The paleobiology of Amphipithecidae, South Asian late Eocene primates

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Abstract

Analysis of the teeth, orbital and gnathic regions of the skull, and fragmentary postcranial bones provides evidence for reconstructing a behavioral profile of Amphipithecidae: *Pondaungia*, *Amphipithecus*, *Myanmarpithecus* (late middle Eocene, Myanmar) and *Siamopithecus* (late Eocene, Thailand).

At 5–8 kg, *Pondaungia*, *Amphipithecus*, and *Siamopithecus* are perhaps the largest known Eocene primates. The dental and mandibular anatomy suggest that large-bodied amphipithecids were hard-object feeders. The shape of the mandibular corpus and stiffened symphysis suggest an ability to resist large internal loads during chewing and to recruit significant amounts of muscle forces from both the chewing and non-chewing sides of the jaw so as to increase bite force during mastication. The large spatulate upper central incisor of *Pondaungia* and projecting robust canines of all the larger amphipithecids suggest that incisal food preparation was important. The molars of *Siamopithecus*, *Amphipithecus*, and *Pondaungia* have weak shearing crests. This, and the thick molar enamel found in *Pondaungia*, suggests a diet of seeds and other hard objects low in fiber. In contrast, *Myanmarpithecus* was smaller, about 1–2 kg; its cheek teeth suggest a frugivorous diet and do not imply seed eating.

Postcranial bones (humerus, ulna, and calcaneus) of a single large amphipithecid individual from Myanmar suggest an arboreal quadrupedal locomotor style like that of howler monkeys or lorises. The humeral head is rounded, proximally oriented, and the tuberosities are low indicating an extremely mobile glenohumeral joint. The great thickness of the midshaft cortical bone of the humerus implies enhanced ability to resist bending and torsion, as seen among slow moving primate quadrupeds. The elbow joint exhibits articular features for enhanced stability in habitually flexed positions, features also commonly found in slow moving arboreal quadrupeds. The short distal load arm of the calcaneus is consistent with, but not exclusive to, slow, arboreal quadrupedalism, and suggests no reliance on habitual leaping.
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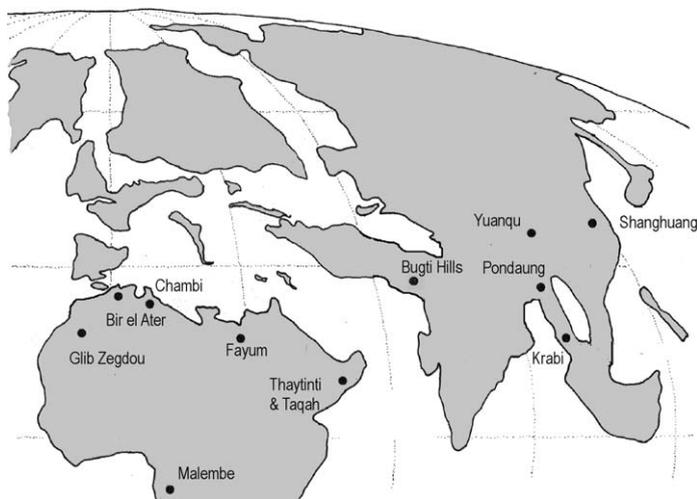 *E-mail address:* rich_kay@baa.mc.duke.edu (R.F. Kay).

Fig. 1. Paleogeography of the Tethyian region in middle to late Eocene times (c. 37 Ma), modified after Smith et al. (1994) by the addition of continental areas north of India. This modification reflects the evidence that India harbors faunas with Eurasian affinities by the early Eocene (Theweissen et al., 2001). Some important late Eocene-Oligocene localities are identified.

Introduction

Large primate taxa *Pondaungia*, *Amphipithecus*, and *Siamopithecus* from the later middle and late Eocene of Myanmar and Thailand form a monophyletic clade called Amphipithecidae (Chaimanee et al., 1997; Ducrocq, 1998, 1999b). Kay et al. (2003) allocate the smaller Myanmar taxon *Myanmarpithecus* to this clade. The fossil evidence for these taxa consists mainly of teeth and jaws. One large-bodied amphipithecid specimen from the Pondaung Formation of Myanmar, assignable to either *Amphipithecus* or *Pondaungia*, is known from parts of the humerus, ulna, and calcaneus (Ciochon et al., 2001; Gunnell et al., 2002). Another specimen associated with a maxilla of *Amphipithecus*, preserves a part of the frontal bone (Gunnell et al., 2002; Shigehara et al., 2002; Shigehara and Takai, in press; Takai et al., 2003). *Myanmarpithecus* is represented by teeth and jaws (Takai et al., 2001) while *Siamopithecus* is represented by teeth, jaws and undescribed facial fragments.

A full historical account of the debate about the phyletic position of amphipithecids is provided by Ciochon and Gunnell (2002b) and Takai and Shigehara (in press). First to be described were *Pondaungia* (Pilgrim, 1927) and *Amphipithecus* (Colbert, 1937), each known from just a few poorly preserved jaws and cheek teeth. In 1994, two papers (Ciochon and Holroyd, 1994; Godinot, 1994) recognized that *Amphipithecus* and *Pondaungia* are closely related taxa within a group now called Amphipithecidae (see Holroyd et al., 2002; Shigehara et al., 2002). Recovery of less fragmentary material of *Amphipithecus* and *Pondaungia* (Jaeger et al., 1998a,b; Chaimanee et al., 2000; Ciochon et al., 2001; Gunnell et al., 2002; Shigehara et al., 2002), the addition of *Myanmarpithecus* (Takai et al., 2001) and *Siamopithecus* to the Amphipithecidae (Ducrocq et al., 1995b; Chaimanee et al., 1997; Ducrocq, 1998, 1999b), as well as better documentation of the orbital anatomy and postcranium has fueled the debate about whether the group has adapoid or anthropoid affinities.

A cladistic analysis of dental, cranial, and postcranial anatomy by Kay et al. (2003) re-examined the phylogenetic puzzle. Kay et al. (2003) reported that it is slightly more parsimonious to root amphipithecids within anthropoids than it is to root them within adapoids. This result is driven largely by similarity in the dental and gnathic regions. In spite of this, they argued that a linkage

Table 1
Listing of the species of Amphipithecidae and the specimens examined for this analysis

Taxon	Geography and age	Principal specimens discussed or measured here
Pondaungia spp. (see below for species allocation)	Pondaung Formation, Myanmar, late middle Eocene	GSI D 201, NMMP 1, 3, 4, 5, 12, 17
Amphipithecus mogaungensis	Pondaung Formation, Myanmar, late middle Eocene	AMNH 32520, NMMP 2, 6, 7, 30
Pondaungia sp./*Amphipithecus mogaungensis*	Pondaung Formation, Myanmar, late middle Eocene	NMMP 20
Siamopithecus eocaenus	Krabi Coals, Thailand late Eocene	TF 3634
Myanmarpithecus yarshensis	Pondaung Formation, Myanmar, late middle Eocene	NMMP 8–11 (parts of one specimen)

Table 2
Estimated body mass (in grams) from m1 measurements (in square mm)

Species	Specimens examined	Mean and range of m1 area	Estimated body mass (all primate regression)	Estimated body mass (strepsirrhine regression)	Estimated body mass (anthropoid regression)
Pondaungia savagei	NMMP 17	39.03	8755	5348	9257
Amphipithecus mogaungensis	AMNH 32520 NMMP 2, NMMP 6, NMMP 7 (average of two sides), NMMP 30	31.90 (27.24–34.65)	6150 (4609–7078)	3880 (2993–4412)	6774 (5264–7678)

Notes: Tooth dimensions from Takai et al. (2001); m1 area formulae from Conroy (1987).

Table 3
Estimated body mass (in grams) from m2 measurements (in mm)

Species	Specimens examined	Mean and range of m2 length	Estimated body mass from m2 length
Pondaungia savagei	NMMP 1, NMMP 3, NMMP 5, NMMP 17	7.26 (7.00–7.65)	6824 (6123–7894)
Pondaungia cotteri	GSI D201	6.6	5174
Amphipithecus mogaungensis	AMNH 32520, NMMP 2, NMMP 6, NMMP 7 (average of two sides), NMMP 30	6.87 (6.80–6.90)	5250 (3611–5874)
Myanmarpithecus yarshensis	MNNP 10	4.17	1392
Siamopithecus eocaenus	TF 3634	6.49	4932

Notes: Tooth dimensions from Takai et al. (2001); m2 length formula from Kay and Simons (1980).

with anthropoids is questionable because of dissimilarities between the amphipithecid humerus and calcaneus and those of late Eocene and early Oligocene African anthropoids (oligopithecids, parapithecids, and propliopithecids). At the very least, this postcranial evidence seems to indicate that the amphipithecids are *outside* the clade of the Eocene-Oligocene African anthropoids. Claims for the anthropoid status of amphipithecids appear especially to be contradicted by the evidence about

Table 4
The relative development of shearing crests on m2 in strepsirrhines

Taxon	n	m2 length	m2 shear	Shear quotient	Major dietary feature
Arctocebus calabarensis	6	3.36	7.33	21.83	Insects
Avahi laniger	7	3.84	8.62	25.54	Leaves
Cheirogaleus major	4	3.43	5.34	−13.01	Fruit
Cheirogaleus medius	6	2.32	4.1	−1.79	Fruit
Eulemur coronatus	4	4.79	9.05	6.1	Fruit
Eulemur fulvus mayottensis	3	5.81	10.41	−0.79	Fruit
Eulemur fulvus rufus	6	5.42	10.72	11.21	Leaves
Eulemur macaco	1	5.63	11.27	12.55	Fruit
Euoticus elegantulus	6	2.36	4.39	3.32	Gums
Euoticus inustus	5	2.15	4.72	21.89	Insects
Galago alleni	7	2.8	5.45	8.26	Fruit
Galago senegalensis	7	2.17	5.33	36.36	Insects
Galagoides demidoff	8	1.94	4.13	18.22	Insects
Hapalemur griseus	4	4.28	9.39	22.81	Leaves
Hapalemur simus	2	5.82	14.56	40.84	Leaves
Indri indri	7	7.04	13.56	8.7	Leaves
Lemur catta	9	4.92	10.16	15.81	Leaves
Loris tardigradus	6	2.88	5.77	11.79	Insects
Microcebus murinus	5	1.58	2.92	1.82	Fruit
Nycticebus coucang	5	3.34	6.26	4.61	Fruit
Otolemur crassicaudatus	6	3.73	6.31	−5.31	Fruit
Perodicticus potto	8	3.07	5.24	−4.69	Fruit
Phaner furcifer	6	2.55	4.6	0.18	Gums
Propithecus diadema	4	6.77	13.65	13.74	Leaves
Propithecus verreauxi	5	6.66	13.1	10.82	Leaves
Varecia variegata	5	6.78	11.91	−0.92	Fruit

All raw measurements in mm. The estimate of shearing development is based on measurements of six lower molar crests [for anatomical details see Kay (1975, 1977)]. A regression line was fitted to the natural log of m2 length (ln m2L) versus the natural log of the sum of the measured crests (ln SH) for frugivorous strepsirrhines. The equation expressing the strepsirrhine line is: ln SH=0.986(ln m2L)+0.60. For each taxon, the expected ln SH was calculated from this equation. The observed (measured) ln SH for each species was compared with the expected and expressed as a residual (Shear Quotient, or SQ): SQ=100* (observed−expected)/(expected). Positive SQ values indicate a degree of shearing capacity higher than expected.

postorbital closure—a key adaptive innovation assumed to have evolved only once at the base of the *Tarsius*+anthropoid clade (Cartmill, 1980; Simons and Rasmussen, 1989; but see Beard and MacPhee, 1994; Ross, 1994). The frontal bone indicates that *Amphipithecus* did not possess postorbital closure (Shigehara et al., 2002; Shigehara and Takai, in press). Therefore, if amphipithecids are anthropoids, then postorbital closure must have evolved independently twice—or it was lost in amphipithecids. We consider either scenario unlikely. Moreover, the dental evidence suggesting an anthropoid relationship is unconvincing

because dental similarities lie more with the later, more specialized, anthropoids from the early Oligocene-taxa like *Propliopithecus* and *Aegyptopithecus*—whereas amphipithecids are less like the smaller more primitive African anthropoids of similar geologic age (late Eocene) such as oligopithecids or early parapithecids.

