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Phyletic Perspectives on Platyrrhine Origins and Anthropoid Relationships

22

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Introduction

As the editors of this volume describe in their preface (Ciochon and Chiarelli, 1980), the preceding papers were solicited from researchers in various disciplines so that we could collectively examine a set of interrelated questions: (1) What are the paleontological origins of the New World monkeys?, (2) what is the nature of the phylogenetic affinity between the catarrhine and platyrrhine primates?, and (3) what is the significance of these questions, and their resolution, for understanding the influence of continental drift upon the modern distributional patterns of the anthropoid primates? We have been asked to evaluate the status of Questions 1 and 2, which are essentially phylogenetic problems, on the basis of the foregoing contributions as well as our own respective researches. We have attempted to do so by reiterating some of the more salient arguments in capsule form and pointing out what we feel are their strengths and weaknesses (see summary in Tables I-III). Our conclusion—in brief—is that a substantial set of first steps has been taken, largely due to the multi-disciplinary persuasion of the contributors to this volume, but many important problems remain: the data on living platyrrhine comparative morphology is still meager; the fossil record of platyrrhines is sparse but tantalizing; comparisons of early catarrhines and platyrrhines have

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hardly begun: too little is still known of omomyid (and adapid) crania and postcrania; the somewhat better-known adapids (not to mention the rarer omomyids) are still poorly understood phyletically; and, especially, without a clear genealogical picture of platyrrhine, catarrhine, and interanthropoid relationships, no scientific model of their deployment can be synthesized.

The papers in this volume reflect a diversity of methods that is both healthy and indicative of the breadth of the attack on these problems, and we doubt that procedural and philosophical differences are significantly responsible for the lack of a consensus on a number of fundamental issues. However, much of the data that has been generated comes in the wake of the featured debates of the last decade, contrasting the strepsirhine-haplorhine, simiolemuriform and prosimian-anthropoid dichotomous models of primate evolution. It seems timely now to recast our questions, and perhaps our search for fossils, if we are to make more rapid progress toward solving the problems of platyrrhine origins and platyrrhine-catarrhine relationships.

Consideration of these two questions began in the late 19th Century. Anatomists early recognized some major distinctions between New and Old World monkeys, reconciling them as examples of convergent evolution. *Tarsius* was also seen to have closer ties to the anthropoids than to Lemuriformes on the basis of placentation and cerebral arteries. Meanwhile, some paleontologists proposed that the "lemur-like" *Notharctus* was ancestral to platyrrhines. Later, this view was extended to view tarsiiiforms as catarrhine ancestors, implying anthropoid polyphyly. Thus, both the approaches and the hypotheses of this volume are rooted in the earliest interpretive works on primate evolution.

Platyrrhine Relationships

The primary orientation of this volume, which focuses on issues of anthropoid origins from the perspective of the New World monkeys, is appropriate for a number of reasons. Not only are the platyrrhines more conservative than catarrhines in many aspects of their morphology, but they have also been shown to represent actual, rather than purely hypothetical, analogs of early catarrhine behaviors and adaptations (e.g., Fleagle, 1980). Nevertheless, fundamental to their heuristic utilization as models of the extinct early catarrhines is the development of a coherent picture of platyrrhine genealogy, which seems far from achieving a uniformity of opinion. For example, the prolonged debate over the ancestral or derived nature of marmoset morphology has important implications for understanding the evolutionary transition marking the rise of the anthropoids. Were primitive platyrrhines, and protoanthropoids, small-bodied, scansorial, claw-bearing frugivore-insectivores (i. e., marmoset-like) or not? If not, what taxon or phyletic group does most closely approximate our expectations of the kind of animal that was an early anthropoid? Perhaps even more important is an appreciation of the

morphological pattern thought to have characterized the earliest New World monkeys, for that suite of features is prerequisite to the establishment of the phylogenetic relationships of the catarrhines and platyrrhines.

