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THE EVOLUTION OF MIMICRY: A SOLUTION TO THE PROBLEM OF PUNCTUATED EQUILIBRIUM

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Once again, "punctuated equilibrium" is oversold to a general audience as the basis for a new, general theory of evolutionary change that is in reality little more than a promissory note (Durant 1985)

The superseding of strict Darwinism may establish the Darwinian style of argument in its most general form as the foundation for a truly synthetic theory of evolution (Gould 1982)

Punctuated equilibrium is a theory that evolution can be separated into two processes: microevolution, which accounts for adaptation, and macroevolution, which accounts for diversity (Gould and Eldredge 1977; Gould 1982). It challenges the prevailing Darwinian and neo-Darwinian view that both adaptation and diversity have a single prime cause: natural selection.

Punctuated equilibrium is therefore in a tradition of theories alternative to strict Darwinism, most recently espoused by Goldschmidt (1940) with ancestry in the mutationist tradition of the early twentieth century (Provine 1971). The study of butterfly mimicry (Clarke and Sheppard 1960*a,b*, 1971, 1972; Sheppard 1961, 1962; Clarke et al. 1968; Turner 1977*b*) has already shown how the gradualist neo-Darwinian view of evolutionary genetics could be synthesized with the mutationist view of Goldschmidt (1945) and Punnett (1915, 1927). In this paper, I use recent studies of mimicry to suggest ways of synthesizing neo-Darwinism with the theory of punctuated equilibrium. Of necessity, I present a summary of much elaborate data and argumentation; other papers give fuller accounts of our theory of the evolution of Müllerian mimicry (Turner 1981, 1983*b*, 1984*c*, 1985*a*; Sheppard et al. 1985); of the historical relations of mimicry theory, adaptationism, and mutationism during the Modern Synthesis (Kimler 1983; Turner 1983*a*, 1985*b*); and of the critique and synthesis of neo-Darwinism and punctuationism (Turner 1983*a,b*, 1986).

PUNCTUATIONISM AS A THREE-PRONGED FORK

According to punctuated equilibrium, therefore, evolution is not more or less smooth, gradual, and continual, as has been supposed for most purposes in most post-Darwinian theories. Rather, most morphological change is held to take place

within geologically short periods, separated by vastly longer periods of comparative stasis (Eldredge and Gould 1972). The rapid, large changes all occur during speciation, that is to say during the branching of the evolutionary tree (cladogenesis); as a result, the evolutionary tree can be represented by a diagram resembling not a conventional spreading bush but an elaborate candelabra with horizontal branches and vertical candles (fig. 8a). As a result, speciation acts as a kind of mutational process, generating species that undergo little change but merely become extinct, or give rise to new and different species by the mutational, punctuational event. Directions, patterns, and trends in evolution are due not, as has been supposed, to natural selection within species (microevolution) but to a process of selection between species (macroevolution) (Gould 1982).

This theory has some profound implications, which can be seen as giving it revolutionary features when compared with neo-Darwinian theory. First, since species are restrained from evolving except when branching (speciation) takes place, there must be some restraining mold in evolution that is broken only at the formation of a new species. Suggestions for the nature of this restraint and its relaxation have included internal developmental restraints, internal molecular restraints, genetic revolution produced by founder effects (invoking the spirit of Mayr 1954), genetic revolution produced by three-phase evolution (invoking Wright 1971 and earlier), developmental macromutations (invoking Goldschmidt 1940), and (more conventionally) ecological release.

Second, most of what is important in evolution—the generation of diversity, trends, and directions—is caused not by natural selection, which produces only adaptive adjustments within evolving lines, but by the interaction of the punctuational process and the process of species selection. Hence, most features of organisms cannot be seen as adaptive (Gould and Lewontin 1979). This destroys most of the intellectual base of the philosophically and politically threatening discipline of sociobiology (Wilson 1975; Dawkins 1982), as well as the less dangerous but equally adaptationist field of evolutionary ecology (Shorrocks 1984). Punctuationalism can be seen as one of a line of theories that can save evolutionary theory from the more uncomfortable implications of strict Darwinism (Bowler 1983, 1984; Turner 1983a, 1984a).

The punctuational theory has been subject to extensive criticism from neo-Darwinists (Levinton and Simon 1980; Charlesworth et al. 1982; Hecht and Hoffman 1986). For the more difficult task of synthesizing it with neo-Darwinism, I find it useful to imagine the punctuational theory as a three-pronged fork (Turner 1986).

Prong 1: Punctuational Evolution

The fossil record reveals a pattern of stasis alternating with periods of extremely rapid change.

Prong 2: Evolution in Jerks

This pattern arises because species, morphologically distinct from their closest relatives, appear rapidly and remain more or less unchanged until they become extinct. Some of the direction of evolution arises at this stage, as a result of a

“direction bias” in the evolutionary jerk (Gould 1982); both this bias and the maintenance of the phenotypic mold (perhaps even its breaking during the jerk) are more likely to be generated internally by the organism than externally by the environment.

Prong 3: The Second Process

Long-term trends and patterns of evolution are therefore created not by evolution within the relatively static species, but by selection acting between species. This consists of two processes (Gould 1982): a “birth bias” (higher rate of speciation in some clades), and a “death bias” (higher rate of extinction); these are directly analogous to natural selection through fertility and mortality at the individual level. (Note that Gould’s arguments normally place “direction bias” in prong 3 but that it seems more rationally to belong to the jerk than to the second process.)

I shall argue that prong 1 is an observation that, even if not universal, is common enough to be taken as a phenomenon in need of explanation; certainly it is shown by the butterflies that I shall consider. I shall, however, argue that prong 2 is a simple misinterpretation of the fossil record, which can be fully explained by neo-Darwinian microevolutionary theory. The model of evolution in jerks is at the very least superfluous; it is in fact less compatible with our overall knowledge than is the conventional theory. Nonetheless, I shall then further argue that prong 3 is a correct and a valuable extension of evolutionary theory: while it is in no way incompatible with neo-Darwinism, it discusses matters beyond the scope of population genetics. With the tricky central prong removed, both the observations (prong 1) and the theory (prong 3) of macroevolution can be painlessly joined onto existing microevolutionary theory to produce a new synthetic theory of evolution.

It would be possible to argue this case purely theoretically, but I shall use a real example, in which we are possessed of an exceptional understanding of evolutionary dynamics: a case study of adaptive radiation. I believe it shows evolution occurring according to this synthetic model.

EVOLUTIONARY DYNAMICS OF MIMICRY

The Problem: Mimicry Rings

The rival gradual and mutational models for the evolution of mimicry supposed respectively that mimics came to resemble their models by a slow, continual process of change (Fisher 1927, 1930; Brower et al. 1971) or that the mimetic pattern was achieved by a single, and final, mutational step (Punnett 1915; Goldschmidt 1945). Empirical work on Batesian mimics in the genus *Papilio* showed that the mimicry was better explained by a synthesis of the two theories (Clarke and Sheppard 1960*a,b*; Clarke et al. 1968). I call this synthetic theory, originated by Poulton (1912) and Nicholson (1927), the *two-stage model*. According to this theory, mimicry normally arises in two steps: a comparatively large mutation achieves a good approximate resemblance to the model; it is followed by gradual evolutionary changes that refine the resemblance, in many cases to a high



FIG. 1.—The five mimicy rings to which most of the long-winged, warningly colored butterflies of the South American rain forests belong. They are represented here by one species from each ring, with the patterns as they appear in Trinidad. (From Sheppard et al. 1985.)

degree of perfection (Sheppard 1962; Ford 1964). However, it was generally accepted, on account of a cogently worded although faulty argument of Fisher (1927, 1930), that Müllerian mimicry did not evolve in this way, but was, as the early students of the subject had believed, the product purely of a gradual process of mutual convergence between the co-mimics (Dixey 1909; Brower and Brower 1972). Only recently have empirical findings about Müllerian mimicry in both moths and butterflies led two groups of researchers to the conclusions that this theory was wrong and that major mutations were involved in the origination of Müllerian mimicry also (Bullini et al. 1969; Turner 1976; Sbordoni et al. 1979; Sheppard et al. 1985). We have therefore adopted the two-stage theory for the explanation of Müllerian mimicry as well.

