and rhinoceroses, as large or larger than most dinosaurs, already existed in the early Cretaceous. We have already seen there is reason to suppose certain animals actually classified as dinosaurs (e.g., ankylosaurs, stegosaurids) can be construed as direct ancestors of creatures classified as mammals (e.g., armadillos, pangolins). Perhaps most remarkable conclusion reached in this chapter is that the famed "extinction of the dinosaurs" appears in large part to be a matter of mistaken classification.

Available evidence seems to exclude the idea that mammalian evolution has been monophyletic (i.e., that all modern mammals are descended from a single, “generalized” ancestor living in the Cretaceous Period). It is certainly more plausible to assume each recent type has arisen from a similar ancient type (e.g., seals from earlier plesiosaurs, bats from pterosaurs). Many of these general types can be traced back to synapsid times. This perspective is consistent, not with divergence and adaptation to vacated "niches" (“adaptive radiation”) and gradual change in isolation, but with descendant forms arising from similar preexisting forms via stabilization processes, a kind of evolution that can be discussed without reference to “branching trees” and that can instead be conceptualized in terms of sets of related forms that give rise to new sets of similar forms. Instead of gradually evolving, isolated lineages (neo-Darwinism's perspective), under stabilization theory we can picture an evolving community of forms. Nor would there be any radiation of placental mammals from a common ancestor living in the late Cretaceous. In fact, the evidence suggests many of the major types of placental mammals arose long before the Cretaceous, in the Triassic or perhaps even in the late Paleozoic and that marsupials arose within a previously diversified placental similarity set. The relative positions of the southern continents in times past seem to indicate that marsupials arose much more recently, subsequent to the separation of Africa and South America (approx. 105 mya). Thus, if we judge only by relative times of origin, marsupials would be a more “advanced” than placentals.

In general, stabilization theory suggests we should seek to explain the origin of any given set of similar forms in terms of their derivation from some preexisting set of forms with similar traits. Under this view no radiation is expected. No single ancestral form is presumed. Instead each similarity set goes on evolving as it generates new member forms via stabilization processes (and as old members become extinct). In this respect, stabilization theory is far more plausible than neo-Darwinian theory, which makes far-fetched assertions about "generalized" ancestors being rapidly and radically altered into a variety of totally dissimilar types (e.g., shrew to whale, shrew to bat, shrew to deer, shrew to monkey, shrew to pangolin, shrew to pig, shrew to seal, etc.). The facts and arguments offered in this chapter, what might be called a scientific taming of the shrew, make patent the implausibility of such claims. This theoretical emperor simply isn't wearing any clothes.

10 Concluding Remarks

That with this bright believing band
I have no claim to be,
That faiths by which my comrades stand
Seem fantasies to me,
And mirage-mists their Shining Land,
Is a strange destiny.
—THOMAS HARDY
The Impercipient

I have now presented the facts and inferences that have convinced me that the typical form treated as a species (1) is produced rapidly by a stabilization process; (2) has a distinctive and characteristic set of traits from the time of its inception that does not change significantly thereafter.[a] The data and their implications seem clear. Why, then, have other biologists not come to similar conclusions? It isn't easy to say. After all, who has seen evidence that one fossil form typically changes gradually into another? Who would deny that a single description generally allows us to identify individual specimens of a fossil form even when vast ages intervene between the times at which they lived? How could a single description suffice if the typical fossil form gradually changes? What biologist would claim that the production of new types of organisms via stabilization processes is poorly known? Perhaps it is only the weight of tradition that has prevented others from advocating the same views.

Perhaps, too, in the absence of a more plausible alternative theory, my colleagues have not been forced by logic to acknowledge counterevidence. They have instead been able to respond to the pattern of sudden change followed by stability observed in the fossil record (see Chapter 6) either with the peripheral

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[a] When I say that there is no significant change, I mean that the amount of change that can occur is limited to the various possible permutations of alleles that can be produced by point mutations and, in sexual forms, by meiotic recombination in a fully paired karyotype (see Chapter 3).

isolates scenario (see p. 159) or with the notion of speedy gradualism (see p. 162). They could claim the preservation of fossils has been too imperfect for gradualism to be properly documented. They could also argue that the reason we do not observe gradual evolution is that it is unobservable within the time span of systematic human observation (though it should be observable in the fossil record, even if we cannot observe it directly). If they had no satisfactory explanation of the fact that the typical hybrid is of reduced fertility, it was enough merely to shrug their shoulders and walk away. Or they could accept inadequate explanations of the general phenomenon of hybrid infertility, such as the Dobzhansky-Muller model (see pp. 191-192). Independent studies could yield conflicting phylogenetic trees and such results could be viewed merely as puzzling and any data that did not agree with the accepted view could be dismissed as statistical "noise." In the absence of a more satisfactory explanation, the claim could be made that conventional theory simply *must* be correct. Any shortcomings of the theory could be dismissed as a matter of future fine-tuning. In this book I have attempted to show that stabilization theory, on scientific grounds, is demonstrably superior to orthodox theory. This alternative theory does, in fact, explain numerous phenomena that seem inexplicable under neo-Darwinian theory. Furthermore, stabilization processes, the mechanisms on which stabilization theory is based, are firmly founded on observation—forms of known origin are typically derived from such processes.

But I cannot pretend certain aspects of stabilization theory have not been previously expressed. Long ago, Locke realized that the word *species* was badly defined. Many others have reached the same conclusion. Cuvier saw that the typical fossil form is morphologically stable over time. So did Lyell. Many others have said the same. In recent years, Gould and Eldredge did evolutionary biology a service by calling attention to this fact once again. De Vries observed and reported that certain forms treated as species arise repeatedly as individuals in the progeny of another type. Others, too, have since corroborated this fact. Goldschmidt realized that processes producing forms treated as distinct species often also change the karyotype. Again, others have since said the same (M. J. D. White, in particular). Ledyard Stebbins and Verne Grant enumerated many of the stabilization processes discussed in this book. They and many others showed that existing forms have actually been derived from such processes. But Stebbins and Grant never extended their claims beyond the plant kingdom and, even there, they never argued that the production of new forms by such processes is typical. Innumerable naturalists, from Linnaeus and Lamarck up to the present, have pointed out that hybridization occurs in a natural setting and that it can produce new types of organisms. Therefore many of the components used to construct the worldview expressed in this book were the insights of others. But perhaps such is the case with any theory.

Many biologists would readily admit new forms do come into being via stabilization processes. But in the case of forms of unknown origin—that is, in the case of the vast majority of all organisms—many still imagine new types come into being gradually under the influence of natural selection. This conclusion violates all scientific tradition, in which we are taught to suppose unobserved cases are probably like observed ones. Somehow, with people who think this way, inductive inference breaks down. They accept that a multitude of forms, once thought to be of gradual origin, are now known to be the products of stabilization processes. But they view these cases as *exceptional* and continue to believe the typical process is gradual natural selection. They refuse to extend the same view even to other, very slightly different types of organisms. By induction, one would suppose that, among forms of unknown origin, the percentage of forms produced by stabilization processes would be about the same as among forms of known origin. And among forms of known origin, virtually all are indeed derived from stabilization processes. Nevertheless, most biologists would admit such processes are the typical source of new forms *only* for those cases where origins are known. They arbitrarily reject it when origins are unknown. They not only fail to estimate the fraction of the unknown cases based on the proportion observed in known cases, but even go so far as to assume the fraction must be small, or even insignificant, when the observed fraction is large. If they cannot appeal to observed cases, on what basis can they justify such a claim? Such thinkers seem happy to explain evolution in terms of processes they have never seen, when they could just as easily construct their explanations in terms of observed processes. But do they really believe a single type of organism, which occurs in a variety of different environments, has been shaped by each of those various environments, even though the same distinctive traits are found in all the individual constituents of that form in all environments where that form occurs? In such cases, isn't it far more plausible to suppose a single form arose via a single stabilization process and that it then spread into a variety of environments to which it was suited? Although biologists quite properly demand evidence from creationists, they themselves gloss over, or are even unaware of, the fact that there is little, if any, evidence demonstrating that the forms they treat as species come into being gradually.

Stabilization theory clarifies recent evolutionary history. But it may make ancient events seem more nebulous, given that orthodox theory makes so many specific, though largely unsubstantiated, claims about ancient evolutionary history. Thinking of evolution in terms of stabilization processes doesn't usually allow us to identify the exact ancient forms remotely ancestral to a modern form. As we pass back through time, it becomes increasingly difficult to say anything conclusive. But stabilization theory does specify the nature of the processes producing new forms and it does allow the positive identification of the immediate ancestors of many particular extant forms treated as species. It provides science with the proof needed to counter allegations that evolutionary study is mere irreligious speculation. In many cases we can now irrefutably show that entities traditionally regarded as "species" are not immutable. That is, it is now known that many such forms have produced other stable types unlike themselves and also treated as species. Given the apparent prevalence of stabilization processes among extant forms, both extant and fossil, we can reasonably suppose such processes have always been at work, even among the earliest known forms of life. I therefore can only believe that all organisms are enmeshed in a web of life, united by ancient strands and new, that "the mingled, mingling threads of life are woven warp and woof." Our ancestral forms must be legion.

Many of the most respected scholars in biology seem completely satisfied with the view that the typical new form comes into being gradually under the influence of natural selection. To me, it accords far better with what we know of evolution to suppose stabilization processes are the usual source of organic innovation. If the reader has been persuaded by the arguments presented in this book, she will find inescapable the logical consequences of the theory, which are broadly destructive of neo-Darwinian theory. If we accept the claim that stabilization theory is better supported than neo-Darwinism, then we must, for example, reject the notion that taxonomic classifications should reflect a branching history of descent, a method of classification that neo-Darwinians term “natural.” We will instead be forced to suppose the history of evolution is analogous to a multidimensional web, not a tree.[a] Taxonomists will no longer be able to pursue their work in the same manner as they now do because they will have no intellectual touchstone by which to judge the validity of their classifications. Indeed, the activity of classifying natural forms would lose much of its zest—for a taxonomist much of the satisfaction provided by the activity of constructing classifications comes from the feeling of getting history right. Under stabilization theory, systems of classification will have no more grandeur than an office filing system. There will be few or no historical implications. Indeed, classifications will no longer be *taxonomic* because the structure of the classification system will not reflect the presumed nature of the relationships of the forms classified. Existing, supposedly taxonomic, classifications will be seen as mere artificial constructs bereft of any basis other than the weight of usage and tradition.

The traditional account of descent will be replaced with a very different one. Instead of divergent trees, there will be similarity chains and similarity sets, sets of organismal types that give rise over time to new sets. Some of the forms in a given generation of a similarity set survive into the succeeding generation. Others go extinct. If we look at any one of the forms occurring in successive generations of a similarity set, we will expect it to show an insignificant amount of change over time. Preexisting forms add new forms to the set via the various stabilization processes. As a result, the composition of the set changes over time as old forms drop out and new ones enroll. Here, no modern set of forms is defined in terms of a single common ancestor (as is typically the case under neo-Darwinian theory). Presumably, some forms will survive longer and produce more offspring forms than others because they have traits favoring survival and the parenting of new forms. Over time, then, such advantageous traits will tend to occur in a larger number of different forms within a similarity set. This picture of descent suggests an interconnectivity of relationship

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[a] The assumption that evolution can be represented as a branching tree is axiomatic to the cladistic approach to taxonomic classification. If this premise is erroneous, then the cladistic approach would itself be nugatory (Panchen 1992).

among forms that is in no way implied by—or even logically consistent with—neo-Darwinian theory.

By describing evolution in terms of similarity sets and by recognizing the existence of forms with traits linking major taxonomic categories, stabilization theory makes arbitrary the exact positioning of the lines of demarcation between higher categories. It suggests distinct higher categories correspond to similarity sets discrete today, but descended from ancient sets connected by extinct intermediate forms. Moreover, it implies that the main way in which natural selection produces new types of organisms is by choosing among forms within such a similarity set, not by selecting among individuals. To investigate the production of new forms via natural selection, evolutionary biologists have long used competition experiments in the laboratory or on computers. The competition is among genetically distinct individuals within a population. Under stabilization theory such experiments would lose their intellectual basis, though they are at present quite popular.

It is my hope there will at last be an end to the interminable disputes over whether this group or that one is truly a "species." I can foresee that our children will look back on our discussions of such issues and fail to understand our concerns. They will accept that geographically and morphologically intermediate hybrid populations connect many distinct types of organisms. They will think, too, that our nomenclatural delineations of such populations, if they understand them at all, were largely arbitrary. For they will see that such distinctions have been ruled not only by differences in form, but also to a great extent by the personal prejudices of those who devised the nomenclature and by traditions that ensconced such prejudices on the throne of accepted usage. In the future, naturalists will only have to consider what type of organism they wish to study. They won't need to decide whether it is a "species" or not. Determining the genus or class or phylum to which a given form belongs will no longer be a crucial issue. The reprieve from the duty to make such decisions will in itself save untold hours of labor and tedium. It will in fact mark the demise of an entire branch of biological research. It will be no small additional blessing that we will be emancipated from the endless, unrewarding, and, in my opinion, medieval tasks of revising the taxonomic hierarchy and defining the word *species.*

Another basic biological concept, that of the common ancestor, also becomes obsolete under stabilization theory. Neo-Darwinian theory claims any two given types of organisms share a single, most recent common ancestor. Likewise, the genes of the two forms are presumed descendants of genes present in the ancestor. No doubt many distinct forms sharing a given trait are descended from some single form with that trait. But it seems just as certain, given the apparent prevalence of hybridization, that traits distinguishing such forms will often be derived from ancestors not held in common. Each living form can have two or more parental forms and those parental forms, in turn, can each have two or more parents of their own. As the ramifications pass back through time, "the" common ancestor simply vanishes.

The terminology used to discuss the various aspects of "species," *speciation, conspecific, interspecific, intraspecific,* etc., will be recalled by historians of biology, but by few others. We will believe that the production of the typical living form has not been a matter of tacking on one trait after another with the passage of time. Instead, we will think that typically an abrupt process creates at a single stroke a functionally integrated whole. We will then realize how much we have yet to learn about the genetic basis of development. No longer will an organic being be seen as if it were shaped for a purpose, as if it were a tool nature had honed and perfected for a particular task. The traits of an organism will be seen merely as adequate to permit its continued existence. We will think of the typical organism as having, from the time of its inception, a particular characteristic set of traits. We will think that many complex structures and traits have arisen at random from the billion trillion trillion varying gametes and zygotes generated by hybrids in past ages, and that some, but not all, of the structures so generated must have been useful to their possessors. When our outlook changes, we will see our own abilities and peculiarities in a more modest light. Along with our "speech and wind-swift thought," we will expect ever to retain certain flaws and shortcomings.

A wide field of research will be opened, in which we shall seek the limits and laws of hybridization. Very little research has been done on the ability of distantly related organisms to interbreed. The more different two parental forms are, the more novel their offspring forms can be. Thus, it is of interest under stabilization theory to know the true limits of hybridization. A research program designed to determine these limits might, for example, select organisms at random and cross them by artificial insemination or pollination. Other studies might seek to elucidate the poorly known phenomenon of a mother's immune response to hybrid offspring within her womb. Hybrids will be seen as wide avenues to new realms of form, not as futile cul-de-sacs abhorred by nature. No longer will they be regarded merely as entities that are selected against. Instead, they will be seen as an important source of variation, the grist of natural selection. For the student of evolution, the study of domestic breeding will become an essential topic. Historical studies of breeding records will allow us to document the origins of many types of organisms. Currently emerging forms will be tracked and surveyed. The production of stabilized forms identical to existing natural forms will be a far more important source of information about origins than the stories of unobserved gradual change that now receive such avid attention. How much more interesting will the study of such matters become when we realize that it is possible, in many cases, to prove how a given form has come into being, when fact constrains imagination. There is even the exciting prospect of being able to recreate certain extinct forms, in those cases where the relevant parental forms are still in existence. Orthodox theory excludes this "Lazarus" option from the realm of possibility. Obviously, an extinct agamosperm or polyploid would be a reasonable target for such a project. But even extinct forms that arose as recombinant derivatives have potential for resurrection.

Our classifications will cease to be perceived as genealogies. Rules of classification will no doubt be more straightforward when we no longer feel compelled to decide whether the entities in question are truly related in the way that we choose to classify them, and we are no longer concerned with whether they are "species." We need not—indeed, in most cases we cannot—discover and trace the many lines of descent in a complex web of ancestry long lost in the depths of time. Nor would traditional systems of classification be able to replicate their topology. It will be far more interesting to reproduce as many types of organisms as possible, and so to verify their origins. Functionless organs will no longer suggest the former existence of long-lost structures serving some purpose now unknown. They will not be vestigial. They will simply be by-products of a stabilization process. Living fossils will become something more than simple illustrations of ancient forms of life. They will become emblematic of the remarkable genetic stability of living forms. Embryology will no longer be seen as the study of a process that somehow recapitulates past events or reveals the general plan of broad classes of organisms. Instead it will be seen in a straightforward way as providing information on the developmental processes that change a zygote into a mature organism. When we can feel assured that natural processes of descent are not reflected in the basic topology of our bifurcating systems of classification, we will feel free to choose other systems with other topologies that suit our convenience and intellectual needs. For example, we might find it easier to list types of organisms linearly by name, as in a dictionary, with cross-references to relevant topics. When we become convinced that those patterns of descent have been largely weblike because forms typically have more than one parental form, the quest for the "true" Tree of Life will be at an end. For, so long as they differ, all things of any kind, even inanimate ones, can be assigned positions in a treelike classification on the basis of their traits. The mere possibility of arranging a set of organisms into such a classificatory scheme does not in any way imply that a process of gradual divergence has produced them. If it did, we could infer that such a process produced the various items in my attic.

Because they describe the behavior of paired chromosomes during meiosis, Mendel's Laws, axiomatic to neo-Darwinian theory, will be far less important in describing processes producing new types of organisms. In general, such rules have nothing to say about stabilization processes. Thus, the traditional ways of thinking about the origins of new forms—the sorts of evolutionary models offered by neo-Darwinian theory—will become largely irrelevant. For the most part, such mechanisms describe how genes subject to Mendel's Laws change in frequency over time under various hypothetical circumstances. Under stabilization theory such processes have only a minor role in the production of new types of organisms. There will be a new emphasis on the role of chromosomes as structural units determining the characteristics of a chromotype and limiting their range of variation. The study of meiotic mechanisms that rearrange and reassort chromosomes will then be directly relevant to our understanding of the production of new forms. Mutations in genes and changes in their regulation will become issues more relevant to the medical student than to the evolutionist.

Interest in ‘isolation mechanisms’ would also be at an end. Most of the models discussed in neo-Darwinian theory describe new forms as evolving in reproductive isolation. Stabilization theory, in contrast, assumes a lack of reproductive isolation (hybridization) greatly increases the potential to create new forms and, thus, further invalidates neo-Darwinian explanations of evolution. Therefore, assumptions concerning the nature of the environmental context in which new types of organisms are likely to arise will also change. Stabilization theory tells us isolated lakes and islands are not the crucibles of change many neo-Darwinians would say they are. Instead, stabilization theory claims new forms arise most frequently in environments where stabilization processes are likely to occur. Therefore we should expect new forms to arise more frequently where the opportunities for highly varied hybridization events are maximized, as in large landmasses or in the oceans and their connected waters.

Geology will gain in evolutionary stature. Fossils are the *only* reliable source of information on rates of morphological change in prehistoric times. Such rates, it will be realized, provide a vital clue to the genetic nature of evolutionary processes. Given the present state of geological knowledge, the conclusion seems unavoidable that the typical fossil form comes into being abruptly at a particular stratigraphic level and remains largely unchanged thereafter until the time of its extinction. This finding is wholly consistent with the hypothesis that new forms typically come into being via stabilization processes. Neo-Darwinians have claimed the fossil record is imperfect. The processes they accept must have occurred, they say, in strata that have not been preserved. Anyone who accepts stabilization theory doesn't have to make such claims. There will be no need to posit undiscovered "small, generalized" common ancestors "radiating" into arrays of diverse, "specialized" descendants. The existence of sets of fossil forms with particular traits will simply imply the existence of ancestral sets of forms with similar traits. Study of the fossil record will focus on identification of such successive similarity sets and on the documentation of discontinuity of origin and stability of form. The science of plate tectonics will allow us to determine where similarity sets with particular characteristics first came into being. The facts of ancient geography will place limits on potential patterns of past migration.

Under neo-Darwinian theory, new forms are imagined as coming into being by a gradual process of natural selection as small differences accumulate over time. Once a type has been shaped by this process, it is maintained in the same way—the type is supposedly ideally suited ("adapted") to its "environmental niche," and is therefore maintained by natural selection that eliminates any individuals with new traits differing from that ideal because they are not as well suited to the "niche." The environment is the great shaper and maintainer under this view. All living beings are the passive products of this process. This milquetoast determinism plays itself out on a cosmic scale.

To me, organisms have a far greater value when they are seen as ancient and unchanging, existing today much a they did when they came into being long ago, in the remoteness of time. They become something more than mere pawns, forever changing at the behest of a tyrannical environment. When a new type of organism comes into being via a stabilization process, the primary selective factor is reproductive stability—a stable reproductive cycle must be established or the new form will fail to maintain itself in existence. If it survives, the new type spreads into all geographic regions to which it is suited and has access. If it ceases to have access to a suitable environment, it simply goes extinct. It does not gradually change into a new type that can tolerate a new environment. Under this view, a form's genetic make-up plays at least as great a role in determining its characteristics as does the environment. In fact, it generally plays a far greater one. Once a new type of organism has stabilized, the environment may place limits on growth, health, and activities, but it does not significantly change the nature or potential of that type of organism, even with the passage of time on a geological scale. Living forms, under this view, are beyond and above the environment.