Whereas a number of contributors to this volume have concluded that the claw-bearing marmosets, Callitrichinae, are quite derived in aspect (e. g., Luckett, 1980; Bugge, 1980; Maier, 1980; Kay, 1980; Hoffstetter, 1980; Gantt, 1980; Martin and Gould, 1980; see also Rosenberger, 1977, 1979), marking somewhat of a transition from the prevailing opinion of preceding decades (e.g., Le Gros Clark, 1959; Napier and Napier, 1967; Hershkovitz, 1977 and before), the details of marmoset and nonmarmoset interrelationships are not agreed upon or even well established in certain cases. To some extent, this is due to a genuine lack of information and the still underdeveloped interest in platyrrhine biology. On the other hand, it seems true also that most current students continue to employ the conventional marmoset vs. nonmarmoset perspective for framing their questions and interpreting their data. Rosenberger (1977, 1979) and some others (e. g., Egozcue and Perkins, 1971; Romero-Herrera *et al.*, 1976, 1978; Dene *et al.*, 1976) have contested the phylogenetic accuracy of that distinction, and we have attempted to document (e. g., Szalay and Delson, 1979) an alternative dichotomy based upon a cladistic split between atelids (*Aotus*, *Callicebus*, saki-uakaris, atelines) and cebids (cebines and callitrichines). Thus far, this notion has received little support from immunological efforts, although the DNA sequencing data of Romero-Herrera and colleagues uphold the major outlines of this interpretation as a parsimonious possibility. The biomolecular-based contributions of this volume (Sarich and Cronin, 1980; Baba *et al.*, 1980) are not mutually consistent and present a number of significant problems. It seems especially important, for example, to determine why the albumin and transferrin data seem to have low resolving power beyond a few almost universally accepted phyletic groupings (*Pithecia*+*Cacajao*; *Ateles*+*Lagothrix*+*Alouatta*; Callitrichinae), and why the Cronin-Sarich estimates of divergence times predict that no relatives of the living forms would exist prior to 15-20 million years ago. The fossil record establishes almost unequivocally that platyrrhines were present as early as 35 million years ago and that species exceedingly like, if not ancestral to, the living squirrel monkey (*Dolichocebus*) and the owl monkey (*Tremacebus*) existed 20-25 million years ago. Given our limited knowledge in this area, we note only that the validity of the molecular clock must continue to be seriously questioned, especially since internal analyses have shown that many of the macromolecules used in clock construction do not evolve at mutually consistent rates (Corruccini *et al.*, 1979).

Platyrrhine Origins

As several authors state or imply, the question of platyrrhine origins may be evaluated within the framework of either of two alternative phyletic ap-

proaches: (1) ancestor–descendant, lineage hypotheses or (2) sister–taxon, cladistic hypotheses. The latter, of course, is an indirect approach to the issue of *origins*, but represents a less complex first step which may remain the only course when the nature of the data so dictates (e. g., in neontological work) or when ancestor–descendant hypotheses are nullified. It is worth pointing out in this regard that except for amino acid sequencing, which assesses the transformation of specific, unit character states from one condition to another, none of the molecular evidence is truly comparable to the essence of cladistic analysis, the inference of shared, homologous derived features. Thus, although couched in cladistic terminology in that clusters of taxa are recognized as “clades” (implying a unique common ancestry) the foundation of such analyses (e. g., Sarich and Cronin, 1980) is essentially phenetic. We do not wish to minimize the significance of phenetic studies, but merely point out that *we* prefer them to play an auxiliary role in the establishment of genealogical relationships.

While a number of authors have suggested definite scenarios of platyrrhine origins, we consider all of these as highly speculative or lacking in robusticity. Proponents of a polyphyletic origination model (e.g., Chiarelli, 1980; Perkins and Meyer, 1980) bear the burden of refuting the contradictory morphological evidence which implies that platyrrhines are in fact monophyletic (see Table I). This objection stands irrespective of the ancestral stock(s) from which these workers would derive the New World monkeys. In advocating a dual origin involving both adapids *and* omomyids, Perkins and Meyer have essentially resurrected the early 20th century hypotheses noted above. In this form, however, it is based on neontological rather than paleontological evidence, thus having little resolution as far as descent is concerned.

