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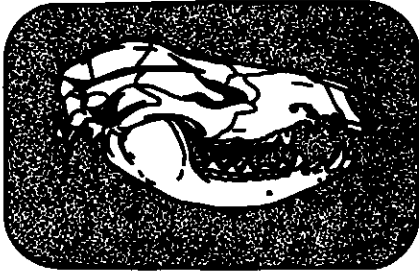
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PALEOSCENE #1. Species In Paleontology

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Introduction

Evolutionary theory is the covering explanation that accounts for the diversity of organisms, living and extinct, and for all of their adaptations. As an explanatory scientific principle, evolutionary theory is of no less consequence for the paleontologist than for the neontologist, even though most understanding of the mechanisms of evolution must come from the study of living organisms. In modern evolutionary theory, species are the central units of the evolutionary process (Mayr, 1963; Futuyma, 1979): it is, after all, species that evolve, as a summation of directional change in the genetics, development, anatomy, physiology, ecology and behavior of their included individuals. Moreover, species are historical entities, each having a unique, monophyletic ancestry, or as Hull (1973, p. 73) has put it, "Having the appropriate past history is necessary for a species to be the species that it is". Parts of some of these historical entities are preserved and made available to paleontology through the fossil record: paleontologists collect and identify fossils that are samples from species of the past, they often infer or attempt to reconstruct evolutionary relationships among past species from the fossils that they collect, and they classify the species that they recognize into some larger, more inclusive framework reflecting evolutionary affinity. Thereafter, species can become the basis for broader paleontological application, as in biostratigraphy and correlation, reconstruction of paleoecological communities and geographical distributions, and in speculations about functional morphology and behavior. For these reasons, species are central in paleontology and one must give some thought to what they are: after all, in paleontology at least, species are not objects to be found (*contra* Forey, 1982),

but are interpretations given to fossil evidence by the mind, within the theoretical framework of a *species concept*.

Constraints on Species Concepts in Paleontology

Time has figured importantly in the geological sciences at least since the days of Hutton, and confronts paleontologists no less than it does geologists: in brief, how can paleontologists investigate the past since they can never examine it directly (see Kitts, 1977)? One way in which accessibility to the past is eased for paleontologists, as for historical geologists generally, is by reliance on the principle of uniformitarianism, a constraining assumption usually met with first in undergraduate textbooks as "the present is the key to the past". In the history of geology, however, this principle has been expressed in different ways depending on which "key" has been of interest at the moment (Ghiselin, 1969a; Gould, 1977). In its modern form, the principle is not a scientific theory about the world ("it is neither true nor false" (Ghiselin, 1969a, p. 14)), nor is it even limited to geology; it states the universality of natural law, the idea that given certain initial conditions in the natural world, certain events will always take place in law-like fashion, independently of time or place (Hull, 1976). In other words, as a uniformitarian, one assumes that natural law has never been suspended in Earth history or even in the Universe at large. In everyday, practical terms, the uniformitarian assumption means that phenomena which are similar between past and present imply similar processes involved in their production.

In the refining of a species concept in paleontology, the uniformitarian assumption is all-important: the paleontologist assumes that organisms of the geological past were arranged in patterns of population organization comparable in ecology and genetics to those of organisms now living. On examining the fossil record, one can determine whether the expectations that stem from the assumption are consistent with the evidence that the record actually provides. By way of illustration, an expectation that might be explored by the paleontologist is whether variation in a sample (from what is arguably a single species of extinct organism) is comparable to variation in homologous characters in a related, living species. Such a comparison would be direct and objective, and might lead to further predictions that in turn could be screened against other fossils. For example, Gingerich (1979a, b) has used this rationale in recognizing species in fossil mammals by reference to tooth size/body size relationships in living mammalian species.

In paleontology, however, a robust uniformitarianism is not enough. A second, related, constraint to reasoning about the past is that imposed by the principle of parsimony or Occam's Razor: when confronted with com-

peting hypotheses, one should choose the simpler alternative that is consistent with the evidence, the alternative requiring fewer assumptions itself in order to be true (Popper, 1968). The principle of parsimony is not a statement about the properties of nature or a description of the empirical world (it is in no sense a claim that nature is "simple"). Instead, the principle assists our reasoning: hypotheses should not be multiplied unnecessarily when reasoning scientifically. Hence, in developing a species concept in paleontology, it is most parsimonious to assume beforehand that the population organization of extinct organisms was comparable to that of organisms now living; then we can see whether the actual evidence that fossils provide is in keeping with this assumption. It is precisely this failure to reason parsimoniously about the past that makes the special creationist concept of Biblical "created kinds" scientifically unacceptable as an alternative to naturally evolved species, nor is there a uniformitarian basis for such units. Without the constraints that parsimony and uniformitarianism provide, paleontological species could be whatever we wished them to be, satisfying whatever preconceptions we might have and without fear of refutation.

The third constraint in developing a species concept for paleontology derives from the material evidence itself that geology and biology provide: fossils are the remains of once-living organisms, and these organisms were connected by descent as a consequence of their reproduction. No strictly geological entities have this property (with the possible exception of certain clay minerals hypothesized to have functioned as abiogenic "organisms" during the early history of the Earth (Cairns-Smith, 1985), nor do organisms living in the modern world have the lengthy dimension in time that the fossil record provides. We know from modern biology that mistakes in the replication and transmission of genetic information governing the development of organisms create the variation that is essential if species and their adaptations are to evolve. These mistakes arise at random in respect to the likelihood of their being adaptive, making it quite impossible for any species, including ourselves, to have evolved toward some prior theological, historical or adaptive goal encompassing design: in short, the results of biotic history that we see as extinct and living species need not have followed the pathways that they did.

The transmission of genetic information in reproduction is nonetheless law-like, thereby meeting the requirement of the uniformitarian assumption (Kitts, 1977), and can be fully described statistically. But the interaction of the laws of heredity with the effects of the environment that determine which kinds of organisms actually develop is both unpredictable and unique for each lineage of organisms through time. No two species can

be the same; no species, once having gone extinct, will ever originate again: "...if a species of dinosaur were to evolve from present-day reptiles which was in every respect, save its phylogenetic history, identical to an extinct species of reptile, it would still be a new, separate species" (Hull, 1973, p. 73). Hence, individual species are unique events in history, established at particular places in space and time, having a beginning and an end, and differing thereby from the "timeless regularities" described by universal law (Simpson, 1960). It is this historical aspect of biology that lends a polarity in time to the evolutionary process and hence to the fossil record itself, and sets biology philosophically off from physics. This polarity in turn permits the use of fossils in the temporal ordering of strata in correlation between outcrops and in the definition of temporal units according to their fossil content. However, the initial ordering of strata at any single outcrop proceeds in-

dependently, by superposition, thereby refuting any claim for tautology or circularity between reconstruction of evolutionary relationships and determination of fossil succession.

Species Concepts

The Typological Species. In its most general uses, the term species refers to the "kinds" of things: "a class of individuals having common attributes and designated by a common name" (Webster's Ninth New Collegiate Dictionary, 1983), as in "species" of minerals or of chemical compounds. Membership of individuals in the class "species" is given by possession of certain characters, and possession of these characters is essential for membership in the species (Ghiselin, 1969a, 1974; Hull, 1976). "Species" in this sense conforms to what Mayr (1963) has called the typological species concept. Typology in taxonomy is an ancient idea, deriving from Plato

and Aristotle (Simpson, 1961 and Ghiselin, 1969a, provide brief, but useful, reviews of the subject): for the classical typologist, variation is an illusion, and only "fixed, unchangeable "ideas" underlying the observed variability...are permanent and real" (Mayr, 1963, p. 5).

The typological species concept is in common use still, and serves a variety of purposes in everyday, non-scientific language, even though the term "species" itself might not be used explicitly: one speaks of "kinds" of chairs or of wheeled vehicles or of eating utensils, when the word "species" instead of "kinds" would do just as well. The individuals that belong to typological "species" display no interaction among themselves by which their affinities to one another can be established and they never did; instead, membership in the group is by possession of attributes-in-common and nothing further.

