

#### 4 PLATYRRHINES, CATARRHINES AND THE ANTHROPOID TRANSITION

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##### INTRODUCTION

Four basic questions are fundamental to our inquiries into the origins and early history of the anthropoid primates: (1) Are platyrrhines and catarrhines monophyletically or diphyletically related? (2) How did their geographical division into New and Old World radiations come about? (3) Who were the ancestors of the anthropoids? (4) What adaptive breakthroughs, if any, were achieved during the anthropoid transition? These large, much debated subjects will be the topic of this paper, scaled down to a size and formulation that will perhaps suggest more questions than it answers. Another equally basic matter, predicated on the others and therefore more interesting in many ways, is: What are the differences between the platyrrhine and catarrhine adaptive radiations, and how can they be explained? That this more comparative concern has received attention only recently (Delson & Rosenberger, 1984) is in large part due to the imbalance of fossil evidence for the Old and New World anthropoids. Despite its interest, it is a question that will not be considered in this paper.

##### *Monophyly or diphyly - how are platyrrhines and catarrhines related?*

The obvious distinctions between living platyrrhines, catarrhines and other primates were well known to the authors of the earliest higher level primate classifications (e.g. E. Geoffroy, 1812; Gray, 1821). More detailed work on skeletal morphology (e.g. Mivart, 1874; Flower, 1866) expanded the range of their differences, and it was this body of evidence that formed the backdrop for theories of the affinities of platyrrhines and catarrhines. Two schools of thought emerged. One suggested that anthropoids were the monophyletic descendants of a single protoanthropoid ancestor that was genealogically linked with a non-anthropoid (variously specified as adapid or omomyid). The other argued that each group arose in parallel from distinct 'lower primate' stock. Wood Jones (1929) attributed the origins of the parallelism hypothesis to St. George Mivart (1874), who was an accomplished primate anatomist, but decidedly aphylogenetic in his thinking. Mivart seemed fascinated by cases of adaptive similarity in disparate taxonomic groups, such as the long armed Ateles and Hylobates, the thumbless Ateles and Colobus and the long faced Alouatta and Papio. The origins of the monophyly theory can probably be traced to primatology's phylogenetically orientated thinkers, such as Elliot Smith (1924), although other prominent phylogeneticists of the period, like Haeckel (1899) and Wood Jones (1929), were convinced that platyrrhines and catarrhines arose independently. The complexity of the problem is evident when one realizes

that Le Gros Clark, one of the masters of comparative primate morphology, opted for monophyly in his first classic synthesis of primate evolution (1934), but seemed swayed by diphyly in his heavily updated revision (1963).

Although the majority of today's workers have rejected the diphyly hypothesis, it was the overwhelming favourite of researchers until the last decade (e.g. Gregory, 1920; Schultz, 1969), and there is lingering support for it (e.g. Groves, 1972; Cachel, 1979, 1981). Since this debate shaped so much of modern primatology, it would seem fitting to attempt a brief, but by no means exhaustive, historical synopsis and critique of the major propositions of the diphyly theory (Fig. 1).

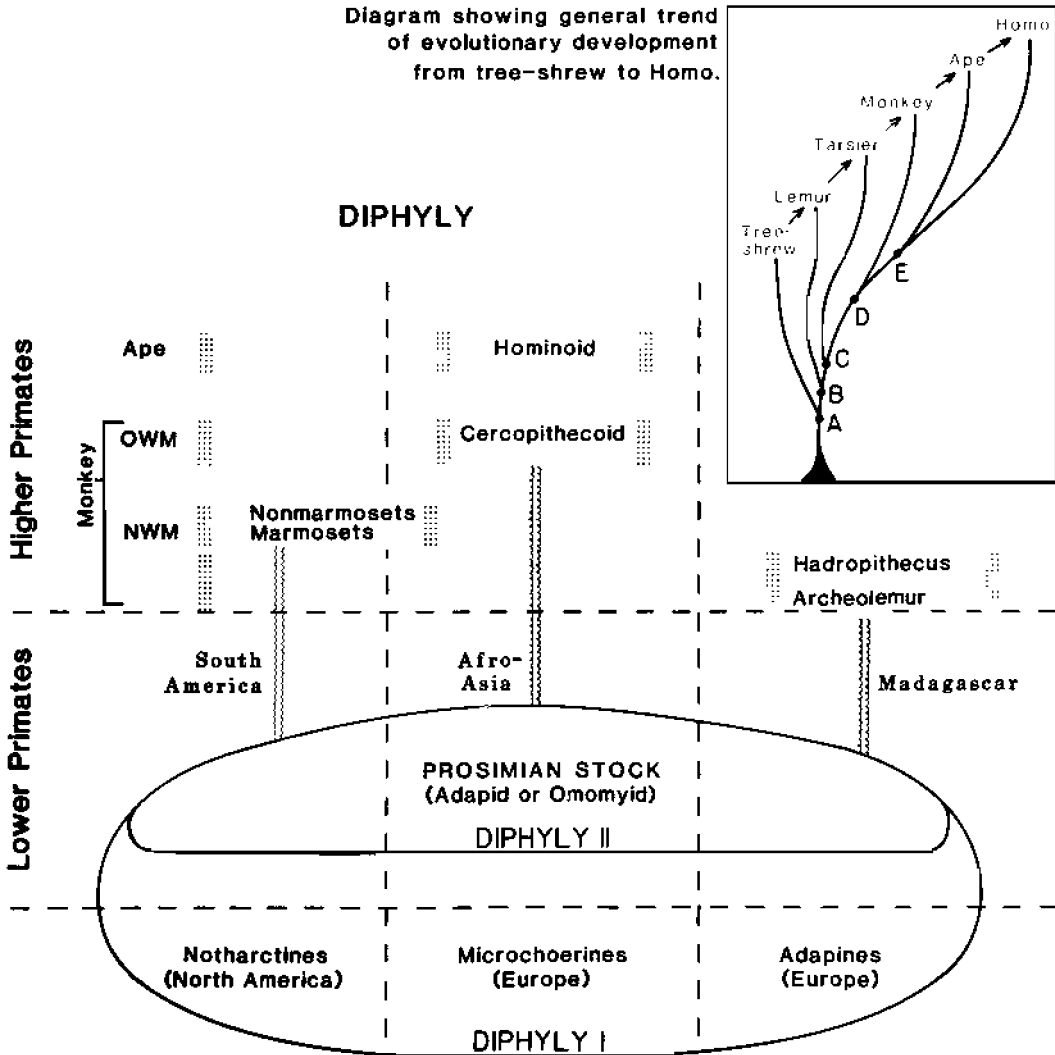
Let us examine three propositions pertaining to taxonomy, evolutionary theory and geography, in sequence:

1. Platyrrhines and catarrhines are markedly different in form, suggesting a lack of affinity and warranting their separation at higher taxonomic levels (e.g. Flower, 1866; Mivart, 1874; Keith, 1934).
2. Primate higher taxa should be ordered and interpreted as successive grades of organization, reflecting the existence of directed evolutionary trends, and suggesting that advanced grades of organization could be attained, or traversed, independently by separate lineages (e.g. Huxley, 1863; Le Gros Clark, 1963).
3. The disjunct distribution of New and Old World faunas were products of parallel evolution, anthropoid primates being just one example (e.g. Wallace, 1876; Matthew, 1915; Simpson, 1961).