Hoffstetter's (1980 and before) argument for the descent of platyrrhines from catarrhines via the Parapithecidae has been specifically considered by a number of workers (Rosenberger, 1979; Szalay and Delson, 1979; Kay, 1980). All of these are firmly in opposition, citing the uniquely derived attributes of parapithecids (relative to eucatarrhines) or platyrrhines (relative to catarrhines) which militate against Hoffstetter's hypothesis (see Table I). Although *Parapithecus* and *Apidium* may resemble *some* platyrrhines in *some* features, these appear to be conservative retentions from the last common ancestor of anthropoids and thus do not signify a special relationship between parapithecids and New (or Old) World monkeys. Furthermore, it is becoming increasingly well established (Szalay and Delson, 1979; Fleagle and Simons, 1979) that parapithecids are dentally derived by comparison to other Fayum catarrhines but are more conservative than cercopithecids and pongines in lacking ischial callosities and in retaining P2. In sum, the evidence suggests that parapithecids are a collateral branch of the catarrhines which did not give rise to any of the living anthropoids.

A similar set of anatomical features and phyletic arguments are applicable to any hypothesis which postulates the descent of platyrrhines from a bona fide catarrhine stock (e.g., Falk, 1980). Even the most basic of catarrhine

Table I. Some Characters of Selected Higher Primate Morphotypes^a

Platyrrhines		
D	Hypoconulid absent on M ₃	Kay (1980)
D	Metaconules highly reduced with paraconules probably absent	Rosenberger (1979)
D	Zygomatico-parietal pterion with lateral orbital fissure	Rosenberger (1977)
U	Intraplacentar maternal vessels present; placental hematopoiesis present	Luckett (1980)
D	Reduction of nasal wing cartilages; enlarged embryonic nasal capsule	Maier (1980)
Catarrhines		
D	Presence of facet "X" on lower molars	Kay (1980)
D	Presence of hypoconulid on M _{1,2}	Szalay and Delson (1979)
D	Loss of lateral orbital fissure	Cartmill (1980)
D	Reduction of presphenopalatine lamina of palatine	Cartmill (1980)
D	Placental disk villous; cytotrophoblastic shell well developed	Luckett (1980)
D	Narrow intermaxillary septum with reduction of wing cartilages and olfactory scrolls; loss of vomeronasal organ of Jacobson	Maier (1980)
Anthropoids		
D	I ² conical and robust	Rosenberger and Szalay (1980)
∓D	Thickened enamel on lower anterior premolar	Kay (1980)
P	Loss of P1; mesiodistally "crowded" premolars	Kay (1980)
D	Symphyseal fusion	Kay (1980) (∓D; and adapids)
P	Type 11B enamel prism pattern	Gantt (1980)
D	Postorbital septum complete or nearly so	Cartmill (1980) (D; and tarsiers)
D	Trabeculate hypotympanic sinus	Rosenberger and Szalay (1980)
D	Loss of stapedia artery	Bugge (1980); Rosenberger and Szalay (1980)
∓A	Ophthalmic artery arises from internal carotid	Bugge (1980) (D)
D	Presence of transverse central cerebral sulcus	Falk (1980)
D	Expanded visual cortex and associated sulci	Falk (1980)
D	Reduced lesser trochanter of femur	Ford (1980) (∓D; ∓P)
D	Loss of femoral third trochanter	Ford (1980) (∓D; ∓P)
D	Distal femoral epiphysis anteroposteriorly compressed	Ford (1980) (∓D; ∓P)
P	Karyotypic similarity	Chiarelli (1980)
D	Primordial amniotic cavity present; amniogenesis by cavitation; bidiscoidal hemochorial placenta; blastocyst attachment by embryonic pole; primary and secondary yolk sac present; trabecular disk uterus simplex; rudimentary villous anchoring; no head-to-head sperm agglutination; sublingua absent	Luckett (1980)

^a Our interpretation of the polarity or status [see Rosenberger (1979) for methods] of each feature is indicated in the left column according to the following conventions: A, ancestral, shared with a sister taxon; D, uniquely derived by comparison to sister taxon; C, convergent, nonhomologous similarity; P, phenetic similarity whose phyletic significance we cannot infer. The right column lists the sources for each character and their interpretation when different from our own. Although we have not attempted to assess character correlation in this tabulation, several sets of character states have been grouped for convenience.

molar patterns (excluding the two poorly-known forms *Oligopithecus*—which we consider probably nonanthropoid—and *Pondaungia*) is too derived to have been ancestral to that of the platyrrhines unless a number of reversals can be documented (see Table 1). This implies that any presumptive platyrrhine ancestor inhabiting the Old World would not be regarded as a catarrhine (even on the basis of the Atlantic Ocean as a major diagnostic feature), but rather as a protoanthropoid.