Any theory of Müllerian mimicry has to take into account the phenomenon of the coexistence of multiple mimicy rings. If one examines the local butterfly fauna in any area of the world, one finds that between all the aposematic (warningly colored and defended) species present there are normally only a limited number of different patterns, normally far smaller than the number of species. Each cluster of species, all sharing a common pattern, is termed a Müllerian mimicy ring. Thus, in the rain forests of South and Central America, most of the long-winged butterflies (ithomiids, danaiids, and heliconians) belong to one of only five different rings (fig. 1; Papageorgis 1975). This phenomenon is worldwide. It has been amply documented in the butterflies of Africa and southeastern Asia (Owen 1974; Ackery and Vane-Wright 1984) as well as in the hymenopterans: both wasps in Hawaii and bumblebees in the northern temperate zone are similarly

clustered into a limited number of Müllerian mimicry rings (Perkins 1912; Plowright and Owen 1980). Since we expect in Müllerian mimicry that all species will share the same pattern, this phenomenon is puzzling; even if the butterflies and hymenopterans might fail to mimic each other (some groups of moths do in fact achieve excellent mimicry of wasps), we would at least expect only one color pattern among the butterflies and one among the bees. It is necessary to account for two apparently contradictory phenomena: evolution has produced a high level of mimicry within each ring, while allowing the separate rings to go on existing side by side. We have to account for both their existence and their coexistence.

The Theory

We (Sheppard et al. 1985) have therefore considered what is known about the generalization behavior of vertebrates (Brower et al. 1971) and in particular the quantitative experiments of Duncan and Sheppard (1965), Schuler (1974), and Goodale and Sneddon (1977): the protection afforded to mimetic pattern falls away the less they resemble the model, until a pattern of very different appearance has no effective protection. Thus, if we represent the warning pattern of a butterfly on a horizontal scale, there will be an envelope of protection around it, which potentially protects patterns that only imperfectly resemble it (fig. 2*a*). Now imagine two such warning patterns in one habitat, similar enough that the envelope of protection afforded to one gives some protection to the more extreme variants of the other (or in ordinary language, suppose that predators that have sampled species A sometimes avoid the more extreme members of species B because they mistake them for A). These two species are subject to natural selection for mutual convergence of their patterns (fig. 2*b*). Eventually they will form a rather accurate Müllerian mimicry ring.

By contrast, if the two species have patterns so dissimilar that predators encountering one never imagine that it might be the other (the envelopes of protection do not overlap the other species' phenotype distribution), then there is no selection whatever for convergence, and the two patterns will remain distinct indefinitely (fig. 2*c*). We have an explanatory theory for both the existence and the coexistence of Müllerian mimicry rings.

But mutations of color patterns are occurring all the time. Suppose that species B happens to produce a mutation whose pattern falls within the envelope of protection afforded to species A (fig. 2*d*). The mimicry need not be perfect, but if it is good enough (in the figure it must lie between the points *x* and *y*), the mutation will have an advantage and will spread. In this way species B may, by a single mutation, become a Müllerian mimic of species A; in other words, species B may switch from one Müllerian mimicry ring to another. Clearly, if the mimicry is not perfect, the two patterns will then gradually converge, making the resemblance ever closer. Like Batesian mimicry, Müllerian mimicry can evolve in two stages: the mutational, one-way convergence stage followed by the gradual, mutual convergence stage. Note that in the first stage, only the less protected species can adopt the pattern of the better protected species; mutations in the other direction are not favored. Note also that one-way convergence is entirely different from the process of gradual advergence described for Batesian mimicry by Brower and Brower (1972).

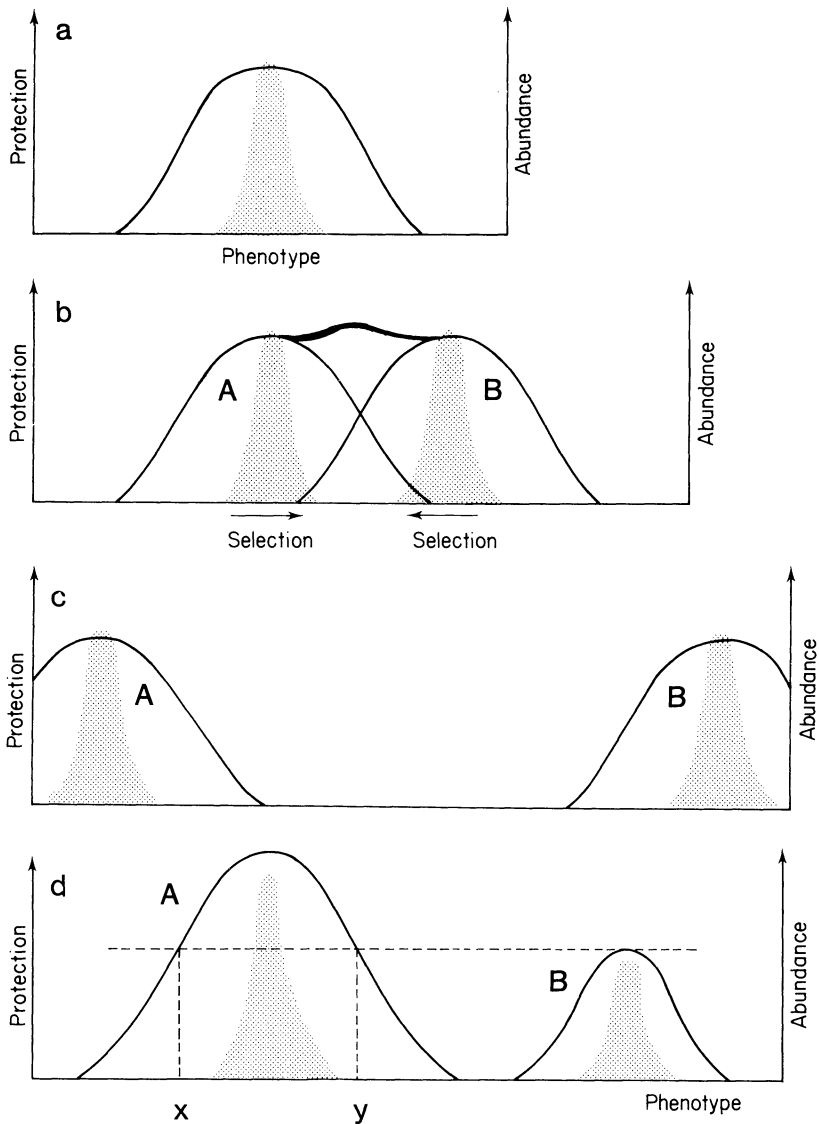


FIG. 2.—A model for the existence, coexistence, and switching of Müllerian mimicry rings. The horizontal scale represents a range of potential phenotypes. The phenotypes of existing species, with their normal variation, are shown by the stippled areas. *a*, A distasteful species, generalized by predators that encounter it, protects not only existing patterns but also a wider range of patterns than actually exists (*heavy curve*). This species is subject to normalizing selection. *b*, Two species already resemble one another fairly closely, such that each gains some protection from the existence of the other. These species are selected for gradual mutual convergence and will become Müllerian mimics. *c*, Two species, or rings of species, with markedly different patterns do not converge on one another, since the predators never confuse the two. Thus, two or more mimicry rings may persist indefinitely in the same habitat. *d*, If two species are not equally protected, one can switch to mimicking the other, even though gradual convergence is impossible, if the less protected species produces a mutant that sufficiently resembles the better protected species. (Based on Sheppard et al. 1985, in Turner 1983*b*, fig. 1. By permission of Academic Press, Inc. (London).)

