

Anatomy of the bony pelvis of a relatively large-bodied strepsirrhine primate from the late middle Eocene Pondaung Formation (central Myanmar)

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Abstract

Recent survey of the fossiliferous variegated mudstones of the PK1 locality (Sabapondaung) in the late middle Eocene Pondaung Formation (central Myanmar) has led to the recovery of a partial right innominate of a relatively large-bodied primate. Given its size and provenance, this bone probably belongs to the same individual represented by the NMMP 20 primate partial skeleton described previously from the same locality. The new fossil, which preserves the region around the acetabulum and the adjacent part of the ilium, clearly exhibits strepsirrhine rather than anthropoid affinities. This addition to our knowledge of the NMMP 20 partial skeleton allows us to reassess the different locomotor interpretations that have been proposed for this specimen. Aspects of pelvic morphology suggest that the NMMP 20 partial skeleton documents a primate that probably engaged in active arboreal quadrupedalism similar to that practiced by medium-sized Malagasy lemurids rather than lorislke slow moving and climbing. Given the conflicting phylogenetic signals provided by NMMP 39 (a talus showing anthropoid affinities) and NMMP 20 (a partial skeleton bearing adapiform affinities), it appears that two higher-level taxonomic groups of relatively large-bodied primates are documented in the Pondaung Formation. The recent discovery of two taxa of sivaladapid adapiforms from the Pondaung Formation indicates that the assumption that the NMMP 20 partial skeleton belongs to an amphipithecid can no longer be sustained. Instead, this specimen apparently documents a third large-bodied sivaladapid species in the Pondaung Formation.

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Introduction

Until recently, the fossil primate fauna from the late middle Eocene Pondaung Formation of central Myanmar was limited

to members of the Amphipithecidae (*Pondaungia Pilgrim*, 1927; “*Amphipithecus*” Colbert, 1937; and *Myanmarpithecus* Takai et al., 2001) and Eosimiidae (*Bahinia* Jaeger et al., 1999), which document two major clades of stem anthropoids in Asia (e.g., Chaimanee et al., 1997, 2000; Jaeger et al., 1998; Beard, 2002, 2004; Marivaux et al., 2003, 2005; Jaeger and Marivaux, 2005; Seiffert et al., 2005; Marivaux, 2006). Amphipithecids have attracted considerable attention since their

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initial discovery in the early part of the twentieth century. Their phylogenetic position remains controversial, with various authorities advocating either anthropoid or adapiform affinities for the group. The highly fragmentary and (at times) systematically ambiguous nature of their fossil record has engendered both confusion and phylogenetic debate (Ciochon and Holroyd, 1994; Godinot, 1998; Takai et al., 2001, 2003; Ciochon and Gunnell, 2002, 2004; Gunnell et al., 2002; Shigehara et al., 2002; Shigehara and Takai, 2004; Takai and Shigehara, 2004; Kay et al., 2004a; Seiffert et al., 2004; Beard et al., 2005). Part of this uncertainty stems from the fact that dental, cranial, and postcranial elements that have been allocated to amphipithecids resemble those of anthropoids in some respects (Simons, 1971; Maw et al., 1979; Ciochon et al., 1985; Jaeger et al., 1998, 2004; Chaimanee et al., 2000; Beard, 2002; Marivaux et al., 2003), while in other details they resemble those of certain adapiforms and omomyiforms (Ciochon et al., 2001; Ciochon and Gunnell, 2002, 2004; Gunnell et al., 2002; Kay et al., 2004b; Shigehara et al., 2002; Takai et al., 2003). However, recent anatomical analyses, along with significant improvements in the fossil record, highlight the problems associated with allocating some of these isolated elements to the Amphipithecidae (e.g., Beard et al., 2005). For example, although both specimens were originally recovered from the Pondaung Formation and referred to Amphipithecidae, it is now difficult to reconcile a very anthropoidlike talus (NMMP 39; Marivaux et al., 2003) with an equally adapiformlike partial skeleton (NMMP 20; Ciochon et al., 2001). A plausible alternative to such a morphological chimera is that the Pondaung primate community was more diverse than earlier workers believed, and that large-bodied primate postcranial elements from this rock unit actually document two higher-level primate taxa.

In November and December 2005, we intensively surveyed the fossiliferous variegated clays at Sabapondaung “Kyitchaung” (also known as PK1 or Paukkaung Kyitchaung 1; see Fig. 1), which previously yielded the NMMP 20 partial skeleton (a complete left humerus, fragments of a right humerus and both left and right ulnae, and the distal half of a left calcaneus) described by Ciochon et al. (2001). Although the fossiliferous outcrops at Sabapondaung are extensive, the small area that yielded the NMMP 20 partial skeleton is quite restricted (Ciochon et al., 2001). Our survey of the dark red-brown mudstone at the same tiny hill (Fig. 1) that yielded NMMP 20 led to the recovery of the partial right innominate of a large-bodied primate. The size of the new element indicates that it could have come from the same individual as the NMMP 20 remains. Moreover, it bears the same distinctive surface patina (gray color with small carbonate concretions) and was recovered from the same stratum at the same locality that yielded the original elements allocated to NMMP 20 (Fig. 1). As such, the new partial innominate can be referred to NMMP 20 with the same degree of confidence that is implicit in the original association of the calcaneal fragment and forelimb elements of this specimen. Although limited to the region around the acetabulum and the adjacent part of the ilium, the fragmentary innominate provides substantial new information about the pelvic anatomy and functional

morphology of this relatively large-bodied primate from the Pondaung Formation.

Description and comparisons

Several isolated but freshly broken bone fragments were recovered and rejoined to obtain the partial right innominate presented in Fig. 2. Most of the breaks in the region around the acetabulum correspond to sutures between pelvic elements (ilium, pubis, and ischium). The specimen preserves the caudal part of the ilium, extending from the cranial margin of the acetabulum to the caudal part of the iliac tuberosity (just cranial to the auricular surface of the sacroiliac joint); the dorsal part of the pubis, including the ventral rim of the acetabulum and the iliopubic eminence; and the cranialmost end of the ischium, which is very limited in length and forms the cranio-dorsal rim of the acetabulum. The cranial part of the ilium (iliac wing, just above the auricular facet), the ventral part of the pubis, and the main body of the ischium have been lost.

Acetabular region

The acetabulum, though incomplete dorsocaudally, is nearly hemispherical in shape and faces laterally. The dorsal, cranial, and ventral margins of the acetabulum are well defined and laterally salient, except for the caudoventral area, which is indented by the acetabular incisura. Inside the acetabular fossa, the lunate surface (the articular facet for the femoral head) forms a circumferential band. The nonarticular surface in the center of the acetabular fossa is surrounded by the lunate surface except at the level of the incisura. According to the measurements and ratios made by Schultz (1969) on various genera of extant primates, the width of the acetabular incisura is generally about half the diameter of the acetabulum (except in *Pan* and *Pongo*, in which the incisura is relatively much smaller). On NMMP 20, although the dorsocaudal rim of the acetabulum is lacking (corresponding to the cranial part of the ischium), the diameter of the acetabulum (measured dorso-ventrally) suggests that the incisura probably displays its maximum width. The ventral rim of the acetabulum is relatively broad and slightly thicker than the dorsal rim in NMMP 20. This feature distinguishes most strepsirrhines from most anthropoid primates (fossils and extant), which show relatively thicker dorsal rims (Schultz, 1969; Gebo et al., 1994). The thickness of the ventral rim relative to that of the dorsal rim, in addition to having potential phylogenetic implications, also conveys functional significance (Fleagle and Simons, 1979), as discussed below.

Ilium

The cranial end of the ilium is lacking due to breakage; hence, total iliac length and cranial breadth remain unknown. Despite this breakage, the caudal part of the bone is particularly well preserved, revealing a robust ilium that is characterized by a distinct delineation of its gluteal, iliac, and sacral planes (tripartite arrangement; Waterman, 1929). In these

