5.2.4 Stratophenetics

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Stratophenetic analysis is an approach to understanding the ancestor–descendant or genealogical relationships of organisms and groups of organisms preserved in the fossil record. The approach is based on: (1) quantitative assessment of morphological (*phenetic*) similarity, interpreted in the context of (2) independent evidence of geological age (furnished by *stratigraphy*). Morphology is important because it is what we can see and study directly in living organisms, and the material record of life in the past is morphological. Time is important because genealogy is sequential. Stratigraphy is the discipline that correlates short sequences of life's history ordered by superposition in local geological sections, building longer composite histories for continents and seaways. Geography too plays a role in phylogenetic inference because organisms propagate within the spatial confines of their geographical ranges.

The goal of stratophenetics, like that of cladistics (Section 5.2.2), is more than a phenetic assessment of affinity or a classification of organisms based solely on morphological similarity. Stratophenetics and cladistics both seek to clarify genealogical relationships. Stratophenetics differs from cladistics in placing more emphasis on time and in seeking ancestor-descendant relationships explicitly. These are expressed in phylogenetic trees rather than cladograms. The ultimate goal is to know the history of life. It is sufficient, in the interim, that stratophenetics continues to augment and extend a well established outline of this history based on fossils, identifying gaps as well as continuity in the historical record.

General approach

The term stratophenetic(s) was coined to characterize palaeontological procedures commonly used in studying phylogenetic relationships in the fossil record (Gingerich 1976, pp. 15—16). These procedures were long employed without a name (see Colbert 1963; Rowell 1970; and others) because the logic seemed self-evident and no competing approaches were advocated by palaeontologists. Responding to the development of phenetics and cladistics by neontologists, Simpson (1976) listed a summary of 'eclectic' or 'evolutionary' systematic procedures, but Simpson's procedures and indeed the names he used to describe them seem unduly broad and vague (but see Section 5.2.3).

A stratophenetic approach to phylogeny involves four steps:

1 *Within-locality or within-sample organization.* Quantitative study of morphological variation in each locality sample of the organisms under study, to identify clusters of specimens belonging to species or other operational taxonomic units (populations, genera, families, etc.) based on morphological similarity at one time and place. A taxon exists only in relation to another, and each taxon in a given time interval or locality must differ by a measurable amount from all others before it can be recognized as distinct.

2 *Stratigraphic organization.* Superposition of localities within local stratigraphic sections and correlation of localities between sections. Correlation is based on sequential change observed in fossils, palaeomagnetic signatures, radiometric dating, and any other geological evidence. Stratigraphic superposition determines the polarity of character transformations observed in a sequence of fossils. Superposition in each local section is determined before correlation between sections. Thus superposition and polarity are independent of correlation.

3 *Stratophenetic linking.* Operational taxonomic units in adjacent time intervals are linked together by their overall morphological similarity, beginning with intervals that have the most taxonomic units and linking those in subjacent (earlier) or superjacent (later) intervals. When a taxon overlaps no other in an adjacent interval, the search for a similar ancestor or descendant is extended to the next subjacent or superjacent interval, and this process may be repeated. Ideally, there is more overlap in the ranges of variation of taxa linked between two adjacent intervals than there is in the ranges of variation of taxa within the same interval. No attempt is made to restrict similarity to shared derived features at this stage because there is no way to determine a priori which characteristics are primitive and which are advanced, and there is no way to determine a priori which advanced features are uniquely derived and which evolved convergently.

Stratophenetic linking can be approached, as Rowell (1970) has done, by looking at species in a multivariate morphometric space with principal component I (or I and II) as a horizontal axis (or axes), lifting species to their appropriate stratigraphic levels on a vertical axis, and drawing connections between similar forms in successive intervals of time. The most *economical* pattern of linking is the one requiring the minimum number of evolutionary lineages connecting all taxa, and the most *complete* pattern is the one with the fewest empty intersections of a lineage passing through a time interval.

4 *Hypothesis testing.* Patterns of stratophenetic linking are phylogenetic hypotheses that are tested each time a new specimen, a new locality sample, or a new taxon is discovered that belongs to the group under study. *Robust* patterns are those that change little as new discoveries are made.

Classification based on phylogeny requires two additional steps:

5 *Grouping.* Operational taxonomic units are grouped into sets of similar forms corresponding to higher taxonomic units (genera, families, etc.). These groups are constrained to include all intermediates in the minimum spanning tree of stratophenetic linking.

6 *Diagnosis:* Groups are distinguished from each

other using combinations of characteristics unique to each group. Shared derived characteristics are particularly important in diagnosing groups from ancestral stocks that preceded them in time. Shared derived diagnostic characteristics are identified *a posteriori* by their distribution on the minimum spanning stratophenetic tree.

