

# Primate postcrania from the late middle Eocene of Myanmar

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Fossil primates have been known from the late middle to late Eocene Pondaung Formation of Myanmar since the description of *Pondaungia cotteri* in 1927. Three additional primate taxa, *Amphipithecus mogaungensis*, *Bahinia pondaungensis* and *Myanmarpithecus yarshensis*, were subsequently described. These primates are represented mostly by fragmentary dental and cranial remains. Here we describe the first primate postcrania from Myanmar, including a complete left humerus, a fragmentary right humerus, parts of left and right ulnae, and the distal half of a left calcaneum, all representing one individual. We assign this specimen to a large species of *Pondaungia* based on body size and the known geographic distribution and diversity of Myanmar primates. Body weight estimates of *Pondaungia* range from 4,000 to 9,000 g, based on humeral length, humeral midshaft diameter, and tooth area by using extant primate regressions. The humerus and ulna indicate that *Pondaungia* was capable of a wide variety of forelimb movements, with great mobility at the shoulder joint. Morphology of the distal calcaneus indicates that the hind feet were mobile at the transverse tarsal joint. Postcrania of *Pondaungia* present a mosaic of features, some shared in common with notharctine and adapine adapiforms, some shared with extant lorises and cebids, some shared with fossil anthropoids, and some unique. Overall, *Pondaungia* humeral and calcaneal morphology is most consistent with that of other known adapiforms. It does not support the inclusion of *Pondaungia* in Anthropoidea.

The first fossil primate described from Myanmar was *Pondaungia cotteri* Pilgrim in 1927 (1) from a locality near Pangan (Pankan) village in the Pondaung Formation of central Myanmar (formerly Burma). Ten years later Colbert (2) described *Amphipithecus mogaungensis* from near Mogaung village in the Pondaung Formation. No other primates were reported from the Pondaung Formation over the next 42 years until four new specimens were discovered at Mogaung in 1978 (3–5). Several new specimens of primates have been reported subsequently from the two earlier areas along with specimens from new localities near Bahin, in the Pondaung Formation (5–9). Mogaung localities are middle Eocene (late Lutetian to early Bartonian) while localities near Pangan and Bahin are late middle (late Bartonian) to late (Priabonian) Eocene (10). A Bartonian age for localities in the Bahin area is supported by a fission-track date of  $37.2 \pm 1.3$  mega-annum (Ma) on zircon crystals from a tuffaceous bed that outcrops at several localities (35).

Primates known from Myanmar include at least four taxa, the original two species plus *Bahinia pondaungensis* (7) and *Myanmarpithecus yarshensis* (36). An additional species of *Pondaungia*, *P. minuta* [holotype NMMP (National Museum of Myanmar Primate) 4] was proposed by Jaeger *et al.* (6), and another species of *Amphipithecus*, “*A. bahinensis*” (NMMP 7) was informally cited by Thein (8). Jaeger *et al.* (6) questioned the distinctiveness of *A. bahinensis*, instead regarding it as *A. mogaungensis*, while Takai *et al.* (5) have questioned the validity of *P. minuta*, a species based on a heavily worn and eroded specimen.

New discoveries of primate remains from the Pondaung Formation are the result of a Myanmar joint government-university initiative begun in 1997 by the Office of Strategic Studies, Ministry of Defense and the University of Taunggyi, Dagon University, and Hlaing College. In April 1997 this team discovered new fossil localities in the Bahin area (Fig. 1) that led to the recovery of the first complete jaw of *Amphipithecus mogaungensis* now designated NMMP 7. At this point, an invitation was made to one of us (R.L.C.) to mount a joint Myanmar-American field project to the Bahin area. On December 26, 1997 members of this international team discovered the first primate postcrania in the Pondaung Formation at a locality less than 2 km from Yarshe kyitchang where NMMP 7 was found (Fig. 1).

## *Pondaungia* Postcrania

All known primate specimens from the Pondaung Formation are dental and cranial remains. Field collecting at a locality about 4 km NW of the village of Bahin (Fig. 1) resulted in the discovery of some associated postcranial elements (NMMP 20) of a relatively large-bodied primate (11). These remains had eroded from a dark red-brown mudstone on a small hillock undistorted by local dipping. The local name for this locality is Sabapondaung kyitchang; it also has been cataloged as Pk1 (see figure 5 in ref. 12). We have assigned these postcrania to *Pondaungia* as it is the largest of the four primate genera now known from the Bahin area (Fig. 2). *Pondaungia* is also the most common primate in the Pondaung Formation, representing 50% of the 20 primate specimens recovered to date.