Thus, interpreting the phyletic position of amphipithecids depends on the weight one wishes to place on one or another part of the known anatomy. The senior author's reading of the available evidence agrees with Ciochon and Gunnell's (Ciochon and Gunnell, in press) assessment that

Table 5
The relative development of shearing crests on m1 in platyrrhines, based on the frugivorous strepsirrhine model described in Table 4

Taxon	n	m1 length	m1 shear	Shear quotient	Major dietary feature
Alouatta caraya	6	6.72	13.09	9.79	Leaves
Alouatta fusca	6	6.7	12.94	8.86	Leaves
Alouatta palliata	10	6.92	13.91	13.35	Leaves
Ateles geoffroyi	10	5.26	9.31	−0.58	Fruit
Brachyteles arachnoides	9	7.22	15.19	18.7	Leaves
Callimico goeldii	3	2.6	5.48	17.23	Insects
Callithrix argentata	4	2.22	4.08	2	Fruit/gum
Cebuella pygmaea	4	1.78	3.26	1.33	Gum/fruit
Leontopithecus rosalia	5	3.09	5.62	1.41	Fruit/insects
Saguinas mystax	5	2.52	4.03	−11.09	Fruit/insects
Aotus trivirgatus	10	3.06	6.16	12.22	Insects/fruit
Cebus apella	5	4.79	7.71	−9.7	Fruit/seeds
Saimiri sciureus	5	2.87	5.54	7.51	Insects/fruit
Cacajao melanocephalus	2	3.97	5.9	−16.849	Seeds/Fruit
Callicebus moloch	10	3.18	5.5	−3.53	Fruit
Chiropotes satanas	5	3.64	5.5	−15.56	Seeds/fruit
Pithecia monachus	4	4	6.78	−5.15	Fruit/seeds

Notes: All measurements in mm. The procedure outlined in the notes for Table 4 was applied to platyrrhines. However, in this case the taxa are platyrrhine and the tooth compared is m1, not m2 as in strepsirrhines.

amphipithecids are adapoids with dental and gnathic convergences toward later larger-bodied Oligocene African anthropoids. Others among us (Shigehara, Takai) prefer the position that amphipithecids are stem anthropoids (Takai and Shigehara, in press). All of us agree that recovery of crucial parts of the basicranium and skeleton could resolve this question.

Whatever the true phylogenetic position of amphipithecids, the available anatomical evidence tells a very interesting story about their paleobiology. In this paper, we summarize this evidence as a first step toward reconstructing their behavioral profile and the community structure of the late Eocene primates.

Geological setting and age

Amphipithecids have been found in Myanmar and Thailand. In Myanmar, the specimens come from several levels of the Pondaung Formation, a package of continental sediments that consists of variegated mudstones and sandstones deposited by meandering rivers and streams at low elevation adjacent to the northern shore of the Tethys Sea (Aung, 1999). The Tethys in later middle and late Eocene times was a discontinuous strait dividing most of present-day Afro-Arabia to the south from Asia and Europe to the north (Fig. 1).

One level in the Pondaung Formation has a reported fission-track age of ∼37 Ma (Tsubamoto et al., 2002) and the formation is overlain by marine beds with foraminifera of late Eocene aspect (Aung, 1999). Both of these lines of evidence establish that Myanmar fossil primates cannot be younger than late middle Eocene.

Siamopithecus comes from coal deposits in the Krabi Basin of Thailand. The faunas with which it is associated suggest a somewhat younger age than the Myanmar beds—probably late Eocene (Ducrocq et al., 1995a; Ducrocq, 1999a; Chaimanee et al., 2000). Thus, the Krabi primates may be roughly contemporaneous with the late Eocene (34 million year old) lower levels of the Jebel Qatrani Formation of Egypt (Kappelman et al., 1992) while the Pondaung primates seem to be at least 3 million years older than both.
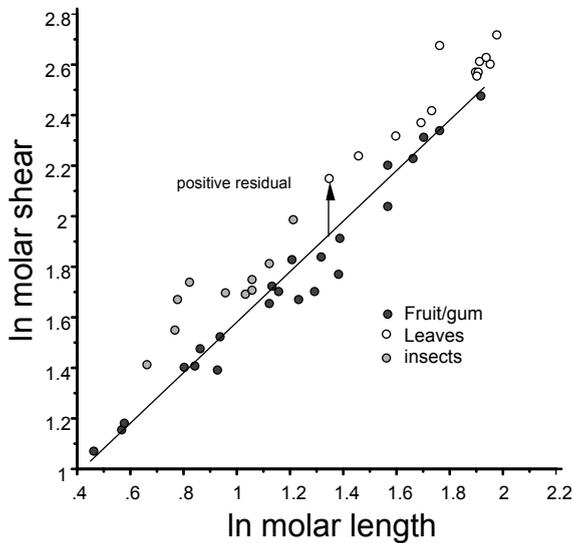
Fig. 2. Illustrating the way shearing quotients are calculated in this paper using extant strepsirrhine primates. A least-squares regression is fit between the natural logarithm of molar length (the independent size variable) and the natural logarithm of the sum of the lengths of six shearing crests on that tooth (dependent variable). The subset of taxa used to fit this line is restricted to species with diets broadly similar in diet (in this case fruit- and gum-eating species ranging in size from *Microcebus murinus* [∼50 g] to *Varecia variegata* [∼3 kg]). The SQ is a residual expressing the discrepancy (in percent) between the observed value of shearing (in real space, as opposed to log space) versus that predicted from the regression line of "best fit". Relative to body size, the greater the sum of the shearing crest lengths, the larger is the shearing quotient (for precise calculations of these quantities, see notes in Table 4). The taxon indicated by the arrow would have a positive residual. Because of the taxa selected to fit the line, the mean SQ for fruit- and gum-eating strepsirrhines is zero.

The species

Amphipithecids are known from four or perhaps five species (Table 1): *Siamopithecus eocaenus* (Thailand), *Amphipithecus mogaungensis* (Myanmar) and *Myanmarpithecus yarshensis* (Myanmar), and *Pondaungia* (Myanmar). The latter seems to be represented by two species, *P. cotteri* and *P. savagei* (Takai and Shigehara, in press), although these could also represent a single sexually dimorphic species. One argument for the former interpretation is that the ratio of the size of the lower canine (or its root socket) to the dimensions of the molars is similar in the larger and smaller specimens. In contrast, there is more size

difference between the canines than between the molars of the two sexes among extant sexually dimorphic primates (Fleagle et al., 1980; Kay, 1982; Kay et al., 1987; Plavcan et al., 1987; Plavcan and Kay, 1988).

All amphipithecids are represented by maxillae, mandibles, and teeth. Frontal bones of *Amphipithecus* have been described (Ciochon and Gunnell, 2002a; Gunnell et al., 2002; Shigehara and Takai, in press; Takai et al., 2003) but further cranial parts for the other species are unknown or undescribed. As inferred from molar size, the body size range of the two morphs (possibly species) of *Pondaungia* brackets the body size of *Amphipithecus*. Numerous specimens of both genera are represented at similar levels in the Pondaung Formation. The only postcranial material pertaining to an amphipithecid is of a large-bodied species from Myanmar that could be either *Amphipithecus* or *Pondaungia*. There is no convincing rationale for allocation of this specimen to a particular genus or species of amphipithecid on the grounds of size, co-occurrence in the same locality, or the more common occurrence of a particular taxon. This specimen is not associated with dental material of either taxon and the locality where it was collected contains neither (see also Egi et al., in press a). Hereafter, the postcranial material will be referred to using only its specimen number (NMMP 20).

An amphipithecid behavioral profile

Body size

Determination of body mass for amphipithecids is based on their molar dimensions as presented in Tables 2 and 3.

Based on the relationship among extant primates between lower first or second molar size and body mass, the larger specimens of *Pondaungia savagei* had a mass of between 5.3 and 9.3 kg (depending on which taxonomic sample of extant primates is used as the model). A specimen assigned to (*P. cotteri*), based on m2 length, weighed about 5.2 kg. (Here and elsewhere in the text, upper teeth are referenced by a capital letter
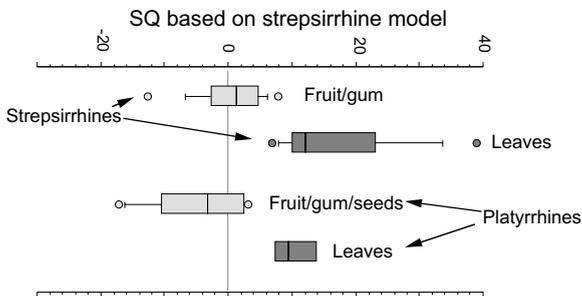
Fig. 3. Box and whisker plots of the distribution of shearing quotients of extant strepsirrhines and platyrrhines based on the frugivorous strepsirrhine model. See Table 4 for details.

while lower teeth are represented by the lower case, viz., M1 and m1.) If the two taxa prove to be sex morphs of one species, males would have been about 10 to 15% larger than females on average in second molar length. This level of dimorphism is not uncommon among anthropoid primates.

The body size of *Amphipithecus mogaungensis* was between 3.9 to 7.6 kg and that of *Siamopithecus eocaenus* was approximately 4.9 kg. These estimates place *Pondaungia*, *Amphipithecus*, and *Siamopithecus* among the largest Eocene primates. The only other taxon that approaches them in size is the 4–8 kg *Leptadapis magnus* from the late Eocene of Europe (Gingerich, 1980). Based on published estimates by Kirk and Simons (2000), no late Eocene African primate approaches these amphipithecids in size.

The body size of *Myanmarpithecus* is estimated to be about 1.4 kg. This animal was comparable in size to *Adapis parisiensis* (late Eocene, Europe). Similar results were obtained independently by Egi and colleagues (Egi et al., 2002, 2004; Egi et al., 2002, in press a, b).

The body sizes of known amphipithecids exceed those of extant insectivorous primates (Kay, 1975; Gingerich, 1980; Kay and Covert, 1984). On this basis we can rule out a primarily insectivorous diet for all of the known species.

Vision, touch, and smell

The orbits of amphipithecids are not sufficiently preserved in any specimen to permit estimation of orbital diameter. However, one specimen of *Amphipithecus* preserves the superior (frontal) portion of a postorbital bar showing that it did not possess postorbital closure (Shigehara and Takai, in press). Postorbital closure stabilizes the periorbital fascia and protects the eye from movements of the muscles of mastication within the infratemporal and temporal fossae. This assists visual acuity and therefore is functionally linked with other adaptations for more acute vision in anthropoids—a retinal fovea and the loss of a tapetum lucidum (Cartmill, 1980; Ross and Hylander, 1996). In contrast, extant strepsirrhines (as they lack post-orbital closure) have excellent visual acuity by mammalian standards, but have less acute vision than do anthropoids (Kay and Kirk, 2000; Kirk and Kay, in press). The absence of postorbital closure in *Amphipithecus* suggests this animal did not possess the acute vision present in modern anthropoids. Indeed, the preserved parts of the orbits of *Amphipithecus* resemble those of *Leptadapis*, an Eocene adapoid that apparently did not possess acute vision as judged from the relative size of the optic foramen (Kay and Kirk, 2000).

The infraorbital foramen is partially preserved in *Pondaungia* (Shigehara et al., 2002). This foramen transmits the infraorbital nerve returning sensory information from the vibrissae and skin of the snout, together with the vasculature that supplies the same region. The small size of this foramen in *Pondaungia* suggests that vibrissae were poorly developed and the rhinarium not well vascularized.

