1.1 Fossils and Evolution

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Summary. Our modern synthetic view of evolution represents the collective wisdom of investigations carried out over five centuries, beginning with the first detailed comparisons of fossils to living organisms. When adequately sampled, fossil mammals exhibit many of the patterns expected of gradually evolving species. Morphological variation in early Cenozoic mammals is comparable to that of modern mammals, and study of successive samples closely spaced in time indicates that species are dynamic, changing continuously and continually at variable rates including rates that characterize their transitions. Anagenesis is an important mode of speciation and (pseudo)extinction. Cladogenesis is also important, but more difficult to document. Species durations are more dispersed than would be expected if they were Poisson-distributed, indicating that they are interdependent and extrinsically determined. All time series can be modelled as random walks at some rate on some scale of time. Successive samples of *Hyopsodus* closely spaced in time are more distinct morphologically than predicted by random genetic drift, suggesting a deterministic component of change (possibly selection). Most evolutionary rates scale as a function of time. Temporal independence of evolutionary rates was previously known only in artificial selection experiments. Here the first instance is reported for evolution on a geological scale of time. Slowing molecular change in primate evolution may be due to natural selection. Repeated regularities cannot be explained by stochastic processes alone, and evolution is more than random.

Introduction

The more dominant and urban we become, the more easily we believe, consciously or unconsciously, that the Earth is a world of our own creation. Progress is no longer moving forward in time, but now a pressing question of good or bad. Observation and description are increasingly replaced by advocacy and definition. Study of evolution is not immune. We do not know a priori how evolution works,

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and it may not work as we think it should. The only way to learn is to observe, quantify, and compare its many patterns on a wide range of time scales, prejudicing perception with as little preconception as possible. Patterns speak for themselves when evidence is sufficient, and evidence is essential in any science. Here I want to review principles that constitute the modern synthetic paradigm of evolution and illustrate new empirical patterns that may be useful in advancing our understanding of how evolution works.

Evolution as a Science

Evolution is an interdisciplinary "historical" and "actual" science. Evolution is *historical* in the sense that it deals with organisms living in the past, patterns of change over long intervals of time, and relationships formed at different times in the past. Evolution is *actual* in the sense that it is ongoing, the underlying process takes place on a time scale of generations, and this can best be studied in the present. Historicism and actualism are complementary and necessary mutually-illuminating approaches to the study of evolution.

Evolution developed from the historical sciences of geology and paleontology, and the fossil record is the only record for much of evolutionary history. The tangible empirical *patterns* of evolution showing progressive change in organisms, faunas, and floras, are facts of geology and paleontology. At the same time, evolution is an integral part of biology because the objects of study, even in the geological past, are organisms related to those living today, because living organisms are products of evolution, and because the ongoing process of evolution is most accessible for study in the present. The intangible theoretical *processes* of evolution, by the very nature of processes, cannot be observed directly but must be interpreted from patterns. Consequently, evolutionary theory has always been debated at some level.

Principles that guide evolutionary studies are rarely discussed explicitly, perhaps because they are many or possibly because they seem self-evident. An outline of evolutionary principles is provided in Table 1. These are conveniently subdivided into perception principles and process principles. All are "first principles" in the sense that they are *basic* principles, but not in the sense that they are in any way a priori principles; each is now based on experience and evidence rather than theory (although each necessarily developed from investigations motivated by theory of some kind, and their importance is enhanced by theory developed subsequently).

Our understanding of the vitality of fossils is based, ultimately, on their detailed similarity to parts of living organisms. This is discussed at length by Rudwick [1]. It is perhaps best exemplified by the important role published illustrations played in conveying similarity of form during the development of paleontology as a science. Comparison of fossils to living organisms began with Gesner's comparison, published in 1558, of a "*Glossopetra*" to the living shark whose teeth it resembled. Similarity is a key word in the principle of vitality of fossils as, we shall see, it is in other principles as well. Similarity reflects the broader scientific principle of sim-

Table 1. Perception and process principles comprising the modern synthetic paradigm of evolution. This list is probably incomplete: certainly additional authorities could be cited. Principles of uniformity (or consistency) and simplicity common to science in general are also assumed

Principle	Discipline	Nature of evidence	Authorities
Perception principles concerning ancient fauna and flora			
1. Vitality of fossils	Paleontology	Detailed similarity of fossils to living organisms	Leonardo da Vinci (ca. 1508) Gesner (1558, 1565)
2. Superposition	Biostratigraphy	Stratified sediments (and most fossils) are deposited from above in a gravitational field	Steno (1669)
3. Succession	Biostratigraphy	Fossil faunas and floras change at successively higher levels in a stratigraphic column	Cuvier and Brongniart (1808) Smith (1815)
4. Correlation	Biostratigraphy	Successions in widely separated columns can be explained by reference to a general composite succession	Cuvier and Brongniart (1808) Smith (1815) Lyell (1832)
Perception principle concerning modern fauna and flora			
5. Finite diversity	Systematic biology	There are a finite number of species; these live in populations of finite size, and vary within finite limits	Ray (1686) Linnaeus (e.g., 1758) and others
Process principles: Anagenesis (transformation)			
6. Continuity	Evolution	Intermediates evidence transition and transformation	Lamarck (1809) Darwin (1859)
7. Variation	Evolution	Species vary and variation is important in their evolution	Darwin (1859)
8. Inheritance	Evolution	Important variations are those inherited from generation to generation	Lucas (1847–50) Darwin (1859)
9. Fecundity	Evolution	Species have the potential for exponential growth in numbers	Malthus (1798–1826) Darwin (1859)
10. Natural selection	Evolution	Natural tendency for heritable variations promoting life and reproductive success to be differentially represented in subsequent generations—this may track complex and random change in the environment	Darwin (1859)
11. Mutation and recombination	Genetics	Random mutation and nearly-random recombination provide the genetic and ultimately phenotypic variability conserved by selection	Mendel (1866) de Vries (1901) and many others
Process principle: Cladogenesis (multiplication)			
12. Geographic separation	Biogeography	Spatial separation disrupts reproductive continuity of contemporary populations—much of this may be driven by random change in the environment	Wagner (1868) Dobzhansky (1937) Mayr (1942)

plicity: organisms and parts of organisms are considered the same or closely related until they are shown to be different. Once form gained precedence over composition, and once fossils bearing complex and detailed resemblance to living organisms were recognized as remains of formerly-living organisms, it became easier to recognize the vitality of fossils for which resemblance was less detailed and, finally, fossils with only the most general form of organisms (or parts of organisms, or traces made or left by organisms). There are, of course, "problematica" for which organic affinity is still uncertain.