As Martin (1973) explained, using primate examples, classifications were an inspirational source for evolutionary hypotheses, rather than the other way around. Additionally, early classifications were usually devised as aids to zoological identification, rather than evolutionary statements. To maintain such a typological structure and convey diagnostic messages, such classifications were exclusive in design, that is, not built upon the inclusive notions akin to the monophyly concept, or genealogy (Mayr, 1982). Consequently, when applied to primates, the differences between platyrrhines and catarrhines were exaggerated; when evolutionary questions were posed, the answers were often correspondingly awry. Thus platyrrhines and catarrhines were assumed to be genetically far removed from one another. *be genetically far removed from one another.*

The gradistic perspective, which implied an inherently progressive ordering of groups not too different from the *scala naturae* paradigm which preceded it (e.g. Mayr, 1982), offered an evolutionary explanation for the set morphological dichotomies that distinguished taxa. The differences between platyrrhines and catarrhines became explicable if each had attained somewhat different levels of evolutionary rank along the trajectory exhibited by living primates (Fig. 1). The similarities of platyrrhines and catarrhines were also thus explained, since the evolutionary trends that guided primate diversification operated in parallel in all groups, enabling each to reach comparable higher grades of organization.

Fig. 1. The gradistic view of anthropoid evolution as a parallel transition. Based upon the ordering of "types" along a scale of progress (see insert) in the human direction, allegedly common evolutionary trends in groups across the order and geographical division of possible ancestral stocks (Diphyly I), later replaced by a less definite ancestral-descendant scheme (Diphyly II).



Grades, like taxa, were typologically defined. The suggestion that higher taxa did, in fact, arise in parallel was but a simple extension of the accepted principle of convergent adaptive evolution at the genus level. As mentioned, Mivart (1874) promulgated this viewpoint, and it was emphatically endorsed even during recent times (Le Gros Clark, 1963). Support for the theory came from the discovery of the extinct subfossil indrioids, such as *Hadropithecus* and *Archaeolemur*, embraced by many researchers (e.g. Wood Jones, 1929; Le Gros Clark, 1963) as a sound example of how parallelism in primate evolutionary trends can produce anthropoid (or monkey-) grade taxa out of an ancestral stock of a lower grade. The interpretation of marmosets as anatomically primitive (e.g. Beattie, 1927) also seemed to suggest that platyrrhines had bridged the higher primate grade separately from the catarrhines, which were never suspected of having such primitive traits as digital claws and minimally convoluted brains.

Given this allegedly factual basis, it was logically inferred that anthropoids had independently evolved their similarities, *in situ*, in the New and Old Worlds. It was frequently surmised that much of Tertiary mammalian evolution was settled during the Eocene, when many modern families first appeared in northern continents. Coupled with the parallelism principle, and armed against the notion of imaginary land bridges across the oceans at middle latitudes, zoogeographers like Wallace (1876) were convinced that Eocene primates, rodents and others independently evolved into more advanced descendants after migrating into southern continents having similar tropical environments. Rather convincing palaeontological evidence for this view was supplied by Leidy (1873), Wortman (1903-4), and Gregory (1920) among others. They began to chart out the phylogenetic history of the major primate groups as an east-west hemispheric divide, which progressed over time via southward dispersal. In many of these studies, North American notharctines were promoted as platyrrhine ancestors, European microchoerines were cited as catarrhine and tarsiid ancestors, and European adapines were possible strepsirhine ancestors. Following Wallace's explicit rationalization, the family-level segregation of these ancestral stocks was emphasized as proof that anthropoids evolved diphyletically in parallel, although Simpson (e.g. 1961) perpetuated the mixture of phylogeny and taxonomy by defining this case of parallelism as an example of monophyly.

In retrospect, one can appreciate how the parallelism hypothesis provided an elegant explanation of platyrrhine-catarrhine similarities before Darwin's monophyly concept became firmly established, and while the approach of character weighting, cladistic analysis and phylogeny reconstruction was not broadly understood. It would also have been solid proof of the theoretical evolutionary patterns championed by the 'New Synthesis'. Like other cases in the history of science, a rethinking of the diphyle theory was perhaps slow in coming because the data were presented as a paradox, to be answered by an unusual solution.

Since that time, revisions in systematic concepts and methods, improved knowledge of the affinities of all the primates, and a vastly improved

fossil record have contributed to the rejection of the hypothesis that platyrrhines and catarrhines have evolved to anthropoid status independently. The genealogical relationships of the early Tertiary primates are better appreciated, but their detail does not resolve into anything resembling the schemes that were conducive to the diphyle theory elaborated by Gregory and others (see Szalay & Delson, 1979; Rosenberger *et al.*, 1985). Geography, which was clearly a stronger barrier to ideas than to animal migration, now weighs less in phylogeny reconstruction. As extrinsic evidence, it is not amenable to tests of homology and polarity, and, at least initially, should be ignored.

The recovery of more early Oligocene catarrhines and platyrrhines has tended to blur their anatomical distinctions. Character analyses of shared platyrrhine-catarrhine traits (e.g. Szalay & Delson, 1979; Lockett, 1980; Delson & Rosenberger, 1980; Cartmill *et al.*, 1981; Rosenberger *et al.*, 1985) provide direct support for their monophyletic descent (see below), despite some nagging anatomical differences which require better evolutionary explanations. The 'arctopithecine' theory of marmoset evolution, which views callitrichines as primitive, has slowly eroded. More convincing analyses have supported the idea that they are a lineage of relatively apomorphic structure and behaviour (e.g. Rosenberger, 1983). The rampant parallelisms that so impressed earlier workers (e.g. toothcombs in lemurs and lorises, suspensory locomotion in gibbons and spider monkeys; incipient or complete postorbital closure in anthropoids, tarsiers and extinct indrioids; the manual dexterity of capuchin monkeys and cercopithecids) are now generally recognized as examples of incidental convergence, and not evidence of true affinity, or as true homology (e.g. in lemuriforms).