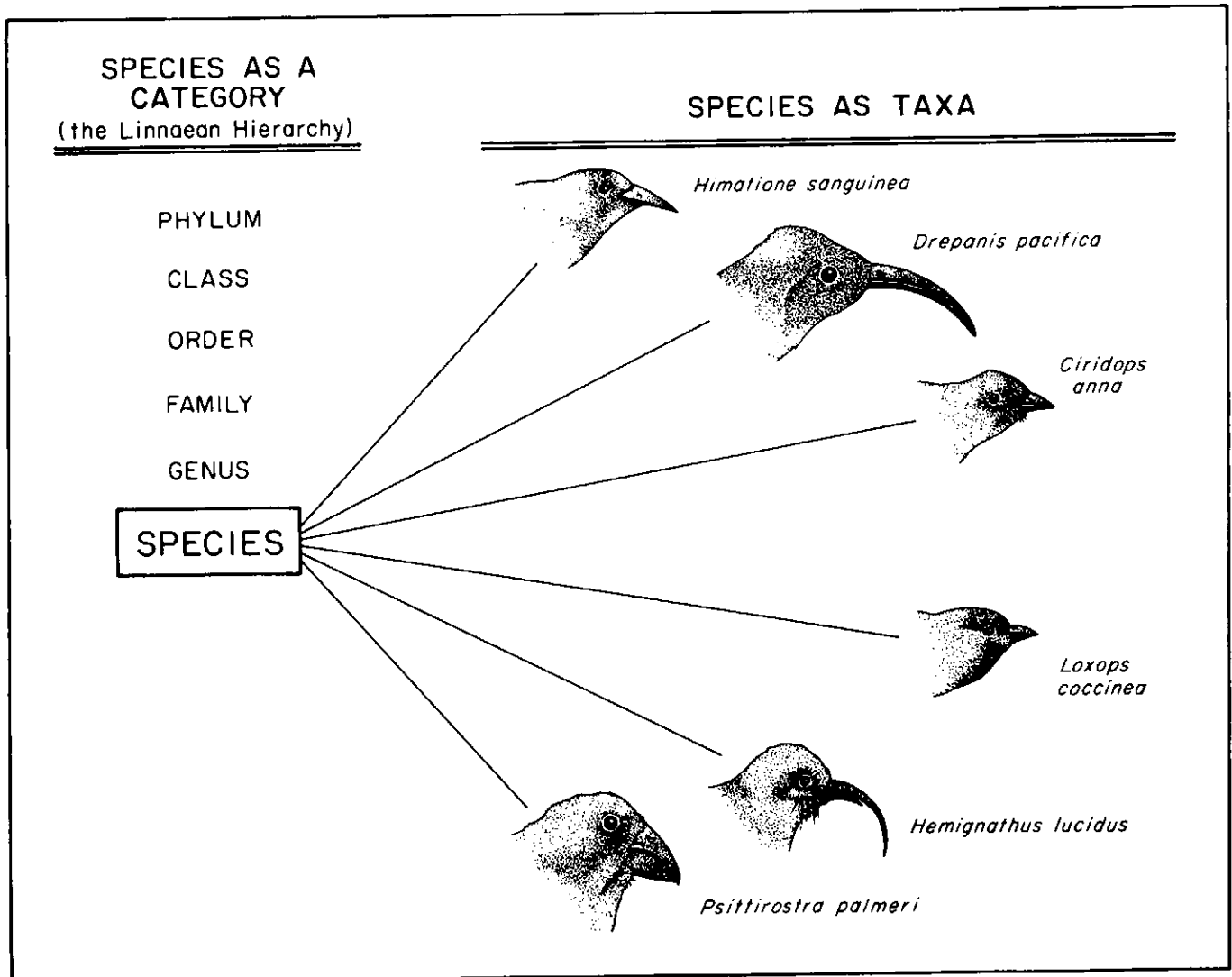


Figure 1 Diagram showing the relationship of "species" as logical class (a category in the Linnaean hierarchy of classification) and "species" as individual (a taxon). The members of "species" meaning "taxonomic category" are taxa (the species *Himatione sanguinea*, *Drepanis pacifica*, etc.), whereas the members of "species" meaning "taxon" are biological individuals (that is, specimens of *Himatione sanguinea*, *Drepanis pacifica*, etc.). The birds are members of the Family *Drepaniidae*, Hawaiian honeycreepers.

The typological species concept was first applied to organisms in a pre-evolutionary context: species in pre-Darwinian zoology or botany were considered to be groups of organisms sharing particular characteristics (usually in structure or anatomy), and accordingly, species of plants and animals differed not at all in logic from "species" of chairs, wheeled vehicles or eating utensils. The typological species concept admitted to no real variation: "species" were constant in their features and were sharply demarcated from one another morphologically, each conforming to an ideal "type"; one "type" could not merge into another. Individual differences, and change and intergradation between "species" had no place in the system, which was static, ahistorical and non-evolutionary (Ghiselin, 1969a). The typological species concept still prevails in some areas of paleontology (Newell, 1956, and see below), and is the basis for the taxonomy of artifacts in archaeology.

The Taxonomic Species. "Species" as a term in modern taxonomy designates a particular unit or category in the Linnean hierarchical classification of organisms (Figure 1); accordingly, the taxonomic species is part of the vocabulary of all biologists and paleontologists. The taxonomic species is the lowest obligate category in the Linnean system, and is followed by "genus", "family", "order", and so on, at successively more inclusive levels in the hierarchy. Although the Linnean system is not the only system by which organisms can be classified, it is almost universally accepted as the most useful system of biological classification, and "species" as a required level in it is not a matter of dispute. In logic, the taxonomic species category is a class; the definition of this class which has the most meaning biologically states that its members are organisms organized in reproductively isolated populations (Ghiselin, 1969a; Hull, 1976; Mayr, 1976) or, more broadly, in evolutionary species (see below). Following Darwin (1859, Figure 1), the higher or supraspecific levels in the system (genus and above) are meant to include groups of species arranged according to their inferred evolutionary relationships, thereby reflecting two historical realities, namely degree of modification and descent of the included species.

The Evolutionary Species. The evolutionary species is a particular kind of taxonomic species, composed of organisms that are united by community of descent. The meaning of "species" in this sense is given by the evolutionary species definition of the late vertebrate paleontologist G.G. Simpson (1951, 1961, 1980): "...a phyletic lineage (an ancestral-descendant sequence of interbreeding populations) evolving independently of others and with its own separate and unitary evolutionary role and tendencies". Among neontological systematists, Wiley (1978, 1981) is a recent champion of Simpson's basic con-

cept. For both, species limits are determined by descent relationship through geologic time, not by the unique possession of genotypic or phenotypic characters or attributes-in-common: more directly, inclusion in a species is by inclusion in a unique, evolving lineage, and the one is but the alternative expression of the other. A strength of the evolutionary species concept is that it is in harmony with the many different patterns of reproduction and speciation that organisms actually exhibit, thereby avoiding the limitations sometimes encountered with other species concepts current in evolutionary biology (Simpson, 1951, 1961, 1980; George, 1956; Wiley, 1978, 1981); consequently, "all organisms, past and present, belong to some evolutionary species" (Wiley, 1978, p. 19).

The evolutionary species of Simpson extends into geological time the widely accepted, but essentially non-evolutionary, biological or genetical species of neontologists (Mayr, 1963; Dobzhansky, 1951, 1970; Simpson, 1961, 1980): in the latter, species are populations of biparental organisms that interbreed among themselves or have the potential of doing so, but do not interbreed with other such populations. "Species" used in this way designates a unit that itself has the logical status of an individual whose own parts or membership is composed of "biological individuals" (meaning "individuals" or "specimens" in an everyday sense) that are joined together by reproductive continuity (Ghiselin, 1984; Hull, 1984; Kitts, 1984). Variation among these parts (the specimens) is the norm, such that species then becomes a statistical concept. Formal, nomenclatorial matters enter here as well: in the Linnean system, particular genetical/evolutionary species are given binomial names (e.g., *Canis latrans*, the coyote); these are proper names of individuals (Ghiselin, 1974; Hull, 1976), unique for each species, and grammatically singular in number (Simpson, 1945).

Genetical/evolutionary species, made up of populations interconnected by reproductive continuity through time, are both a logical expectation of evolutionary theory and are believed to be empirically real. Accordingly, genetical/evolutionary species are claimed to be *natural* units in the belief that there really are such entities in nature at present (Mayr, 1949), and — if we accept the constraints of uniformitarianism, parsimony and heredity — in the past as well, in unbroken continuity with those of the present. The biological individuals within these units are the focus of processes, the most important of which is natural selection, that have brought about the diversity and adaptations of all organisms, living and extinct, irrespective of time or place. As such, these units exist independently of the communities of paleontologists and neontologists and any rivalries between them: *given the unity of past with present, there should be no separate paleontological species concept or paleonto-*

logical species definition, although paleontologists do confront problems unique to them in determining the limits of *particular species*, as discussed below.