In fact, we know actual organisms have an active, creative nature. An animal typically selects an environment suited to its unchanging nature. A bird that cannot tolerate the cold of winter flies to tropical climes. A landed fish will flip and flop until it drops back into the water. Even a plant passively selects its environment since a seed will mature only in a setting that suits its nature. A banana tree does not grow on an arctic island. Indeed, a plant or animal will often alter its environment and, in the process, make that environment either more or less habitable. The environment does not create a nest. Each type of nest is a characteristic environment created by a particular type of animal that builds a certain type of nest. Through their ability to produce oxygen, photosynthetic organisms have completely changed the atmosphere of the earth, and, in consequence, have vastly altered the array of forms that exist there. Even the lowly worm, crawling blind through the soil, shapes its world. Under stabilization theory, the living organism is the initiative force and creative power—a positive agent, selecting and reconstructing its environment. It is not mere wax upon which an indifferent environment writes at will. Each living thing has its own potent nature. In fact, its choice of environment and its actions upon that environment are aspects of its nature. Yeats saw better than Darwin:

> O body swayed to music, O brightening glance,
> How can we know the dancer from the dance?

On the basis of stabilization theory, we may conclude that evolutionarily successful forms will spawn many offspring forms, heirs to their genes, when they themselves cease to exist. Each form of organism has a birth and death, just as an individual does. But living forms are more stable than an individual because they do not undergo gradual change in the time between inception and demise. Under this view, elimination of certain types of individuals does not result in progress toward perfection. It merely reduces the scope of diversity. Indeed, severe selection against all types deviating from a single ideal would eventually reduce a form to a clone-like uniformity in which no change, progressive or otherwise, would be possible.

It is encouraging to imagine a world in which individual competition and selfishness cease to be biological givens, where each type of organism has a fixed nature that holds its own against an impotent environment. There is hope in this view of life, in which nature is no longer "red in tooth and claw," where the necessity of struggle ceases to be an axiom. In such a world we will be able to abandon the factory metaphor, turn our backs on the efficient assembly line, and instead embrace alternative ideals more consistent with our own nature. Relieved of the grim duty of destroying our imagined competitors for the sake of mere survival, we can escape Darwin's ruthless ratios of increase and rise to a higher moral plane where we, as individuals and as societies, can build ourselves environments filled with "sounds and sweet airs, that give delight and hurt not." And in this new world we will be able to study, and perhaps come fully to know, the origins of living forms.

Nor is that other point to be passed over, that the Sphinx was subdued by a lame man with club feet; for men generally proceed too fast and in too great a hurry to the solution of the Sphinx's riddles; whence it follows that the Sphinx has the better of them, and instead of obtaining the sovereignty by works and effects, they only distract and worry their minds with disputations.

FRANCIS BACON, *The Sphinx*

There are some who think that they have found the truth, the so-called dogmatists, such as Aristotle, Epicurus, the Stoics, and certain others. On the other hand, Clitomachus, Carneades, and the other Academicians assert that the truth is impossible to find. But the skeptics go on searching.

SEXTUS EMPIRICUS, *Outlines of Pyrrhonism*

Strange friend, past, present, and to be;
Loved deeplier, darklier understood;
Behold, I dream a dream of good,
And mingle all the world with thee.

ALFRED, LORD TENNYSON, *In Memoriam*

Appendix A: *The Limits of Directional Selection*

Directional selection is selection resulting in a directional shift in the population mean along a continuum, for example the continuum height. In the absence of mutation, this sort of selection, in itself, can have only limited effect. That limit is reached when an optimum allele is present at all loci affecting a quantitative trait. The following reasoning explains why:

If there were n loci for height and two extreme alleles, t_i and s_i, at any given locus i (where individuals with the allele t_i at locus i are taller than those having any other allele at locus i, and those with the allele s_i are shorter), then the shortest possible person would have the genetic constitution $s_1s_1, s_2s_2, s_3s_3, \ldots, s_ns_n$ (two alleles at each locus since humans are diploid), and the tallest would have $t_1t_1, t_2t_2, t_3t_3, \ldots t_nt_n$, whereas, someone of intermediate height might have the constitution $s_1t_1, s_2t_2, s_3t_3, \ldots, s_nt_n$. The variation of height in the population would be nearly continuous due to the many different possible combinations of alleles that a person might have at these loci. In a real situation there would also be an environmental component causing further variation. For example, difference in nutrition during growth would cause variation in height. However, under such circumstances, the amount that meiotic recombination could increase or decrease height would be limited. The shortest person that could be produced by directional selection would have the genetic constitution $s_1s_1, s_2s_2, s_3s_3, \ldots, s_ns_n$ and the tallest possible individual would have the alleles $t_1t_1, t_2t_2, t_3t_3, \ldots t_nt_n$.

Once all individuals in the population had two tall alleles at all n loci, further directional selection among variants produced by meiotic recombination alone would never produce taller progeny. In general, an optimal pair of alleles will exist for each locus affecting any quantitative trait. When the optimal pair for each such locus is actually present at each locus, then the limit of variation will have been reached.

Directional selection will not be able to bring about a progression outside those limits unless mutation creates some new allele with more potent effect than any preexisting allele (or hybridization introduces such an allele).

The conclusions of the preceding paragraph can be reached without experiment or observation. They are *a priori* given the known nature of meiotic recombination. It would therefore be pointless to carry out experimentation to verify them. Nevertheless, in the first decades of the twentieth century before the nature of meiotic recombination was well understood, researchers actually did carry out experimentation and found that such limits can quickly be reached. These were the so-called "pure line" studies.

The first researcher to demonstrate by means of experimentation this limitation of selection was the Danish botanist Wilhelm Johanssen (1903, 1915), who studied size change in an initially variable population of beans. In each generation he selected the largest and the smallest individuals and self-fertilized them. After only a few generations he had two stabilized populations, one small, the other large, and no amount of subsequent selection made beans in the larger line any larger. Nor did it make the small beans any smaller. The two lines had both become pure (genetically invariant) so that the small line was homozygous for small alleles at all size-governing loci, and the large line was homozygous for large alleles at all such loci. Johansen obtained similar results using barley.

Likewise, Pearl (1915) subjected chickens to long-term selection for increased egg production. Again, there were definite limits to the amount of increase that could be achieved. William Ernest Castle (1915), Sewell Wright's professor at the Bussey Institution, argued that Pearl's study was flawed. Castle asserted that his own experiments with hooded rats were much more reliable and that they had shown selection could go on changing a character indefinitely.

Pearl (1916) adequately defended himself against Castle's attack. Indeed, Castle believed in error that selection actually changed alleles, what were then called "Mendelian factors."[908] For example, he thought directional selection for darker rats would actually *create* alleles for darker coat color. This notion is false. In fact, experiments carried out in his own laboratory later convinced him of his error and he formally retracted his claim that selection could change "Mendelian factors" (Castle 1919a, 1919b). Since Castle's notion of creating new alleles through selection was erroneous, his belief that selection would continue to change coat color indefinitely in a certain direction was mistaken too. As soon as rats in Castle's study became homozygous at all loci affecting coat color, further selection would have been to no avail.

Studies like Castle's aimed at "taking variability beyond the range of variability in the original control stock." Castle's methods did in fact produce individuals with coat colors outside the range of variation seen in the control population. But such findings are spurious. They do not demonstrate selection can go on altering a trait indefinitely. Extreme individuals homozygous for all extreme alleles affecting a quantitative trait would occur with such low frequency that one would not expect to observe them in a small unselected laboratory population. But in a natural population, in the long run, they would in fact occur. So, due to small sample sizes, they would not be observed in any control stock, even though the alleles to produce them through meiotic recombination did exist in the control population. And yet they could be produced by continued selection.

Various other early workers carried out experiments similar to Johanssen's. In particular, Jennings' (1909) work with *Paramecium* and Hanel's (1907) with *Hydra* yielded similar results. For example, in selecting for size in *Paramecium,* Jennings (1909: 331) says that in initial generations great progress is made in increasing the mean size of the population.

> But finally we reach a stage in which all but the largest race have been excluded. Thereafter we can make no further progress. In vain we choose for breeding the largest specimens of the lot; all belong to the same races so that all produce the same progeny. Selection has come to the end of its action.

Neo-Darwinians later viewed pure line research as an attack on the validity of the notion of evolution via natural selection (when it in reality it merely showed that the effects of selection are limited in the absence of mutation and hybridization). For this reason pure line research has often been misrepresented. For example, Mayr (1982: 585) says Johanssen claimed "selection cannot produce a deviation from the mean in a self-fertilizing species." What Johanssen actually said was that selection *can* produce a deviation from the mean, but that *the deviation cannot be indefinitely increased*. This is in fact true if the only source of variation is meiotic recombination (as has already been shown by *a priori* reasoning).

Later studies supposedly refuting these early findings, such as the much heralded work of Kettlewell (1955) on industrial melanism in moths, focused on the fact that steady changes in the mean measures of traits can be accomplished by selection in initially variable populations. But all such studies gloss over the fact that there is always a limit to such change when the source of variation is meiotic recombination alone.

In general, the karyotype defining a chromoset also defines the limits of variation that can be observed in the corresponding somaset since:

(1) a finite set of loci in that karyotype will have an effect on the expression of any given trait; and

(2) each such locus will have a finite set of alleles. Some allele for each locus must exist that maximizes (or minimizes) expression of that trait.

Once an organism is homozygous at each locus for the allele having the extreme effect at that locus, selection can do no more (in the absence of mutation and hybridization).

Appendix B: *Polyploidy (Modes of Production)*

Most natural polyploids arise in one of two ways: (1) somatic chromosome multiplication; and (2) unreduced gametes. Evidence suggests that the latter of these two modes is the commoner in both animals and plants.

The production of a polyploid offspring via somatic multiplication requires a doubling of the chromosome number to occur in some part of the parent organism. So it requires the production of a polyploid shoot, bud, or fragment that can in some way (i.e., via sexual reproduction, agamospermy, vegetative reproduction, or some combination thereof) go on to maintain itself as a new type of organism. This doubling must initially occur in a single cell of the organism. That cell must then initiate new growth and proliferate to become a distinct multicellular polyploid portion of the parent organism. Individual polyploid cells commonly occur in plants otherwise composed of diploid cells, but the frequency with which such cells initiate new growth and give rise to polyploid offspring forms is poorly known.[909]

Somatic multiplication was once thought to be the primary mode of polyploidization in plants.[a] More recent literature, however, suggests unreduced gametes are the most common source of plant polyploids,[910] as has long been assumed for animals.[911] A wide variety of organisms produce unreduced gametes, which are usually either diploid or triploid.[912,b] For example, Franke (1975) lists 31 plant families for which they have been reported. It is often suggested that the union

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[a] Indeed, the fact that the hybrid that gave rise to *Primula kewensis* produced polyploid shoots in three successive years (Grant 1981), suggests that somatic doubling must be a fairly common process. Darwin (1875: vol. I, 425–427) notes many reports of hybrid plants exhibiting features that, from a modern perspective, strongly suggest somatic mosaicism. Herbert (1837: 336–337) describes some early cases that may be like that of *P. kewensis.*

[b] Grant (1952) noted that adverse growing conditions increased the rate of diploid gamete production in *Gilia.*

of two unreduced gametes must be a very rare event, but this claim appears to have been made only in considering such unions as a percentage of all gametic unions. If, however, one considers the fact that gametes are produced in vast numbers and that the expected rate at which unreduced eggs will be fertilized by unreduced male gametes is equal to the fraction of all male gametes that are unreduced, then it becomes apparent such unions must be very numerous indeed.

For example, suppose a very small fraction of the eggs produced by a particular population were diploid, say one egg in a million, and that a similarly low fraction of all male gametes produced by that population were diploid. If the population contained one million females each producing one million gametes, then they would produce a total of one trillion gametes, one million of which would be diploid. Among these million diploid gametes, one would be expected to be fertilized by a diploid male gamete giving rise to a tetraploid offspring. Thus, even with the assumption of this unrealistically low rate of diploid gamete production, a tetraploid would be produced by such a population in every generation. In the case of a tetraploid capable of self-fertilization or of vegetative reproduction, the production of even one individual could result in a new type of organism getting established.

However, actual rates at which diploid gametes occur are far higher than assumed in the example (see citations listed in Note 913). In a broad survey of plants, Ramsey and Schemske (1998) found the mean frequency of diploid gametes produced by non-hybrid individuals was 0.56 percent (about one gamete in 200).[a] Applying this rate in the example just given would give $0.0056 \times 10^{12} = 5.6 \times 10^{9} =$ 5,600,000,000 diploid eggs. Under the assumption that 0.56 percent of the male gametes were also diploid, 0.56 percent of these 5,600,000,000 diploid eggs would be fertilized by a diploid male gamete. That is, $0.0056 \times 5{,}600{,}000{,}000 = 31{,}360{,}000$ tetraploid offspring would be produced in every generation. This is a very large number indeed.

Moreover, hybridization greatly promotes the formation of diploid gametes. Ramsey and Schemske (1998) say that in studies of hybrids the mean reported rate of diploid gamete production was 50-fold greater (27.52%) than in non-hybrids.[b] In fact, unreduced gametes are often the *only* functional ones in hybrids produced by interbreeding between distinct chromosets.[914] We have already encountered two examples of this phenomenon (*Tripsacum dactyloides* × *Zea mays:* p. 92; *Brassica oleracea* × *Raphanus sativus:* p. 94). In hybrid populations the union of unreduced gametes must therefore be rampant and the production of polyploids by the union of such gametes must surely be accordingly amplified. In some hybrid zones polyploids are, no doubt, produced en masse on an ongoing basis. Indeed, in recent years it has been empirically verified that many polyploids are derived from their progenitors repeatedly via separate polyploidization events producing separate polyploid

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[a] The gene 'elongate' on maize (*Zea mays*) Chromosome 3 increases the number of diploid eggs produced (Alexander 1957; Rhoades 1956).

[b] Harlan and deWet (1975) list 68 genera in which functional diploid gametes were produced by F_1 diploid hybrids.

individuals. For example, in the border region between Washington and Idaho, over a 50-year period, two types of tetraploid goatsbeard, *Tragonopagon mirus* and *T. miscellus,* probably formed, respectively, on 12 and 20 separate occasions.[915] Hedrén et al. (2001: 1868) say this appears to be a general pattern.

Many polyploids produced by the union of unreduced gametes would get established as new forms even if they were obligate outcrossers (i.e., organisms capable of reproducing by sex, but incapable of self-fertilization, agamospermy, or vegetative reproduction). Consider the example of the hypothetical tetraploid just given. Such tetraploids are normally quite fertile since they have fully paired karyotypes. In that example we saw many such tetraploids were produced. These could interbreed to produce a line of descendants. Moreover, new tetraploid individuals of this sort, and their karyotypically identical tetraploid descendants, normally produce hybrids of low fertility when they backcross with either of their diploid parents.[916] They would thus have no tendency to be swamped out of existence by interbreeding with their initially more numerous parents. Only when fertilized by others of their own kind would they produce significant numbers of fertile offspring. In this way they could maintain themselves as a new stable chromotype and, presumably, as a new somatype as well.

Appendix C: *Zygotic Doubling*

Zygotic doubling is an additional way in which polyploidy can arise. This mode, which is less common in a natural setting than either of the two other main ways of producing polyploids (i.e., somatic multiplication and the union of unreduced gametes), involves a doubling of the chromosome number in the zygote. All reported cases of zygotic doubling seem to involve artificial processes (e.g., exposure to chemicals, heat and cold shock, and hydrostatic pressure). While similar conditions to those used to artificially induce doubling are no doubt found at times in a state of nature, this mode of polyploidization is poorly known in a natural setting and requires further investigation to assess its significance.

For example, maize zygotes exposed 24 hours after pollination to 40˚C produced 1.8 percent tetraploid and 0.8 percent octoploid seedlings.[917] Dorsey (1936) obtained similar results by heat shocking rye (*Secale*), wheat (*Triticum*), and rye-wheat hybrids. Polyploidy has also been induced by this means in many other plants, as well as in fungi, insects, amphibians, and fish by various combinations of heat shock, cold shock, chemical treatment, radiation, centrifugal force, and hydrostatic pressure[918].

Astaurov (1936, 1957, 1967a, 1967b) used an artificial process of this sort to create a parthenogenetic silkworm. He subjected unfertilized domestic silkworm (*Bombyx mori*) eggs to a temperature of 46˚C for 18 minutes and then treated them with hydrochloric acid. Individuals developing from such eggs are almost exclusively parthenogenetic tetraploid females. Hybridization is often used in conjunction with physical inducers of polyploidy such as those just mentioned.[919] For example, Astaurov went on to produce a sexual derivative by (1) crossing his new tetraploid with wild silkworm males (*B. mandarina*); (2) fertilizing triploid eggs from the resulting hybrid with haploid sperm from *B. mori* to produce a fertile sexual tetraploid. Since this new form was reproductively isolated from its parents, Astaurov claimed it should be treated as a species and named it *B. allotetraploidus.*[920]

Appendix D: *Rates of Aneuploid Production*

It is hard to assess just how often new forms arise via the addition or deletion of individual chromosomes. Series of related aneuploid forms are known among plants.[921] The members in such series are believed to be derived from each other by individual aneuploid steps. For example, in the genus *Crepis,* four different chromosome numbers (n = 3, 4, 5, and 6) occur.[922] Distinct forms within the genus therefore often differ with respect to chromosome number. Kim (1992) says aneuploids resulting from a decrease in chromosome number are more common among plants than are those resulting from an increase.

But among animals, viable aneuploids seem more often to result when chromosomes are added and when the chromosomes involved in the change are small.[923] Viable autosomal trisomies have long been known in the mouse.[924] Chickens with extra copies of certain small chromosomes are viable.[925] Such is the case, too, with Down's syndrome in which affected individuals have three copies of Chromosome 21 ("trisomy 21"), one of the smallest human chromosomes. However, Shoffner et al. (1979) describe a viable F_2 hybrid, from the cross *Anser rossii* × *A. canagicus* (Emperor goose × Ross's goose), that was trisomic for its largest chromosome. Also, Mayr et al. (1985) report that a calf trisomic for chromosome 21, one of the medium-sized bovine chromosomes, was viable.

Not every type of organism can produce new forms by simply adding or deleting individual chromosomes. Nor, in the case of those that can, is the production of viable aneuploid offspring possible for every chromosome. In the human case, addition or deletion of most chromosomes is lethal. Individuals with only a single copy of any human autosome die before birth.[926] Down's syndrome is the only human trisomy involving an autosome that results in viable individuals who normally reach maturity.[927] Recall that an autosome is any chromosome other than a sex chromosome (viable sex-chromosome aneuploids also occur in humans[928]). But the overall frequency at which new forms are produced by such processes is poorly known.

Appendix E: *H. J. Muller and Polyploidy*

Primarily because of the claims of H. J. Muller, many biologists have believed animal polyploids must be rare. Muller (1925) asserted that polyploidy could not have a relevant role in the evolution of sexual animals because chromosomal duplication would be incompatible with animal sex-determination mechanisms. This argument is flawed in at least four ways. First, as Westergaard (1940, 1958) and Stebbins (1950) pointed out, Muller's argument is based on the presumption that the sex-determining mechanism of fruit flies (*Drosophila*), which depends on the ratio of the number of X chromosomes to autosomes (i.e., chromosomes other than the X and Y), is typical for animals as a whole. Such is not the case. A Y-dominant system, where sex is determined by the presence or absence of a Y chromosome is more usual.[929] But a variety of additional sex-determination systems exist among animals besides the two just mentioned. Even mammals do not always have standard X-Y sex determination. For example, Sharp and Hayman (1981) note that male swamp wallabies (*Wallabia bicolor*) have two Y chromosomes. Most turtles and all crocodiles have no sex chromosomes and sex is determined by egg incubation temperature, not chromosomes.[930] Indeed, as Mable (2004: 454) points out, "In reality, little is known about the factors that control sex determination in the vast majority of dioecious organisms."

Second, in certain categories of animals sex chromosomes are not well differentiated.[931] Such is the case, for example, among lizards,[932] and many polyploid lizards of hybrid origin have been reported.[933] Bogart (1980: 361) states that "of all the polyploids and possible ancestors [of those polyploids] in amphibians and reptiles, only *Cnemidophorus tigris* seems to have discernable sex chromosomes." White (1973a: 586) notes that sex chromosomes are lacking in the salamander families Cryptobranchidae and Hynobiidae, both of which are characterized by high chromosome numbers (which is consistent with the idea that the members of these families are polyploid).[934]

Third, as Stebbins (1950: 367) points out, the tetraploid plant "*Melandrium* *dioicum* ... has long been known to possess a typical X-Y sex-determination mechanism, with the male as the heterozygous sex." Muller (Muller 1925: 351) said his explanation predicted that such plants would not be found. It is now known that heteromorphic sex chromosomes are in fact found in a number of plant groups.[935] Moreover, many animals do not reproduce sexually, particularly invertebrates. Even Muller (1925: 352) granted that "amongst groups of animals like earthworms and fresh-water snails, which are normally hermaphroditic, tetraploidy or even higher forms of polyploidy might occur as readily as amongst most plants." Judging from available reports, it seems that polyploids of hybrid origin are fairly common among invertebrates as well as in vertebrates, among fish, amphibians, and reptiles, but rare among birds and mammals.