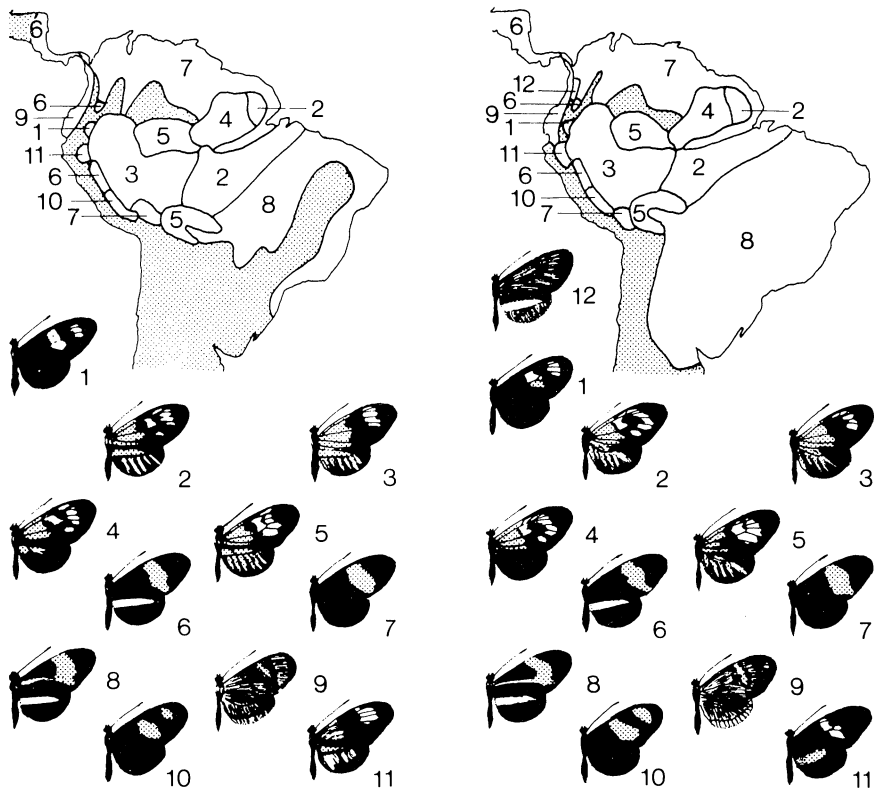


FIG. 3.—Parallel Müllerian mimicry of the races of *Heliconius melpomene* (left) and *H. erato* (right), somewhat simplified. Each race of one species (with the exception of *H. erato* race 12) can be seen to be mimicked by a race of the other, with a closely similar geographical distribution. (A detailed map showing further variants is given in Sheppard et al. 1985.) Hybridization zones (see, e.g., Mallet 1986) are omitted. Colors are black, red (stippled), and yellow or (in Ecuador) white. (From Turner 1981, fig. 2. Reproduced with permission of Annual Reviews, Inc.)

The Evidence

There is ample experimental evidence for the large mutations that have switched butterflies and moths from one mimicry ring to another. The simplest cases were found by Bullini et al. (1969) in *Zygaena ephialtes* and by K. Brown and Benson (1977) in *Heliconius hermathena*. Both species switch mimicry rings in different parts of their range, and the switching is largely accomplished by a single mutation that changes large parts of the color pattern (an illustrated map for *H. hermathena* can be found in Turner 1982, 1983*b*, 1984*c*, 1985*a*; Sheppard et al. 1985). The most extensive investigation (Sheppard et al. 1985) has been into the parallel mimics *H. melpomene* and *H. erato*, which show an enormous amount of racial divergence while maintaining nearly completely faithful, strict mimicry of each other (fig. 3; color illustrations in Turner 1971, 1975). We have good data about the genetic composition of eight races of *H. erato* and six races of *H.*

melpomene. (Mallet [1986] has added a further race of each species.) In both species, all the major changes of pattern between the races are switched by major mutations that remove or add large areas of color: the whole of a red patch or a yellow bar or extensive parts of several apparently independent yellow markings. All told, we know of 14 such major genes in *H. erato* and 12 in *H. melpomene* (Sheppard et al. 1985; genetic [linkage] maps illustrated in Turner 1984*b,c*). We also have clear evidence for the second, gradual stage in the evolution of the patterns, in the form of polygenic adjustments to the patterns produced by the major genes. For example, the thin rays on the hindwings of some races of *H. melpomene*, which are under the control of a major gene, remain but become considerably altered in shape when the gene is backcrossed into a race that does not exhibit the ray pattern.

THE GENETIC PALEONTOLOGY OF *HELICONIUS*

Tempo and Mode

Evolution in these butterflies is clearly not gradual in the genetic sense, nor is it purely saltational. Is it gradual in the longer term? The substitution of a major gene in the species over a hundred millennia would be a saltational change at the genetic level but would be a gradual change in geological time. In the absence of fossils this question cannot be answered for certain, but luckily a combination of genetics, cladistics, and paleoclimatology allows us to infer what has happened with a greater than average degree of accuracy. It was first pointed out by Haldane (1924) that when new mutations become established in populations under natural selection, there is a large or overwhelming tendency for dominant rather than recessive mutations to establish themselves. The reason is that recessive mutations cannot be expressed and therefore cannot be selected until they have risen to a rather high frequency by random drift, whereas dominant mutations are steadily selected when they are still at low frequencies. In this way most of the genes producing industrial melanism in moths are dominant to the original form of the species (Kettlewell 1973). It is not that recessive melanic mutations do not occur; they do, but they seldom establish themselves in populations. This effect, which I have called "Haldane's sieve" (Turner 1981, 1983*b*) is overwhelming in large populations and by no means negligible in small ones. It allows us with a high degree of probability (although obviously not with certainty) to put a direction on any evolutionary change whose genetics is well understood; normally, the recessive allele is ancestral. With the ancestral and derived genetic states thus established, it is a matter of no great difficulty to produce minimum cladograms using the weighted-invariant-step method (Farris et al. 1970).

