NEWS

Rethinking Anthropoid Origins

The adaptive and phylogenetic origin of Anthropoidea has long been a major research focus of paleoprimatology.[1] Yet despite decades of research, several questions remain unanswered, and new questions have arisen. For example, is *Tarsius* more closely related to strepsirrhines or anthropoids? What are the implications of early and fragmentary African and Asian fossils with respect to the paleobiology and phylogeny of later anthropoids? How early in anthropoid evolution did visual specializations like trichromacy arise and what importance do they have for the adaptive origin of anthropoids? More than forty paleontologists, functional morphologists, molecular systematists, and neurobiologists attended the Anthropoid Origins Symposium organized by Callum Ross (Stony Brook University) and Richard Kay (Duke University) in late April, 2001, at the Powdermill Nature Reserve (Carnegie Natural History Museum) to address these questions.

THE *TARSIUS* PROBLEM

The phylogenetic position of *Tarsius* has been enigmatic for as long as systematic research on primates has been conducted. One would think that the morphological and reproductive features that *Tarsius* shares with anthropoids, such as a postorbital septum, anterior accessory cavity of the middle ear, retinal fovea, dry rhinarium and hemochorial placentation, would make most systematists quite comfortable with a monophyletic Haplorhini (*Tarsius* + Anthropoidea). Traditionally, however, this has not been unanimously accepted. The application of molecular systematic methods has complicated the issue because such analyses usually generate conflicting results. Often, the difference between the most parsimonious molecular solution resulting in either a monophyletic Haplorhini or a monophyletic Prosimii (*Tarsius* + Lemuriformes) is just a few steps.

The results presented at the symposium on molecular approaches to primate systematics suggest that although resolution is not at hand, the methods used are becoming more interesting and data-intensive. William Murphy, Eduardo Eizirik, and Stephen O'Brien (National Cancer Institute) presented the results of their cladistic analysis of eighteen eutherian and two metatherian orders, based on nearly 10,000 base pairs of fifteen nuclear genes and three mitochondrial genes.[2] This is one of the largest molecular systematic assaults on mammalian supraordinal relationships attempted to date. These investigators found a monophyletic Euarchonta (Primates, Dermoptera, and Scandentia) with Primates as the sister group to a Scandentia-Dermoptera clade. This result conflicts with several studies based on neurological and morphological data, which have found Dermoptera to be more closely related to Chiroptera and Scandentia to be the sister group to Primates. Regarding primate intraordinal relationships, Murphy and colleagues found a monophyletic Prosimii, using both parsimony and maximum-likelihood search algorithms. However, they were the first to point out that the topology supporting Prosimii and that supporting Haplorhini did not significantly differ when the Kishino-Hasegawa test was applied. That test evaluates whether the best phylogenetic estimates from one topology differ significantly from those of another. One particularly vexing problem is the long branch that represents *Tarsius,* which has had ample time to accrue nucleotide homoplasy. The next step for this research group is to sequence additional species of tarsiers in order to “divide up” the tarsier branch and perhaps resolve this issue.

In contrast, an alternative approach focusing on unique integrated genomic elements found clear evidence to support a tarsier-anthropoid sister-group relationship. Jürgen Schmitz and Hans Zischler (German Primate Center) analyzed the origin and distribution in primates of short interspersed nuclear elements (SINEs), integrated elements of the nuclear genome between 70 and 500 base pairs, which, it has been argued, once arisen, are largely convergence-free due to the improbability of wide-scale simultaneous nucleotide homoplasy. Schmitz and Zischler focused on the 7SL RNA-derived Alu-SINEs in strepsirrhines, anthropoids, and *Tarsius*. They discovered three Alu-SINEs that are exclusively shared by *Tarsius* and anthropoids. In addition, Schmitz and Zischler were unable to find any Alu-SINEs shared by *Tarsius* and strepsirrhines to the exclusion of anthropoids. The three haplorhine Alu markers also independently and separately evolved on chromosomes 7, 9, and 12. Schmitz and Zischler cite this evidence as supporting the improbability that these markers evolved convergently. These data are compelling in their support of a monophyletic Haplorhini. However, it is difficult at present to consider them in lieu of nuclear and mitochondrial sequence data. The use of SINEs for phylogeny reconstruction is new and not without problems, such as how to code for large-scale deletion events and lineage sorting.[3,4]