Fourth, there have been many more studies of polyploidy in plants than in animals. Even sixteen years after Muller's paper Fankhauser (1941: 507) commented that

> Spontaneous deviations from the normal somatic chromosome number have been investigated extensively in populations of plants, partly because of the ease with which the chromosome number of each individual may be determined in root-tip preparations. Comparatively little information is available concerning the range and frequency of such aberrations among mammals.

Even in those cases where changes in chromosome number were in fact studied in animals, the interest was in connection with embryological and developmental effects, not evolution and breeding.[936] Thus, it appears Muller presumed polyploidy was rare in animals because reports, especially ones bearing on the origin of new animal forms through polyploidization, were rare at the time he wrote. But reports could not possibly have been common in 1925 since adequate technology to carry out the necessary studies was not yet available. Given evidence now available, it appears polyploidization is far more important in animal evolution than Muller supposed.

Appendix F: *Recombinational Stabilization: Theory*

Verne Grant was once the most prominent proponent of the idea that recombinational stabilization from interchromoset matings might be a frequent source of new types of plants. However, he ultimately concluded (e.g., Grant 1981: 269–270) that such events are rare in a natural setting. However, he appears to have left the effects of spatial and stochastic factors out of account. McCarthy et al. (1995), who conducted computer simulations of recombinational stabilization, did take such factors into account. These studies suggest that, in large hybrid populations, the occurrence of such events is almost inevitable over evolutionary time.

These simulations provided an important insight, that is, the production of such recombinant derivatives can be viewed as a single statistical event. In any one generation, in any one small portion of a hybrid zone, the complex series of matings leading to the emergence of a new recombinant derivative is an unlikely event. But from a statistical, stochastic perspective, each new generation is a new random trial. So is each new portion of the hybrid zone. So the statistics of recombinational stabilization are those of a random trial repeated a huge number of times. Under such circumstances, as any statistician knows, the probability of a positive outcome approaches unity as the number of trials becomes very large. Somewhere, sometime enough individuals of the recombinant type happen to occur in the same vicinity and mate. As a result, more individuals of that type are present in that vicinity in the next generation, further increasing the probability that individuals of the recombinant type will mate and produce more of their own kind. This amplifying cycle results in the recombinant type getting established as a new form.

However, the results of these simulations published in McCarthy et al. (1995) have been misrepresented in recent publications. For example, Mavárez et al. (2006: 868) say, “Homoploid hybrid speciation [i.e., the production of a new stable recombinant derivative]—hybridization without change in chromosome number—is considered very rare. This has been explained by the theoretical prediction that reproductive isolation between hybrids and their parents is difficult to achieve.” In support of the second of these two quoted statements, they cite McCarthy et al. (1995), which does not contain or imply any "theoretical prediction" that supports this assertion. Indeed, in summarizing the results of our theoretical work on the subject we specifically stated (ibid: 509) our results indicate the stabilization of recombinant derivatives of interchromoset matings

> is a workable mode of evolution, not only in the laboratory but also in nature. So long as the sterility of the hybrids is not absolute, the potential exists for the rapid reassortment of entire chromosomes into novel combinations whenever the new combination is advantageous. In this way, natural selection is able to exploit the rich genetic variability of the typical hybrid zone.

Clearly, this is no prediction that such events are rare. Coyne and Orr (2006: 341) said our model (i.e., McCarthy et al. 1995) ignored most ecological aspects. This is unfortunate," they say,

> since, as Grant (1981: 251–253) emphasized, a new hybrid type might be partially or fully isolated from its parental species by 'external' or ecological factors. If a new hybrid genotype can, for instance, occupy a habitat in which the parental species are fairly unfit, its chances of survival increase.

This criticism neglects an important point—the stabilization of a new recombinant derivative from interchomoset matings relies on a type of isolation that is "internal." Such a derivative differs from its parents with respect to structural rearrangements. Therefore matings of derivative individuals with either of the parental types result in structurally heterozygous offspring. Such is the case in any environment, no matter what the ecological factors might be. This is why McCarthy et al. left ecological factors out of their model. We wished to evaluate whether processes of this sort could effectively produce stable derivatives even when they were not favored by an environmental advantage. Obviously, if the process works in a given situation where the derivative is not assumed to have an environmentally based advantage, it will work all the better when actually given such an advantage. However, the important finding of our study was that stabilization could occur *even when no such advantage was assumed*. There is no need to assume the existence of "an ecologically novel (and initially empty) habitat" as Coyne and Orr (2006: 341) imply.

There are statements in Buerkle et al. (2000) that may have caused Mavárez et al. (2006) and Coyne and Orr (2004) to misunderstand the predictions of theory as they are expressed in our paper (i.e., in McCarthy et al. 1995). Buerkle et al. (2000: 443) say the McCarthy et al. model "described conditions that favour a special case of recombinational speciation [i.e., of the process of stabilization of a new recombinant derivative derived from interchromoset matings], one in which a novel species is generated but both parental species become locally extinct" and that our model predicts a "complete genetic merger" of the parental populations. They go on to say that in most cases where such processes have been documented "the parental types continue to coexist with the derived hybrid species." Gross and Rieseberg (2005: 243) make a similar statement. Coyne and Orr cite Buerkle et al. (2000) to make the statement that "with weak ecological selection, hybrid speciation almost never occurred, while with strong ecological selection it occurred in 20% of simulation runs. Most important, in all cases the novel hybrid genotype was successfully established—and persisted for many generations—without extinction of either parental species." These are distortions of our findings. The implication is that the process as modeled by McCarthy et al. is a rare, special case, and that their own version of the model (which is actually a special case of our original model) better represents naturally occurring processes.

However, in order to focus on the early stages of the process, McCarthy et al. modeled only *a very small portion of the interface region between two hybridizing populations*, the region where the new recombinant derivative first arises. We were only interested in evaluating whether a recombinant derivative derived from interchromoset mating could get established in a small area within a hybrid zone. We did not evaluate how far or under what circumstances it would spread to other regions. Thus, it is true that the new recombinant derivatives in our model typically displaced the parental types. It also true, however, that our results, based on the tiny space that we modeled, in no way imply that the parental forms are driven to extinction elsewhere.

Referring to our model, Rieseberg (1997: 368) says "it seems unlikely that the hybrid genotypes would be more fit than the parentals in all habitats in the hybrid zone." Such an assumption would seem unlikely indeed—if we had made it. But we didn't. Rieseberg apparently misunderstood our model. We only assumed hybrids were at an advantage within the small portion of the zone being modeled. Moreover we only assumed one particular recombinant derivative was at an advantage, not all hybrid types that could be derived from the cross. Indeed, when we included in our simulations regions (within the small portion of the zone being modeled) where the new recombinant derivative was at a disadvantage versus the parental types, the derivative did not spread into those regions. But we did not publish these results since we deemed them self-evident. We merely wanted to see whether recombinant derivatives of interchromoset matings could get established and, if so, to investigate what factors were conducive to them doing so. To get established a new recombinant derivative has to occupy an initial limited territory.

Buerkle et al. (2000) do differ somewhat from McCarthy et al. (1995) with respect to the particulars they claim to be conducive to the this process. Nevertheless, they reach conclusions similar to those already reached in McCarthy et al. with regard to the general feasibility of the process. Thus, they (ibid: 450) note that the model can indeed lead to the production of a new stable recombinant derivative reproductively isolated from its parental forms. In fact, in McCarthy et al. the recombinant derivative is *always* reproductively isolated (at least partially so) because, in matings with both parental types, it produces structurally heterozygous hybrids of reduced fertility.

Neither of the two most cited theoretical papers on the topic (Buerkle 2000 and McCarthy et al. 1995) make any theoretical prediction that this process is rare. Nor do they suggest that "reproductive isolation between hybrids and their parents is difficult to achieve." In fact, the prediction made in our study is quite the contrary. There are additional misunderstandings of our model. For example, Coyne and Orr (2004) state that recombinational stabilization "is more likely if it is fast: if stabilization of a recombinant genotype that is also reproductively isolated from both parentals required, say, a thousand generations, speciation would probably not occur." This claim is inconsistent with the actual mathematics associated with the stabilization of recombinant derivatives. Thus, suppose p is the probability that the stabilization of recombinant derivative begins in any particular generation X. Further call such a beginning the "initiation of a transition." Then X, the number of generations to the initiation of a transition, is a geometric random variable with mean $E(X) = 1/p$. And the probability that k generations will be needed to initiate one transition is

$$\Pr(k=X) = p(1 - p)^{k-1}$$

In the quotation above, Coyne and Orr say that if stabilization of a recombinant derivative took "a thousand generations, speciation would probably not occur." However, if the mean expectation of the time to transition were 1000 generations, we would have $E(X) = 1/p = 1000$, which implies that $p = .001$. The probability that k generations or less would be needed to initiate a transition would therefore be

$$1 - (1 - p)^k = 1 - (1 - 0.001)^{1000} = 1 - 0.999^{1000} \approx 1 - 0.3677 = 0.6523.$$

In other words, if the expected time required to initiate a transition were 1000 generations, then such a transition would be more likely than not to initiate sometime during the first 1,000 generations. The actual probability would be 0.6523. So the probability that initiation would occur sometime subsequent to 1,000 generations would be 0.3477. Note, too, that as k approaches infinity, $1 - (1 - p)^k$ approaches one. This is true for any value of p such that $0 < p \leq 1$. Therefore, from the standpoint of probability theory, the initiation of a transition becomes a mathematical certainty as the number of generations increases without bound. In ordinary language then, given the passage of a very large number of generations, we expect a transition to initiate even when the probability of its initiation in any given generation is very small. So Coyne and Orr's assertion is mistaken.

Finally, it should be mentioned that certain authors (Rieseberg 1997; Coyne and Orr 2004: 350) have suggested our theoretical study (McCarthy 1995; McCarthy et al. 1995) showed inbreeding was somehow essential to stabilization of the recombinant derivative and that selfing was essential. Granted, all other things being equal, the model suggested a higher selfing rate increased the probability of producing a stable derivative, but this is the effect of only one variable (selfing rate), when all other relevant variables are held constant. True, all other things being equal, high selfing rates among the hybrids make the production of recombinant derivatives much more likely. However, since (1) outcrossing is a heritable trait, and (2) hybridization cannot occur in the absence of outcrossing, one does not expect most hybrid populations to have high selfing rates. Therefore, since most hybrid populations will be composed of outcrossers, one expects many recombinant derivatives also to be outcrossers.

Moreover, in McCarthy et al. (1995) Figure 5 indicates that transitions do occur (after many generations) when the selfing rate, $s = 0$, that is when outcrossing is obligate. The graph indicates this for a fitness advantage of $\alpha = 2.0$ (transitions also occurred for lower values of α, but this is not indicated due to vertical truncation of the graph). In general, the results can be interpreted as indicating that in a strictly outcrossing population transitions will occur, but at rare. This is true whether the advantage of the recombinant derivative over the parental types is marked or not (only when the advantage is more marked transitions will occur less rarely). This finding should not be interpreted as a conclusion that outcrossing recombinant derivatives should be rarer than selfing ones. Instead, it should be seen for what it is: our computer simulations produced a pattern where there are typically long periods of stability punctuated by rare events where a new type suddenly appears. This model therefore provides a genetic explanation of the pervasive pattern seen in the fossil record itself where the typical fossil form is stable for millions of years and the advents of new forms are sudden, very rare events.

Appendix G: *Underreporting of Hybridization*

There is good reason to believe that underreporting of hybridization is widespread. That is there are probably many types of hybrids that do occur, but that have not yet been reported. In addition, many other natural hybrids that are reported are probably more common than generally supposed. Various factors contribute to this underreporting.

In many cases, hybrids are common within a particular region (the hybrid zone) but occur only rarely elsewhere (e.g., the already mentioned hybrids between the Black-headed and Rose-breasted grosbeaks). Surveys taking into account the entire ranges of the parental forms are therefore likely to convey the impression that hybrids are rare, when in fact they are common in regions where the parent types come into contact. On the other hand, although a new type of organism would be expected to arise within the confines of a hybrid zone, once established, it might spread far beyond the limits of the zone so that it would no longer be possible to infer its connection with its parents can no longer be inferred on the basis of spatial distribution. It is known that many natural allopolyploids have ranges larger than those of their parents.[937] Under such circumstances it might not occur to an investigator that the organism in question was of hybrid origin. The possibility might therefore go uninvestigated.

Short and Robbins (1967: 542) assert that "the remarkable appearance of intergeneric [avian] hybrids renders them more likely to be noticed by collectors and banders than the usually less obvious hybrids between congeneric species." In other words, hybrids between very distinct parents are often very obvious. But the kind of hybrids that probably occur most frequently, those between similar somatypes, are more difficult to detect and therefore less likely to be reported.[938] For example, Clausen et al. (1945) note that the allopolyploid Townsend's cordgrass (*Spartina townsendii*) has been mistaken for both of its parents, smooth cordgrass (*S. alterniflora*) and small cordgrass (*S. maritima = S. spartina*). They also say a figwort known as Plumas County beardtongue (*Penstemon neotericus*) has been confused with both of its parents, mountain blue penstemon (*P. laetus*) and azure penstemon (*P. azureus*). Similarly, Short and Horne (2001: 453) state that two birds, the Thick-billed and Lesser honeyguides (*Indicator conirostris* and *I. minor*), are so similar that hybridization is hard to detect. Hybrids between the similar Eastern and Western meadowlarks (*Sturnella magna* and *S. neglecta*) are another example.[939] This difficulty probably accounts, at least in part, for the lack of reported hybrids in certain taxonomic categories. Thus, according to Holyoak (2001), the dearth of reports of hybridization among caprimulgids (nighthawks, whip-poor-wills, etc.) may simply result from difficulties in recognizing hybrids between birds that are themselves often hard to distinguish.

Despite the fact that most hybrids are intermediate in appearance, those from certain crosses closely resemble one parental form, even when those forms greatly differ. One hybridizer of begonias (Brilmayer 1960: 188) notes, for example, that wax begonias *Begonia semperflorens* (familiarly known as "semps"), "are such forceful parents that, no matter what other type they are crossed with, the result is another, even though slightly different, semp." Stebbins (1950: 309) notes that some hybrids "may resemble one or the other of their parental species so closely that they have not been recognized as distinct by systematists." He gives as an example *Nasturtium microphyllum,* which so closely resembles ordinary watercress, *N. officinale,* that it was thought to be an autopolyploid form. However, Stebbins (ibid) states that it is now thought to be a hybrid between *N. officinale* and some species of a different but related genus, *Cardamine.* He also mentions (ibid) *Madia citrigracilis,* which he says "was at first thought to be a form of *M. gracilis,* but later … was synthesized artificially via the triploid hybrid between *M. gracilis* and the very different diploid species *M. citriodora.*" Clausen et al. (1945) list a variety of plant hybrids that have been confused with their parents due to similar morphology. Grant (1981: 304) notes that many similar examples have been added since 1945, and that "this pattern of variation can be said to be a common one." An example among birds is the population on Mangere Island, New Zealand, which was thought to be the only extant population of Forbe's Parakeet (*Cyanoramphus forbesi*). Using genetic techniques, Chan et al. (2006) showed that at least 81 percent of the birds in that population are hybrids between Forbe's Parakeet and the Red-crowned Parakeet (*C. novaezelandiae*), even though many of the birds in the population appeared to be *C. forbesi* on the basis of morphology. Another example is the hybrid between Egyptian Goose (*Alopochen aegyptiacus*) and the Ruddy Shelduck (*Tadorna feruginea*) Finn 1907: 18) says this not uncommon hybrid is very similar to *T. ferruginea* and that "the very marked characteristics of the Egyptian goose disappear almost completely except in [the pink color of] the legs." It may well be that this phenomenon, of F_1 hybrids looking almost identical to one of their parents, is itself underreported since such hybrids would only be detected if their parentage were known. Who knows how many hybrids masquerade as pure individuals in this manner?

In crosses producing partially fertile hybrids, backcross hybrids are often highly similar to the parental type to which the backcross occurs. As Stebbins (1950: 310) notes, if "a polyploid has originated from hybridization between two closely related species, with chromosomes partly homologous to each other, some derivatives of this polyploid may be hardly distinguishable from autopolyploids of one or the other parental species. And if through backcrossing, such a polyploid acquires a preponderance of genes derived from one or the other of the parental species, it may fall entirely within the range of variation of the latter" (such misclassification is especially likely given the fact that hybrid specimens are often mistakenly used in defining the range of variation characteristic of their pure parents). When hybrids between Long-tailed Finch (*Poephila acuticauda*) and Black-throated Finch (*P. cincta*) backcross to either parent, the resulting hybrids are almost identical to that parent.[940] Many animals that appear on the basis of their morphology to be pure American bison (*Bison bison*) contain a significant percentage of cattle nuclear genes.[941] The Black-throated Green Warbler (*Dendroica virens*) and Townsend's Warbler (*D. townsendi*) hybridize in southwestern Canada (Alberta). Dunn and Garrett (1997: 305) say genetic analysis showed a bird was hybrid even though it "was exactly identical to Townsend's in appearance."[a,b] Vallender et al. (2007) genetically analyzed 48 birds with plumage identical to that of a Golden-winged Warbler (*Vermivora chrysoptera*). They were taken from a region where Golden-winged Warblers regularly hybridize with Blue-winged Warblers (*V. pinus*). Of the

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[a] The Townsend's Warbler hybridizes, too, with the Hermit Warbler (*Dendroica occidentalis*) in Washington State (U.S.). Rohwer et al. (2001) found that throughout a 2,000 km coastal strip to the north, birds that look like pure Townsend's warblers are for the most part cytoplasmically hybrid (i.e., they have Hermit Warbler mtDNA). In many types of crosses, backcross hybrids are more fertile and thus more likely to backcross again to the same parent, so that their progeny will be even more similar to that parent, and so forth. Such hybrids can be very hard to identify.

[b] Insensitive techniques often result in underreporting, too. Some genetic studies of hybrid zones suffer from poor experimental design. A sufficient number of markers must be used to prevent high rates of false negatives, especially in cases where later generation backcross hybrids occur (Arnold 1997). Thus, among hybrids of known parentage descended from matings between the Red-legged and Rock partridges (*Alectoris rufa* and *A. graeca*), Negro et al. (2001) found that six RAPD primers that produced 11 markers allowed detection of all F_1 hybrids and first backcrosses to Red-legged Partridge, and all but one hybrid among 18 second backcrossses, but only 18 out of 27 third backcrosses. If the same method were applied to evaluate birds in a hybrid zone many hybrid birds would be overlooked. Bensch et al. (2002) found similar a problem in studies of specimens from the Pyrenees contact zone between two other birds, the Iberian and Common chiffchaffs (*Phylloscopus brehmii* and *P. collybita*). A larger number of markers allowed detection of hybrids among birds previously believed, on the basis of song and mtDNA, to be pure parentals.

48 birds, seemingly pure on the basis of plumage, 11 (23%) turned out to be hybrids.

Many types of organisms are difficult to study because they breed in inaccessible habitats (e.g., tropical rainforests, remote islands, cliffs, the depths of the sea) or have habits that make them harder to investigate (e.g., are nocturnally active). Hybridization among such organisms, although it may occur frequently, would likely go unobserved. Many organisms are also poorly known because their diet makes them difficult to keep in captivity. Gramivorous birds (e.g., finches) are easily kept and have been extensively hybridized in captivity. In comparison, captive hybridization is very poorly studied for insectivores such as tanagers and wood warblers. In addition, many hybrids are observed, but not formally reported. For example, according to the Birds Australia Rarities Committee,[942] there are several "reliable, but unpublished reports" of hybrids in Australia between the Sooty and Pied Oystercatcher (*Haematopus fuliginosus* and *H. longirostris*).

Biologists working in the field or classifying specimens have tended to think of hybrids as very rare. But an observer does not look for something she does not expect to see. Over the years, then, many encounters with hybrids have likely gone unreported, written off as sightings of aberrant individuals or morphs. However, knowledge of avian hybridization is on the increase. Randler (1998, 2001b) suggests that a growing awareness of the existence of hybrids and improved identification literature have brought about the recent large increase in avian hybridization reports. Higgins and Davies (1996: 307) say certain new sandpiper hybrids lately reported probably reflect "increasing interest in plumages, hybridization and field identification of waders rather than changes in breeding habits and distribution." The common occurrence of hybridization in plants is now widely recognized, at least among botanists, agricultural breeders, and horticulturalists. Even today, though, it is not unusual to encounter the assumption that natural animal hybrids are so rare that they are unlikely to be seen. This attitude tends to prevent consideration, for example, that a collected specimen might be hybrid, or that a given type of organism might be of hybrid origin, and in the long run results in systematic reporting bias.