Once these strictures are recognized, much of the literature about the "kinds" of "species" can be laid to rest as a literature of only historical interest, and barely so at that: typological "species", morphological "species", phenetic "species", paleontological "species" and so on are terms that have figured importantly in past discussions of what a species might be (and there are still other terms that are not included here); but these are terms that either designate *classes* of individuals united by shared attributes as opposed to descent relationship, or entities that are thought to differ owing to the different kinds of *evidence* by which they are recognized, or even units that differ because of the kinds of *specialists* to whom they are of greatest interest (as in the "species of the systematist" or the "species of the biologist" (Trueman, 1979)! In an evolutionary context, promotion of such species concepts cannot be a legitimate goal because they do not define biological populations nor do they have evolutionary significance (Simpson, 1980, p. 149).

A bitter controversy in the literature has centered in recent years on the "operationalism" of the Mayrian genetical species concept, concerning the means by which the boundaries of particular species are to be recognized (see, for example, Ehrlich, 1961; Sokal, 1963; Sokal and Camin, 1965; Sokal and Corvello, 1970). One objection to the genetical species concept has been that the reproductive patterns of plants and animals can vary in space and time, so it may be difficult or impossible to determine the "potential" for interbreeding between geographically separated populations. In other instances, contiguous populations may interbreed freely across some parts of their geographic range where they replace one another geographically, but not in other parts, where they overlap and are reproductively isolated from each other (the ring-species of Rensch, 1960). Further, in actual practice, the taxonomic boundaries of Recent species are normally determined by the distribution of morphological characters in preserved museum specimens and not (directly) by reproductive criteria at all, and of course morphological characters are virtually the only evidence available for delimiting species in paleontology. Would it not be better to acknowledge frankly the morphological basis of species and define the concept by reference to morphological criteria alone, such as: "A species is a group of animals or plants all of which are similar enough in form to be considered as minor variations of the same organism" (Trueman, 1979)? And in fact, such a definition of species has an understandable appeal to paleontologists; for example, Gingerich (1979a), in keeping with a long tra-

dition in paleontology (see Sylvester-Bradley, 1956), has viewed species as "phenetic clusters within a multivariate morphometric space" for "operational" reasons, since "data are usually not available to support inferences about interbreeding or reproductive isolation" (p. 43), and, more strongly, "(interbreeding) becomes pure conjecture in the context of past or future organisms" (Gingerich, 1985, p. 29; and he has elaborated further on "operationalism" and the species in paleontology in 1979b.).

However, Hull (1968, 1971) and Ghiselin (1969a) have effectively dealt with the "operationalist" critique, and in so doing, have clarified for systematists, including paleontologists, the relationships in science between theoretical statements and the material evidence relating to them. Simpson (1980, p. 149), a paleontologist, not a philosopher, sees the issue in the same way: "The fact that a species, as a group, is actually diagnosed in morphological terms, does not conflict with definition of the species as a category, in genetical terms. *The basis for definition of a category is quite different from the evidence available for decision as to whether a particular group of organisms meets that definition*" (emphasis added). As a somewhat similar example, free from the polemics that have attended the discussion of species concepts, one might define the theoretical term "life" (a category) in particular ways and one might include in that definition reference to unique properties that living things possess or to special processes that they display. Nevertheless, there are systems in the natural world about which we might legitimately disagree concerning their status as living: are viruses, or crystals, proteinoids or DNA molecules living (or, more paradoxically, are the abiogenic "organisms" of Cairns-Smith (1985) "alive")? Each of these has some, but not all, of the attributes of living systems. But our difficulty in deciding whether or not particular systems such as these (the things defined) are living has no logical bearing on the validity of our definition of life, which has a firm empirical content nonetheless: in the real world, we can easily determine in most cases whether or not a system is living, that is, whether the natural units that we encounter actually meet the criteria posed by our definition. Similarly, the difficulty that the taxonomist (paleontologist or neontologist) may experience in determining the species status of a natural population (either living or extinct) from a museum (or other) sample has no relevance to the question of the validity of the biological/genetical species concept or its extension in geological time as the evolutionary species concept: Hull (1968, p. 449-450, footnote) and Simpson have emphasized that the genetical (evolutionary) definition is intended to define the category term "species" itself in terms of interbreeding or reproductive isolation or evolutionary role, but not to define the name of any single species (the name of a particular taxon).

The "operationalist" problem, however, has at least one other facet that is sometimes bothersome to theorists and is relevant to paleontology (see below): it is impossible to classify in a non-arbitrary way continuous phenomena in a classification made up of discontinuous categories having well-marked boundaries. For example, in an ecological time scale, speciation (the multiplication of species) is commonly a gradual process, leaving daughter species genetically and phenotypically continuous with their parent stock. While the daughters are reproductively isolated from each other on completion of the process and are objectively real species on that account, where "operationally" should the line be drawn separating parent from daughter species, given the intergrading sequence of generations between the two (Figure 2)? Biologists commonly hold that the evolutionary process has not stopped; if evolution is still continuing now, living populations of plants or animals that separately represent steps along the way from parent to sympatric but non-hybridizing daughter species should exist in nature. That they do, and that, in so doing, they create some inconvenience for the practicing taxonomist, can hardly refute the validity of the genetical/evolutionary species concept; instead, species *in statu nascendi* are an expectation of the evolutionary process, and provide important confirmation for it, irrespective of any taxonomic problems that might result. In the interests of good science, one hopes that at least most systematists would agree with Raup and Stanley (1978, p. 109) in believing that it is better to describe the results of evolution by a "theoretically valid method, but one dif-

ficult to apply, than by a theoretically invalid method that owes its existence to convenience".

Species in Paleontology

Even after agreement is reached on a scientifically meaningful definition of the species category — and it is the contention of this essay that the Simpsonian conception of evolutionary species is best in this regard for *both* paleontology and neontology — paleontology is still a discipline that meets seemingly unique and perhaps intractable problems in actually delimiting species boundaries (that is, in defining the *names* of particular species). This comes about from properties of the fossil record that are widely known and that influence taxonomic practice in major ways: (1) the fossil evidence is always incomplete such that no individual is preserved in its entirety, as it was when alive, not only in respect to its anatomy, but also in other biological attributes, such as genetics and behavior, that can never be observed in fossils directly; (2) no lineage of organisms is preserved with generation succeeding generation in all of their members through successive strata at any one outcrop or combination of them; and, (3) the reproductive status of extinct organisms can never be established by observation. Whereas the impact of an incomplete record might be thought to be crippling to meaningful paleontological research, what is important is not whether the evidence that paleontology requires is complete in some absolute sense (*for the evidence is never complete in any scientific investigation, not just in paleontological investigation*), but whether it is com-

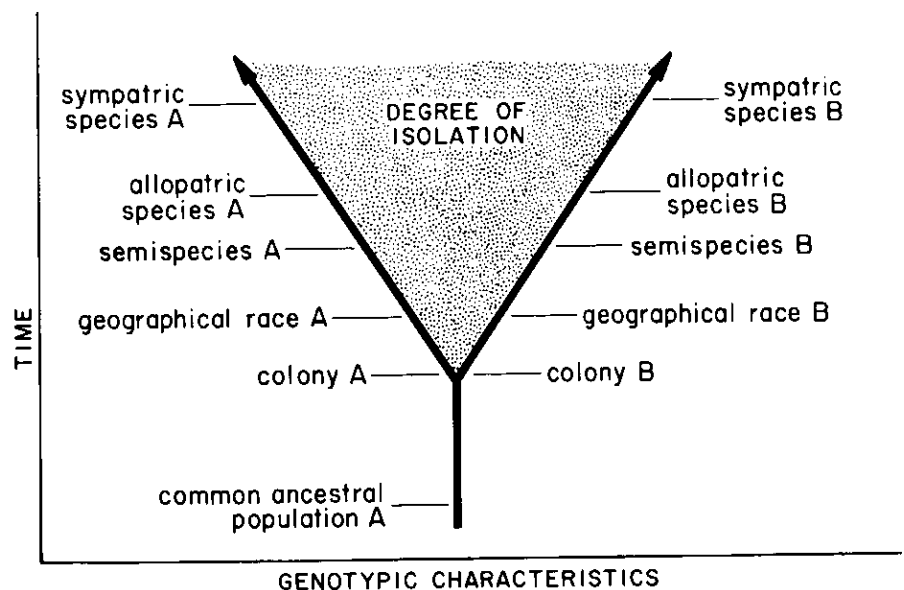


Figure 2 Diagram showing the gradual divergence of populations from a common ancestral species to two daughter species fully isolated reproductively from each other. At present, populations can be found at any stage in this process — an expectation of evolutionary theory and of the supposition that evolution is still continuing. The fact that such populations can be found has been mistakenly claimed to contradict the genetical/evolutionary species concept; it does not. (Diagram modified from Grant, 1963).

plete *enough* to give a reliable basis for inference about that part of the real world under investigation. Even that special deficiency — the inability to determine the reproductive status of extinct species directly — is no cause for despair, for the neontologist himself is unable to determine the reproductive status of living species "directly". Instead, he extrapolates from observations of interbreeding or reproductive isolation among the individuals that make up his sample to the unexamined parts of the entire population under study; thereafter, he formulates an hypothesis for as yet unexamined cases that in turn can be tested by additional observations. In any case, it would be quite impossible to observe reproduction in *all* individuals within the populations that are the focus of an investigation, including those having the potential for interbreeding but that did not (and ignoring the trivial circumstances of species nearing extinction (whooping cranes, for example) in which all members of the species are actually known). This is not to argue that the limits of species can be determined with equal confidence in neontology and paleontology, for one can still assess the reproductive status of *some* individuals in living species, an impossibility with extinct organisms; but probably the more important inequality between neontological and paleontological species stems from the likelihood that paleontological samples on which species are based are normally affected by sedimentological factors governing the temporal resolution of rock strata and the fossils that they contain, resulting in a blurring of ecologic and genetic boundaries in pooled populations over time (Schindel, 1980, 1982; and see below).