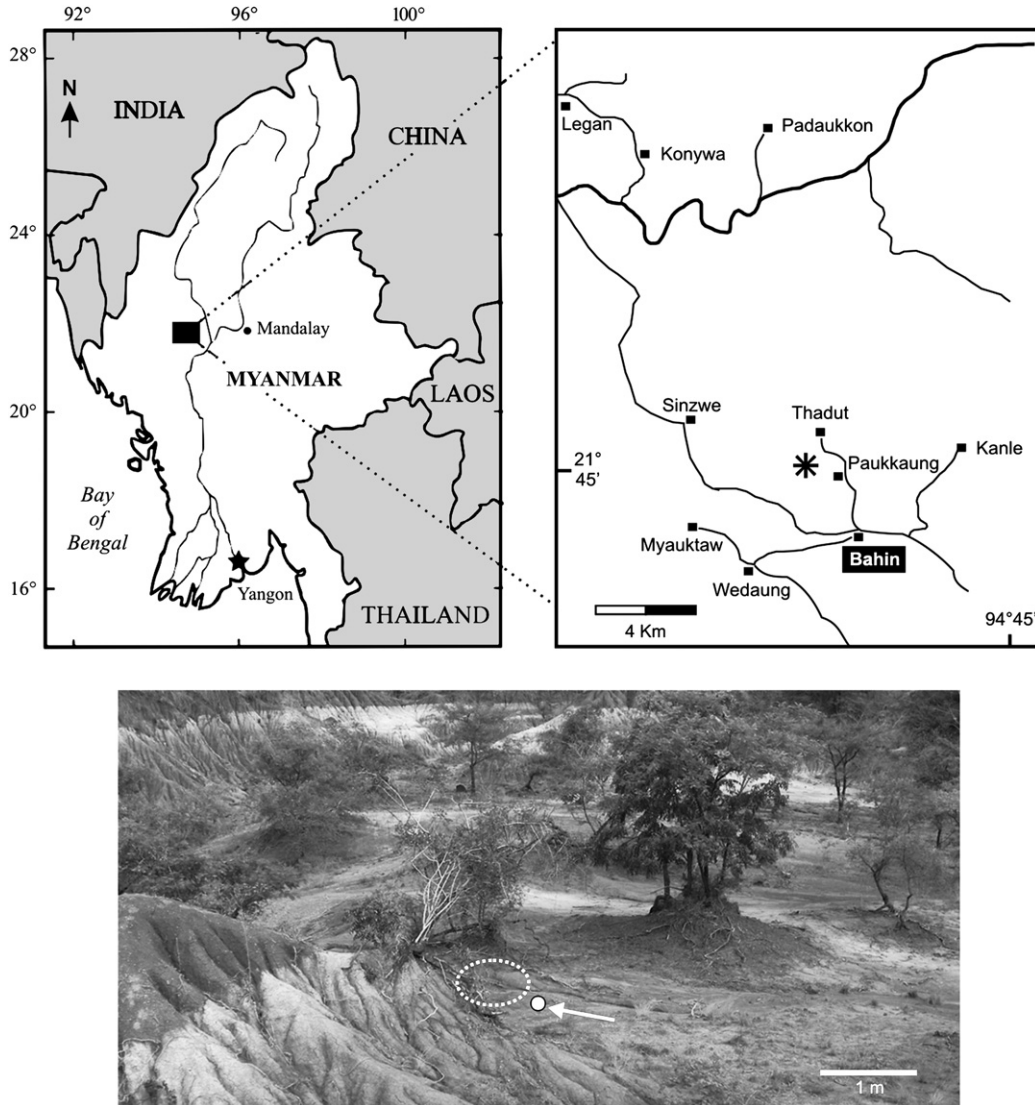


Fig. 1. Location map of the fossiliferous locality of Paukkaung Kyitchaung no.1 (PK1, Sabapondaung; denoted by an asterisk) in central Myanmar. The photograph shows a view of the small hillock from which the NMMP 20 partial skeleton was found several years ago (denoted by a white dashed circle). The white point (indicated by the arrow) located just to the right of the dashed circle indicates the place where the pelvic fragments were found.

respects, the ilium of NMMP 20 differs remarkably from the rodlike ilium of *Tarsius* and certain strepsirrhines (such as lorises and cheirogaleids; e.g., Grand and Lorenz, 1968).

In NMMP 20, the sacral plane faces medially, the iliac plane faces ventrally, and the gluteal plane faces laterally with almost no deviation from the plane of the acetabulum. Considering this latter aspect of the gluteal plane, the ilium of NMMP 20 resembles those of strepsirrhines (notably lemuriforms). In contrast, among anthropoid primates of similar body size (such as cebids), the entire ventral part of the gluteal plane is rotated with respect to the plane of the acetabulum so that it faces dorsolaterally (e.g., Waterman, 1929). The gluteal and iliac planes are separated by the margo acetabuli, which bears the femoral process (anterior inferior iliac spine) just anterior to the cranial margin of the acetabulum, and from which a slender and bladlike crest extends cranially.

In ventral view, a short gap separates the cranial edge of the acetabulum from the femoral process. The gluteal surface is

relatively wide at the level of the sacral tuber and becomes slightly wider just before the break. The dorsal and ventral (iliac blade) edges of the gluteal surface delimit a narrow and concave fossa, which broadens cranially. On the margo acetabuli, the extensive V-shaped pattern of breakage suggests that the femoral process was prominent and would have projected strongly ventrolaterally, as in some extant strepsirrhines (such as *Lemur*, *Eulemur*, *Daubentonia*, *Varecia*, *Hapalemur*, *Lepilemur*) and Paleogene adapiforms (e.g., *Notharctus*). There is a shallow but distinct depression on the ventral aspect of the femoral process.

Dorsally, the margo ischiadicus, which separates the sacral plane from the gluteal plane, is smoothly rounded and broadens cranially to form the postgluteal plane. The posterior iliac spine (sacral tuber) juts out slightly from the rest of the iliac body, defining the cranial edge of the greater sciatic notch. Ventrally, the iliac plane is particularly well delineated and distinct from the sacral plane, and both are separated by

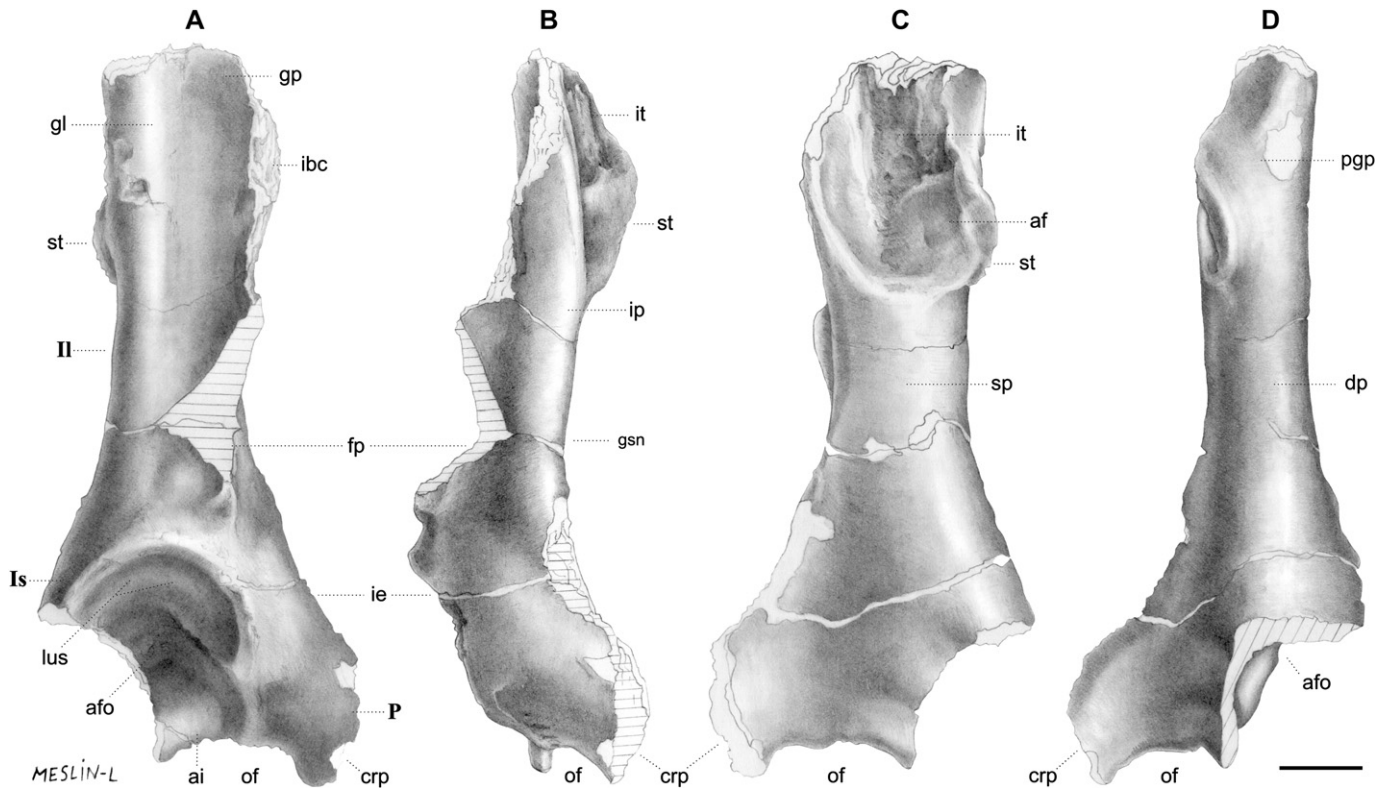


Fig. 2. NMMP 20, fragmentary right innominate bone from Sabapondaung Kyitchaung (PK1), in lateral (A), ventral (B), medial (C), and dorsal (D) views. Terminology and abbreviations: **af**, auricular facet; **afo**, acetabular fossa; **ai**, acetabular incisura; **crp**, cranial ramus of pubis; **dp**, dorsal plane; **fp**, femoral process (tubercle for the rectus femoris muscle); **gl**, gluteal line; **gp**, gluteal plane; **gsn**, greater sciatic notch; **ibr**, iliac blade-like crest; **ie**, iliopubic eminence; **II**, ilium; **ip**, iliac plane; **Is**, ischium; **it**, iliac tuberosity; **lus**, lunate surface; **of**, obturator foramen; **pggp**, postgluteal plane; **P**, pubis; **sp**, sacral plane; **st**, sacral tuber (posterior iliac spine). Scale bar = 5 mm. Original art by Laurence Meslin (copyright CNRS-Meslin).

the margo pubicus. This condition resembles that observed in several extant strepsirrhines (lemurids, indrids, and lepilemurids) and differs from that developed in many platyrrhines, in which the iliac plane is poorly delineated and confluent with the sacral plane (e.g., Fleagle and Simons, 1995).

Just before the cranial break, at the level of the medial auricular surface, the iliac plane slightly curves laterally, a condition particularly well marked in extant lemurids and fossil notharctids (e.g., Gregory, 1920). At the junction of the pubic margin, the breadth of the iliac plane is greater than that measured at the level of the auricular surface. As in extinct and extant strepsirrhines and most nonateline platyrrhines, the iliac plane of NMMP 20 becomes slightly narrower as it extends cranially away from the acetabular region. This condition differs from that observed in living catarrhines and ateline platyrrhines, in which the iliac plane increases in width cranially relative to the acetabular region (e.g., Gebo et al., 1994; Fleagle and Simons, 1995).

Functional interpretation

Materials and methods

Rollinson and Martin (1981) proposed a classification of locomotor categories (in relation to body size) among living primates (adapted from Napier and Walker, 1967; revised in

Martin, 1990: 480) that serves as a useful reference for investigating the relationships between behavior and morphology in primate locomotion (Table 1). These locomotor categories may be subdivided by considering the length (L) of limbs (intermembral index = forelimb L/hindlimb L; Mollison, 1910). Such a broad classification of primate locomotor behavior has certain limitations and intermediate cases may be expected. This classification only groups data into meaningful categories that facilitate analysis and interpretation.