The writer's own experience with birders and ornithologists reveals that individual variation is often overlooked in the rush to classify specimens and sighted birds. While many hybrids are obviously intermediate between two types, many others not so exactly intermediate will end up classified as pure individuals of the type to which they tend. For example, two songbirds, the Tufted Titmouse and the Black-crested Titmouse (*Parus bicolor* and *P. atricristatus*), have a hybrid zone in the south central United States. A USGS website[943] notes that "there is a tendency for observers to specifically identify all titmice detected on routes in or near this hybrid zone." This predisposition to record hybrids as pure parentals guarantees underreporting. Dittman and Cardiff (2003: 12) say that although there may well be natural hybrids between Cave Swallows (*Hirundo pelodoma*) and Cliff Swallows (*Hirundo pyrrhonota*) "we will have to assume that birds of mixed-species colonies are 'pure' until demonstrated otherwise." One might well question why Dittman and Cardiff feel compelled to make such an assumption, particularly when they themselves point out that some individuals classified as Cliff Swallows may well be hybrids of this sort. Regarding this propensity of birders to overlook hybrids, famed ornithologist David Sibley remarks (1994: 164) "the human brain has a remarkable capacity to ignore glaringly inappropriate features while categorizing a bird based on other, more familiar, features. My experience is that an unexpected hybrid does not stand out at first glance."

In fact, there is a tendency for writers to talk of variation "within a species," even when much of the variation is known to be the product of hybridization with some other type of organism. For example, it is well known that most polyploids are derived from hybridization (see Chapter 5). But polyploids are often treated as conspecific with their diploid relatives, which obscures the fact that hybridization has occurred. Lewis (1980b) lists many examples. Kaufmann (1990) says that in the field hybrids between the Red-naped and Yellow-bellied sapsuckers (*Sphyrapicus nuchalis* and *S. varius*) can't be identified with certainty because "the parental forms are similar enough that a bird which seems intermediate could just be an extreme variant of one form or the other." Actually, since these two birds are in fact known to hybridize extensively (McCarthy 2006), any bird that seems intermediate is almost certainly a hybrid, not just "an extreme variant." However, in all those cases where hybridization between two types of organisms has not yet been recognized, this tendency to describe hybrids as extreme variants of one or the other of the parental forms will certainly obstruct recognition of the true situation and is bound to decrease the number of hybrids reported.

Appendix H: *Darwin's Assessment of Hybridization*

A careful reading of Darwin's writings other than the *Origin* shows that he did come to believe that hybridization is a significant source of variation and of new types of organisms. But at the same time it suggests that when the *Origin* was first published he had not yet come to believe hybridization had a significant role in breeding and that in the *Origin* he downplayed any significance he did see. One suspects also that, having had so much success with the initial editions of the *Origin,* he might have hesitated to incorporate new information and opinions on hybrids in later editions that would have contradicted views he had expressed in the first edition.

Certainly, he made conflicting statements regarding the significance of hybridization, just as he did regarding the meaning of *species,* and with respect to the importance of saltation. Thus, in the first chapter of the *Origin* (1859), Darwin strongly expresses the opinion that new types of organisms rarely arise through hybridization:

> When in any country several domestic breeds have once been established, their occasional intercrossing, with the aid of selection, has, no doubt, largely aided in the formation of new sub-breeds; but the importance of the crossing of varieties has, I believe, been greatly exaggerated, both in regard to animals and to those plants which are propagated by seed. In plants which are temporarily propagated by cuttings, buds, &c., the importance of the crossing both of distinct species and of varieties is immense; for the cultivator here quite disregards the extreme variability both of hybrids and mongrels, and the frequent sterility of hybrids; but the cases of plants not propagated by seed are of little importance to us, for their endurance is only temporary. Over all these causes of Change I am convinced that the accumulative action of Selection, whether applied methodically and more quickly, or unconsciously and more slowly, but more efficiently, is by far the predominant Power.[944]

So here he expresses the opinion that hybridization is of very little importance in producing new sexual forms. In a letter to Hooker dated July 13, 1856, he had also dismissed hybridization: "With respect to crossing, … I think you misunderstand me. I am very far from believing in hybrids: only in crossing of the same species or of close varieties." Also in the first chapter of the *Origin* he says:

> There can be no doubt that a race may be modified by occasional crosses, if aided by the careful selection of those individual mongrels, which present any desired character; but that a race could be obtained nearly intermediate between two extremely different races or species, I can hardly believe. Sir J. Sebright expressly experimentised for this object, and failed. The offspring from the first cross between two pure breeds is tolerably and sometimes (as I have found with pigeons) extremely uniform, and everything seems simple enough; but when these mongrels are crossed one with another for several generations, hardly two of them will be alike, and then the extreme difficulty, or rather utter hopelessness, of the task becomes apparent. Certainly, a breed intermediate between *two very distinct* breeds could not be got without extreme care and long-continued selection; nor can I find a single case on record of a permanent race having been thus formed.[945]

Here, too, he discounts hybridization, but only to the extent of dismissing the feasibility of producing a breed intermediate between two parent forms. He does, however, say the parents can be modified by hybridization. But in the eighth chapter he makes statements that seem directly to contradict the opinions just quoted. There he says

> A doctrine which originated with Pallas, has been largely accepted by modern naturalists; namely, that most of our domestic animals have descended from two or more aboriginal species, since commingled by intercrossing. On this view, the aboriginal species must either at first have produced quite fertile hybrids, or the hybrids must have become in subsequent generations quite fertile under domestication. This latter alternative seems to me the most probable, and I am inclined to believe in its truth.[946]

If this quotation were read alone and one had not seen those quoted before it, it would seem clearly to show that Darwin was convinced that intermediate breeds *can* be produced by hybridization. But the eighth chapter of the *Origin* is not a discussion of possible sources of natural variation. It is a single long polemic against the idea that God specially endows hybrids with sterility in order to keep the "species" immutable. Darwin introduced Pallas' doctrine, not to support the idea that breeds can be produced by hybridization, but to attack the idea of special endowment. Apparently, he failed to notice the inconsistency. For elsewhere, in his discussion of the probable sources of the variation on which natural selection acts, he makes no mention of Pallas. At the time of the first publication of the *Origin,* Darwin wrote Lyell and assured him that he largely discounted Pallas with regard to the production of new forms through hybridization. The passage in the letter, dated October 31, 1859, reads as follows:

> That you may not misunderstand how far I go with Pallas and his many disciples I should like to add that, though I believe that our domestic dogs have descended from several wild forms, and though I must think that the sterility, which they would probably have evinced, if crossed before being domesticated, has been eliminated, yet I go but a very little way with Pallas & Co. in their belief in the importance of the crossing [i.e., hybridization] and blending of the aboriginal stocks. You will see this briefly put in the first chapter.[947]

In a subsequent letter to Lyell (January 1865), Darwin continued to avow his belief that only the accumulation of minor variation was significant: "The more I work, the more I feel convinced that it is by the accumulation of such extremely slight variations that new species arise."[948]

And yet, it seems Darwin did in fact come to attribute more significance to hybridization. In a letter to Huxley dated December 22, 1866, at the time that he was completing work on *Variation of Animals and Plants under Domestication* (1868), Darwin confides "Now that I have worked up domestic animals, I am convinced of the truth of the Pallasian view of loss of sterility under domestication, and this seems to me to explain much."[949] In *Variation* he makes strong statements affirming the efficacy of hybridization in producing new breeds. For example, the following extended quotation from *Variation* shows that he was well aware that new breeds had been obtained from hybridization:

> There can be no doubt that crossing, with the aid of rigorous selection during several generations, has been a potent means in modifying old races, and in forming new ones. Lord Orford crossed his famous stud of greyhounds once with the bulldog, in order to give them courage and perseverance. Certain pointers have been crossed, as I hear from the Rev. W. D. Fox, with the foxhound, to give them dash and speed. Certain strains of Dorking fowls have had a slight infusion of Game blood; and I have known a great fancier who on a single occasion crossed his turbit-pigeons with barbs, for the sake of gaining greater breadth of beak.
>
> In the foregoing cases breeds have been crossed once, for the sake of modifying some particular character; but with most of the improved races of the pig, which now breed true, there have been repeated crosses,—for instance, the improved Essex owes its excellence to repeated crosses with the Neapolitan, together probably with some infusion of Chinese blood.[950] So with our British sheep: almost all the races, except the Southdown, have been largely crossed; "this, in fact, has been the history of our principal breeds."[951] To give an example, the "Oxfordshire Downs" now rank as an established breed.[952] They were produced about the year 1830 by crossing "Hampshire and in some instances Southdown ewes with Cotswold rams:" now the Hampshire ram was itself produced by repeated crosses between the native Hampshire sheep and Southdowns; and the long-woolled Cotswold were improved by crosses with the Leicester, which latter again is believed to have been a cross between several long-woolled sheep. Mr. Spooner, after considering the various cases which have been carefully recorded, concludes, "that from a judicious pairing of cross-bred animals it is practicable to establish a new breed." On the continent the history of several crossed races of cattle and of other animals has been well ascertained. To give one instance: the King of Wurtemburg, after twenty-five years' careful breeding, that is, after six or seven generations, made a new breed of cattle from a cross between a Dutch and a Swiss breed, combined with other breeds.[953] The Sebright bantam, which breeds as true as any other kind of fowl, was

> formed about sixty years ago by a complicated cross.[954] Dark Brahmas, which are believed by some fanciers to constitute a distinct species, were undoubtedly formed in the United States, within a recent period, by a cross between Chittagongs and Cochins.[955] With plants there is little doubt that the Swede-turnip originated from a cross; and the history of a variety of wheat, raised from two very distinct varieties, and which after six years' culture presented an even sample, has been recorded on good authority.[956]
>
> Until lately, cautious and experienced breeders, though not averse to a single infusion of foreign blood, were almost universally convinced that the attempt to establish a new race, intermediate between two widely distinct races, was hopeless "they clung with superstitious tenacity to the doctrine of purity of blood, believing it to be the ark in which alone true safety could be found." [Here, Darwin is quoting Spooner[957]] Nor was this conviction unreasonable: when two distinct races are crossed, the offspring of the first generation are generally nearly uniform in character; but even this sometimes fails to be the case, especially with crossed dogs and fowls, the young of which from the first are sometimes much diversified. As cross-bred animals are generally of large size and vigorous, they have been raised in great numbers for immediate consumption. But for breeding they are found utterly useless; for though they may themselves be uniform in character, they yield during many generations astonishingly diversified offspring. The breeder is driven to despair, and concludes that he will never form an intermediate race. *But from the cases already given, and from others which have been recorded, it appears that patience alone is necessary; as Mr. Spooner remarks, "nature opposes no barrier to successful admixture; in the course of time, by the aid of selection and careful weeding, it is practicable to establish a new breed." After six or seven generations the hoped-for result will in most cases be obtained; but even then an occasional reversion, or failure to keep true, may be expected.*[958] [italics added]

The final, italicized passage makes his attitude clear. Here, in *Variation,* he is saying new breeds can in fact be produced by hybridization. This claim directly contradicts the views he expresses in the first chapter of the *Origin,* to the effect that new breeds cannot be obtained in this way. Indeed, on the next page Darwin asserts that

> the several kinds of dogs are almost certainly descended from more than one species, and so it is with cattle, pigs and some other domesticated animals. Hence the crossing of aboriginally distinct species probably came into play at an early period in the formation of our present races. From Rutimeyer's observations there can be little doubt that this occurred with cattle; but in most cases one form will probably have absorbed and obliterated the other, for it is not likely that semi-civilised men would have taken the necessary pains to modify by selection their commingled, crossed, and fluctuating stock. Nevertheless, those animals which were best adapted to their conditions of life would have survived through natural selection; and by this means crossing will often have indirectly aided in the formation of primeval domesticated breeds.[959,a]

Of the origin of dogs, elsewhere in *Variation* he says

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[a] In the same place, Darwin (1868: vol. II, 98, citing von Gärtner 1849: 553), also comments that "Gärtner has given five cases of hybrids, in which the progeny kept constant; and hybrids between *Dianthus armeria* and *deltoides* remained true and uniform to the tenth generation."

> From the resemblance in several countries of the half-domesticated dogs to the wild species still living there—from the facility with which they can often be crossed together—from even half-tamed animals being so much valued by savages, and from the other circumstances previously remarked on which favour their domestication, it is highly probable that the domestic dogs of the world have descended from two good species of wolf (viz., *C. lupus* [i.e., Grey Wolf] and *C. latrans* [i.e., Coyote]), and from two or three other doubtful species of wolves (namely, the European, Indian, and North African forms), from at least one or two South American canine species, from several races or species of the jackal, and perhaps from one or more extinct species.[960]

So in *Variation* Darwin clearly affirms the idea that new breeds can be produced by hybridization. In his own words, "patience alone is necessary."

To some extent, it seems Darwin's contradictory statements can be attributed to his changing attitudes on hybridization. In an 1862 letter to Hooker, Darwin wrote: "I formerly thought with [i.e., concurred with] you about rarity of natural hybrids, but I am beginning to change."[961] In *Variation* (1868: vol. II, 110) Darwin strongly endorses Pallas' claim that fertility can recover during the establishment of a hybrid breed.

> The indirect evidence in favour of the Pallasian doctrine appears to me to be extremely strong. In the earlier chapters I have attempted to show that our various breeds of dogs are descended from several wild species; and this probably is the case with sheep. There can no longer be any doubt that the Zebu or humped Indian ox belongs to a distinct species from European cattle: the latter, moreover, are descended from two or three forms, which may be called either species or wild races, but which co-existed in a state of nature and kept distinct. We have good evidence that our domesticated pigs belong to at least two specific types, *S. scrofa* and *Indica,* which probably lived together in a wild state in South-eastern Europe. Now, a widely-extended analogy leads to the belief that if these several allied species, in the wild state or when first reclaimed, had been crossed, they would have exhibited, both in their first unions and in their hybrid offspring, some degree of sterility. Nevertheless the several domesticated races descended from them are now all, as far as can be ascertained, perfectly fertile together. If this reasoning be trustworthy, and it is apparently sound, we must admit the Pallasian doctrine that long-continued domestication tends to eliminate that sterility which is natural to species when crossed in their aboriginal state.

He even comments (1868: vol. II, 97) that he could have produced a stable hybrid breed himself if he had wished it:

> I crossed some Labrador and Penguin ducks, and recrossed the mongrels with Penguins; afterwards most of the ducks reared during three generations were nearly uniform in character, being brown with a white crescentic mark on the lower part of the breast, and with some white spots at the base of the beak; so that by the aid of a little selection a new breed might easily have been formed.

This method of breeding sounds surprisingly similar to the production of a new stabilized recombinant derivative (see Chapter 4). In *The Descent of Man* (1871), too, with regard to interbreeding of human races, he describes a process of this same sort:

> Whether a heterogenous people, such as the inhabitants of some of the Polynesian islands, formed by the crossing of two distinct races, with few or no pure members left, would ever become homogeneous, is not known from direct evidence. But as with our domesticated animals, a cross-breed can certainly be fixed and made uniform by careful selection in the course of a few generations, we may infer that the free inter-crossing of a heterogeneous mixture during a long descent would supply the place of selection, and overcome any tendency to reversion; so that the crossed race would ultimately become homogeneous, though it might not partake in an equal degree of the characters of the two parent-races.[962]

Thus, Darwin did come to attribute more significance to hybridization in his later years. His comments in later correspondence, and in later publications (other than later editions of the *Origin*) show that he came to view hybridization as a viable source of variation on which subsequent selection, particularly artificial selection, could act. He clearly thought new stable forms could be obtained from such a process, and that a hybrid population could "ultimately become homogeneous" under the influence of selection. However, his new views on the subject never gained significant expression in any edition of the *Origin,* his most widely read book. Certainly such ideas were never canonized among the dogmas of neo-Darwinian theory.

One of Darwin's greatest talents was his remarkable ability to assuage the ire of his opponents, which he accomplished in large part by his great personal charm. However, his desire to keep on good terms with others seems to have led him to shun certain controversial issues. The best-known example is the long delay between the publication of the *Origin* (1859) and his public admission of his belief that humans are descended from apelike ancestors (*The Descent of Man,* 1871). In the *Origin* his references to this idea were entirely oblique. There he limited himself to a single vague statement: "Light will be thrown on the origin of man and his history."[963] Lamarck (1809: 170) had long before described a process by which humans might have evolved from apes.[a] Mayr (1982: 352) says Lamarck presented his views on human origins "with far more courage than Darwin fifty years later in the *Origin.*"

Perhaps Darwin simply felt that altering later editions of the *Origin* to reflect his changed assessment of hybridization would have aroused unwanted opposition. It would be interesting to know whether he ever ran across Daniel Defoe's poem *The True Born Englishman* (1701) and considered hybridization in connection with his own origins:

Thus from a mixture of all kinds began,

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a. Even Linnaeus speaks of the apes as the "nearest relations of the human race" in *The Cousins of Man,* a work published long after his death (Lönnberg 1919). This shows that long before Darwin Linnaeus thought apes and humans were related by descent.

That het'rogeneous thing, an Englishman:
In eager rapes, and furious lust begot,
Betwixt a painted Britain and a Scot.
Whose gend'ring off-spring quickly learn'd to bow,
And yoke their heifers to the Roman plough:
From whence a mongrel half-bred race there came,
With neither name, nor nation, speech nor fame.
In whose hot veins new mixtures quickly ran,
Infus'd betwixt a Saxon and a Dane.
While their rank daughters, to their parents just,
Receiv'd all nations with promiscuous lust.
This nauseous brood directly did contain
The well-extracted blood of Englishmen.

Appendix I: *Stability of Sexual Chromosets*

Stabilization theory claims that the karyotype of a sexual chromoset remains stable because, relative to other members of a population otherwise composed of individuals with fully paired karyotypes, structural heterozygotes are at a severe reproductive disadvantage. For if an alteration in chromosome structure (structural rearrangement) did arise by mutation in a sexual chromoset, it would do so in a single gamete. When that gamete combined with another gamete to form a zygote, the individual that developed from that zygote would have one chromosome of the usual type paired with one showing the new structural arrangement and would therefore be structurally heterozygous. Such an individual would typically be far less fertile than those members of the population with fully paired karyotypes.

Whether a particular arrangement is, or is not, advantageous (from a reproductive standpoint) depends, then, not only upon the intrinsic genetic content of the affected chromosome(s), but upon whether the arrangement is common or rare in the population at large. In the absence of hybridization, new structural arrangements are extremely rare. As long as the original structural arrangement is the type found in the vast majority of the population, individuals having the new arrangement will be at a strong reproductive disadvantage. Because a new structural heterozygote would be 1) of low fertility and 2) would be exceedingly unlikely to find a mate having the same rearrangement because a *new* arrangement would be excessively rare—in fact, unique. Low fertility means there will be few offspring. The inability to find a "matching" mate means progeny will either be 1) homozygous for the old arrangement or 2) again heterozygous and so, again, of low fertility. Under such circumstances it is in no way likely that a homozygote for the new arrangement would ever arise, but even if it did, it would again face the same problem of finding a matching mate (and so would almost certainly produce heterozygous offspring of low fertility). Moreover, new arrangements arising in a non-hybridizing population would bear no new genes of any kind, let alone advantageous ones. So there would be no improvement in selective advantage. There would therefore be no selection for the new arrangement to help it get established in the population. Strong selection would be necessary to overcome the marked adverse effect of unpaired chromosomes on fertility. In consequence, it is not easy to see how the karyotype of one chromoset would be converted with time into the karyotype of a new chromoset, if the changes had to take place in a gradually evolving, isolated population (Key 1968). That is, there will be powerful selection for karyotypic stability.

This argument can be converted to the language of population genetics and take advantage of an established result: the original form of the chromosome is an “allele present at high frequency." The newly arising structural arrangement is an "allele present at very low frequency." The heterozygote has a lower fitness than either of the two possible homozygotes. The situation just described is termed *underdominant selection*. With underdominant selection, an allele initially present at an extremely low frequency will be eliminated from the population.[964] New structural arrangements will therefore be eliminated from a non-hybridizing population.