Typological Species in Paleontology. "Species" known only from fossils range from typological "species" to genetical/evolutionary species. Typological "species" have proved particularly important in applied biostratigraphy, paleobotany and ichnology, with the guiding principle in these disciplines being that individuals of the same "species" look alike, clustering phenetically about a type specimen, and those that can be grouped in different clusters belong to different "species" (Newell, 1956). Specimens showing minor departures from the structure of the type specimen can be awarded different species names, or are otherwise singled out taxonomically (Newell, 1956). Recognition of genetical/evolutionary species is also dependent on morphological resemblance, but morphological resemblance of a special kind, interpreted in special ways, as discussed below.

Biostratigraphy. Clearly, typological "species" have had great utility in geological studies. In applied biostratigraphy, correlation of rock strata relies on similarity of fossil content; it matters not at all for the purposes of the biostratigrapher as technician what the source of the similarity among the fossils of interest might be (Scott, 1976), for basically

it is the rocks in time, not the fossils themselves, that are of primary concern. The fundamental hypothesis is that similar fossils imply similar age (whether that is always the case is, of course, a different matter; see, for example, Flynn *et al.*, 1984, for discussion of homotaxis and heterochrony in biostratigraphy), and in this context, fossils are to the biostratigrapher as potsherds are to the archaeologist — the fossils might just as well be discarded beer cans or bottle caps, whose "style" of manufacture has changed through time (Youngquist (1967) provides an explicit defense of this view). The proven utility of conodonts and of pollen and spores in applied biostratigraphy provides an excellent example: successive time horizons are recognized at small increments of phenotypic change within a given stratigraphic interval (and with much finer resolution than is possible than by any non-paleontological means), even though little or nothing is inferred about genealogical relationships among the fossil taxa or parts of life histories that the fossils represent. Hence, applied biostratigraphy, while valid on its own terms and an important source of information in historical geology, does not address the problem of organization of extinct populations into evolutionary units and how these might best be recognized and interrelated, questions of central interest to paleontology as a science.

Paleobotany. Paleobotany confronts difficult problems in determination of species limits, as exemplified by the recent comprehensive textbooks by Taylor (1981) and Stewart (1983). Only rarely is an extinct vascular plant species known from a complete specimen, and thus different names usually are given to fossils occurring separately as leaves, fruits, wood, roots, stems, flowers, cones, etc.; furthermore, different modes of preservation (as with compression-impression fossils versus three-dimensional "petrifications") of the same parts in the same species are normally different in appearance and are then given different species names. In fact, the incomplete, disaggregated parts of individual plants in what were undoubtedly single living species are usually identified as belonging to different genera, and are named accordingly as "form" taxa or "organ" taxa, strictly typological groups (see Beck, 1970, for example). Hence, in paleobotany, "species" of whatever conception play only a minor role, limited for the most part to meeting the formal requirements of taxonomic nomenclature (see discussion in Stewart, 1983, p. 21-27).

Ichnology. Ichnology, the study of tracks, burrows, traces, etc., confronts even more intractable problems in recognizing species: the discipline is currently of heightened interest in at least sedimentology and paleoecology, in the interpretation of ancient sedimentary environments. The objects of interest are sources of information about attributes of the substrate, water depths, wave

action, and other environmental parameters; however, the biological origins of the fossils are of little consequence in this connection. In ichnology, morphologically similar biogenic traces are given the same Linnean name, irrespective of their genealogical affinities or stratigraphic age, so that, for example, some ichnological genera range from Precambrian to Recent, a span many times greater than for any known phylogenetic genus. As ichnologists recognize, phylogenetically distant organisms can produce closely similar traces, and, conversely, the same organism can produce different traces under different environmental conditions, or at different times as a consequence of different behavioral repertoires. Only rarely is the trace-maker found associated with the trace, but even that discovery provides no basis for the supposition that the organism in question is limited in capacity to only the manufacture of that trace or even that other, similar traces must have been produced by that same kind of animal. Hence, it is safe to say that ichnology has no necessary phylogenetic component, at least in so far as its tasks are sedimentological and paleoecological (which is not to claim that ichnologists never attempt to interpret traces from a phylogenetic point of view, the study of traces as valuable guides to identifying important stages in early metazoan evolution (Glaessner, 1984) being a particular case in point). Indeed, widespread recognition of the special status of ichnological problems in taxonomy is given by the use of special ichnological categories ("ichnogenus", for example), although this practice is not universally advocated, even by ichnologists (see Frey and Pemberton (1985) for a recent review) and has not been formally recognized by the International Code of Zoological Nomenclature.

Parataxa. For all cases such as these, some systematists have believed that the paleontological community would be better served by introduction of the global concept of *parataxa* for fossils grouped together in "species" or higher taxa solely on the basis of their similarity (Simpson, 1961; Crowson, 1970). Parataxa in paleontology would then be overtly acknowledged logical classes whose dimensions are determined only by similarity, without implication of uniqueness of descent or sources of resemblance. Higher taxonomic categories could be designated by the prefix "para-", as "paragenus", "parafamily", etc., so as to identify clearly a system in which successively more inclusive classes are hierarchically arranged without imputation about genealogical relationship. "Species" in such a system would simply be the least inclusive class based on similarity in the hierarchy (parataxon classification was presented to the 1958 International Congress of Zoology, but was not recognized then (Simpson, 1961) or since). Yet other authors maintain that even with limited knowledge, it is nonetheless best to attempt to delimit taxa according to evo-

lutionary criteria, with the awareness that the discovery of additional information promises to bring strictly typological species increasingly into an evolutionary context (Simpson, 1961). It is doubtful, however, that this promise holds for ichnology, and use of parataxa or some other special, non-Linnean system would probably be a legitimate methodology for that discipline.

Evolutionary Species in Paleontology. If it can be agreed that in paleontology the term "species" should be applied to a category based only on reproductive relationship through time and not on similarity, the methodological problem still remains: how are individual species to be recognized from fossil evidence — evidence from organisms that are no longer living and hence unable to exhibit reproductive or any other interaction with one another?

The evidence determining the limits of particular species in paleontology is mostly anatomical similarity, but anatomical similarity of a particular kind. The aim is recognition of *homologous* similarity, that is, similarity owing to community of descent, and *within* the boundaries of the species in question. Similarity of attributes having a distribution more extensive than that of the species in question is spurious to determination of the boundaries of that species, whether the similarity arose at some earlier time, in a more remote ancestry, or arose convergently, from a different ancestry entirely. Further, species are composed of individuals no two of which are alike; accordingly, variation is an integral part of the evolutionary species, both in time and in space, and is not an attribute to be viewed as an aberration, with each variant being designated by a different Linnean name.