How, then, do recent advocates find support for the diphyle interpretation? Cachel (1981) questions studies dealing directly with the issues (see Ciochon & Chiarelli, 1980) and wrongly defines the platyrrhine-catarrhine riddle as "...the question of monophyly or diphyle of the anthropoid grade" (Cachel, 1981:168). It is the applicability of the 'grade' concept, in this particular case, or in general, which is in question; since Darwin's clear statement of the phylogeny concept, propinquity of descent has been the null hypothesis explaining similarities shared jointly by species. Darwin, who was a 'phylogeneticist' (as opposed to Huxley, who was a 'gradist'), wrote, in his Descent of Man:

Every naturalist, who believes in the principle of evolution will grant that the two main divisions of the Simiadae, namely the Catarrhine and Platyrrhine monkeys, with their subgroups, have all proceeded from one extremely ancient progenitor, before they had diverged to any considerable extent from each other... The many characters which they possess in common can hardly have been independently acquired by so many distinct species..." (1871 p. 197-8).

To refute Darwin, one would have to successfully challenge the assumption that such similarities, especially if derived, are nonhomologous. With the single exception of the postorbital septum (see below), there are no

potential anthropoid synapomorphies whose homology has been seriously questioned on the basis of anatomy. Nor does functional rationalization detract from the phyletic valence of potential synapomorphies simply because we can better envision why something evolved, which seems to be the premise of some arguments (Cachel, 1979). Rather, it makes pure similarity stronger evidence of affinity, because it implies the inextricability of phylogeny and adaptation.

There is another aspect that distinguishes these alternative views of platyrrhine-cathartine relationships. Only one is subject to robust biological tests. The monophyly hypothesis is a relatively straightforward cladistic proposition. It may be wrong, but it lays out a set of facts that have predictive value. It can be corroborated by absorbing new data, explaining additional anthropoid synapomorphies. It is not weakened by zoogeographic uncertainties surrounding mechanisms that drive groups to disjunction. Nor is debate over the potential sister-groups of the anthropoids of relevance. Parenthetically, its credibility is increased now that the notharctine-platyrrhine/microchoerine-cathartine scenario has been thoroughly discredited, without any alternative candidates being proposed as the twin, separate ancestors to the platyrrhines and cathartines.

On the other hand, the diphyly hypothesis is a more complex phylogenetic and adaptational argument. It rests entirely on the differences between platyrrhines and cathartines, relegating their similarities to trivia. As an ancestral-descendant hypothesis with no clear statement of the identity of its dual antecedents, it is a phylogenetic hypothesis without roots in the world of experience. If framed as a cladistic hypothesis in which platyrrhines and cathartines each have their own nonanthropoid sister-taxa, it would be amenable to test, but I know of no such proposition. If framed in purely gradistic terms, i.e. anthropoids are descendants of a single non-strepsirrhine, non-tarsiiform species that had not yet evolved traits such as the fused mandibular symphysis, postorbital plate or cellular petrosal bulla, it would still not be testable so long as the classic tests of homology, analogy and polarity determination are deemed unacceptable (e.g. Cachel, 1981). The only recourse, given a disbelief in the validity of classic tests, would be to locate an actual common ancestral species and examine its morphology, a virtual impossibility.

#### *Zoogeography of early anthropoids*

Hoffstetter (1980) rekindled an old debate when he proposed that the Oligocene cathartines from the Fayum supported the hypothesis that a transatlantic migration of Old World anthropoids gave rise to platyrrhines. Such crossings over land bridges stretching between widely separated continents were favourite images among 'philosophical' zoologists of the nineteenth century. It was rejected by more modernistic diphyly and monophyly advocates (e.g. Wallace, 1876; Matthew, 1915; Elliot Smith, 1924), all of whom preferred a dispersion of anthropoids via the northern continents. Hoffstetter, on the other hand, presented his case in a direct, comprehensive fashion, based upon the premises that: (1) anthropoid monophyly implied a common origin in the southern continents where they are basically endemic; (2) Egyptian parapithecids displayed morphology consistent with a hypothetical platyrrhine ancestor; (3) Africa and South

America were closer together during the middle and late Eocene, when platyrrhines and catarrhines probably emerged and (4) the same explanation is applicable to a second contentious group that may have migrated into South America simultaneously, the caviomorph rodents, thought by Hoffstetter and colleagues (Lavocat, 1980) to be the sister-group of the African phiomysid rodents.

Some of the weaknesses of this hypothesis have been outlined (e.g. Kay, 1980; Delson & Rosenberger, 1980) but let me cite several examples. Parapithecids are an unlikely ancestral stock for the platyrrhines because, as their anatomy becomes better known, so too grows the list of autapomorphic specializations (e.g. Szalay & Delson, 1979; Kay & Simons, 1983) that mark them as a divergent collateral catarrhine branch. Postulating a different catarrhine group as a possible platyrrhine sister-taxon, such as the pliopithecids (e.g. Fleagle & Bown, 1983), is questionable on similar grounds. Their general dental anatomy, which serves to unite catarrhines as monophyletic (e.g. Kay, 1977), is more derived than the platyrrhine pattern. The latter probably lacked such catarrhine traits as strongly differentiated talonid cusps, hypoconulids on first and second molars, auxiliary wear facets on the back of the trigonid, subequal trigonid-talonid elevation and advanced reduction of upper molar metaconules. Some of these features even suggest an extra-African origin for catarrhines, which negates that crux of the transatlantic argument, the African endemism of the catarrhines. The Burmese *Pondaungia* displays them, possibly because of a common ancestry shared with catarrhines after the platyrrhine-catarrhine split (Delson & Rosenberger, 1980).