In order to assess which locomotor category and subcategory (i.e., postural activities) among living primates corresponds structurally with the NMMP 20 innominate, we performed linear discriminant analyses (LDA). For the different subcategories proposed by Martin (1990; Table 1), pelvic girdles of about 40 genera of extant primates (strepsirrhines and anthropoids; Appendix 1) in the collections of the Museum National d'Histoire Naturelle in Paris (France) were measured and compared directly with NMMP 20. Measurements included those proposed by Schultz (1969), Fleagle and Simons (1979), and several others deriving from our personal observations (Appendix 1). All measurements were taken to the nearest 0.01 mm using a Stainless digital caliper.

A total of 24 measurements were obtained on the pelvis (ilium, pubis, and ischium) of living primates. Only 13 of these measurements were possible on NMMP 20. For the discriminant analyses, these 13 measurements were regarded as

Table 1

Classification of locomotor categories among living primates (adapted from Napier and Walker, 1967; Rollinson and Martin, 1981; Martin, 1990)

Major category	Size group	Subcategory (activity)	Code	Representatives
Vertical-clinging-and-leaping	Small	(Leaping in trees and hopping on the ground)	A1	<i>Galago*</i> , <i>Tarsius*</i>
	Medium	(Leaping in trees and hopping on the ground)	A2	<i>Avahi*</i> , <i>Hapalemur*</i> , <i>Indri*</i> , <i>Lepilemur*</i> , <i>Propithecus*</i>
Arboreal quadrupedalism	Small	Clawed (climbing, springing, branch running)	B	<i>Callimico</i> , <i>Callithrix</i> , <i>Cebuella*</i> , <i>Leontopithecus*</i> , <i>Saguinus*</i>
		Unclawed, agile (climbing, springing, branch running)	C	<i>Cheirogaleus*</i> , <i>Allocebus*</i> , <i>Microcebus*</i> , <i>Mirza*</i> , <i>Phaner*</i>
		Unclawed, slow-climbing type (cautious climbing, no leaping or running)	D	<i>Arctocebus</i> , <i>Loris*</i> , <i>Nycticebus*</i> , <i>Perodicticus*</i>
		Branch-running-and-walking type (climbing, springing, branch-running)	E1	<i>Daubentonia*</i> , <i>Lemur*</i> , <i>Eulemur*</i> , <i>Varecia*</i>
	Medium	Branch-sitting-and-walking type (climbing and ground-running)	E2	<i>Aotus*</i> , <i>Callicebus*</i> , <i>Cebus*</i> , <i>Chiropotes</i> , <i>Pithecia*</i> , <i>Saimiri*</i>
			F	<i>Cercocebus</i> , <i>Cercopithecus*</i> , <i>Macaca</i> , <i>Mandrillus</i>
		Old World suspensory type (arm-swinging and leaping)	G	<i>Colobus*</i> , <i>Nasalis*</i> , <i>Presbytis*</i> , <i>Pygathrix</i> , <i>Rhinopithecus</i>
		New World suspensory type (arm-swinging with use of prehensile tail, little leaping)	H	<i>Alouatta*</i> , <i>Ateles*</i> , <i>Brachyteles</i> , <i>Lagothrix*</i>
Large	Ground-standing-and-walking type (with digitigrady)	J	<i>Cercocebus</i> , <i>Erythrocebus*</i> , <i>Macaca</i> , <i>Mandrillus</i> , <i>Papio</i> , <i>Theropithecus</i>	
			<i>Gorilla</i> , <i>Pan</i>	
Terrestrial quadrupedalism	Medium	Ground-standing-and-walking type (with digitigrady)	J	<i>Cercocebus</i> , <i>Erythrocebus*</i> , <i>Macaca</i> , <i>Mandrillus</i> , <i>Papio</i> , <i>Theropithecus</i>
	Large	Knuckle-walking		<i>Gorilla</i> , <i>Pan</i>
Arboreal arm-swinging	Medium	True brachiation	K	<i>Hylobates*</i>
	Large	Arm-swinging and quadrumanous climbing Occasional brachiation, climbing	L	<i>Pongo</i> <i>Gorilla</i> , <i>Pan</i>
Terrestrial striding bipedalism	Large	(Standing, striding, running)	M	<i>Homo</i>

*Indicate that these taxa were used in the LDA (see Materials and Methods section).

variables and the locomotor subcategories (related to intermembral index and body weight) proposed by Martin (1990) were regarded as grouping factors. Two matrices were examined, one including a minimum (10) of locomotor subcategories (A–K), and the other including a maximum of subcategories (12, if we consider that A and E can be subdivided into A1 and A2 and E1 and E2, respectively; Table 1). The LDA matrices were analyzed with R-1.7.1 (MASS package; Ihaka and Gentleman, 1996). Analyses were conducted with size-standardized variables. Finally, in order to obtain an approximation of the size of the missing parts in NMMP 20 (i.e., the ischium, pubis, and cranial part of the ilium), linear regressions were performed on the complete data matrix to estimate the values of the 11 missing variables. These values are simply indicative and were not considered in the LDAs.

Results

The plots of discriminant factors derived from the LDA are presented in Fig. 3. In both analyses, the position of the NMMP 20 partial innominate was predicted by projecting its corresponding transformed variables (canonical variates) onto the linear discriminants. These predictions clearly show that the pelvic morphology of NMMP 20 matches that of the medium-sized quadrupedal primates, more specifically, the arboreal quadrupeds (subcategory E in Table 1; see Fig. 3A). The analysis utilizing the maximum number of locomotor subcategories suggests that the morphology of the NMMP 20 partial innominate is more similar to that of quadrupedal strepsirrhine lemurs (subcategory E1 in Table 1),

such as *Lemur*, *Eulemur*, *Varecia*, and *Daubentonia*, than to that of quadrupedal anthropoids (subcategory E2) such as the medium-sized platyrrhine monkeys *Aotus*, *Callicebus*, *Cebus*, *Pithecia*, and *Saimiri* (Fig. 3B). Although the posterior probability of NMMP 20 being a medium-sized primate capable of hindlimb motion similar to that of extant lemurid arboreal quadrupeds is particularly strong (0.99), these results must be viewed somewhat cautiously inasmuch as they are based on limited morphological evidence due to the fragmentary nature of the fossil.

The estimated dimensions of the missing parts of NMMP 20 are provided in Appendix 1 (labeled with an asterisk). Figure 4 illustrates a reconstruction (lateral and ventral views) of the NMMP 20 innominate based on these estimated dimensions.

Locomotor abilities

Despite its fragmentary condition, the NMMP 20 partial innominate exhibits a suite of osteological features that reflect functional attributes related to locomotor behavior. The pelvic girdle transmits the body weight to the femur and provides areas for attachment of various hindlimb muscles (see Waterman, 1929). Several important muscles arise along the ilium, including both the gluteal group of extensors (gluteus medius, gluteus minimus [scansorius], gluteus superficialis) and one quadriceps extensor (rectus femoris), and a number of important hip flexors (e.g., tensor fasciae femoris, iliacus, sartorius, rectus femoris).

As noted by Anemone (1993: 168), “the length of the ilium affects the dynamic characteristics of these muscles in a number of ways.” Unfortunately, the most cranial part of the ilium of NMMP 20 is lacking, and as a result, there is no clear information on the total length and shape of the iliac wing. From that which is preserved on NMMP 20, the predicted dimensions of the missing parts indicate that the total length of the ilium would be approximately twice as long as the lower iliac length (the distance between the center of the acetabulum and the auricular surface [Leutenegger, 1970; Fleagle and Simons, 1979]), meaning that about 28% of the cranial part of the ilium is missing (Fig. 4). Furthermore, based on the shape of the caudal part of the ilium, it is clear that the cranial part of the iliac wing was broad rather than narrow since the gluteal surface is relatively wide at the level of the sacral tuber and becomes slightly wider just before the break. The expanded iliac wing on NMMP 20 (Fig. 4) would therefore indicate a large area for the attachment of the gluteal muscles on the gluteal surface, thus suggesting powerful femoral extensors. However, the capacity for rapid extension of the thigh would have been less than in specialized leaping primates, in which the gluteal muscles (especially the gluteus medius) are much more powerful and fast due to a significant lengthening of the ilia (for further details, see Anemone [1993]). The NMMP 20 pelvis has a relatively short ilium (particularly the lower part) compared with specialized extant leapers (e.g., *Tarsius*, *Galago*), and its length corresponds instead to that of active quadrupedal primates engaged in arboreal locomotion (Table 1).

One of the most striking features observed on the preserved caudal part of the ilium in NMMP 20 is the extensive development of the anterior inferior iliac spine, which forms a prominent femoral process projecting ventrolaterally. This area of the gluteal plane is the site of origin for the rectus femoris (part of the quadriceps femoris), which is one of the powerful extensors of the leg at the knee joint, and also, but to a lesser extent, a flexor of the femur at the hip. Given the relatively large size of the femoral process in NMMP 20, it could be inferred that the rectus femoris was particularly well developed and powerful in this fossil primate. The femoral process is well developed in lemurs that are characterized by active quadrupedalism, notably the arboreal quadrupedal runners and climbers, which can also be fairly proficient leapers (e.g., cheirogaleids and lemurids). In NMMP 20, this process is noticeably more expanded cranially, thereby providing a larger area of origin for the sartorius (e.g., Gregory, 1920; Rose and Walker, 1985), which flexes the thigh and extends the knee. Ventrally, the well-delineated and bandlike iliac plane extends cranially over the auricular surface and provides origin for the iliopsoas. As stated in the description, there is a shallow depression on the ventral aspect of the femoral process, which probably means that the iliopsoas was more widely anchored caudally on the iliac plane. The iliopsoas, in association with the tensor fasciae femoris (arising from the blade-like iliac crest, which is poorly preserved in NMMP 20), is an important flexor of the femur at the hip joint during the recovery stroke of locomotion. Unlike large-bodied suspensory atelines and catarrhines, which exhibit a ventral expansion of the iliac

plane for the attachment of the iliopsoas (in relation to their peculiar mode of arboreal locomotion), the iliac plane in NMMP 20 narrows somewhat cranially as both the auricular surface and iliac tuberosity broaden. This osteological feature indicates that the iliopsoas was not expansively developed cranially, a condition that matches that of medium-bodied arboreal quadrupeds that engage in a branch-running-and-walking (climbing, springing) type of locomotion.