Three principles from stratigraphy are important in evolutionary studies. Superposition of sedimentary strata, the strata that contain fossils, is ultimately a consequence of the Earth's gravitational field. Sedimentation in this context dictates that strata deposited closer to the center of the Earth, lower in any local stratigraphic section, were deposited before strata that overlie them. This principle is important in polarizing the chronology of any local stratigraphic section. Faunal and floral succession is based on the observation that organisms preserved as fossils often differ at different levels in a stratigraphic section. Faunal and floral correlation is another perception principle, resulting in this case from the observation that successions in individual stratigraphic sections can be correlated and thereby assembled into a composite master succession consistent with the temporal ordering or polarity of all individual sections. This master succession is the basis for the geological time scale (now calibrated radiometrically), and it is the tangible basis for evolution as a history of life.

Development of systematic biology in the seventeenth and eighteenth centuries clarified the nature of biological species in the modern world, and components of this clarification are grouped under the perception principle of finite diversity. Enumeration of species, however incomplete, indicated that the number of species living at any time and place was finite. Each was recognized to be composed of a variable but finite (if uncountable) number of individual organisms, and each was recognized to vary within finite limits (this variation was long taken to represent a kind of "error" about an ideal modal form, the most perfect individuals being those most similar to the "type" or mode; hence the subsequent importance of variation as a process principle).

Darwin [2], building on a foundation of paleontological, geological, and biological wisdom conveyed by Lamarck [3] and Lyell [4], is deservedly credited with the process principles explaining transformation of individual species into others, the process subsequently termed anagenesis. The principle of continuity in time and form is a principle of broader interest in empirical science, but it lies at the heart of Darwinian gradualism and deserves mention here. Lamarck illustrates this principle near the end of Chapter III in his *Philosophie Zoologique*:

Naturalists who did not perceive the changes undergone by most animals in course of time tried to explain the facts connected with fossils . . . by the supposition of a universal catastrophe . . . Unfortunately this facile method of explaining the operations of nature, when we cannot see their causes, has no basis beyond the imagination which created it . . . [3]

Continuity of intermediates linking ancestral and descendant species provides tangible evidence of transition and transformation, evidence of their "cause" that is otherwise unattainable.

The four corners of Darwinian transformation theory are the principles of variation, inheritance, fecundity, and natural selection. The first goes beyond observing that species vary within finite limits to recognize that individual variation is essential to any process of selection. Inheritance connects variants in one generation to those in the next, and the only important variations from an evolutionary point of view are those that are inherited. Fecundity refers to the potential species have for unlimited exponential growth, and fecundity leads, through increasing density, to competition and hence natural selection favoring organisms with heritable variations promoting life and reproductive success. [Competition, like selection, is infinitesimal in a system at equilibrium, which is the normal condition in nature. This makes both difficult to measure, and a null result is the expected outcome in most instances.] Fecundity and concomitant competition impose an extrinsic biotic selective regime on individual organisms, and Darwin was well aware that the extrinsic physical environment imposes its own independent additive selective regime. Competitive exclusion is one possible consequence of the biotic selective regime.

The development of genetics clarified the mechanism of inheritance, identifying mutation and recombination as the source of genetic variation and ultimately variant organisms conserved by selection. The final process principle is the principle of geographic separation disrupting reproductive continuity of contemporary populations, which is necessary to explain cladogenesis or the multiplication of species. This was incorporated into evolutionary theory during the modern evolutionary synthesis of genetics, systematics, biogeography, and paleontology.

These principles, taken together, are the modern synthetic paradigm of evolution. A new paradigm can be developed by adding new principles or by showing that earlier ones are misinterpreted. There is some hierarchy here. The first principles listed (vitality of fossils, superposition, etc.) lie deeper in the paradigm, and reinterpretation would necessarily affect most subsequent principles. Some biologists claim that Darwin's *Origin of Species* is not about the origin of species at all because it does not discuss cladogenesis, and cladogenesis is the only mode of speciation. Cladogenesis is the least understood mode of speciation and it is the subject of much current interest, but to argue that it is the only mode ignores both the history of ideas and the hierarchical priority of principles. Transformation of species was a problem that had to be solved before their multiplication came into focus as a derived and different problem.

Fossils, Species, and Speciation

Principles of the modern synthetic paradigm of evolution listed in Table 1 can be used to explore the meaning of species and speciation in the context of the fossil record and evolutionary history. Like the modern synthetic paradigm as a whole,

study of species and speciation clearly involves more than the actualist's finite diversity principle (principle 5 in Table 1), and information from many additional sources is required. Paleontological and biostratigraphic contributions to Darwinian evolution were necessarily sketched with broad strokes in the nineteenth century, and this remained true in development of the modern synthetic paradigm (e.g., [5]) Even today, we strain the fossil record in attempting to characterize species and speciation. However the fossil record is the only historical record we have, and it is important to consider what it shows.