The impressions of the olfactory lobes are preserved on the ventral surface of the frontal of *Amphipithecus* (Takai et al., 2003; Shigehara and Takai, in press). These lobes appear to have been relatively much larger than in *Tarsius*, living anthropoids, and the early Oligocene anthropoid *Aegyptopithecus*, but similar in relative size to those of living and fossil strepsirrhines including *Leptadapis*, and the early Oligocene anthropoid *Simonsius* (Kay and Cartmill, 1977; for discussion see Radinsky, 1977; Stephan et al., 1984; Bush et al., in press). The large size of the amphipithecid olfactory apparatus suggests that these animals utilized olfactory communication to a similar degree as extant strepsirrhines.
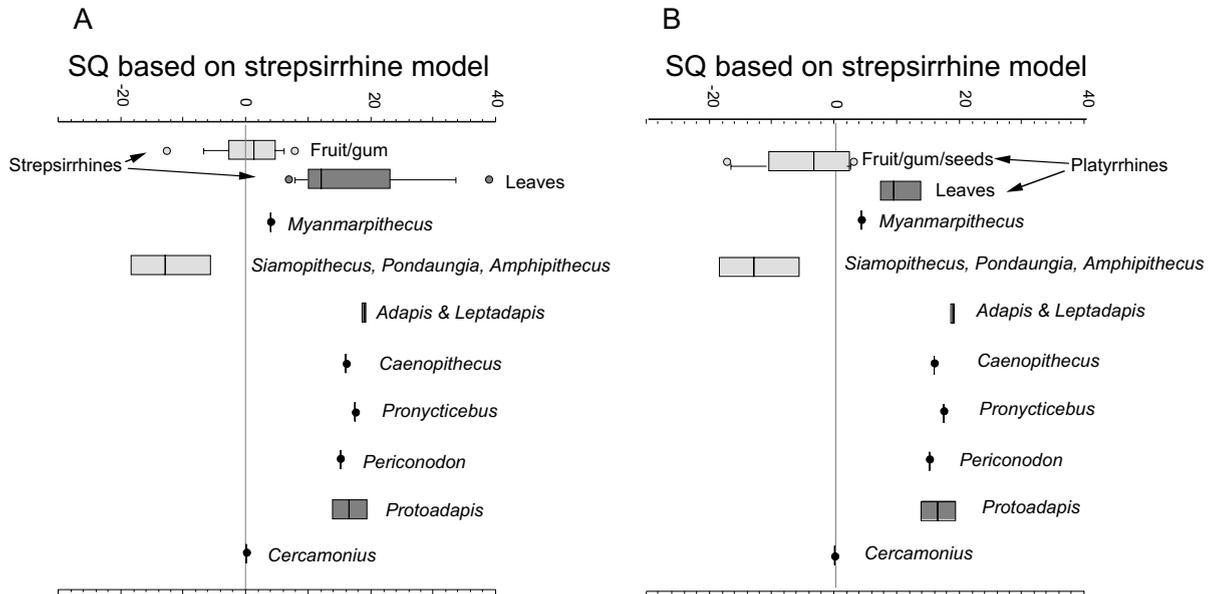
Fig. 4. SQs of amphipithecids, adapoids, and extant taxa compared: A) amphipithecids and European adapoids compared with the strepsirrhine model; B) amphipithecids and European adapoids compared with the platyrrhine model.

Diet and feeding behavior

Upper incisors

The only known upper incisor material of an amphipithecid is an upper central incisor of *Pondaungia* (Shigehara et al., 2002). This tooth is spatulate and the cross-section of its root is labiolingually broad, suggesting that it was optimized to resist powerful labiolingual bending stresses engendered while slicing off a bite of food. Furthermore, this upper central incisor is very large (relative to the size of the upper molars) and falls within the range of extant platyrrhines, between folivorous (*Alouatta* and *Brachyteles*) and frugivorous anthropoids (*Cebus*, *Ateles*, and *Chiropotes*) (Shigehara et al., 2002). It is tempting to interpret this as an indication that *Pondaungia* had a mixed frugivorous and folivorous diet. However, the picture is considerably more complex. In relative terms, living lemuriforms have smaller incisors than anthropoids and the more folivorous species have *larger* incisors than the more frugivorous ones. The relatively large size of the upper incisor of *Pondaungia* is more appropriately understood as an adaptation for powerfully separating a bite of food by means of an orthal jaw movement (i.e., predominantly up and down). Anthropoids often husk fruit or strip bark using their incisors in an orthal power stroke. Extant lemuriforms have small incisors that are not buttressed in the buccolingual axis (Shigehara et al., 2002), perhaps because they more often use their canines and postcanine teeth rather than the incisors to bite off food items (Kay and Hiiemae, 1974). The incisor proportions of *Pondaungia* suggest that this amphipithecid used its incisors for powerful incision (as in fruit-husking anthropoids) whereas European and North American adapoids did not.

Molar shearing and diet

The morphology of the cheek teeth provides insight into the physical properties of the foods eaten by a species (Kay, 1975; Rosenberger and Kinzey, 1976; Kay and Covert, 1984; Strait, 1991; Anthony and Kay, 1993; Williams and Covert, 1994; Fleagle et al., 1997; Meldrum and Kay, 1997). In particular, the relative development of shearing crests on molar crowns varies in a
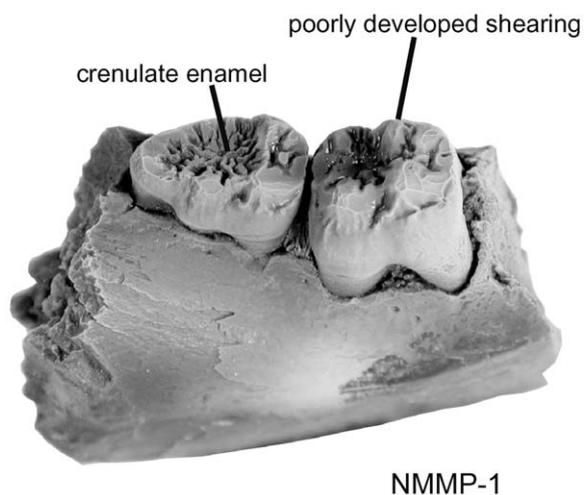
Fig. 5. Occlusolateral view of *Pondaungia savavei* (NMMP 1), showing the poorly developed shearing and crenulate enamel characteristic of the species.

predictable way with dietary differences. This shearing development has been quantified by examining the summed lengths of molar shearing crests relative to molar size.

One size-adjusted measure of molar shearing in primates is a "shearing quotient" (SQ). The SQ concept is based on interspecific comparisons (see Fig. 2 for explanation). Tables 4 and 5 summarize the species means for tooth length, shearing crest length, and the SQs for a broad selection of m2s of extant strepsirrhines and m1s of platyrrhines.

As summarized in Fig. 3, living strepsirrhines that ingest large amounts of foods high in fiber (e.g., leaves) or chitin (e.g., insects) have positive SQs and, therefore, relatively better developed molar shearing crests than species that ingest less fibrous foods such as fruit or gum.

The trends that relate shearing development to diet hold most clearly within monophyletic groups that have a common structural design. These trends tend to be less reliable between such groups (Kay and Covert, 1984; Kay and Ungar, 1997; Kirk and Simons, 2000). To test the applicability of our frugivorous strepsirrhine equation to other primates, we used it to calculate SQs in platyrrhine primates for which the diets are well

documented[1]. The results fit predictions. Living platyrrhines that eat leaves or insects have positive SQs compared to fruit-, gum-, or (in some extant platyrrhines) seed-eaters. Examining the platyrrhine SQ data more closely in Table 5, it is notable that SQs of seed-eating platyrrhines fall below or are at the low end of the range of the gum- and fruit-eating taxa.

Amphipithecid residuals (SQs) derived from the extant frugivorous strepsirrhine model are compared with the SQs of extant strepsirrhines and platyrrhines of known diet in Fig. 4a, b. Irrespective of the model chosen, the inference is the same: *Amphipithecus*, *Pondaungia* (Fig. 5), and *Siamopithecus* all have relatively poorly developed molar shearing. The degree of molar shear development among amphipithecids is similar to that of living species that have low-fiber diets. Shearing development in large-bodied amphipithecids is especially similar to that of extant seed-eating platyrrhines. *Myanmarpithecus* has considerably better developed shearing than other amphipithecids; nevertheless, it exhibits far less shearing than do extant folivorous strepsirrhines and platyrrhines. For this taxon, we infer a mixed diet consisting primarily of fruit with substantial components of leaves or insects as a protein source. A plausible body size and dietary analog for *Myanmarpithecus* is the living platyrrhine *Callicebus*.

The contrast in shearing development of amphipithecids and European adapoids of similar geologic age is stark (Table 6). Large late Eocene European adapoids, with the exception of *Cercamonius*, have SQs that fall clearly among the folivorous extant taxa (Fig. 4a, b). This difference begs a paleoenvironmental explanation. Studies of mammalian faunas in South America show a higher percentage and absolute number of frugivores than folivores in regions of higher rainfall (Kay and Madden, 1997). A latitudinal effect is also observed: richness of frugivore species decreases as latitude and seasonality (temperate conditions) increase (Kay and Madden, 1997).

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[1] Whereas m2s are used in strepsirrhines, for platyrrhines, m1s are used because m2 is often greatly reduced, and m3 is lost.

Table 6
The relative development of shearing crests on m1 or m2 in amphipithecids and larrge-bodied European Adapoidea using the strepsirrhine model described in Table 4

Taxon	Specimen number	n	m1 or m2 length	m1 or m2 shear	SQ from strepsirrhine model
Amphipithecus mogaungensis	NMMP 7, 30	2 (m1)	5.72	10.03	−3.13
Amphipithecus mogaungensis	NMMP 6, 30	2 (m1)	5.58	9.26	−8.16
Pondaungia savagei	NMMP 1, 3	2 (m2)	6.48	9.66	−17.77
Myanmarpithecus yarshensis	NMMP 10	1 (m2)	3.97	7.43	3.91
Siamopithecus eocaenus	TF 3634	1 (m2)	5.88	8.61	−19.09
Adapis magnus	–	2 (m2)	7.72	16.71	19.20
Adapis parisiensis	–	11 (m2)	4.59	9.82	18.64
Caenopithecus lemuroides	–	1 (m2)	5.81	12.19	15.95
Cercamonius brachyrhynchus	–	1 (m2)	5.81	10.51	−0.03
Periconodon lemoinei	–	1 (m2)	3.45	7.14	15.10
Pronycticebus gaudryi	–	1 (m2)	3.68	7.78	17.49
Protoadapis recticuspidens	–	2 (m2)	4.53	9.30	13.80
Protoadapis klatti	–	1 (m2)	4.31	9.27	19.29

Thus, the observed differences in guild structure between European adapoids and South Asian amphipithecids could be a consequence of drier or more seasonal climatic conditions in Europe, versus more humid, equable climatic conditions in South Asia during the late Eocene.

Molar enamel thickness

The teeth of species that specialize in eating hard seeds or in splitting open tough, hard fruits have thicker enamel (Kay, 1981) or more specialized enamel structure (Martin et al., 1994) than closely-related frugivorous and folivorous species. While precise measurement of enamel thickness is not possible for any amphipithecid, one broken specimen of *Pondaungia* (NMMP 12) reveals that its enamel is very thick (Fig. 6). This is evidence that *Pondaungia* incorporated substantial quantities of hard objects like certain seeds in its diet at least at some times of the year.

Mandibular morphology

Siamopithecus, *Amphipithecus*, and *Pondaungia* have unfused mandibular symphyses, but their symphyseal surfaces are rugose (Fig. 7). This significant morphological relief indicates that the two symphyseal plates were tightly held together by ligaments and the bony interdigitations resisted

displacement in the plane of the symphysis. Thus, the amphipithecid symphysis was probably stronger than those of many primates with unfused symphyses. Arguably, they fall among species with Class III symphyses (see Scapino, 1981). In sagittal view, the symphyseal cross-section shows prominent superior and inferior transverse tori that help form a deep genioglossal pit. This combination of stiffness and buttressing could have facilitated the recruitment of significant balancing-side jaw-muscle forces during chewing.