Stratophenetic linking at the species level

Within-locality organization, stratigraphic organization, phenetic linking, and hypothesis testing are all illustrated in Fig. 1, which outlines the North American radiation of eight species of Carpolestidae and nine species of Plesiadapidae (archaic primates) found in a 1400 m stratigraphic section on Polecat Bench (and shorter sections measured nearby) in northwestern Wyoming. Solid lines represent the means and probable ranges of seventeen species-level taxa (*Elphidotarsius · florencae, Pronothodectes jepi,* etc.) recognized in studies by Rose (1975) and Gingerich (1976). Species differ principally in size, but they also differ in other morphological characteristics (dental formula, enamel crenulation, incisor form, etc.). Within-locality organization involves grouping specimens

representing all species-level taxa within each fossil-bearing locality; stratigraphic organization involves correlating all localities bearing the same or closely similar taxa and arranging these in stratigraphic order for comparison.

Phenetic linking of similar species-level taxa in adjacent intervals is shown with dashed lines in Fig. 1. The result suggests that there is a single carpolestid lineage and a single plesiadapid lineage below 500 m, while two carpolestid daughter lineages and two plesiadapid daughter lineages are present in some intervals above 500 m. Each pattern is economical in that the relationships of all species in each family require no more lineages than the maximum number of coexisting taxa; and each pattern is reasonably complete in that there is only one extended interval (800–1200 m) where lineages lack representative specimens or intermediate taxa.

The patterns shown in Fig. 1 are tested every time a new carpolestid or plesiadapid is found in northwestern Wyoming. There have been *c.* 80 new specimens found since 1976. These are superimposed in Fig. 1 as solid circles and associated integers. All fall within or near the dashed lines of the original patterns of linking, indicating that the original stratophenetic hypotheses of relationship
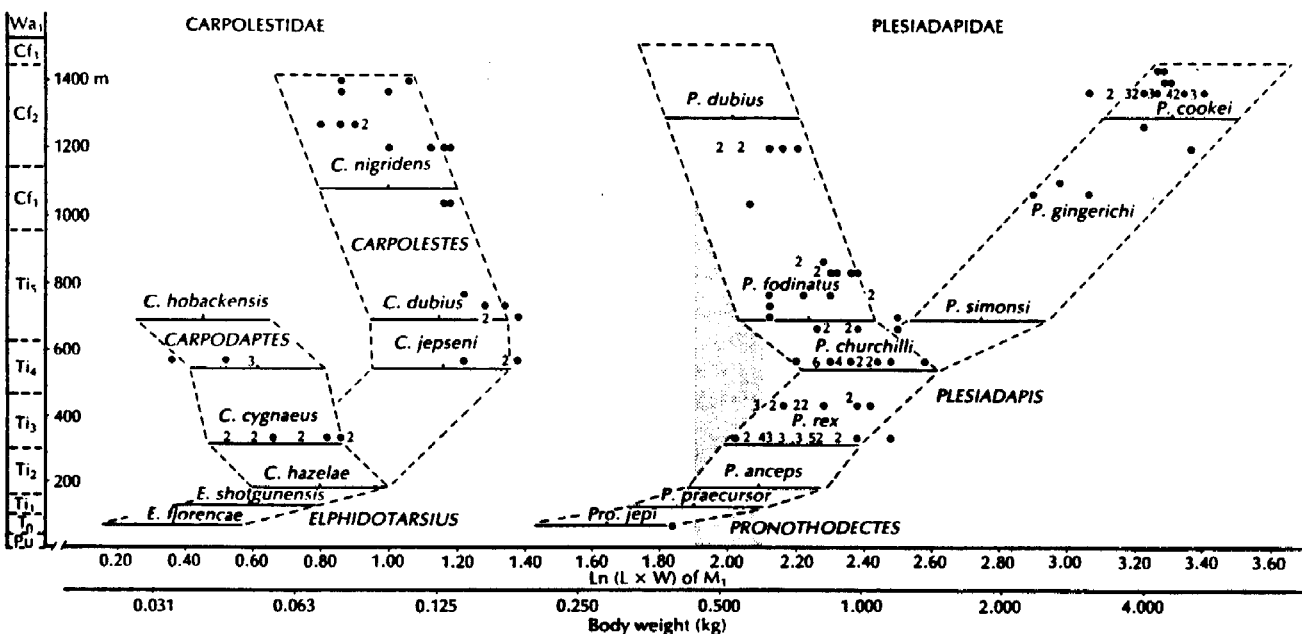

