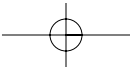
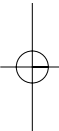
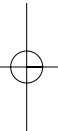
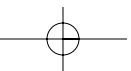
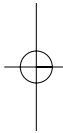
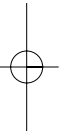
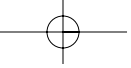


PART FIVE

# The Future of Anthropoid Origins





## CHAPTER TWENTY-FIVE

# Anthropoid Origins: Retrospective and Prospective

*Callum F. Ross and Richard F. Kay*

## INTRODUCTORY COMMENTS

As discussed in the chapter on Evolving Perspectives on Anthroidea (Ross and Kay, chapter 1, this volume), the research in this book revolves around hypotheses regarding: the phylogenetic relationships within Anthroidea; the relationships of Anthroidea to other living and fossil primates; and the functional and adaptive significance of the features characterizing the early branches of anthropoid evolution.

## ANTHROPOID PHYLOGENETIC RELATIONSHIPS

### Relationships of Primates to Other Mammals

Although the three major clades of extant primates (strepsirrhines, anthropoids, and tarsiers) are generally agreed to be monophyletic, the relationships among them are not agreed upon. Two of these clades must be more closely related to each other than to the other, but it is not clear which. Strepsirrhines,

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tarsiers, and anthropoids are descended from very early divergence events within the primate clade and definitive determination of the character states at these basal primate nodes requires that the primate outgroup be known. Thus, uncertainty surrounding relationships among primate higher taxa, including Anthropoidea, is due in part to lack of agreement on the relationships of Primates to other mammals.

Eizirik et al. (this volume) summarize the relationships between primates and other living mammals based upon molecular genetic evidence. Studies based on large molecular data sets (Murphy et al., 2001a, 2001b) derive concordant topologies for basal placental mammal clades that have living descendants. One of those clades has two groups: The Euarchonta (Primates, Dermoptera, Scandentia) and Glires (Rodentia and Lagomorpha). However, the monophyly of Euarchonta with respect to Glires and relationships among orders within the Euarchonta are not determined with high statistical support. A more recent study combining and expanding these data sets further supports Euarchonta monophyly and within it a clustering of Scandentia and Dermoptera, with Primates as the most basal extant lineage in this clade (Murphy et al., 2001b).

The molecular evidence is, of course, mute as to the relationships of extinct clades of mammals to the living taxa. Still the leading candidate for a relationship to Primates is the Plesiadapoidea, a diverse group of Paleocene and Eocene mammals best known from skulls and skeletons found in Europe and North America. The most extensive phylogenetic analysis of plesiadapoids and other extinct groups relevant to primate origins is that of Silcox (2001). Using lepticids and *Asioryctes* as outgroups, Silcox found dermopterans, bats, and tree shrews to clade with an extinct group, the Plagiomenidae, as the sister group to a primate–plesiadapiform clade. She confirms *Altiatlasius* and *Altanius* to be euprimates. Similar results are obtained by Bloch and Boyer (2002) although they argue that Carpolestidae and Plesiadapidae together may be the sister clade to Primates based primarily on the presence in primates and carpolestids of a grasping hindfoot. For the latter scenario to be correct, however, several more or less unlikely evolutionary events would be required: (a) The crown primate ancestor would have descended from a stem species that possessed a number of anterior dental peculiarities shared by carpolestids and plesiadapids; and (b) plesiadapoids would have acquired and then lost the grasping hindfoot, which *Plesiadapis* lacks (Bloch and Boyer, 2003; Kirk et al., 2003). Moreover there is continuing uncertainty as to whether carpolestids

and plesiadapids had a petrosal bulla. Such a claim is advanced by Bloch and Silcox (2003) but it is just as likely that the bulla of *Plesiadapis* and *Carpolestes* was composed of an entotympanic, as in paromomyids (Kay et al., 1992; Silcox, 2003), that was fused with the petrosal in adult life as it is in scandentians.

Kay and colleagues (Kay et al., 1997, this volume; Ross et al., 1998) include some plesiadapoid and scandentian material in their analysis of the relationships among primate higher taxa. However, the data sets of Bloch, Boyer, and Silcox contain more data on putative primate outgroups. Combination of the two extensive data sets would provide insight into the stability of primate ingroup relationships under different assumptions regarding primate outgroups.

### Relationship of Anthropoids to Other Primates

**The Living Groups:** Molecular and morphological data are internally discordant as to the relationships of three groups of living primates—Strepsirrhini, *Tarsius*, and Anthropoidea. Is *Tarsius* a sister-group to anthropoids (forming the clade Haplorhini), or a sister-group to Strepsirrhini (forming the clade Prosimii)? Whilst this argument has been underway for more than a century (Cartmill and Kay, 1978) and despite lack of a congruence of the data, we still are inclined in favor of Haplorhini.

The morphological case for a haplorhine clade has deep historical roots (Cartmill and Kay, 1978; Fleagle and Kay, 1994; Kay et al., 1997; Le Gros Clark, 1971; Ross et al., 1998). Derived osteological, placental, and soft-tissue characters each support affinities between tarsiers and anthropoids to the exclusion of strepsirrhines (Hubrecht, 1897; Luckett, 1975, 1976, 1993; Martin, 1990; Schmitz and Zischler, this volume; Schmitz et al., 2001, 2002). The phylogenetic analysis of Kay et al. (this volume) bringing together these data in a total-evidence parsimony analysis yields a haplorhine clade. Notably however, data sets partitioned into cranial, dental, and postcranial components yield mixed support for Haplorhini. Cranial evidence matches the total evidence results. Dental data, however, yields an Anthropoidea–Strepsirrhini clade under some analytical assumptions and a Haplorhini–Strepsirrhini dichotomy under others. These discrepancies highlight the underlying reasons why various authors in recent years continue to hue to conflicting anthropoid/strepsirrhine versus anthropoid/*Tarsius* clades (Kay and Williams, 1994; Ross, 1994; Shoshani et al., 1996; Simons and Rasmussen, 1989b).

Much of the disagreement stems from the conflicting signals from these admittedly arbitrary data partitions and the incompleteness of our data from the fossil groups (discussed later).

Molecular evidence concerning whether there is a haplorhine/strepsirrhine dichotomy is also mixed. Murphy et al. (2001a) and Eizirik et al. (this volume) interpret DNA sequence data as supporting a Prosimii clade, whereas study of SINE elements leads Schmitz et al. (2001) to support the Haplorhini hypothesis. Eizirik et al. (this volume) analyze a large concatenated data set composed of nuclear genes. They find identical topologies of an Anthropeida/Prosimii basal split using Bayesian phylogenetics (BAY), maximum likelihood (ML), and minimum evolution (ME) approaches. However, they note that the branch connecting tarsiers to strepsirrhines receives only weak statistical support ranging from 61% to 95%. In either alternative (Haplorhini or Prosimii) there must have been an extremely rapid set of divergence events separating stem anthropoids versus strepsirrhines, and tarsiers from one of the other two major primate lineages.

Using a different molecular approach, Schmitz and Zischler (this volume; see also Schmitz, 2000, 2002) identify three SINE markers suggesting a common ancestry of tarsiers and anthropoids. This is the strongest molecular evidence to date for the existence of Haplorhini. They argue that the independence and meaningfulness of the three haplorhine SINE markers is supported by the following.

1. The locations of the markers on three different chromosomes at the human locations exclude a derivation of the three retropositions from the same SINE-amplification event.
2. For each marker they identify the direct repeats in all haplorhine representatives and unoccupied retroposition target sites in all strepsirrhines and nonprimate outgroups. This clearly rules out a larger deletion comprising the SINE itself together with its adjacent nuclear flanking DNA, which could potentially lead to an erroneous interpretation of the strepsirrhine condition as the ancestral absence-state.
3. The possibility of a lineage-sorting phenomenon due to ancestral polymorphism is unlikely because of the multiple independent retropositional events on the same branch, resulting in congruent retropositional evidence.
4. They do not detect conflicting PCR patterns, that is, patterns clustering *Tarsius* and strepsirrhines or strepsirrhines and anthropoids together.