The shape of the primate mandibular corpus is often correlated with diet, as animals that eat tougher and harder foods often have more robust corpora than other closely-related species (Bouvier, 1986; Hylander, 1988; Ravosa, 1991). However, primate corpus morphology is not a diagnostic indicator of diet because primates that eat different foods overlap significantly in their corporal morphology (Fig. 8). Relative to m1 width, mandibular corpus breadth (at m1) of the *Pondaungia* and *Amphipithecus* specimens is greater than those of most living primates (Fig. 8A). The relative corpus breadth of the *Siamopithecus* fragment falls within the range of anthropoid seed-eaters and folivores and at the upper end of the anthropoid frugivore range. The relative depth of the corpus of these species falls within the range of living primate folivores and frugivores
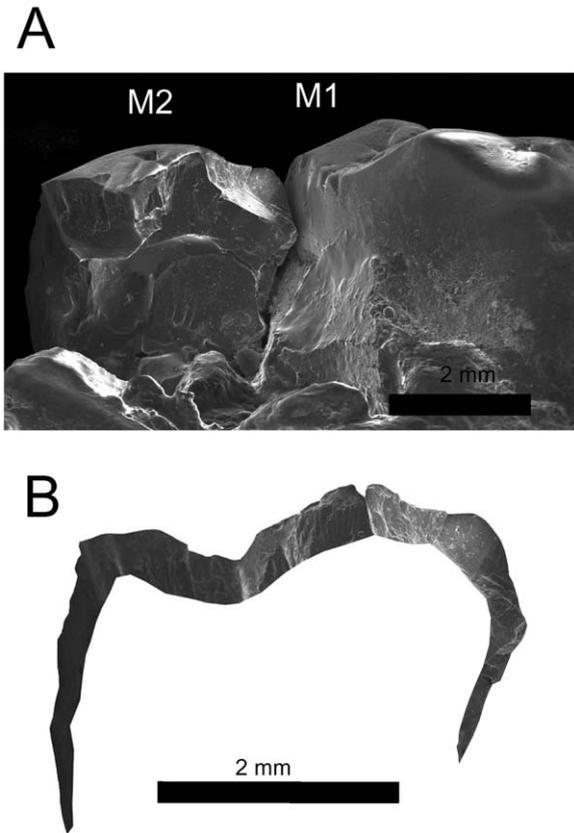
Fig. 7. Mandible of *Amphipithecus mogaungensis* (MNNP 7, left side) in medial view showing p3-m2 and the rugose unfused symphysis.

Fig. 6. *Pondaungia savagei* (NMMP 12 =NMMP KU 0003): A) medial view of M1 and broken M2; B) the traced outline of the occlusal surface and exposed dentine-enamel junction along the natural break on M2.

(Fig. 8B). We hypothesize based on these comparisons that *Pondaungia*, *Amphipithecus* and *Siamopithecus* could have withstood similar internal loads in their corpora during chewing and biting as do living primate folivores and many seed-eaters.

Locomotion

Parts of two humeri, an ulna, and a nearly complete calcaneus of a single individual (NMMP 20) are referable to Amphipithecidae (a talus has recently been discovered; Jaeger, personal communication). These bones provide an opportunity to make some inferences about the probable locomotor behavior of one member of this family. Ciochon and colleagues (Ciochon et al., 2001; Ciochon and Gunnell, 2002a; Gunnell et al., 2002;
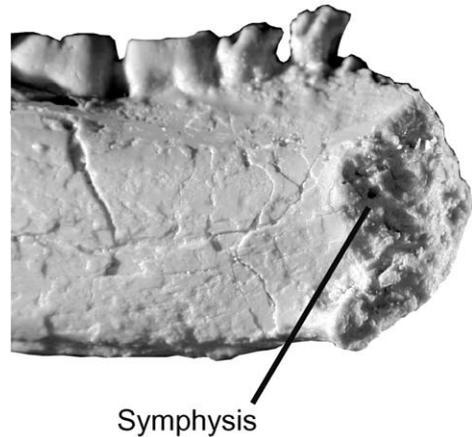
Ciochon and Gunnell, in press) call attention to morphological similarities between NMMP 20 and some extant strepsirrhines and with the North American Eocene adapoid *Notharctus*. These authors do not suggest that amphipithecids were vertical clingers and leapers like *Notharctus*. Rather, they find many features that suggest quadrupedalism. Here we add quantitative and qualitative observations that support and clarify the conclusions of previous authors suggesting that NMMP 20 was a slow-moving arboreal quadruped (like a modern lorisid) and was similar to the middle and late Eocene European adapoids *Adapis* and *Leptadapis*, but quite unlike *Notharctus*. Such inferences about locomotor behavior rely on a number of anatomical features that are functionally correlated with the modes of locomotion employed by extant species.

Proximal humerus

The morphology of the shoulder (and elbow; see below) of extant primates reflects habitual locomotor behavior (Ashton et al., 1968; Walker, 1974; Feldesman, 1976; Szalay and Dagosto, 1980; Bown et al., 1982; Gebo and Simons, 1987; Rose, 1988; Harrison, 1989; Rose, 1989; Tilden, 1990; Ciochon, 1993; Rose, 1993, 1994; Schmitt, 1996; Richmond et al., 1998; Schon-Ybarra, 1998), range of motion (Zeimer, 1978; O'Conner and Rarey,
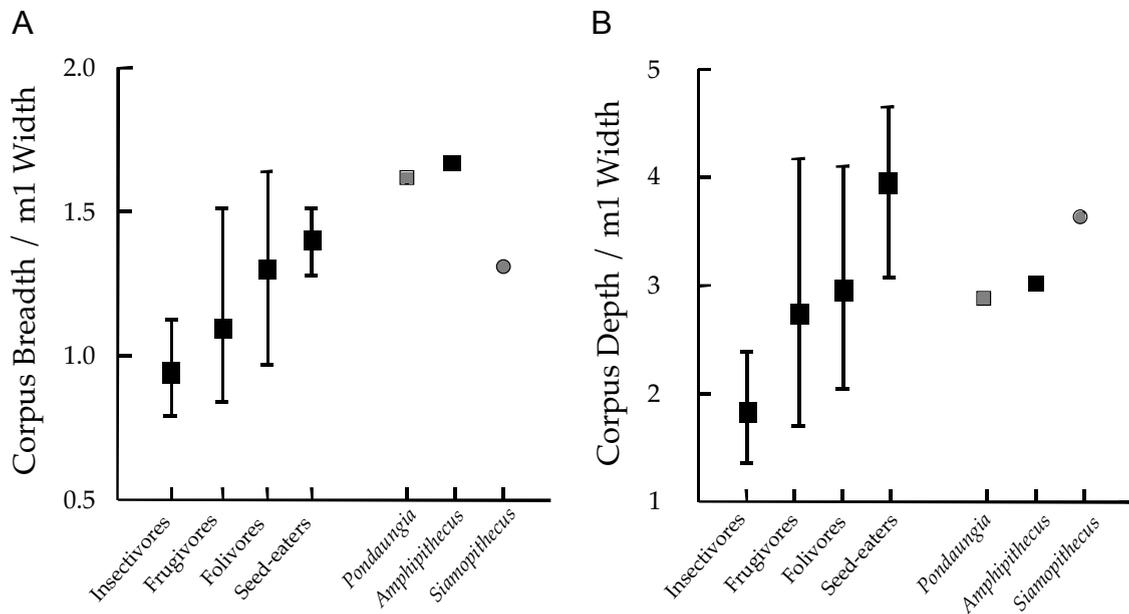
Fig. 8. Comparison of means and ranges of size-adjusted amphipithecid corpus dimensions and extant primate insectivores, frugivores, folivores, and seed-eaters: A) ratio of corpus breadth at m1 divided by m1 width; B) ratio of corpus depth at m1 divided by m1 width. The living primate samples include 13 insectivores, 42 frugivores, 29 folivores, and 6 seed-eaters. The six seed-eaters were all anthropoids, while the remaining dietary groups include both living strepsirrhine and haplorrhine species. Species were assigned to dietary categories based on their primary dietary component. *Pondaungia* sample: NMMP 4; *Amphipithecus* sample: AMNH 32520, NMMP 1, 2, 6, 7; *Siamopithecus* sample: TF 3634.

1979), and the external forces associated with different locomotor modes (Demes et al., 1998; Schmitt, 2003).

Based on comparisons among extant primates, a number of features of the proximal humerus point towards a loris-like slow arboreal quadrupedal mode of locomotion for NMMP 20. In terrestrial quadrupeds and species that engage in vertical clinging and leaping behaviors (hereafter VCL), the tuberosities for insertion of the rotator cuff muscles rise well above the summit of the glenohumeral articular surface (Jolly, 1967; Gebo, 1988; Rose, 1988; Harrison, 1989). Among active arboreal quadrupeds (AAQ), the humeral tuberosities and summit are of nearly equal height (Jolly, 1967; Gebo, 1988; Rose, 1988; Harrison, 1989). In contrast, among living slow-moving arboreal quadrupeds, the tuberosities are far below the summit, that is to say, the humeral head projects distinctly superior to the tuberosities (Jolly, 1967; Gebo, 1988; Rose, 1988; Harrison, 1989). These morphological contrasts are made

clear in Fig. 9. In NMMP 20 the tuberosities are positioned well below the summit of the articular surface of the humeral head as in the slow-moving arboreal quadrupeds.

The articular surface of the humeral head of NMMP 20 is oriented proximally (Ciochon et al., 2001; Ciochon and Gunnell, 2002a; Gunnell et al., 2002) (Fig. 9). This is consistent with the positioning of the tuberosities below the articular summit and indicates that the shoulder joint was optimized for overhead reaching and bridging (Jolly, 1967; Walker, 1974; Gebo, 1988) and experienced reduced stability in protracted positions (Rose, 1989; Schmitt, 1996). Notably, the articular surface is oriented more acutely to the long axis of the shaft (i.e., more cranially) than in most arboreal quadrupeds and primates that habitually cling to and leap from vertical supports (Schmitt, 1996). The articular surface orientation of NMMP 20 is most like that of a loris (Fig. 9) or *Alouatta*, the howler monkey (Schon-Ybarra, 1998).
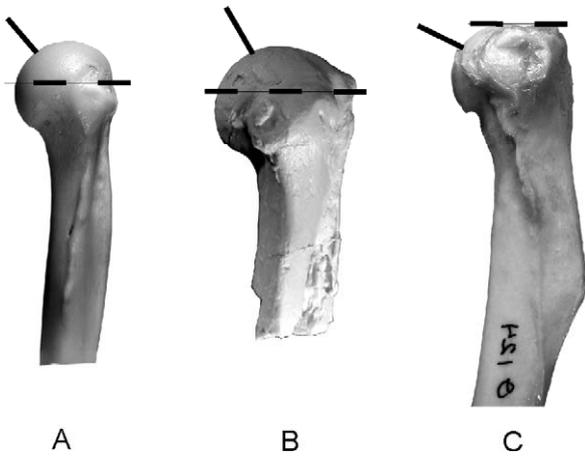
Fig. 9. Medial views of the proximal humeri of: A) *Nycticebus coucang*, a slow-moving arboreal quadruped; B) NMMP 20; and C) *Propithecus verreauxi*, a vertical clinging and leaping species. The position of the tuberosities is illustrated by the dashed line. The median orientation of the glenohumeral articular surface is depicted by the lines arising from the head of each specimen.