Such a piece of genetic cladistics is shown for *Heliconius melpomene* and *H. erato* in figure 4. There are a number of things to note. First, the overall ancestors and all the extinct patterns reconstructed at the major nodes of the trees show a very close mimetic resemblance between the two species. They appear to have been evolving in parallel rather than converging. Brower and Brower (1972) indeed suggested that Müllerian mimicry might arise as the result of parallel

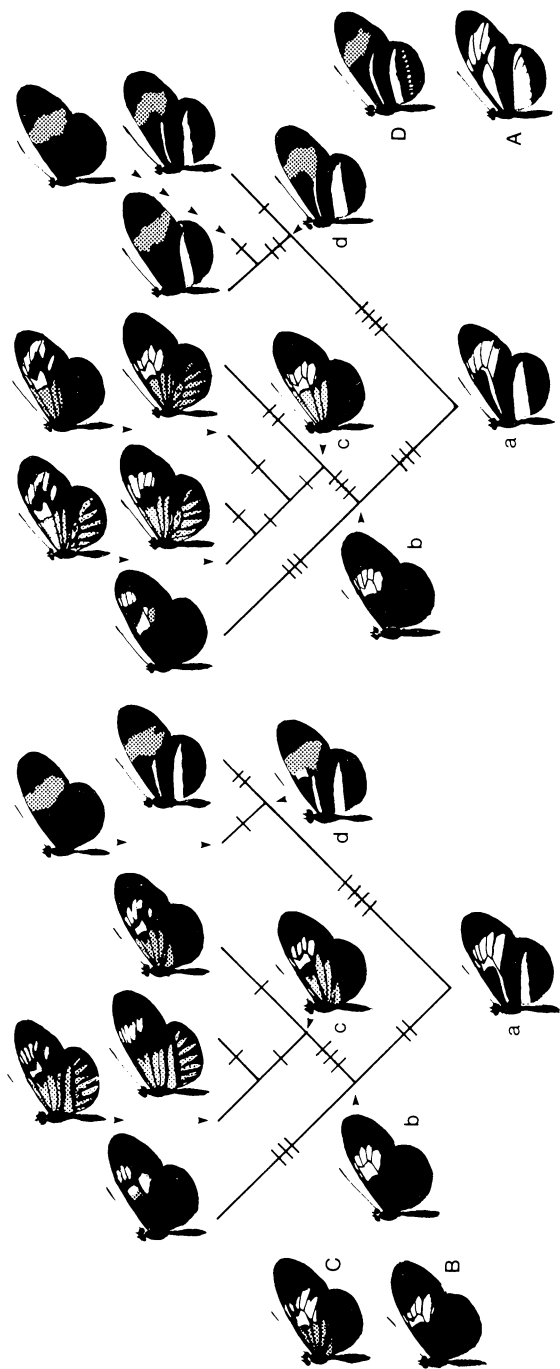


FIG. 4.—Punctuational evolution reconstructed by genetic cladistics: cladograms of some of the races of *Heliconius melpomene* (left) and *H. erato* (right). Minimum trees (selected for illustration from a number of equal-length trees obtained) have been computed by the method of Farris et al. (1970), using the genetic composition (not the phenotypes) of the races as the data set. Cross bars represent the substitution of a major genetic change in the pattern (it is possible to work out roughly what these are by comparing the butterflies at each end of the branch); butterflies *a-d* are reconstructed ancestors at the nodes of the trees; *A-D* are existing species that still show these patterns, which *H. melpomene* and *H. erato* may have mimicked in the past. The extant races at the top correspond with those in figure 3 (left to right, upper row first): races 2, 7; 1, 3, 4, 8 (*H. melpomene*); and 2, 4, 7; 1, 3, 5, 6, 8 (*H. erato*). (From Turner 1983*b*, fig. 8. Reproduced with permission of Academic Press, Inc. (London).)

evolution following the retention of patterns inherited from a common ancestor, and it is possible that the initial mimicry (*a* in fig. 4) is an ancestral pattern. This parallel radiative divergence is indeed the obvious explanation for their extraordinary parallel mimicry; it would be a coincidence beyond belief if the dozen and a half modern races of *H. erato* had all converged independently from different ancestors on the dozen and a half sympatric races of *H. melpomene* that they now mimic. Second, the reconstructed patterns all seem to have belonged to mimetic associations that still exist somewhere in South America, although some are now only sparsely represented (depicted in the margins of fig. 4). Most importantly, the reconstructed pattern of the overall ancestors (*a* in fig. 4) is still exhibited by close relatives of both *H. melpomene* and *H. erato* (one is illustrated at *A*) and is therefore probably close to the ancestral pattern as it really was.

The reconstruction reveals that an astonishing diversity of pattern has been produced by a relatively small number of genetic changes, shown by the cross bars on the arms of the cladograms. Each of these represents the substitution of a major gene (fig. 4).

We now ask whether the pattern of evolution is revealed as gradual or punctuational. This amounts to asking how long the substitutions take relative to the total length of time represented by the branch of the tree. Obviously, there is no certainty about this, but the overwhelming odds are that the substitutions occupy a relatively small part of the available time. First, under natural selection, a new phenotype produced by a single gene moves from a low frequency of 10^{-x} to a high frequency of $1 - 10^{-x}$ in only $10^{x/2}/s$ generations, where s is the selection coefficient (Turner 1983*b*). If $x = 3$ (a generous margin for detecting a rare variant) and $s = 0.01$, this period is only 3200 generations or, in *Heliconius*, about 320 yr (actually shorter, if we allow s to change in a positively frequency-dependent manner, which it must do in a Müllerian mimic). Our best guess is that the trees span at least the period of the last glaciation (a minimum of 30,000 yr), and possibly much longer. In other words, the gene substitutions probably occupied only a short period of the available time. Seen in fossils or in time-lapse photography, the butterflies would show a clear pattern of punctuational evolution, switching from one stable, static color pattern to another in something very like a geological instant.

Extinction as a Driving Force

What causes the stasis and the switching? Stasis in these butterflies is easily explained by the theory of Müllerian mimicry. Warning patterns are consistently subject to stabilizing selection (demonstrated experimentally by Benson [1972]), since deviants are not clearly recognized as having the warning pattern and are therefore sampled. It is this effect that produces the stable, coexisting mimicry rings. Our theory of Müllerian mimicry also suggests a reason for the switching: the capture of *H. melpomene* and *H. erato* by other, better protected mimicry rings at different places and different times. Some of these rings are shown in the margin of figure 4.

The historical setting in which this capture took place was, we believe, the shrinkage of the rain forest into a number of more or less isolated refuges during

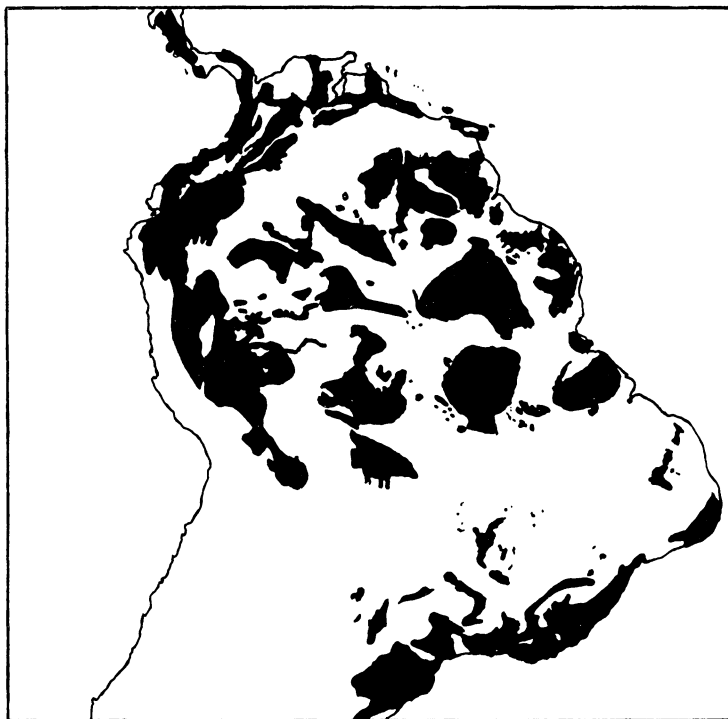


FIG. 5.—The probable geographical origin of the extant races of *H. melpomene* and *H. erato* (fig. 3); that is, the approximate location of South American rain forests at the peak of the last glaciation, ca. 18,000 years ago, deduced from a combination of biogeographical and paleoecological data. (Redrawn after fig. 16.36 by K. Brown in Prance 1982.)