For the past fifteen years I have supervised detailed field study of a richly fossiliferous stratigraphic section spanning the Paleocene-Eocene transition in a continental intermontane basin, the Clarks Fork Basin, in the Western Interior of North America. This ongoing investigation was initiated to document species level and faunal level evolutionary change at an important epoch boundary during the interval when most modern orders of mammals appeared. The study is yielding patterns of change through time like the one shown in Fig. 1, where forty-five successive samples show an overall increase in tooth size of the early Eocene mammal *Hyopsodus*. These forty-five samples have a weighted mean standard deviation of 0.048 units on a proportional logarithmic scale, and the mean value changed by a factor of 3.3 standard deviations in a time interval of about 1.6 million years (or about 1.6 million generations). During this time the initial species, *Hyopsodus loomisi* McKenna 1960 changed into *Hyopsodus latidens* Denison 1937. The transition appears to have occurred in the stratigraphic interval between 1780 and 1815 m. The pattern of change in Fig. 1 illustrates anagenesis, with smaller *H. loomisi* giving rise to larger *H. latidens*. Evolutionary rates range from −4.17 to +3.31 darwins, and the transition from *H. loomisi* to *H. latidens* between 1780 and 1815 m is +1.22 darwins; the between-species rate of change here is well within the range of within-species change. In addition, there is some evidence from earlier work in the contiguous Bighorn Basin [6] to suggest a branching event at about level 1800 m time, with *H. loomisi* giving rise to a rare species *H. simplex* (not known from the Clarks Fork Basin) as well as *H. latidens*.

We can summarize information in Fig. 1 by saying that two species are involved: the first, *H. loomisi*, appeared suddenly, with no evidence of cladogenesis at its origin, and ranged from level 1520 to 1780 m, for a minimum duration of about 0.7 million years (m.y.); and the second, *H. latidens*, appeared at level 1815 m, with clear indication of anagenesis and some suggestion of cladogenesis at its origin (based on evidence from a contiguous geographic area). The latter species persisted through level 2110 m and beyond for a minimum duration of about 0.8 m.y. Variability of tooth size in moderately large samples of *Hyopsodus* from individual sampling levels is typical of that in mammalian species living today. Availability of successive samples from a 1.6 m.y. interval of geological time tells us things we cannot otherwise know about the tempo and mode of change in biological species evolving through time.

Table 2 summarizes information on forty-six late Paleocene and early Eocene mammalian species in the Clarks Fork Basin based on stratigraphic plots of morphology (principally tooth size and, by inference, body size) documented in a number of recent publications. Twenty-five species have closely related congeners pres-
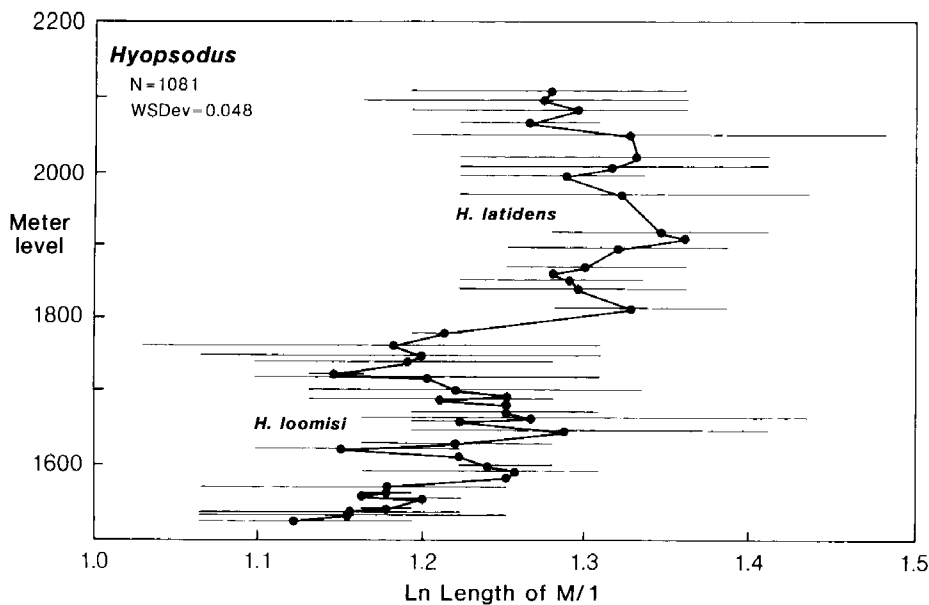
Fig. 1. Gradual evolutionary size change in forty-five successive samples of *Hyopsodus loomisi* and *Hyopsodus latidens* from a stratigraphic section in the early Eocene of the Clarks Fork Basin, Wyoming. This part of the section includes 1.6 million years of evolutionary time. Abscissa is natural logarithm of first molar length (mm). Ordinate is stratigraphic level in meters. *Heavy line* connects mean values of successive samples. *Lighter horizontal lines* show sample ranges. Total number of specimens plotted here is 1081. Samples have a weighted mean standard deviation of 0.048 (which is also typical of extant mammalian species). Rate of change *between* species in the interval from 1780 to 1815 m (+1.22 darwins) is well within the range of rates of change *within* species (-4.17 to $+3.31$ darwins)

ent in lower stratigraphic levels. Seven show no offset from their putative ancestral species, but eighteen species show some indication of an offset in morphology (as *H. latidens* shows relative to *H. loomisi* in Fig. 1). Anagenesis is inferred in all twenty-five transitions. Cladogenesis is documented in one transition (evolution of *Prototomus martis* from *Prototomus phobos*), and it may be involved in an additional eleven transitions. Seventeen species, including the first modern Primates (*Canlius*), Artiodactyla (*Diacodexis*), Perissodactyla (*Hyracotherium*), and hyaenodontid Creodonta (*Acarictis, Prototomus, Arfia,* and *Prolimnocyon*) make their first appearance at level 1520 m. Four species make first appearances at level 1815 m. Coordinated appearances indicate that species origins are often correlated in time (the same is true of extinctions), making both intrinsic and/or random causes of origination and extinction highly improbable, and suggesting that faunal turnover is environmentally determined. Inferences about extinction are necessarily based on disappearances of species, which can never be demonstrated conclusively. Modes of extinction suggested in Table 2 are based on knowledge of the presence or absence of conspecifics or congeners in other stratigraphic sections. These modes suggest