However, in intrachromoset hybridization, structural heterozygotes are often produced in millions, generation after generation. These heterozygotes, and their hybrid offspring, are spatially concentrated in the hybrid zone. Because they are spatially concentrated, the inbreeding among the hybrids is increased, which in turn increases the chances of producing small, local groups of individuals that are structurally homozygous for a new arrangement (and so can breed among themselves to stabilize the new arrangement). Such hybrids may possess new, advantageous gene combinations not present in either pure parent. If a karyotype specifies a new hybrid chromoset at an advantage relative to its two parents, spatial, stochastic computer simulations show the new karyotype can become established in the population despite the reproductive disadvantages inherent in structural heterozygosity, and can rapidly replace the parental karyotype.[965] On a geological timescale, this process of replacement would appear almost instantaneous (the hybrid zone between the new type an its parents would spread as a front, passing over, in just a few generations, any particular geographic site sampled by a paleontologist). The observed pattern would be one of long-term stability followed by an abrupt transition to the new type—the pattern actually observed in the fossil record for a wide variety of fossil forms.[966] When, however, this same computer simulation was altered so that 1) all individuals were identical (i.e., so that no hybridization was assumed) and 2) structural rearrangements were allowed to arise in the population at realistic rates, no new chromosets whatsoever were ever generated.[967]

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Notes

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1. *Sic et Non*.
2. Darwin (1859: 257).
3. Darwin (1859: 259-60).
4. Darwin (1859: 254).
5. Rendered by E. M. McCarthy.
6. Smith (1880: 34-35).
7. *The Revised English Bible with Apocrypha.*
8. King James Version.
9. Hutchins (1952k, p. 18b), Book II, line 852.
10. Hutchins (1952e: 304), Book XXI.
11. Fargard XIII. Translated in Zirkle (1935: 14).
12. Rendered by E. M. McCarthy.
13. *The Revised English Bible with Apocrypha* (9:12).
14. Book II, Ch. 46. Macaulay translation (1890).
15. Book III. Ch. 153, Hutchins (1952d: 122).
16. Book VIII, Ch. 28 (Hutchins 1952b, II: 132).
17. *The Revised English Bible with Apocrypha,* (13:15).
18. Book II (translation: W. E. Leonard 1921).
19. Book V (W. E. Leonard translation).
20. Hutchins (1952i: 381-382).
21. III, 46.
22. Hutchins (1952i: 5).
23. Book VIII, lxix.
24. Book VIII, lxi.
25. Morfill and Charles (1896).
26. V, 48. Translated by E. M. McCarthy.
27. I, v, 5.
28. II, 69. Scholfield (1958, vol. I)
29. White (1998).
30. Translated by E. M. McCarthy. Original Latin: "Gryphes vocantur, quod sit animal pennatum, et quadrupes. Hoc genus ferarum in Hyperboreis montibus nascitur. Omni parte corporis leones sunt; alis et facie Aquilis similes, et equis vehementer infesti. Nam et homines visos discerpunt."
31. Ch. II. Translated by E. M. McCarthy. Original Latin: "Mulum namque scimus, quia ex equa et asino promiscuum genus ducit, sicut e contra ex equo et asina burdo, voluptatem solere coeundi sine fructu appetere generandi."
32. Quoted in *Oxford English Dictionary* (*s.v.* kind, II, 10). Translated by E. M. McCarthy. Original Old English: "Ne forseoh þu næfre þine gecynd."
33. Wicklow was granted to Maurice Fitzgerald in 1174. Extract from: *Topographia Hibernica*, § II, xxi. Translated by E.M. McCarthy. Original Latin: "In partibus de Wikingelo, tempore quo Mauricius Giraldi filius terram illam et castrum obtinuerat, visus fuit homo prodigiosus, si tamen eum hominem dici fas est. Habebat enim totum corpus humanum praeter extremitates, quae bovinae fuerant. A juncturis namque quibus et manus a brachiis, et pedes a tibiis porriguntur, ungulas bovis expressas praeferebat. Caput ei sine crine totum; tam in occipite, quam anteriori parte, calvitio deforme; raras tantum lanugines per loca pro capillis habens. Oculi grossi; tam

rotunditate quam colore bovini. Facies oretenus subinde plana; pro naso, praeter duo narium foramina, nullam eminentiam habens. Verba ei nulla. Mugitum enim tantum pro sermone reddebat. Curiam hic Mauricii diu frequentabat; quotidie ad prandiam veniens, et quod ei dabatur ad vescendum, intra fissuras ungularum, quas pro manibus gestabat, stringens, ori apponebat."

34. Translated by E.M. McCarthy. Original Latin: "Onocentaurum autem vocari aiunt, eo quod media pars hominis species, media asini esse dicatur, sicut et hippocentauri; quod equorum hominumque in eis natura conjuncta fuisse putatur, Centauris autem species vocabulum indidit, id est hominem equo mistum, quos quidam fuisse equites Thessalorum dicunt, sed pro eo quod discurrentes in bello velut unum corpus equorum scilicet et hominum viderentur, inde centauros fictos asseverant. Porro Monocentaurum nomen sumpsisse ex tauro et homine, qualem bestiam inclusam dicunt fabulose in Labyrintho fuisse."
35. *Sancti Benardi opera,* Paris, 1690, Vol. I, p. 538, ch. xii. Translated in Allen (1888: 111).
36. Translated by E. M. McCarthy. Original Latin: "Hybrida dicitur qui nascitur ex ignobili matre."
37. *De Animalibus,* Ch. 8.
38. Hutchins (1952a: 371). Question LXXIII, i, 3.
39. Original Italian: E 'n su la punta de la rotta lacca l'infamia di Creti era distesache fu concetta ne la falsa vacca; e quando vide noi, sé stesso morse, sì come quei cui l'ira dentro fiacca.
40. Paré (4th ed., Ch. 25). Translated by E. M. McCarthy. Original French: "Du temps que le Pape Iules fcond fufita tant de malheurs en Italie & gu'il eul la guerre contre le Roy Louys douziefme 1512, laquelle fut fuyuie d'vne fanglante bataille donnee pres de Rauenne: peu de temps apres on veit naiftre en la mefme ville vun monftre ayant vne corne à la tefte, deux ailes, & vn feul pied femblable à celuy d'vn oyfeau de proye : à la ioncture du genoil un œil."
41. Bevington IV iv 79
42. Hutchins (1952d: 159b).
43. Hutchins (1952d: 213a).
44. Hutchins (1952c: 386).
45. In: *The History of Serpents.*
46. Marquette (1959). Translated by E. M. McCarthy. Original French: "Comme nous côtoyons des roches affreux pour leur hauteur et pour leur longueur; nous vîmes sur un de ces roches deux monstres en peintures qui nous firent peur d'abord et sur lesquels les sauvages les plus hardis n'osent pas arrêter longtemps les yeux; ils sont gros comme un veau. Ils ont des cornes en tête comme des chevreuils; un regard affreux, des yeux rouges, une barbe comme d'un tigre, la face a quelque chose de l'homme, le corps couvert d'écailles, et la queue si longue qu'elle fait tout le tour du corps passant par dessus la tête et retournant entre les jambes elle se termine en queue de poisson."
47. Marquette (1959). Translated by E. M. McCarthy. Original French: "Comme nous côtoyons des roches affreux pour leur hauteur et pour leur longueur; nous vîmes sur un de ces roches deux monstres en peintures qui nous firent peur d'abord et sur lesquels les sauvages les plus hardis n'osent pas arrêter longtemps les yeux; ils sont gros comme un veau. Ils ont des cornes en tête comme des chevreuils; un regard affreux, des yeux rouges, une barbe comme d'un tigre, la face a quelque chose de l'homme, le corps couvert d'écailles, et la queue si longue qu'elle fait tout le tour du corps passant par dessus la tête et retournant entre les jambes elle se termine en queue de poisson."
48. LXI, 319 (OED, *s.v. mule*).
49. Dicey (1863: vol. I, 298-209).
50. Darwin (1872, vol. I, 222).
51. *s.v. bastard.*

52. Burroughs (1918: 133).
105. Book I, line 1. Translated by E. M. McCarthy. Original Latin: "In nova fert animus mutatas dicere formas corpora."
106. Darwin (1859: 170).
107. Lovejoy (1936: 7).
108. Even Buffon (1749–1804: XIX, 20) was aware hybrids capable of producing offspring are usually not as fertile as their pure parents.
109. Plato used *genus* and *eidos* interchangeably. He never used *eidos* in the sense of a category subordinated to the category *genus* (Mayr 1982: 255).
110. *Metaphysics,* IV, 5.
111. First Part, Q. 84, Art. I. Quoted from Hutchins (1952a: 441).
112. Rickaby (1905).
113. Lovejoy (1936: 228); Mayr (1982: 158–159).
114. Mayr (1982: 159).
115. Quoted in Lovejoy (1936: 228).
116. First Part, Question 98, Art. 1; Hutchins (1952a: 517).
117. Woodward (1695: 246–247).
118. Goldsmith (1763).
119. Rousseau (1928).
120. Quoted (s.v. mule) in the *Oxford English Dictionary*.
121. Hutchins (1952h: 73).
122. *Encyclopedia Britannica* (1967: vol. XI, 921).
123. Trench (1846: 15).
124. Freeburg (1918: 166).
125. Cuvier et al., eds., (1839–1844: vol. IV, 4462). Translated by E. M. McCarthy. Original French: "Dans les espèces mixtes, c'est-à-dire dans celles des animaux qui, comme le mulet, proviennent de deux espèces différentes, il y a, comme dans les espèces pures, des degrés différents de fécondité ou plutót d'infécondité."
126. Schiede (1825). Lasch (1829) also listed naturally occurring hybrids.
127. *Fundamenta botanica* (No. 157, 1736). Translated by E. M. McCarthy. Original Latin: "Species tot sunt diversae quot diversas formas ab initio creavit infinitum Ens."
128. Larson (1968: 293–295).
129. Smith (1821: vol. II, 376).
130. i.e., *Oratio de Telluris habitabilis incremento* (1744).
131. Larsen (1968).
132. Larsen (1968: 295).
133. Fries and Hulth (1907–1922: vol. IV, 140). Translated in Larson (1968: 295). See also: Linnaeus (1756).
134. Fries and Hulth (1907–1922: vol. IV, 127). Translated in Larson (1968: 295).
135. Larsen (1968: 295).
136. Translated in Grant (1981: 245).
137. Translated in Zirkle (1935: 194).
138. Zirkle (1935: 194).
139. Von Hofsten (1958); Zimmermann (1953).
140. Darwin (1859: 254).
141. Quoted in Morton (1847: 271).
142. Translated in Elliot (1914: 39).

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143. See Kölreuter (1761-1766) and additional papers cited in Schiede (1825: 12).
144. Kölreuter (1761–1766) in *Ostwald's Klassiker der exakten Wissenschaften,* no. 35, p. 29. (1893, Leipzig: Wilhelm Engelmann). Translated by E. M. McCarthy. Original German: "So unwahrscheinlich es ist, dass von zwoen verschiedenen Gattungen von Thieren, die in ihrer natürlichen Freyheit gelebt, jemals ein Bastart erzeugt worden, so unwahrscheinlich ist es auch, dass bey der ordentlichen Einrichtung, die die Natur bey dem Pflanzenreiche gemacht hat, eine Bastartpflanze entstanden sey. Die Natur, die jederzeit, auch bey der grössesten scheinbaren Unordnung, die schönste Ordnung beobachtet, hat dieser Verwirrung bey den wandelnden Thieren ausser andern Mitteln hauptsächlich durch die natürlichen Triebe vorgebeuget, und bey den Pflanzen , bey denen ihre allzu nahe Nachbarschaft, der Wind und Insekten zu einer widernatürlichen Vermischung täglich Gelegenheit geben, wird sie denen davon zu besorgenden Wirkungen ohne Zweifel durch eben so sichere Mittel ihre Kraft zu benehmen gewusst haben. Vermuthlich sind es eben dieselben, die bey den Thieren, ausser den natürlichen Trieben, statt finden."
145. Callender (1988: 45-46).
146. Callender (1988: 46).
147. Gärtner (1849: 14-15). Translated by E. M. McCarthy. Original German: "Die Bastardbefruchtung wird noch in. neuester Zeit von mehreren Botanikern als Plan und Zweck der Natur betrachtet, besonders von solchen, welche glauben, dass artenreiche Gattungen nur auf dem Wege der Bastardzeugung haben entstehen können, wie Knight, W. Herbert, H. Lecoq, L. Reichenbach, u. m. a. [und mehere andere]. … Schon Kölreuter hat diese Hypothese bestritten, und es wird sich im weiteren Verlauf unserer Untersuchung über die Natur der Bastarde ergeben, dass das Wesen der reinen Art dieser Annahme widerspricht."
148. See: Stauffer (1987: 390).
149. Part 3, Ch. 5, Div. 1, p. 343.
150. Ray (1693: vol. I, 40). Translated by E. M. McCarthy. Original Latin: "Ut Plantarum numerus iniri possit, & earundum divisio rectè institui, oportet ut notas aliquas seu indicia specificæ (ut vocant) distinctionis investigemus. Nobis autem diu multúmque indagantibus nulla certior occurrit quàm distincta propagatio ex semine. Quæcunque ergo Differentiæ ex ejusdem seu in individuo, seu specie plantæ seminae oriuntur, accidentales sunt, non specifcæ. … Nam quæ specie differunt speciem suam perpetuò servant, neque hæc ab illius semine oritur, aut vice versa."
151. *An Essay Concerning Human Understanding* (Book III, Ch. 6, § 14).
152. Ibid (Book III, Ch. 6, § 13).
153. Stauffer (1987: 402).
154. Mayr (1982: 273).
155. Quoted in translation by Mayr (1942: 119).
156. Darwin and Seward (1903: 252).
157. Darwin (1872: xvi).
158. Quoted on Internet (ucmp.berkeley.edu/history/matthew.html).
159. Buffon (1749–1804: vol. IV, 384–386). Translated by E. M. McCarthy. Original French: "… l'âne ressemble au cheval plus que le barbet au levrier, et cependant le barbet et le levrier ne font qu'une même espèce, puisqu'ils produisent ensemble des individus qui peuvent eux-mêmes en produire d'autres, au lieu que le cheval et l'âne sont certainement de différentes espèces, puisqu'ils ne produisent ensemble que des individus viciés et

inféconds. … on peut toûjours tirer une ligne de séparation entre deux espèces, c'est-à-dire, entre deux successions d'individus qui se reproduisent et ne peuvent se mêler, comme l'on peut aussi réunir en une seule espèce deux successions d'individus qui se reproduisent en se mêlant."

160. Darwin (1859: 245).
161. Darwin (1909: 11).
162. *An Essay Concerning Human Understanding,* Book III, Ch. 6, 23.
163. Buffon (1749–1804: vol. XVI, xii). Translated by E. M. McCarthy. Original French: "Et qui sait tout ce qui se passe en amour au fond des bois? qui peut nombrer les jouissances illégitimes entre gens d'espèces différentes?"
164. Darwin (1909: 98).
165. McCarthy (2006).
166. Even Mendel (1866: 5) was aware of this difficulty. See (Mayr 1982: 712).
167. Darwin (1872, vol. I, 222).
168. Winker et al. (2007).
169. Cracraft (1983, 1989); Zink and McKitrick (1995).
170. Paterson (1985).
171. Winker et al. (2007).
172. Darwin (1887: vol. I, 88).
173. Darwin (1859: 44).
174. *An Essay Concerning Human Understanding,* Book III, Chapter 11, §25.
175. Winker et al. (2007).
176. Darwin had a long dispute with his friend, the botanist Joseph Hooker, over whether the primrose and cowslip should be treated as conspecific (Darwin maintained they should be treated separately). See Darwin and Seward (1903: vol. I, 252).
177. Sometimes it seems such choices are more a matter of local custom than anything more rational. Often researchers in different parts of the world will apply different criteria in classifying taxa even within the same class of organisms. For example, in speaking of related fern diploid-tetraploid pairs, Wagner and Wagner (1980: 208) note that "in the tropics—thus far at least—the tendency has been to treat the diploids and tetraploids as the same species, but in the temperate regions they are being treated increasingly as separate species or subspecies."
178. Thompson (1992: 1038) says fossils deformed under pressure within the earth have often been treated as distinct species from undeformed specimens of the same type: "A great number of described species, and here and there a new genus (as the genus *Ellipsolithes* for an obliquely deformed *Goniatite* or *Nautilus*), are said to rest on no other foundation."
179. McCarthy (2006).
180. Piálek et al. (2001: 615-616).
181. Translated by E. M. McCarthy. Original German: "etwas Complicirtes, Etwas, das nur als Wort eine Einheit ist."
182. *Novum Organum,* First Book, §43.
183. Translated by E. M. McCarthy. Original German: "diesem so vielfachen Dinge, für welches das Volk nur Ein Wort hat."
184. The following sources were used. *Mammals:* Duff and Lawson (2004); *Reptiles and amphibians:* MavicaNET (mavicanet.ru/directory/eng/1421.html); *Birds:* Sibley and Monroe (1990); *Fish:* Fishbase (fishbase.org/search.php?lang=English); Invertebrates: University of Michigan Museum of Zoology, Animal Diversity Web

(http://animaldiversity.ummz.umich.edu/site/); *Plants:* The International Plant Names Index (ipni.org/index.html) and the USDA Plant Database (http://plants.usda.gov/java/profile?symbol=SCPH).

185. Second Book, §29.
186. Barton and Hewitt (1985).
187. Gould (1993).
188. McCarthy (2006); Petitjean (1969).
189. Wishart et al. (1988: 1665).
190. Arnold (2006).
191. Anonymous (1979); Basrur (1969); Bonhomme et al. (1983, 1984); Carver and Taliaferro (1992: 136); Dawson (1965); Detlefson (1914: 11); Fedyk and Krasinska (1980); Lay and Nadler (1969); McCarthy (2006); Nijman (2003: 10); Pinter (1971); Sandnes (1957); Stauffer et al. (1997: 183); Stebbins (1969: 33); Verkaar et al. (2003: 565); von Gärtner (1849); Winter et al. (1988a, 1988b); Wishart et al. (1988); Zimmermann (1965); Zong and Fan (1988, 1989).
192. Anonymous (1979); Basrur (1969: 117).
193. Gray (1958: 91–92); see also Sandnes (1957).
194. Christopher et al. cite Sax (1929).
195. Stauffer (1987: 388).
196. Darwin (1859: 256).
197. Anderson (1949); Blair (1972); Christopher et al. (1991); Cleland (1962, 1972); Darwin (1859, 1868); Gärtner (1849); Gray (1958, 1972); Grant (1981); Harrison (1993); Harte (1994); Hawkes (1982–1983); Herbert (1837); Kawamura (1950b); Kölreuter (1761–1766); Lewis (1980a); Linnaeus (1756); McCarthy (2006); McCarthy (in prep.); Pandian and Koteeswaran 1998; Pinkava (1985); Reuther et al. (1968); Richards (1973); Sander (1947); Sander and Wreford (1961); Schultz (1980); Schwartz (1972); Soltis and Soltis (1992); Stauffer (1987: 388–462); Stebbins (1950, 1959, 1971); Syvanen and Kado (2002); Wagner 1954; White (1978).
198. Steffens et al. (1983).
199. For example, Hancock (1964); Lopyrin and Loginova (1953); Steklenev (1972).
200. Dain (1980); Moore et al. (1982).
201. Rockwell et al. (1961: 33).
202. Denis et al. (1987); Tucker et al. (1989).
203. Pinheiro et al. (1989) also report a female geep that was fertile in a backcross with a ram. Stewart-Scott et al. (1990) give an account of another geep, produced in New Zealand.
204. Rockwell et al. (1961: 33).
205. Anderson (1939); Antonius (1950); Chandley et al. (1974); Craft (1938); Gray (1972); Groth (1928); Lloyd-Jones (1916); Makino (1955); McCarthy (in prep.); Rong et al. (1985, 1988); Ryder et al. (1985); Smith (1939); Zong and Fan (1988, 1989). Although a complement of histologically normal oocytes are present in fetal female mules and hinnies, their stock of germ cells is severely depleted at birth (Benirschke and Sullivan 1966; Taylor and Short 1973).
206. For example, Wagner (1841: 33).
207. Stauffer (1987: 393).
208. Banaszek et al. (2000a); Basrur (1969: 117); Ching (1988); Clausen and Goodspeed (1925, Figs. 4–6); Close et al. (1996); Cole and Hollander (1950, Table IV); Ernst 1918; Fedyk and Krasinska (1980); Grubb (1981: 6); Gustafsson (1946: 102); Guyer (1900: 40,

1902); Kawamura (1950a: 69, 1952: 145); LaChance (1984); McCool (1990); Pala and Lissia-Frau (1966); Poddubnaya-Arnol'di (1982); Redi et al. (1984); Shrigley (1938, 1940); Shumov and Rubtsov (1981); Smith (1912a, 1912b); Steklenev (1983: 61, 62); Steklenev and Elistratova (1992); Stephan (1903); Swan (1985); Swan and Christidis (1987); Winter et al. (1988a, 1988b); Wishart et al. (1988); Yamashina (1943); Zhang and Duan (1991); Zong and Fan (1989).

209. Basrur (1969: 117); see also Anonymous (1979).
210. Ching (1988); Clausen and Goodspeed (1925), Figs. 4–6; Ernst (1918); Gustafsson (1946: 102); Mayr (1982: 643); Poddubnaya-Arnol'di (1982).
211. Poddubnaya-Arnol'di (1982).
212. Poddubnaya-Arnol'di (1982).
213. Darwin (1859: 266).
214. Tranah et al. (2004).
215. McCarthy (2006).
216. McCarthy (2006).
217. Mitchell (2000).
218. Gorman (1969).
219. Sibley (1994).
220. Brilmayer (1960: 188).
221. Brainerd (1924: 165).
222. Schultz (1989).
223. Darwin (1868: vol. II, 267).
224. Darwin cites Kölreuter, *Nova acta Academiae scientiarum imperialis petropolitanae* (1794: 391).
225. Darwin cites von Gärtner (1849: 507, 516, 572).
226. Wichura (1865).
227. See also: Lotsy (1915).
228. Hirayoshi and Nakamura (1943); Li (1987); Stebbins (1948, 1959).
229. Kushner and Kitaeva (1938b); Lakoza (1938); McCarthy (in prep.); Potts (2004); Tapper (1985).
230. Maksudov and Panchenko (2002: 199).
231. Stebbins (1969); Stebbins and Ferlan (1956).
232. Rockwell et al. (1961: 203–204).
233. Patrikeev et al. (2008: 44).
234. Darwin (1839: vol. III, 384–385).
235. Darwin cites Sageret (1826: 36, 28, 30).
236. Darwin cites *The Gardener's Magazine and Register of Rural & Domestic Improvement* (1832: vol. VIII, 52).
237. Darwin cites *Transactions of the Horticultural Society of London* (1814): vol. I, 25.
238. Darwin cites Chevreul (1846: 189).
239. Darwin cites Wiegmann (1828: 32, 33).
240. Darwin cites *The Gardener's Magazine and Register of Rural & Domestic Improvement* (1831: vol. VII, 696).
241. Darwin cites *The Gardeners' Chronicle and Agricultural Gazette* (1846: 601).
242. Darwin cites Knight (1799: 201).
243. Darwin cites *Bulletin de la Société botanique de France* (1855: vol. II, 327).
244. *Pinus nigricans* is a synonym of *P. nigra* (also known as Corsican Pine).