the progressive drying and cooling of Amazonia during the last glaciation (fig. 5; K. Brown et al. 1974; Prance 1982). Different races of *H. melpomene* and *H. erato* appear to have adopted different patterns in different refuges, mainly as a result of the long-term changes in faunal and perhaps even floral composition that must inevitably occur in such ecological islands (Turner 1977a, 1982, 1985a). As they become progressively isolated from the other fragments of the once continuous habitat, plant and animal species become progressively extinct. Once this happens, the whole ecological structure is changed: some mimetic butterflies may disappear; over the long term, the abundance of others may be radically altered by the extinction of food plants, parasites, competitors, competitors of food plants, and so on. What was formerly a rare and not well protected pattern may become the pattern that is the best protected in one particular refuge. Any species that can reach that pattern by means of a single mutation will do so. As a result, the ring that is best protected and hence most mimicked locally differs from refuge to refuge, and widespread species like *H. melpomene* and *H. erato* differentiate into numerous sharply contrasted races.

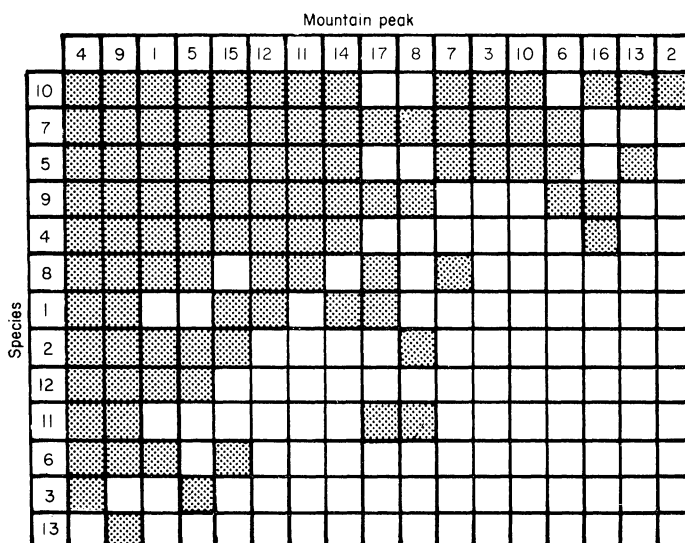


FIG. 6.—Disorderly but by no means random extinction of species in a group of refuges, shown by the boreal mammalian fauna of a series of mountain peaks now isolated by desert in the Great Basin of the western United States. Stippling indicates the presence of a species. For the names of the species and mountains, see J. Brown (1971), from whose data this diagram has been constructed. (From Turner 1977a, fig. 3. Copyright by J. R. G. Turner.)

The kind of extinction pattern that I am postulating cannot be demonstrated for the now rejoined refuges of Amazonia, but it is clearly shown by J. Brown's (1971) study of the mammalian fauna of the forested mountaintops in the otherwise arid Great Basin. As figure 6 shows, each refuge has its characteristic faunal composition, arising from the disorderliness (not randomness) of the extinctions. Different species became extinct in different islands.

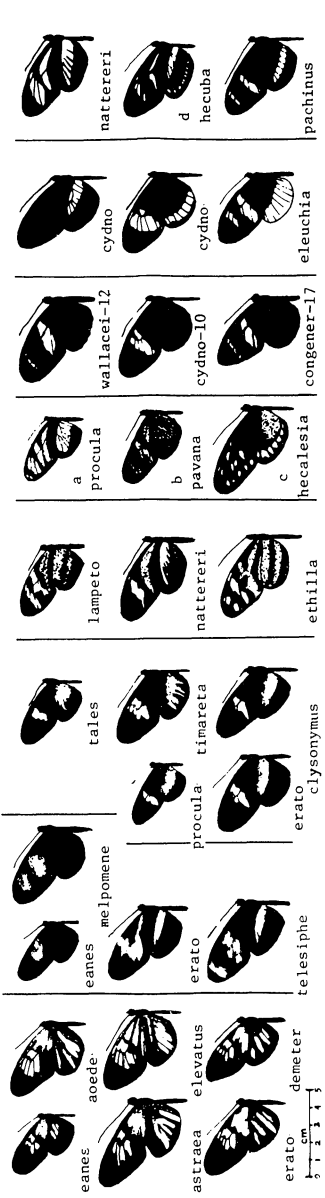
TESTING PUNCTUATED EQUILIBRIUM

These butterflies then allow us to test the prongs of punctuated-equilibrium theory. With prong 1 (stasis and change), the butterflies are clearly highly compatible, perhaps showing the effect more strongly than many other organisms. With prong 2 (evolution in jerks), they are equally clearly at complete variance. The punctuational changes have not been associated with speciation; they take place only between races of the same polytypic species. We could, of course, suggest that these races will eventually become full species, as many of them may, and that the punctuational changes are therefore associated with speciation. We could also argue that the punctuational changes must have occurred after a cladogenic event, even though that led only to the formation of a geographic race. Both these statements make prong 2 true only in a tautological sense: if there are not two different branches of the evolutionary tree, then we cannot perceive a difference between them. We can see this by a little thought experiment. Suppose that

| Genus/group | Dennis-Ray (red, yellow) | Red on FW, (yellow on HW) | Red on HW, yellow on FW | "Tiger" ithomiine | Other mimetic* | Blue and yellow, FW | White or yellow on HW & usually FW | Black with yellow bars |
|-----------------------|--|--|--|--|---|--|--|--|
| <i>Euclides</i> | <i>eanes</i> (pt) <i>vibilia</i> (pt) <i>tales</i> | <i>procula</i> (pt) <i>tales</i> (pt) | <i>isabella</i> <i>lampeto</i> | <i>procula</i> <i>vibilia</i> <i>pavana</i> <i>godmani</i> ^c <i>hecuba</i> ^d | <i>eanes</i> (pt) | <i>hecule</i> (pt) <i>timareta</i> (pt) <i>cydno</i> (pt) <i>luciana</i> (pt) <i>leucadia</i> <i>sara</i> (pt) <i>antiochus</i> (pt) congener | — | — |
| <i>Neruda</i> | <i>aoede</i> | — | — | — | <i>metharme</i> <i>doris</i> (pt) <i>xanthocles</i> (pt) | <i>doris</i> (pt) | — | <i>doris</i> (pt) <i>hecuba</i> (pt) |
| <i>Laparus</i> | <i>xanthocles</i> (pt) | — | <i>hierax</i> | — | <i>burneyi</i> (pt) <i>wallacei</i> | — | — | — |
| <i>Heliconius</i> II | <i>burneyi</i> <i>egeria</i> | — | — | — | — | — | — | — |
| <i>Heliconius</i> III | <i>astraea</i> <i>melpomene</i> (pt) <i>timareta</i> (pt) <i>elevatus</i> | <i>melpomene</i> (pt) <i>besckei</i> | <i>melpomene</i> (pt) <i>timareta</i> (pt) | <i>nattereri</i> ♀ <i>numata</i> <i>hecule</i> <i>ethilla</i> <i>hecalesia</i> (pt) | <i>atthisd</i> <i>cydno</i> (pt) ^c <i>cydno</i> (pt) ^d | <i>cydno</i> (pt) | — | <i>nattereri</i> ♂ <i>pachinus</i> <i>luciana</i> (pt) |
| <i>Heliconius</i> IV | <i>erato</i> (pt) <i>demeter</i> | <i>erato</i> (pt) <i>hermathena</i> <i>telesiphe</i> | <i>erato</i> (pt) <i>clysonymus</i> <i>hortense</i> <i>ricini</i> | <i>hecalesia</i> (pt) <i>charitonia</i> (pt) ^d | <i>erato</i> (pt) <i>sara</i> (pt) <i>antiochus</i> (pt) <i>sapho</i> <i>eleuchia</i> | — | — | <i>hewitsoni</i> <i>sara</i> (pt) <i>charitonia</i> (pt) |
| Other Genera | <i>Podotricha</i> <i>telesiphe</i> | <i>Podotricha</i> <i>telesiphe</i> | — | — | — | — | — | <i>Philaethria</i> (3 species) |