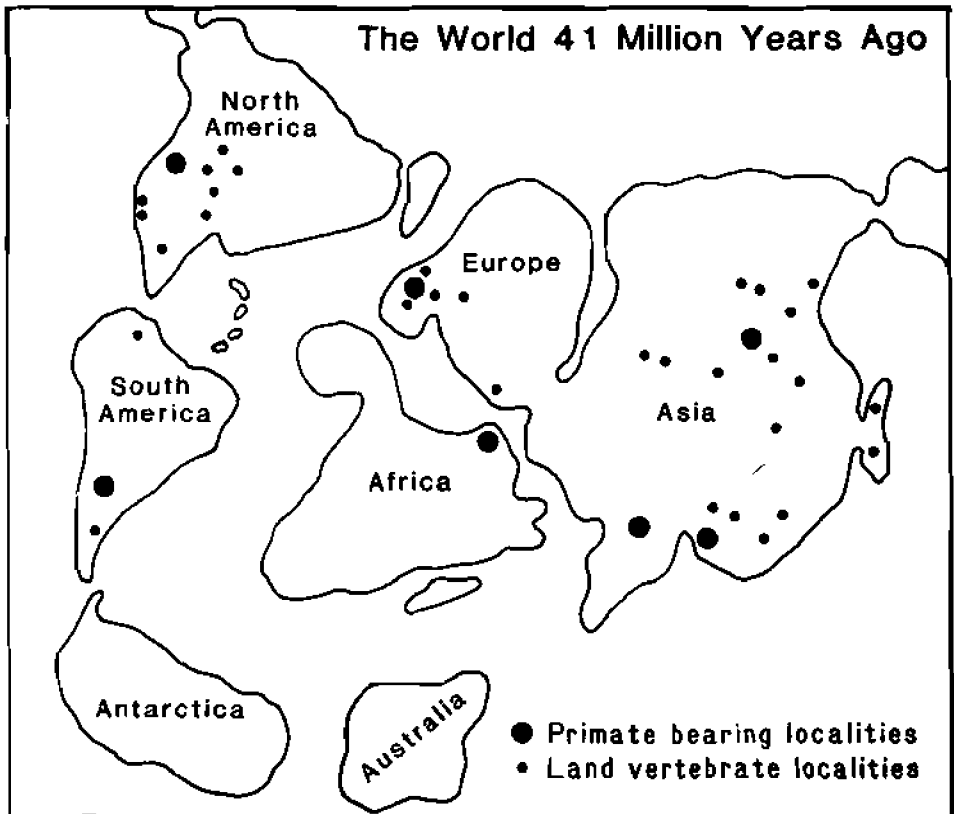
Regarding the former positions of the continents, a factor that should be treated separately from the biological data, both transatlantic and trans-caribbean crossings seem to stretch the human imagination. Overwater distance during the Palaeogene would probably have been less of an impediment to primate dispersal than accessibility to island stepping-stones, now that sunken and/or resutured landmasses are thought to have been scattered between South America, and both North America and Africa (e.g. Sykes *et al.*, 1982; Tarling, 1980), in interrupted chains. Finally, the cladistic links between the African and South American rodents have been seriously challenged in a recent symposium on rodent phylogeny (Lockett & Hartenberger, 1985).

The timing of the arrival of primates in South America, and the allegedly equivalent emergence of related taxa and similar morphologies in Africa, is now also being reconsidered. A revised calibration of upper Fayum beds places them earlier in time, circa 32 million years ago, (Bown & Simons, 1984). New dates for the *Branisella* zone at LaSalla, Bolivia, are about 25 Mya (MacFadden, pers. comm.), roughly ten million years younger than previously thought (Marshall *et al.*, 1977). By comparison with the anthropoid morphotype, therefore, the earliest known catarrhines were highly modified dentally perhaps ten million years before the earliest known platyrrhines, which themselves are more primitive in some ways (Rosenberger 1981a, b) but more derived in others.

No resolution to the palaeozoogeography question is likely to come without

the recovery of fossils from more African and South American localities, which presently represent nothing more than two oases in an otherwise desert of palaeontological ignorance. We might profit, however, by placing the question in a broader context. It appears that continental Africa and South America interacted with Eurasia and North America, respectively, throughout the Tertiary, giving passage to different mammals at various times. The Fayum contained a circum Tethyeen fauna during the early Tertiary (e.g. Cooke, 1972; Savage & Russell, 1983), sharing many elements with southern Europe, the Indo-Pakistan region and central north Asia (Fig. 2). Identical genera, families and (probably) sister-taxa are present outside Africa and as far westward as North America, ranging in time from late Palaeocene to Oligocene (Table 1). This implies that the Fayum accumulated (and probably supplied) a rather cosmopolitan mammalian fauna, with the flux of the Tethys. The Fayum primates may have had an important

Fig. 2. A reconstruction of the world's continents during the late Eocene, made by Savage & Russell (1983). Several orders, families and genera of mammals (Table 1) were distributed across the northern continents and into Africa. Protoanthropoids could have been part of this fauna but were eventually divided, as when platyrrhines became isolated in South America. Eocene and Oligocene primate localities are emphasized.





geographic linkage with Asian forms (not having close relatives in the Eocene-Oligocene Paris Basin) and may be represented by a diverse assemblage of taxa because they were affected en masse by palaeogeography. The parapithecids and eucatarrrhines may have close ties with forms akin to Pondaungia, as already mentioned. Oligopithecus, which does not appear to have any catarrhine or anthropoid synapomorphies, (less even than Pondaungia possibly has) deserves more serious comparisons with Indian Indraloris (Szalay & Delson, 1979), with the Chinese Hoangonius and with Tarsius. There is also little doubt that the African ancestors of the Malagasy strepsirrhines will some day turn up, as Africa probably supported them en route to Madagascar. These points tend to argue against an Africa to South America dispersal route in pleading the anthropoids as a special case, for they would be the only group suspected of bridging the Atlantic and surviving the trip, and they would be the only ones to head westward.

In the western hemisphere, a similar pattern prevailed, with important phyletic and geographic connections between North America and South America (see McKenna, 1980). The didelphid Alphadon was present in the late Cretaceous of both continents, when the water barrier between them was even greater than in the Eocene. The contemporaneous condylarth, Perutherium, resembles others from the Palaeocene and Eocene of North America, Europe and Asia. The exclusively North American soricomorph insectivores also seem to have contributed to the Neotropical realm during the Palaeogene, leaving Solenodon and Nesophontes as descendants that are now confined to the Greater Antilles (MacFadden, 1980). Thus, a smaller number of taxa are thought to have been involved in an interchange between the Americas than between Africa and Eurasia, but this may reflect a more difficult passage across the geophysically complex proto-Carribean Basin. Primates and rodents may simply represent one or two other cases of incidental dispersal.

#### *Ancestors of the anthropoids*

The three viable theories specifying the sister-group, or ancestral stock, from which anthropoids arose are respectively the adapid-anthropoid, tarsiid-anthropoid and omomyid-anthropoid hypotheses (Fig. 3). The adapid-anthropoid hypothesis is based on a variety of dental characteristics shared jointly by certain fossils and all anthropoids, and the case for it has been made most eloquently by Gingerich (e.g. 1975, 1977, 1980). Previous formulations of this position (e.g. Gregory, 1920; Le Gros Clark, 1963) were fallaciously influenced by the scala naturae doctrine, an (apparent or uncertain) acceptance of a diphyletic Anthropoidea, a misunderstanding of the affinities of Palaeogene primates, and the accidental nature of palaeontological discovery (Rosenberger et al., 1985). Some of the cranial evidence supporting the adapid-anthropoid hypothesis has been challenged recently (e.g. Rosenberger & Szalay, 1980; Delson & Rosenberger, 1980; Cartmill et al., 1981).