Table 2. Modes of origin and estimated minimum durations of forty-six late Paleocene and early Eocene mammalian species in the Clarks Fork Basin, Wyoming (*Hyopsodus* from Fig. 1; remainder from [7] and other recent papers by the author)

Species	Origin level (m)	Offset on origin	Anagenesis	Cladogenesis	Extinction level (m)	Extinction mode	Estimated duration (m.y.)
Insectivorous mammals							
Palaeanodon parvulus	1300±	—	—	—	1530	Anagenesis?	0.5
Palaeanodon nievelti	1520	Yes	Yes?	Yes?	2000	Real extinction?	1.3
Palaeanodon n.sp.	1720	Yes	Yes?	Yes?	2050+	Anagenesis?	0.9
Herbivorous mammals							
Cantius torresi	1520	—	—	—	1520	Anagenesis?	0.2
Cantius ralstoni	1525	Yes?	Yes?	—	1680	Anagenesis	0.4
Cantius mckennai	1685	No	Yes	—	1990	Anagenesis	0.8
Azygonyx xenicus	1100±	—	—	—	1215±	Anagenesis	0.3
Azygonyx ancylion	1220±	No	Yes	—	1380±	Anagenesis	0.4
Azygonyx latidens	1385±	No	Yes	—	1470±	Anagenesis	0.2
Azygonyx grangeri	1475±	No	Yes	—	1515	Cladogenesis?	0.1
Azygonyx gunnelli	1520	Yes	Yes?	Yes?	1525	Real extinction?	0.2
Azygonyx sp.	1520	Yes	Yes?	Yes?	1720	Real extinction?	0.5
Esthonyx spatularius	1520	—	—	—	1780	Anagenesis?	0.7
Esthonyx bisulcatus	1815	Yes?	Yes?	—	2000+	Anagenesis?	0.5
Hyopsodus loomisi	1520	—	—	—	1780	Cladogenesis?	0.7
Hyopsodus latidens	1815	Yes?	—	Yes?	2110+	Cladogenesis?	0.8
Thryptacodon cf. antiquus	1100±	—	—	—	1515	Cladogenesis?	1.1
Thryptacodon barae	1520	Yes	Yes?	Yes?	1520	Real extinction?	0.2
Thryptacodon antiquus	1525	Yes	Yes?	Yes?	1820±	Anagenesis?	0.8
Chriacus sp.	1100±	—	—	—	1800±	Anagenesis	1.9
Chriacus badgleyi	1520	Yes	Yes?	Yes?	1520	Real extinction?	0.2
Ectocion osbornianus	1000±	—	—	—	2100	Real extinction?	3.0
Ectocion parvus	1520	Yes	Yes?	Yes?	1520	Real extinction?	0.2
Diacodexis ilicis	1520	—	—	—	1520	Anagenesis	0.2
Diacodexis metsiacus	1525	No	Yes	—	2140+	Anagenesis?	1.6

Diacodexis robustus	1550	—	—	—	2100+	Anagenesis?	1.5
Hyracotherium sandrae	1520	—	—	—	1520	Real extinction?	0.2
Hyracotherium grangeri	1520	Yes	Yes?	—	1780	Anagenesis?	0.7
Hyracotherium aemulor	1790	Yes	Yes?	—	2000	Cladogenesis?	0.6
Hyracotherium pernix	2005	Yes	Yes?	Yes?	2100+	Anagenesis?	0.3
Carnivorous mammals							
Acarictis ryani	1520	—	—	—	1720	Real extinction?	0.5
Prototomus deimos	1520	—	—	—	1780	Real extinction?	0.7
Prototomus phobos	1525	—	—	—	2100±	Cladogenesis?	1.0
Prototomus martis	1680	Yes	Yes	Yes	1950	Anagenesis	0.7
Galecyon mordax	1525	—	—	—	1780	Real extinction?	0.7
Arfia junnei	1520	—	—	—	1520	Anagenesis?	0.2
Arfia zele	1525	Yes	Yes?	—	1585±	Anagenesis	0.2
Arfia shoshoniensis	1590±	No	Yes	—	1780	Anagenesis	0.5
Arfia opisthotoma	1815	No	Yes	—	2100	Real extinction?	0.8
Prolimnocyon eerius	1520	—	—	—	1520	Anagenesis?	0.2
Prolimnocyon haematus	1525	—	—	—	1780	Cladogenesis?	0.7
Prolimnocyon atavus	1720	Yes	Yes?	Yes?	2200+	Anagenesis	1.3
Uintacyon rudis	1200±	—	—	—	1780	Anagenesis	1.6
Miacis winkleri	1520	—	—	—	1680	Anagenesis?	0.4
Miacis deutschi	1690	Yes	Yes?	—	1780	Anagenesis?	0.2
Miacis exiguus	1815	Yes	Yes?	—	2060	Cladogenesis?	0.7