Although it is incomplete and somewhat crushed in a way that prevents accurate measurements, the acetabular region of NMMP 20 also preserves some interesting features that aid in reconstructing the locomotor abilities of this Pondaung primate. As mentioned previously, we regard the acetabular incisura as being virtually complete in NMMP 20 based on the tight correlation between acetabular diameter and the size of the incisura among primates (Schultz, 1969; Fleagle and Simons, 1979). This observation is corroborated by linear regressions against other pelvic dimensions (Appendix 1). As such, the acetabular incisura in NMMP 20 appears to have been relatively broad. A moderately deep acetabular fossa associated with a broad incisura suggests that the femoral head was capable of a wide range of motion (especially rotation) (Elftman, 1929; Jenkins and Camazine, 1977).

The acetabulum of NMMP 20 also bears a ventral rim that is slightly thicker than its dorsal rim. This osteological feature characterizes all extant and fossil strepsirrhines regardless of their locomotor behavior, and it is therefore of significant phylogenetic interest (Fleagle and Simons, 1979). In NMMP 20, the difference between the thickness of the dorsal and ventral acetabular rims is less marked ($VBA/DBA = 109$; $R1$ in Appendix 1) than in most strepsirrhines of similar body size ($VBA/DBA [R1] \geq 117$, and more generally, > 120 ; Appendix 1). Some strepsirrhines, notably those with tendencies toward vertical-clinging postures and hindlimb suspension, are remarkable in having a ventral rim that is considerably thicker than its dorsal counterpart (e.g., *Propithecus* and *Indri*, with $VBA/DBA [R1] > 170$; Appendix 1). Among strepsirrhine primates generally, the enhanced thickness of the ventral acetabular rim means that joint reaction forces frequently pass through the ventral rim, whereas in the more pronograde anthropoid primates, which show a relatively thicker dorsal rim, the greatest joint reaction forces almost certainly pass dorsally (Schultz, 1969; Fleagle and Simons, 1979). The fact that the ventral rim of the acetabulum in NMMP 20 is moderately thicker than the dorsal rim, as is the case in *Lemur*, *Cheirogaleus*, *Allocebus*, *Lepilemur*, and *Galago* ($VBA/DBA [R1]$ between 110 and 120), would indicate that the joint reaction forces passed through the ventral and dorsal rims almost equally, thus suggesting a relatively generalized form of locomotion characterized by a wide range of postural activities (i.e., clinging, leaping, active quadrupedal branch-running and climbing, and suspension; see Table 1).

To summarize, the morphological evidence available from both the ilium and acetabular region of the NMMP 20 partial innominate suggests that this Pondaung primate must have been capable of hindlimb motion approximating that of extant medium-sized lemurids, which are active arboreal quadrupeds

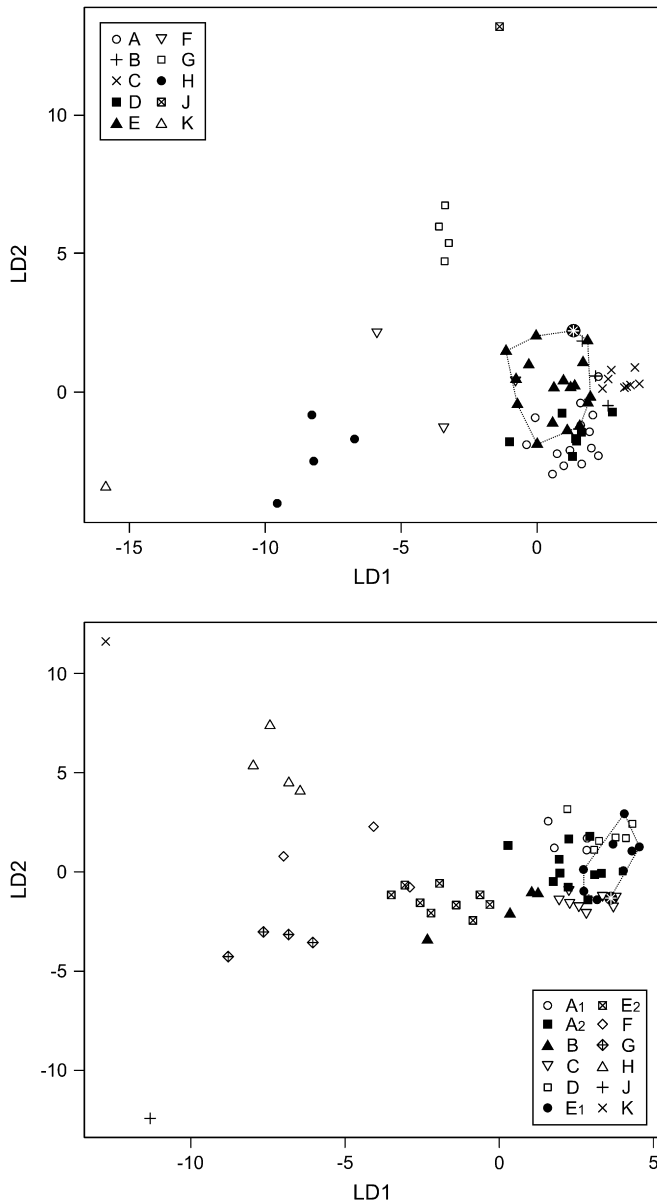


Fig. 3. Plots of discriminant scores derived from linear discriminant analyses: **A**, results of analysis that included a minimum (10) of locomotor subcategories (A–K); **B**, results of analysis that included a maximum of subcategories (12, if A and E are subdivided into A1 and A2 and E1 and E2, respectively). The position of the NMMP 20 partial innominate is denoted by the white asterisk embedded in a gray circle. A total of 24 measurements were obtained on the pelvis (ilium, pubis, and ischium) of living primates. Only 13 of these measurements were possible on NMMP 20 and used as variables in these analyses. These variables were size-standardized for the analyses.

and fairly proficient leapers. *Eulemur*, *Varecia*, and *Lemur* perhaps could be the best modern analogs in terms of postural activities and locomotor repertoire. Unfortunately, the preservation of NMMP 20 does not allow for measurement of ischial length (Napier and Walker, 1967) and orientation (Fleagle and Anapol, 1992), which are particularly indicative of locomotor habits. Our estimation based on linear regressions (Appendix 1) indicates that the length of the ischium in NMMP 20 would have been roughly similar to lower iliac length ($ISL/LIL = 98$; R^2 in Appendix 1; see also Fig. 4),

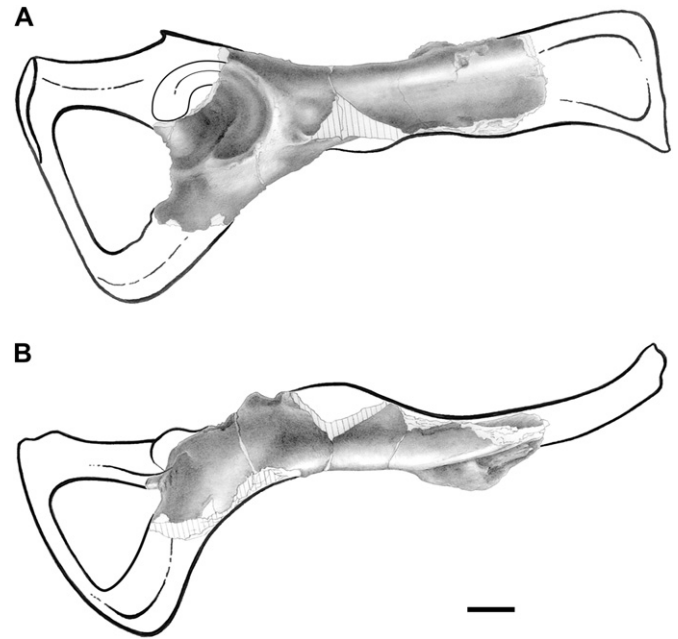


Fig. 4. Reconstruction of the NMMP 20 right innominate, based on estimated dimensions: **A**, lateral view; **B**, ventral view. Scale bar = 5 mm. Original art by Laurence Meslin and Laurent Marivaux.

meaning that this part of the innominate probably was relatively long compared with those of extant leapers (such as *Tarsius*, *Galago*, *Lepilemur*, *Propithecus*, *Avahi*, *Hapalemur*, and *Indri*) and slow-climbers (*Loris*, *Nycticebus*, *Perodicticus*, and *Arctocebus*). A relatively long ischium is consistent with the inference of an active quadrupedal mode of locomotion (e.g., Anemone, 1993).

Discussion

In their original description of the NMMP 20 partial skeleton, Ciochon et al. (2001) reported that the postcranial elements available to them displayed a mosaic of characteristics recalling those of adapiforms (notharctines and adapines), some extant strepsirrhines (lorises and lemurs), omomyids, platyrrhines, and, to a lesser extent, certain fossil anthropoids. With regard to functional interpretations, Ciochon et al. (2001) concluded that the primate taxon represented by NMMP 20 practiced some form of arboreal quadrupedalism, but they noted that more precise locomotor reconstructions were not possible given discrepancies in the functional implications (active vs. slow) of individual elements making up NMMP 20. Indeed, Ciochon et al. (2001: 7676) interpreted the morphology of the unique tarsal bone (a distal calcaneus) as evidence that this primate might be a “slow-climbing arboreal quadruped” similar to living lorises (e.g., *Nycticebus*, *Loris*) and fossil adapines (e.g., *Adapis*), while the morphology of the forelimb (especially the distal humerus) indicated that it was an “arboreal, leaping quadruped like extant lemurs” and fossil notharctines (e.g., Gebo et al., 1991; Rose and Walker, 1985). Subsequently, detailed functional analyses of the NMMP 20 partial skeleton led Kay et al.