Table 7
Humeral articular surface shape (mean values). See Figure 10 for range of values

Species	AH/ML	PD/ML
NMMP 20	31	96
Slow arboreal quadrupeds	31	92
Alouatta sp.	34	93
Active arboreal quadrupeds	33	83
Vertical clingers and leapers	39	77

Notes: The measurements are (1) the length of the base (chord) of a contour along the central proximodistal (superior-inferior) surface of the humeral head (PD), (2) the same for a central mediolateral contour (ML), and (3) the central height of the ML contour from its base (AH). This sample includes: 40 specimens of active arboreal quadrupeds sampling 5 species (*Varecia variegata*, *Eulemur fulvus*, *E. rubriventer*, *E. macaco*, *Otolemur crassicaudatus*), 57 specimens of vertical clingers and leapers sampling 6 species (*Lepilemur* sp., *Avahi laniger*, *Propithecus verreauxi*, *Indri indri*, *Hapalemur griseus*, and *Galago senegalensis*), and 10 specimens of slow climbers sampling four species (*Loris tardigradus*, *Nycticebus coucang*, *Alouatta* sp., and *Perodicticus potto*).

Comparing the humeral head's breadth, width, and depth using the metrics of Schmitt (1996), NMMP 20 has a nearly equal mediolateral breadth relative to its proximodistal length and is relatively flat when its depth is compared either with its proximodistal length or mediolateral length. Fig. 10 and Table 7 show representative values for these measures in living primates, NMMP 20, and middle Eocene *Smilodectes* and *Notharctus*. Primates that engage in habitual vertical clinging and leaping are separated from both active arboreal quadrupeds (Schmitt, 1996) and from slow-moving arboreal quadrupeds (the lorisoids *Loris, Nycticebus, Perodicticus,* and the platyrrhine
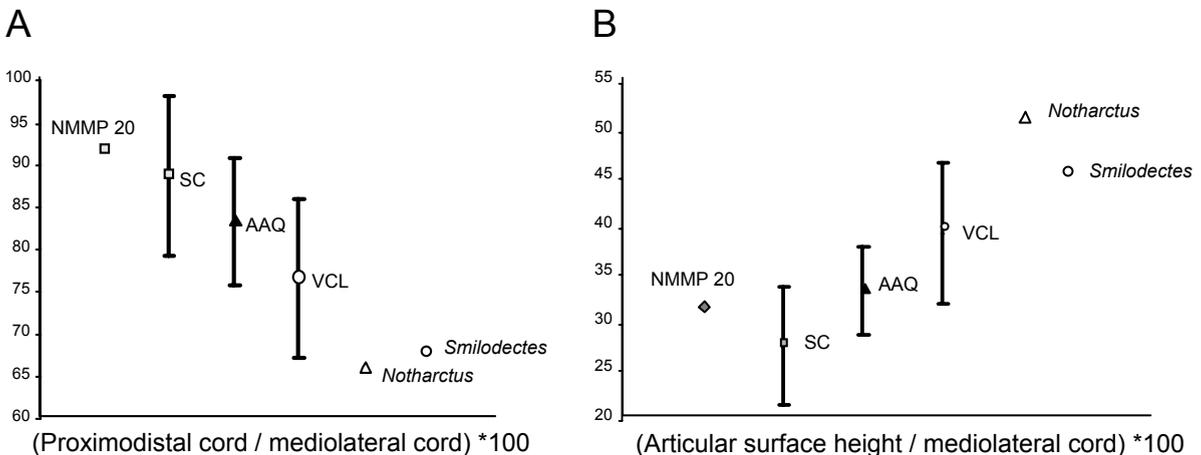

Fig. 10. A) Means and ranges of humeral head shape. B) Humeral head inflation in slow climbers (SC), active arboreal quadrupeds (AAQ), and vertical clingers and leapers (VCL). Humeral head shape is defined, and species and sample sizes are listed in Table 8.
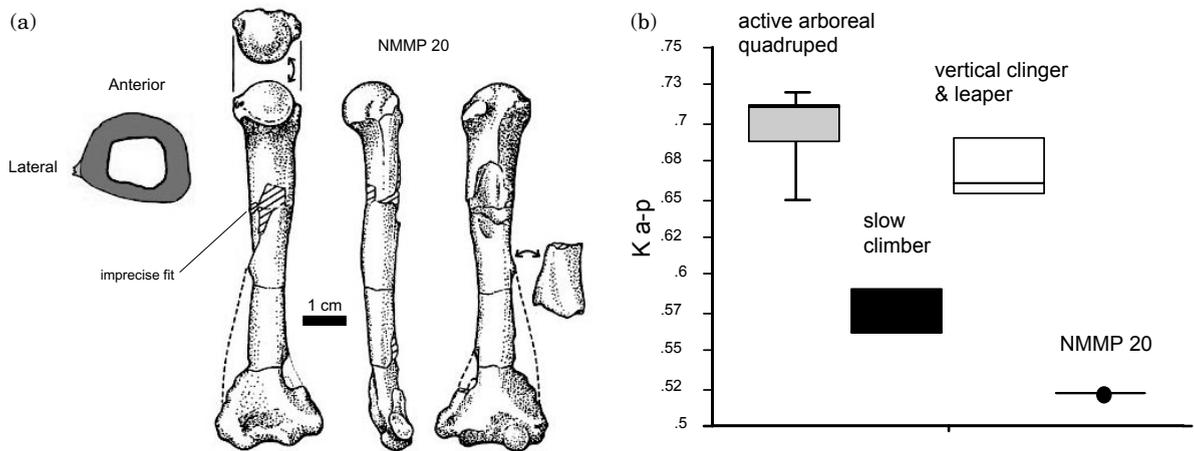
Fig. 11. A) Reconstruction of the humerus of NMMP 20 after Ciochon et al. (2001) and the outline of the natural mid-shaft cross-section showing the distribution of cortical bone and the medullary canal. While acceptable in other respects, the humeral length of this specimen may be underestimated in this reconstruction because we found it impossible to connect the proximal and distal parts at a natural break as they have done. B) Anteroposterior values for the quantity K described in the text for samples of active arboreal quadrupeds, slow climbers, and vertical clingers and leapers (data from Runestad [1994]). NMMP 20 measured for this study.

Alouatta). NMMP 20 falls among the cautious arboreal quadrupeds. The articular surface is dissimilar in shape to that of *Notharctus* and *Smilodectes*, and also differs from those extant primates that habitually cling and leap from vertical supports.

Humeral cross-sectional anatomy

The relative thickness of the cortical walls of the humeral shaft can be examined along a plane of a postmortem fracture that occurs at a level approximately 60% distally on a left humerus (Fig. 11). The details of this cross section further support the hypothesis that NMMP 20 was a slow-moving quadruped. The internal and external dimensions of the humeral shaft were measured along the major axis (approximately in the mediolateral plane) and minor axis (approximately along the anteroposterior plane). These dimensions are used to estimate cortical area (CA) following Runestad (1994, 1997). The ratio of internal diameter to external diameter (K) can also be estimated following the methods of Currey and Alexander (1985) and Demes and Jungers (1993). The values for CA and K are larger for this specimen than for any leaper or active arboreal quadruped of similar body size (Fig. 11, Table 8). CA is most similar to

that of *Adapis* and *Leptadapis*, (values from Runestad). Runestad (1997) reports relatively high values for CA in slow climbing lorises. The values for K show that this specimen has extraordinarily thick cortical bone in both AP and ML planes and approached only by extant lorises and *Daubentonia* (Table 8)[2].

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[2] We assume that overall increase in bone mass reflects a need to maintain safety factors in the face of increased load. However, the direction and frequency of load are difficult to infer from such data. It is important to note that there is considerable debate among bone biologists concerning the critical stimulus (or stimuli) that trigger bone modeling or remodeling. Some argue that the critical stimulus is the magnitude of the strain engendered in the bone during loading, not the number of loading cycles (Rubin and Lanyon, 1984; Wahlen et al., 1988; Beaupré et al., 1990a,b; Skerry and Lanyon, 1995). On the other hand many authors (Lanyon and Rubin, 1985; Martin and Burr, 1989; Rubin et al., 1994) do not believe that peak functional strains are the only stimulus, or even the most important of the various stimuli, to have osteoregulatory capabilities. In addition to strain magnitude Rubin et al. (1994) describe other stimuli including the fabric tensor, strain frequency, strain rate, strain gradients, electrokinetics, piezoelectricity, strain history, and strain energy density that may have osteoregulatory effects. We take as our working hypothesis that strain magnitude, or some combination of magnitude and frequency (Jacobs et al., 1998; Robling et al., 2000), functions as an important stimulus for osteogenic response.

Table 8
Cortical properties of the cross-section of the NMMP 20 humerus compared with those of extant primates

Species	Body weight	Cortical area	K a-p	K m-l	Locomotion
Nycticebus coucang	658	12	0.56	0.59	slow climber
Perodicticus potto	860	13.8	–	–	slow climber
Loris tardigradus	300	3.5	0.56	0.53	slow climber
Cheirogaleus major	436	5.6	0.71	0.58	active arboreal quadruped
Cheirogaleus medius	180	3.14	0.72	0.67	active arboreal quadruped
Daubentonia madagascarensis	2700	26.4	0.6	0.66	slow climber
Propithecus verreauxi	5794	33.7	0.65	0.63	vertical clinger and leaper
Varecia variegata	3000	26.98	0.7	0.69	active arboreal quadruped
Indri indri	7500	37.94	0.66	0.67	vertical clinger and leaper
Otolemur crassicaudatus	1200	12.47	0.65	0.63	active arboreal quadruped
Avahi laniger	1175	9.28	0.7	0.68	vertical clinger and leaper
Lemur catta	2423	15.45	0.71	0.7	active arboreal quadruped
NMMP 20	5500	39	0.52	0.46	–
Notharctus sp.	2700	24	–	–	–
Smilodectes sp.	2400	25	–	–	–
Leptadapis sp.	10000	72	–	–	–
Adapis 1	2000	20	–	–	–
Adapis 2	3500	34	–	–	–

Notes: Cortical area in NMMP 20 was measured using the methods of Runestad (1994, 1997). The quantity "K" is the ratio of internal diameter to external diameter estimated following the methods of Currey and Alexander (1985) and Demes and Jungers (1993). Data for extant species and adapoids from Runestad (1994).

Distal humerus

As noted by Ciochon and colleagues (Ciochon et al., 2001; Ciochon and Gunnell, 2002a), the elbow joint of NMMP 20 (Fig. 12) shows functional similarities to those of lorises and notharctine primates (although not to the exclusion of European adapines). Using indices described by Szalay and Dagosto (1980), Ciochon and Gunnell (in press) suggest that *Pondaungia* falls within the arboreal quadrupedalism distribution. However, they note that the shallow olecranon fossa and moderately developed olecranon process of the ulna indicate that the arm may not have been capable of as much elbow extension as in arboreal quadrupeds. Results from our own analysis of these indices concur with the conclusions of Ciochon and Gunnell. However, in addition to the features of the olecranon, we would add several other features that suggest a relatively slow moving quadrupedal locomotor mode for NMMP 20. In this specimen, the large, rounded capitulum is the dominant feature of the elbow joint. However, this is not diagnostic of any particular locomotor