Paleocene-Eocene Mammals of North America   Pleistocene Mammals of Europe
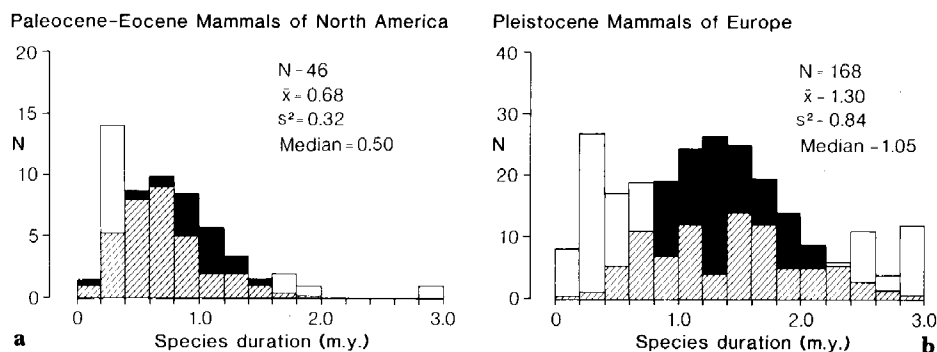

Fig. 2. Empirical distributions of estimated minimum durations of **a** Paleocene-Eocene, and **b** Pleistocene mammalian species (*open*) silhouetted against Poisson distributions (*shaded*) with the observed mean durations or half-lives λ (*cross-hatching* shows overlap of the two distributions). Paleocene-Eocene durations from Table 2. Pleistocene durations from [8]. Both empirical distributions are strongly skewed, making the median more appropriate than the mean as a measure of central tendency. Modal species duration is 0.2–0.4 m.y. in both studies, and median durations are 0.50 and 1.05 m.y. respectively. Note excess of both short and long duration species relative to Poisson model (χ^2 shows both to be significantly different than Poisson at $P < 0.01$), indicating that durations are neither independent nor an intrinsic property of species

that extinction is real in twelve out of forty-six cases. The remaining thirty-four extinctions are "pseudoextinctions," involving cladogenesis in eight cases and anagenesis in twenty-six cases. Anagenesis is probably more common than cladogenesis, but the latter is difficult to document.

Estimated minimum durations of the forty-six species are also listed in Table 2. These provide some idea of the rate at which speciation proceeds in nature. The mean of this distribution is 0.68 m.y., the median is 0.50 m.y., and the mode lies between 0.2 and 0.4 m.y. Taking the median as an appropriate measure of central tendency, a typical rate of early Eocene speciation is 2 species per m.y. The empirical histogram of durations for forty-six species suggests a Poisson distribution with a species half-life (λ) equal to the sample mean (empirical histogram is silhouetted against this Poisson distribution in Fig. 2a). However the empirical histogram differs significantly from a Poisson distribution in having too many species of both short and long duration. An empirical histogram for Pleistocene mammals shows the same deviations from expectation (Fig. 2b). Persistence of species is not a Poisson process.

The thirteen Paleocene-Eocene species originating by anagenesis alone have a mean duration of 0.54 m.y., while the twelve species originating with some indication of cladogenesis have a mean duration of 0.62 m.y. These differences are not significant. Both groups have medians of 0.50 m.y. Only one species (*Hyopsodus latidens*) is bounded by cladogenic branching at both its origin and extinction, and it has a duration (0.8 m.y.) slightly longer than average. It may be noted in passing that most species studied here are paraphyletic in that descendant species are

excluded from the taxon. All are monophyletic in the traditional sense, but the only holophyletic species are terminal taxa disappearing through real extinction.

The distribution of species durations for Paleocene-Eocene mammals resembles that for Pleistocene mammals (Fig. 2) except that the median duration of Palcocene-Eocene species is about half that of Pleistocene species. Median durations and speciation rates are sensitive to time scales of sampling, as are evolutionary rates in general [9]. The Paleocene-Eocene species are sampled on a finer time scale than the Pleistocene species, which probably explains the difference and may mean that the Palcocene-Eocene median duration is more representative than the Pleistocene median. It is also possible that the median duration of species has increased (and their rates of turnover have decreased) over the course of Cenozoic time, but confirmation will require sampling on a common time scale.

Randomness, Rate, Direction, and Progress

Much in evolution appears to be random or stochastic, and randomness is explicitly included in the modern synthetic paradigm. The origin of phenotypic variation is attributed to random genetic mutation and recombination (principle 11 in Table 1) which can, by themselves, produce change through random genetic drift. This mechanism promoting random change is countered by the deterministic process of selection (principle 10 in Table 1). However, the environment may change randomly due to the interaction of many independent factors and a deterministic process tracking random environmental change may produce a pattern that is random. In addition, much of the spatial separation necessary for cladogenesis may be driven by random change in the environment (principle 12 in Table 1).

Is the pattern of size change in *Hyopsodus* shown in Fig. 1 purely random, or does it have determined elements? All time series can be represented as random walks at some rate on some time scale; hence the pattern in Fig. 1, like every time series, is random on some scale. A general random walk at any rate on any time scale is so general a model that it can never be rejected. The real question of interest is whether the pattern of size change in *Hyopsodus* can be explained by the one known mechanism producing random change in evolution: genetic drift?

Any random walk has two rates: (1) an intrinsic rate based on the divergence distance at each time step, and (2) a stochastic net rate limited by the intrinsic rate, but taking into account random changes in direction as well. Genetic drift produces a sampling variance in the mean phenotype per generation equal to the genetic variance divided by effective population size [10]. Genetic variance is equal to the product of heritability and phenotypic variance [11], and the intrinsic rate of drift is equal to the square root of heritability multiplied by phenotypic variance divided by effective population size. The net rate of genetic drift including the effect of random fluctuations is the intrinsic rate multiplied by $\pm z_\alpha$ (± 1.96 for $\alpha = 0.05$) and divided by the square root of time in generations.