NMMP 20 includes a nearly complete left humerus, missing only fragments of the supinator crest, a right humerus with a complete proximal end, a portion of the shaft, and a broken distal end, a right proximal ulna preserving the distal part of the trochlea and the radial articular surface, a left proximal ulna preserving the olecranon process and proximal trochlea, the distal half of a left calcaneum, two other long bone shaft fragments, and a fragmentary vertebral centrum (Figs. 3–5).

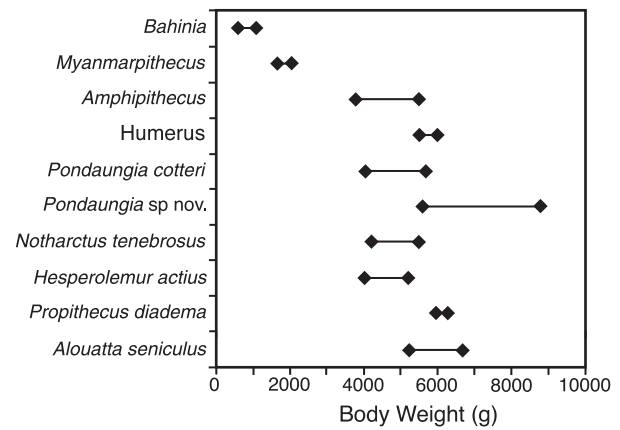
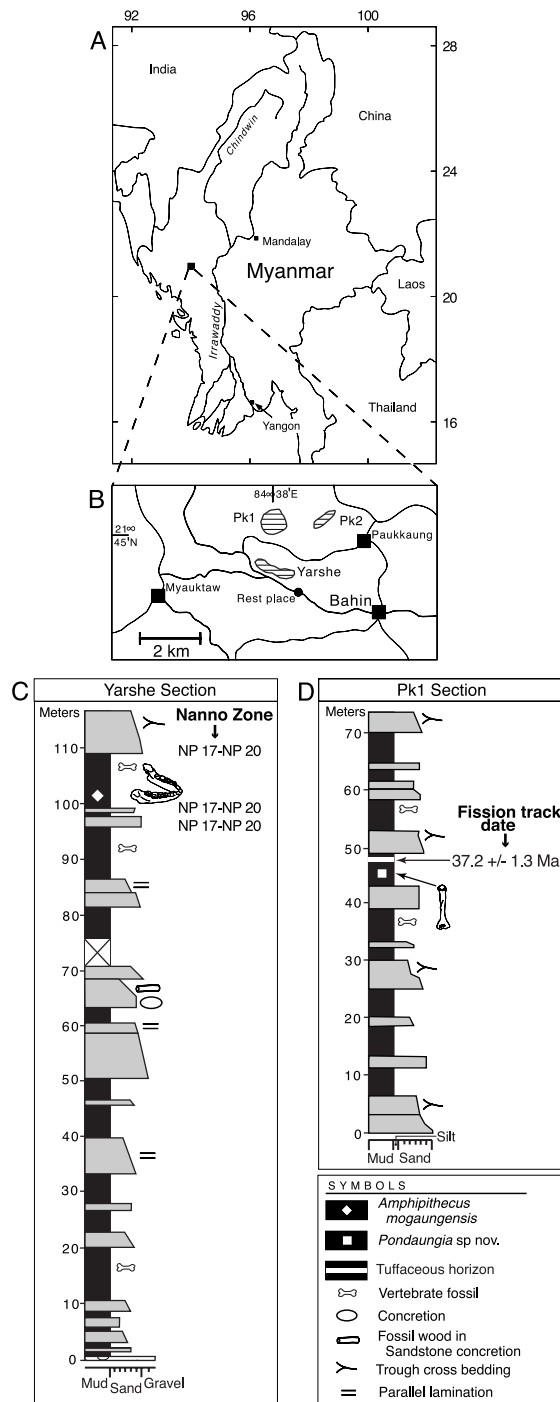
The humerus of *Pondaungia* (Fig. 3 C–E) is 95.6 mm in length (see Tables 1 and 2 for humeral and calcaneal measurements), comparable to humeral length in extant ring-tail lemurs (*Lemur catta*). Based on humeral length/midshaft diameter to body weight relationships (13, 14), we estimate the body weight of *Pondaungia* to have been between 5 and 6 kg. This compares favorably with an estimated body weight of 4 to 9 kg for all specimens of *Pondaungia* by using tooth size as a proxy for body weight (15).