While evolutionary species in a paleontological context are to be delimited by homologous similarities whose distribution matches that of a unique descent community, the necessary inferences from morphology to reproductive isolation may not always be easily made: for example, many living animal and plant species have life histories in which they undergo one or more somatic metamorphoses, as from a larval to adult stage in certain animals, or in an alternation of generations (in both animals and plants); in such cases, successive stages can differ substantially in appearance (Figure 3). Species can be markedly sexually dimorphic, as well, with one sex phenotypically quite unlike the other (Figure 4), or even polymorphic, with individuals having different phenotypes, independently of sex or age (Figure 5). Conversely, sibling species are those that are reproductively isolated but that are phenotypically closely similar to each other, and ecological "species", prominent in higher vascular plants, can occur where conditions of the substrate or variation in other environmental parameters may produce very different phenotypes within a single reproductive species (Figure 6; and see Mishler and Don-

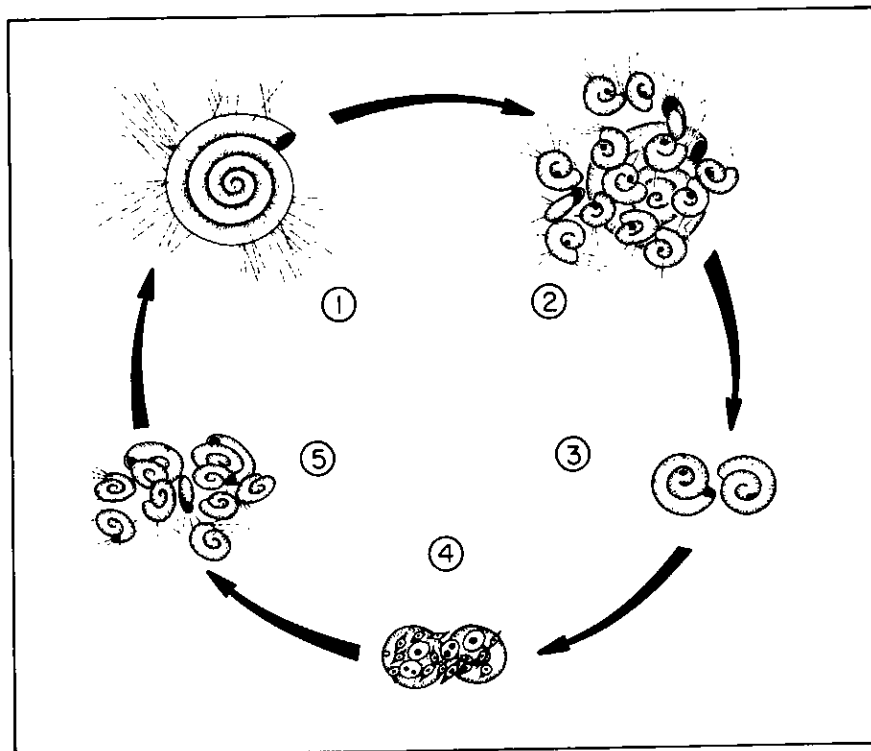


Figure 3 Five morphologically different stages in the life history of a single species of foraminiferan. (Redrawn from Moore et al., 1952).

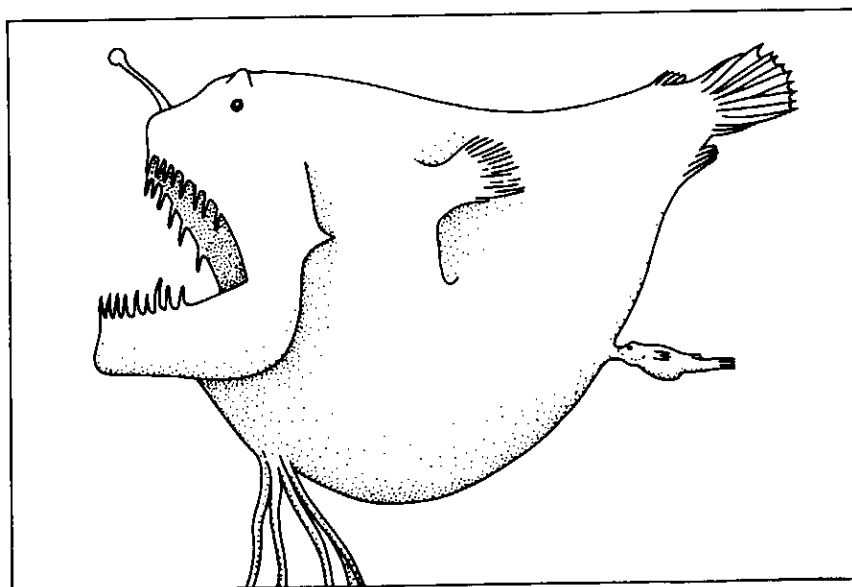


Figure 4 Sexual dimorphism in a species of deep-sea fish (the tiny male is attached to the posterior ventral part of the female); both specimens belong to the same species (reproductively isolated population), but they obviously differ markedly in appearance. If one adheres to a morphological species concept, these two individuals would have to be classified in two different species! (Illustration after Gould, 1983).

oghue (1982) for other uncertainties concerning species concepts in botany); comparable environmental effects on morphology are known in some animals (Palmer, 1985). As a general, cautionary note in this connection, present understanding of the speciation process in living organisms furnishes no credible evidence that phenotypic novelties necessarily arise in new species in correlation with the advent of reproductive isolation (Levinton and Simon, 1980; Lande, 1980; Bell and Haglund, 1982; Levinton, 1983; Lewin, 1985), yet this must minimally be the case if an equivalence between reproductive community and morphological group is validly to be assumed. Obviously, if any of the above factors affected extinct species as they do those now living (and, for reasons of uniformitarianism and parsimony, it is assumed that they did so), they would often be beyond recognition by the paleontologist. Indeed, Thomas Schopf (1979), a distinguished invertebrate paleontologist, was quite pessimistic about recognition of species in a biological sense from fossil materials at all.

Another difficulty special to paleontology stems from the time dimension: in continuous lines of descent of fossil specimens, where are the boundaries between ancestral and descendant species to be drawn? In practice, this conundrum is rarely one that is real: the samples of fossils on which species inferences are based are discontinuous stratigraphically at some scale (Newell, 1956), and the gaps in stratigraphic distribution are relied on to postulate the boundaries between different species wherever "significant" stratigraphic gaps coincide with "significant" morphological discontinuities. It remains an unavoidable matter of judgment by the paleontologist as to what might be deemed

"significant", but the usual "rule of thumb" is to include within a species a range of morphological variation comparable to that in the same features in related living species, and to distinguish between species by gaps similar in dimension to those separating their living relatives; if none are known, comparison can be made to gaps between species in living analogues. The techniques available for recognition of such species in paleontology are well described in the literature and will not be reviewed here; Sylvester-Bradley (1956), Beerbower (1960), Raup and Stanley (1978) and Simpson (1980) are among those providing useful introductions to actual practice in this regard.

Sometimes, however, examples of apparently continuous clinal change stratigraphically are discovered (Williamson, 1981; Gingerich, 1979a, 1985; Bell and Haglund, 1982), and it is these that are particularly problematic, reflecting a complex interplay between theory and methodology: the apparently simple question as to how the boundaries between what some paleontologists would call successive species (sometimes termed "chronospecies", "paleospecies", "phyletic" or "successional" species, although "chronospecies" and "paleospecies" have also been used as terms to designate units more nearly like Simpson's "evolutionary" species) are to be drawn, does not have a simple answer, one that finds all, or even perhaps most, paleontologists in agreement (see Simpson, 1951; Rhodes, 1956). Obviously, reproductive isolation is, even in principle, of no consequence here: offspring generations cannot have mated with earlier, dead generations in the same lineage, which are nonetheless parts of the same evolutionary species.

One view now current would apply the term "species" to the entire segment that occurs between cladogenetic events, that is, between the branching of a parental species to its daughters, irrespective of the amount of phyletic evolution (Figure 7) occurring in the daughter lineages after their inception (Wiley, 1981). Given a dense enough record, recognition of such lineages seems straightforward and has the added strength of bringing practice closely into accord with theory, in an emphasis on inferred reproductive continuity within evolutionary species through time. But even when species are defined according to cladogenetic criteria to meet the demands of theory, practical matters of decision eventually must intrude: as the discovered record becomes more and more dense, an infinite regress of choices needs to be made to identify the precise point at which reproductive isolation is imposed — an obvious *reductio ad absurdum* creating the necessity for an ultimately impossible decision.

Most paleontologists would recognize new species at approximate cladogenetic events to the degree that the evidence permitted, but would continue to designate other new "species" within a single evolving lineage, justified by the accumulated degree of difference from earlier members and by stratigraphic convenience. Figure 8 shows a diagram from Gingerich (1977) representing species that have been recognized in both senses. Gingerich (1976a, b, 1979a, b, 1985) has elaborated what he has called the stratophenetic method for delimiting species in paleontology: "(1) organization of data, with organisms from each geological horizon clustered into species (see below) and these horizons arranged in temporal order based on stratigraphic superposition, (2) phenetic

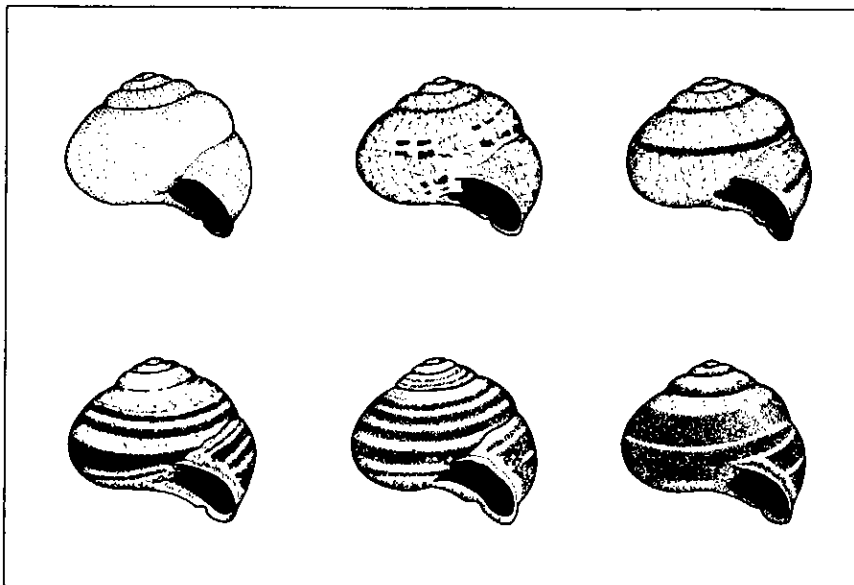


Figure 5 These snails, whose shells are polymorphic for colour, all belong to the same species (reproductively isolated population). (Illustration after Dowdeswell, 1958).