(2004a) and Kay (2005) to reconstruct NMMP 20 as a slow-moving arboreal quadruped resembling modern lorises and/or the Eocene adapiforms *Adapis* and *Leptadapis* (following the locomotor pattern for adapines presented by Dagosto [1983, 1993]).

The discovery of an additional postcranial element belonging to the NMMP 20 partial skeleton allows us to reassess the different locomotor interpretations that have been proposed previously for this specimen. As we noted earlier, the NMMP 20 innominate does not support lorislake locomotor reconstructions for this Pondaung primate. The innominate of extant lorises is characterized by an ilium that is relatively long (particularly its lower iliac length), straight, and narrow (and therefore rodlike) and that lacks clear delineation of the different planes (gluteal, iliac, and sacral), does not possess a femoral process on the margo acetabuli, and that has an extremely short ischium. In contrast, the NMMP 20 partial innominate bears an ilium that is moderate in length and clearly segregated into gluteal, iliac, and sacral planes. Furthermore, the gluteal plane is expanded, and the large femoral process on the margo acetabuli projects strongly laterally. These aspects of pelvic morphology suggest that the NMMP 20 partial skeleton represents a primate in which active arboreal quadrupedalism like that practiced by medium-sized Malagasy lemurids (which are active above-branch quadrupeds and fairly proficient leapers) was probably an important part of its locomotor repertoire. Nonetheless, more hindlimb elements will certainly be needed to verify and refine this interpretation.

The initial discovery of the NMMP 20 partial skeleton marked an important turning point in the ongoing debate over the phylogenetic affinities of the Amphipithecidae. Virtually all workers agree that the postcranial morphology of NMMP 20 resembles that of living and fossil strepsirrhine primates, including various adapiforms (e.g., Ciochon et al., 2001; Ciochon and Gunnell, 2002, 2004; Gunnell et al., 2002; Kay et al., 2004b). The addition of the new partial innominate to the inventory of elements available for NMMP 20 extends the list of similarities shared by this partial skeleton from the Pondaung Formation and various strepsirrhines. For example, the NMMP 20 innominate possesses a ventral acetabular rim that is relatively thicker than the dorsal rim, a gluteal plane of the ilium that faces laterally rather than dorsolaterally, a well-delineated iliac plane that is distinct from the sacral plane, and a prominent and ventrolaterally projecting femoral process, all of which are characters that indicate strepsirrhine rather than anthropoid affinities. Most authorities have assumed that the NMMP 20 partial skeleton represents an amphipithecoid on the basis of its large size and the apparent absence of large-bodied primates other than amphipithecoids from the Pondaung Formation. Accordingly, the numerous postcranial characters shared by NMMP 20 and various strepsirrhine primates have led some workers to conclude that amphipithecoids are specialized adapiforms with dentitions that are merely convergent upon those of early Cenozoic anthropoids (Ciochon et al., 2001; Ciochon and Gunnell, 2002, 2004; Gunnell et al., 2002; also see Kay et al., 2004b).

While the morphological evidence pointing toward strepsirrhine affinities for the NMMP 20 partial skeleton is now more compelling than ever, two recent discoveries from the Pondaung Formation require us to revisit the assumption that NMMP 20 represents an amphipithecoid. The first of these discoveries is NMMP 39, a well-preserved left talus of a relatively large-bodied primate, which, unlike NMMP 20, displays derived anatomical features typical of haplorhines, particularly anthropoids (Marivaux et al., 2003). Because aspects of talar morphology are among the most diagnostic postcranial features distinguishing strepsirrhines from haplorhines (e.g., Gebo, 1986, 1988; Dagosto, 1988), it is difficult to imagine that the NMMP 39 talus belongs to the same higher-level primate taxon as the NMMP 20 partial skeleton. The conflicting phylogenetic signals provided by NMMP 39 (suggesting anthropoid affinities) and NMMP 20 (suggesting adapiform affinities) indicate that postcranial elements of two higher-level taxa of large-bodied primates occur in the Pondaung Formation. Only one of the large-bodied taxa represented by postcranial remains can correspond with the Amphipithecidae, which are otherwise documented only by teeth and jaws.

The second recent advance germane to this discussion is the discovery of the first primates other than anthropoids from the Pondaung Formation. Beard et al. (in press) described isolated teeth and postcranial elements (including a relatively complete talus and calcaneus) attributed to two new genera and species of sivaladapid primates, which are the first undoubted adapiforms to be recorded from the Pondaung Formation. Although neither of the new Pondaung sivaladapids is large enough to be a viable taxonomic candidate for the NMMP 20 partial skeleton, their description demonstrates that sivaladapids constituted a distinct, if uncommon, component of the Pondaung primate fauna. Of greater importance is the fact that tarsal elements referred to one of the new Pondaung sivaladapids provide a fresh means of evaluating the likely affinities of the large-bodied primate postcranial elements from the Pondaung Formation. The talus attributed by Beard et al. (in press) to a new Pondaung sivaladapid differs from the NMMP 39 talus in numerous respects, notably including the shape and orientation of the lateral articular facet for the fibula. These morphological differences indicate that NMMP 39 represents a primate that is only distantly related to Sivaladapidae, in agreement with the original description of this isolated talus as representative of an anthropoid (Marivaux et al., 2003). On the other hand, despite its much smaller size, the sivaladapid calcaneus described by Beard et al. (in press) closely resembles that of NMMP 20. The morphology of both of these Pondaung calcaneal specimens is similar in: (1) lacking the extreme calcaneal foreshortening that characterizes adapid and loriseid primates, (2) having a posterior calcaneal facet that is broad with respect to its length, (3) having a peroneal tubercle that is relatively proximal in position, and (4) having a deep cuboid pivot that is offset toward the plantomedial side of the calcaneocuboid facet (rather than being located more centrally on the plantar surface of the facet). As a matter of fact, these remarkable similarities in calcaneal morphology, coupled with the numerous adapiformlike features that occur

throughout the rest of the NMMP 20 postcranial skeleton, lead us to strongly suggest that NMMP 20 could document a third sivaladapid species in the Pondaung Formation.

Conclusion

The new fragmentary innominate, considered here to belong to the same individual represented by the NMMP 20 partial skeleton from Sabapondaung (PK1), provides substantial new information about the pelvic anatomy and functional morphology of a relatively large-bodied strepsirrhine primate from the Pondaung Formation. The presence in the same rock unit of a relatively large talus (NMMP 39) that exhibits haplorhine (particularly anthropoid) rather than strepsirrhine affinities demonstrates that there are two large-bodied primate taxa in the Pondaung Formation, no matter how one parses the taxonomic allocations of these isolated postcranial elements. Based on recent discoveries of small-bodied sivaladapid adapiforms from the Pondaung Formation (Beard et al., in press), it appears that NMMP 20 documents additional sivaladapid diversity in the middle Eocene of Myanmar. Medium- and large-bodied sivaladapid adapiforms are well known from late Eocene–Oligocene sites in southern China (Guangxi Zhuang Autonomous Region, *Guangxilemur tongi* Qi and Beard, 1998), peninsular Thailand (Krabi, *Wailekia orientalis* Ducrocq et al., 1995), and Pakistan (Bugti Hills, *Guangxilemur singsilai* Marivaux et al., 2002), where they occur in

association with amphipithecids (Thailand, Pakistan) and eosimiids (Pakistan). If future discoveries corroborate the sivaladapid affinities of NMMP 20, the anthropoid affinities of the Amphipithecidae will no longer be disputed on the basis of conflicting signals from the postcranium and dentition.

Acknowledgements

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Appendix 1

List of measures carried out on pelvis (ilium, pubis and ischium) of living primates and NMMP 20