* a = various primitive Ithomiinae, b = *Actinote* (Acraeinae), c = *Tithorea* (Ithomiinae), d = *Elzunia* (Ithomiinae).

FIG. 7.—Adaptive radiation, or convergent and divergent evolution, in *Heliconius* and the related genera. Classification by morphology (genera and subgenera) on one axis and by color pattern on the other shows that morphological groups have radiated into different color patterns, examples of which are shown beneath. The whole pattern can be seen as the long-term extension of parallel evolution of the type seen in figure 3; pt, in part. (Updated from Turner 1968 in K. Brown 1981, fig. 3. Reproduced with permission of Annual Reviews, Inc.)



indeed a punctuational change cannot occur unless there is another population of the species somewhere that does not undergo the change. Let us say that the population of *H. melpomene* in Trinidad is about to change its pattern radically as a result of changed ecological circumstances in that island. The punctuated-equilibrium theory, strictly interpreted, states that such a change can take place only if there is a population of *H. melpomene* on the mainland that is not evolving. If *H. melpomene* is extinct everywhere but in Trinidad, then the punctuational change cannot occur. The statement is so obviously ridiculous that the reader may wonder why I have made it. It is the clear implication of the statements made unequivocally by both Stanley (1979) and Gould (1979) that punctuated phyletic change does not occur and that all significant punctuational change occurs when the tree branches. Quite clearly, as all critics have pointed out (e.g., Levinton and Simon 1980; Charlesworth et al. 1982; Gingerich 1985; Palmer 1985; Seeley 1986), punctuational change is very likely to occur sometimes without branching.

It might be possible to save prong 2 by claiming that species differences in *Heliconius* are of a different kind from those observed between the races of *H. melpomene* and *H. erato*, and that all of this is therefore totally irrelevant to the question of evolution in jerks (that is certainly the kind of claim made by Goldschmidt). Although I cannot disprove this suggestion, I think it unlikely. There is an enormous adaptive radiation and convergence of patterns within this group (fig. 7) that looks just like the pattern of radiation and convergence between *H. melpomene* and *H. erato* writ large. Our ability to produce, both in theory and in the laboratory, the patterns of related species by rearranging genes found in extant races of *H. melpomene* and *H. erato* suggests that the genetics of trans-species differences are no different from the genetics of interracial differences (the patterns in question are depicted in Turner 1984*b*, 1986).

It is harder to assess prong 3 (the second process) in these butterflies, but I believe they probably do demonstrate that it occurs. Within the heliconians, a considerable preponderance of species have patterns of the same general type as *H. melpomene* and *H. erato*: that is, black with striking yellow, red, white, and blue marks. Species with a more conventional, complicated fritillary pattern of black spots on orange are very much in the minority. Although some species have switched between these patterns, I believe it is more reasonable to suppose that this evolutionary trend toward the black, simple patterns has been produced by a greater rate of speciation in the subgenus *Heliconius* (probably induced by their tendency to inhabit the interior of the forest and thus suffer population fragmentation during the glaciation) and by a much lower rate of speciation in *Dione* and the similar genera of open-country butterflies that have the more complicated orange patterns.

THE NOT-THE-PUNCTUATED-EQUILIBRIUM THEORY

"Another Way of Seeing" the Candelabra

Accepting that *Heliconius* conform to prong 1 and prong 3, what sort of evolutionary theory do we get if we dispense with prong 2, that is if we assume

that major and/or rapid evolutionary change occurs independently of speciation and cladogenesis? This assumption leads to the conclusions that speciation without morphological change produces sibling species and that morphological change without speciation produces the allegedly nonexistent punctuated phyletic evolution; for some proportion of the time, naturally, both processes (or neither) will be taking place. The evolutionary tree drawn with these assumptions is shown in figure 8*b*. It looks similar to the candelabra tree of figure 8*a* but separates morphological change and cladogenic or specific isolation on separate horizontal axes. Gradual change is omitted, or shown as stepwise punctuational change, not because I believe it does not occur, but to keep the perspective of the drawing and of the argument from becoming excessively ambiguous.

The question is, what would evolution following this pattern, the one suggested by our findings with *Heliconius*, look like in the fossil record? Obviously, isolation is extremely difficult to detect (reproductive isolation is impossible, geographical isolation requires sampling more extensive than is yet available for most groups). This amounts to saying that all fossil species are merely morphospecies; it means that what we see in the fossil record is an image of this tree rotated so that the branches representing cladogenesis are facing end on toward us and are invisible (imagine the figure as a rotating, three-dimensional computer graphic). This produces the effect shown in figure 8*c*, in which only the morphological changes are detected. If these are in addition so rapid as to occupy periods shorter than the best resolution of the fossil record, we see figure 8*d*, a series of morphological "species" appearing suddenly and just as suddenly disappearing, with no evolutionary continuity and no apparent evolutionary change. This is indeed the pattern that punctuationalists tell us is observed in the fossil record.

Given figure 8*d*, it is all too easy to assume that all the "gaps" represent evolutionary jerks (that is simultaneous morphological change and cladogenesis) and to connect the vertical bars into the candelabra model of figure 8*a*. In short, I suggest that the candelabra model is an attractive but naive misinterpretation of a fossil record that has been generated by something much more like figure 8*b*.

If my suggestion is correct, then the usual criterion by which punctuated phyletic change has been refuted in the fossil record (Stanley 1982)—that the ancestral species does not disappear when the descendant species appears—cannot be used as evidence on this point at all. The apparently persistent ancestral form may well be another related species that speciated from the stock some considerable time before but that is indistinguishable from its relative until one or the other of them undergoes a punctuational change; then one of the invisible branches of the tree pops out from behind the sibling form that is concealing it. I call this the "popping out from behind" model.

It is important to remember, when considering how likely this explanation is, that while many extant species are sibling species of this kind, many more are siblings in the fossil record. Whole genera and even families there present indistinguishable morphologies because so little of the phenotype survives fossilization. How many species of butterfly or passerine could we recognize if we were presented only with their skeletons?