5. In anthropoids and *Tarsius*, the Alu SINE located on human chromosome 7 is truncated for 21 bps in the 5' portion. Most parsimoniously, according to Schmitt and Zischler, this deletion is a fourth event (in addition to the SINE data itself) that must have taken place prior to the haplorhine–tarsier split. It provides further independent evidence that these Alu sequences are identical by descent rather than by convergence.

Seiffert et al. (Seiffert et al., this volume) present an analysis similar to that of Kay et al. (Kay et al., this volume) that yields a Prosimii clade with weak support. The morphological character set is very similar between the two studies. However, there are substantial differences in that Seiffert et al. combine morphological and molecular characters. Given the differences between their results and ours, it is useful to note some of the analytical differences between the studies.

*Results from analytical choices and of various partitions of data.* It is important to know what part of the data provides the best support for a Prosimii clade. In particular, it is unclear what the morphological characters in the data of Seiffert et al., analyzed alone, would show. This issue is critical in this case given the discrepancies mentioned above between the molecular sequence data on one hand and the SINE data on the other.

*Taxon choice.* *Tupaia*, a representative of Scandentia, was the only outgroup selected by Seiffert et al. to root their primate ingroup. Work over the past decade by Beard, Bloch, Kay, Silcox, and others (Beard, 1993; Bloch and Boyer, 2002, 2003; Bloch and Silcox, 2003; Kay et al., 1992; Silcox, 2001) suggests that Paleocene/Eocene Plesiadapoidea may be sister to Primates, to tree shrews, or to *Cynocephalus*, or that plesiadapoids may be a paraphyletic assemblage with respect to these groups. Substantial morphological data has been published for a number of plesiadapoid taxa but none is included in Seiffert et al.'s analysis. We raise this as a problem because the rooting of the in-group is fundamental to determining whether the phylogenetic analysis yields a haplorhine/strepsirrhine dichotomy or a Prosimii versus Anthropoidea clade.

*The molecular data set.* Seiffert et al. chose a small subset of nucleotide characters from the nuclear IRBP and mitochondrial cytochrome B sequences reported by Yoder and Yang (Bloch and Silcox, 2001; Yoder and Yang, 2000). It is unclear why this molecular data set was chosen over the one reported by Murphy et al. (2001b) containing 8,182 bp (Eizirik et al., this volume).

Nor is it apparent why data for *Cynocephalus* was excluded from the analysis given that Murphy's data suggest that Scandentia plus *Cynocephalus* are sister to Primates. Leaving *Cynocephalus* out of an analysis that includes molecular data could materially effect the rooting of the primate 'in-group' (discussed earlier).

As will appear from the forgoing, the validity of Haplorhini is as hotly debated today as it was 25 years ago. The molecular sequence data weakly supports a Prosimii versus Anthroidea basal split. On balance, however, combined total morphological evidence together with the evidence of molecular SINE markers support Haplorhini, an arrangement we favor. Much remains to be done, however, before all workers will be convinced of one pattern or the other. Some progress could be made through a combined analysis of the extensive morphological and molecular data sets now available.

***Which Extinct Taxa are Haplorhine?*** Kay et al.'s (this volume) analysis suggests that the crown haplorhine clade (*Tarsius* + Anthroidea) is nested within Omomyidae (making Omomyidae a paraphyletic taxon) although partitioned data sets (cranial, dental, and postcranial) yield mixed support for the haplorhine–strepsirrhine dichotomy. Indeed, the adapoid–anthropoid hypothesis receives weak support from the dental evidence and (because of ambiguous rooting) is not ruled out by the postcranial evidence. However, an adapoid–anthropoid clade receives no support from analyses of cranial evidence, or from any total morphological evidence. Rather, most of the evidence supports the hypothesis of an adapoid–strepsirrhine clade exclusive of anthropoids and tarsiers.

Seiffert et al. (this volume) offer a substantially different phylogenetic scenario from the one favored by Kay et al. A number of the fundamental issues concerning the validity of the Haplorhini have already been reviewed above. In one analysis, Seiffert et al. "force" a haplorhine arrangement using the "backbone" option of PAUP. Under this constraint, they find *Tarsius* to be nested within Omomyidae and Anthroidea to be sister to omomyids. Why does their conclusion differ from ours? A partial explanation is the controversy surrounding allocation to *Eosimias* of an isolated petrosal fragment from the fissure–fills of Shanghuang Province. This petrosal is extremely similar to omomyids, leading Ross and colleagues to assign the specimen to omomyids (Hylander et al., 2000; Ross and Covert, 2000; Ross et al., 1998). If the petrosal actually belongs to *Eosimias*, as MacPhee et al. (1995) hypothesize, this

would constitute the most significant evidence for a *Tarsius* + Omomyidae clade (as opposed to the *Tarsius* + Anthropoidea clade). However, as noted by Ross and colleagues, the allocation of this specimen is doubtful (Ross, 2000; Ross et al., 1998).

As Ross and Covert (2000) note, the documentation of an extensive radiation of small primates in the Eocene of China possessing omomyid-, anthropoid-, or haplorhine-like tarsal bones (Gebo et al., 2000) provides nonanthropoid (i.e., non-eosimiid) possibilities for the source of the Shanghuang petrosal. It also suggests that there is a diversity of early Eocene haplorhines, the dentition, and cranial anatomy of which are currently completely unsampled. In the context of such a diversity of poorly sampled taxa around the anthropoid basal node, the lack of robustness to phylogenetic analyses of anthropoid relationships cautions against definitive conclusions regarding the phylogenetic position of Anthropoidea.

### Relationships among Basal Anthropoids

#### *Possible Asian anthropoids*

*Amphipithecidae*. Larger south Asian taxa *Pondaungia*, *Amphipithecus*, *Siamopithecus*, and perhaps *Myanmarpithecus*, are now generally regarded as forming a monophyletic clade Amphipithecidae (Chaimanee et al., 1997; Ducrocq, 1998, 1999; Jaeger et al., 1999; Kay et al., 2003, this volume; Takai and Shigehara, this volume). But where do amphipithecids belong on the primate tree? Study of the numerous amphipithecid specimens discovered in recent years has led the authors in this volume to very different conclusions. Several favor anthropoid affinities for amphipithecids. One view is that amphipithecids are a stem anthropoid group (Beard, 2002; Chaimanee, this volume; Chaimanee et al., 1997, 2000; Takai and Shigehara, this volume). Another possibility is that amphipithecids are catarrhine anthropoids closely related to the Propliopithecidae of the early Oligocene Africa (Jaeger et al., 1998b). Still others suggest that amphipithecids have nothing to do with anthropoids and are instead aberrant members of the Adapoidea (Kay et al., this volume) or even Notharctinae (Ciochon and Gunnell, this volume; Ciochon et al., 2001).

These different phylogenetic assessments stem from reliance placed on various lines of evidence. Some are persuaded that amphipithecids are anthropoid owing to derived dental and gnathic similarity with anthropoids and the dissimilarity of those anatomic aspects to notharctine adapoids (Ba Maw et al.,

1979; Jaeger et al., 1998a; Kay, 1980; Shigehara et al., 2002; Takai and Shigehara, this volume). Others doubt the amphipithecoid–anthropoid link because amphipithecoids differ from (and are more primitive than) anthropoids in humeral and calcaneal anatomy (Ciochon and Gunnell, this volume; Ciochon et al., 2001). Also, for amphipithecoids to be anthropoid, postorbital closure, which amphipithecoids lack (Takai and Shigehara, this volume), would have to be evolved in parallel between amphipithecoids and anthropoids or evolved and lost in amphipithecoids (Kay et al., this volume; Seiffert et al., this volume). (Jaeger [personal communication] offers a solution to this problem: The possibility that the postcranial bones and frontals ascribed to amphipithecoids may belong to another otherwise unknown adapoid.)

