

Paleoprimatology at the Pyramid of the Sun

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Evolutionary anthropologists seek to understand aspects of the biology, behavior, ecology, and evolution of primates and humans. One valuable source of data for addressing such issues is the fossil record, which for primates extends at least as far back as the earliest Eocene. At the 60th annual meeting of the Society of Vertebrate Paleontology in Mexico City last October, more than 500 paleontologists convened to discuss the latest discoveries in paleontology, touching on such diverse taxa as dinosaurs, horses, rodents, crocodilians, and, of course, primates. Herein we discuss new fossils relevant to the study of primate evolution, as well as new advances in the phylogenetic analysis of fossil data.

THE FOSSILS

The late middle Eocene Pondaung Formation of Myanmar (formerly Burma) has yielded several fossils, such as *Pondaungia*, *Bahinia*, and *Amphipithecus*, which may offer clues to the origin and early evolution of anthropoids. Gregg Gunnell (University of Michigan Museum of Paleontology) and colleagues presented new postcranial fragments of a primate, including a complete left humerus, fragments of the right humerus, and fragments of both ulnae. Although these postcrania were not associated with dental remains, these researchers tentatively assigned the specimens to *Amphipithecus*, based mainly on their size. Numerous aspects of the morphology suggest strong strepsirrhine affinities. Focusing on the morphology of the left humerus, Gunnell interprets the locomotor adaptations as being consistent with a slow climber, not dissimilar to *Loris*. If these postcranial elements do represent *Amphipithecus*, then they further

strengthen the argument that *Amphipithecus* is an adapiform.¹

Gary Schwartz (George Washington University) and coworkers reported on the dental development rates of the Malagasy subfossil *Palaeopropithecus ingens*. Extant indriids are known to have a highly accelerated dental eruption rate relative to that of all other primates, which is likely to correlate with rapid life-history strategies. The analysis of daily enamel accretion rate as collected from histological sections of *Palaeopropithecus* molars indicates that this taxon is similar to extant indriids in having accelerated dental precocity. However, the rate of enamel accretion is far faster than that in any extant primate, implying that although these animals had precocial dental (and likely overall) development, the life-history strategies of such a large-bodied animal differ greatly from anything seen among living primates.

Jonathan Bloch and colleagues (University of Michigan Museum of Paleontology) showed tantalizing views, including crania and much of the postcranium, of a new paromomyid plesiadapiform that was extracted from a limestone block in the Clarks Fork Basin of Wyoming. Paromomyids have been important to Archontan relationships (the Grand-order that includes primates, tree shrews, bats, dermopterans, and plesiadapiformes). During the last decade and a half, it has been suggested that some paromomyids, based on the possible gliding morphology of the postcranium, are sister taxa to modern dermopterans or "flying lemurs." Bloch and colleagues, based on their analysis, dispute this claim, suggesting that this very early and primitive paromomyid shares no recognizable synapomorphies with dermopterans. However, a more extensive analysis of

the taxonomic status of this fossil and the implications for Archontan systematics must await next year's presentation by this group.

Since the molecular revolution of cladistics, systematists have sought ways to integrate fossil and molecular evidence in phylogenetic analyses. The total-evidence approach was discussed in two different papers as the most amenable method of incorporating these different lines of evidence. Marcia Delanty and Callum Ross (Stony Brook) presented the results of their analysis of tarsiid relationships. *Tarsius* has long been thought to represent the sister taxon to anthropoids based on morphological data (derived rhinarium, postorbital septum, retinal fovea, anterior accessory cavity of the middle ear, and hemochorial placentation). On the other hand, molecular datasets and analyses often fail to resolve the phylogenetic position of *Tarsius*. In addition, the relationships of *Tarsius* and anthropoids to the fossil superfamilies Omomyoidea and Adapoidea are a continuing source of discussion and controversy. Delanty and Ross addressed these issues by combining mitochondrial and rRNA data with a large morphological dataset coding not only extant taxa but each relevant fossil group, and conducted a total-evidence analysis. Although their results differed based on assumption sets and data partitions, the most surprising and controversial result supported a monophyletic Prosimii (*Tarsius* + Strepsirrhini), as well as other traditional groupings such as Anthropoidea + Omomyoidea. A monophyletic Prosimii is very likely driven by the molecular component of the dataset and will undoubtedly lead to more work on this topic.