In the dentition, the essential phenetic resemblance linking adapids and anthropoids includes such features as a fused mandibular symphysis, spatulate incisors, canine sexual dimorphism, canine honing premolars and upper molar morphology (e.g. Gingerich, 1980). These have been reexamined critically (Rosenberger et al., 1985) and seriously challenged as a suite

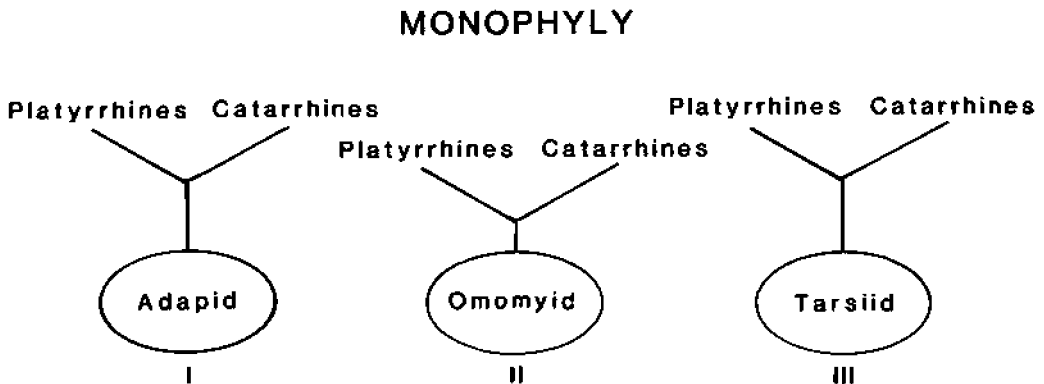
Table 1. Comparison of the geographical distribution of Fayum mammals during the Eocene and Oligocene (compiled from various sources). The co-occurrence of genera in Europe, Asia, North America and Africa suggests the existence of a cosmopolitan Laurasian fauna, and significant interchange between Africa and Eurasia. The contrastingly sparse overlap between Fayum groups and South American eutherians, and their restriction to the ordinal level, suggests that Transatlantic crossings are inconsistent with the global zoogeographic pattern for nonvolant, terrestrial mammals. The presence of non-anthropoid primates in the Fayum, such as Oligopithecus, and the possibility that Eocene forms like Pondaungia of Burma are phyletically anthropoids - and more primitive than catarrhines - implies that catarrhines may not be endemic to Africa and that anthropoids arose on some other continent.

Fayum Mammalia	Europe	Asia	North America	South America
PROTOEUTHERIA	•	•	•	
INSECTIVORA	•	•	•	
MACROSCELIDEA				
CHIROPTERA	•		•	•
Phyllostomatidae				•
PRIMATES	•	•	•	•
Parapithecidae				
<u>Quatrania</u>				
<u>Parapithecus</u>				
<u>Apidium</u>				
Pliopithecidae				
<u>Propliopithecus</u>				
<u>Aegyptopithecus</u>				
Family indet.				
<u>Oligopithecus</u>				
RODENTIA	•	•	•	•
CREODONTA	•	•	•	
Hyaenodontidae	•	•	•	
Apterodon	•			
Pterodon	•	•		
Isohyaenodon	•	•		
PROBOSCIDEA		•		
Moeritheriidae		•		
SIRENIA				
EMBRIHOPODA		•		
HYRACOIDEA				
ARTIODACTYLA	•	•	•	
Cebochoeridae	•			
<u>Mixotherium</u>	•		•	
Anthracotheriidae	•	•	•	
<u>Rhagatherium</u>	•			
<u>Brachyodus</u>		•		
MARSUPIALIA				
Didelphidae	•		•	•

of potential synapomorphies. Rosenberger *et al.* (1985) attempted to show that the anterior dentitions of those adapids most similar to anthropoids manifest a non-homologous similarity, and are less comparable anatomically than our vague terminology allows. They interpreted the anterior dentitions of each group as reflecting divergent adaptive orientations. They claim, for example, that notharctines display a pattern laid over a bauplan that is strepsirhine and not anthropoid. The pattern exhibits a reduction in the importance of the anterior dentition in ancestral adapids, away from the primitive primate pattern where they play significant harvesting roles, towards a more lemuriform-like sniffing and grooming complex (Rosenberger & Strasser, 1985). This postulated preadaptation to a tooth-combed anatomy rules out a phyletic adapid from anthropoid ancestry. Adapids are thus viewed as bona fide representatives of the autapomorphous strepsirhine clade. In contrast, anthropoids augment the plesiadapiform-like pattern (see below), where food harvesting predominates over the grooming or communicative faculties associated with the anterior dentition and snout.

The tarsiid-anthropoid hypothesis is based upon a number of cranial similarities thought to be exclusively shared by Tarsius and the anthropoids, to the exclusion of omomyids (Cartmill & Kay, 1978; Cartmill, 1980; Cartmill *et al.*, 1981). These characters include details of the middle ear and the postorbital septum. Some suggested synapomorphies, such as the partitioning of an anterior bullar cavity and the relocation of the posterior carotid foramen, have been challenged as convergences (Rosenberger & Szalay, 1980; Packer & Sarmiento, 1984). The homologizing of an enlarged postorbital bar in Tarsius and a complete postorbital septum in anthropoids (see below) has also been disputed (Delson & Rosenberger, 1980). Added to these criticisms is the factor of phylogeny. Although the position

Fig. 3. Anthropoid monophyly, and the three current candidates for their ancestral stock. Omomyids (II) appear to be the most likely stem group.



of tarsiers among the haplorhines is in dispute, advocates of the tarsiid-anthropoid hypothesis bear the burden of falsifying a series of possible synapomorphies in the skulls, dentitions and postcrania of *Tarsius* and the microchoerines (e.g., Simons, 1972; Gingerich, 1981; Rosenberger, in prep.) which would preclude them from sharing in a sister-group relationship with anthropoids.