Taxon	Code	Collection number, sex	α	DIA	DPA	WIA	DBA	VBA	MBA	LIL	IL
Pondaung primate		NMMP 20	*163.73	13.7	8	*6.14	9.44	10.32	17	25.7	*57.69
<i>Tarsius syrichta</i>	A1	CG 1884-411 F	160	3.9	2.65	2.2	1.93	1.41	5.8	14.03	23.13
<i>Tarsius spectrum</i>	A1	CG 1976-940	160	4.05	2.37	2.67	1.67	2.54	5.31	13.18	20.43
<i>Galago senegalensis</i>	A1	CG 1971-18	165	6.88	3.42	4.11	3.26	3.9	8.58	17	28.9
<i>Galago alleni</i>	A1	CG 1976-240	165	5.53	3.31	2.11	2.27	2.5	7.57	13.9	24.67
<i>Propithecus verreauxi</i>	A2	CG 1981-770	150	15.7	7.57	8.08	5.3	9.1	15.1	26.2	62.6
<i>Propithecus verreauxi</i>	A2	CG 2005-255 M	155	16.62	8.84	8.38	6.25	11.1	16.83	27.84	62
<i>Indri indri</i>	A2	CG 1982-977	155	20.02	10.66	11.92	6.35	13.49	20.53	33.11	80.98
<i>Lepilemur ruficaudatus</i>	A2	CG 1994-2462	170	9.62	5.01	4.76	4.62	5.49	8.96	22.89	45.22
<i>Lepilemur edwardsi</i>	A2	CG 2002-13 F	170	8.3	5.2	4.5	3.84	4.48	10.09	18.27	38.47
<i>Lepilemur</i> sp.	A2	CG 1951-9	170	8	4.66	3.4	4.56	4.62	12.02	23.45	42.43
<i>Avahi laniger</i>	A2	CG 2002-68 F	145	9.83	4.67	4.01	4.33	5.2	12.14	28.35	48.32
<i>Avahi laniger</i>	A2	CG 1901-519	145	8.66	4.31	4.6	4.26	5.48	11.75	21.11	39.64
<i>Hapalemur griseus</i>	A2	CG 2000-377	155	8.1	5.02	4.04	4.77	5.9	12.61	22.12	42.61
<i>Hapalemur sinus</i>	A2	CG 1940-318	155	8.52	4.6	4.6	3.46	4.87	10.61	23.18	43.84
<i>Saguinus midas</i>	B	CG1998-230 M	155	7.34	4.03	3.12	4.17	3.89	8.49	15.86	31.39
<i>Saguinus midas</i>	B	CG 2005-250 F	155	7.33	3.71	3.17	4.48	3.4	9.17	15.7	31.99
<i>Cebuella pygmaea</i>	B	CG 1998-150 M	155	3.78	1.99	1.84	2.32	1.68	4.64	11.06	18.9
<i>Leontopithecus rosalia</i>	B	CG 1953-30 M	155	7.35	3.87	4.34	4.58	2.68	10.87	14.35	31.62
<i>Mirza coquereli</i>	C	CG 1986-424 M	175	5.29	3.21	3	3.65	4.47	8.86	15	28.12
<i>Phaner furcifer</i>	C	CG 2002-43 M	165	5.82	3.21	2.95	3.66	4.72	9.87	15.38	29.88
<i>Cheirogaleus medius</i>	C	CG 2005-254 F	170	4.28	2.65	1.9	2.66	3.28	6.79	12.09	22.63
<i>Cheirogaleus medius</i>	C	CG 1912-21A	170	4.06	2.25	2.02	2.87	3.4	6.55	12.65	21.53
<i>Cheirogaleus medius</i>	C	CG 1912-21B	170	4.15	2.12	1.92	2.72	3.51	5.87	12.54	21.42
<i>Cheirogaleus major</i>	C	CG 2002-45 F	180	5.46	3.52	3.95	3.73	3.9	7.6	13.95	30
<i>Allocebus trichotis</i>	C	CG 2002-1 M	170	3.36	1.5	1.64	2.4	2.59	4.44	7.22	14.1
<i>Microcebus murinus</i>	C	CG 2002-57 F	170	2.48	1.23	1.2	1.79	1.6	3.85	8.02	16.28

(continued on next page)

Appendix 1 (continued)

Taxon	Code	Collection number, sex	α	DIA	DPA	WIA	DBA	VBA	MBA	LIL	IL
<i>Nycticebus coucang</i>	D	CG 1977-759	180	8.61	4.86	4.39	3.54	7.11	10.47	22.54	40
<i>Nycticebus pygmaeus</i>	D	CG 1990-428	160	7.74	4.32	4.64	4.36	6.17	10.47	24.15	36.73
<i>Nycticebus coucang</i>	D	CG A-3963	180	7.04	3.8	3.21	3.47	5.32	9.28	19.14	33.94
<i>Perodicticus potto</i>	D	CG 2004-405 M	165	11.05	6.2	4.54	6.63	7.98	19.53	27.66	53.07
<i>Perodicticus potto</i>	D	CG 1958-773	165	10.12	5.54	5.36	5.6	6.71	13.55	26.05	50
<i>Loris gracilis</i>	D	AC A-3927	170	5.19	3.17	3.04	3.34	4.86	7.93	18.55	28.4
<i>Loris tardigradus</i>	D	CG A-3956	170	4.93	3.2	2.38	2.7	4.76	7.75	15.33	23.56
<i>Daubentonia madagascariensis</i>	E1	CG 1992-4 M	160	13.34	7.03	8.7	5.81	9.58	14.73	25.36	57.18
<i>Varecia variegata</i>	E1	CG 2004-403 F	155	16.28	9.52	7.23	8.91	11	23.29	30.36	64.35
<i>Lemur catta</i>	E1	CG 1992-1857 M	165	10.6	6.23	6.07	6.87	8.06	15.83	26.88	55.45
<i>Eulemur fulvus fulvus</i>	E1	CG 1996-2161 M	165	11.16	6.88	5.53	5.51	8.63	16.04	28.8	60.06
<i>Eulemur fulvus fulvus</i>	E1	CG 1996-2159 M	165	11.48	6.85	5.57	6.08	8.7	16.6	30.86	61.51
<i>Eulemur macaco</i>	E1	CG 1997-1399 F	165	12.02	6.37	7.19	6.18	8.32	16.08	29.24	55.86
<i>Eulemur macaco</i>	E1	CG 2005-816	165	13.73	7.43	6.65	8.59	11.5	19.71	28.88	62.98
<i>Eulemur mongoz</i>	E1	CG 1987-252 M	165	9.53	5.15	5.35	4.02	7.98	12.56	27.21	49.42
<i>Pithecia pithecia</i>	E2	CG 1998-233 M	160	11.4	5.41	6.77	6.88	5.44	15.38	26.22	55.2
<i>Pithecia pithecia</i>	E2	CG 2001-1979 M	160	11.3	5.99	7.67	6.61	5.39	14.63	23.23	49.61
<i>Saimiri sciureus</i>	E2	CG 2000-1052 M	165	7.94	4.42	4.17	4.89	4.11	10.83	18.02	38.28
<i>Saimiri boliviensis</i>	E2	CG 2004-288 F	165	7.07	3.74	3.41	4.82	2.42	11.64	19.58	37.65
<i>Callicebus cuprea</i>	E2	CG A. 3985	160	8.68	4.6	5.44	5.58	4.38	13.66	20.25	42.36
<i>Cebus</i> sp.	E2	UMC-V9	160	12.6	7.36	6.67	9.04	6.68	16.81	27.27	59.61
<i>Cebus apella</i>	E2	CG 1962-1371 F	160	11.11	5.37	6.89	6.8	4.28	15.38	30.78	58.42
<i>Cebus apella</i>	E2	CG 1963-47 M	160	11.8	7.35	7.36	9.78	6.28	18.7	26.75	55.63
<i>Aotus trivirgatus</i>	E2	CG 1967-20 M	165	8.37	4.31	4.91	4.6	3.17	11.76	18.78	40.3
<i>Cercopithecus rufiventer</i>	F	CG 2005-258 M	145	13.47	8.34	8.03	8.45	6.71	22.01	34.54	73.51
<i>Cercopithecus solatus</i>	F	CG 1990-44 M	150	16.05	10.15	8.75	13.28	8.73	21.95	45.31	94.28
<i>Miopithecus talapoin</i>	F	CG 1998-1949 F	150	7.79	4.39	3.7	6.59	2.9	11.92	26.68	48.87
<i>Procolobus verus</i>	G	CG 1963-1375 F	155	13.69	7.56	5.97	11.99	6.97	23.87	37.05	79.62
<i>Nasalis larvatus</i>	G	CG 1880-1147	150	19.84	10.56	9.89	13.1	11.09	25.06	31.24	79.9
<i>Trachypithecus holotype</i>	G	CG 1934-546 M	140	17.17	11.24	9.06	15.18	11.88	26.54	39.66	91.37
<i>Presbytis mitratus</i>	G	CG A-3849	150	19.11	11.57	8.23	13.96	10.19	23.39	32.87	81.39
<i>Alouatta seniculus</i>	H	CG 1998-235 F	150	18.55	9.7	10.8	10.3	10.27	30.52	59.26	97.07
<i>Alouatta</i> sp.	H	CG 2000-409	150	18.54	9.39	10.58	8.53	8.53	29.32	55.97	94.27
<i>Lagothrix</i> sp.	H	CG 1972-190	155	18.37	10.31	10.36	9.88	7.94	25.38	46.57	88.53
<i>Ateles ater</i>	H	CG 1960-129 M	155	18.46	9.92	9.58	10.27	7.13	21.11	35.16	68.64
<i>Erythrocebus patas</i>	J	CG 1996-2165 M	145	19.81	12.59	9.38	19.1	11.81	27.82	42.12	104.57
<i>Hylobates leucogenys</i>	K	CG 2000-403 F	155	20.6	12.55	7.84	11.25	9.91	25.42	50.79	100.09