The placement of amphipithecoids as stem anthropoids in the phylogenetic analyses of Kay et al. (this volume) and Seiffert et al. (this volume) is interesting but not compelling. As Seiffert et al. note,

missing data certainly make this hypothesis one of the least stable aspects of our maximally parsimonious topology ... it is almost equally likely that these taxa may, in fact, not be anthropoids at all but rather highly specialized adapiforms that have convergently evolved anthropoid-like dental and gnathic features (Ciochon et al., 2001; Gunnell et al., 2002).

Kay et al. (this volume) test the sensitivity of their own placement of Amphipithecidae with adapoids or stem anthropoids using various weighting schemes for postorbital closure. They find that support for the position of amphipithecoids at either position on the primate clade is very weak.

*Eosimiidae.* The status of middle and late middle Eocene Asian Eosimiidae has undergone a radical shift in the past few years. Beard et al. (1996a) described *Eosimias sinensis* (middle Eocene, China) as an anthropoid on the basis of fragmentary dental and gnathic remains. Since then, a nearly complete lower jaw and other dental material of another species, together with eosimiid foot bones all support the anthropoid status of this taxon (Beard, 2002; Beard et al., 1996b; Gebo et al., 2000; Tong, 1997). Another eosimiid *Bahinia* (late middle Eocene, Myanmar) is represented by a rostrum and lower jaw (Jaeger et al., 1999). All contributors in this book recognize *Eosimias* and *Bahinia* as Anthrozoidea. Kay et al.'s analysis of the dental and postcranial material of *Eosimias* and *Bahinia* confirms the eosimiid status of *Bahinia* and reaffirms the conclusion (Kay et al., 1997; Ross et al., 1998) that eosimiids are stem anthropoids sister to a clade consisting of crown anthropoids, parapathecoids,

and oligopithecids. Seiffert et al. (this volume) agree with this assessment. They note,

perhaps the most compelling Asian candidate for anthropoid status is now late middle Eocene *Bahinia* ... a genus that, if nothing else, appears to be generalized enough in certain features ... to approximate a reasonable *bauplan* for later Eocene Afro-Arabian anthropoids.

They caution, however, that many eosimiid characters argued by others to be anthropoid resemblances (e.g., deep mandibles, flattened molar cusps, and missing paraconids) resemble only early Oligocene African anthropoids but do not resemble acknowledged African anthropoids of the late Eocene like parapithecids and oligopithecids. They suggest that many resemblances between eosimiids and later anthropoids may thus be a consequence of parallelism.

***Stem and Crown Anthropoids of Africa:*** A number of Oligocene to Recent extinct taxa are acknowledged by all current workers to belong to crown Anthroidea. Of the Oligocene taxa, Propliopithecidae *sensu stricto* (*Aegyptopithecus*, *Propliopithecus*, and *Moeripithecus*; early Oligocene, Africa) are catarrhines and *Branisella* (late Oligocene, South America) is a platyrrhine. Some advocate the crown anthropoid status of a number of African later Eocene taxa whilst others regard all of them to be stem anthropoids. Two clusters of taxa are relevant in this regard:

- Oligopithecidae (late Eocene, Africa; including *Oligopithecus* and *Catopithecus*); and
- Parapithecidae (later Eocene- early Oligocene, Africa; including *Qatrania*, *Abuquatrana*, *Apidium*, *Parapithecus*, *Simonsius*, and possibly *Serapia*, *Arsinoea*, and *Proteopithecus*).

All phylogenetic analyses undertaken by the participants support the clade Anthroidea including Eosimiidae (discussed earlier), Oligopithecidae, and Parapithecidae (sometimes paraphyletic) (Ducrocq, 1999; Gunnell and Miller, 2001; Kay et al., this volume; Seiffert et al., this volume).

As Seiffert et al. (this volume) note, new postcranial material of *Proteopithecus*, *Catopithecus*, and *Aegyptopithecus* (Ankel-Simons et al., 1998; Seiffert and Simons, 2001; Seiffert et al., 2000; Simons and Seiffert, 1999), greatly alters the most parsimonious placement of these taxa from the arrangement advocated by Ross et al. (1998). In particular, both Kay et al. (this volume) and Seiffert et al. (this volume) agree that the new material (a) casts doubt on the proposed monophyly of *Oligopithecus* and *Catopithecus* with

*Proteopithecus*, (b) reduces the likelihood that *Proteopithecus* might form a monophyletic group with platyrrhines, and (c) strengthens the hypothesis that parapithecids are basal to other late Eocene–early Oligocene African anthropoids. But there is a difference of opinion about the position of oligopithecids vis à vis catarrhines.

### Origins of Catarrhine and Platyrrhine Primates

Recent workers discussing anthropoid origins consider Africa to be the source of platyrrhine primates of the Neotropics (Fleagle and Kay, 1987; Hoffstetter, 1977, 1980; Kay and Williams, 1994a; Simons and Seiffert, 1999; Takai et al., 2000). There is general agreement that early Oligocene Propliopithecidae are catarrhines (see above). But are there also platyrrhine representatives in the late Eocene or early Oligocene of Africa? Seiffert et al. (this volume) and others view *Proteopithecus*, a basal member of the parapithecoid clade, as a plausible candidate for platyrrhine ancestry (Kay and Williams, 1994a; Miller and Simons, 1997; Simons and Seiffert, 1999; Takai et al., 2000). Kay et al. argue that *Proteopithecus* and other parapithecids are stem anthropoids. Likewise Seiffert et al. place *Proteopithecus* outside crown Anthropoidea. Seiffert et al. argue further that *Catopithecus*, despite its many primitive features (e.g., a partially fused mandibular symphysis), is nevertheless a catarrhine as previously thought (Fleagle and Kay, 1987; Gunnell and Miller, 2001; Rasmussen, 2002; Seiffert et al., 2000; Simons, 1972; Simons and Rasmussen, 1996; Simons et al., 1994). An essential feature of the argument is that oligopithecids (*Catopithecus*) are basal catarrhines in that reduction has occurred in both in the number of premolars (from three to two). However, aside from this, there is virtually nothing pointing to an oligopithecoid–catarrhine link *to the exclusion of platyrrhines*. Kay et al. interpret the premolar reduction as a parallel development and links *Catopithecus* with a more inclusive clade of *all* crown anthropoids (platyrrhines + catarrhines).

## ANTIQUITY OF THE MAJOR CLADES

### Fossil Evidence

Depending upon the differing interpretations of the fossil evidence, summarized above, fossil evidence allows us to place the following minimum limits on the branching of the major clades of primates.

**Haplorhine–Strepsirrhine split (>55 Ma):** Kay et al. place *Donrussellia* and *Cantius* amongst basal Strepsirrhini and *Teilhardina americana*, *Tetonoides*, and *Anemorhysis* among basal Haplorhini. These placements constrain the haplorhine–strepsirrhine split to be older than earliest Eocene, that is, greater than 55 Ma. If, as Seiffert et al. argue, the fundamental split occurred between Prosimii and Anthropoidea, the timing would still be greater than 55 Ma.

**Tarsius–Anthropoidea split (>45 Ma):** Kay et al.’s analysis cannot rule out the possibility that the anthropoid clade might be as old, or older, than the earliest known omomyids and adapoids. They find crown Haplorhini (*Tarsius* + Anthropoidea) to be nested within the Omomyidae. The earliest omomyids occur at  $\approx 55$  Ma, the first tarsiid (*Xanthorhysis*) is middle Eocene ( $\sim 45$  Ma), and the first stem anthropoid (*Eosimias*) is also middle Eocene. If we follow Seiffert et al.’s phylogenetic hypothesis that a *Tarsius*–Anthropoid split did not occur, the only datum constraining the antiquity of anthropoids would be the geological age of *Eosimias* at about 45 Ma.