The humeral head is rounded and extends proximally well beyond the greater and lesser tuberosities. The head is oriented proximoposteriorly (Fig. 3D) and the bicipital groove is very

Abbreviations: NMMP, National Museum of Myanmar Primate; UM, University of Michigan.

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**Fig. 2.** Distribution of estimated body weights of Myanmar primates compared with two notharctines, one lemuriform and one platyrrhine. Body weight estimates of fossil taxa are based on tooth size for all taxa except *Pondaungia* postcrania, which is based on humeral length and humeral midshaft diameter (13, 14).

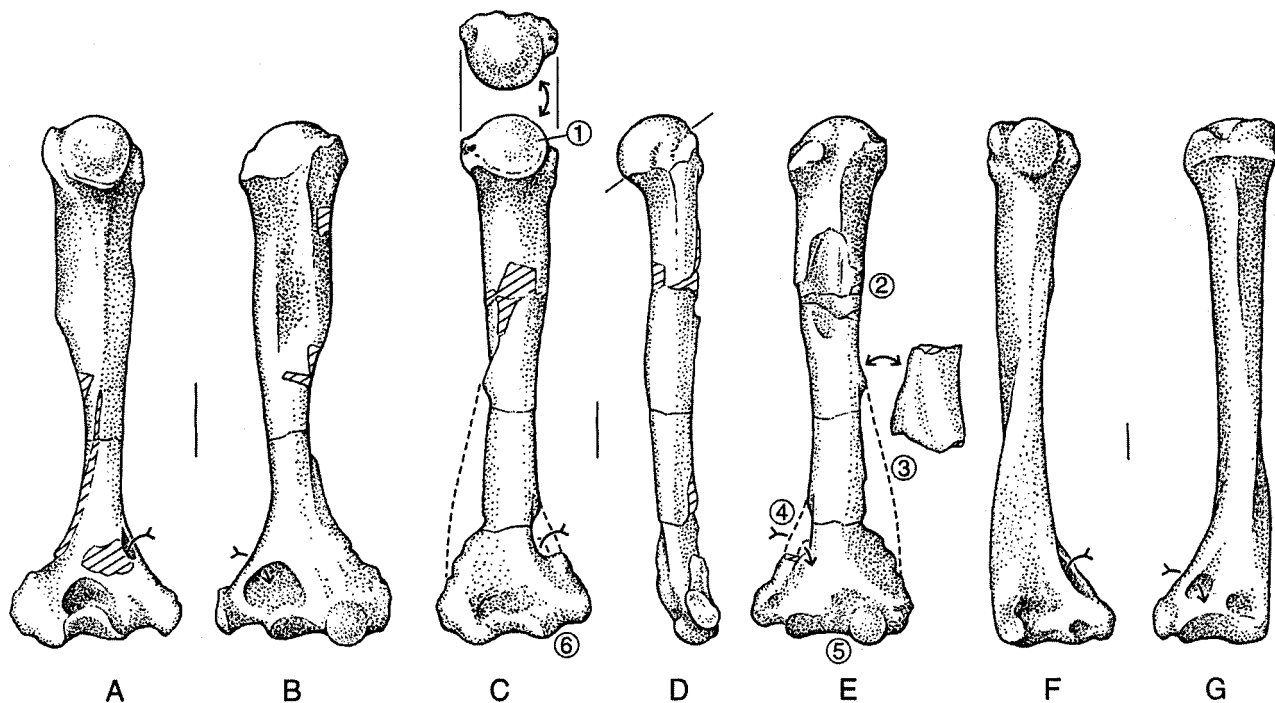
shallow and relatively broad. The deltopectoral crest is not well developed and the *teres* tubercle is only slightly better developed. Distally, the humerus of *Pondaungia* has a round capitulum that is separated from the trochlea by a well developed gutter (16). An entepicondylar foramen is present and the medial epicondyle is extended medially and lacks a distinct dorsoepitrochlear pit (17). The lateral epicondyle is laterally extended and the capitular tail is prominent. The olecranon fossa is relatively shallow. A large and well developed supinator crest begins at the lateral condyle and extends proximally beyond the midshaft.