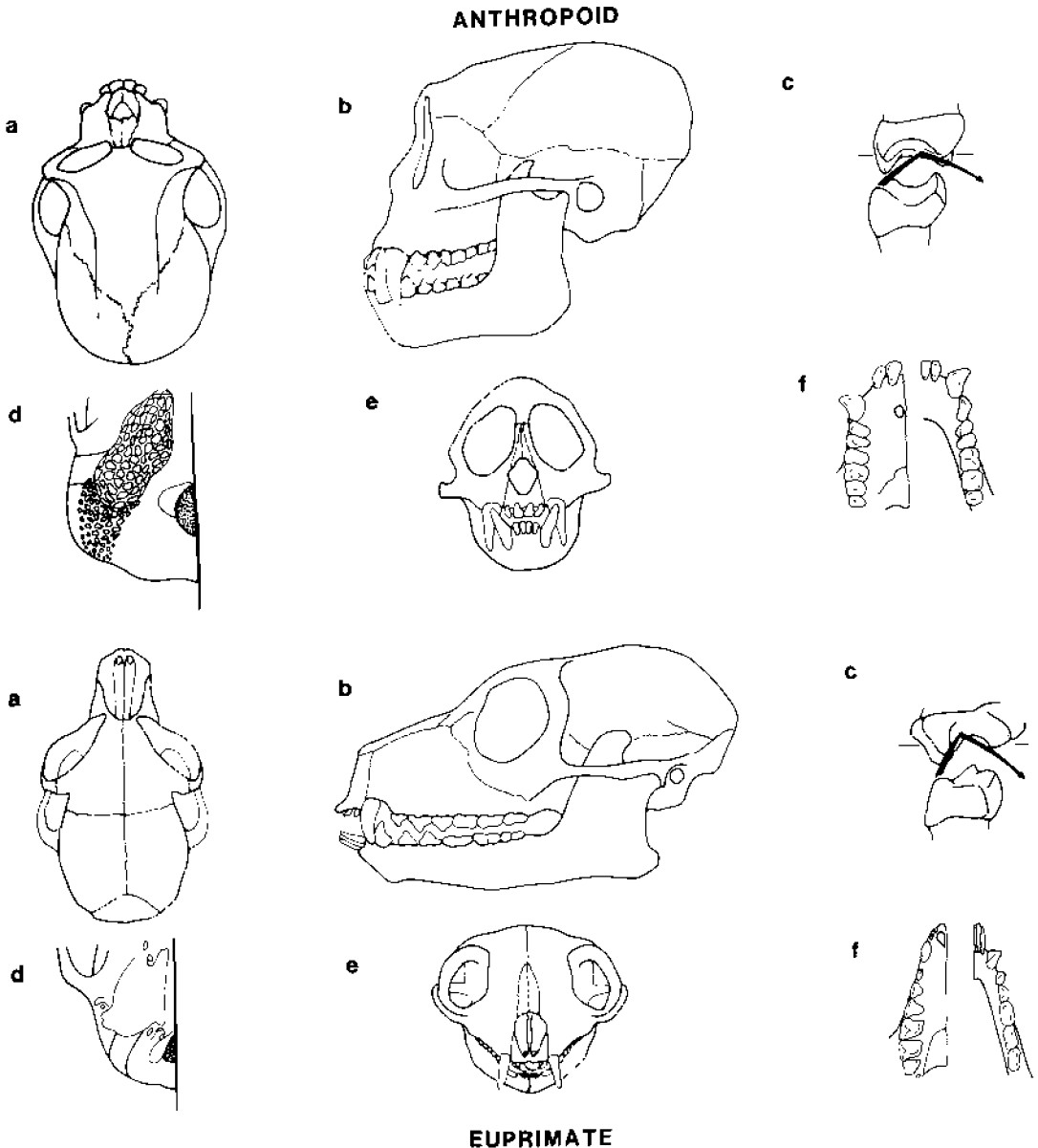
The third option, the omomyid-anthropoid hypothesis, is based upon features demonstrating the monophyly of living haplorhines (Luckett & Szalay, 1978) and the presence in omomyids of apparently derived homologies shared with anthropoids (Rosenberger & Szalay, 1980) such as an apical interorbital septum, abbreviated face, enlarged brain and, possibly, fused frontal bones (Fleagle & Rosenberger, 1983). Those who object to this viewpoint, citing the presence of a fused tibiofibula and tarsal elongation (e.g. Gingerich, 1980), have been answered by the discovery of omomyid material showing neither of these derived, non-anthropoid conditions (Dagosto, 1985). This model is also supported by its ability to provide a preadaptive morphological substrate for the evolution of the anthropoid head.

#### *The anthropoid transition*

The list of shared derived features which characterize the Anthropoidea is drawn from diverse anatomical systems, ranging from the brain to the reproductive tract and the femur (e.g. Falk, 1980; Luckett, 1980; Ford, 1980). But as Cartmill (1982) pointed out, these still give us little insight into the lifestyle of early anthropoids, or the nature of the anthropoid transition. On the other hand, the cranial skeleton includes the highest concentration of anthropoid synapomorphies, which suggests that a study of the anthropoid head might shed more light on the subject. Several of these synapomorphies, such as the fused mandibular symphysis, the postorbital septum and the large, spatulate incisors have been discussed as significant contributions to a masticatory apparatus adapted to a frugivorous diet (e.g. Beecher, 1979; Cachel, 1979; Rosenberger et al. 1985). I am in essential agreement with this view, for reasons other than those given by Beecher, Cachel and others. Let me propose a model for the evolution of the anthropoid synapomorphies as adaptations to critical functions (see Rosenberger & Kinzey, 1976) for the harvesting of tough-coated fruits and, possibly, fruits with hard edible contents, such as seeds and nuts. The model is framed as a contrast of strepsirhine and anthropoid structure and function and uses forms like *Lemur* and *Notharctus* as representatives of the primitive euprimate anatomy (Fig. 4).

Anthropoid skulls are distinguished by features of the dentition, mandible, facial structure, craniofacial hafting and structure of the ossified petrosal bulla. I propose that the transition to the Anthropoidea involved the evolution of a masticatory apparatus designed to produce a powerful anterior bite employing the incisors and the anterior premolars effecting strong static stresses within the cranium. Further, the anatomical substrate for this complex was a haplorhine heritage; the particular mechanical solutions were conditioned by other architectural developments that emerged in the omomyid relatives of the anthropoids in response to different selective pressures.

Fig. 4. Comparison of (top) anthropoid (Cebus) and (bottom) euprimate (Lemur) skulls and dentitions to suggest some of the modifications involved in the anthropoid transition: (a) fused frontal bones, (b) recession of face, closure of orbit by enlargement and fusion of zygomatic bone to braincase. (c) enhanced grinding stroke of chewing cycle, (d) cancellous petrosal bones, (e) fused mandibular symphysis, (f) frontation and enlargement of incisors, blunting of premolars,



The most distinctive component of the anthropoid dentition is the morphology of the incisors. Anthropoid upper incisors are quite different from those of adapids (Rosenberger *et al.* 1985), with which they have been compared. They are relatively robust, high-crowned, buccolingually thickened teeth with strong roots, and are aligned mostly in the frontal plane (Fig. 4). They reciprocate with lowers that are solidly implanted across a fused mandibular symphysis. Anthropoid upper premolars tend to be more transversely extensive and anteroposteriorly compact than is the case among other primates. They also have subsequal protocones and paracones rather than a dominating buccal cusp, and there is a fairly large intervening occlusal basin. Molars tend to have larger occlusal basins and have crowns of lower relief than those of many omomyids, suggesting a transition at some point to a greater emphasis upon lingual phase processing during the chewing cycle (Kay & Hiiemae, 1974). Thus, in general, the molar teeth of anthropoids are designed for more crushing and grinding and less shearing, and the premolars for more crushing than puncturing during the preparatory cycle.