245. *Ulmus effusa* is a synonym of *U. laevis.*
246. Darwin cites von Gärtner (1849: 259, 518, 526, et seq.).
247. Darwin cites Kölreuter (1761–1766, Fortsetzung 1, 1763: 29; Fortsetzung 3: 44, 96); as well as *Acta Academiae scientiarum imperialis petropolitanae* (St. Petersburg), 1782 part 2: 251; and *Nova acta Academiae scientiarum imperialis petropolitanae* (1793: 391, 394; 1795: 316, 323).
248. Darwin cites Wichura (1865: 31, 41, 42).
249. Darwin cites Wichura (1865: 43) and M. J. Berkeley, *Journal of the Royal Horticultural Society,* Jan. 1866: 70.
250. Darwin cites von Gärtner (1849: 394, 526, 528).
251. Darwin cites Kölreuter, *Nova acta Academiae scientiarum imperialis petropolitanae* (1795: 316).
252. Darwin (1859: 20; 1872: 15).
253. Barton and Hewitt (1989).
254. Frith and Beehler (1998).
255. Hershkovitz (1977); Peres et al. (1996).
256. Nowak (1999: 1115).
257. Short and Horne (2001); Winkler and Christie (2002).
258. Short (1982).
259. McCarthy (2006); Sibley and Monroe (1990); Stiles and Skutch (1989).
260. Due to hybridization these birds are now sometimes lumped.
261. Short et al. (1983).
262. Due to hybridization these birds are now sometimes lumped.
263. Dagg (1962, 1968); Kingdon (1979); Lönnberg (1912); Stott (1959).
264. McCarthy (2006).
265. Benedict (1999a: 139).
266. Anderson (2006); Lockley (1992, 1996); Meise (1936b); Niethammer and Bauer (1960); Schifferli and Schifferli (1980); Schöll (1960).
267. McCarthy (2006).
268. Elstrand (1992); Rhymer and Simberloff (1996).
269. McCarthy (2006).
270. Higgins et al. (2001).
271. Hegde et al. (2006); McCarthy et al. (1995).
272. Arnold and Hodges (1995); Brochmann (1984); Echelle and Connor (1989); Gillespie (1985); Good et al. (2000); Grant (1981); Hegde et al. (2006); Kamal and Mair (2005); Levin et al. (1996); Manwell et al. (1963); Martin and Cruzan (1999); Perry et al. (2001); Sauer (1957); Wilson and Brown (1953); Wynn (1986).
273. McCarthy (2006).
274. Anderson and Daugherty (1974); Misra and Short (1974).
275. Harrison (1993: 6).
276. Arnold (1992, 1993, 1997); Bailey and Gilbert (1960); Bullini (1994); Bullini and Nascetti (1994); Cayouette and Morisett (1985); Coyne and Orr (2004); Gallez and Gottlieb (1982); Grant (1981); Hubbs (1955); Mayr (1942: 97, 268–270); McCarthy (2006); Rieseberg (1997); Seehausen (2004); Standley (1990); Stebbins (1957, 1958: 183); Wang et al. (1994); Wallace (2003); White (1978).
277. Grant (1981); Stebbins (1971).
278. Rieseberg (1991), Rieseberg et al. (1990, 1991, 1993, 1995, 1996); Welch and Rieseberg

(2002).

279. Clausen et al. (1940–1958: vol. I, 1947); Stebbins (1950: 279).
280. Foster (1937); Riley (1938, 1939).
281. Arnold and Hodges (1995); Bock (1984); Darwin (1859, 1868); Gray (1958, 1972); Hubbs (1955); McCarthy 2006; McCarthy (in prep.); Schwartz (1972); Stauffer (1987: 388–462).
282. See among many others: Capanna (1973); Crabtree and Buth (1987); DeMarais et al. (1992); Dev (1987); Dowling and DeMarais (1993); Echelle and Echelle (1978); Fulgione et al. (2001); Goodfellow et al. (1984); Goodfriend and Gould (1996); Gould and Woodruff (1990); Hebert (1985); Heller and Sevgili (2005); Hutchinson and Donnellan (1992); Johnston (1969); Lack (1940, 1945); Lanham (1981, 1984); Lieder (1983, 1987); Manwell et al. (1963); Mavárez et al. (2006); Mayr (1932); McCarthy (2006); McCarthy (in press); Meager and Dowling (1991); Meise (1975); Menezes and Weitzman (1990); Menzel (1977); Meyer et al. (2006); Miller and Smith (1981); Mina (1992); O'Foighil et al. (1996); Osinov (1993); Pala et al. (1982); Parham and Shi (2001); Ross (1958); Roy et al. (1994a, 1994b); Rudd (1955); Salazar et al. (2005); Salzburger et al. (2002); Sanders (1961); Schwarz et al. (2005); Schelly et al. (2006); Schwenk and Spaak (1995); Scriber and Ording (2005); Smith (G. R.) et al. (1979, 1983); Smith (P. F.) et al. (2003); Sperling and Harrison (1994); Stuart and Van der Willigen (1980); Sweader (1937); Tominaga et al. (2005); Verhulst (2005); Verkaar et al. (2004); Wayne and Jenks (1991); Yonekawa et al. (1988).
283. McCarthy (2006).
284. McCarthy (2006).
285. Arnold (2006).
286. McCarthy (2006).
287. Boehm (1954); Brooksbank (1949); Cain (1955); Collar (1997); Ford (1987); Forshaw (1973: 226, 233; 1981); Hobbs (1956; 1958); Irwin et al. 2001); Juniper and Parr (1998); Keast (1961); Meise (1975).
288. Gray (1972); McCarthy (in prep.).
289. Schuchmann (1999); Sibley and Monroe (1990).
290. Grimmett et al. (1998: 420); Rasmussen and Collar (1999a, 1999b, 1999c).
291. See Stebbins (1950: 281–282).
292. Tucker (1952).
293. Carver and Taliaferro (1992); Esuperanzi (2005: 302); Soliman (1992).
294. Colard, J.-C. (1992); De Faveri (1989); Natale and Pidalà (2004).
295. Esuperanzi (2005: 301-302). Translated by E. M. McCarthy. Original Spanish: "Buena parte de los híbridos, si no fuese porque a veces nos dan indicaciones acerca de la afinidad genética de las dos especies, solamente servirían para exhibirlos en los concursos y poco mas. Pero si los híbridos resultan ser fértiles el asunto ya cambia totalamente, porque se los puede emplear para crear una nueva especie intermedia entre las dos de partida o para trasladar una mutacion de una especie a otra."
296. Birkhead (2003); Duncker (1927a, 1927b, 1928, 1934).
297. Esuperanzi (2005).
298. Translated in Shuckard (1848: 270).
299. Eriksson et al. (2008).
300. Bradley et al. (1994, 1996); Epstein (1971); Frisch et al. (1997); Hanotte et al. (2000).
301. Internet: spotswoodbengals.com/bengal_history.htm; textfiles.com/fun/purebred.cat

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302. See: ftp://ftp.fao.org/docrep/fao/009/ah759e/ah759e16.pdf.
303. The word *introgression,* often used in discussions of hybrid variation, has had various definitions. As originally defined by Anderson and Hubricht (1938: 396), it was the "infiltration of germ plasm from one species into another through repeated backcrossing of the hybrids to the parental species." This definition, however, is problematic because it involves the word *species,* which is not clearly defined (Chapter 1). More recently, there has been an attempt to limit use of the term to situations involving permanent infiltration of genes from one population into another (Heiser 1973; Stebbins 1959). Thus, Rieseberg and Wendel (1993: 7) define it as the "permanent incorporation of alien alleles into a new, reproductively integrated population system," But here, too, a problem arises with the definition of the term "integrated population system." There is also the problem of saying what constitutes "infiltration." In the case of many crosses, the genetic influence of natural hybridization is very local and affects only individuals in the immediate vicinity of the contact zone. In the case of others, the effect may be detectable hundreds of kilometers away. How should one draw a line between these two cases? What is "infiltration" and what is not? In fact, the main difficulty with "introgression" is that it is thought of as an introduction of genes from one entity (usually thought of as a "species") into another. Actually, natural hybridization between two populations treated as species generally has a genetic effect only on individuals in the vicinity of the contact zone. No genes are introduced into other individuals elsewhere. Over the remaining geographic ranges of the two interbreeding populations, all individuals remain pure and genetically unaffected. The same distinction exists with the term *introduction*. There, a trait is introduced into only a subset of the target stock. Indeed, the whole idea of introducing genes into a "genetic background" is probably misleading. In many cases, what is called "introduction into a target stock" is really crossing individuals of the target stock with individuals of some other type to produce hybrid individuals with genetic complements of mixed parental origin. Esuperanzi (2005: 302) suggests that birds produced by repeated backcrossing to as single parent should be regarded as belonging to that parental type only when they contain less than 1/16 blood from the other parent. But this is clearly arbitrary. Why not 1/8 or 1/32? Even when the intention is to transfer a single gene to the target stock other genes often are transferred at the same time. For example, Carver and Taliaferro (1992: 131) note that even when the primary purpose is to transfer disease resistance to a crop, other traits such as yield may also be increased. If backcrossing occurs to one parental type or the other, the relative contributions of the two parents to the genetic complements of the resulting hybrids will vary in accordance with the amount of backcrossing that occurs. But no matter how many backcrosses to the target stock occur, so long as the traits of the offspring are discernibly mixed, they are hybrids, distinct from the target stock type. For the foregoing reasons, the terms *introduction* and *introgression,* though widely used in the literature on hybridization, are avoided in this book.
304. Asker and Jerling (1992: 249).
305. Darrow (1966: 73).
306. Austin (2005: 22).
307. Austin (2005: 24).
308. Buffon (1749–1804: vol. XVI, xxii). Translated by E. M. McCarthy. Original French: "les métis qu'ils produisent peuvent, en s'unissant, produire d'autres individus semblables à eux, et former par conséquent de nouvelles espèces intermédiaires."

309. Zirkle (1935: 107–110).
310. Quoted in Zirkle (1935: 115).
311. Translated in Zirkle (1935: 132).
312. Stebbins (1959: 232).
313. Translated in Zirkle (1935: 196).
314. Darwin (1859: 45).
315. Lewin (2000).
316. Coyne and Orr (2004: 401).
317. Sawatzki and Cooper (2007).
318. Hughes et al. (2005).
319. Sawatzki and Cooper (2007).
320. Ferguson-Smith et al. (1998); Ruvinsky and Graves (2005: 352).
321. Darlington (1932, 1937); Delneri et al. (2003); Ford and Clegg (1969); Forejt (1996); Grant (1985); Griffeths et al. (1999); Gustavsson (1990); King (1980); King (1993: 164–168); Lewis (1966); McCarthy (2006); McCarthy et al. (1995); McClintock (1945); Piálek et al. (2001); Searle (1993); Stebbins (1950: 218–226, 1971); White (1973: 219, 1978).
322. Callan and Lloyd (1960); Stebbins (1945, 1950: 221–222, 1958, 1971); Stebbins et al. (1946); White (1973: 338-339).
323. Sawatzki and Cooper (2007).
324. Stebbins (1950: 223, 1958, 1971).
325. Carson (1981); Carson and Stalker (1968); Carson et al. (1967); Powell (1997); Wasserman (1960); White (1973: 338); Zouros (1982).
326. Capanna (1973); Corti and Ciabatti (1990); Searle (1991).
327. Britton-Davidian et al. (1989); Capanna (1982); Gropp et al. (1982).
328. Arevalo et al. (1993, 1994); Capanna (1973); Grant (1985); Macey and Dixon (1987); McCarthy (2006); McCarthy et al. (1995); Nelson et al. (1987); Sites et al. (1993); Stebbins (1971); White (1973a, 1978).
329. Capanna (1973); King (1993: 150); Liming and Pathak (1981); Liming et al. (1980).
330. White (1978).
331. Britton-Davidian et al. (1989); Capanna (1982); Gropp et al. (1982); King (1990: 270).
332. Baverstock et al. (1983, 1986)); King (1990: 270).
333. Hauffee and Searle (1993); Lewis (1966); McCarthy et al. (1995); Rieseberg et al. (1995); Shaw et al. (1983; White (1973).
334. White (1973a: 169).
335. Dobzhansky et al. (1977); Karpechenko (1927).
336. Lewin (1987: 55).
337. Dobzhansky (1941); Huxley (1953).
338. Bee and Close (1993); Close and Bell (1997); Sharman et al. (1990).
339. Heiser (1947).
340. Hovanitz (1943).
341. McCarthy (2006).
342. McCarthy (2006).
343. Dunn and Garrett (1997: 273).
344. Barton and Hewitt (1989); Endler (1973, 1977); Haldane (1948); May et al. (1975); Slatkin (1973).
345. McCarthy (2006).

346. McCarthy (2006).
347. Barton and Hewitt (1985); Bazykin (1969); Key (1968); Moore (1977); Remington (1968).
348. Barton and Gale (1993).
349. Aprea et al. (2007); Arevalo et al. (1993, 1994); Banaszek et al. (2000b, 2002, 2003); Brünner and Hausser (1997); Capanna (1973); Dosselman et al. (1998); Dowler (1989); Fredga and Narain (2000); Hauffe and Piálek 1997; Lamborot (2001); Lamborot and Eaton (1992); Macey and Dixon (1987); McCarthy et al. (1995); Moska (2003); Narain and Fredga (1996, 1997); Piálek et al. (2001); Polyakov et al. (2002, 2003); Ratkiewicz et al. (2000, 2003); Searle (1984, 1991, 1993); Sites et al. (1993, 1995); Stangl (1986); Strasburg and Kearney 2005; Sudman et al. (1987); White (1973a, 1973b, 1978); Wyttenbach et al. (1999); Zahavi et al. (1956).
350. Macey and Dixon (1987); Stebbins (1971); White (1978).
351. de Vries (1902: 728).
352. Rockwell et al. (1961: 162).
353. Gustafsson (1943).
354. Asker and Jerling (1992: 121); Coyne and Orr (2004: 18).
355. White (1973a: 696).
356. Dhar et al. (2006).
357. Wagner 1992; Werth and Wagner (1990: 701).
358. Stebbins (1959); Stebbins and Walters (1949).
359. Baldwin (1941); Stebbins (1947, 1950: 316).
360. Stebbins (1950).
361. Stebbins (1950: 222).
362. Soltis and Soltis (1993).
363. Dvorak et al. (1998).
364. Zhang et al. (2002).
365. Zhang et al. (2002).
366. DeWet (1980); Fankhausen (1945: 35–36); Ramsey and Schemske (1998).
367. Manglesdorf and Reeves (1939); Newell and deWet (1973).
368. DeWet and Harlan (1974).
369. DeWet and Harlan (1974).
370. Stebbins (1950); Pandian and Koteeswaran (1998).
371. Pandian and Koteeswaran (1998); Similarly, Bogart (2003) notes that triploid females in the Salamander genus *Ambystoma* produce both reduced and unreduced eggs.
372. Grant (1971: 192); Müntzing (1930, 1932).
373. Grant (1971: 192). The production of triploid eggs by the triploid intermediate in this case is not implausible given that Pandian and Koteeswaran (1998) report that a triploid form of the fish *Misgurnus anguillicaudatus* "simultaneously spawns small, intermediate and large eggs carrying n, 2n and 3n genomes."
374. Pandian and Koteeswaran (1998); Ueda et al. (1986); Vigfusson (1970).
375. Digby (1912); Pellew and Durham (1916); Newton and Pellew (1929); Upcott (1939).
376. *Epilobium torreyi* is called *Boisduvalia stricta* by Seavy (1992).
377. Seavey (1992).
378. *Epilobium pallidum* is called *Boisduvalia macrantha* by Seavy (1992).
379. Sheridan et al. (1989).
380. Grant (1981: 379–400).

381. King and Stansfield (1985: 397).
382. Cleland (1962, 1972).
383. Grant (1981: 386).
384. Cleland (1962); Darlington (1937).
385. Grant (1981: 386–387).
386. Grant (1981: 397); Renner (1942).
387. Grant (1981: 397); Renner (1942).
388. Grant (1981: 397); Renner (1942).
389. Grant (1981); Suomalainen et al. (1987: 21).
390. White (1973a: 701).
391. Ramsey and Schemske (1998).
392. Johnson and Leefe (1999); Johnson et al. (1999).
393. Suolamainen et al. (1987: 176).
394. Hewitt (1975); White et al. (1977).
395. Honeycutt and Wilkinson (1989); White et al. (1977); White and Contreras (1978).
396. Drosopoulos (1976, 1978).
397. Coyne and Orr (2004); Grant (1981: 443); Richards (1973).
398. Grant (1981), Richards (1997); Sepp and Paal (1998).
399. Sepp and Paal (1998); Walters (1986).
400. Simmonds (1966, 1976).
401. Werth and Wagner (1990: 700).
402. Werth and Wagner (1990: 700).
403. Werth and Wagner cite Hauke (1963) and Wagner and Hammitt (1970).
404. White (1973a: 696); Suomalainen et al. (1987).
405. Grant and Grant (1971a); Kearney and Peebles (1942, 1964).
406. See also: Benson (1950, 1969, 1982); Benson et al. (1940); Kearney and Peebles (1942, 1964); Peebles (1936).
407. McCarthy (2006).
408. Schultz (1969).
409. That is, they are *hybridogenetic*.
410. Whetherington et al. (1987).
411. Dessauer et al. (1996).
412. Dawley and Goddard (1988); Dawley et al. (1987); Goddard and Dawley (1988); Goddard and Schultz (1993); Goddard et al. (1989, 1998).
413. Although such hybrids may have *P. neogaeus* mtDNA.
414. Margulis and Schwartz (1998: 364).
415. Bermudes and Margulis (1987); Margulis (1970); Margulis and Schwartz (1998). For example, it is believed mitochondria, which retain residual bacterial DNA, are descended from a bacterium related to *Rickettsia prowazeki* (Andersson et al. 1998; Gray 1998).
416. Rockwell et al. (1961: 204).
417. Grant (1966a, 1966b, 1981, 1985); Rieseberg (1991); Rieseberg and Soltis (1991); Rieseberg et al. (1990); Stebbins (1950, 1957). A wide variety of examples of fertility improving in later generation avian hybrids are listed in McCarthy (2006). A full listing of all studies documenting this phenomenon across all types of hybrids is beyond the scope of this book. Only a few will be listed here classified by the genera in which hybridization was studied. Most of the avian cases listed in McCarthy (2006) involve domestic genera: e.g., *Anas, Chrysolophus, Gallus, Columba, Carduelis, Serinus,*

Lonchura. Numerous cases are known in plants. In *Apoceynum* hybrids: Anderson (1936); in *Viola*: Brainerd (1924) and Clausen (1926, 1931); in *Galeopsis:* Müntzing (1930); in *Delphinium:* Lewis and Epling (1959); in *Plemonium:* Ostenfeld (1929); in *Bromsus, Elymus,* and *Nicotiana*: Stebbins (1950: 287); in *Tragopogon:* Winge (1938); in *Phaseolus:* Lamprecht (1941); in *Triticum:* Stebbins (ibid, citing Zakharjevsky 1940); in *Godetia:* Håkansson (1946, 1947) and Hiorth (1942); Stebbins (ibid) notes that "Constant, true-breeding lines have been extracted from such fertile segregates in *Galeopsis, Tragopogon, Phaseolus, Triticum, Viola,* and *Godetia.* Many cases are also reported for mammals, e.g., in *Bos:* Lotsy (1922), von Nathusius (1911) Winter et al. (1988a, 1988b); in *Odocoileus:* Wishart et al. (1988).

418. Darwin cites *Bulletin de la Société botanique de France,* vol. viii, 612 (Dec. 27, 1861).
419. Darwin (1868: vol. II, 110).
420. Darwin (1868: vol. II, 109) says Pallas proposed this doctrine in *Acta Academiae scientiarum imperialis petropolitanae* (1780: part ii., 84, 100).
421. Darwin (1869: 308).
422. Darwin (1871: vol. I, 241).
423. For example, Grant (1981).
424. For example, Wagner (1992),
425. For example, Stebbins (1959).
426. See also: Grant (1966a, 1966b); Rieseberg et al. (1996); Stebbins (1957).
427. Arnold and Bennett (1993); Gallez and Gottlieb (1982); Randolph (1966); Rieseberg (1992); Rieseberg et al. (1990, 1995, 1996); Wagner (1992). See also: Conant and Cooper-Driver (1980); Muller (1952); Raven and Raven (1976); Ross (1958); Stebbins and Ferlan (1956); Straw (1955); Stutz et al. (1979).
428. Gerrasimova (1939); Grant (1966a, 1966b, 1981); Grieg (2002); Harini and Ramachandra (2003); Stebbins (1957)
429. McCarthy et al. (1995).
430. McCarthy et al. (1995); White (1973: 215–232).
431. McCarthy et al. (1995).
432. Ferrel et al. (1980); Roy et al. (1994a, 1994b); Wayne and Jenks (1991).
433. DeMarais et al. (1992); Dowling and DeMarais (1993).
434. Song et al. (2002, 2003).
435. Wolfe et al. (1998).
436. Werth and Wagner (1990: 701).
437. Borgen et al. (2003); Brochmann et al. (2000).
438. Brochmann et al. (2000); Humphries (1976).
439. Marchant and Higgins (1990: 1333).
440. Gillespie (1985); McCarthy (2006).
441. Buchan (1977) gave a similar estimate (7.3%).
442. McCarthy (2006).
443. Salazar et al. (2005); Mavárez et al. (2006).
444. Grant (1981: 251); Lewis and Epling (1959).
445. Stebbin's *Sitanion jubatum* is a synonym of modern *Elymus multisetus.*
446. For example, Mayr (1963).
447. Arnold (1997); Bever and Felber (1992); Grant (1981); Jackson (1976); Karpechenko (1927); Levin (1983); Lewis (1980a); Löve and Löve (1957); Masterson (1994); Ramsey and Schemske (1998); Soltis and Soltis (1993, 1999); Stebbins (1950, 1971); Tate et al.