The proximal ulna of *Pondaungia* (Fig. 4) has a moderately long olecranon process. The trochlea is relatively shallow and is angled mediolaterally. The radial articular surface is proximodistally elongate and positioned on the anterolateral surface of the ulna. The proximal shaft of the ulna just distal to the trochlea is anteroposteriorly deep and mediolaterally narrow and lacks distinct grooves for muscle attachment.

The calcaneal fragment of *Pondaungia* (Figs. 4B and 5) preserves the distal half. The peroneal tuberosity is very small and is located proximally just plantar to the proximal calcaneal facet. The proximal calcaneal facet is relatively broad and angled plantomedially. The distal calcaneal facet (sustentacular facet) is mediolaterally narrow and extends nearly to the distal margin of the calcaneum. The calcaneocuboid articular facet is oriented dorsomedially to plantolaterally with a very deep cuboid pivot that opens plantomedially. The pit for the cuboid pivot notches the calcaneocuboid facet medially. There is a relatively large anterior plantar tubercle.

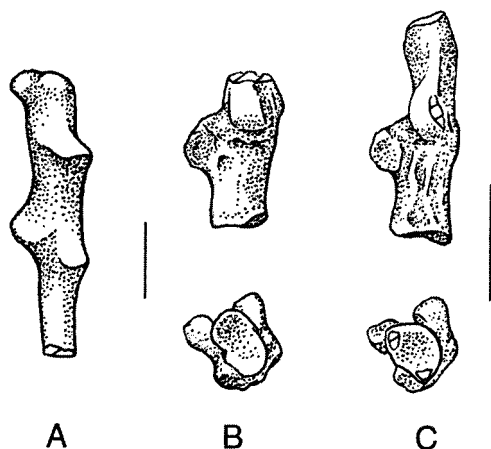
### Comparisons

Comparisons of *Pondaungia* postcranial elements with those of selected extant and fossil primates reveals several similarities but some differences as well. In general, the proximal part of the humerus is similar to that of slow lorises (*Nycticebus coucang*) and some cebid platyrrhines (*Cebus apella*). The shape of the humeral head is rounded and broad, resembling extant *Cebus* but unlike *Nycticebus*, where the head is tapered proximally and distally. The proximal extension of the head is similar to that in extant *Nycticebus* (16) and North American middle Eocene notharctines (*Notharctus* and *Smilodectes*). The head extends farther proximally than in *Cebus* and differs from extant lemurs and Egyptian Oligocene *Aegyptopithecus* where the head and greater tuberosity extend nearly equidistant proximally (Fig. 3A, B, F, and G). The head angles proximally more so than in *Nycticebus*, *Smilodectes*, or *Aegyptopithecus*, about as in extant