specialization—it is present in both slow quadrupeds and vertical clingers and leapers (Szalay and Dagosto, 1980; Rose, 1993). In NMMP 20, the capitulum and trochlea are separated by a narrow, shallow *zona conoidea*. The *zona conoidea* is variably developed in slow-moving lorises but is more distinct in howler monkeys (Schon-Ybarra, 1998). A *zona conoidea* would serve to stabilize the radius, especially in flexed positions (Rose, 1988). More importantly, the capitulum of NMMP 20 has a well-developed anterolateral flange or tail with a distinct and deep ridge (Fig. 13). Leaping strepsirrhines and lorisoids have well developed capitular tails; indeed, in *Loris* this tail is formed into a distinct lateral flange to stabilize the radius (Szalay and Dagosto, 1980; Rose, 1993). A distinct capitular tail with a deep ridge is also found in *Alouatta* (Schon-Ybarra, 1998). Finally, NMMP 20 has a large cone-like trochlea with a relatively large lateral expansion like that of lorisids (Rose, 1993). Taken as a package, the large, round capitulum, truncated cone-like trochlea, and the strong capitular tail compellingly suggest that loris-like
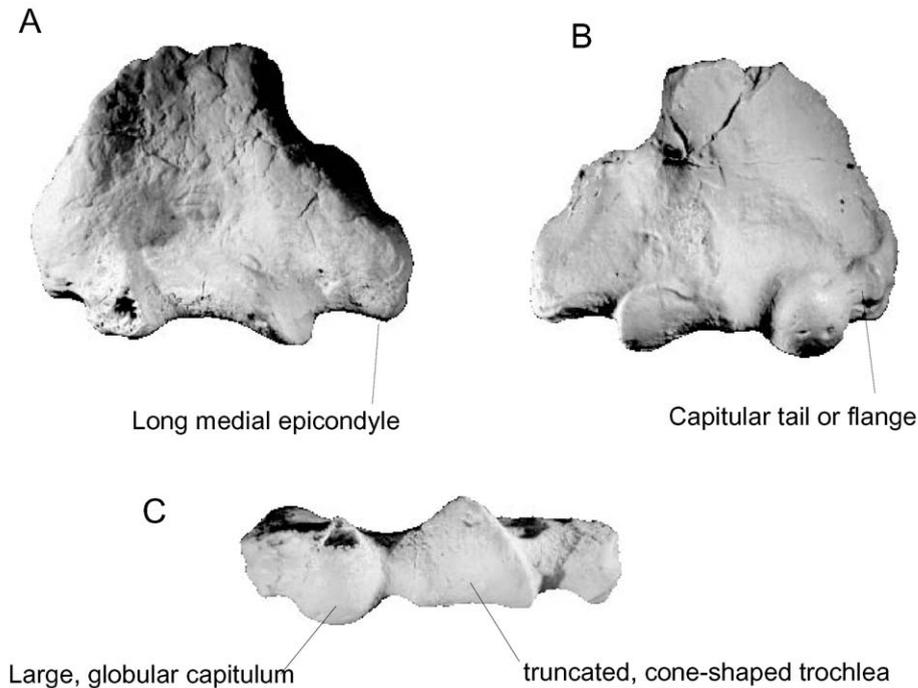
Fig. 12. Posterior (A), anterior (B), and distal (C) views of the distal humeral fragment of NMMP 20.

cautious arboreal quadrupedalism was an important part of the locomotor repertoire of this animal (Fig. 13).

Calcaneus

The NMMP 20 calcaneus is incomplete proximally: a part of the heel is broken away. As a consequence, only the load-arm can be measured. Because useful functional information can be gained from the ratio of calcaneal load-arm length to lever-arm length (e.g. Gebo, 1986a,b; Martin, 1990), an investigation was undertaken to see whether calcaneal breadth can be used as a proxy for lever-arm length. For this purpose, we use data on load-arm and lever-arm lengths and calcaneal breadth in Gebo (1986a). For calcaneal breadth to serve as a reliable surrogate for lever-arm length, it must be shown first, that calcaneal breadth and lever-arm length are highly correlated and second, that the deviations away from the general trend are matched (Fig. 14). In this case, the two variables are highly correlated: 87% of the variance in

calcaneal breadth is "explained" by calcaneal lever arm length (Fig. 14A). Residuals (expressed as a percentage of expected) are calculated from the least-squares bivariate regression of lever-arm length (independent variable) versus load-arm length (dependent variable). Similar residuals are calculated by substituting calcaneal breadth as the independent variable (Fig. 14B). The residuals of the two comparisons are very highly correlated: 97% of the variance in one residual is "explained" by the other (Fig. 14B).

Two very different trajectories of calcaneal proportions are followed with increased body size in primates (Fig. 15). In "tarsi-fulcrumators" like *Tarsius*, cheirogaleids, and galagos, the tarsus is greatly elongated, whereas in "metatarsi-fulcrumators" (including other extant strepsirrhines and anthropoids), elongation of the foot occurs in the metatarsal region (Morton, 1924). These two pathways of foot elongation are not certain indicators of locomotor behavior because the metatarsi-fulcrumator group includes active
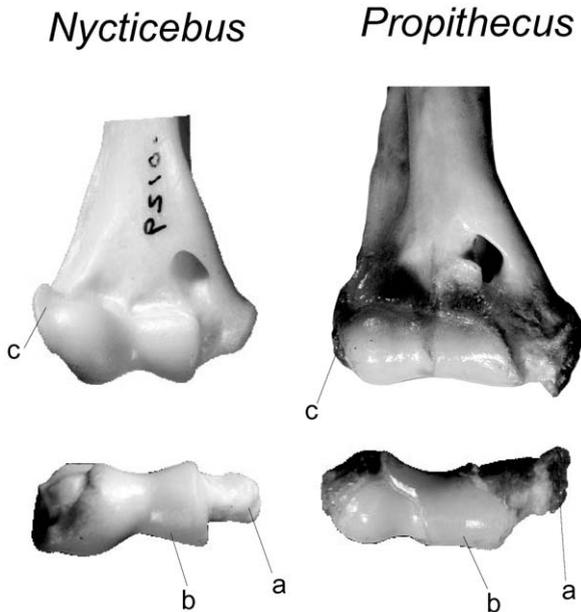
Nycticebus   Propithecus

Fig. 13. Anterior and distal views of the distal humeri of *Nycticebus coucang*, a slow-moving arboreal quadruped, and *Propithecus verreauxi*, a vertical clinging and leaping species. Symbols: a, medial epicondyle; b, trochlea; and c, capitular tail.

quadrupeds as well as leapers. Interestingly, early Oligocene anthropoids and living anthropoid primates have shorter load arms than strepsirrhines for a given calcaneal breadth (Fig. 15). Eocene North American and European adapoids fall among the strepsirrhine metatarsi-fulcrumators, as does NMMP 20.

Summary and conclusions

Amphipithecidae—*Pondaungia*, *Amphipithecus*, and *Myanmarpithecus* (late middle Eocene, Myanmar) and *Siamopithecus* (late Eocene, Thailand)—is a clade of middle and late Eocene primates. Several of the authors of this paper believe amphipithecids to be stem anthropoids, while others subscribe to the view that they are adapoids with dental and gnathic features that converge on those of larger-bodied Oligocene African anthropoids.

The upper and lower teeth, mandibular structure, as well as humeral and calcaneal fragments,

provide detailed evidence of the behavioral profile of amphipithecids. At 5–8 kg, *Pondaungia*, *Amphipithecus*, and *Siamopithecus* were as large as any known Eocene primates, and comparable in size to the largest extant platyrrhines and strepsirrhines. The mandibular corpora of amphipithecids are robust, the symphyses are vertically oriented, and there are strong transverse tori. The mandibular symphysis is unfused but rugose surfaces would have allowed little movement. Collectively, these features suggest an ability to resist large biting and chewing loads, and to recruit muscle forces from the contralateral side of the jaw, thus increasing the muscle force available for mastication. The robust, spatulate upper central incisor and projecting robust upper canine of *Pondaungia* suggest powerful biting as in the fruit husking and seed predation of certain living anthropoids. Similar inferences are possible from the robust lower canines of *Amphipithecus* and *Siamopithecus*. The molars of *Siamopithecus*, *Amphipithecus* and *Pondaungia* have weak shearing crests. This fact and the thick enamel found in *Pondaungia* (unknown in the other taxa) suggest a hard-object, low-fiber diet. Collectively, the dental and mandibular anatomy suggests that large-bodied amphipithecids were seed predators. *Myanmarpithecus* was a smaller, most likely frugivorous, species.

The humerus and calcaneus of a single individual have been attributed to *Pondaungia* but the material is equally likely to belong to *Amphipithecus*. The humeral head of this specimen (NMMP 20) indicates a wide range of motion in all planes, including overhead reaching. It is rounded and proximally oriented with low tuberosities, indicating an extremely mobile shoulder like that of living lorises and *Alouatta*. The humerus has exceptionally thick midshaft cortical bone, as seen among slow-moving primate quadrupeds. The elbow joint exhibits articular features for enhanced stability in habitually flexed positions, including an anteriorly expanded capitulum and an expanded, grooved capitular tail. These distal humeral features, along with a large medial epicondyle, are shared with *Alouatta*, a slow moving quadruped. The distal humerus of deliberate arboreal quadrupedal lorisids is less similar—the enlarged
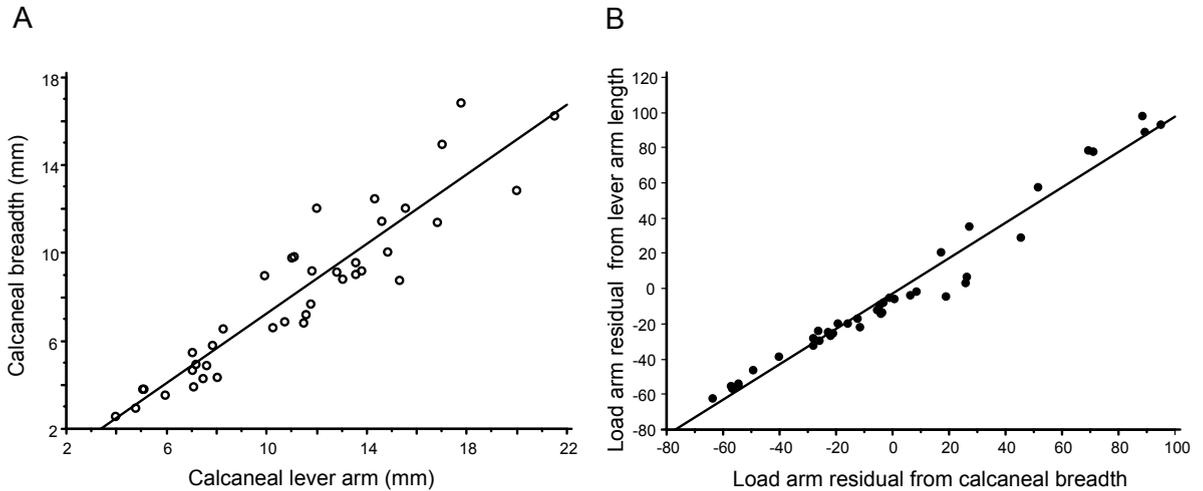
A

B

Fig. 14. Comparison of calcaneal breadth and calcaneal lever arm in extant primates. A) Least-squares regression line fitted to calcaneal lever arm (independent variable) and calcaneal breadth (dependent variable). The correlation between the two variables is 0.930. B) Least-squares regression line fitted to the residuals from 1) the bivariate regression of lever-arm length (independent variable) versus load-arm length (dependent variable) and 2) lever-arm length (independent variable) versus calcaneal breadth (dependent variable). The correlation between the residuals is 0.986—species with relatively long load arms also have relatively broad calcanei. Data from Gebo (1986a).
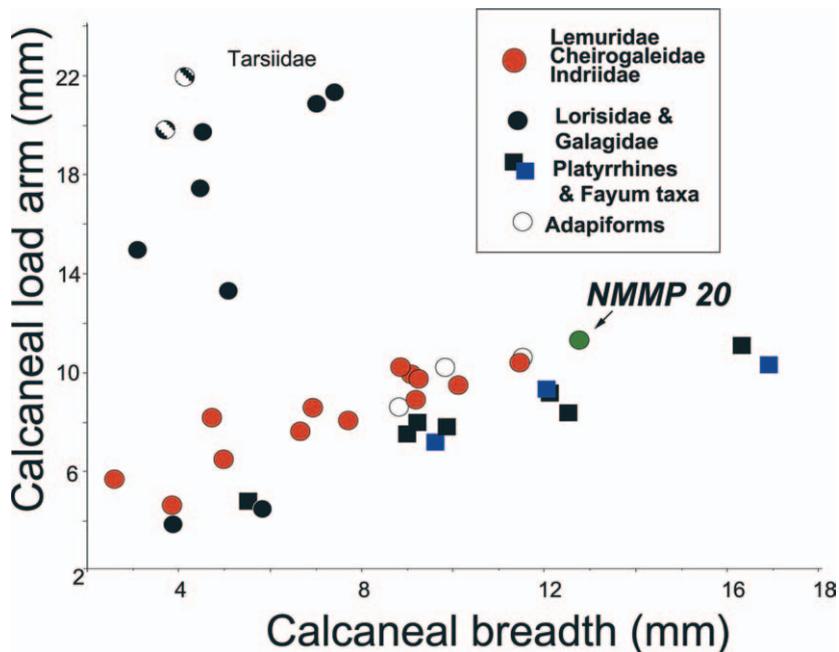

Fig. 15. Bivariate plot of calcaneal load-arm vs. calcaneal breadth for a broad range of small- to medium-sized strepsirrhines and haplorrhines. NMMP 20 falls with living metatarsi-fulcrumating strepsirrhines and adapoids. Comparative data from Gebo (1986a).

capitulum and capitular tail are the only features in the above list common to both. The short distal load arm of the calcaneus also is consistent with, but not exclusive to, slow arboreal quadrupedalism. Taken together, the locomotor signal suggested by the different postcranial features is remarkably consistent. No features link this large amphipithecid exclusively with a vertical clinging and leaping or simple leaping locomotor pattern. NMMP 20 represents an above-branch quadruped, most likely a slow-moving one.