(2005).

448. For wheat, Stebbins cites McFadden and Sears (1946); for cotton, Beasley (1940), Hutchinson and Stephens (1947), and Stephens (1947); for tobacco, Goodspeed and Clausen (1928), Greenleaf (1941, 1942), and Kostoff (1938).
449. Blanc and Wolfe (2004); Bowers et al. (2003); Vision et al. (2000).
450. Paterson (2005); Paterson et al. (2004); Wang et al. (2005).
451. Wolfe and Shields (1997)
452. Margulis and Schwartz (1998: 373).
453. Furlong and Holland (2004); Gu et al. (2002); Mable (2004); Meyer and Schartl 1999); McLysaght et al. (2002); Nadeau and Sankoff (1997); Ohno (1970); Spring (1997); Van de Peer and Meyer (2005).
454. Grant (1981); Leitch and Bennett (1997); Stebbins (1971); Swanson (1957).
455. Stebbins (1950, 1971: 133).
456. Stebbins (1950: 182–183); Wettstein (1937).
457. Amores et al. (1998); Meyer and Schartl (1999); Osborn et al. (2003); Schultz (1980); Soltis and Soltis (1993).
458. Gregory and Mable (2005: 444–477).
459. Gregory and Mable (2005); Meyer and Schartl (1999); Van de Peer and Meyer (2005).
460. The entire family Salmonidae has long been known to be tetraploid (Allendorf and Thorgaard 1984; Phillips and Ráb 2001; Svärdson 1945). Moreover, triploids occur in commercial stocks and hybridization among salmonids is known to promote modern polyploids (Allendorf and Thorgaard 1984; Capana et al. 1974; Thorgaard et al. 1982).
461. According to Gregory and Mable (2005: 452) the family Catostomidae (suckers) is believed to have "originated about 50 million years ago as an allotetraploid hybrid between two cyprinidlike ancestors." See also: Uyeno and Smith (1972).
462. Gregory and Mable (2005: 448–456). Examples of teleost hybrids are unending. The population described under the name *Corydoras aeneus* (Bronze Corydoras), a callichthyid catfish of northern South America, is a complex of diploid and tetraploid individuals (Turner et al. 1992). Other members of the same genus, although not as yet fully investigated, also show signs of polyploidy, specifically, large variation in chromosome counts and DNA content (Oliveira et al. 1992, 1993). In Poeciliidae (Cyprinodontiformes) there is the well-known case of the Amazon Molly (*Poecilia formosa*). It is a unisexual produced by hybridization between *P. latipina* and *P. velifera* (Schartl et al. 1995; Sola et al. 1992). The genus *Cobitus* (Cypriniformes, Cobitae) contains bisexual diploids, unisexual triploids, and both unisexual and bisexual tetraploids (Vasil'ev et al. 1999). Both the triploids and tetraploids were produced by hybridization (Janko et al. 2003; Vasil'ev et al. 1999). In the same family, the Weatherfish (*Misgurnus fossilis*) appears to be tetraploid (Raicu and Taisescu 1972) and in Hubei province, China, one population of the Oriental Weatherfish (*Misgurnus anguillicaudatus*), which is elsewhere diploid, is tetraploid (Zhang et al. 1998). Mating these tetraploids with diploids produces triploids. The resulting males are sterile, but the females are fertile and produce both haploid and triploid eggs.
463. Not all members of Cyprinidae are known polyploids, but more than 50 taxa treated as species from several cyprinid subfamilies have been identified as polyploid (Buth et al. 1991). Gregory and Mable (2005: 454) say "it seems that polyploidy has evolved independently on several occasions in the Cyprinidae, and even sometimes within single genera." The Common Carp (*Cyprinus carpio*) is an allotetraploid (David et al. 2003;

Larhammar and Risinger 1994; Zhang et al. 1995). The Iberian minnow, *Tropidophoxinellus alburnoides* (also known as *Leuciscus alburnoides* and *Rutilis alburnoides.*), another cyprinid, is actually an elaborate complex of diploid and polyploid forms with separate spatial distributions (Alves et al. 2001). Genetic analyses have demonstrated that the entire complex is the product of hybridization (Alves et al. 1997, 2001; Carmona et al., 1997; Pala and Coelho 2005).

464. Among elasmobranchs (sharks, rays, and skates) some are thought to be tetraploid or octoploid, which suggests that polyploidy may be fairly prevalent among cartilaginous fishes (Chondrichthyes) as a whole (Gregory and Mable 2005; Olmo et al. 1982; Schwartz and Madock 1986; Stingo and Capriglione 1986; Stingo and Rocco 2001). Kendall et al. (1994) demonstrated triploidy in a female Nurse Shark (*Ginglymostoma cirratum*). Gregory and Mable (2005) say it has been suggested polyploidy may be prevalent among lungfishes (Sarcopterygii, Lepidosireniformes). In particular, Vervoort (1980) reported that the Slender Lungfish (*Protopterus dolloi*) is tetraploid. Polyploidy among chondrosteans such as paddlefish and sturgeons (Acipensiformes) has long been recognized (Ohno et al. 1969). These fishes can be arranged in three karyotypic groups (1) those with ~120 chromosomes; (2) those with ~250; and (3) those with about 500 (Birstein et al. 1997; Ludwig et al. 2001). Corresponding increases in DNA content of their genomes confirm their polyploid nature (Birstein et al. 1997; Blacklidge and Bidwell 1993; Gregory and Mable 2005: 446). The 120 chromosomes of the Mississippi Paddlefish, *Squalus spathula,* can be arranged into 30 quartets of matching chromosomes (Dingerkus and Howell 1976). Blacklidge and Bidwell (1993) say *Acipenser brevirostrum* (Shovelnose Stugeon) is 12-ploid, resulting perhaps from hybridization between a tetraploid and octoploid followed by autopolyploid duplication. The whole group (Acipensiformes) is generally thought to have arisen through polyploidy from a diploid ancestor with 2n = 60 (Birstein et al. 1997).
465. Viable polyploids are almost unknown in birds. However, since birds are vertebrates and vertebrates now appear to be derived from ancient polyploidization events, presumably all birds have some polyploidy in their past. Moreover, the lack of reported avian polyploids may simply reflect that bird karyotypes typically contain large numbers of very small chromosomes and have not lent themselves to cytological analysis (e.g., Hobart et al. 1982). As Fechheimer and Jaffe (1966) point out, "karyological investigations in birds have been restricted because of inherent and procedural difficulties [Here Fechheimer and Jaffe cite Shoffner (1965)]. The relatively large number of small chromosomes seen in birds, the number and morphology of which cannot easily be ascertained, has been one discouraging factor. Another is the fact that the leucocyte culture technique developed by Moorhead et al., [1960] while generally applicable to mammals, is unsuitable for feral birds." Tiersch et al. (1991) did report a viable triploid Blue-and-Yellow Macaw (*Ara ararauna*). Also, Sarvella (1973) reported triploidy in a hybrid between common pheasant (*Phasianus colchicus*) and domestic fowl (*Gallus gallus*). Fechheimer et al. (1983) give an account of diploid-triploid mosaicism in domestic fowl. Perhaps recent improvements in techniques will lead to the identification of more avian polyploids.
466. Noting the existence of tetraploid, hexaploid, and octoploid frogs, Bogart (1980) states that "the number of known bisexual polyploid [frog] species (or populations) has increased dramatically in the past few years … Many of the polyploid species have been found to have morphologically very similar diploid 'cryptic species'." Among anurans

(frogs and toads) a wide variety of examples are known of sexual polyploids. For example, in the family Bufonidae: *Bufo danatensis* (Pisanetz 1978), *B. viridis* (Mazik et al. 1976), and *Bufo* sp. (Bogart amd Tandy 1976); in Hylidae: *Hyla versicolor* (Wasserman 1970) and *Phyllomedusa burmeisteri* (Batistic et al. 1975); in Leptodactylidae: *Ceratophrys dorsata* (Beçak et al. 1967), *C. ornata* (Barrio and Rinaldi de Chieri 1970; Bogart 1967; Bogart and Wasserman 1972), *Odontophrynus americanus* (Barrio and Pistol de Rubel 1972; Beçak et al. 1966, 1967, 1970; Bogart 1967; Bogart and Wasserman 1972), and *Pleurodema bibroni* (Barrio and Rinaldi de Chieri 1970): *kriegi* (ibid); in Pipidae: there are *Xenopus ruwenzoriensis* and *X. vestitus* (Fischberg and Kobel 1978; Tymowska and Fischberg 1973); in Ranidae: *Dicroglossus occipitalis* (Bogart amd Tandy 1976) and *Pyxicephalus delalandii* (Bogart amd Tandy 1976). The three members of siren family Sirenidae are apparently all polyploid (Morescalchi and Olmo 1974; Morescalchi et al. 1986).

467. Ehrlich and Wilson (1991); Grant (1981); Hedrén et al. (2001); Stebbins (1966a, 1971); Whitham et al. (1991),
468. Amores et al. (1998); Osborn et al. (2003); Schultz (1980); Soltis and Soltis (1993).
469. Grant (1981); Stebbins (1950: 308).
470. Mable (2004).
471. See also: Schultz (1980: 327).
472. Goldman et al. (1983); Städler et al. (1996)
473. Städler et al. (1996).
474. Bogart (1980). See also: Bogart (1969, 1972).
475. Grant (1981: 348–352).
476. Grant (1981: 298).
477. For example, DenNijs and Peloquin (1977).
478. Clausen et al. (1945); Stebbins (1947, 1950, 1959).
479. Brochmann et al. (2004); Clausen et al. (1945); Grant (1981: 305–306); Gregory and Mable (2005); Jackson (1976); Levi (1983); Lewis (1980a); Soltis and Soltis (1993, 2000); Stebbins (1947, 1950, 1959, 1971); Van de Peer and Meyer (2005).
480. Spring (2003); Van de Peer and Meyer (2005: 333).
481. Grant (1981: 11).
482. Margulis and Schwartz (1998: 239).
483. Margulis and Schwartz (1998: 249).
484. Margulis and Schwartz (1998: 297).
485. Bogart (1980); Darevsky (1992); Darevsky et al. (1985).
486. Berger (1977); Cuellar (1976); Günther (1975); Kawamura (1939); Tompkins (1978); Uzzell (1963, 1964).
487. Ayre (1984); Black and Johnson (1979).
488. Benazzi-Lentati and Benazzi (1981).
489. Gibson (1981).
490. Yamaguchi and Lucas (1984).
491. Diploid agamosperms do, however, occur (e.g., Czapik 1985; Jankun and Kovanda 1988; Muniyamma and Phipps 1985).
492. Grant (1981: 424).
493. Grant (1981: 428 and Fig 31.4).
494. Ernst (1918); Rosenberg (1917); Maslin (1971); Stebbins (1950); Schultz (1971); Winge (1917).

495. Asker and Jerling say "apomicts" not agamosperms, but they make it clear (1992: 53, Figure 19) they mean the same thing by apomixis as is meant by agamospermy in this book.
496. Kruse (1969); Mujeeb-Kazi (1981); von Bothmer et al. (1988).
497. Stebbins (1932, 1935).
498. Nygren (1946, 1948, 1951).
499. Babcock and Stebbins (1938).
500. Rollins (1944).
501. Gustafsson (1946–1947: 121–124).
502. Gustafsson (1943).
503. Grant (1981: 424).
504. Ellerström and Zagorcheva (1977).
505. Johnson and Leefe (1999); Johnson et al. (1999).
506. Citing McAllister (1986).
507. McAllister (1986).
508. Avise (1992); Moore (1984); Vrijenhoek et al. (1977, 1989); Whetherington et al. (1987).
509. Boissinot et al. (1997); Cole et al. (1988, 1993, 1995); Cordes and Walker (2006); Darevsky et al. (1985); Densmore, Wright, and Brown (1989); Densmore et al. (1989); Dessauer et al. (1996); Fu et al. (1998); Kearney and Shine (2004); Kearney et al. (2005); Kizirian and Cole (1999); Moritz et al. (1989a, 1989b); Reeder et al. (2002); Sites et al. (1990); Taylor et al. (2001); Townsend (2000); Uzzell and Darevsky (1973); Vrijenhoek et al. (1989); Vyas et al. (1990); Walker et al. (2004); Woolley and Crews (2004).
510. Darevsky et al. (1985); Uzzell and Darevsky (1975).
511. Darevsky et al. (1985); Uzzell and Darevsky (1975).
512. Bogart (1980); Echelle et al. (1989); Gomez et al. (2004); Grant (1981); Honeycutt and Wilkinson. (1989); Hubbs (1955); Keller and Spaak (2004); Kraus and Miyamoto (1990); Kraus et al. (1991); McFadden and Breton-Hutchinson (2004); Morgan-Richards and Trewick (2005); Nascetti et al. (2003); Trewick et al. (2005); Vrijenhoek et al. (1989).
513. Asker and Jerling (1992: 114); Darevsky et al. (1985); Pamilo (1987); Spillane (2001); White (1973a).
514. Grant (1981: 426–427).
515. Grant (1981: 463).
516. Grant (1981).
517. Grant (1981: 7).
518. White (1973: 744).
519. Margulis and Schwartz (1998: 324).
520. Margulis and Schwartz (1998: 281).
521. Margulis and Schwartz (1998: 208).
522. Darwin and Seward (1903: vol. I, 362).
523. Darwin (1859: 43).
524. Arnold (1997); Arnold and Bennett (1993); Borgen et al. 2003; Brochmann et al. 2000); de Vries (1901–1903); DeMarais et al. (1992); Gallez and Gottlieb (1982); Grant (1981, 1985); Hirai et al. 2000); McCarthy (2006); McCarthy, in prep.; Mayr (1942: 265, 269–270); Meise (1936a); Randolph (1966); Rieseberg (1992); Rieseberg et al. (1990, 1995, 1996); Taylor et al. (1996); Sang et al. (1995); Song et al. (2002); Stebbins (1971); Wang et al. (1994, 2001); Wolfe et al. (1998).
525. Deonier et al. (2005); King (1993); Sumner (2003).

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526. Ferguson-Smith et al. (1998); Ruvinsky and Graves (2005: 352).
527. Grant (1966a, 1966b, 1966c, 1981: 269–270).
528. Buffon (1749–1804: vol. XVI, xii). Translated by E. M. McCarthy. Original French: "Tout ce que nous faisons par art peut se faire, et s'est fait mille et mille fois par la Nature."
529. Asker and Jerling say "apomicts" not agamosperms, but they make it clear (1992: 53, Figure 19) that they mean the same thing by apomixis as is meant by agamospermy in this book.
530. McCarthy (2006).
531. Milner (1993: 341); Sander (1947); Sander and Wreford (1961).
532. Rienikka (1995: 83).
533. Anderson (1939); Anderson and Hubricht (1938); Anderson and Stebbins (1954); Arnold (1997: 7); Stebbins (1959, 1971); Grant (1953, 1981, 1985); Heiser (1949); Soltis and Soltis (1993); Syvanen and Kado (2002); Tate et al. (2005).
534. Arnold (1997: 7–8).
535. Arnold (1997: 7–8).
536. Kölreuter (1761–1766).
537. Mable (2004).
538. Bickham (1984)
539. White (1973a: 581).
540. White (1973a: 571–681).
541. Mayr (1982: 730).
542. Gardner (1997); Pfenninger et al. (2002); Schwartz (1972).
543. Anonymous (2002); Baker et al. (1981); Clayton (1996a, 1996b, 1996c, 1996d); Fujita (1990); Grant (1997); Grant and Grant (1997); Inhelder (1962); Kirchhof-Glazier (1979); Krzywinski (1993); Laland (1994); Lorenz (1952, 1972); Mattson and Evans (1974); Morris (1970); Payne et al. (2000); Rao and Whittaker (1996); Reik and Walter (1998); Rowley and Chapman (1986); Schusterman et al. (1992); Slagsvold et al. (2002); Slagsvold and Hansen (2001); ten Cate (1986, 1987); ten Cate and Mug (1984); Verfurth (1983).
544.Kendrick et al. (1998).
545. McCarthy (2006).
546. *The Ibis* (1896: 261).
547. Baker et al. (1981); Grant and Grant (1996a).
548. DeLong (1982); Miller 1996).
549. Translated in Lovejoy (1936: 79).
550. Translated in Lovejoy (1936: 80).
551. Lovejoy (1936).
552. Russell (1982: 214).
553. Translated in Lovejoy (1936: 144).
554. Mayr (1982: 200).
555. Pennisi (1998).
556. Bruce and Ayala (1979); Cohen et al. (1997); Dev (1987); Gallez and Gottlieb (1982); Hutchinson and Donnellan (1992); Inglis (1985); Lee (1993); McDade (1992); Martin and Birmingham (1998); McFadden and Breton-Hutchinson (2004); Menezes and Weitzman (1990); Mina (1992); Panchen (1992); Rabinowitz et al. (1983); Rieseberg and Soltis (1991); Rieseberg et al. (1991); Ruvolo et al. (1991); Sang et al. (1997); Taylor, et

al. (1996).
557. Page x.
558. Arnold (1992, 1997); Grant (1981); Stebbins (1971); Soltis and Soltis (1993, 1995).
559. For example, Macnair and Cumbes (1989); Mayr (1942, 1963).
560. Ripley (1977).
561. Ripley (1977).
562. For example, Dobzhansky (1940b); Mayr (1963).
563. For example, Harrison (1990); Hatfield and Schluter (1999); Hewitt (1988); Templeton (1981).
564. Book 1, IV, 5.
565. Lyell (1832, vol. II, 20).
566. Cuvier (1827: 103).
567. De Deguileville (1975).
568. Darwin (1859: 32).
569. Huxley coined the term agnostic to describe himself.
570. Milner (1993: 393).
571. Huxley (1860; 1901: 189); Mayr (1982: 742).
572. Gillispie (1996: 130).
573. Lyell (1881: 442–443).
574. Lyell (1835: vol. III, 372–377).
575. Lyell (1835: vol. II, 418, vol. III, 393–396).
576. Lyell (1835: vol. III, 373).
577. Lyell (1835: vol. III, 395).
578. Darwin (1859: 299).
579. Darwin (1859: 342).
580. Desmond and Moore (1991); Milner (1993); Sedgwick (1860).
581. Translated in Osborn (1894: 47–48).
582. Mayr (1982: 544).
583. Osborn (1894).
584. Russell (1982: 68), citing Geoffroy Saint-Hilaire (1833: 80).
585. Russell (1982: 305).
586. Russell (1982: 242).
587. In von Baer (1864–1876, vol. II). See: *Über den Zweck in den Vorgängen der Natur, Über Zielstrebigkeit in den organischen Körpern inbesondere,* and *Über Darwins Lehre.*
588. Russell (1982: 244).
589. Owen (1866–1868: vol. III, 797).
590. Bateson (1894: 18). Bateson and de Vries were bellwethers of genetic thought during the early years of the twentieth century. In addition to *genetics,* Bateson coined many of the terms used in the field of genetics today, such as *allele*, *homozygote*, and *heterozygote* (Cremer 1985: 191).
591. Translated by Huxley in his essay *Criticisms on "The Origin of Species"* (1864); reprinted in Huxley (1893–1894: vol. II, 88).
592. Translated in Russell (1982: 243).
593. Translated in Russell (1982: 243).
594. Huxley (1860).
595. Lovejoy (1936).
596. Darwin (1887: 107).

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597. Darwin (1869: 103–104).
598. Eldredge (1971); Eldredge and Gould (1972).
599. Eldredge (1995: 3).
600. Eldredge (1971).
601. Quoted from http://aleph0.clarku.edu/huxley/SM2/PTyp.html.
602. Benton (1993: 720).
603. Stokes (1982: 348).
604. Li (1963).
605. Lemche (1957); Margulis and Schwartz (1998: 290).
606. Benton (1993: 353).
607. Mayr (1982: 617).
608. Bush (1975); Mayr (1963); Mayr and Ashlock (1991).
609. See Gould (1980a: 183–184); Eldredge (1995: 119).
610. Darwin (1859: 194).
611. Boorstin (1983: 316).
612. Epistle of Paul the Apostle to the Hebrews, 11:1.
613. Cuvier (1827: 21–23, 344–354).
614. Cuvier (1827: 10).
615. Cuvier (1827: 242).
616. Milner (1993: 6).
617. Sedgwick (1860).
618. Quoted in Darwin (1872: xvii-xviii).
619. Mayr (1982: 536).
620. Milne-Edwards (1867: 429), translated in Russell (1982: 245).
621. Allen (1969).
622. De Vries (1902: 726).
623. De Vries (1901–1903, 1902: 726).
624. De Vries (1901–1903, 1902: 724).
625. De Vries (1901–1903, 1902: 726).
626. De Vries (1901–1903, 1902: 725).
627. De Vries (1901–1903: vol. I, 32–33).
628. Cleland (1962, 1972); Darlington (1937); Emerson (1935); Harte (1994: 102–109, 133).
629. Emerson (1935); Gates (1909); Lutz (1907).
630. Emerson (1935).
631. De Vries (1901–1903: vol. I, 68–69).
632. De Vries (1901–1903, 1905: 799, 802).
633. De Vries (1901–1903: vol. I, 76).
634. Darwin (1868: vol. I, 406).
635. Darwin (1868: vol. I, 224).
636. Darwin (1868: vol. I, 92).
637. Darwin (1859: 29–30).
638. Darwin (1859: 23).
639. Darwin (1887: vol. III, 85).
640. The Buffon quotation in the footnote was translated by E. M. McCarthy. Original French: "Il est donc fort possible, comme nous l’avons déjà insinué, que les bisets, les ramiers et les tourterelles, dont les espèces paroissent se soutenir séparément et sans mélange dans l’état de nature, se soient néanmoins souvent unies dans celui de domesticité ; et que de leur mélange, soient issues la plupart des races de nos

pigeons domestiques, dont quelques-uns sont de la grandeur du ramier, et d'autres ressemblent à la tourterelle par la petitesse, par la figure, etc. et dont plusieurs enfin tiennent du biset ou participent de tous trois."