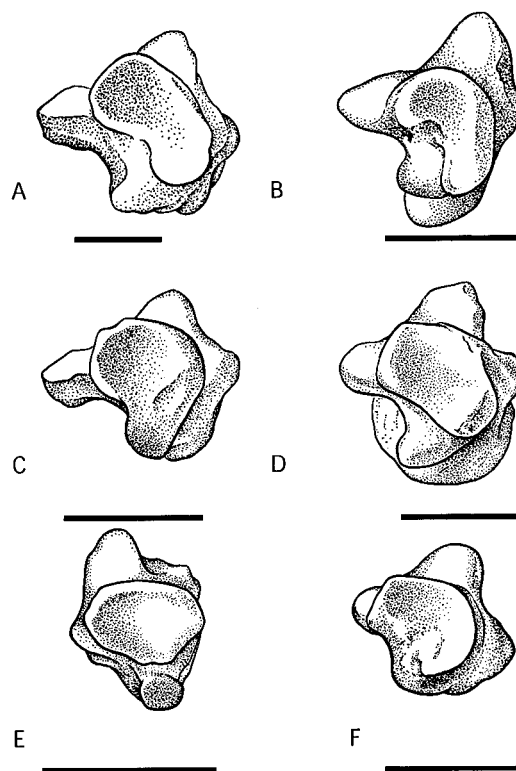


**Fig. 3.** Right humerus (reversed) of *Smilodectes mcgrewi* [University of Michigan (UM) 100603] in posterior (A) and anterior (B) views; left humerus of *Pondaungia* (NMMP 20a) in posterior and proximal (C), medial (D), and anterior (E) views, portion of right humerus (NMMP 20b) in anterior view shown in E to indicate extent of supinator crest; left humerus of *Aegyptopithecus zeuxis* (Duke Primate Center 1275) in posterior (F) and anterior (G) views. Circled numbers denote the following features of *Pondaungia*: 1) rounded, proximally extended head; 2) very reduced deltopectoral crest; 3) extensive supinator crest; 4) presence of entepicondylar foramen (arrows on all figures indicate foramen); 5) rounded capitulum separated from trochlea by gutter; 6) absence of dorsoepitrochlear pit [note presence of deep pit in *Aegyptopithecus* (F)]. Line in D indicates proximoposterior orientation of humeral head in *Pondaungia*. Scales represent 1 cm.

*Cebus*, but not as much as in extant brachiators such as gibbons (*Hylobates*). The broad and shallow bicapital groove is similar to the condition found in lorises, lemurs, and Eocene notharctines but unlike *Cebus* and *Aegyptopithecus* where the groove is somewhat deeper. Like lorises and cebids that have reduced proximal humeral muscle attachment areas (16), the deltopectoral crest is very weak and the *teres* tuberosity is small. Deltopectoral crests are much stronger in extant lemurs, fossil notharctines, and some fossil anthropoids like *Proteopithecus* (18), *Aegyptopithecus* (19), and parapithecids (20).



**Fig. 4.** (A) Composite right proximal ulna (olecranon process reconstructed from left side) of *Pondaungia* (NMMP 20c, 20d) in anterior view. (B) Left distal calcaneum of *Pondaungia* (NMMP 20e) in dorsal (Upper) and distal (Lower) views. (C) Left calcaneum of *Cantius nunienus* (UM 102167) in dorsal (Upper) and distal (Lower) views. Scales represent 1 cm.



**Fig. 5.** Calcaneocuboid facet of (A) *Pondaungia* (NMMP 20e), (B) *Nycticebus coucang* (University of Michigan Museum of Zoology, UMMZ 113354), (C) notharctine adapiform *Cantius* (UM 80737), (D) adapine adapiform *A. parisiensis* (unnumbered cast in UM collection), (E) omomyid *Omomys* (UM 98604), and (F) *Saguinus* sp. (unnumbered specimen in UM collection). All specimens are drawn to the same size. Scales represent 1 cm.

**Table 1. Distal humeral indices after Szalay and Dagosto (22)**

Locomotor category	Taxon	TAI	THWI	TCI	RTWI	MEI	AI
Arboreal quadruped	<i>Varecia variegata</i>	44.5	86.9	88.2	80.4	18.7	82.1
	<i>Lemur catta</i>	47.8	101.6	103.4	81.3	12.8	79.1
	<i>Cheirogaleus major</i>	43.9	80.3	85.6	79.2	22.3	71.1
	<i>Hapalemur griseus</i>	41.0	81.3	66.7	70.8	25.4	70.0
	Mean	44.3	87.5	86.0	77.9	19.8	75.6
Vertical clinging and leaping	<i>Indri indri</i>	34.7	111.8	64.2	53.0	12.5	80.9
	<i>Propithecus verreauxi</i>	31.1	136.3	46.6	45.0	19.5	74.4
	<i>Avahi laniger</i>	36.5	112.8	51.4	57.4	21.6	72.1
	<i>Galago senegalensis</i>	43.0	107.1	75.9	72.4	28.8	71.1
	<i>Tarsius</i> sp.	40.0	130.6	66.5	66.7	25.7	60.8
	Mean	37.1	119.7	60.9	58.9	21.6	71.9
Slow climbing	<i>Perodicticus potto</i>	33.6	124.3	45.7	50.7	29.3	72.6
	<i>Nycticebus coucang</i>	38.5	131.3	57.8	62.5	23.6	74.3
	<i>Loris tardigradus</i>	32.8	170.5	43.7	48.9	16.6	76.6
	Mean	35.0	142.0	49.0	54.0	23.2	74.5
Fossil taxa	<i>Pondaungia</i>	47.3	95.0	110.1	89.9	25.0	62.4
	<i>Smilodectes gracilis</i>	35.5	106.1	55.8	55.1	27.5	68.5
	<i>Adapis parisiensis</i>	39.9	75.9	65.5	66.1	22.6	69.5
	<i>Shoshonius cooperi</i>	48.8	76.2	—	150.0	—	70.5
	<i>Omomys carteri</i>	40.9	100.0	—	69.2	—	68.8
	<i>Aegyptopithecus zeuxis</i>	47.9	82.9	108.9	92.1	27.1	70.6