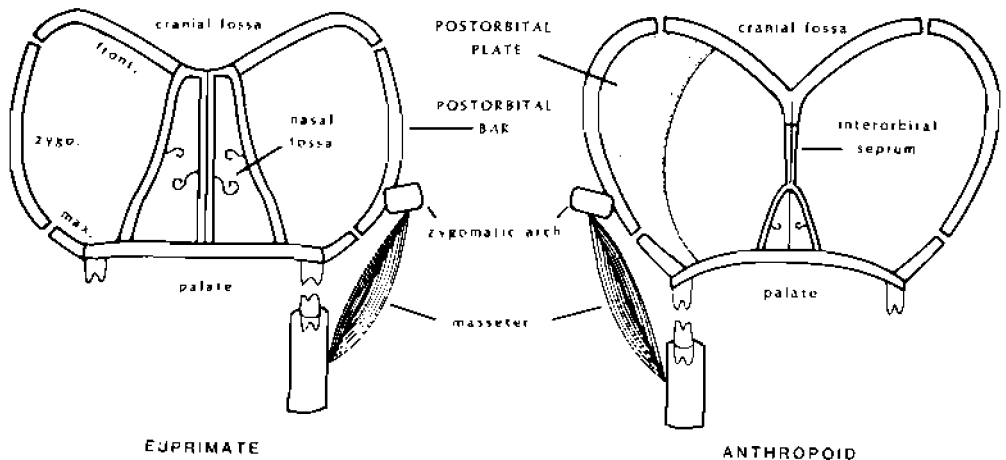
What is being proposed, in simple terms, is that the anthropoid head reflects a shift in design from a primitive euprimate pattern, in which the tooth-bearing facial skull is braced against the cerebral skull by an envelope of midline structures, to an architecture in which central and lateral trusses are more prominent (Fig. 5). Geometrically, this corresponds to a repositioning of the face from a precerebral to a more subcerebral location so that the face is hatted below the forebrain, rather than in front of it. The primitive euprimate condition, still exemplified by many primitive strepsirhines, has a cone-shaped face joined to the anterior cranial fossa at its base. Widely separated orbits are divided by an impressive inter-orbital plate that is continuous with the upper portion of the maxillary and nasal bones. This represents the outer, upper surface of the cone. The more important structures completing the cone laterally, inferiorly and internally are the medial walls of the orbits, the hard palate and connecting bones, e.g., the palatine and maxilla. During mastication, forces transmitted to the facial skull probably cause the face to bend and, to some extent, twist up against its moorings. Much of this load is probably distributed through the core of the cone. But, with the molar teeth and the temporomandibular joint and muscles of mastication positioned laterally, the postorbital bar will also probably be affected (see Endo, 1973; Roberts, 1979). The bar, being a T-shaped member connecting the frontal bone to the maxilla and temporal through the strut-like processes of the zygomatic, must also be loaded.

The contrasting anthropoid pattern is built around a greatly narrowed central complex, and a lower, recessed face (Figs. 4,5). The reduced nasal fossa and convergent orbits produce a relatively narrow interorbitum, eliminating the broad wedge between the eye sockets and reducing the capacity of this craniofacial junction to resist any twisting of the face upon the braincase. The medial orbital walls are more closely spaced and are less effective in bracing against lateral forces. The entire face tends to be tucked in below the frontal bone, making the tooththrows more nearly perpendicular to the line of action of masseter and much of

temporalis. The upper, lateral, aspect of the face is completely sutured to the sidewall of the cranium by the ossified postorbital septum. Thus, the anthropoid face is essentially hung from the neurocranium by a series of parallel pillars formed by the thin plates of the interorbitum and the postorbital septa.

Having a fully fused mandibular symphysis, anthropoids may transmit relatively large amounts of force to the mandible and, presumably, the rest of the masticatory periphery, in comparison with strepsirhines (see Hylander, 1979b for a contrast between *Macaca* and *Galago*). With enlarged, relatively vertical incisors, and premolars effecting relatively large amounts of resistance by virtue of their increased crushing-grinding surface area, the pattern of forces absorbed by the face of an anthropoid may be assumed to be different from that seen in strepsirhines. These distinctions are exaggerated because strong facial loadings occur antagonistically, and in unison. With a fused symphysis, the jaw can be powered by muscles on both sides of the head (Hylander, 1984) without dissipation of force through twisting of an open joint at the front of

Fig. 5. Schematic frontal section of hypothetical euprimate (left) and anthropoid (right) skulls at the craniofacial junction, i.e., near optic foramen. The large nasal fossa acts as a central core of the face, bracing it against the neurocranium. The narrow inter-orbital septum, a consequence of olfactory reduction and orbital convergence in preadapted omomyids, is less able to resist twisting of the face about a central axis, as when masseter is active and the zygomatic is tensed against the resisting food and temporo-mandibular joint. The postorbital plate is a lateral pillar which compensates for loss of central stability.



the lower jaw (e.g. Beecher, 1979) thus making parasagittal bite points more efficient. In the anthropoids, therefore, loads can be concentrated at the front of the face. With a fused symphysis, contralateral biting forces would be resisted by the parallel pillars at the craniofacial junction.

In this model the postorbital plate is viewed as a mainstay in the connection of cranial components, resisting the tendency to twist the face about the narrow central interorbital strut. Due to the fused anthropoid symphysis, contraction of the masseter (which arises along the lower border of the zygomatic arch) will produce a large tensile component in the postorbital bar, tending to separate it from the frontal at their suture. By increasing the length of the suture and, more importantly, adding a perpendicular extension that connects the postorbital bar to the sidewall of the skull, increasing the size of the zygomatic bone and giving it mechanical support, the tendency to pull or rotate the lateral pillar out of position is counteracted. The addition of a third, inferiorly placed, suture (i.e. the zygomaticomaxillary) adds mechanical integrity to the zygomatic plate. Thus, postorbital closure braces the facial skull against twisting produced by the system and reinforces the origin of the masseter muscle against enlarged forces.

The dentition is an important source of vibration. The zygomatic arch, under the bending influences of the masseter, and the articular surface of the temporomandibular joint, which is heavily loaded by the condyle (Hylander, 1979a) likewise contribute bone vibration. The transmission of such bone conducted sounds to the hearing mechanism via this heavily sutured and braced anthropoid skull must be insulated, possibly by the development of porous, spongy bone in the petrosal (cf. Fleischer, 1979).