641. Desmond and Moore (1991: 427).
642. Desmond and Moore (1991: 459).
643. Desmond and Moore (1991: 427, 459).
644. Morgan (1903: 299).
645. Harte (1994: 100).
646. Babcock (1918).
647. Provine (1971, 1986: 138–142).
648. Provine (1986: 44).
649. Provine (1971, 1986: 138–142).
650. *Novum Organum,* First Book, §70.
651. Jennings (1935: 45).
652. Schindewolf (1993: 351).
653. Schindewolf (1993: 351).
654. Schindewolf (1993: 393).
655. Simpson (1944: 206).
656. For example, Robson and Richards (1936).
657. Willis (1940: 52–54).
658. Willis (1940).
659. Quoted in Wright (1941: 345).
660. Goldschmidt (1982: 243).
661. Goldschmidt (1982).
662. Khudr et al. (1973).
663. Goldschmidt (1982: 249).
664. Goldschmidt (1982: 199).
665. Goldschmidt (1982: 395).
666. Goldschmidt (1980: 396).
667. Goldschmidt (1952: 96).
668. For example, Dobzhansky (1940a: 357); Mayr (1942: 155).
669. King and Wilson (1975); Prager et al. (1976); Wilson (1975).
670. Lewis (1966).
671. Grant (1981: 172); Key (1968); Templeton (1981: 33–35).
672. Goldschmidt (1982: 207).
673. Key (1968).
674. Desmond and Moore (1991: 39).
675. Desmond and Moore (1991: 90).
676. Darwin (1887: vol. I, 47). Darwin's son Francis (ibid: 26) says Darwin wrote his autobiography in 1876.
677. Darwin (1887: vol. I, 82).
678. Bateson (1894: 11).
679. Butlin (2005).
680. Bateson (1909); Dobzhansky (1937a); Muller (1942).
681. Darlington (1932, 1937); Delneri et al. (2003); Ford and Clegg (1969); Forejt (1996); Grant (1985); Griffeths et al. (1999); Gustavsson (1990); King (1980); King (1993: 164–168); Lewis (1966); McCarthy (2006); McCarthy et al. (1995); McClintock (1945);

Piálek et al. (2001); Searle (1993); Stebbins (1950: 218–226, 1971); White (1973: 219, 1978).

682. Ferguson-Smith et al. (1998); Ruvinsky and Graves (2005: 352).
683. Grant (1985); Griffiths et al. (1999); White (1973a: 215–232).
684. Huxley (1898: 150). See also: Huxley (1901: 257).
685. Huxley (1901: vol. II, 309).
686. Darwin (1866: 312, 1869: 318, 1872: 248).
687. Darwin (1872: 262).
688. Darwin and Seward (1903: vol. I, 296)
689. Darwin and Seward (1903: vol. I, 297).
690. Huxley (1901: vol. II, 14).
691. Darwin (1871: vol. I, 222–223, footnote).
692. Darlington (1932, 1937); Delneri et al. (2003); Ford and Clegg (1969); Forejt (1996); Grant (1985); Griffeths et al. (1999); Gustavsson (1990); King (1980); King (1993: 164–168); Lewis (1966); McCarthy (2006); McCarthy et al. (1995); McClintock (1945); Piálek et al. (2001); Searle (1993); Stebbins (1950: 218–226, 1971); White (1973: 219, 1978).
693. Maynard Smith (1971, 1978, 1988); Mogie (1992); Williams (1975).
694. Lyell (1835: vol. III, 331).
695. Lyell (1835: vol. I, 113).
696. Manfredi Romanini (1985).
697. Capanna (1973: 690); King (1993: 150).
698. See for example Dobzhansky (1935, 1937a, 1937c); Dobzhansky and Socolov (1939); Dobzhansky and Sturtevant (1938); Sturtevant and Dobzhansky (1936).
699. *Le Règne Animal* (Cuvier 1817, I: 5–6). Translated by E.M. McCarthy. Original French: "Comme rien ne peut exister s'il ne réunit les conditions qui rendent son existence possible, les différentes parties de chaque être doivent être coordinées de manière à rendre possible l'être total, non-seulment en lui même, mais dans ses rapports avec ceux qui l'entourent."
700. Hutchins (1952b: vol. I, 275–276). Darwin (1872: xiii) cites this passage.
701. *On the Nature of Things,* Book I. Translated in Hutchins (1952h: 8).
702. Minelli (1993).
703. Pennisi (1998).
704. Whittaker (1959, 1969); Margulis and Schwartz (1982, 1998); Whittaker and Margulis (1978).
705. Margulis and Schwartz (1998: 111).
706. Campbell (1987: 518, 524).
707. Margulis and Schwartz (1998: 192).
708. Margulis and Schwartz (1982: 82; 1998: 148–151).
709. Margulis and Schwartz (1982: 84; 1998: 146).
710. Margulis and Schwartz (1998: 193, Fig. B).
711. Helbert et al. (1997).
712. Margulis and Schwartz (1998: 168).
713. Darwin (1868: vol. I, 133–134).
714. Frost (1914).
715. Obst et al. (1988).
716. Aguinaldo et al. (1997); Brusca and Brusca (1990); Margulis and Schwartz (1982: 222;

1998: 300, 301); Pearse et al. (1987: 454).
717. Margulis and Schwartz (1998: 292); Pearse et al. (1987: 384).
718. Pearse et al. (1987: 419, 656).
719. Morris (1998: 109-110); Schindewolf (1993: 28); Whittington (1985).
720. Stanek (1969).
721. Margulis and Schwartz (1982: 194).
722. Margulis and Schwartz (1982: 204).
723. Walker (1983: 1035).
724. Nowak (1999: 187-188).
725. Nowak (1999).
726. Nowak (1999).
727. Nowak (1999).
728. Nowak (1999: 1422-1423).
729. Nowak (1999).
730. Nowak (1999).
731. Obst et al. (1988).
732. Margulis and Schwartz (1982).
733. Branch (1988); Dixon et al. (1988: 89); Obst et al. (1988).
734. McGavin (2000: 170); Stanek (1969: 366).
735. Stanek (1969: 294).
736. Chen et al. (1998); Desmond and Moore (1991: 514); Lambert (1991: 24, 115, 118-124); Norman (1985: 44, 50-54); Sloan (1999); Winter et al. (1988).
737. Hanzák (1967: Fig.15).
738. Thomas (1999).
739. Murphy et al. (2001).
740. Benton (1993: 563); Bone and Goto (1991); Bone et al. (1991); Ghirardelli (1968: 356-357, 363); Margulis and Schwartz (1982: 233); Morris (1998); Whittington (1985).
741. Gould (1980a: 42); Moore and Miller (1979).
742. Margulis and Schwartz (1998: 125, 196).
743. Margulis and Schwartz (1982: 82; 1998: 148-151).
744. Margulis and Schwartz (1982: 84; 1998: 146).
745. Margulis and Schwartz (1998: 193, 194 Fig. B).
746. Margulis and Schwartz (1998: 196).
747. Campbell (1987: 551) ; Helbert et al. (1997); Margulis and Schwartz (1982).
748. Margulis and Schwartz (1998: 125, 194, 347).
749. Doolittle (1999, 2000); Margulis and Schwartz (1982: 42, 62, 72, 74; 1998: 117-118); Martin (1999); Minelli (1993: 131, 134); Reichenbach (1984); Xiong et al. (1998).
750. Benton (1993: 779, 804); Margulis and Schwartz (1998: 400, 404).
751. Margulis and Schwartz (1998: 408-411, 416).
752. Margulis and Schwartz (1998: 125, 192).
753. McCarthy (2006).
754. McCarthy (2006).
755. Frost (1914).
756. Boucher et al. (2003); Duncan et al. (1989).
757. Martin (1999).
758. Hardy (1986).
759. Benton (1993: 3).

760. Margulis and Schwartz (1998).
761. Margulis and Schwartz (1998: 123).
762. Benton (1993).
763. Golubic and Knoll (1992: 60).
764. Golubic and Knoll (1992: 60).
765. Quoted in Darwin (1872: xvi).
766. Geoffroy Saint-Hilaire (1796, 1847: 71–72, 134–135, 432).
767. Hutchins (1952f: 579).
768. Milner (1993: 60).
769. Rádl (1905–1909: vol. I, 71)
770. See among many others: Campbell (1987); Futuyma (1986); Kemp (1982, 2004); Romer (1966); Stokes (1982).
771. Darwin (1859: 116); Desmond and Moore (1991).
772. Bowler (1989: 144).
773. Bowler (1989: 130).
774. Ospovat (1976, 1981).
775. Darwin and Seward (1903: vol. I, 73).
776. Darwin (1859: 435, 1872: xvii).
777. See also: Carpenter (1851).
778. Desmond and Moore (1991: 367).
779. Quoted in Desmond and Moore (1991: 368).
780. Darwin (1859: 435).
781. Wittgenstein (1961: 117).
782. For example, see Woodburne et al. (2003).
783. Lambert (1991: 115); Norman (1985: 38).
784. Dates for the various geological time periods mentioned in this book are taken from the website ucmp.berkeley.edu/help/timeform.html.
785. Broili (1927, 1938, 1939); Goldfuss (1831); Lambert (1991: 22); Seeley (1870); Sharov (1971); Wellnhofer (1991).
786. Wellnhofer (1991: 164).
787. Wellnhofer (1991: 161).
788. Wellnhofer (1991: 164).
789. Wellnhofer (1991: 164).
790. Romer (1966).
791. Romer (1966: 336).
792. Norman (1985: 10).
793. Campbell (1987: 650)
794. Nowak (1991, p.1289); Rosas (1994); Walker (1983: 118, 454, 857).
795. Nowak (1999).
796. Walker (1983: 1169)
797. Frair et al. (1972); Paladino et al. (1990).
798. Obst et al. (1988: 284).
799. Gibbons (1995).
800. Romer (1966).
801. For example, Stokes (1982: 362).
802. Case (1934).
803. Dixon et al. (1988: 189); Gregory and Broom (1926).

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804. Colbert (1948); Dixon et al. (1988: 189).
805. Strickberger (2000).
806. Dixon et al. (1988: 192); Kemp (1982: 138).
807. Kemp (1982: 86, Fig. 29).
808. Dixon et al. (1988: 193); Romer (1966: 185).
809. Farlow and Brett-Surman (1997).
810. Dixon et al. (1988: 160–161); Weishampel et al. (1990).
811. Norman (1985).
812. Romer (1966: 370); Weishampel et al. (1990: 475).
813. Walker (1983).
814. Barlow (1984); Savage and Russell (1983: 46).
815. Fidalgo et al. (1986); Politis and Gutierrez (1998).
816. Dixon et al. (1988: 209); Romer (1966: 161); Weishampel et al. (1990).
817. Norman (1985: 154).
818. Weishampel et al. (1990: 454).
819. Anderson and Jones (1984).
820. Walker (1983: 470).
821. Dixon et al. (1988: 156); Norman (1985: 154).
822. Bakker (1986); Dixon et al. (1988: 156).
823. Kingdon (1971: 367); Walker (1983: 459, 471).
824. Walker (1983: 470).
825. Walker (1983).
826. Emry (1970); Fox (1991); Rose et al. (1977); Savage and Russell (1983).
827. Norman (1985: 153).
828. Walker (1983: 470).
829. Norman (1985: 153).
830. Norman (1985: 153).
831. Dixon et al. (1988: 160).
832. McKenna (1980: 61); Romer (1966: 232, 237); Savage and Russell (1983: 169).
833. Benton (1993: 757); Briggs (1987: 89); Savage and Russell (1983: 231, 232, 284); Simpson (1980).
834. Smith et al. (1994); Teeling, et al. (2003); Woodburne and Case (1996).
835. Romer (1966: 382); Savage and Russell (1983: 232).
836. Savage and Russell (1983: 89).
837. Savage and Russell (1983: 65, 66, 67, 72, 81, 82, 97, 101, 105, 106, 115).
838. Dixon et al. (1988: 201); Simons (1972); van Valen (1994); van Valen and Sloan (1965).
839. Smith et al. (1994).
840. Dixon et al. (1988: 209); Storch and Richter (1992).
841. Nowak (1999: 1243).
842. Nowak (1999: 1715).
843. Romer (1966: 337).
844. Romer (1966: 200).
845. Romer (1966: 200; also compare Figs. 309A and 437B).
846. Forsyth-Major (1893); Friant (1933); Hinton (1926); Savage and Russell (1983: 117).
847. Korth (1994: 23).
848. For example, Clemens and Kielan-Jaworowska (1979: 99).
849. Dixon et al. (1988: 252); Reguero et al. (2007); Riggs and Patterson (1935); Romer

(1966).
850. For example, see Dixon et al. (1988: 252).
851. See Savage and Russell (1983).
852. Carroll (1988); Internet: www.ucmp.berkeley.edu/mammal/eutheria/chirofr.html.
853. Carroll (1988); Habersetzer et al. (1992).
854. Carroll (1988); Internet: www.ucmp.berkeley.edu/mammal/eutheria/chirofr.html.
855. Quoted in Desmond and Moore (1991: 288).
856. Fenton (1992: 9–10).
857. Fenton (1992: 9–10).
858. Romer (1966: 145).
859. Romer (1966: 145).
860. Wellnhofer (1991).
861. Wellnhofer (1991).
862. Wellnhofer (1991).
863. Nesov (1981); Williston (1902).
864. Wellnhofer (1991).
865. Bateson (1894).
866. Walker (1983).
867. Benton (1993: 755); Romer (1966: 380).
868. Romer (1966: 385).
869. Dixon et al. (1988: 248); Romer (1966: 387); Savage and Russell (1983: 46).
870. Romer (1966: 385).
871. Romer (1966: 264); Savage and Russell (1983: 44).
872. Archibald and Clemens (1984); Clemens et al. (1979: 48–49).
873. Kellogg (1998).
874. Piperno and Sues (2005).
875. Dixon et al. (1988); Kemp (1982: 147, Fig. 55).
876. Kemp (1982: 86).
877. Romer (1966: 336).
878. Gingerich et al. (1983); Romer (1966: 297); Savage and Russell (1983: 123).
879. Boyden and Gemeroy (1950); Slijper (1966: 312).
880. http://darla.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Pakicetid.html
881. McGowan (1973, 1978a, 1978b); Norman (1985: 21, 178); Romer (1966: 329, 371); Taylor (1987).
882. The teeth of *Mosasaurus* are pictured in Camper (1786: Tab. XV, fig. 6); Lingham-Soliar (1995: 169, fig. 15); Williston (1898: Plate XIX).
883. The teeth of *Hainosaurus* are pictured in Lindgren (2005: 1160, fig. 2).
884. Van Regerten Altena (1956).
885. Lingham-Soliar (1995: 156).
886. Lingham-Soliar (1995: 156).
887. Walker (1983).
888. Walker (1983).
889. Walker (1983).
890. Walker (1983).
891. Walker (1983).
892. Walker (1983).
893. Savage and Russell (1983: 106).

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894. Rabinowitz et al. (1983).
895. For example, see Romer (1966, Fig. 280).
896. Benton (1993: 706); Romer (1966).
897. Benton (1993); Romer (1966); Savage and Russell (1983).
898. Ameghino (1889, 1895, 1902). Lydekker (1896: 85) also identified *Pyrotherium* as an elephant. See also: Andrews (1904: 101).
899. Simpson (1984: 98).
900. For example, Andrews (1904: 101).
901. Savage and Russell (1983: 114); Shoshani and Tassy (1996: 64).
902. MacFadden and Frailey (1984, Fig. 2 & Table 1); Shoshani and Tassy (1996, Plate 8.3).
903. Barbour (1977: 243).
904. Kielan-Jaworowska et al. (1979: 222).
905. Kielan-Jaworowska et al. (1979: 222).
906. For example, Martin (1977).
907. Romer (1966: 379).
908. Provine (1986: 38–41).
909. Ramsey and Schemske (1998: 469).
910. DeWet (1980); Felber (1991); Jackson (1976); Mable (2004); Rabe and Haufler (1992); Ramsey and Schemske (1998); Watanabe et al. (1991).
911. Bogart and Wasserman (1972); Fankhauser (1945).
912. Bogart (1969, 1972, 1980); DenNijs and Peloquin (1977); deWet (1980: 6); Harlan and deWet (1975); Franke (1975); Grant (1981); Mable (2004); Ramsey and Schemske (1998); Richards (1977); Volpe (1970).
913. Burton and Husband (2000); de Haan et al. (1992); Husband (2004); Husband and Schemske (2000); Maceira et al. (1992); Rabe and Haufler (1992); Ramsey and Schemske (1998).
914. DeWet (1980: 7).
915. Soltis and Soltis (1999).
916. Stebbins (1950).
917. Randolph (1932).
918. Astaurov (1936, 1957, 1967a, 1967b, 1977); David and Pandian (2006); Dasgupta (1962); Fankhauser (1945); Ferrier and Jaylet (1978); Maniotis (1980: 174–175); Pandian and Koteeswaran (1998); Parmenter (1933); Rugh and Marshland (1943); Suomalainen et al. (1987); Volpe and Dasgupta (1962).
919. Pandian and Koteeswaran (1998).
920. See Suomalainen et al. (1987: 129–130).
921. Grant (1981); Stebbins (1950).
922. Babcock (1947).
923. Muscarella et al. (1985).
924. Griffen and Bunker (1964, 1967).
925. Delany et al. (1988); Muscarella et al. (1985).
926. Griffiths et al. (1999).
927. The only other human autosomal trisomics that do not die *in utero* are trisomies 13 and 18. Both show severe physical and mental abnormalities and neither long survives birth. See Griffiths et al. (1999); Hassold et al. (1991).
928. White (1973: 580).
929. Bull (1983); Orr (1990).

930. Ferguson-Smith (2007).
931. Mable (2004).
932. Bickham (1984),
933. Gregory and Mable (2005: 472–473).
934. White cites Iriki (1932) and Makino (1934, 1935, 1939). In the same place, he states, citing Kezer (1962) and Seto et al. (1964), that no cytologically visible sex chromosomes exist in the salamanders *Necturus maculosus* and *Proteus anguinus*.
935. Charlesworth (2002).
936. Fankhauser (1945: 20).
937. Lewis (1980b); Grant (1981); Stebbins (1950).
938. Randler (2004).
939. Jaramillo and Burke (1999).
940. Immelmann (1982).
941. Halbert et al. (2005).
942. www.birdsaustralia.com.au.
943. www.mp2-pwrc.usgs.gov/bbs/AOUsplt1.htm.
944. Darwin (1859: 43).
945. Darwin (1859: 20).
946. Darwin (1859: 253–254).
947. Darwin and Seward (1903: vol. I, 127–128).
948. Darwin and Seward (1903: vol. III, 33).
949. Darwin and Seward (1903: vol. I, 274).
950. Darwin cites Richardson (1847) and Youatt and Sidney (1860).
951. Darwin cites Spooner (1859, *Journal of the Royal Agricultural Society of England,* vol. XX, part ii) and Howard (*The Gardeners' Chronicle and Agricultural Gazette,* 1860: 320).
952. Darwin cites *The Gardeners' Chronicle and Agricultural Gazette* (1857: 649, 652).
953. Darwin cites *Bulletin de la Société impériale zoologique d'Acclimatation* (1862: vol. IX, 463) and Moll and Gayot (1860: 32).
954. Darwin cites *The Poultry Chronicle* (1854: vol. II, 36).
955. Darwin incorrectly cites "Tegetmeier (1866)." Almost surely he intended Tegetmeier and Weir (1867).
956. Darwin cites *The Gardeners' Chronicle and Agricultural Gazette* (1860: 320).
957. Darwin cites Spooner (1859, *Journal of the Royal Agricultural Society of England,* vol. XX, part ii).
958. Darwin (1868: vol. II, 95–97).
959. Darwin (1868: vol. II, 98).
960. Darwin (1868: vol. I, 22).
961. Darwin and Seward (1903: vol. II, 285).
962. Darwin (1871: vol. I, 241).
963. Darwin (1859: 488).
964. Hartl and Clark (1989: 154, Table 3 & pp. 163–165). See also: Barton and Rouhani (1991).
965. McCarthy (1995); McCarthy et al. (1995).
966. For more details, see McCarthy (1995) and McCarthy et al. (1995).
967. McCarthy, unpublished.