TAI, trochlear articular index; RTWI, relative trochlear width index; THWI, trochlear height-width index; MEI, medial epicondylar index; TCI, trochlear-capitular index; AI, articular index.

Distally, *Pondaungia* humeri share less in common with lorises and cebids and are instead more similar to middle Eocene notharctine adapiforms. The rounded capitulum and the distinct gutter separating the capitulum and trochlea are found in notharctines. Platyrrhines such as *Cebus* and *Saguinus* have

distinct trochlear gutters but their capitula are less rounded. The trochlea is deep medially and tapers laterally as in notharctines and *Nycticebus*, but differs from the more cylindrical trochlea found in omomyids and extant anthropoids. The large, rounded, distally extended capitulum of *Pondaungia* is shared with arboreal quadrupedal leapers such as lemurs and cheirogaleids (21). In contrast to *Pondaungia*, lorises have a rather flattened capitulum that is continuous with the trochlea (16). Fossil anthropoids like *Catopithecus*, *Proteopithecus*, *Propithecus*, and *Aegyptopithecus* have weakly rounded capitula that are continuous with the trochleae (18–19). Table 1 summarizes distal humeral measurements and indices (22) for a number of extant and fossil taxa (23, 24). Most of these indices group *Pondaungia* with extant arboreal quadrupeds.

**Table 2. Calcaneal measurements and indices after Gebo et al. (29)**

Taxon	C2	C3	C4	C5	C6	C8	C4/C3	C6/C5
Calcaneal measurements								
<i>Pondaungia</i>	13.3	9.5	5.1	6.8	9.2	11.9		
<i>Cantius ralstoni</i>	6.6	5.6	2.2	4.6	3.3	7.4		
<i>Cantius mckennai</i>	7.8	5.5	2.9	5.2	4.0	8.2		
<i>Cantius trigonodus</i>	8.9	6.9	3.2	4.9	3.7	8.8		
<i>Cantius abditus</i>	10.2	7.6	3.7	6.5	4.8	9.6		
<i>Notharctus venticolis</i>	12.0	8.7	4.1	7.8	6.0	10.4		
<i>Notharctus tenebrosus</i>	11.6	7.1	4.1	7.6	6.3	9.1		
<i>Smilodectes gracilis</i>	10.7	8.0	3.9	5.5	4.7	10.5		
<i>A. parisiensis</i>	7.1	5.5	3.5	5.0	5.0	4.9		
<i>A. magnus</i>	12.4	10.6	5.9	9.5	8.9	10.8		
<i>Omomys carteri</i>	5.1	3.1	2.2	3.5	2.5	7.6		
Calcaneal indices								
<i>Pondaungia</i>							53.7	135.3
<i>C. ralstoni</i>							39.3	71.7
<i>C. mckennai</i>							52.7	76.9
<i>C. trigonodus</i>							46.3	75.5
<i>C. abditus</i>							48.7	73.8
<i>N. venticolis</i>							47.1	76.9
<i>N. tenebrosus</i>							57.7	82.9
<i>S. gracilis</i>							48.8	85.5
<i>A. parisiensis</i>							63.6	100.0
<i>A. magnus</i>							55.7	89.5
<i>O. carteri</i>							71.0	71.4

Measurements of comparative primate sample from ref. 29. C2, calcaneal width at sustentaculum; C3, length of posterior calcaneal facet; C4, width of posterior calcaneal facet; C5, width of calcaneo-cuboid facet; C6, height of calcaneo-cuboid facet; C8, length of distal calcaneum.