Taxon	Code	Collection number, sex	WILS	CRWIP	CAWIP	IGCRW	IGCAW	FPW	ISL	DSWIS	MLWIS
Pondaung primate		NMMP 20	9.37	8.96	10.42	*18.99	11.33	12.5	*25.31	*9.24	*5.69
<i>Tarsius syrichta</i>	A1	CG 1884-411 F	2.4	2.3	1.84	5.14	2.06	2.79	6.78	3.37	1.57
<i>Tarsius spectrum</i>	A1	CG 1976-940	2.01	1.35	2.02	4.29	2.45	2.34	5.82	2.65	1.33
<i>Galago senegalensis</i>	A1	CG 1971-18	4.05	1.84	3.55	9.46	5.52	4.79	10.39	4.04	2.95
<i>Galago alleni</i>	A1	CG 1976-240	3	1.77	2.47	7.51	3.51	3	7.93	3.42	2.06
<i>Propithecus verreauxi</i>	A2	CG 1981-770	8.3	6.15	9.7	30.19	13.66	18.3	21.5	7.7	4.5
<i>Propithecus verreauxi</i>	A2	CG 2005-255 M	7.25	7.4	9.83	26.37	12.67	16.87	20.67	6.74	4.38
<i>Indri indri</i>	A2	CG 1982-977	11.62	9.3	11.57	40.91	15.31	19.42	30.41	12.88	6.3
<i>Lepilemur ruficaudatus</i>	A2	CG 1994-2462	5.53	3.66	4.97	14.65	5.89	7.74	17.34	5.18	3.31
<i>Lepilemur edwardsi</i>	A2	CG 2002-13 F	4.28	4.03	4.21	7.98	4.82	7.22	16.42	5.33	2.77
<i>Lepilemur</i> sp.	A2	CG 1951-9	4.38	4.45	5.23	14.77	7.29	7.94	16.17	4.96	2.27
<i>Avahi laniger</i>	A2	CG 2002-68 F	5.77	9.77	5.27	21.63	11.08	11.36	16.34	6.46	3.1
<i>Avahi laniger</i>	A2	CG 1901-519	4.66	7.43	4.39	15.48	8.3	8.71	14.21	5.37	3.39
<i>Hapalemur griseus</i>	A2	CG 2000-377	6.41	5.42	5.28	16.73	7.02	9.9	17.87	4.85	3.33
<i>Hapalemur sinus</i>	A2	CG 1940-318	4.62	4.4	4.58	12.27	5.69	7.1	17.38	3.24	3.29
<i>Saguinus midas</i>	B	CG1998-230 M	5.03	3.39	4.72	10.09	7.89	7.94	16.79	5.93	2.86
<i>Saguinus midas</i>	B	CG 2005-250 F	5.7	3.31	4.6	10.9	7.84	8.08	16.57	5.22	3.3
<i>Cebuella pygmaea</i>	B	CG 1998-150 M	2.99	1.39	1.97	9.91	4.35	3.99	9.24	2.57	1.36
<i>Leontopithecus rosalia</i>	B	CG 1953-30 M	7.39	4.08	3.21	12.21	9.01	9.13	17.95	3.29	3.19
<i>Mirza coquereli</i>	C	CG 1986-424 M	3.74	2.93	3.48	6.36	5.79	5.27	14.29	3.33	2.46
<i>Phaner furcifer</i>	C	CG 2002-43 M	3.65	2.96	3.8	8.08	4.37	5.73	12.69	3.62	2.45
<i>Cheirogaleus medius</i>	C	CG 2005-254 F	2.86	2.61	2.7	4.91	4.11	4.09	10.26	2.82	1.64
<i>Cheirogaleus medius</i>	C	CG 1912-21A	2.43	2.24	2.97	4.57	3.2	3.63	9.48	2.6	1.48
<i>Cheirogaleus medius</i>	C	CG 1912-21B	2.39	2.21	2.8	4.71	3.05	3.92	9.9	2.74	1.42
<i>Cheirogaleus major</i>	C	CG 2002-45 F	3.56	2.3	3.72	6.51	4.23	5.05	15.28	3.84	2.16
<i>Allocebus trichotis</i>	C	CG 2002-1 M	1.98	1.9	2.56	3.22	2.46	2.38	9.18	2.1	1.25

Appendix 1 (continued)

Taxon	Code	Collection number, sex	WILS	CRWIP	CAWIP	IGCRW	IGCAW	FPW	ISL	DSWIS	MLWIS
<i>Microcebus murinus</i>	C	CG 2002-57 F	1.85	1.83	1.66	3.7	1.94	2.66	8.28	2.02	1.07
<i>Nycticebus coucang</i>	D	CG 1977-759	4.56	3.16	4.53	9.08	5.37	5.01	17.39	5.84	2.4
<i>Nycticebus pygmaeus</i>	D	CG 1990-428	4.2	3.38	4.85	7.04	5.28	5.07	13.14	5.9	2.46
<i>Nycticebus coucang</i>	D	CG A-3963	3.29	3.29	3.7	8.15	4.77	3.51	12.37	4.91	2.29
<i>Perodicticus potto</i>	D	CG 2004-405 M	6.67	4.66	5.92	13.97	7.92	7.35	18.9	6.82	3.96
<i>Perodicticus potto</i>	D	CG 1958-773	4.98	7.72	5.64	10.26	6.49	4.76	15.23	6.04	3.23
<i>Loris gracilis</i>	D	AC A-3927	2.8	2.33	2.65	6.52	3.32	3.3	7.6	4.82	1.88
<i>Loris tardigradus</i>	D	CG A-3956	2.6	1.64	3.57	4.89	3.46	2.34	6.5	3.92	1.52
<i>Daubentonia madagascariensis</i>	E1	CG 1992-4 M	7.77	6.21	9.1	16.6	8.23	10.25	26.73	8.6	5.07
<i>Varecia variegata</i>	E1	CG 2004-403 F	11.01	8.4	10.21	20.03	12.82	16.85	25.98	12.21	5.32
<i>Lemur catta</i>	E1	CG 1992-1857 M	7.39	5.62	9.49	16.93	8.81	12.1	21.71	6.1	5.05
<i>Eulemur fulvus fulvus</i>	E1	CG 1996-2161 M	7	7.7	8.63	19.13	10.75	13.41	22.52	6.06	4.28
<i>Eulemur fulvus fulvus</i>	E1	CG 1996-2159 M	7.73	7.03	9	18.47	10.98	14.28	23.47	6.81	4.39
<i>Eulemur macaco</i>	E1	CG 1997-1399 F	7.46	6.92	7.74	23.19	11.63	14.25	21.72	6.46	3.76
<i>Eulemur macaco</i>	E1	CG 2005-816	9.44	7.63	10.42	29.58	15.92	15.21	25.2	8.43	4.92
<i>Eulemur mongoz</i>	E1	CG 1987-252 M	6.03	4.41	6.27	16.31	7.5	8.59	20.51	5.2	3.92
<i>Pithecia pithecia</i>	E2	CG 1998-233 M	7.11	10.31	5.92	19.78	14.09	11.88	24.68	7.76	4.49
<i>Pithecia pithecia</i>	E2	CG 2001-1979 M	6.72	10.73	6.69	17.53	13.73	11.68	24.57	7.17	4.67
<i>Saimiri sciureus</i>	E2	CG 2000-1052 M	6.28	5.39	3.97	12.62	9.42	8.27	19.52	5.42	3.36
<i>Saimiri boliviensis</i>	E2	CG 2004-288 F	6.98	2.15	2.84	13.26	8.08	7.1	17.47	5.75	3.25
<i>Callicebus cuprea</i>	E2	CG A. 3985	7.33	4.48	4.43	12.83	10.15	10.4	23.28	5.27	2.85
<i>Cebus</i> sp.	E2	UMC-V9	11.35	6.84	7.61	20.79	17.28	13.56	27.64	9.79	6.31
<i>Cebus apella</i>	E2	CG 1962-1371 F	8.52	6.41	5.18	20.61	13.68	11	26.81	6.99	4.15
<i>Cebus apella</i>	E2	CG 1963-47 M	9.42	6.41	7.5	19.15	13.63	12.83	26.79	8.32	6
<i>Aotus trivirgatus</i>	E2	CG 1967-20 M	6.29	3.03	3.08	10.57	7.15	8.2	20.14	5.92	3.18
<i>Cercopithecus rufiventer</i>	F	CG 2005-258 M	9.02	9.96	6.9	25.23	17.19	13.58	37.71	11.04	5.58
<i>Cercopithecus solatus</i>	F	CG 1990-44 M	12.55	16.04	11.56	33.52	23.74	17.7	49.12	13.3	8.52
<i>Miopithecus talapoin</i>	F	CG 1998-1949 F	6.98	8.1	3.86	15.63	11.6	9.07	21.91	6.45	3.89
<i>Procolobus verus</i>	G	CG 1963-1375 F	13.34	14.81	8.07	31.46	22.88	16.15	40.77	11.03	9.62
<i>Nasalis larvatus</i>	G	CG 1880-1147	14.38	13.46	12	34.85	21.05	16.55	36.17	14.23	8.7
<i>Trachypithecus holotype</i>	G	CG 1934-546 M	14.69	16.45	12.73	35.32	24.14	20.48	44.21	17.22	9.28
<i>Presbytis mitratus</i>	G	CG A-3849	14.5	16.55	11.32	35.24	24.26	20.47	39.95	14.02	9.57
<i>Alouatta seniculus</i>	H	CG 1998-235 F	16.45	20.4	9.73	29.03	26.26	20.1	34.99	15.53	6.92
<i>Alouatta</i> sp.	H	CG 2000-409	14.08	21.14	10.18	32.44	27.84	21.3	36.44	16.72	6.21
<i>Lagothrix</i> sp.	H	CG 1972-190	13.89	14.1	9.57	26.42	23.6	15.88	37.9	14.98	6.97
<i>Ateles ater</i>	H	CG 1960-129 M	10.95	14.91	10.89	28.25	19.3	14.47	31.71	13.26	4.84
<i>Erythrocebus patas</i>	J	CG 1996-2165 M	18.42	19.42	11.26	47.28	29.06	24	59.81	15.3	9.71
<i>Hylobates leucogenys</i>	K	CG 2000-403 F	11.66	26.92	13.04	37.92	30.38	15.9	41.32	10.94	7.34