**Platyrrhine–catarrhine split (>34 or >36 Ma):** Kay et al.’s analysis identifies Parapithecidae and Oligopithecidae as stem Anthropoidea not relevant to the timing of the platyrrhine–catarrhine split. They posit that the catarrhine–platyrrhine split must have occurred before 34 Ma because the earliest known catarrhines, the propliopithecids *Propliopithecus* and *Moeropithecus* come from the early Oligocene ( $\sim 34$  Ma) and the earliest platyrrhine is *Branisella* at 26 Ma (late Oligocene, Bolivia). Seiffert et al. suggest that, by at least 36 Ma, the supposed catarrhine *Catopithecus* had appeared.

### Molecular Evidence

How do dates derived from the fossil record square with molecular evidence concerning branching times? Eizirik et al. (this volume) present estimates of the above branch times on the basis of molecular evolution and employing a Bayesian model employing various fossil calibrations. Their data suggest a  $\sim 46$  Ma date for the platyrrhine–catarrhine split. Eizirik and colleagues further suggest that the times of divergences among the major primate clades are very ancient (prior to the Cretaceous–Tertiary boundary). They report the most basal split within Primates to be between *Tarsius* and strepsirrhines at 77.2 Ma (95% confidence interval of 62.7 to 96.3 Ma), and a branch time of 71.4 Ma (confidence interval 57.8 to 89.1 Ma) for Anthropoidea versus Prosimii.

The timing of cladogenesis of these major groups, based on paleontological evidence (presented above), is younger than that found by the molecular data. Indeed, only one paleontologically determined branch time falls within the range of estimates from their molecular data. Of course, it is likely that the actual branch times will likely be older than the fossil record indicates given the likely occurrence of “ghost lineages” in an incomplete fossil record (Martin, 1993). At the same time, underlying assumptions about time estimate based on molecules continue to be challenged (Yi et al., 2002), so it appears entirely feasible that the molecular clock is yielding inaccurate results.

A second finding of Eizirik et al. is that the splitting among the basal lineages of primates occurred very rapidly. The paleontological evidence is in agreement with that of the molecular in this respect. Given the instability of Kay et al.’s findings concerning which group of omomyids may be sister to crown haplorhines, it is quite feasible that crown haplorhines might have diverged within just a few million years of the basal split between haplorhines and strepsirrhines. The alternative Prosimii versus Anthropoidea interpretation of Seiffert et al. yields the same predictions about rapid divergence. However, we disagree with Eizirik et al. (this volume) about what rapid diversification might imply about morphological evolution. They contend that it is “unlikely, even if Haplorhini is ultimately found to be correct, that an extensive suite of shared-derived characters uniting tarsiers and anthropoids had the opportunity to arise during their ancient and short span of common evolutionary history.” To us, the fact of the rapid diversification and the variety and nature of the evolutionary divergence between *Tarsius* and anthropoids from other primates, suggests that the origins of crown haplorhines was characterized by a very rapid pulse of profound evolutionary modification.

One issue receiving little discussion in this volume is the possibility that extant anthropoids might not be derived from any of the currently known groups of primates. At the time of their discovery, eosimiids were touted as a possible “third group” (i.e., nonomomyid and nonadapid) from which Anthropoidea might be derived (Culotta, 1992). Subsequent work has placed eosimiids firmly within Anthropoidea, and Anthropoidea within a tarsier + Anthropoidea clade, which is in turn nested within omomyids (Kay et al., 1997, this volume; Ross et al., 1998). However, an argument can be made that the tarsier-anthropoid clade might not have anything to do with omomyiforms (Ross, 2003). Separate tarsier and anthropoid clades certainly date at least to the middle Eocene. If *Algeripithecus* and *Tabelia* are any indication, the

tarsier and anthropoid clades had already diverged in the early Eocene, making the extant haplorhine clades almost as old as the first adapiforms and omomyiforms. Dental similarities between early adapiforms and omomyiforms suggest they shared a common ancestor in the late Paleocene (Rose, 1995). If molecular clock estimates are correct in placing the tarsier–anthropoid–strepsirrhine splits prior to the late Paleocene, then it is not possible for both adapiforms to have given rise to strepsirrhines *and* omomyiforms to have given rise to haplorhines. Thus, the possibility still remains that the major clades of extant primates (Strepsirrhini, Tarsiiformes, Anthroidea) are not derived from either adapiforms or omomyiforms, and that the latter taxa are completely independent, dead-end radiations of primates (Ross, 2003).

## EVOLUTION OF ANTHROPOID ADAPTATIONS

The adaptive hypotheses presented in the chapter Evolving Perspectives on Anthroidea (Ross and Kay, Chapter 1, this volume) make predictions regarding the sequence and context in which anthropoid synapomorphies arose. We evaluate these hypotheses using the phylogeny accepted at the end of section on Anthropoid Phylogenetic Relationships in this chapter and the data presented by the contributors to this volume (Bush et al., this volume; Dominy, this volume; Heesy and Ross, this volume; Kirk and Kay, this volume) to evaluate hypotheses regarding the evolution of the visual system and masticatory apparatus : that is, character state reconstructions are optimized for nodes on the accepted phylogeny and used to test the adaptive hypotheses.

### Visual System

A significant amount of new information on the anthropoid visual system is presented in this volume. Kirk and Kay present estimates of visual acuity in a range of extant and fossil primates derived from optic canal and orbit measures; Bush et al. estimate visual acuity in the fossil anthropoid *Parapithecus* (= *Simonsius*) *grangeri*; Ross summarizes the evidence on the functional morphology and comparative anatomy of the retinal fovea in vertebrates, including haplorhines; Simons presents new data on the orbit orientation of *Simonsius*; Tetreault et al. present new data on ganglion cell density in tarsiers, dwarf lemurs, and mouse lemurs; and Dominy, Jacobs, and Heesy and Ross discuss the evolutionary significance of color vision in primates. These data

provide the opportunity to evaluate various hypotheses regarding the evolution of the primate visual system.

**Activity Pattern:** One of the most fundamental aspects of an animal's ecology is its diel activity pattern, and this is no less the case for anthropoids. The shift to diurnality that occurred in the anthropoid or haplorhine stem lineage has been hypothesized to be of fundamental importance for anthropoid/ haplorhine biology, morphology, and subsequent evolutionary trajectories (Cartmill, 1980; Heesy and Ross, this volume; Kay et al., 1997; Ross, 1996, 2000; Ross and Kay, this volume). Hypotheses regarding anthropoid origins make specific predictions regarding the morphological and ecological contexts in which this shift to diurnality occurred. Heesy and Ross (this volume) reconstruct orbit diameter in *Bahinia*. The specimen is shown in Figure 8 of Kay et al. (this volume). Using the partial orbital margin and molar size as a size surrogate, they conclude that it was probably a diurnal animal. *Bahinia* is generally agreed to be a basal anthropoid, probably an eosimiid (Beard, 2002; Jaeger et al., 1999; Kay et al., this volume; Seiffert et al., this volume), so these results support the hypothesis that the anthropoid clade was primitively diurnal. The emphasis on molar shearing and small body size suggest that *Bahinia* ate a mix of fruit and insects. The parsimony analysis of Heesy and Ross (this volume) suggests that diurnality arose in the anthropoid stem lineage, although functional considerations suggest this might have occurred in the haplorhine stem lineage. Either way, *Eosimias* is predicted to have been diurnal. *Eosimias* was small (ca. 100 g) with very well developed molar shearing and therefore was predominantly insectivorous, as was the putative outgroup to primates, *Tarsius* and fossil tarsiers. Together, these data suggest that the shift to diurnality in stem anthropoids/stem haplorhines occurred in the context of a predominantly insectivorous diet, albeit with an increase in the amount of fruit eaten. These new data support Cartmill's (1980) contention that the retinal fovea evolved as an adaptation for visual predation on insects. Ross' (2000) hypothesis that the shift to diurnality occurred at small body size in a predominantly insectivorous lineage is likewise supported. Hypotheses by Cachel and Rosenberger that the shift to diurnality in anthropoid evolution resulted in increased fruit consumption are supported, although there is no evidence that this was associated with symphyseal fusion as suggested by those authors (Cachel, 1979; Rosenberger, 1986).