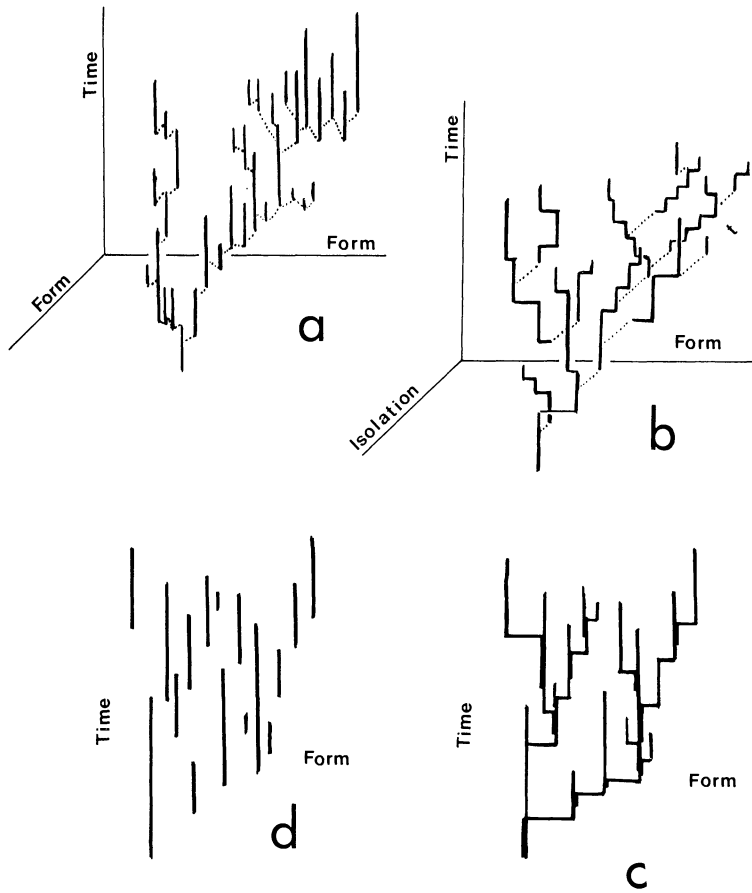


FIG. 8.—Various ways of depicting and explaining punctuational evolution. *a*, In the candelabra model (Eldredge and Gould 1972), large morphological changes and speciation are assumed to be highly correlated. *b*, In the “popping out from behind” model, it is assumed that speciation-cladogenesis and rapid morphological change are not strongly correlated. If we are unable to detect the branching events (e.g., if the species are sibling species or if the morphological changes that occur do not fossilize), evolution of type *b* appears as in *c*, that is, as if the tree is viewed directly from in front. If large morphological changes occupy only relatively short periods of time, as is suggested in the study of *Heliconius* (fig. 4), then the fossil record will present the picture shown in *d*, an illusion of evolution occurring without intermediate stages, in which branching and morphological change appear to take place simultaneously. This in turn leads to the misinterpretation of the evolutionary process seen in *a*. (From Turner 1983*a*; 1986, fig. 5, by courtesy of Dahlem Konferenzen. Copyright 1985 by J. R. G. Turner.)

The causes of stasis and phyletic punctuational change in *Heliconius*, both needed to generate the "popping out from behind" model, seem to be fairly clear. Stasis is produced by normalizing selection on the warning patterns. Punctuational change is produced by a combination of genetic mutation and a change in the ecological balance, resulting from extinctions, which alters the ecological structure of the community in such a way that new phenotypes are favored over the old. The process is rather like a photographic negative of the opening and closing of ecological niches: extinction empties or depauperates both niches and mimicry rings. The species that remain tend to evolve so as to occupy the emptier ecological niches on the one hand, and the more fully occupied mimicry rings on the other.

How General Is the Model?

It is, of course, a mistake to think that one organism tells us everything about evolution. We know that the way things are in *Heliconius* must be one way in which evolution proceeds, but we cannot be sure that the result is general. The best I can claim for these findings is that in science we are safer working outward from facts we have established, even if these prove to be true only in limited circumstances, than basing theories on pure speculations unsupported by any facts at all. The *Heliconius* system looks like a good starting point.

Many geneticists will question the likelihood that such punctuational changes are produced by single mutations as in *Heliconius* (Charlesworth 1982). I leave this question open. As far as the overall features of evolution are concerned, it makes little difference whether the changes are produced by single large mutations or by several smaller ones. The speed of evolution depends much more on the strength of selection (and the generation time) than it does on the genetic architecture of the trait selected. With a coworker, I have simulated two-locus systems with various kinds of rather strong epistasis and found that, even with extremely strong inter-locus epistasis and loose linkage, the time required to alter the frequency of the phenotype is seldom altered by more than one order of magnitude from that predicted if the trait is governed by a single gene (Turner and M. Mukherjee, unpubl. data). It is easy enough to show that except for extremely large populations of big organisms with long generation times, changes of more than 50,000 yr demand selection coefficients so small that the directional change would be swamped by random drift. Except for the tracking of slow secular changes in the environment, population genetics predicts that evolution by natural selection will be punctuational! Punctuated equilibrium does indeed arise as a valid prediction from neo-Darwinian theory.

Of greater uncertainty is the cause of stasis. It is rather simply explained in *Heliconius* as the result of normalizing selection on the warningly colored patterns, which are known to be subject to strong pressure to continue waving their established trademark in the face of the predators (Benson 1972). As I have argued above, the cause of punctuational change, less certainly but quite probably, is a change in the ecological balance resulting from changing patterns of colonization and extinction, which in turn renders ecological niches (mimicry rings) relatively more or less occupied. It is not clear whether a similar argument necessarily

applies to other features of other organisms. It is surely true that extinction creates holes in the ecological hyperspace, into which remaining species may evolve, and that in the absence of such holes, there may be little evolutionary change. (This is, more or less, a return to Lyell's [1832] concept of the occupancy of stations in the economy of life; see also Hodge 1983.) Punctuation and stasis might be generated by the alternate saturation and opening of the ecological space. Against this, one can argue that fossil species appear to remain constant during periods of time that are so long that they can hardly encompass total ecological stability. However, this objection again runs up against the problem that only part of the organism is revealed in the fossil. Parts that are not fossilized may well be changing. The fossil record must surely overestimate the amount of stasis.

It is also possible that the hard fossilized parts of animals are atypical of the phenotype in another way, in that they must represent an approach to optimum solutions to mechanical problems. Although the occupancy of the ecological space may change rather frequently, the laws of physics do not. The almost optimal solution to a mechanical problem may remain adaptive over a wide range of ecological circumstances.

“Species Selection”

Gould (1982) has named three causes as responsible for prong 3 (the second process): differential extinction, differential rate of speciation, and a consistent bias in the direction of the evolutionary jerks. Because no explanation seems to be forthcoming for such a bias in direction other than natural selection as understood by neo-Darwinists, I propose that such “bias” is an example of an evolutionary trend caused by persistent (but if the change is punctuational rather than gradual, clearly not continual) natural selection. I consider only the first two processes to belong truly to the “second process.”

One must also make clear distinctions between the ways in which these second-process phenomena might produce evolutionary patterns or trends (Levinton et al. 1986). Let us say a particular character, such as knobs on the test of a sea urchin, becomes commoner in some particular phylad, not because of individual selection within species but because there are two clades. By ancestry, all species in clade A have knobs, and all species in clade B lack them. By greater rates of extinction or speciation there come to be more species in the “with knobs” clade (A) than in the “without knobs” clade (B). Such a trend could be considered a result of “species selection” (the usually favored term for my second process; for the many possible meanings of “species selection,” see Hoffman 1984) only if the knobs were causally contributing to the lowered extinction rate or to the enhanced speciation rate of the species in clade A. If the increase in knobs resulted simply from the random extinction of species (which, as is normally the case with random events, would generate an apparent bias in favor of one clade or the other), it should more properly be attributed to random species drift. If, however, species were becoming extinct or speciating nonrandomly, but as a result of possessing other features quite unconnected with the knobs (such as larger population size, when the knobs had no effect on population dynamics), then the knobs could be

said to be increasing in frequency by species hitchhiking, a term we developed in Dahlem by analogy to the hitchhiking effect in population genetics (Maynard Smith 1978; Levinton et al. 1986). It seems to be the same as the "effect hypothesis" of Vrba (1980, 1984). Such distinctions are, of course, hard to make in practice on fossils, but it is important to make them in theoretical discussions.