Fig. 1 Pattern of stratophenetic linking in early Cenozoic Carpolestidae and Plesiadapidae. Evolution of tooth size (logarithm of length multiplied by width of first lower molar) and, by inference, evolution of body size (estimated weight in kilograms) are given on the horizontal axis, but the pattern of linking shown here is based on all characteristics preserved in carpolestid and plesiadapid fossils. The vertical axis is a metre level in one master stratigraphic section in northwestern Wyoming (U.S.A.). Standard subdivisions of the Palaeocene and Early Eocene time-scale are also shown. The phylogenetic hypothesis shown here has proved to be robust in that new discoveries (solid circles and associated integers representing multiple specimens) have required little change in the basic pattern of linking. (From Gingerich 1976, 1980, with additions.) Reproduced, with permission, from the *Annual Review of Earth and Planetary Science,* Vol. 8 © 1980 by Annual Reviews Inc.
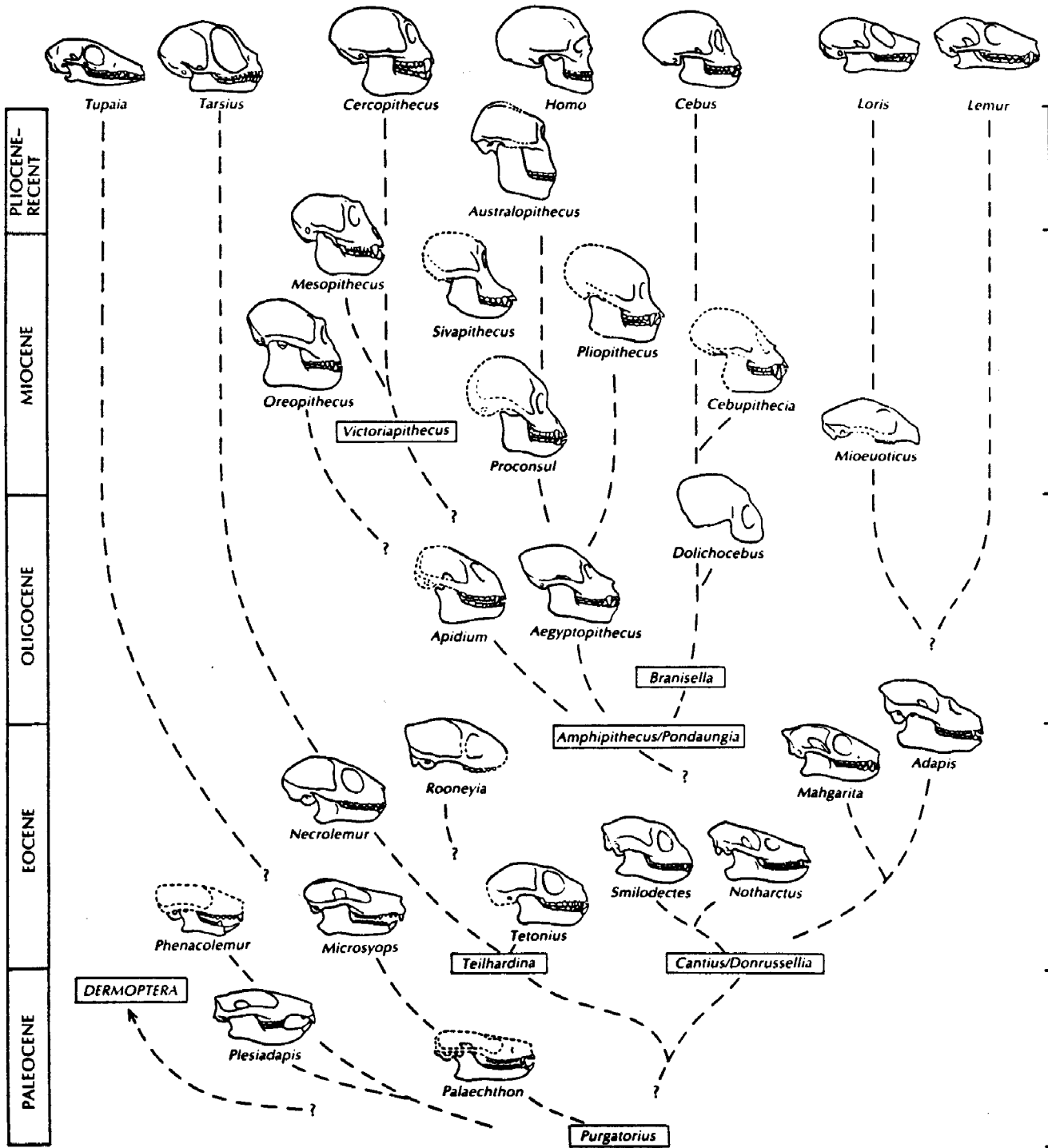
Fig. 2 Stratophenetically constructed outline of primate phylogeny. Morphology (form) is arrayed on the horizontal axis, and the vertical axis encompasses Cenozoic time. Fossil primates known from partial or complete skulls are ordered in form and in time relative to other known fossils. Note that the extant superfamilies Cercopithecoidea, Hominoidea, and Ceboidea are represented by a relatively dense fossil record, while there are many gaps in the historical record of Tupaioidea, Tarsioidea, Lorisoidea, and Lemuroidea. Linkages marked by queries require additional evidence. (From Gingerich 1984.)