**Visual Acuity:** Anthropoids exhibit unusually high visual acuity, being matched in this regard only by avian raptors (Ross, 2000). This high acuity is hypothesized to have arisen as an adaptation to diurnal visual predation at

small body size (Cartmill, 1980; Ross, 1996, 2000) with its subsequent cooption for visual signaling among group-living conspecifics (Bush et al., this volume). One of the features facilitating high acuity in anthropoids (and diurnal birds) is the large axial diameter of the eye relative to the corneal diameter (Ross, 2000). A larger axial diameter increases the distance from the lens to the retina, enlarging the size of the image on the retina. (This difference in eye shape is reflected in differences in orbit shape only at small body size because the negative allometry of eye size vis á vis orbit size means that larger orbits contain relatively more material than just the eye: Kay and Kirk, 2000b, 2000c; Ross, 2003; Schultz, 1940.)

Other correlates of high visual acuity found in the retina are reviewed by Ross (2000) and Kirk and Kay (this volume). These include: A high concentration of ganglion cells in the central retina accompanied by a decrease in the size of the ganglion cell receptive fields; presence of short-wavelength filters to ameliorate the effects of chromatic aberration; absence of *tapeta lucida*; and presence of a retinal fovea. The high concentration of ganglion cells in the central retina is associated with an increase in the size of the optic canal relative to the orbit diameter. This can be quantified using an optic foramen index (OFI) (Kay and Kirk, 2000b) equal to 100 times the ratio of optic foramen area to orbit area. Kirk and Kay (this volume) show that extant diurnal haplorhines have higher OFIs than similarly sized extant strepsirrhines. Where data are available, diurnal haplorhines also have higher visual acuity than strepsirrhines, suggesting that the OFI is a reasonable means of estimating relative visual acuity in fossil primates. Kirk and Kay then calculate optic foramen quotients (OFQs), which express the observed OFI as a percentage of the OFI expected for an animal of comparable body size. Separate regressions are used to estimate this quotient, one for diurnal anthropoids and one for nocturnal strepsirrhines. When OFQs are calculated for fossil primates, Kirk and Kay find that the only fossil primate that overlaps the anthropoid values for OFQ is the fossil anthropoid, *Simonsius* (= *Parapithecus*) *grangeri*. Kirk and Kay reconstruct *Simonsius* as possessing high acuity vision and the relatively small orbits of *Simonsius* as indicating that it was diurnal. Together these data suggest that diurnality and high acuity vision characterized the earliest fossil anthropoids for which data are available. Visual acuity estimates are needed for eosimiids, more primitive stem anthropoids, to test Cartmill's and Ross' (Cartmill, 1980; Ross, 2000) hypotheses regarding anthropoid origins.

***Orbital Convergence and Frontation:*** Extant anthropoids are distinguished from other mammals by the combination of highly convergent and highly frontated orbits (Cartmill, 1970; Ross, 1995a, 2000), that is, anthropoids converge their orbits towards the front of the rostrum rather than towards the top of the skull. Thus, strepsirrhines like *Loris*, or adapoids like *Adapis* exhibit anthropoid-like degrees of orbital convergence, but only in the context of very low frontation.

The functional significance of high orbital frontation in anthropoids is opaque. Various hypotheses “explain” increased frontation as a consequence of increased relative brain size, increased basicranial flexion, recession of the face, and increasing resistance of the face to bending and shearing loads (Cartmill, 1970; Ross, 1995a, 2000) but none is particularly convincing.

Hypotheses regarding the advantages of increased orbital convergence in basal primates are usually founded on the assumption that orbital convergence is related to bringing the optic axes more into line with the visual axes (Allman, 1977; Cartmill, 1992; Pettigrew, 1978). Bringing the optic axis and visual axes together improves the quality of the image on the visual axis, establishing a context in which selection for increased visual acuity might produce a retinal fovea. Under this model, high convergence in anthropoids is a precondition for the evolution of high visual acuity.

Another possible explanation for high convergence in anthropoids derives from the observation that increased orbital convergence is accompanied by increased width of the binocular visual field (Ross, 2000). Allman (Ross, 2000) hypothesizes that this increases the distance over which accommodation and vergence movements of the eyes can be used to estimate distance, a particularly useful trait in a visual predator engaged in manual prey capture. Clearly, measures of optic axis orientation, visual axis orientation, degree of visual field overlap, and orbit orientation are needed for extant primates so that these hypotheses can be fully evaluated and the functional significance of variation in orbit orientation in fossils can be assessed.

Whatever the causes of high orbital convergence and frontation, one of the consequences is the rostral migration of the line of action of the anterior temporal muscles relative to the orbital contents. Ross (1995b, 1995c) hypothesizes that this necessitates the presence of a postorbital septum and suggests that the reorientation of the orbits in stem anthropoids would necessitate the evolution of the septum, even in the absence of the high visual acuity characteristic of anthropoids.

In this light, the orbit orientation data for fossil anthropoids from the Eocene of Africa are important. Simons (this volume) presents estimates of orbital convergence in many taxa, including the well-preserved parapathecoid *Simonsius grangeri*. *Simonsius* exhibits a combination of orbital convergence ( $51^\circ$ ) and frontation ( $62^\circ$ ) unknown in crown anthropoids, falling instead amongst strepsirrhines and tarsiers in these measures. Its orbital convergence is lower than that of all other anthropoids. Simons' estimates of convergence in *Apidium* ( $58^\circ$ ) suggest that it also lay below the range of crown anthropoids, and that *Proteopithecus* ( $59^\circ$ ) lay at the lower end of the crown anthropoid range. *Catopithecus* ( $60^\circ$ – $66^\circ$ ) (Simons and Rasmussen, 1996) had slightly higher values for convergence than *Proteopithecus*. Estimates of frontation in African taxa other than *Simonsius* (= *Parapathecus grangeri*) and *Aegyptopithecus* are difficult to make because the specimens are crushed, but Simons estimates that *Apidium bowni* had lower frontation even than *Parapathecus*.

Although Simons' estimates of orbital convergence in *Apidium*, *Catopithecus*, and *Proteopithecus* are obtained using slightly different methods from those used by others, they are probably broadly comparable. *Catopithecus* and *Proteopithecus* resemble similarly sized extant anthropoids in their degree of orbital convergence, whereas *Apidium* and *Simonsius* are less convergent than extant anthropoids in their size range. This suggests that parapathecoids differed from other anthropoids in their orbital convergence, and probably had lower degrees of frontation than extant taxa.

The significance of these data for hypotheses relating to anthropoid origins depends upon the phylogenetic placement of these taxa. Parapathecoids are generally accepted to be the clade of fossil primates most closely related to crown anthropoids, but debate persists regarding the relationships of *Catopithecus* and *Proteopithecus*. Accepting the phylogeny of Kay et al. (this volume), with *Proteopithecus* as a basal parapathecoid and *Catopithecus* as the sister-taxon to crown anthropoids, the degree of orbital convergence seen in *Catopithecus*, *Proteopithecus*, *Leontopithecus*, *Callimico*, and *Saimiri* is a reasonable approximation to the primitive condition for anthropoids exclusive of eosimiids. The degree of frontation in this part of the stem lineage is unknown at present due to distortion of the relevant fossils, but there is at present no reason to believe that it resembled the parapathecoids in this respect (Simons, this volume).