It is also important to note that in terms of the "popping out from behind" model, Gould's birth bias does not represent the results of true speciation at all. It results only from the generation of new morphospecies that happen to be distinguishable by some character other than the one (the knobs on the sea urchin) that interests us and defines our clade. The clade appears to have more species not necessarily because it contains more species, but only because it contains more species with distinctive morphologies. Indeed, given that some characters are likely to remain constant within a clade (perhaps that is how we define it) and others to evolve, the creation of apparent trends in this way is virtually inevitable.

IS PUNCTUATIONISM "EFFECTIVELY DEAD"?

Where does this synthesis, if correct, leave the punctuated-equilibrium model? Since Gould (1982) regarded prong 2 (evolution in jerks) as the essential difference between punctuated equilibrium and neo-Darwinism, its removal might seem fatal to the Gould-Eldredge model. This, however, is excessively pessimistic. Without prong 2, long-term stasis (prong 1) still requires investigation and, if proved not to be an illusion produced by the conditions of fossilization, explanation. Likewise, even without prong 2, evolutionary patterns and trends will still be generated on a longer time scale and by processes other than those considered in microevolutionary theory. (At the very least, such patterns will be generated purely at random by extinction.) It makes no difference whether the entities (species, phyletic lines) whose rates of proliferation and extinction generate the pattern have become phenotypically distinct through evolutionary jerks (punctuational events), through rapid or punctuated phyletic change, or indeed through gradual phyletic evolution. The theory of the second process (prong 3) stands quite independent of the theory of evolution in jerks. If we like, prong 2 is a Wittgenstein ladder: climbing up it has clearly helped us to understand prong 3, but once we reach that point the ladder can be kicked away. Or to use terms more familiar to evolutionary theorists, the candelabra model of evolution is analogous to the models that population geneticists construct: infinite populations (such as can never exist), the better to understand the action of natural selection, and totally neutral phenotypes (which probably seldom exist above the molecular level), the better to study the effects of random genetic drift. The candelabra model is a mental construct that allows us to see what evolution would be like in the hypothetical absence of microevolutionary processes. Once we have understood the second process (prong 3) in this way by removing microevolution from our thoughts, we are in a much better position to see how the macroevolutionary patterns of prong 3 might be imposed on the products of microevolution. We can, for instance, understand much more clearly that an apparent trend in the fossil record is not necessarily the result of cumula-

tive microevolutionary change; it may be alternatively, or additionally, generated by the differential patterns of extinction and speciation that constitute the second process. An example that would, I think, be perfectly acceptable to most evolutionists as a theoretical suggestion (although it might be factually incorrect) is the familiar one of individual natural or sexual selection tending to increase body size in mammals, producing a microevolutionary trend, with an additional macroevolutionary counter trend superimposed because species with large body size tend to become extinct.

Where does such a synthesis as this leave natural selection as the “onlie begetter” of evolutionary change? Such patterns, be they random or ordered, as are generated by the second process must be imposed on a diversity of phenotypes created by microevolution; that is to say, barring whatever proportion of these phenotypes are produced by random genetic drift, by natural selection. The second process does not create organic diversity, any more than natural selection creates genetic diversity. Selection sorts the genetic diversity created by mutation; the second process sorts the phenotypic diversity created by microevolution. The truly interesting question is whether natural selection, out of all these processes, is the only one that creates functional order. Mutation and random drift are subspecies of the second law of thermodynamics and create only chaos. Is the second process similarly chaotic, or does it have powers analogous to those of natural selection? Whatever answer we obtain, clearly most of the features that come to distinguish the phenotypes of organisms above the molecular level, however they may be subsequently sorted, have been generated by natural selection and are therefore in that sense adaptive.

SYNTHESIS

The synthesis of neo-Darwinism and punctuationism that both Gould (1982) as a proponent of punctuated equilibrium and I (Turner 1983*a*) as a critic have anticipated seems not to be particularly difficult. That evolution proceeds at an uneven speed (prong 1) is no great surprise to population geneticists (although most would question the rigid bimodality of rate implied by the candelabra model). That some changes can be very rapid indeed was well established in the Modern Synthesis (Kettlewell 1973). Long-term stasis, although at least one neo-Darwinist (Haldane 1954) had recognized and attempted to explain it, sits less easily with population genetics. It may be explained by a combination of ecological packing, imperfect fossilization, and for the fossilized hard parts selection against deviations from mechanical optima.

Prong 2, the view that speciation is highly correlated with large morphological changes (evolution in jerks) is probably simply a misinterpretation of the fossil record: evolution in reality is more like figure 8*b* than figure 8*a*. It should be noted, however, that this prong is neither as essential to punctuationism nor as incompatible with neo-Darwinism as one might think. In particular, providing that no special “mold-breaking” mechanism is required to account for the evolutionary jerks, such large morphological changes as are associated with speciation (with

whatever degree of correlation) are presumably generated by adaptation, selection, and random drift, mixed in still unknown proportions. All of these are well-explored aspects of neo-Darwinism.

Similarly, contrary to the impression given by many arguments both for and against, prong 3 (the second process) does not critically depend on the correctness of prong 2 (evolution in jerks). The imposition of longer-term and larger-scale patterns on the products of microevolution is a legitimate area of study independent of the formulation of population-genetic theories, and it leaves neo-Darwinism largely intact. Whether those patterns are significant or nonrandom and whether the processes that generate them account for more that is interesting in evolution than do the processes of microevolution are still matters of inquiry. For instance, that the processes of differential birth and extinction of species may generate what appear to be evolutionary trends does little to alter my view that most of the morphological and physiological features of organisms are the result of adaptation to their past and present environments.

SUMMARY

It has been suggested that the punctuational pattern of morphological change observed in the fossil record demands a new theory of evolution, largely superseding neo-Darwinism. I argue here that the processes of microevolution already known in actual populations account for punctuational evolution and that the apparent pivot of the punctuational theory—the high correlation of speciation with large morphological change—is itself an illusion generated by the fossil record. I suggest that the “candelabra” model of evolution of Eldredge and Gould represents evolution less realistically than the “popping out from behind” model proposed here.

This argument is supported by a study of the dynamics and genetics of the evolution of Müllerian mimicry. On the basis of a theory that explains the existence and coexistence of mimicry rings, one can build a historical and cladistic reconstruction of evolution in *Heliconius*, a group of butterflies apparently undergoing punctuational changes that are not accompanied by speciation.

I therefore argue that punctuational theory can be synthesized with neo-Darwinism: (1) punctuational change is fully compatible with what is known of the genetics of populations; (2) morphological change and speciation are not closely correlated; (3) nonetheless, the so-called processes of “species selection” may generate evolutionary patterns additional to those produced by the processes of microevolution. There is, however, considerable misconception at present about the nature of “species selection.” “Direction bias,” for example, appears to be largely explicable by individual natural selection.

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