are robust and require little modification to accommodate the new evidence found to date.

It is worth noting that the patterns of strato-

phenetic linking shown here are *divergent upward*, i.e. contemporary lineages are found to join at their bases rather than their tops. The important and

long-known generalization that phylogenetic trees diverge rather than converge through time is an empirical result of stratophenetic analysis.

Stratophenetics and cladistics at higher taxonomic levels

Stratophenetics and cladistics can be viewed as alternative approaches to the reconstruction of phylogeny. Which approach is more appropriate in any particular instance depends on the nature of the historical record available for the group under study. Where there is a dense and continuous fossil record available for a group of closely similar species, like the example discussed above (Fig. 1), it is appropriate to analyse the evidence stratophenetically. Numerous intermediate forms provide evidence of transition, and the taxa differ in so few characteristics that it would be difficult to make meaningful cladistic inferences.

At the opposite end of the spectrum, there are groups of organisms (e.g. some insects, bony fishes, . perching birds) for which the fossil record is notably discontinuous and includes only a fraction of the morphological diversity observed to be living today. Here stratophenetic analysis can contribute little, and cladistic inference may be warranted. Cladistic inference is rarely carried out in a vacuum, however, and it is usually appropriate to structure inferences to take advantage of broad outlines of relationship evidenced in the fossil record.

The evolutionary diversification of the mammalian order Primates (Fig. 2) is an example where the phylogenetic tree obtained from stratophenetic linking provides only an outline of the history of the group. Genera illustrating each of the seven superfamilies of living primates are arranged across the top of the diagram. Genera known from skulls in the fossil record, representing one of the living superfamilies or one of three extinct superfamilies, are positioned beneath their most similar living relatives in the appropriate interval of geological time. Stratophenetic linking based on all the evidence of morphological similarity (dashed lines) shows likely genealogical relationships at the family or superfamily level. Of the living groups, Tupaioidea may be related to Microsyopoidea and Plesiadapoidea, but there is a very large gap in their fossil record. Tarsioidea extend back into the Eocene (to *Necrolemur* and its allies), but here again there is a very large gap in the Late Cenozoic. Cercopithecoidea, Hominoidea, and Ceboidea have a reasonably dense fossil record in the Late

Cenozoic, and they appear to converge on *Apidium*-like and *Aegyptopithecus*-like forms in the Middle Cenozoic. Lorisoidea and Lemuroidea have poor fossil records, and they may or may not be derived from Eocene Adapoidea.

Consideration of all the morphological and geographical evidence in a stratigraphic context identifies parts of the historical record that are better known than others; such consideration identifies areas of questionable relationship (origin of lemurs and lorises, for example) that may repay a cladistic analysis carried out in the context of a stratophenetically based outline of primate history (Gingerich 1984). The scale is different, and the pattern of phylogeny is less complete, but the principles of stratigraphic organization and phenetic linking used to produce the outline of primate phylogeny shown here are the same as those used to link species of *Plesiadapis* in Fig. 1.

Conclusions

Stratophenetics differs from cladistics in placing more emphasis on time and in seeking ancestor–descendant relationships explicitly. These relationships may be at the species level, or more broadly drawn at higher taxonomic levels. Stratophenetics as a general approach to phylogeny at any taxonomic level seeks to identify taxa intermediate between others in form, in space, and in time, because intermediates provide the only positive evidence that a given transition occurred.

Stratophenetic outlines are phylogenetic trees constructed with time as an integral component. Phylogenetic trees are more informative than cladograms in relating the divergence of major taxonomic groups to geological time. In addition, stratophenetic outlines have heuristic value in identifying what we do *not* know (as well as what we know), thus identifying gaps in the historical record worthy of investigation. Time is a fundamental dimension in evolutionary studies, and a major goal of palaeontology should continue to be the study of the diversification of major groups of organisms in relation to geological time.

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