Thus, the available data on orbit orientation do not falsify Ross's (1995b, 1996) hypothesis regarding the original functional significance of the

postorbital septum. Under this model, the orbit frontation and convergence of *Simonsius grangeri* are secondarily reduced. A possible explanation for the retention of the postorbital septum in *Simonsius* can be advanced on the basis of closer examination of the *Simonsius* skull and of the illustrations provided by Simons (this volume). It appears that the most anterior fibers of the temporal muscles took origin from the brain case above the orbits, almost as far medially as the medial orbital wall. Such a position would not be possible were a postorbital septum not present as the line of action of these anterior temporal muscle fibers would pass through the orbit (Ross, 1995b). This suggests that the presence of a postorbital septum in the lineage leading to *Simonsius* allowed relatively anteriorly placed temporal muscles, possibly as a consequence of having relatively large muscles and a relatively small brain. An analogous situation exists in tarsiers, in which the presence of a septum in their ancestral lineage allowed them to have enormous eyes positioned in relatively highly convergent and frontated orbits.

**Color Vision:** Primates are distinguished from most other mammals in that several lineages have evolved trichromatic color vision. Most mammals can only distinguish two hues, but catarrhine primates (including humans) and *Alouatta* exhibit routine trichromacy, while two species of marsupials are trichromatic (Arrese et al., 2002), and platyrrhines and a few strepsirrhines exhibit sex-linked polymorphic trichromacy (Dominy, this volume; Heesy and Ross, 2001, this volume; Jacobs, this volume). Tarsiers are dichromatic. Two questions are currently debated: How has chromacy evolved in Primates, and what is the function of trichromacy?

Heesy and Ross (2001) optimize chromacy and activity pattern onto a primate phylogeny and conclude that basal primates and stem strepsirrhines were nocturnal and dichromatic, that the stem lineage of haplorhines is most parsimoniously reconstructed as nocturnal and dichromatic,<sup>1</sup> and that the stem lineage of anthropoids possessed either polymorphic trichromacy or routine trichromacy. The data presented in this volume do not enable more conclusive statements regarding the degree of chromacy in stem anthropoids. The catarrhine stem lineage appears to have possessed fully routine trichromacy at some point before the divergence of the catarrhine crown group. The platyrrhine stem lineage probably possessed polymorphic trichromacy.

<sup>1</sup> Jacobs (this volume) notes that although there are two cone types in tarsiers, they are disjunctly distributed in the retina (Hendrickson et al., 2000) making it unlikely that they are functional dichromats.

The platyrrhine condition of polymorphic trichromacy is sometimes viewed as an “inferior” version of the full trichromacy seen in catarrhines. If true, then full, routine trichromacy would be an unlikely reconstruction for the stem anthropoid visual system because it would require that natural selection favored the return to an inferior version of chromacy in the platyrrhine stem lineage. Polymorphic trichromacy of platyrrhines would then be a more plausible condition for stem anthropoids, with only catarrhines and *Alouatta* chancing on the appropriate mutations to evolve full trichromacy. This interpretation is open to challenge, however, for two reasons.

First, the gene duplications needed to produce full trichromacy are common among mammals (Lynch and Conery, 2000), suggesting that a fully trichromatic variant, if selected, would likely have been available to the anthropoid stem lineage. Second, polymorphic trichromacy might be an alternative adaptively stable strategy, selected for instead of full trichromacy (Dominy, this volume; Regan et al., 2001). Dichromacy confers the ability to “break” color camouflage (Caine and Mundy, 2000; Morgan et al., 1992) giving its possessor an advantage in locating cryptic objects, whereas trichromats have an advantage in locating red fruits against a green background. Groups with both kinds of individuals might plausibly benefit from being able to utilize both kinds of food resources. For example, Dominy and colleagues (Dominy, this volume; Dominy et al., 2003) suggest that polymorphic trichromacy is adaptive for groups utilizing small conspicuous fruits during times of fruit abundance and large cryptic palms and figs during times of fruit scarcity. If adaptive advantages such as these do indeed accrue to primate groups with polymorphic trichromacy, then the polymorphisms in extant platyrrhines might not be primitive retentions from an evolutionarily challenged anthropoid stem lineage, but evolutionarily stable strategies for exploiting a wide range of food resources. This by no means necessitates that the stem lineage of extant anthropoids was fully trichromatic, but it does make it plausible for either full trichromacy or dichromacy to have characterized the last common ancestor of extant anthropoids.

Lucas et al. (1998) and Dominy et al. (2003) argue that full trichromacy was not present in the crown anthropoid stem lineage, but arose in stem catarrhines as an adaptation for identifying juvenile leaves as a fallback resource. They demonstrate that not only are young leaves appropriately colored to be readily identified by trichromats, but the leaf color also signals various nutritional qualities. In this regard it is interesting that the gene

duplication producing trichromacy in catarrhines is dated to 35 Myr (Yokoyama and Yokoyama, 1990) and some degree of folivory is indicated for several basal anthropoids from the Africa, dated to 34–36 Myr: Stem catarrhines *Aegyptopithecus*, *Propliopithecus*, and *Moeripithecus*<sup>2</sup> (Kay, 1980; Kay and Kirk, 2000a, 2000b). However, it is important to remember that these fossil taxa were primarily frugivorous, with only small components of their diet being leaves. Based on parsimony, although the earliest stem anthropoids were primarily insectivorous when they adopted diurnality, a high level of frugivory characterizes the entire anthropoid, platyrrhine, and catarrhine stem lineages (Heesy and Ross, this volume). Moreover, parsimony does not resolve whether “basal” anthropoid, crown anthropoid, and platyrrhine nodes were dichromatic, polymorphically trichromatic, or routinely trichromatic (Heesy and Ross, this volume). Thus, whether full routine trichromacy or polymorphic trichromacy evolved first in stem anthropoids, it was most likely to have occurred in the context of significant reliance on frugivory (Regan et al., 2001).

The fossil record of visual acuity is relevant for hypotheses regarding the evolution of chromacy. The midget ganglion cell system characteristic of anthropoid primates may be a precondition for the evolution of color vision (Jacobs, this volume; Mollon, 1991b). The midget ganglion cell system mediates high acuity vision (Rodieck, 1988) and is found in both platyrrhines (trichromats and dichromats) and catarrhines (Mollon, 1989, 1991a). It has been proposed that the midget ganglion cell system was subsequently coopted for color vision (Regan et al., 2001). The presence of midget ganglion cells in platyrrhines and catarrhines suggests that this system evolved as an adaptation for high acuity vision prior to the divergence of the two anthropoid crown lineages. This is consistent with hypotheses that the shift to diurnality in stem anthropoids occurred in the context of visual predation on insects (Ross, 2000). These adaptations to high visual acuity may have predisposed this anthropoid crown clade to the evolution of trichromacy, either for detecting fruits or immature leaves against the background of tropical rainforests (Sumner and Mollon, 2000a, 2000b).

<sup>2</sup> The fossil anthropoid *Catopithecus* has also been reconstructed as incorporating leaves in its diet (Kirk and Simons, 2000), and is a possible basal catarrhine (Seiffert et al., 2000). Revised body size estimates suggest that neither oligopithecid was large enough to have been folivorous (Heesy et al., n.d.). Moreover, there is also some evidence that *Catopithecus* was not a stem catarrhine, but a stem anthropoid instead (Kay and Mitchell, 2003; Kay et al., this volume; Ross and Kay, this volume) making its dietary proclivities irrelevant for evaluating Dominy’s hypothesis.