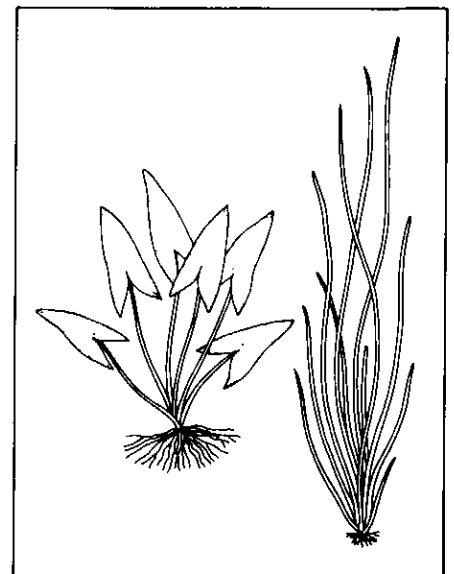


Figure 6 Both plants belong to the same species (reproductively isolated population), but differ phenotypically owing to different environments in which they live. (Illustration after Futuyma, 1979).

linking of closely similar species samples in each horizon with those in adjacent horizons to form a minimal spanning tree of evolutionary lineages, and (3) critical testing of the resulting pattern of lineages in the light of new discoveries" (Gingerich, 1979, p. 454-455). Raup and Stanley (1978, p. 104) have clearly expressed the biological rationale for this procedure: "If we think of a chronologic series of populations and choose one of these as an arbitrary starting point, then, barring termination of the lineage, there will be a point at which the accumulated differences are such that the later populations *would* be reproductively isolated from the initial population *if* they were living at the same time. At this point a new species has been formed by phyletic transition".

The differences between "species" arising by branching of a unitary parental lineage and arbitrarily delimited units arising from phyletic transition within a single lineage (Figure 9) are hence treated in different ways by different systematists. Gingerich (1985)

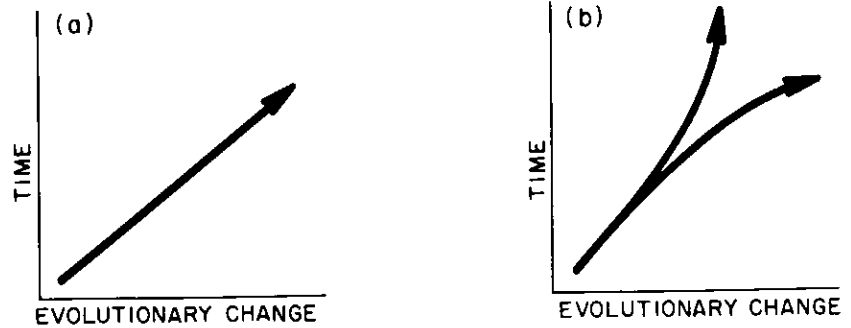


Figure 7 Diagram showing the difference between phyletic evolution or anagenesis (change in a single species) and cladogenesis (multiplication of species or speciation). (Diagram after Grant, 1963).

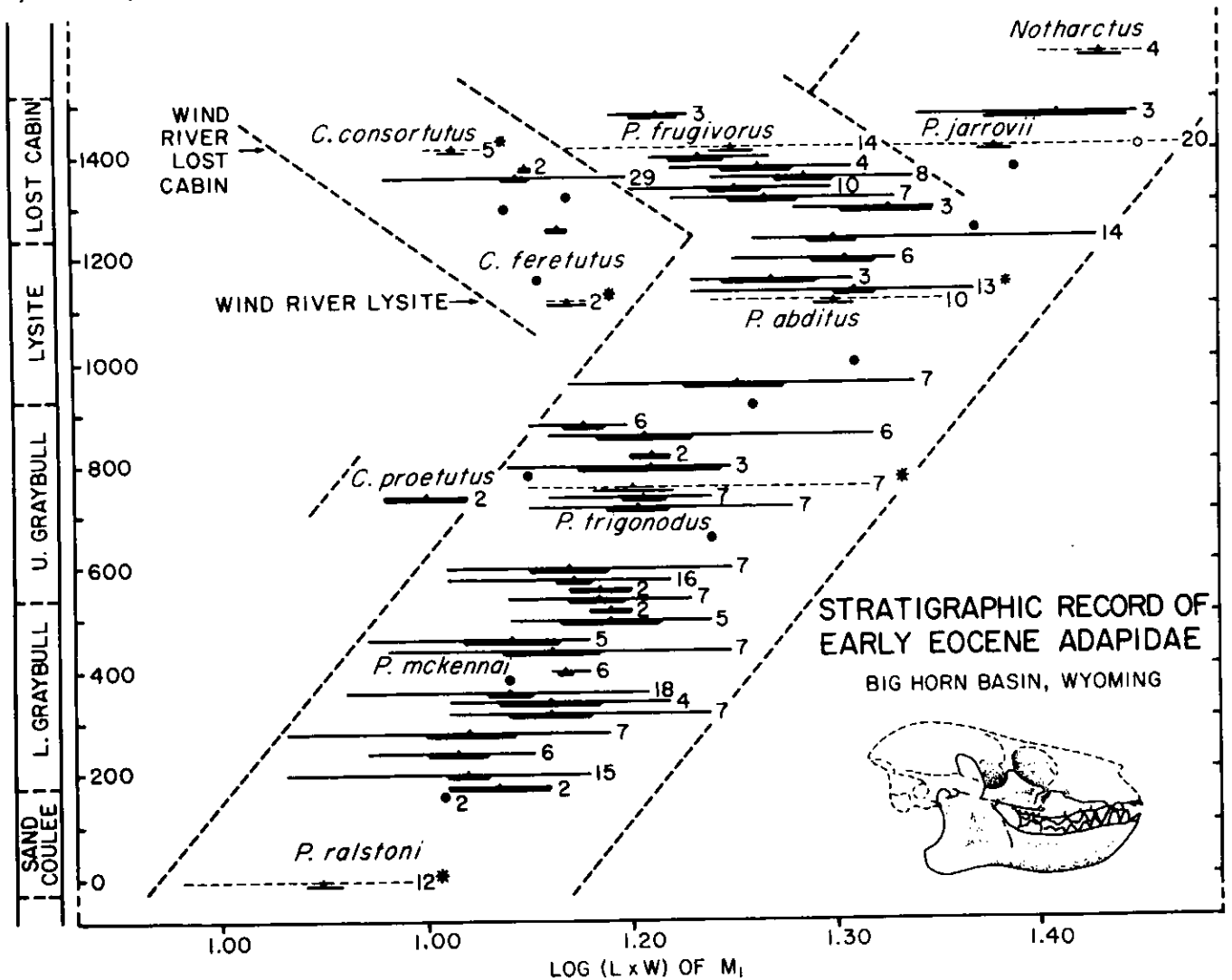


Figure 8 Phylogeny of early Eocene adapid primates from Wyoming, illustrating anagenetic "species" and cladogenesis (multiplication of species) in what appear to be continuous lines of descent in the fossil record. (Diagram from Gingerich, 1977).

uses the term "speciation" for both processes, thereby equating the two, and because of his particular, morphological, concept of the species category, no logical inconsistency results. But that seems not enough: a definition of the species category in terms of phenetic "overall" resemblance is at odds with an evolutionary context — as in applied biostratigraphy, it ignores the source of resemblances in the units being compared and, hence, begs the necessary question as to their origin, which lies in the dynamic, social interaction between the parts of the species in its function as a reproductively inclusive unit and, hence, as a unique evolutionary unit (Rhodes, 1956; Ghiselin, 1969a, 1974); and it misconstrues the nature of the evidence it invokes, for as Ghiselin (1969b) has succinctly pointed out (and see Hull, 1968), there is no such quality as "resemblance overall", only "resemblance over some"! Further, if cladogenetic events, which multiply the numbers of reproductively isolated daughter populations (the usual meaning of "speciation"), delimit "real" species, the logic by which subsequent arbitrary morphological subdivisions of each such species could themselves be species too, is elusive: non-equivalent units are thereby lent identity. Hull's (1979, p. 431-432) comments in this connection can scarcely be improved on: "Species are integrated lineages developing continuously through time (Simpson, 1961; Mayr, 1963; Ghiselin, 1974; Hull, 1976; Wiley, 1978). Cohesiveness at any one time and continuity through time are what matter, not phenotypic or even genotypic similarity. Some lineages may diverge extensively through time without splitting; some

not. It does not matter. *A continuously evolving lineage should no more be divided into distinct species than an organism undergoing ontogenetic development should be divided into distinct organisms*" (emphasis added).