Anthropoid Origins

Given that none of the known anthropoids is ancestral to platyrrhines (or to catarrhines), the next questions for consideration relate to the monophyly of anthropoids and their relationships to other primates. The majority of authors in this volume have accepted the concept that anthropoids are monophyletic (Table 1), thus implying the prior existence of an ancestral species which displayed at least some of the characteristic anthropoid morphology. On the other hand, no authoritative response has yet been counterposed to widespread doubts as to anthropoid monophyly (e.g., Simpson, 1945; Gazin, 1958; Simons, 1972; Cachel, 1979). Other than brief reviews such as this one, there is still no published, detailed objective analysis of the anthropoid morphotype which goes beyond conventional wisdom and the *scala naturae*, such as that provided by Le Gros Clark (1959). The concern over monophyly has largely been based upon the supposition that the postorbital septum evolved convergently among platyrrhines and catarrhines, coupled with a healthy mistrust of the zoogeographic requirements engendered by the monophyly hypothesis. The ontogenetic and distributional patterning of the bony mosaic at the pterion among all primates is a topic worthy of detailed analysis. Major distinctions do contrast platyrrhines and catarrhines (see also Rosenberger, 1977; Cartmill, 1980), and these probably do bear on the evolution of postorbital closure.

Nonetheless, following the consensus of this volume, we may turn to an assessment of the ancestry of the earliest anthropoid, a problem much debated of late as a result of the prominent controversy among primate systematists during the past decade. Most of the morphological and biochemical evidence seems to support the view that the haplorhine primates (anthropoids plus tarsiiiforms) are also monophyletic (Table II and below; see Rosenberger and Szalay, 1980; Kay, 1980; Hoffstetter, 1980). Gingerich (1980), however, argues that this interpretation is incorrect. He suggests, alternatively, that the living lemuriforms are more closely related to anthropoids than is *Tarsius*, and that Eurasian adapids were ancestral to both the living strepsirhines and the anthropoids. Cartmill and Kay (1978) have provided a shred of indirect support for Gingerich's thesis by questioning the traditional acceptance of a close relationship between lemuriforms and adapids and hinting that the latter

Table II. Some Characters Common to Tarsiiforms and Anthropoids^a

Tarsiiforms and anthropoids			
1.	P	Semispatulate incisors variably present	Orlosky (1980); Rosenberger and Szalay (1980)
2.	P	Mesiodistally "crowded" premolars	Kay (1980) (D)
3.	P	Nannopithecus-fold replaced by postprotocrista (variably)	Kay (1980) (D)
4.	P	Premetacristid well developed on M _{2,3} (variably)	Kay (1980) (D)
5.	P	Trigonid low, talonid basin expanded (variably)	Kay (1980) (D)
6.	P	Reduced lower third molars (variably)	Kay (1980) (D)
7.	D	Short, deep, low-hafted facial skull	Rosenberger and Szalay (1980)
8.	D	Apical interorbital septum	Luckett (1980)
9.	D	Diminished nasal fossa; probable lack of olfactory recess	Rosenberger and Szalay (1980)
10.	D	Reduced stapedial artery; enlarged promontory artery	Rosenberger and Szalay (1980)
11.	D	Medially positioned carotid foramen	Rosenberger and Szalay (1980)
12.	D	Anteromedially enlarged hypotympanic sinus	Rosenberger and Szalay (1980)
13.	?D	Downturned humeral trochlea	Rosenberger and Szalay (1980)
14.	D	Enlarged occipital lobes; reduced olfactory lobes	Rosenberger and Szalay (1980)
15.	?D	Loss of coronofacial sulcus	Rosenberger and Szalay (1980)
Tarsius and Anthropoids			
1.	?D*	Haired rhinarium; fused nasal processes	Luckett (1980)
2.	D*	No choriovitelline placenta; rudimentary allantois; well-developed body stalk; ovarian bursa reduced or absent; primordial amniotic cavity transitory; invasive attachment; monodiscoidal hemochorial placenta	Luckett (1980)
3.	C	Postorbital septum	Cartmill (1980) (D)
4.	P*	Presence of fovea centralis	Cartmill (1980) (D)
5.	C	Anterior position of carotid foramen	Cartmill (1980) (D)
6.	A	Incipient enlargement of internal carotid artery	Bugge (1980) (D)