Heritability, phenotypic variance (or standard deviation), generation time, and effective population size are all known to some degree for mammals, and these can all be measured or estimated for *Hyopsodus*. The first ten samples of *Hvopsodus*
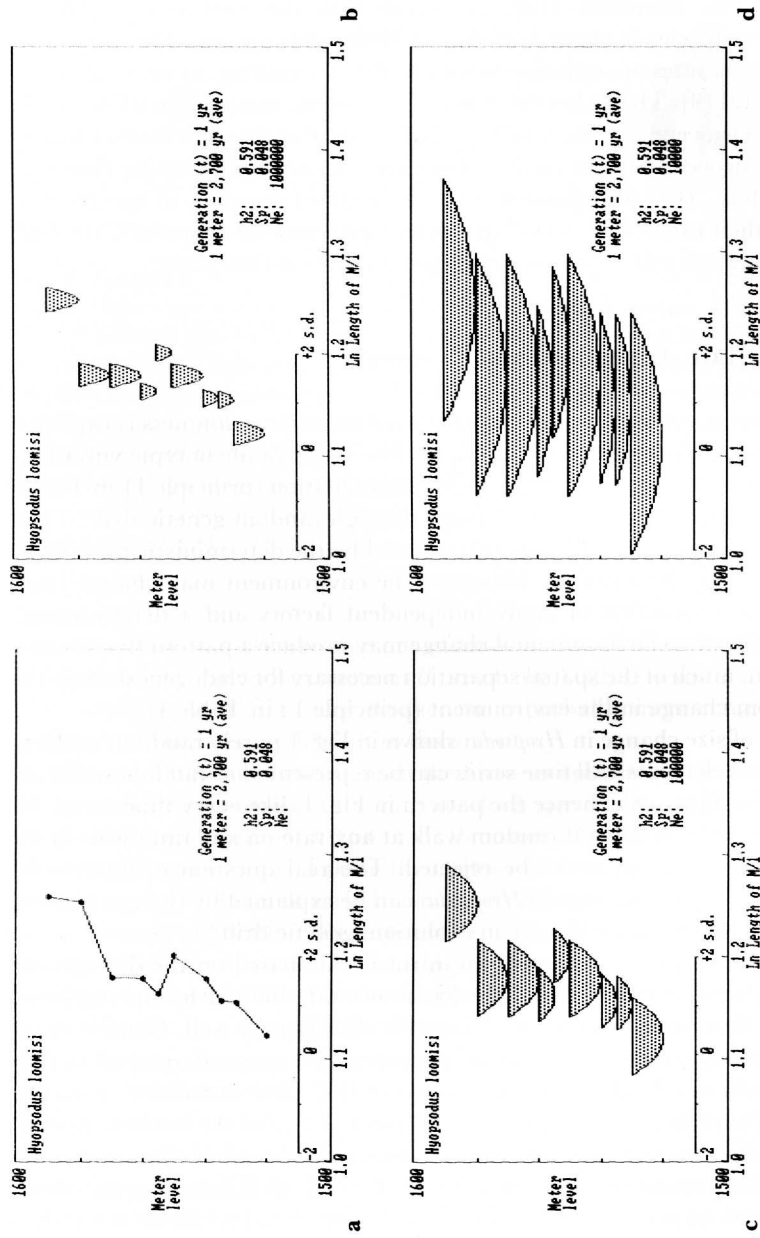
Fig. 3. Random genetic drift in a time series of *Hyopsodus loomisi*. Samples shown here are the first (lowest) ten samples in Fig. 1. Abscissa is natural logarithm of molar length (mm). Ordinate is meter level in measured stratigraphic section. **a** Mean values show an apparent random stratigraphic section. **a** Mean values show an apparent random walk with changes in rate and direction over time. **b** 95% confidence intervals (*shaded*) for tooth size change expected to result from random genetic drift given a generation time of one year, sedimentation rate of 1 m per 2,700 years, heritability of 0.591, phenotypic standard deviation of 0.048 (variance = 0.0023), and effective population size of one million. **c,d** Same simulation for effective population sizes of 100,000 and 10,000

plotted in Fig. 1 are analyzed in detail in Fig. 3 to illustrate this approach to testing evolutionary time series against expected change produced by random genetic drift. A reasonable value for the heritability of first lower molar length is 0.591 averaged from studies on humans and mice. The weighted mean phenotypic standard deviation measured in *Hyopsodus* is 0.048. A generation in *Hyopsodus*-sized mammals is usually one year. The effective size of mammalian populations is debated, but an effective population of one million may be reasonable given the size of the area being sampled, typical densities of *Hyopsodus*-sized mammals in modern faunas, and the abundance of *Hyopsodus* in fossil faunas. These values yield non-overlapping 95% confidence intervals (*shaded symbols* in Fig. 3b) indicating that most transitions between samples are unlikely to result from genetic drift. Similar computations using effective population sizes of 100,000 and 10,000 are shown in Figs. 3c and 3d. In the latter case all confidence intervals overlap and drift is a possible explanation. This does not answer the random walk question definitively, but recasts it appropriately in terms of effective population size. *Hyopsodus* is one of the most common early Eocene mammals and it was distributed over large areas of relatively homogeneous flood plain in western North America. Populations of *Hyopsodus* were clearly large, and it is reasonable to assume effective population sizes were large also. Thus it appears unlikely that random genetic drift was the mechanism producing change shown in Fig. 1.

It is relatively easy to test the idea that *Hyopsodus* is tracking a random pattern of global environmental change. If the pattern of change in *Hyopsodus* shown in Fig. 1 reflects response to a global environmental signal, then other species should have responded in a highly correlated way. This is not the case. Thus we are left with a complex pattern of change that is unlikely to represent genetic drift and unlikely to track any global environmental signal. The pattern of change may have been shaped by natural selection in response to a complex of biotic and other environmental signals. Progress, surviving and moving forward in time, need not lead anywhere in particular. This is especially true in a world densely populated with competing opportunistic species.