The dietary contrast between the mostly folivorous large-bodied European adapoids and the seed-eating and frugivorous south Asian amphipithecids is notable. This observed difference in guild structure might indicate that late Eocene Europe was drier, exhibited greater seasonal contrasts, or was less predictable compared to the later Eocene of South Asia.

Acknowledgements

References

Anthony, M.R.L., Kay, R.F., 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. Am. J. Sci. 283A, 356–382.

Ashton, E.H., Flinn, R., Oxnard, C.E., Spence, T., 1968. The adaptive and classificatory significance of certain quantitative features of the forelimb in primates. J. Zool. 179, 515–556.

Aung, A.K., 1999. Revision of the stratigraphy and age of the Primates-bearing Pondaung Formation. In: Tun, T. (Ed.), Proceedings of the Pondaung Fossils Expedition Team. Office of Strategic Studies, Ministry of Defense, Yangon, Myanmar, pp. 131–151.

Beard, K.C., MacPhee, R.D.E., 1994. Cranial anatomy of *Shoshonius* and the antiquity of Anthropoidea. In: Fleagle, J.G, Kay, R.F. (Eds.), Anthropoid Origins. Plenum Press, New York, pp. 55–98.

Beaupré, G.S., Orr, T.E., Carter, D.R., 1990a. An approach for time-dependent bone modeling and remodeling—application: a preliminary remodeling situation. Jour. Orthopae. Res. 8, 662–670.

Beaupré, G.S., Orr, T.E., Carter, D.R., 1990b. An approach for time-dependent bone modeling and remodeling—theoretical development. Jour. Orthopae. Res. 8, 651–661.

Bouvier, M., 1986. A biomechanical analysis of mandibular scaling in Old World monkeys. Am. J. Phys. Anthrop. 69, 473–482.

Bown, T.M., Kraus, M., Wing, S., Fleagle, J.G., Tiffany, B., Simons, E.L., Vondra, C., 1982. The Fayum primate forest revisited. J. Hum. Evol. 11, 624–648.

Bush, E.C., Simons, E.L., Allman, J., in press. Brain anatomy of *Parapithecus grangeri*. In: Ross, C., Kay, R.F. (Eds.), Anthropoid Origins: New Visions. Kluwer/Plenum, New York.

Cartmill, M., 1980. Morphology, function and evolution of the anthropoid postorbital septum. In: Ciochon, R., Chiarelli, B. (Eds.), Evolutionary Biology of the New World Monkeys and Continental Drift. Plenum Press, New York, pp. 243–274.

Chaimanee, Y., Suteethorn, V., Jaeger, J.-J., Ducrocq, S., 1997. A new late Eocene anthropoid primate from Thailand. Nature 385, 429–431.

Chaimanee, Y., Thein, T., Ducrocq, R.-M., Soe, A.N., Benammi, M., Tun, T., Lwin, T., Wai, S., Jaeger, J.-J., 2000. A lower jaw of *Pondaungia cotteri* from the late middle Eocene Pondaung Formation (Myanmar) confirms its anthropoid status. Proc. Natl. Acad. Sci. 97, 4102–4105.

Ciochon, R., 1993. Evolution of the Cercopithecoid Forelimb: Phylogenetic and Functional Implications from Morphometric Analyses. University of California Press, Berkeley, CA.

Ciochon, R., Gingerich, P.D., Gunnell, G.F., Simons, E.L., 2001. Primate postcrania from the late middle Eocene of Myanmar. Proc. Natl. Acad. Sci. 98, 7672–7677.

Ciochon, R., Gunnell, G.F., 2002a. Chronology of primate discoveries in Myanmar: influences on the anthropoid origins debate. Yearb. Phys. Anthrop. 45, 2–35.

Ciochon, R., Gunnell, G.F., 2002b. Eocene primates from Myanmar: historical perspectives on the origin of Anthropoidea. Evol. Anthrop. 11, 156–168.

Ciochon, R., Gunnell, G.F., in press. Eocene large-bodied primates of Myanmar and Thailand: morphological considerations and phylogenetic affinities. In: Ross, C., Kay, R.F. (Eds), Anthropoid Origins: New Visions. Kluwer/Plenum, New York.

Ciochon, R.L., Holroyd, P.A., 1994. The Asian origin of Anthropoidea revisited. In: Fleagle, J.G., Kay, R.F. (Eds.), Anthropoid Origins. Plenum Press, New York, pp. 143–162.

Colbert, E.H., 1937. A new primate from the upper Eocene Pondaung formation of Burma. Am. Mus. Novit. 651, 1–18.

Conroy, G.C., 1987. Problems of body-weight estimation in fossil primates. Int. J. Primatol. 8, 115–137.

Currey, J.D., Alexander, R.M., 1985. The thickness of the walls of tubular bones. J. Zool. 206, 453–468.

Demes, B., Jungers, W.L., 1993. Long bone cross-sectional dimensions, locomotor adaptations and body size in prosimian primates. J. Hum. Evol. 25, 57–74.

Demes, B., Stern, J.T. Jr, Hausman, M.R., Larson, S.G., McLeod, K.J., Rubin, C.T., 1998. Patterns of strain in the macaque ulna during functional activity. Am. J. Phys. Anthrop. 106, 87–100.

Ducrocq, R.-M., 1999a. The late Eocene Anthracotheriidae (Mammalia, Artiodactyla) from Thailand. Palaeontolograph. 252, 93–140.

Ducrocq, R.-M., Chaimanee, Y., Suteethorn, V., Jaeger, J.-J., 1995a. Mammalian faunas and the ages of the continental Tertiary fossiliferous localities of Thailand. Journal of Southeast Asian Earth Sciences 12, 65–78.

Ducrocq, S., 1998. Eocene primates from Thailand: are Asian anthropoideans related to African ones? Evol. Anthrop., 97–104.

Ducrocq, S., 1999b. *Siamopithecus eocaenus*, a late Eocene anthropoid primate from Thailand: its contribution to the evolution of anthropoids in southeast Asia. J. Hum. Evol. 36, 613–635.

Ducrocq, S., Jaeger, J.-J., Chaimanee, Y., Suteethorn, V., 1995b. New primate from the Paleogene of Thailand, and the biogeographical origin of anthropoids. J. Hum. Evol. 28, 477–485.

Egi, N., Takai, M., Shigahara, N., Tsubamoto, T., 2002. Body mass estimates for Pondaung primates. Primate Research 18, 1–18.

Egi, N., Takai, M., Shigahara, N., Tsubamoto, T., in press a. Body mass estimates for Eocene eosimiid and amphipithecid primates using prosimian and anthropoid scaling models. Int. J. Primatol.

Egi, N., Tun, S.T., Takai, M., Shigahara, N., Tsubamoto, T., in press b. Relative geographical and body size distributions of the Pondaung primates with a comment on the taxonomic assignment of NMMP 20, a postcranium of Amphipithecidae. Anthropological Science (Japan).

Feldesman, M.R., 1976. The primate forelimb: a morphometric study of diversity. Univ. Oregon Anthropol. Papers 1, 1–149.

Fleagle, J.G., Kay, R.F., Simons, E.L., 1980. Sexual dimorphism in early anthropoids. Nature 287, 328–330.

Fleagle, J.G., Kay, R.F., Anthony, M.R.L., 1997. Fossil New World monkeys. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), Mammalian Evolution in the Neotropics. Smithsonian Institution Press, Washington, DC, pp. 473–495.

Gebo, D., 1986a. The anatomy of the prosimian foot and its application to the primate fossil record. Ph.D. Dissertation, Duke University.

Gebo, D., 1986b. Anthropoid origins—the foot evidence. J. Hum. Evol. 15, 421–430.

Gebo, D., 1988. A hominoid proximal humerus from the Early Miocene of Rusinga Island, Kenya. J. Hum. Evol. 17, 393–401.

Gebo, D., Simons, E.L., 1987. Morphology and locomotor adaptations of the foot in early Oligocene anthropoids. Am. J. Phys. Anthrop. 74, 83–101.

Gingerich, P., 1980. Eocene Adapidae, paleobiology, and the origin of South American Platyrrhini. In: Ciochon, R., Chiarelli, B. (Eds.), Evolutionary Biology of the New World Monkeys and Continental Drift. Plenum Press, New York, pp. 123–138.

Godinot, M., 1994. Early North African primates and their significance for the origin of Simiiformes (=Anthropoidea). In: Fleagle, J.G., Kay, R.F. (Eds.), Anthropoid Origins. Plenum Press, New York, pp. 235–296.

Gunnell, G.F., Ciochon, R., Gingerich, P.D., Holroyd, P.A., 2002. New assessment of *Pondaungia* and *Amphipithecus* (Primates) from the late middle Eocene of Myanmar, with comments on 'Amphipithecidae'. Contrib. Mus. Paleont. Univ. Mich. 30, 337–372.

Harrison, T., 1989. New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. J. Hum. Evol. 18, 3–54.

Holroyd, P.A., Ciochon, R.L., Gunnell, G.F., Kay, R.F., Takai, M., Godinot, M., 2002. What's in a name? Family-group name taxonomy of larger-bodied southeast Asian Eocene Primates. J. Hum. Evol. 43, 755–758.

Hylander, W.L., 1988. Implications of in vivo experiments for interpreting the functional significance of "robust" australopithecine jaws. In: Grine, F.E. (Ed.), Evolutionary History of the "Robust" Australopithecines. Gruyter, New York, pp. 55–83.

Jacobs, C.R., Yellowley, C.E., Davis, B.R., Zhou, Z., Cimbala, J.M., Donahue, H.J., 1998. Differential effect of steady versus oscillating flow on bone cells. J. Biomech. 31, 969–976.

Jaeger, J.-J., Chaimanee, Y., Ducrocq, S., 1998a. Origin and evolution of Asian hominoid primates. Paleontological data versus molecular data. C. r. Acad. Sci., Paris 321, 73–78.

Jaeger, J.-J., Soe, U.A.N., Aung, U.A.K., Benammi, M., Chaimanee, Y., Ducrocq, R.-M., Tun, T., Thein, U.T., Ducrocq, S., 1998b. New Myanmar middle Eocene anthropoids. An Asian origin for catarrhines?. C. r. Acad. Sci., Paris 321, 953–959.

Jolly, C.J., 1967. The evolution of the baboons. In: Vartborg, H. (Ed.), The Baboons in Medical Research. 2. University of Texas Press, Austin, pp. 23–50.

Kappelman, J., Simons, E.L., Swisher, C.C., 1992. New age determinations for the Eocene-Oligocene boundary sediments in the Fayum Depression, Northern Egypt. J. Geol. 100, 647–667.