The presence of an entepicondylar foramen is a primitive feature shared with a number of fossil and extant primates. *Pondaungia* has a relatively shallow olecranon fossa, lacks a dorsoepitrochlear pit, and possesses a strong, well developed supinator crest, features shared with notharctines and extant lemurs. Lorises have a relatively deep olecranon fossa and a relatively weak supinator crest. Extant platyrrhines like *Cebus* and fossil anthropoids such as *Aegyptopithecus* and *Propithecus* have relatively deep olecranon fossae and deep and distinct dorsoepitrochlear pits. *Cebus* has a reduced supinator crest whereas *Aegyptopithecus* and *Propithecus* have relatively strong and expanded supinator crests. Omomyids have a moderate dorsoepitrochlear pit (24) as does a distal humerus attributed to the Asian possible anthropoid *Eosimias* (25), but some platyrrhines (e.g., *Saguinus*) lack a dorsoepitrochlear pit. *Catopithecus* resembles *Pondaungia* in sharing a relatively shallow olecranon fossa but is more like other Fayum anthropoids in having a deep dorsoepitrochlear pit (18). Additionally, all of the Fayum anthropoids and most platyrrhines have strong, posteriorly angled medial epicondyles in contrast to *Pondaungia* where the medial epicondyle is strong but not posteriorly angled, being more similar to notharctines and extant lemurs in this characteristic.

*Pondaungia* has an ulnar olecranon process (Fig. 4A) comparable in relative length to that of extant lemurs and notharctine

**Table 3. Morphological comparisons of *Pondaungia* with some extant and fossil primates**

<i>Pondaungia</i> character	Notharctines	Fayum anthropoids	Extant lorises	Extant cebids	Adapines	Omomyidae
Round, broad humeral head	X			X		X
Humeral head proximally extended	X		X			
Humeral head proximal angle				X		
Bicipital groove shallow	X		X			X
Weak deltopectoral crest			X	X		
Rounded capitulum	X					X
Distinct trochlear gutter	X			X		X
Trochlear shape	X		X			
Dorsoepitrochlear pit weak/absent	X		X			
Strong supinator crest	X	X				X
Medial humeral condyle straight	X		X			X
Calcaneal distal tuber elongate	X					X
Proximal calcaneal facet broad					X	
Peroneal tubercle proximal					X	
Robust anterior plantar tubercle					X	
Calcaneocuboid facet dorsoplantar			X		X	

X indicates shared character state.

adapiforms. It is relatively much longer than in lorises and somewhat shorter than in *Aegyptopithecus* (26). The trochlear notch is relatively shallow as in lemurs, notharctines, and *Aegyptopithecus* and unlike *Nycticebus* where it is relatively deeper. The distal trochlea is angled medially as in lemurs and notharctines and unlike lorises and *Aegyptopithecus*, which have the distal trochlea aligned nearer to the long axis of the ulnar shaft. The radial articular facet is placed on the anterolateral aspect of the ulnar shaft and is flattened as in notharctines. This differs from lemurs, lorises, and *Aegyptopithecus* where the radial notch is more lateral and more anteroposteriorly oriented. *Pondaungia* has a relatively anteroposteriorly deep proximal ulnar shaft as in lemurs and *Aegyptopithecus* and unlike lorises and notharctines where the proximal shaft is relatively less expanded.

Among extant taxa, the distal calcaneum of *Pondaungia* most closely resembles lemurs, whereas among fossil taxa it is most closely comparable with adapine adapiforms (*Adapis parisiensis* and *Adapis magnus*) (Fig. 5). The distal tubercle is relatively longer in *Pondaungia* compared with *A. parisiensis* but is about as long as in *A. magnus*. The proximal calcaneal facet is relatively broad as in *Adapis* and unlike North American notharctines where it is relatively narrower. The peroneal tubercle is somewhat more robust in *Pondaungia* compared with *Adapis* but is positioned more proximally as in adapines compared with the more distal position in notharctines. The anterior plantar tubercle is relatively robust as in extant lemurs and fossil adapines, relatively larger than in notharctines.

The *Pondaungia* calcaneocuboid facet is different from that in lemurs and notharctines but is similar to that of *Adapis*, especially *A. parisiensis* (Table 2). The facet is oriented nearly dorsoplantarly, is relatively narrow mediolaterally, and has a very deep pit that notches the facet medially (Fig. 5). The orientation of the calcaneocuboid facet of *Pondaungia* is similar to that seen in *Nycticebus* and *A. parisiensis*, but the depth of the joint surface and the depth of the pit are much greater in *Pondaungia*.