### Auditory System

**Anterior Accessory Cavity:** Air-filled accessory spaces attached to the middle ear cavity are common among primates. Tarsiers and anthropoids are unique among mammals in possessing an anterior accessory cavity pneumatizing the anterior moiety of the petrosal plate (Cartmill and Kay, 1978; MacPhee and Cartmill, 1986). This cavity is present in all petrosals of anthropoids so far recovered (see discussion of a possible petrosal of *Eosimias* above). As noted previously (Ross, 2000) cavities such as these are expected to facilitate a broader range of sensitivity than a single-chambered system (Lombard and Hetherington, 1993; Moore, 1981). Recent statistical analysis of primate audiograms (measures of hearing sensitivity at different frequencies) suggests that haplorhines have increased low frequency sensitivity compared with strepsirrhines (Coleman, 2002), confirming this prediction. Other primates (lorises and galagos) also possess dual-chambered middle ear cavities (evolved independently of haplorhines) but do not have significantly greater low frequency sensitivity than their single chambered (lemurid) relatives. The precise functional consequences of different intrabullar configurations are currently being investigated (M. Coleman, personal communication).

### Masticatory Apparatus

**Symphyseal Fusion:** The morphology of the masticatory apparatus has featured prominently in hypotheses regarding anthropoid origins. Much of this debate has focused on hypotheses about the function of fusion of the mandibular symphysis in all crown anthropoids. The discovery that the oligopithecoid *Catopithecus* and the parapithecoid *Arsinoea* had partially fused symphyses (Rasmussen and Simons, 1992; Simons, 1992; Simons and Rasmussen, 1989a), and the eosimiids *Eosimias* (Beard et al., 1996a) and *Bahinia* have unfused symphyses (for *Bahinia*, see Figure 8 in Kay et al., this volume) makes it possible to evaluate these hypotheses through comparative analyses within the evolving anthropoid stem lineage. However, the anthropoid stem lineage also documents other alterations to the morphology of the feeding apparatus along with the increased symphyseal fusion: that is, greater isognathy (widths of upper and lower dental arcades are roughly similar) (Ravosa and Hylander, 1994), relatively larger molar crushing surfaces (Hiiemae and Kay, 1973; Kay, 1973), more isodontic molars (upper and lower molars roughly the same width) and more vertically oriented superficial masseter muscles than strepsirrhines (Ravosa

et al., 2000). Recent work by Matt Ravosa and his colleagues has seen the development of hypotheses regarding the functional relationships among these features and their significance for the evolution of the anthropoid masticatory apparatus (Ravosa, 1999; Ravosa and Hogue, this volume; Ravosa et al., 2000; see also Ross, 2000).

As reviewed by Ravosa and Hogue (this volume), *in vivo* studies of extant primates reveal differences in patterns of muscle recruitment between anthropoids on one hand and *Otolemur* and *Lemur* on the other. Anthropoids exhibit relatively greater activity of balancing-side muscles during mastication than *Otolemur* and *Lemur* (i.e., lower W/B EMG ratios) (Hylander et al., 2000, 2002). This increased recruitment serves to increase the magnitude of dorsoventral shear occurring at the mandibular symphysis; fusion of the symphysis functions to strengthen the symphysis under this loading regime (Beecher, 1979; Hylander, 1979; Ravosa and Hylander, 1994). This is the dorsoventral shear model of symphyseal fusion. Ravosa and Hogue report comparative data indicating that the dorsoventral shear model also explains increased fusion in many nonprimate mammalian taxa. They hypothesize that symphyseal fusion evolved in several anthropoid lineages (parapithecids and crown anthropoids) to resist increased dorsoventral shear associated with increased recruitment of balancing-side muscles in order to process tougher foods.

In extant anthropoids, elevated magnitudes of balancing-side muscle activity are most pronounced in the deep masseter. In addition to its elevated recruitment, the balancing-side deep masseter delivers peak force well after the working side deep masseter, and after the working and balancing superficial masseters (Hylander and Johnson, 1994; Hylander et al., 1987, 2000, 2002), whereas in *Otolemur* and *Lemur* the balancing deep masseter peaks prior to the working masseters (Hylander et al., 2000, 2002). This late activity of the balancing-side deep masseter of anthropoids is associated with a "wishboning" loading regime at the mandibular symphysis late in the power stroke (Hylander and Johnson, 1994; Hylander et al., 1987). This wishboning loading regime highly strains and stresses the anthropoid symphysis (Hylander, 1984) and symphyseal fusion has been argued to function to strengthen the symphysis under this loading regime as well (Ravosa and Hylander, 1994). This is the wishboning model of symphyseal fusion. This hypothesis receives support from recently published data on *Propithecus*, which has independently evolved a rigid, partially fused symphysis and an anthropoid-like muscle recruitment pattern

characterized by low W/B EMG ratios in the deep masseter and late activity in the balancing-side deep masseter (Hylander et al., 2003).

The relatively greater recruitment of the balancing-side deep masseter of anthropoids has been suggested to be important for augmenting transversely oriented forces during the power stroke of mastication (Ravosa, 1999; Ravosa et al., 2000). These augmented forces are not recruited during Phase II because bite forces are very low and decreasing during Phase II movements (Hylander and Johnson, 1994; Hylander et al., 1987; Wall et al., 2002). Instead, analyses of simultaneous jaw kinematics, mandibular corpus strain, and symphyseal strain in macaques reveal that peak strain in the mandibular symphysis occurs after peak strain in the working side corpus and maximum intercuspatation, but prior to the initiation of jaw opening (Hylander and Johnson, 1994). Hence, it can be hypothesized that the transversely oriented components of force from the balancing-side deep masseter are “wishboning” the symphysis and exerting transversely oriented bite force after the vertical components of force from the working and balancing adductors have dorsoventrally sheared the symphysis and bent and twisted the working side corpus. These transversely oriented forces probably act to crush food between Phase II facets.

Of course this does not explain why the balancing-side deep masseter is active *late* in the power stroke. One possibility is that fusion of the symphysis to strengthen the mandible against increased vertically oriented forces also stiffened the symphysis, making it impossible for independent rotation of the hemimandibles to assist in moving the teeth out of occlusion. Late balancing-side deep masseter activity evolved to compensate for this increased stiffness with wishboning of the symphyseal region being the price paid. As Ravosa and Hogue (this volume) review, most nonprimate mammals with fused symphyseal joints also show the late activity of balancing-side deep masseter. The exception that proves the rule is *Pteropus giganteus*, in which the “immobile symphysis, large canines and hinge-like temporomandibular joint impose constraints upon lateral excursions as long as the jaws are in a closed position” (de Gueldre and de Vree, 1988, p. 103). Together these data support the hypothesis that the late activity of the balancing-side deep masseter in mammals with fused symphyseal joints functions to move the mandible out of centric occlusion (Hylander et al., 1987; Ravosa, 1999; Weijs et al., 1999). Weijs et al. (1999, p. 243) posit that in rabbit the late activity of balancing side posterior deep masseter “probably disengages the teeth by pulling the jaw across the midline, beyond

symmetric occlusion. It may, thus, help clear the food from the teeth and reset the mandible for the next chewing cycle.” (See also, Hiiemae and Crompton, 1985, p. 268). Ravosa also suggests that the late balancing-side deep masseter activity in anthropoids compensates for the fact that their superficial masseters are more vertically oriented than in strepsirrhines, compromising their ability to move their mandible through the power stroke (Ravosa, 1999; Ravosa et al., 2000c). The widespread distribution of symphyseal fusion and late balancing-side deep masseter activity in mammals provides ample opportunity to determine whether muscle orientation might be responsible for wishboning loading regimes outside of primates.