ASIAN AND AFRICAN ANTHROPOIDS

Within the last decade, Asia has become a crucial area for the discovery of Eocene primate fossils, which are clarifying the traits that define early anthropoids. The importance these new specimens hold for the study of early anthropoid evolution was demonstrated by two papers, one by Chris Beard (Carnegie Museum) and Jingwen Wang (Chinese Academy of Sciences)

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and the other, Dan Gebo (Northern Illinois University) and Marian Dagosto (Northwestern University), on eosimiids, a family of putative basal anthropoids from central China, as well as some as yet unnamed anthropoid taxa. Perhaps the single most important aspect uniting these new fossils, which may number more than ten species from the Shanghuang fissure fillings alone, is that they are extremely small, all approximately less than 150 grams in body mass. In several cases these species are so small that modern primatology lacks a living analog of similar size from which the biology of the fossil forms can be inferred.[5] Even within this truncated range of sizes, several size classes are apparent, suggesting significant diversity among these middle Eocene anthropoids. In addition, eosimiid ankle morphology preserves a mosaic of omomyiform and haplorhine traits, which Gebo and Dagosto interpret as indicating the transition from prosimian grade to anthropoid grade locomotor morphology. Importantly, eosimiid ankle fossils, particularly the talus, show none of the derived traits uniting adapiformes and strepsirrhines.[6]

New discoveries from the late middle Eocene of Myanmar (formerly Burma) are clarifying the relationships of *Amphipithecus* and *Pondaungia,* both of which have been suggested to be anthropoids based on descriptive and cladistic analyses of their dentition. One problem posed by amphipithecids is that they are more than an order of magnitude larger in reconstructed body mass than the slightly older eosimiids. Based on their reanalysis of amphipithecid dentition, Gregg Gunnell (University of Michigan) and Russell Ciochon (University of Iowa) suggested that similarities in molar and mandibular morphology that cladistically link amphipithecids with catarrhines, such as bunodonty, subequal trigonid and talonid heights, enamel crenulation, and deep mandibles and symphyses, are functionally related to a diet of tough, fibrous foods requiring heavy mastication. Gunnell and Ciochon were led to this reanalysis by their discovery of unassociated postcranial remains that they attribute to *Pondaungia,* based on size and the known distribution of fossil primates in the Eocene deposits of Myanmar. These postcrania, in particular the humerus, strongly resemble notharctine adapiform (for example, *Smilodectes*) postcranial morphology in the possession of a rounded humeral head, brachialis flange, large medial condyle, and round capitulum separated from the trochlea. New cranial material also demonstrates that *Amphipithecus* did not have a complete postorbital septum, a synapomorphy of Haplorhini. Gunnell and Ciochon made a strong case that amphipithecids are not anthropoids at all, and should be included in the Notharctidae.

The Fayum of Egypt has long been the most significant source of fossil material of early anthropoids. Elwyn Simons (Duke University) emphasized the preeminent importance of the Fayum when he unveiled a nearly complete skull of *Parapithecus grangeri,* previously known only from mandibular and dental remains. Based on the relatively small size of the orbits, Simons infers that *Parapithecus* was diurnal. Like *Apidium* and *Aegyptopithecus,* this specimen of *Parapithecus grangeri* shows the platyrrhine-type morphology of the ring-shaped ectotympanic at the rim of the external auditory meatus. A bizarre feature of this specimen of *Parapithecus* is that it preserves four small upper incisor alveoli. In contrast, known and well-preserved *Parapithecus* mandibles lack lower incisors, instead having two tusk-like canines. *Parapithecus* may possess a catarrhine-like frontal-alisphenoid contact at pterion, unlike the parietal-zygomatic contact in platyrrhines and, perhaps, in the other parapithecid, *Apidium phiomense.*[7] The latter point is important because the polarity of the pterion trait is unclear. Parapithecids, the outgroup to crown anthropoids, may show both conditions.

Erik Seiffert and Elwyn Simons (Duke University) described new postcranial elements of *Proteopithecus sylviae* and *Catopithecus browni,* previously known mainly from cranial material, and incorporated these data into a cladistic analysis. Their data demonstrate that *Proteopithecus* and *Catopithecus* are quite dissimilar in postcranial morphology. *Proteopithecus* preserves several traits that are similar to those of parapithecids, such as a narrow trochlea, the placement of the entepicondylar foramen, and a bicipital groove, whereas *Catopithecus* is similar to propliopithecids in trochlear width and medial placement of the entepicondylar foramen. Seiffert and Simons incorporated these data into Ross and colleagues' extensive cladistic matrix[8] and demonstrated that *Catopithecus* and oligopithecids are stem catarrhines, whereas Ross and colleagues found *Catopithecus* and oligopithecids to be stem anthropoids.