^a "Variable" features are not present in all taxonomic groups; asterisked features not observable in fossils. For key to symbols see also notes to Table I.

group may be closer to the haplorhine clade, with the lemuriforms and plesiadapiforms being somewhat further removed. We regard both of these as less likely hypotheses (see also Rosenberger and Szalay, 1980), further suggesting that other resemblances between adapids and lemuriforms (e.g., the freely suspended ectotympanic and the lack of an ossified annulus membrane [=? reduced linea semicircularis]) may well turn out to be synapomorphies.

Gingerich's (1980 and before) hypothesis of adapid-anthropoid ties is predicated upon (1) the presence of more than a dozen itemized points of resemblance shared between them (Table III); (2) recognition of presumed morphologically intermediate forms that are difficult to allocate [e.g., *Pro-*

Table III. Some Characters Common to Adapids and Anthropoids

1.	C	Body size greater than 500 g	Gingerich (1980) ^a
2.	C	Tendency to fuse the mandibular symphysis	Gingerich (1980); Kay (1980) (?D)
3.	C	Vertical, spatulate incisors	Gingerich (1980)
4.	C	I ₁ smaller than I ₂	Gingerich (1980)
5.	C	Interlocking canine occlusion	Gingerich (1980)
6.	C	Canines moderately large and projecting	Orlosky (1980) (P)
7.	C	Canines sexually dimorphic	Gingerich (1980)
8.	A	Canine-premolar "honing"	Gingerich (1980); Kay (1980)
9.	P	Molarized P4	Gingerich (1980)
10.	P	Tendency toward quadrate lower molars	Gingerich (1980)
11.	A	Nontubular [partially free] ectotympanic ^b	Gingerich (1980)
12.	P	Relatively short calcaneum	Gingerich (1980)
13.	A	Unfused tibia-fibula	Gingerich (1980)

^a None of the characters enumerated by Gingerich were stipulated as shared, derived conditions—merely as similarities indicative of close relationship. See also notes to Table I.

^b Gingerich has claimed that the ectotympanic is partially free in early anthropoids. See text, p. 453 for our refutation of this claim.

toadapis ("Cercamoniis") *brachyrynchus*, *Amphipithecus*, *Hoanghoniis*, *Oligopithecus* and *Pondaungia*); (3) the intermediate stratigraphic position of these dubious taxa and the continuous nature of the Paleogene primate record; and (4) the geographic distribution of adapids and early anthropoids. As examples of "extrinsic" nongenetic evidence, we regard the last three points as having only a secondary relevance to the issue. A phyletic hypothesis should be based upon testable statements about homologous similarities. Other forms of information may sharpen the argument but cannot supersede morphology and genealogical reasoning, either positive or negative. Moreover, the fossil records of adapids and omomyids are in fact replete with stratigraphic and morphologic gaps, uncertainty about the evolutionary significance of incomplete fossils should militate against their being used in grand hypotheses; and the temporal sequence of *taxa* has far less significance than the temporal sequence of *characters*, which tells us little in this case.

The morphological evidence for adapid-anthropoid links also suffers upon close scrutiny. Many of the characters involved are probably correlated, a point often glossed over by most workers, including ourselves (e.g., features 2-4, 5-8, and 12-13 of Table III), so their sheer number is not as impressive as it might seem. Some of these resemblances are likely to represent convergences on the anthropoid condition (characters 2, 3-4, 5-8, and 9-10; see Cartmill and Kay, 1978; Kay, 1980; Rosenberger and Szalay, 1980) or are primitive for the euprimates (features 10, 12, and 13) or otherwise are of limited genealogical value (condition 1). Some authors have employed terms such as *spatulate* incisors, *molarized* premolars, and *quadrate* lower molars in describing shared character states among these primates. Such biologically imprecise terms do not permit clear understanding of the details of any potential similarity, so that determination of homology vs. convergence is not