Some comparative examples may be cited in support of the hypothesis that novel loading conditions influence a selectional response in the postorbital bar of strepsirhines, which by extension suggests that similar processes could have directed the evolution of full postorbital closure. For example, in Loris the orbits are extremely convergent and supporting central elements are correspondingly reduced. As compensation for the consequent reduction in static stability, the peripheral elements of the face are modified. The diameters of the lateral maxillary process, inferior and lateral aspect of the postorbital bar and zygomatic arch are all enlarged to increase their resistance against bending. In Hadropithecus, the fused mandibular symphysis increases the masticatory component of contralateral forces and adds to the amount of tension borne by the zygomatic arch via the masseter. The arch and lateral orbital pillar are consequently greatly strengthened. A similar condition occurs in Adapis, which also has a fused symphysis, although it retains the primitive elongate snout.

A number of explanations have been given for the evolution of the postorbital plate. Cartmill (1980) lists five: (1) support of the eye, (2) protection of the eye, (3) increased attachment for anterior temporalis, (4) bracing the eye and orbit against tension from masticatory muscles,



and (5) insulation of the foveate eye from temporalis contractions (see Figure 6). These interpretations have been variously applied to the post-orbital plate of anthropoids (2,3,5), the enlarged postorbital bar of tarsiers (1,5) and the unenlarged bar of ancestral euprimates (2,4). Perhaps the best developed arguments proposed in recent years are those given by Cachel (1979) and Cartmill (1980). Cachel explains the anthropoid condition as an adaptation to increase the surface of attachment for the anterior temporalis, thought to be especially useful in incisivation. Cartmill (1980) suggests that the explanation for the morphology in tarsiers and anthropoids is that posterior closure of the orbit is necessary to keep the fovea bearing eyeball from oscillating as temporalis contracts during chewing. The model proposed above is compatible with Cachel's hypothesis, though it emphasizes different factors. It is markedly different from Cartmill's, in part because our interpretations of tarsier affinities are mutually exclusive.

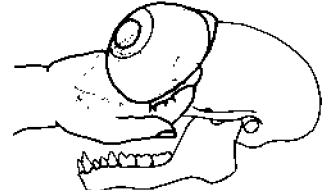
Fig. 6. Six theories for the evolution of the postorbital septum: (a) eyeball protection; (b) attachment surface for anterior temporalis; (c) eyeball support in tarsiers; (d) insulating the foveate eyeball from oscillating with temporalis activity; (e) resisting bending under muscular tension; (f) bracing the facial skull against twisting and securing the masseter against the non-rotating dentaries.



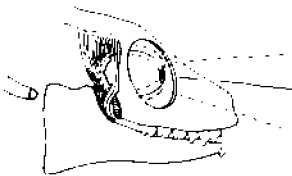
(a) eyeball protection



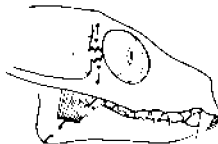
(b) muscle attachment



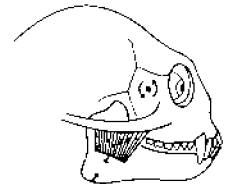
(c) eyeball support



(d) eyeball insulation



(e) muscle-force brace



(f) craniofacial bracing

*Summary and conclusions*

Anthropoids are a monophyletic subgroup of the Haplorhini. The diphyly theory of anthropoid origins fails to address the contradictory implications of shared derived similarities found in platyrrhines and catarrhines. Instead, it focuses upon differences between the two groups, which have been considerably reduced by new information about the anatomy of the Oligocene African catarrhines. The diphyly theory is steeped in the gradistic tradition of primatology, which overemphasizes the possibilities of parallelism without falsifying the Darwinian null hypothesis that similarity in form and function is an indication of affinity.

The current geographical separation of platyrrhines and catarrhines into New and Old World realms postdates the emergence of the Anthropoidea. The morphological evidence indicates that catarrhines, of any sort, are too derived to be direct ancestors of the platyrrhines, and hints at the possibility that catarrhines have more primitive, extra-African relatives in the Indo-Pakistan region. Such a relationship favours Laurasia as the geographical source for protoanthropoids. Fayum primates are but one element of a changing Tethyan mammalian fauna. South America similarly absorbed various early Tertiary mammals that found their way across the tectonically-active nuclear Central America and proto-caribbean. Since the Tertiary history of mammals on both these southern continents mirrors one another in pattern, the invocation of a special circumstance, that is, a unique westward transatlantic dispersal, is not necessary to explain the disjunction of the anthropoids.

Anthropoids are probably the descendants of a haplorhine ancestral stock that would nominally be classified as omomyid. The latter were widespread in Laurasia during the Eocene and included cranial and dental morphs sufficiently primitive to be ancestral to the higher primates. Tarsiids are an unlikely sister taxon because they are highly autapomorphic and they are probably related to a different omomyid subgroup. Non-primitive similarities shared with anthropoids tend to be convergences. Adapids are probably the early members of the greater lemuriform clade, a modified group sharing no immediate ancestry with haplorhines after the differentiation of each from ancestral euprimates. A few adapids have apparently converged upon anthropoids, leading some to conclude that they are possibly anthropoid ancestors.

The anthropoid transition was adaptively predicated upon a haplorhine cranial morphology, typified by such features as an abbreviated, low face, a small nasal cavity and craniofacial hafting along a narrow interorbitum. Reinforcement of the craniofacial junction by the development of a post-orbital plate enabled the anthropoid skull to absorb eccentric loads that tend to twist the face up against the neurocranium, to apply powerful biting force with the incisors and premolars, to secure the zygomatic bone against the tension of masseter, and to transfer forces across the fused mandibular symphysis to either side of the face and toothrows. The pneumatization of the petrosal bone may serve to insulate the hearing mechanism from vibrations transmitted through the more solidly fused anthropoid head. Thus, the adaptive shift of the masticatory apparatus was probably related to a critical reliance upon resistant fruits, such as

legumes (with their hard coverings) and seeds, when less costly fruits were unavailable. Additional shared derived features of anthropoids help to delineate the other dimensions of their formative ecological niche and many of these are unrelated to feeding. For example, the coordination of a relatively large brain with acute vision made possible the coding of a huge amount of visual information stemming from the environment, which far exceeded the amount of 'smell' data cues that lemuriforms or primitive euprimates could extract. The sheer cognitive advantages of early anthropoids should not be ignored in models detailing their mode of origin.

By drawing together the approaches of phylogenetic reconstruction and functional analysis, rather than perpetuating the false dichotomy that has divided them in systematic endeavours, future work will add clarity to discussions on the major topics of anthropoid evolution. More pointed tests of homology, and more satisfactory interpretations of character polarity, should help generate powerful heuristic models of the adaptive transition that resulted in Anthrozoidea, and the separate radiations of the New and Old World lineages. If the fossil record continues to grow as it has done recently in both hemispheres, the next decade of research on platyrrhines, catarrhines and the anthropoid transition will prove even more rewarding than the past century of excitement, discovery and controversy.

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