Taxon	Code	Collection number, sex	PL	MLWP	CCWS	CCLOF	DVWOF	IPL	R1	R2	R3
Pondaung primate		NMMP 20	*25.57	3.47	9.09	*17.97	*16.67	*38.37	109	98	224
<i>Tarsius syrichta</i>	A1	CG 1884-411 F	12.28	0.84	1.19	3.81	5.72	16.14	73	48	165
<i>Tarsius spectrum</i>	A1	CG 1976-940	7.78	0.73	1.64	3.8	5.97	12.41	152	44	155
<i>Galago senegalensis</i>	A1	CG 1971-18	10.59	1.4	4.31	4.97	8.1	18.18	120	61	170
<i>Galago alleni</i>	A1	CG 1976-240	9.29	0.62	3	7.13	4.59	15.07	110	57	177
<i>Propithecus verreauxi</i>	A2	CG 1981-770	27.57	2.26	5.86	16.69	15.25	37.71	172	82	239
<i>Propithecus verreauxi</i>	A2	CG 2005-255 M	21.51	1.82	6.34	14.98	12.28	33.82	178	74	223
<i>Indri indri</i>	A2	CG 1982-977	26.58	2.59	7.12	19.37	15.87	42.37	212	92	245
<i>Lepilemur ruficaudatus</i>	A2	CG 1994-2462	15.36	1.65	2.6	11.12	10.28	23.01	119	76	198
<i>Lepilemur edwardsi</i>	A2	CG 2002-13 F	13.63	1.59	2.69	10.01	7.71	21.84	117	90	211
<i>Lepilemur</i> sp.	A2	CG 1951-9	19.18	1.38	3.24	11.95	12.56	23.97	101	69	181
<i>Avahi laniger</i>	A2	CG 2002-68 F	18.06	1.16	4.24	11.31	8.9	27.25	120	58	170
<i>Avahi laniger</i>	A2	CG 1901-519	14.66	1.48	4.47	10	8.1	22.59	129	67	188
<i>Hapalemur griseus</i>	A2	CG 2000-377	19.72	1.89	4.18	12.47	12.77	26.84	124	81	193
<i>Hapalemur sinus</i>	A2	CG 1940-318	13.92	1.77	3.14	11.61	9.57	23.77	141	75	189
<i>Saguinus midas</i>	B	CG1998-230 M	13.54	1.58	2.79	10	8.4	24.63	93	106	198
<i>Saguinus midas</i>	B	CG 2005-250 F	14.1	1.6	2.06	12.18	9.66	23.91	76	106	204
<i>Cebuella pygmaea</i>	B	CG 1998-150 M	9.69	0.73	1.39	7.1	7.33	14.82	72	84	171
<i>Leontopithecus rosalia</i>	B	CG 1953-30 M	16.01	1.1	2.84	11.26	12.7	26.07	59	125	220
<i>Mirza coquereli</i>	C	CG 1986-424 M	13.83	1.15	2.48	10.52	9.22	19.56	122	95	187
<i>Phaner furcifer</i>	C	CG 2002-43 M	11.12	1.19	3.34	9.92	6.3	19.68	129	83	194
<i>Cheirogaleus medius</i>	C	CG 2005-254 F	12.2	0.76	1.37	7.82	9.55	16.6	123	85	187
<i>Cheirogaleus medius</i>	C	CG 1912-21A	9.91	0.88	1.8	7.04	7.57	14.3	118	75	170
<i>Cheirogaleus medius</i>	C	CG 1912-21B	9.62	0.96	1.84	7.08	7.34	13.99	129	79	171

(continued on next page)

Appendix 1 (continued)

Taxon	Code	Collection number, sex	PL	MLWP	CCWS	CCLOF	DVWOF	IPL	R1	R2	R3
<i>Cheirogaleus major</i>	C	CG 2002-45 F	12.66	0.64	2.52	9.36	9.48	19.38	105	110	215
<i>Allocebus trichotis</i>	C	CG 2002-1 M	9.25	0.73	1.28	5.71	5.5	11.61	108	127	195
<i>Microcebus murinus</i>	C	CG 2002-57 F	7.73	0.51	1.09	4.44	4.96	10.34	89	103	203
<i>Nycticebus coucang</i>	D	CG 1977-759	23.92	1.43	5.2	15.85	13.39	33.42	201	77	177
<i>Nycticebus pygmaeus</i>	D	CG 1990-428	20.91	1.42	3.87	8.87	11.65	25.76	142	54	152
<i>Nycticebus coucang</i>	D	CG A-3963	21.16	1.27	3.61	9.23	11.86	26.89	153	65	177
<i>Perodicticus potto</i>	D	CG 2004-405 M	29.87	2.38	5.96	13.5	16.4	36.49	120	68	192
<i>Perodicticus potto</i>	D	CG 1958-773	26.63	1.79	5.47	12.12	13.08	34.11	120	58	192
<i>Loris gracilis</i>	D	AC A-3927	14.72	0.96	3.3	7.1	5.1	19.67	146	41	153
<i>Loris tardigradus</i>	D	CG A-3956	10.99	0.79	2.84	6.37	4.74	15.87	176	42	154
<i>Daubentonia madagascariensis</i>	E1	CG 1992-4 M	21.13	1.34	7.47	18.55	14.45	40.89	165	105	225
<i>Varecia variegata</i>	E1	CG 2004-403 F	26.69	2.54	10.34	18.13	13.4	38.71	123	86	212
<i>Lemur catta</i>	E1	CG 1992-1857 M	20.97	1.71	4.32	17.49	15.44	33.33	117	81	206
<i>Eulemur fulvus fulvus</i>	E1	CG 1996-2161 M	26.48	2.12	5.24	17.85	18.53	35.7	157	78	209
<i>Eulemur fulvus fulvus</i>	E1	CG 1996-2159 M	26.76	2.51	6.02	17.88	18.45	35.83	143	76	199
<i>Eulemur macaco</i>	E1	CG 1997-1399 F	24.7	1.9	5.03	17.06	16.59	35.08	135	74	191
<i>Eulemur macaco</i>	E1	CG 2005-816	24.85	2.71	8.3	17.81	18.93	39.64	134	87	218
<i>Eulemur mongoz</i>	E1	CG 1987-252 M	21.27	1.77	3.53	16.48	14.26	28.55	199	75	182
<i>Pithecia pithecia</i>	E2	CG 1998-233 M	18.6	1.78	4.08	16.87	14.07	35.32	79	94	211
<i>Pithecia pithecia</i>	E2	CG 2001-1979 M	15.47	2.52	4.53	16.38	12.91	33.94	82	106	214
<i>Saimiri sciureus</i>	E2	CG 2000-1052 M	14.17	1.5	4.47	12.91	9.72	27.26	84	108	212
<i>Saimiri boliviensis</i>	E2	CG 2004-288 F	18.81	1.53	2.3	10.37	11.8	29.23	50	89	192
<i>Callicebus cuprea</i>	E2	CG A. 3985	15.6	1.23	3.85	15.91	13.17	31.84	78	115	209
<i>Cebus sp.</i>	E2	UMC-V9	22.23	2.44	7.3	17.66	14.24	40.31	74	101	219
<i>Cebus apella</i>	E2	CG 1962-1371 F	24.42	2.17	2.71	17.47	16.22	38.48	63	87	190
<i>Cebus apella</i>	E2	CG 1963-47 M	20.42	1.73	6.11	16.25	13.4	38.14	64	100	208
<i>Aotus trivirgatus</i>	E2	CG 1967-20 M	16.84	1.41	3.27	13.42	13.49	30.45	69	107	215
<i>Cercopithecus rufiventer</i>	F	CG 2005-258 M	26.05	1.93	6.45	21.71	15.62	50.52	79	109	213
<i>Cercopithecus solatus</i>	F	CG 1990-44 M	33.61	2.42	6.88	30	20.12	67.32	66	108	208
<i>Miopithecus talapoin</i>	F	CG 1998-1949 F	24.98	1.39	3.95	13.43	10.28	37.4	44	82	183
<i>Procolobus verus</i>	G	CG 1963-1375 F	34.33	2.8	7.3	22.27	15.36	53.08	58	110	215
<i>Nasalis larvatus</i>	G	CG 1880-1147	29.57	2.36	7.75	22.87	13	52.71	85	116	256
<i>Trachypithecus holotype</i>	G	CG 1934-546 M	33.94	2.02	10.15	25.13	15.09	59.72	78	111	230
<i>Presbytis mitratus</i>	G	CG A-3849	30.61	2.3	9.49	27.07	18.05	58.29	73	122	248
<i>Alouatta seniculus</i>	H	CG 1998-235 F	46.22	3.31	9.18	26.7	20.3	64.66	100	59	164
<i>Alouatta sp.</i>	H	CG 2000-409	41.58	3.08	8.09	27.2	19.82	61.53	100	65	168
<i>Lagothrix sp.</i>	H	CG 1972-190	38.81	3.49	6.77	24.9	20.18	56.07	80	81	190
<i>Ateles ater</i>	H	CG 1960-129 M	26.53	2.89	6.61	18.34	13.64	40.89	69	90	195
<i>Erythrocebus patas</i>	J	CG 1996-2165 M	41.31	4.13	9.45	38.4	30.95	79.28	62	142	248
<i>Hylobates leucogenys</i>	K	CG 2000-403 F	38.64	2.06	8.86	24.17	24.24	57.4	88	81	197

Abbreviations are as follows: α , angle between ilium and ischium (cranio caudal axis); **DIA**, maximum diameter of acetabulum; **DPA**, maximum depth of acetabulum; **WIA**, maximum width of incisura acetabuli; **DBA**, minimum dorsal breadth of acetabular rim; **VBA**, minimum ventral breadth of acetabular rim; **MBA**, minimum medial breadth of acetabular rim; **LIL**, lower iliac length; **IL**, ilium length; **WILS**, minimum width of ilium sacral plane; **CRWIP**, cranial width of ilium iliac plane (level of auricular surface); **CAWIP**, caudal width of ilium iliac plane; **IGCRW**, maximum cranial width of ilium wing (gluteal plane); **IGCAW**, maximum caudal width of ilium wing (level of caudal auricular surface); **FPW**, minimum caudal width of ilium wing (femoral process); **ISL**, ischium length; **DSWIS**, minimum dorsoventral width of ischium; **MLWIS**, minimum mediolateral width of ischium; **PL**, pubis length; **MLWP**, minimum mediolateral width of pubis; **CCWS**, minimum craniocaudal width of pubis; **CCLOF**, maximum craniocaudal length of obturator foramen; **DVWOF**, maximum dorsoventral width of obturator foramen; **IPL**, ischium—pubis length. Indices used for specific comparisons through the text: **R1**, (VBA/DBA) \times 100; **R2**, (ISL/LIL) \times 100; **R3**, (IL/LIL) \times 100. The estimated dimensions of the missing parts of NMMP 20 innominate are indicated with an asterisk. Measurements were taken to the nearest 0.01 mm using a Stainless digital caliper.

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