SEEING RED

Most Old World monkeys, apes, and humans see the color red but male and some unlucky female platyrrhines, as well as most strepsirrhines, do not. Opsins are the proteins in the photosensitive pigments within the retinal cone receptors of vertebrates. Only primates that have abundant wavelength-specific opsins (short for blue, middle for green, and long for red) can make detailed color discriminations, and only those that also possess the red opsins are trichromatic. What is the adaptive significance of trichromacy to primates? The great comparative neurologist, Polyak,[9] thought that trichromacy evolved to detect yellow-to-red fruits against a background of green leaves, and that fruit color and trichromacy had dynamically co-evolved. Studies have indeed demonstrated that trichromacy is useful for sighting and identifying yellow-to-red fruits against vari-luminant and vari-chromatic backgrounds.[10,11] Nevertheless, is trichromacy an adaptation for frugivory? Nathaniel Dominy and Peter Lucas (University of Hong Kong) discussed an alternative explanation, that trichromacy, at least for large-bodied catarrhines, is much more useful for detecting young, nutritious leaves. Young leaves may often be colored red, which to a dichromat looks dark green, and therefore much more like mature, undesirable leaves, a possible anti-folivore strategy on the part of angiosperm species. The fascinating and controversial finding by Dominy and Lucas is that the timing of red color cues for leaves is highly correlated with nutritional value and desirability, whereas yellow-to-red color cues for "ripe" fruits are not. This is opposite of what would be expected if angiosperms were targeting primates as seed dispersers by coloring fruits bright yellow or red. Indeed, Dominy and Lucas' data instead support the hypothesis that catarrhine trichromacy evolved to counter the red camouflage of young leaves.

Trichromacy has long been thought

to be restricted to anthropoids. Ying Tan (University of Massachusetts at Boston) and Wen-Hsiung Li (University of Chicago) screened several strepsirrhine species and found that *Varecia variegata rubra* and *Propithecus verreauxi coquereli* possess sex-linked polymorphic medium (green) and long (red) opsin genes. As a consequence of this, heterozygous females with this polymorphism may have functional trichromacy; that is, these females may have different alleles that are sensitive to the green-red portion of the spectrum.[12] Opsin gene polymorphisms were previously thought to exist only in platyrrhines and some humans, although the platyrrhine pattern of polymorphism is unique in that multiple alleles vary across species.[13] Based on the medium/long opsin polymorphism in *Varecia variegata rubra* and *Propithecus verreauxi coquereli,* as well as their discovery of a greater diversity of long opsins in strepsirrhines and *Tarsius,*[12] Tan and Li argued that the last common ancestor of all primates also possessed a polymorphic opsin and was therefore trichromatic. Because cone photoreceptors never capture sufficient light at night to function, trichromacy is virtually useless to a nocturnal animal, a fact that led Tan and Li to suggest that the last common ancestor of all primates was also diurnal. This notion conflicts with inferences of nocturnal activity in fossil Eocene primates and the most parsimonious solution for the evolution of nocturnality in basal primates,[14] a point that Chris Heesy and Callum Ross made in a subsequent presentation. However, the apparent sequence similarities among medium/long and long opsins genes found in several strepsirrhines and *Tarsius* does suggest homology, supporting the possibility that the last common ancestor of all extant strepsirrhines and haplorhines may indeed have had polymorphic color vision.

What, then, is the adaptive significance of trichromacy to anthropoids? Gerald Jacobs (University of California, Santa Barbara) pointed out that dichromats can discriminate approximately 10,000 hues, whereas trichromats can discriminate more than 2 million, granting trichromats an enormous advantage for image sensitivity, discrimination, and processing. From these data, one can suggest that the advantages of trichromacy probably are not restricted to foraging but may instead be integrated into virtually all components of a species' visual ecology. Teasing apart the selective factors favoring the evolution of trichromacy in primates may be a very difficult task.

The importance of this symposium was not in resolving issues in primate phylogenetics and functional morphology. It seems unlikely that anyone who advocated a monophyletic Haplorhini or Prosimii before this symposium now thinks otherwise. Instead, the most exciting aspects of this meeting were the diversity of approaches and methods used by these researchers, and the wealth of neontological and fossil data now available to primatology. This bodes well for the future.

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