The proximally extended and rounded humeral head of *Pondaungia* allows for great range of motion at the shoulder joint including above shoulder extension and adduction of the humerus (27, 28). The well developed supinator crest and the rounded capitulum indicate that the forelimb was mobile at the elbow and probably at the wrist as well. Supination is an important movement for suspension and the well developed supinator crest in *Pondaungia* indicates that supinator musculature was well developed (21). The shallow olecranon fossa and the moderately developed olecranon process of the ulna suggest

that the arm may not have been capable of complete extension. This combination of features indicates that the forearm and arm were capable of a wide range of movements, suggesting that *Pondaungia* used a variety of different supports including horizontal and vertical branches and that it may have been capable of both above and below branch locomotion. The deep, rounded, and medially oriented calcaneocuboid joint indicates that great range of motion was available at the transverse tarsal joint.

The overall morphological pattern of *Adapis* postcrania led Dagosto (23) to interpret these fossil primates as slow-climbing arboreal quadrupeds, similar to living lorises. Although *Pondaungia* is similar to *Adapis* and *Nycticebus* in some morphological features, especially of the calcaneum, interpretations of other postcranial elements of *Pondaungia* do not provide evidence to support this interpretation. Other morphological features, especially that of the distal humerus, suggest that *Pondaungia* was more like fossil notharctines, primates interpreted to have been arboreal, leaping quadrupeds like extant lemurs (16, 29).

#### Anthropoid Status of *Pondaungia*

Phylogenetic implications of *Pondaungia* postcrania are difficult to assess. Table 3 summarizes some humeral and calcaneal comparisons of *Pondaungia* with some extant and extinct primate taxa. Humeral morphology is a mosaic of lorine, cebid, omomyid, and notharctine character states with only the proximal humerus showing any unequivocally derived conditions (proximally rotated head, reduced deltopectoral crest). It is clear that *Pondaungia* is not closely allied with cebids or lorines. *Pondaungia* has previously been aligned with notharctines on the basis of dental features (30). At present it is difficult to determine whether any of the notharctine-like features of the *Pondaungia* humerus are apomorphic within primates, but among the various competing hypotheses of the phylogenetic position of *Pondaungia*, the evidence from this element is more consistent with *Pondaungia* being a closer relative of notharctines than being a stem anthropoid. Recent claims of anthropoid status for *Pondaungia* (9) are not supported by the known postcranial evidence. Humeral and calcaneal morphology is entirely inconsistent with the hypothesis that *Pondaungia* is a catarrhine (6, 31, 32).

The plantarly rotated, medially oriented calcaneocuboid pivot that is notched medially apparently is unique to *Pondaungia*, although *A. parisiensis* and extant lorises show similar patterns. The only postcranial character state that *Pondaungia* shares in

common with Fayum anthropoids is a strong supinator crest, but this is also shared with notharctines.

Recent phylogenetic analyses of dental features have aligned *Pondaungia* and *Amphipithecus* with propliopithecine catarrhines (6, 31), but it is now clear that the known postcrania of *Pondaungia* are entirely at odds with this hypothesis. This evidence indicates to us that, unless the lineage leading to *Pondaungia* underwent a number of highly unlikely morphological reversals, this genus cannot be nested within the clade containing Eocene-Oligocene anthropoids from the Fayum. This, in turn, implies that the dental features aligning *Pondaungia* with propliopithecine catarrhines are functional convergences, for late Eocene Fayum taxa such as *Proteopithecus* exhibit a much more primitive dental morphotype but already exhibit typically anthropoid postcrania (18, 33) and complex anthropoid apomorphies such as postorbital closure (34). Whether the anthropoid-like dental features of *Pondaungia* are derived from a dental morphotype like that of notharctines, that of eosimiids, or that of primitive Paleogene Afro-Arabian anthropoids remains to be determined. Given the emerging cranial and postcranial fossil evidence from the late middle Eocene of Myanmar, however, it now appears that the possible notharctine, or at least adapiform, affinities of *Pondaungia* and its close relatives once again deserve serious consideration. The discov-

ery of this associated partial skeleton draws attention to the importance of further fieldwork at the various Myanmar localities with the objective of finding combined dental, cranial, and postcranial remains that may be relevant to the question of anthropoid origins.

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