### SOCIAL BEHAVIOR IN EARLY ANTHROPOIDS

Previous models of anthropoid origins posit that the shift to diurnality in the anthropoid stem lineage was accompanied by increased gregariousness, primarily as a response to predation (Kay et al., 1997; Ross, 1996, 2000; Ross et al., 1998). Müller and Thalmann (2000) argue that the shift to diurnality in the ancestral haplorhine was accompanied by a shift from a dispersed multi-male system to a gregarious multi-male system. Plavcan (this volume) provides a thorough critique of the assumptions underlying these hypotheses, and Kappeler (1997) reviews evidence against the simple “diurnal = gregarious, nocturnal = solitary” model. As Plavcan points out, there are other ways to avoid predation, such as crypsis and if early anthropoids were as tiny as suggested by Gebo and Dagosto (this volume), crypsis might have been a more attractive strategy. However, in support of the hypothesis that early anthropoids were group living, they do appear to have had relatively large canines, and there is some suggestion of sexual dimorphism in canine size in eosimiids. However, to the extent that early anthropoids (indeed, early primates) fell outside the size range of extant primates, it will be difficult to make definitive statements about their behavior, ecology, and social structure. Gebo and Dagosto (this volume) summarize this dilemma succinctly:

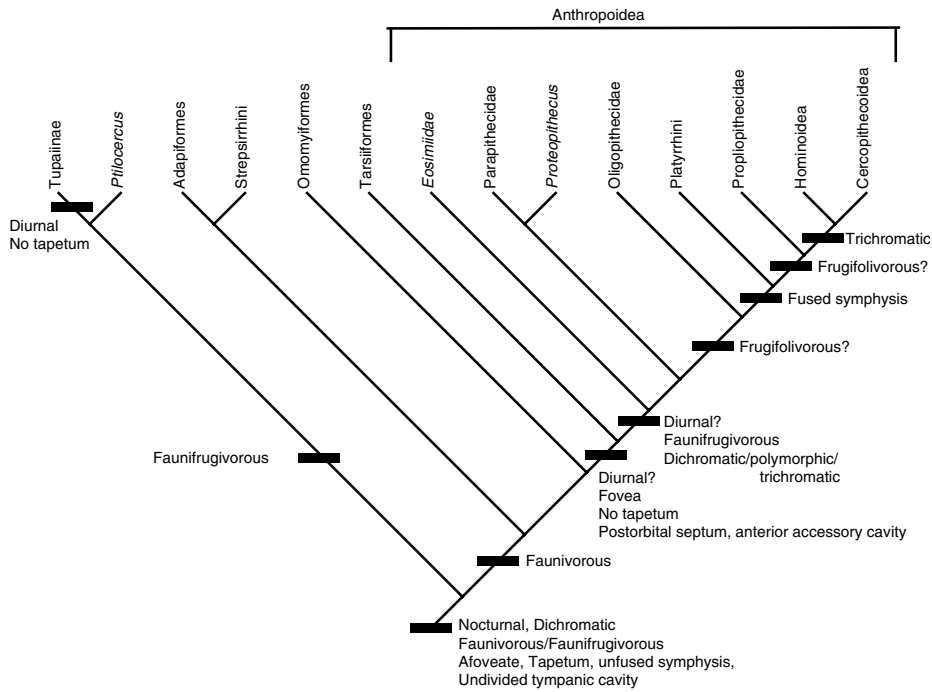
“The extreme smallness of these Shanghuang anthropoids suggests a very different way of life for stem anthropoids than current models based on larger ancestral forms. Clearly, tiny body sizes and the implied high metabolic rate (Kleiber, 1961; McNab, 1980) must modify our views of early anthropoid evolution. Finding food, reproductive output, escaping predators, home

range, and group size might have been quite different from living anthropoids, perhaps radically different. Clearly, we need to rethink our views of anthropoid life history traits for such a small ancestral form.”

**CONCLUDING SUMMARY**

It is now possible to provide a narrative summary of the sequence of events that led to the origin and diversification of anthropoid primates, including a definition of the adaptive features that make them distinct and have enabled them to successfully occupy a wide array of environments on all but two continents. Figure 1 illustrates the sequence of changes in diet, activity pattern, and color vision documented in this volume. The data are primarily from Heesy and Ross (this volume); the tree structure on which the traits are optimized is derived from Kay et al. (this volume).

The origin of Primates was associated with a shift to nocturnal visual predation in the shrub layer of tropical rainforests. The increased orbital convergence seen at this node functioned to improve the quality of the image falling



**Figure 1.** Sequence of changes in diet, activity pattern, and color vision among primates.

on the retina in animals unable to constrict their pupils because of their dimly lit environment. They probably possessed some kind of tapetum to brighten the retinal image (as seen in *Prilocercus*; Emmons, 2000), although increased visual field overlap would have also facilitated this. The prey of these early primates was probably almost entirely insects. There is no evidence that these animals were anything but dichromatic (Heesy and Ross, 2001). Their mandibular symphysis was unfused, their middle ear had a single, undivided cavity. The social organization of these early primates probably resembled the dispersed, multi-male system prevalent in nocturnal strepsirrhines (Müller and Thalmann, 2000).

The lineage leading to crown haplorhines (tarsiers and anthropoids) diverged from these basal primates in acquiring a divided middle ear cavity and some unusual features related to the visual system. The tapetum behind the retina was lost, a retinal fovea was added, along with short wavelength filters, and a bony partition evolved to separate the eye from the muscles in the temporal fossa. These features of the visual system all function to increase visual acuity, and there are good reasons to believe that they evolved in a diurnal environment, with the nocturnality characteristic of tarsiers being secondarily evolved (Cartmill, 1980; Kirk and Kay, this volume; Ross, 1996, 2000, this volume). If these features did evolve as adaptations to high acuity visual predation in low light levels, they made it easy for stem anthropoids to shift to a diurnal activity pattern.

In retrospect, the shift to diurnality by a lineage of small, arboreal, primarily faunivorous, visual predators was as fundamental a shift in behavior and ecology as can be imagined. Small, diurnal, arboreal, insectivorous mammals are rare in tropical rainforests (Charles-Dominique, 1975; Ross, 1996). These early anthropoids would have competed directly with many bird species occupying similar niches, possibly explaining the similarly high visual acuity in birds and anthropoids (Ross, 1996; Ross et al., n.d.). In addition to the retinal fovea, short wavelength filters, postorbital septum, and lack of a tapetum also seen in tarsiers, anthropoids further increased their degree of orbital convergence. If this resulted in even closer alignment between the visual and optic axes, the quality of the retinal image would have improved even more.

Suggestions that early anthropoids reduced competition with birds by fusing their mandibular symphyses to enable them to harvest obdurate fruit resources (Cartmill, 1980, citing Beecher, 1979) are incorrect. Significant frugivory developed along with partial symphyseal fusion in the late Eocene

(*Arsinoea*, *Catopithecus*), and full symphyseal fusion in the early Oligocene in the parapithecids (Ravosa, 1999; Ravosa and Hogue, this volume). The earliest anthropoids apparently competed successfully with diurnal, insectivorous, tropical birds, but exactly how remains unclear. Perhaps early anthropoids were able to obtain insects from a wide variety of arboreal locations, whereas sympatric birds resembled extant birds in being specialized for more specific, restricted food sources.

The social behavior of these earliest anthropoids cannot be determined without better data on sexual dimorphism in canine size (Plavcan, this volume). Models suggesting that anthropoids (or stem haplorhines) evolved gregariousness when they became diurnal (Müller and Thalmann, 2000; Ross, 1996, 2000) remain to be evaluated. It is also unclear whether the extent to which these models apply to tiny animals in the size ranges hypothesized for early anthropoids by Gebo and Dagosto (this volume).

The origin of crown anthropoids (i.e., platyrrhines and catarrhines) was accompanied by the development of a fused mandibular symphysis. In other respects, basal crown anthropoids much resembled oligopithecines such as *Catopithecus*. Fusion of the symphysis was probably accompanied by increased recruitment of balancing side jaw muscles during the power stroke of mastication, and by late activity in the balancing-side deep masseter. Increased recruitment of balancing-side muscles would increase the amount of force exerted during the power stroke and was probably associated with consumption of "tougher diets, variably consisting of thick-coated, unripe fruits and/or leaves" (Ravosa, 1999, p. 65). The catarrhine lineage is distinguished from these basal crown anthropoids by the adoption of full trichromacy, probably by a primarily frugivorous lineage, although possibly to facilitate visual detection of young leaves.

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