Evolutionary Rates in Microevolution and Macroevolution

Evolutionary rates calculated on different scales of time have been used to argue that different groups of animals evolved at different rates [5], and that the same groups evolved at different rates at different times [12]. Empirical distributions of evolutionary rates have the form shown in Fig. 4a. Each is bounded above by structural limits to size and, to some degree, by our inability to perceive two groups to be related if they have changed too much in too little time. Empirical distributions of rates are bounded below by our limited ability to measure small differences. These upper and lower limits have slopes of −1.0 when plotted on log axes against the time interval over which they are calculated. We calculate evolutionary rates, dividing by time because we want to characterize the process of change by numbers independent of time interval, but most rates are not indepen-
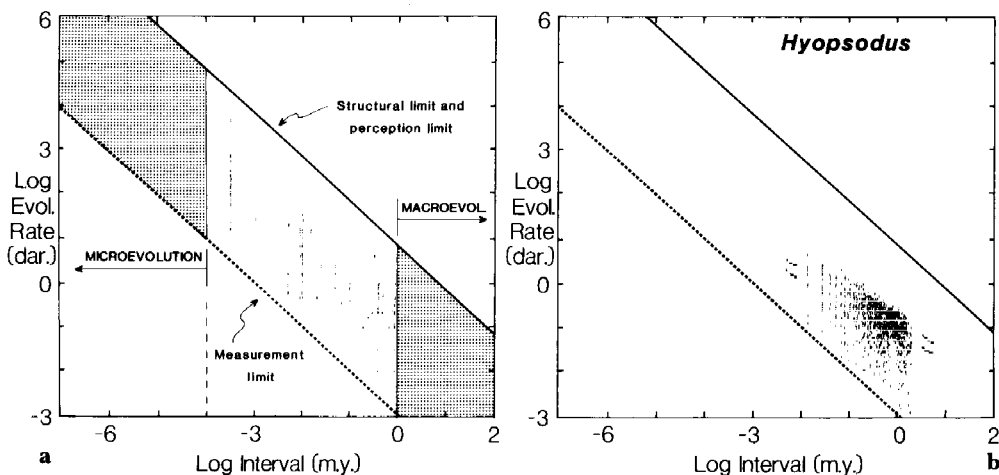
Fig. 4. a Relationship of microevolutionary rates on short time scales to macroevolutionary rates on long time scales. Rates are expressed in units of proportional change per million years (darwins, [9,13]). *Stippled* area of diagram at upper left represents evolutionary change in a laboratory setting on scales of time up to about 100 years. *Stippled* area at lower right represents evolutionary change in a geological setting on scales of time exceeding 1 m.y. Both of these are reasonably well studied, but evolution on intermediate time scales is poorly documented. Some rates in this interval are known and these appear to unify micro- and macroevolution as parts of one continuum. **b** Empirical distribution of evolutionary change in tooth size for *Hyopsodus* shown in Fig. 1. These rates fall within the poorly sampled central region of Fig. 4a. Regression slope of the distribution (−0.62) is shown for two intercepts by *short parallel lines*. Note that this is below an artifactual rate slope of −1.0, but well above a real process rate slope of zero (0.0). Calculated evolutionary rates are almost always lower when measured over longer intervals of time due to time averaging and other artifacts

dent of time. Dividing the same proportional difference or distance by longer and longer intervals of time (one consequence of time-averaging) artificially produces lower and lower rates (the slope of this artifact is −1.0). As we saw above, random walks produce change proportional to one over the square root of time ($t^{-0.5}$) and random walks scale with a slope of −0.5 on a plot like that in Fig 4. Pure selection or any other process producing change as a function of time should be indepen- dent of time and produce a line of zero (0.0) slope on such a plot; rates for selection experiments where time is measured in generations approach this ideal.

Misperceptions based on comparison of rates measured over different intervals of time enhance the distinction between microevolution and macroevolution. Micro- evolution deals with change on such short intervals of time (typically the experi- ence of a human lifetime, or less than 100 years) that "average" rates lie below the measurement limit, and rates, when calculated, are always high (*stippling* in upper left of Fig. 4a). Macroevolution deals with change on such long intervals of geolog- ical time that "average" rates lie above the structural/perception limit, and rates,

when calculated, are always low (*stippling* in lower right). In recent years, rates measured on intermediate scales of historical time and finely-divided geological time have become available and we are beginning to fill the artificial gap (*unshaded*) separating microevolution on short time scales from macroevolution on long time scales.

One such study of rates on intermediate scales of time, based on the *Hyopsodus* of Fig. 1, is illustrated in Fig. 4b. Here 1081 rates are plotted, representing each combination of successive samples representing different scales of time from about 14,000 years to 1.9 m.y. (the two highest samples used are not shown in Fig. 1). Of the total, 810 rates are positive, representing change to larger size, and 271 rates are negative, representing change to smaller size. Species with different histories have different proportions of positive and negative rates. If the two species are considered to be in stasis on the scale of their durations, then each might be considered to exhibit gradual change at zero net rate on that time scale, but each species is clearly dynamic on finer time scales.

The most interesting aspect of the rate distribution for *Hyopsodus* shown in Fig. 4b is its slope. Regression of rate on interval yields a slope of -0.6, which lies below the artifactual rate slope of -1 but just above the random walk rate slope of -0.5 and well above the process rate slope of 0.0. The observed value of -0.6 does not mean that the distribution was produced by a random process (we concluded above that it probably was not), but may simply represent the combination of a small amount of process and a large amount of artifact. Ideally, any rate versus interval distribution should have a slope near zero over some range of intervals, telling us that it represents a real process rate.

Another example can be taken from the fossil record and molecular evolution. This is illustrated in Fig. 5. A slowdown of molecular change has been widely observed in primate evolution by Goodman [15,16] and others. This slowdown is observed in all studies when multiple ties to the fossil record are used for calibration [14]. Results of sixteen studies employing immunological distance, augmented amino acid sequence difference (distance), nucleic acid hybridization, and augmented nucleotide sequence difference (distance) are shown in Fig. 5, all standardized to the same molecular distance at 25 m.y. divergence (arbitrarily chosen to be 50 units for comparison). All exhibit some slowdown, but the six nucleotide sequence studies stand out in showing the greatest slowdown.