In contrast, the total-evidence analysis of callitrichid relationships presented by Felicia Brenoe (Stony

Brook) was, in some respects, more successful. Brenoe applied total-evidence methodology to the analysis of extant callitrichids as well as the fossils *Lagonimico* and *Patasola*, using a morphological dataset compiled from the literature and both mitochondrial genes (12S, 16S, cytochrome b) and nuclear genes (epsilon globin and beta2 microglobin). The combined morphological and molecular results were strongly supported with a single, completely resolved tree. Surprising, a highly nested *Callimico* + *Patasola* + *Lagonimico* clade was found. This implies that the taxa may have re-evolved third molars and hypocones, the loss which are putative synapomorphies of the callitrichid clade.

MISSING DATA SYMPOSIUM

The potential for large amounts of missing data has long been a confounding factor in evolutionary studies that include fossils. This issue was the subject of a symposium entitled "Missing Data—Practical Problems and Theoretical Issues," in which several speakers addressed the problems posed by missing data and some possible solutions.

An abundance of missing data in certain taxa or characters can often add to the number of most parsimonious trees produced in a phylogenetic analysis, increasing instances of ambiguous character optimization and leading to reduced resolution in consensus trees. For this reason, fragmentary fossil taxa or characters that cannot be scored in such taxa are sometimes entirely excluded from data matrices either before or after analysis. Are these practices justified?

Maureen Kearney (George Washington University, now at Field Museum of Natural History) argued that methods that exclude data a priori are ill-conceived because the information content of incomplete taxa cannot be easily judged before analysis. Methods that involve identification and removal of problematic taxa a posteriori do not fare much better, as they are liable to obscure the true reason for ambiguous optimizations, which may be due to missing data or character conflict. An alternative is to include all available data and examine consensus trees to determine the source of am-

biguity. Using a measure called the Clade Concordance Index, the amount of ambiguity in consensus trees derived from character conflict can be determined and ambiguity that arises as an artifact of missing data can be suppressed. This method allows the amount of information gleaned from fragmentary taxa to be maximized while simultaneously minimizing the undesirable effects of missing data.

Kearney's method employs a total evidence approach, followed by careful examination of resulting consensus trees. The total evidence approach, while not universally accepted, is operationally sound and, under ideal conditions (complete data for all taxa) would encounter few obstacles. However, 99% of all life is extinct, and thus exists only as fossilized remains, which are always missing some data. Maureen O'Leary (Stony Brook), an advocate of total evidence analyses, addressed some of the operational difficulties encountered when using this approach.

Hypotheses of relationships that are based on non-fossilizable data cannot be tested for the majority of taxa, and are therefore subject to a weakened parsimony criterion. Non-fossilizable data, however, often comprise 80% or more of data matrices. Thus, the total evidence approach is operationally confounded by the fact that most taxa are extinct. To avoid this pitfall, some authors advocate partitioned analyses, segregating morphology and molecules or cranial and postcranial characters, and then comparing resulting phylogenies with one another. The problem with this approach, called taxonomic congruence, is that the partitions themselves are, in a biological sense, completely arbitrary. O'Leary suggests, however, that two biological data partitions actually do exist: fossilizable and non-fossilizable data. A thorough phylogenetic analysis, therefore, should consider not only total evidence, but also taxonomic congruence between these two partitions.

In addition to the discussions on the proper handling of missing data, some authors gave valuable insight into the effects of missing data on the support measures used to evaluate confidence in phylogenetic trees. Peter Makovicky (American Museum of Natural History) examined two com-

mon methods of measuring support: bootstrap and Bremer support. By incrementally adding missing values to existing data matrices, it was shown that Bremer support predictably decreases. Bootstrap values showed a similar trend, but exhibited far greater variability with regard to the overall size of the data set. Although both methods may show tendencies to overestimate support, Bremer support is less likely to do so, and therefore more appropriate for dealing with paleontological data sets and the unique problems posed by missing data. The use of current methods for assessing confidence may, however, lead to the acceptance of false phylogenetic hypotheses.

Mark Wilkinson (Natural History Museum, London) echoed this concern, calling for better support measures that are not excessively sensitive to unstable taxa. Instability that leads to poorly resolved consensus trees may often be caused by a concentration of missing data in a small subset of taxa, rather than missing entries scattered throughout a data matrix. The detection of such unstable taxa can be achieved using double decay analysis. This method improves on traditional decay analyses by revealing strong phylogenetic signals that are otherwise obscured by large amounts of missing data.

REFERENCES

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