Regardless of these theoretical considerations, it nevertheless remains useful, indeed important, to recognize for particular purposes arbitrarily delimited segments within evolutionary species; some of these purposes are stratigraphic and geological, and are wholly legitimate in themselves. Matched segments of evolving lineages are of great interest to stratigraphers in temporal correlation of rocks, and are no less objective because they are defined arbitrarily (by way of analogy, Hull (1979) has drawn attention to the arbitrarily-defined, but objective, units of everyday time, that is, seconds, minutes, and hours; and Newell (1956) earlier had pointed out that political boundaries are arbitrary but no less objective on that account). Naming or otherwise labelling of these segments need not involve Linnean binomials (Newell, 1956, p. 73); that being the case, it does not follow that an appropriate nomenclature cannot be developed for them, as increments of morphological change distributed in stratigraphic succession. Maglio (1973), for example, developed a system of this very kind in designating stratigraphically successive stages for dental changes within evolutionary species lineages of extinct elephants (Figure 10); White and Harris (1977) used a comparable system to designate morphological stages in the evolution of East African fossil pigs (Suidae).

Are Paleontological and Neontological Species Equivalent?

As paleontologists have become increasingly sensitive to the relevance of population biology and ecology to interpretation of the fossil record — in this connection, a particular focus in recent years has centered on paleontological evidence and the geometry of species evolution (Eldredge and Gould, 1972; Stanley, 1979; Gingerich, 1983, 1984) — the question arises naturally as to the faithfulness with which the fossil record preserves population-level biological events of the past: can, for example, we really "see" the origin of species in the fossil record or do we see a more or less rarified account somewhat removed from the actual events? More specifically, does the paleontological "window" give direct access to population events occurring at single time horizons or at time horizons of known dimension to each other — or do the fossil occurrences that paleontologists normally encounter and that provide the data for most paleontological investigation represent a summation of events over broader scales in time, perhaps numbering in the thousands, tens of thousands, or even hundreds of thousands of years? From recent taphonomic and sedimentologic analyses of the fossil record (Schindel, 1980, 1982; Behrensmeier, 1982, 1983; Retallack, 1984), there seems to be little doubt that the second alternative is the general case, a function of what has been termed "temporal completeness" or the "ratio between time represented by intervals of preservation versus the time span of the whole section" (Dingus, 1984, p. 424; Sadler, 1981; Dingus and Sadler, 1982; Sadler and Dingus, 1982; Schindel, 1982). The issue here seems strictly geological, being one of sedimentology and stratigraphy governing the occurrence of fossils and the interpretation of the temporal record that they provide.

However, rare sedimentological settings are known that permit one to conclude that no significant temporal mixing has occurred, and that single populations in ecological time have been sampled. For example, certain Eocene lacustrine shales in British Columbia that contain exceptionally well-preserved teleost fish and insects were initially deposited as varves, sedimentary couplets each of which appears to represent an annual cycle of deposition (M.V.H. Wilson, work in progress). At any one outcrop, the stratigraphic position of a fossil in relation to that of other fossils occurring at the same locality can be determined in years, by counting directly the layers intervening between the fossiliferous horizons. The longest section of these shales that has been discovered encompasses nearly 700 years. Bell and Haglund (1982) report on similar occurrences of an extinct stickleback fish, *Gasterosteus doryssus*, from Miocene varved lake sediments in Nevada. Quite clearly in settings of this kind, the paleontological "window" provides unencumbered

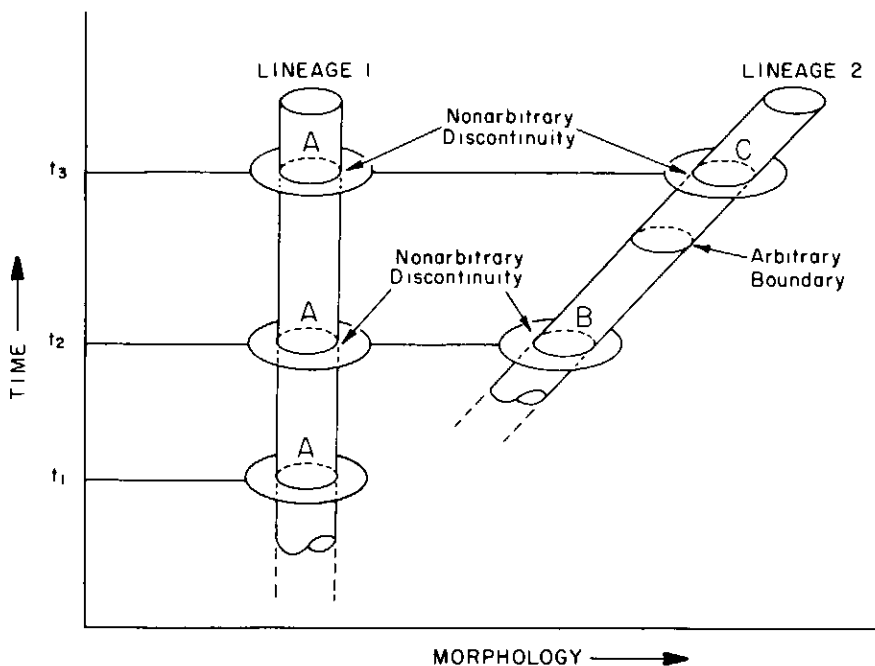


Figure 9 Summary diagram showing relationship between reproductively isolated, genetical species at any single time horizon (non-arbitrary discontinuity separating species A and B at t_2 and A and C at t_3), successional "species" (B and C) delimited arbitrarily in lineage 2, and evolutionary species in the sense of Simpson (1951, 1961) (lineages 1 and 2). (Diagram from Gingerich, 1978b).

access to events in an ecological time frame, such that time can be ignored as an unknown variable affecting what one interprets as species composition.

By way of comparison, however, and illustrative of the more usual circumstance, *Didelphodon vorax* is a common North American Upper Cretaceous opossum-like marsupial, found in fluvial deposits in Alberta, Saskatchewan, Montana and Wyoming. From a biostratigraphic perspective, the deposits in which *D. vorax* occurs are contemporaneous with each other, being Lancian in age (Russell, 1975). Potassium-argon dates from the Red Deer River Valley (Lerbekmo *et al.*, 1979) indicate that *D. vorax* was present in at least Alberta for approximately the last two million years of the Cretaceous (radiometric dates bracketing the occurrences of *D. vorax* are not known from other parts of its geographic range). It seems likely that "*D. vorax*", which morphologically forms a single "species", may very well represent a pool of somewhat divergent reproductive communities both in space and in time (see Newell, 1956, p. 67), thereby comprising a composite unit whose ecologic and genetic boundaries are not as sharp or clear-cut as those of living opossum species, nor as those implied by the occurrences of fossil teleosts in the varves of localized lake basins of Tertiary age. As a consequence of uncertainties of this kind, the genus, not the species, has conventionally

been viewed as the working taxonomic unit in paleontology (Newell, 1956; Wilson, 1967), an artificial device useful for recognition of broader evolutionary patterns, but not one that faithfully portrays biological events transpiring at the population level.

Summary

1. Owing to considerations of uniformitarianism and parsimony, and to the continuity of descent of organisms through time, there should be no separate species concepts for paleontology and neontology.

2. The most realistic concept of species in paleontology is based on evolutionary, not typological, principles, in keeping with the central theme of paleontology, which is not applied biostratigraphy, but elucidation of the history of life (Newell, 1956).

3. The most realistic species concept for all organisms is the evolutionary species concept of Simpson (1951, 1961): "a species is a phyletic lineage (an ancestral-descendant sequence of interbreeding populations) evolving independently of others and with its own separate and unitary evolutionary role and tendencies". The evolutionary species has significant dimension in time and is independent of particular reproductive patterns, and is thereby freed from the limitations of the Mayrian genetical species concept.