Molecular change takes place by random replacement of nucleotides in linear sequences and hence simple distances should be equivalent to morphological change that involves proportion. Plotting rates of molecular evolution in the framework of Fig. 4 (see inset in Fig. 5) tells us little directly about the relationship of molecular rates to morphological rates, but molecular rates do not follow the same pattern of decreasing rate with increasing time interval for intervals of millions of years. Molecular rates have the flat zero-slope relationship to time scale that indicates they represent a real process acting over long intervals of geological time (and millions of generations). Natural selection is normally considered to be a microevolutionary process that acts on a generational time scale, but there may be levels of selection that act in weak and diffuse ways over macroevolutionary time as well. Nucleotide substitution rates or mutation rates may be mitigating factors
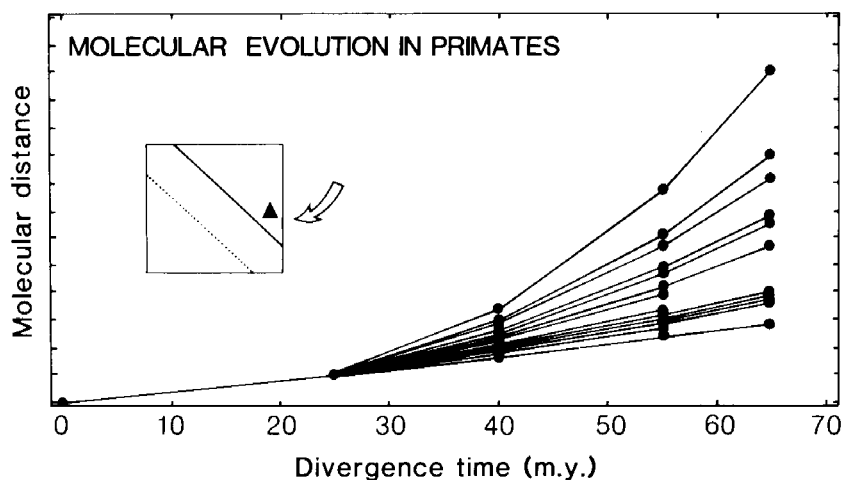
Fig. 5. Molecular slowdown in primate evolution, based on temporal scaling of sixteen empirical studies [14]. Curves are modelled using four Cenozoic divergence times, and all molecular distances are scaled to an arbitrary standard of 50 units at 25 m.y. divergence to facilitate comparison. There is some evidence of a speedup in molecular evolution of mammals in the early Cenozoic (not shown here). Rates are given by slopes of tie-lines between all points in an individual study. Greatest slowdown is in six nucleotide sequence studies. Least slowdown is in immunological distance, amino acid sequence, and nucleic acid hybridization studies. Slowdown implies that the intrinsic rate of the process is changing over time. If the process is selection, then slowdown might be explained as progressive commitment of a greater proportion of molecular sequence to function. Inset shows approximate distribution of molecular rates (*solid triangle*) from any one of these studies in context of the rate distribution of Fig. 4. Vertical position of rectangle is uncertain, and each study falls at a different level. Slope of rate distribution for each study is approximately zero

here. The proportion of selectively neutral substitutions is probably also a factor. Rates of molecular evolution clearly deserve much further study. Zero-slope scaling of rates with interval length indicates that a real process is involved, and slowdown implies that the intrinsic rate of the process is changing over time. If the process is selection, balanced by mutation, then slowdown might be explained as progressive commitment of a greater proportion of molecular sequence to function.

Discussion

The characterization of species and speciation given here depends on evolutionary principles 1–7 in Table 1, and it is consistent with principles 8–12 as well. Further, these principles appear sufficient to explain patterns of morphological change in species observed to date. Any "expansion" of evolutionary theory or "paradigm shift" must clearly identify those principles in error and identify any new principles. It must provide new evidence and explain why previous patterns were misleading.

Species are dynamic groups of individual organisms that are themselves "individual" in the sense that they are recognized and not defined. This does not mean species are fixed entities. Speciation includes both anagenesis and cladogenesis, and species exhibit rates of change between speciations that are as high as those observed during speciation. There are major reorganizations of diversity at intervals (principally era, period, and epoch boundaries) in the paleontological record coordinated with major changes in the physical environment. These impose change on species and whole floras or faunas that are distinct from change resulting from random mutation and deterministic selection.

Some of the most important problems of evolution concern the relative importance of random independent versus non-random dependent processes. Darwinian theory requires both. It is fashionable to argue that evolution is all random; that selection acting on individual organisms is unimportant or nonexistent. The fossil record provides evidence on these questions, but it is important to recognize that different patterns emerge at different scales of inquiry, and scale itself is important in interpreting observed patterns.

It is generally accepted that the number of species and the total range of morphology represented by all species taken together has increased over time. Some of this increase can be explained by our perspective looking at the historical record of life in hindsight, and some of the regularity disappears when examined on a finer scale. Species-level diversification takes place continuously at rates sufficient to account for present diversity in millions, or tens of millions of years. Dispersion and diversity are not the problem. These are the patterns expected from random processes.

There are also surprising regularities. The phenotypic variability of mammalian species in the Eocene 50 million years before present was the same as it is today, the number of species in mammalian faunas is similar, and the spacing of species relative to each other is similar. Lineages of Eocene mammals mimic random walks through time, but some cannot be explained by the only random walk for which we have a mechanism: random genetic drift. Brain size has increased independently in different orders of mammals, and temporal calibration of molecular clocks indicates that these have slowed down in parallel in different orders. Repeated regularities cannot be explained by random processes alone, and these examples are part of the extensive evidence fossils provide that evolution is more than random.

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