possible in these cases. Moreover, one feature (number 11 of Table III) is based on a specimen which we suggest may be misidentified. The only evidence that any anthropoids ever had a free, intrabullar ectotympanic comes from a broken bone allocated by Gingerich (1973) to *Apidium* (in part on the basis of its recovery alongside a molar of that genus). Such features of this presumed squamous temporal fragment as (1) the orientation of the "zygomatic process"; (2) the morphology of the "postglenoid process" and its surrounding anatomy; (3) the very large size of the bone by comparison to other fragments of *Apidium*; and (4) the extreme lateral position of the "ectotympanic" inferred by Gingerich lead us to doubt that this bone derives from a primate, much less represents the otherwise well-known *Apidium phiomense*. Finally, Gingerich and other proponents of the adapid ancestry hypothesis have not adequately dealt with much of the positive evidence supporting the tarsiiform-anthropoid theory [although Gingerich (1980) has made several important points in this vein]. If we are to believe that Adapidae is the sister-taxon of anthropoids, we must be persuaded by morphological and systematic argument that the characters identified as haplorhine synapomorphies (Table II) are either conservative retentions or nonhomologous (convergent) shared traits. To ignore counterarguments is not to refute them.

As noted above, we believe that the tarsiiform hypothesis of anthropoid origins, which presumes that the protoanthropoid was omomyid-derived, is the best available interpretive scheme for explaining the bulk of the evidence. The strength of this hypothesis lies in the complementary nature of the results from character analyses of a variety of data sets obtained from both extant and extinct taxa (Table II) combined with the phenetic support from biomolecular studies (for example, see Baba *et al.*, 1980). Moreover, the incorporation of nullifying counterarguments against the adapid-anthropoid alternative scheme allows us to reject opposing interpretations based on the same anatomical systems (see above). Clearly, additional work can further sharpen this hypothesis by excluding many of the known genera or lineages from potential ancestral status (see Kay, 1980; Rosenberger and Szalay, 1980) and by the recovery of more informative cranial and postcranial remains.

Cartmill (Cartmill, 1980; Cartmill and Kay, 1978) has attempted to go beyond this conservatively vague statement of tarsiiform-anthropoid affinities in offering the intriguing hypothesis that *Tarsius* itself, rather than some unknown or unrecognized tarsiiform or omomyid, is most closely related to anthropoids. Some of the evidence against this view has been presented by Rosenberger and Szalay (1980), but Cartmill (1980) has marshalled additional points in support. It appears to us that the key to this question lies in comparisons between *Tarsius* and microchoerine omomyids, some of which share with *Tarsius* such derived features (by comparison to strepsirhines and/or *Rooneyia*) as tibio-fibular fusion and major calcaneal elongation (see Gingerich, 1980; Szalay and Delson, 1979), a narrow interorbital region and somewhat enlarged orbits (Cartmill and Kay, 1978), and a secondarily narrowed external auditory tube and reduced subtympanic recess of the bulla (Rosenberger and

Szalay, 1980). If these homologies and polarities are correct, the hypothesis most compatible with the many autapomorphies of *Tarsius* would recognize microchoerines, rather than anthropoids, as the closest relatives of tarsiers. This concept, supported by Simons (1961) but rejected by Szalay (1976), requires further analysis before it will be widely accepted.

Furthermore, we remain unconvinced that Cartmill's (1980) admittedly fragile reconstruction of orbit and eyeball evolution among the haplorhines is correct (see also Rosenberger and Szalay, 1980). The enormous bony ring and flanges which make up the tarsier eye socket resemble those of *Aotus*, whose ocular and orbital morphology is derived among platyrrhines (Rosenberger, 1979). Whatever advantage a postorbital enclosure might provide when a retinal fovea is present, as it is in *Tarsius* (apparently) and in anthropoids other than *Aotus*, the anatomical association of these two structures need not be causally linked. Although Cartmill (1980) implied that all strepsirhines have a tapetum lucidum while all haplorhines (save *Aotus*) possess a fovea, the literature is replete with queries to this simple picture. Pariente (1979) has reported foveae in *Lemur catta* and *Hapalemur griseus*, both of which lack an anthropoid-like postorbital septum, while Wolin and Massopust (1970) indicate doubts about the presence of a true fovea in *Tarsius* and the distribution of tapeta in strepsirhines. Cartmill (1980) has suggested that *Tetonius*, an early omomyid, may have possessed a tapetum on the basis of its relatively large orbital size, but we offer an alternative interpretation. Cartmill and Kay (1978) indicated that smaller species have relatively larger orbits than do larger relatives, and most mammals do not have either a tapetum or a fovea, suggesting this lack to be the ancestral condition. If *Tetonius* (and by implication other omomyids) were diurnal animals lacking either derived feature, the eyes would have been large to gather the unconcentrated light, especially in a small animal which was vision-oriented. Such a conservative omomyid might give rise to diurnal foveate anthropoids, while the microchoerines and *Tarsius* might have evolved parallel, canalized specializations independently, involving both the fovea and the postorbital septum.