4. In logic, the evolutionary species category is a class whose members are particular

species that have the status of individuals; recognition of particular species (taxa) from morphological data, as in paleontology, does not conflict with the definition of the species category in terms of a unitary reproductive community and unique evolutionary role through time.

5. Arbitrarily defined segments of evolutionary species cannot themselves be species; nevertheless, it can be useful to recognize such segments as stratigraphically successive morphological stages designated numerically (or by some other convention not utilizing Linnean binomial names).

6. The boundaries of paleontological species are normally affected by a pooling of samples in space and time, and accordingly may be less clear-cut than for living species, although in special sedimentological environments, paleontological species composition can be seen in an ecological, rather than geological, time frame. Even though known from fossil materials, such examples may be closely comparable to genetical species in the living biota.

Acknowledgements

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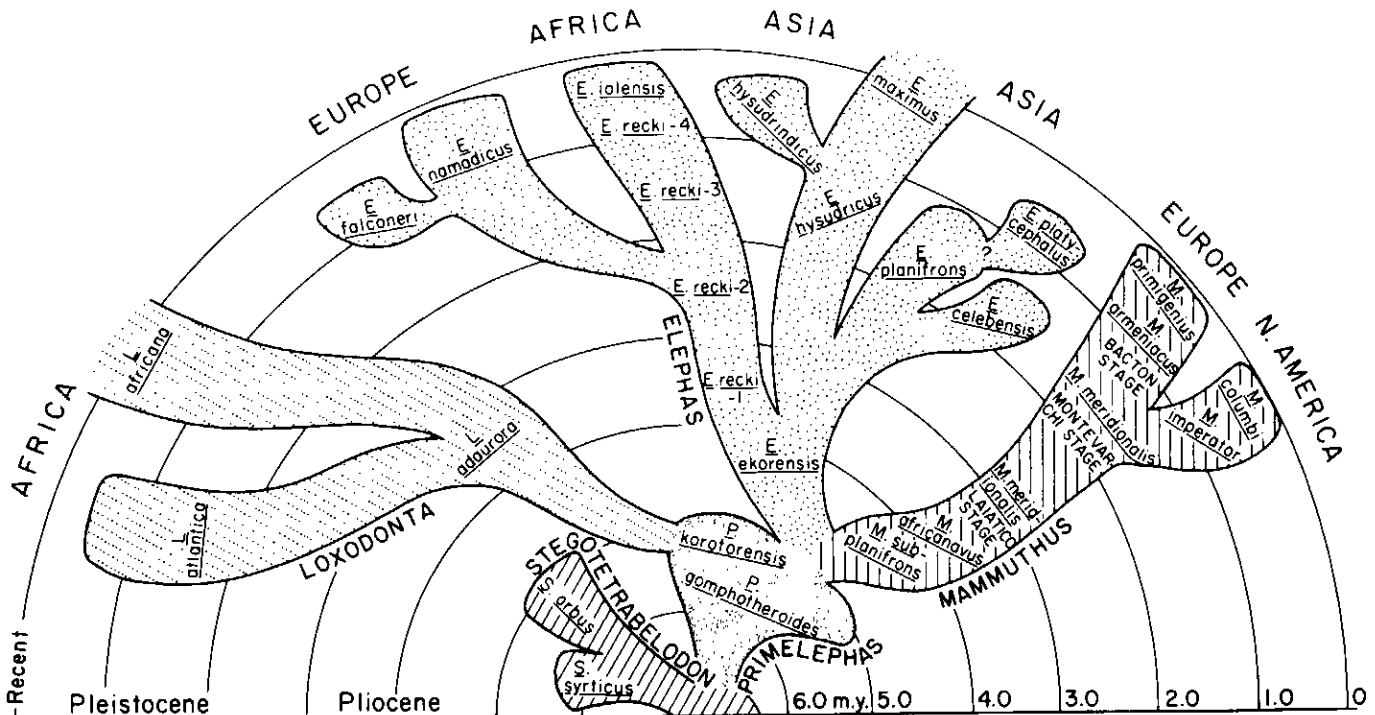


Figure 10 Phylogeny of the elephants illustrating stages of evolution with evolutionary species (four numbered stages in *E. recki*, and stages bearing locality names of the documenting specimens for *Mammuthus*; note, however, that successional "species" are recognized in the terminal branches of *Mammuthus*). (Diagram from Maglio, 1973).

References

Textbooks in Evolution

Contemporary evolutionary biology is a vigorous field, incorporating information from paleontology, ecology, systematics, and population and molecular genetics. Listed here are some standard works in which the properties of living species and their position in the evolutionary process are discussed, information that is essential for paleontologists, no less than for neontologists.

Dobzhansky, T., 1951, *Genetics and the Origin of Species*: Third Edition, Columbia University Press, New York, 364 p.

Dobzhansky, T., 1970, *Genetics of the Evolutionary Process*: Columbia University Press, New York, 505 p.

Dobzhansky wrote from the point of view of a population geneticist, and was a leader in the development of modern evolutionary theory.

Futuyma, D.J., 1979, *Evolutionary Biology*: Sinauer Associates, Inc., Sunderland, Massachusetts, 565 p.

An excellent undergraduate textbook explaining evolutionary mechanisms; reviews contributions from paleontology to evolutionary theory.

Mayr, E., 1963, *Animal Species and Evolution*: Harvard University Press, Cambridge, Massachusetts, 797 p.

Mayr's is perhaps the classic modern textbook on evolution, written from the point of view of a neontological systematist.

Rensch, B., 1960, *Evolution Above the Species Level*: Columbia University Press, New York, 419 p.

Stanley, S.M., 1979, *Macroevolution*: W.H. Freeman and Company, San Francisco, 332 p.

A stimulating attempt by an invertebrate paleontologist to integrate paleontological and biological information into modern evolutionary theory.

Textbooks in Systematics

General works in which the principles of animal systematics are presented. For the purposes of this essay, these works are particularly helpful in delimiting the differences between the category species (a taxonomic level in the Linnean hierarchy), and the taxon species (populations of organisms united by community of reproduction). These works also include important discussions of the problems posed by species in paleontology.

Crowson, R.A., 1970, *Classification and Biology*: Atherton Press, Inc., New York, 350 p.

This provocative book includes novel treatment of the problems that fossils pose for classification in a cladistic system. Crowson is an entomologist.

Simpson, G.G., 1961, *Principles of Animal Taxonomy*: Columbia University Press, New York, 247 p.

Sylvester-Bradley, P., 1956, *The species concept in palaeontology*: Systematics Association, Publication 2, 145 p.

A compilation of essays some of which now seem quaint, others of which are very modern in their point of view.

Wiley, E., 1981, *Phylogenetics: the theory and practice of phylogenetic systematics*: John Wiley and Sons, New York, 439 p.

Wiley, an ichthyologist, amplifies Hennigian systematic theory and practice in this textbook.

Textbooks in Paleontology

These include important discussions of the species in paleontology.

Beerbower, J.R., 1960, *Search for the Past*: Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 562 p. *Beerbower's text pioneered the treatment of fossils from a modern, biological, conceptual point of view.*

Raup, D.M. and Stanley, S.M., 1978, *Principles of Paleontology*, Second Edition: W.H. Freeman and Company, San Francisco, 481 p.

Probably the single most important contemporary textbook in paleontology, having a strong conceptual basis.

The Philosophy of Science

The works below include discussion of the philosophy of science applied to problems in historical sciences, such as paleontology.

Ghiselin, M.T., 1969a, *The Triumph of the Darwinian Method*: University of California Press, Berkeley, California, 287 p.

Gould, S.J., 1977, *Ever Since Darwin*: W.W. Norton and Company, Inc., New York, 285 p.

Hull, D.L., 1973, *Darwin and His Critics*: Harvard University Press, Cambridge, Massachusetts, 474 p.

Includes important introductory essays on reasoning in science, with application to paleontological issues.

Kitts, D.B., 1977, *The Structure of Geology*: Southern Methodist University Press, Dallas, Texas, 180 p.

A very important book examining the philosophic foundations of geology and paleontology.

Popper, K.R., 1968, *The Logic of Scientific Discovery*, Second Edition: Harper and Row, Publishers, Inc., New York, 480 p.

Probably the most important contemporary treatise on the logic of science.

Paleobotany

These titles provide introduction to the paleobotanical literature generally and a discussion of the special problems in systematics that paleobotanists confront.

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"Operationalism" and the Biological Species Concept

A selection of papers criticizing the biological species concept and advocating "operationalism" in systematics; and rebuttals.

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Discussion as to the different meanings of the term "species" in systematics.

Ghiselin, M.T., 1974, *A radical solution to the species problem*: Systematic Zoology, v. 23, p. 536-544.

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