Kay, R.F., 1975. The functional adaptations of primate molar teeth. Am. J. Phys. Anthrop. 43, 195–216.

Kay, R.F., 1977. The evolution of molar occlusion in Cercopithecidae and early catarrhines. Am. J. Phys. Anthrop. 46, 327–352.

Kay, R.F., 1981. The nut-crackers: A new theory of the adaptations of the Ramapithecinae. Am. J. Phys. Anthrop. 55, 141–152.

Kay, R.F., 1982. Sexual dimorphism in the Ramapithecinae. Proc. Natl. Acad. Sci. 79, 209–212.

Kay, R.F., Cartmill, M., 1977. Cranial morphology and adaptation of *Palaechthon nacimienti* and other Paromomyidae (Plesiadapoidea? Primates), with a description of a new genus and species. J. Hum. Evol. 6, 19–35.

Kay, R.F., Covert, H.H., 1984. Anatomy and behaviour of extinct primates. In: Chivers, D.J., Wood, B.A., Bilsborough, A. (Eds.), Food Acquisition and Processing in Primates. Plenum Press, New York, pp. 467–508.

Kay, R.F., Hiiemae, K.M., 1974. Jaw movement and tooth use in recent and fossil primates. Am. J. Phys. Anthrop. 40, 227–256.

Kay, R.F., Kirk, E.C., 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. Am. J. Phys. Anthrop. 113, 235–262.

Kay, R.F., Madden, R.H., 1997. Mammals and rainfall: paleo-ecology of the middle Miocene at La Venta (Colombia, South America). J. Hum. Evol. 32, 161–199.

Kay, R.F., Plavcan, J.M., Glander, K.E., Wright, P., 1987. Sexual selection and canine dimorphism in New World monkeys. Am. J. Phys. Anthrop. 77, 385–397.

Kay, R.F., Simons, E.L., 1980. The ecology of Oligocene African Anthropoidea. Int. J. Primatol. 1, 21–37.

Kay, R.F., Ungar, P., 1997. Dental evidence for diet in some Miocene catarrhines with comments on the effects of phylogeny on the interpretation of adaptation. In: Begun, D.R., Ward, C., Rose, M. (Eds.), Function, Phylogeny and Fossils: Miocene Hominoids and Great Ape and Human Origins. Plenum Press, New York, pp. 131–151.

Kay, R.F., Williams, B.A., Ross, C., Takai, M., Shigehara, N., 2003. Anthropoid origins: a phylogenetic analysis. In: Ross, C., Kay, R.F. (Eds.), Anthropoid Origins: New Visions. Kluwer/Plenum, New York.

Kirk, E.C., Kay, R.F., in press. The evolution of high visual acuity in the Anthropoidea. In: Ross, C., Kay, R.F. (Eds), Anthropoid Origins: New Visions, Kluwer/Plenum, New York.

Kirk, E.C., Simons, E.L., 2000. Diet of fossil primates from the Fayum Depression of Egypt: a quantitative analysis of molar shearing. J. Hum. Evol. 40, 203–229.

Lanyon, L.E., Rubin, C.T., 1985. Functional adaptation in skeletal structures. In: Bramble, D.M., Leim, K.F., Wake, D.B. (Eds.), Functional Vertebrate Morphology. Belknap Press, Cambridge, pp. 1–25.

Martin, L.B., Kinzey, W.G., Maas, M.C., 1994. Enamel thickness in pitheciine primates. Am. J. Phys. Anthrop. 18(Suppl.), 138.

Martin, R.B., Burr, D.B., 1989. Structure, Function, and Adaptation of Compact Bone. Raven Press, New York.

Martin, R.D., 1990. Primate Origins and Evolution: A Phylogenetic Reconstruction. Chapman and Hall, London.

Meldrum, D.J., Kay, R.F., 1997. *Nuciruptor rubricae*, a new pitheciin seed predator from the Miocene of Colombia. Am. J. Phys. Anthrop. 102, 407–427.

Morton, D.J., 1924. Evolution of the human foot, II. Am. J. Phys. Anthrop. 7, 1–52.

O'Conner, B.L., Rarey, K., 1979. Normal amplitudes of pronation and supination in several genera of anthropoid primates. Am. J. Phys. Anthrop. 51, 39–44.

Pilgrim, G.E., 1927. A *Sivapithecus* palate and other primate fossils from India. Mem. Geol. Soc. India 14, 1–26.

Plavcan, J.M., Kay, R.F., 1988. Sexual dimorphism and dental variability in platyrrhine primates. Int. J. Primatol. 9, 169–178.

Plavcan, J.M., Kay, R.F., Albrecht, G.H., 1987. Sexual dimorphism and dental variability among extant platyrrhines. Am. J. Phys. Anthrop. 72, 243.

Radinsky, L., 1977. Early primate brains: fact and fiction. J. Hum. Evol. 6, 79–86.

Ravosa, M.J., 1991. Structural allometry of the mandibular corpus and symphysis in prosimian primates. J. Hum. Evol. 20, 3–20.

Richmond, B.G., Fleagle, J.G., Kappelman, J., Swisher, C.C. III, 1998. First hominoid from the Miocene of Ethiopia and the evolution of the catarrhine elbow. Am. J. Phys. Anthrop. 105, 257–277.

Robling, A.G., Burr, D.B., Turner, C.H., 2000. Partitioning of a daily mechanical stimulus into discrete loading bouts improves the osteogenic response to loading. J. Bone and Min. Res. 15, 1596–1602.

Rose, M.D., 1988. Another look at the anthropoid elbow. J. Hum. Evol. 17, 193–224.

Rose, M.D., 1989. New postcranial specimens of catarrhines from the middle Miocene Chinji formation, Pakistan: descriptions and a discussion of the proximal humeral functional morphology in anthropoids. J. Hum. Evol. 18, 131–162.

Rose, M.D., 1993. Functional anatomy of the elbow and forearm in primates. In: Gebo, D. (Ed.), Postcranial Adaptation in Nonhuman Primates. Northern Illinois University Press, DeKalb, pp. 70–95.

Rose, M.D., 1994. Quadrupedalism in Miocene catarrhines. J. Hum. Evol. 26, 387–412.

Rosenberger, A.L., Kinzey, W.G., 1976. Functional patterns of molar occlusion in platyrrhine primates. Am. J. Phys. Anthrop. 45, 261–298.

Ross, C., Hylander, W.L., 1996. In vivo and in vitro bone strain in owl monkey circumorbital region and the function of the postorbital septum. Am. J. Phys. Anthrop. 101, 183–215.

Ross, C.F., 1994. The craniofacial evidence for anthropoid and tarsier relationships. In: Fleagle, J.G., Kay, R.F. (Eds.), Anthropoid Origins. Plenum Press, New York, pp. 469–547.

Rubin, C.T., Gross, T.S., Donahue, H.J., Guilak, F., 1994. Physical and environmental influences on bone formation. In: Brighton, C., Friedlander, G., Lane, J. (Eds.), Bone

Formation and Repair. American Academy of Orthopaedic Surgeons, Rosemont, IL, pp. 61–78.

Rubin, C.T., Lanyon, L.E., 1984. Dynamic strain similarity in vertebrates: an alternative to allometric limb bone scaling. J. theoret. Biol. 107, 321–327.

Runestad, J.A., 1994. Humeral and femoral diaphyseal cross-sectional geometry and articular dimensions in Prosimii and Platyrrhini (Primates) with applications for reconstruction of body mass and locomotor behavior in Adapidae (Primates; Eocene). Ph.D. Dissertation, Johns Hopkins University.

Runestad, J.A., 1997. Postcranial adaptations for climbing in Loridae (Primates). J. Zool. 242, 261–290.

Scapino, R., 1981. Morphological investigation into functions of the jaw symphysis in carnivorans. J. Morphol. 167, 339–375.

Schmitt, D., 1996. Humeral head shape as an indicator of locomotor behavior in extant strepsirhines and Eocene adapids. Folia primatol. 67, 137–151.

Schmitt, D., 2003. The relationship between forelimb anatomy and mediolateral forces in primate quadrupeds: implications for interpretation of locomotor behavior in extinct primates. J. Hum. Evol. 44, 49–60.

Schon-Ybarra, M.A., 1998. Arboreal quadrupedalism and forelimb articular anatomy of red howlers. Int. J. Primatol. 19, 599–613.

Shigehara, N., Takai, M., in press. Facial fragments of Amphipithecus. In: Ross, C., Kay, R.F. (Eds), Anthropoid Origins: New Visions. Kluwer/Plenum, New York.

Shigehara, N., Takai, M., Kay, R.F., Aung, A.K., Soe, A.N., Tsubamoto, T., Thein, T., 2002. The upper dentition and face of *Pondaungia cotteri* from central Myanmar. J. Hum. Evol. 42, 143–166.

Simons, E.L., Rasmussen, D.T., 1989. Cranial anatomy of *Aegyptopithecus* and *Tarsius* and the question of the tarsier-anthropoidean clade. Am. J. Phys. Anthrop. 79, 1–23.

Skerry, T.M., Lanyon, L.E., 1995. Interruption of disuse by short duration walking exercise does not prevent bone loss in the sheep calcaneus. Bone 16, 269–274.

Smith, A.G., Smith, D.G., Funnell, B.M., 1994. Atlas of Mesozoic and Cenozoic Coastlines. Cambridge University Press, Cambridge.

Stephan, H., Frahm, H.D., Baron, G., 1984. Comparison of brain structure volumes in primates. VI: non-cortical visual structures. J. Hirnforsch. 25, 385–403.

Strait, S.G., 1991. Dietary reconstruction in small-bodied fossil primates. Ph.D. Dissertation, State University of New York, Stony Brook.

Szalay, F.S., Dagosto, M., 1980. Locomotor adaptations as reflected on the humerus of Paleogene Primates. Folia primatol. 34, 1–45.

Takai, M., Shigahara, N., Egi, N., Tsubamoto, T., 2003. Endocranial cast and morphology of the olfactory bulb of *Amphipithecus mogaungensis* (latest middle Eocene of Myanmar). Primates 44, 137–144.

Takai, M., Shigehara, N., in press. New specimens of the Pondaung primates (latest middle Eocene, central Myanmar). In: Ross, C., Kay, R.F. (Eds), Anthropoid Origins: New Visions, Kluwer/Plenum, New York.

Takai, M., Shigehara, N., Aung, A.K., Soe, A.N., Tun, S.T., Tsubamoto, T., Thein, T., 2001. A new anthropoid from the latest middle Eocene of Pondaung, central Myanmar. J. Hum. Evol. 40, 393–409.

Theweissen, J.G.M., Williams, E.M., Hussain, S.T., 2001. Eocene mammals from northern Indo-Pakistan. J. Vert. Paleontol. 21, 347–366.

Tilden, C.D., 1990. A study of locomotor behavior in red-bellied lemurs (*Eulemur rubriventer*). Am. J. Primatol. 22, 87–100.

Tsubamoto, T., Takai, M., Shigehara, N., Egi, N., Aung, A.K., Maung, M., Danhara, T., Suzuki, H., 2002. Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. J. Hum. Evol. 42, 361–369.

Wahlen, R.T., Carter, D.R., Steel, C.R., 1988. Influence of physical activity on the regulation of bone density. J. Biomech. 221, 825–837.

Walker, A., 1974. Locomotor adaptations in past and present prosimian primates. In: Jenkins, F. (Ed.), Primate Locomotion. Academic Press, New York, pp. 349–381.

Williams, B.A., Covert, H.H., 1994. New early Eocene anaptomorphine primate (Omomyidae) from the Washakie Basin, Wyoming, with comments on the phylogeny and paleobiology of anaptomorphines. Am. J. Phys. Anthrop. 93, 323–340.

Zeimer, L.K., 1978. Functional morphology of the forelimb joints in the wooly monkey *Lagothrix lagothricha*. Contrib. primatol. 14, 1–130.