Conclusion

In summation, we agree with the majority of authors in this volume in supporting strict monophyly of both catarrhines and platyrrhines (although we offer a different internal arrangement of the ceboids). Anthropoids, too, are most likely monophyletic, with the earliest representatives presenting at least some of the synapomorphies listed in Table I. Such an early anthropoid would not have been greatly similar in dental details to any of the known Oligocene to modern platyrrhines or catarrhines. Comparing the several most widely accepted hypotheses of origin for ancestral anthropoids, we think that the tarsiiform genealogical tie is the most firmly established (Table II). Not

only does morphology (Table III and refutation above) not support a set of homologous synapomorphies between adapids and anthropoids, but there are important stratigraphic lacunae in the supposed continuum as well. All suggested refinements of the tarsiiform-anthropoid concept suffer from significant difficulties and appear to be based mainly on negative evidence, essentially related to our limited knowledge of omomyid morphology and interrelationships. Microchoerines may be the sister-taxon of modern *Tarsius*, but it is doubtful that this clade is especially close to the protoanthropoids. On the other hand, we suggest that features of the anterior dentition in forms such as *Arapahovius* (perhaps *Tetonius*) and *Ourayia*, which are little if at all known cranially or postcranially, probably include derived homologies shared with anthropoids. Thus we take the conservative stand that the ancestral higher primate originated somewhere in or near the Omomyidae.

Finally, in the spirit of speculation (and of paleogeography, to which this book is dedicated), we offer our current deployment scenario, already put forward in essence by Szalay and Delson (1979). It appears that the east Asian adapid *Lushius* and omomyid *Altanius* have their most significant morphological resemblances to western North American anaptomorphine omomyids, lending primate support to the Bering connection as a mammalian migration route during the Eocene. Similarly, a primate connection between eastern Asia and Africa is suggested by (1) the disjunct presence of *Hoan-ghonius* and *Oligopithecus*, both probably nonanthropoid; and (2) a possible phyletic link between the still poorly-known *Pondaungia* of Burma and the Fayum catarrhines (see Szalay and Delson, 1979; Gingerich, 1980; Kay, 1980). Recent studies of Mediterranean rodents (Adrover *et al.*, 1978), Turkish embrithopods (Sen and Heintz, 1979) and Pakistani proboscideans and cetaceans (West, 1980) suggest further links of these regions and taxa to Fayum relatives. Thus, as Gingerich (1980) delineates in his Fig. 4 (but with different taxa involved), some early euprimates could have occupied a single biotic community spanning the circum-Pacific region and differentiated there into the protoanthropoid stock. With the apparent world-wide oceanic regression during the late Eocene, the formative catarrhine branch (of which *Pondaungia* may represent an offshoot) might have crossed the narrowing western Tethys and entered Africa, while the protoplatyrrhines managed to cross into South America from the north (see also Wood, 1980).* As with all paleogeographic hypotheses, this one is not easily amenable to testing in the precise manner applicable to morphological theories, but must stand or fall on consensus

*Many authors in this volume have preferred a trans-Atlantic rafting dispersal of protoanthropoids from Africa to South America. We reject such dispersal not only because of the problems of dehydration, salt poisoning, and exposure facing any rafted primate unable to estivate, but also on phyletic grounds. No known Old World anthropoid is conservative enough to be ancestral to platyrrhines, even the earliest of which lack several of the catarrhine derived characters found in Fayum and Pondaung fossils. Thus, rafting requires postulation of an unknown source group, as well as serendipitous paleocontinental relationships and paleoceanographic conditions.

analyses of a variety of data. We await the next incarnation of this volume (or at least of the questions it has posed) for such a consensual evaluation.

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