

PSEUDOPOTTO MARTINI: A NEW GENUS AND SPECIES OF EXTANT LORISIFORM PRIMATE

JEFFREY H. SCHWARTZ

NUMBER 78
ANTHROPOLOGICAL PAPERS OF
THE AMERICAN MUSEUM OF NATURAL HISTORY
NEW YORK: 1996

PSEUDOPOTTO MARTINI: A NEW GENUS AND SPECIES OF EXTANT LORISIFORM PRIMATE

JEFFREY H. SCHWARTZ

Research Associate, Department of Anthropology American Museum of Natural History Professor, Department of Anthropology University of Pittsburgh

ANTHROPOLOGICAL PAPERS OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 78, 14 pages, 9 figures, 2 tables Issued January 23, 1996

Price: \$2.60 a copy

ABSTRACT

Two specimens—one represented by a virtually complete skeleton and adult dentition and the other by skull, mandible, and mixed dentition—in the collections of the Anthropological Institute and Museum, University of Zürich-Irchel, that had been cataloged as *Perodicticus potto* do not possess the salient features of this prosimian primate. Although these specimens are cladistically lorisiform, and in some features are variably similar, especially to *Arctocebus*, *Nycticebus*, and *Perodicticus*, they do not share the suite of apomorphies that unites these extant lorisids plus the fourth genus, *Loris*, as a clade. The postcrania (preserved for one specimen) are primitive relative to those

of lorisids in having a long tail and lacking a distinctly hooked ulnar styloid process. Both specimens are dentally primitive relative to lorisids in retaining a more buccally emplaced cristid obliqua and lacking deep hypoflexid notches on the lower molars, as well as in having relatively longer lower middle and last premolars. Nevertheless, these specimens appear to be more closely related to the lorisid clade than the more well-known lorisiform groups, the cheirogaleids and the galagids. In light of their dissimilarity to any other known lorisiform primate, a new genus and a new species are named to accommodate this previously unrecognized prosimian.

INTRODUCTION

The lorisid¹ genus, *Perodicticus*, commonly known as the potto, is distributed throughout tropical West Africa, from the Guinea coast to the Congo and Ubangi rivers, and as far east as the Great Rift Valley (e.g., Booth, 1958). Although late 18th and early 19thcentury taxonomists had recognized as many as seven species within the genus (see review by Allen, 1912), these were reduced by Schwarz (1931) to four subspecies of a single species, *Perodicticus potto*, on the grounds that differences among forms are only those of size and pelage pattern and coloration. This has been the general consensus in subsequent reviews of primates (Hill, 1953; Napier and Napier, 1967; Groves, 1974), although a recent morphological as well as metrical study demonstrated that different morphs of Perodicticus can be delineated and that each morph should be recognized as a separate species (Schwartz and Beutel, in press). In the latter investigation, all morphs shared the basic apomorphies that distinguish Perodicticus from other lorisids.

In this context, it is of interest that two specimens in the collections of the Anthro-

¹ Jenkins (1987) pointed out that, although the family name Lorisidae has been used consistently by systematists, Loridae Gray, 1821, actually has priority. In keeping with familiarity, and a forthcoming appeal to suppress Loridae (Schwartz et al., in prep.), the family name Lorisidae is used here.

pological Institute and Museum, University of Zürich-Irchel (AMZ), that had been identified as *Perodicticus potto* are not only unlike any known species or variety of potto, but unlike any known prosimian. One of the specimens, from the Adolph Schultz collection (AMZ-AS 1730), is a subadult male and according to the Institute's records was collected in the Cameroons. It is represented by only a skull and mandible and a mixed (permanent and some deciduous) dentition. The other specimen (AMZ 6698) is listed in the Institute's records as having come from "Equatorial Africa" via the Zürich Zoo. The specimen is represented skeletally and dentally, but its pelage was not saved. It is identified in the Institute's records as "female, adult." All permanent teeth had erupted and the cranial vault sutures are well coalesced; epiphyseal lines are visible on the proximal humerus, distal femur, tibia, fibula, radius, and ulna. In light of the fact that it had spent some time in a zoo environment, it is important to note that aside from traces of osteoporosis and periostitis [which are pathological conditions commonly found in zoo specimens (B. Senut, personal commun.)], there is nothing developmentally or morphologically abnormal about this individual. The major detraction is that a previous researcher, who did not recognize this specimen as being atypical of P. potto, had been allowed to carve the teeth from the right sides of upper

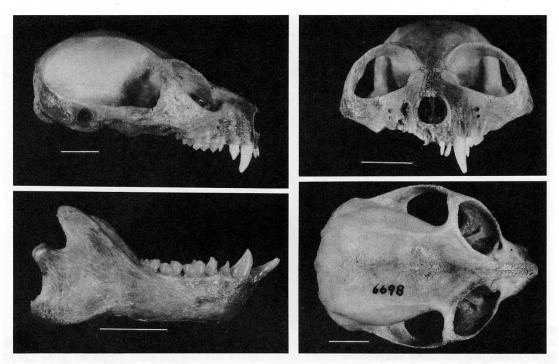


Fig. 1. Skull and mandible of type specimen of AMZ 6698 (type, *Pseudopotto martini*). Scale bar = 1 cm.

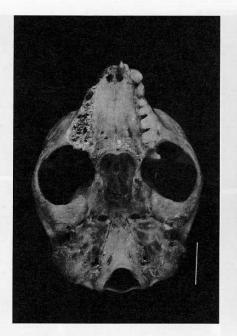
and lower jaws. Of less serious note is that the teeth are somewhat translucent, presumably having become so during the process of skeletonization.

THE SPECIMENS

AMZ 6698 consists of essentially a complete skeleton and skull of an adult animal. Overall, the skull is in good condition (figs. 1, 2). Slight indications of periostitis are noted on the nasal bones and around the orbits. Aside from damage to the right alveolar margin, the alveolus of the right upper canine is cracked open along the face and the left central incisor is partially broken. The skull is characterized by the following features: poorly developed temporal lines; anteriorly facing orbits with minimally elevated rims; lacrimal canal situated within inferior margin of orbit; arcuate rather than straight zygomatic arches; bizygomatic width greater than maximum biorbital width; minimally projecting nasal bones and anterior nasal spine; snout not squared up by stout canine root (i.e., the snout

is not "puffy"); thick but not too tall postglenoid plate; petrosal ossified laterally into short tube. In addition, there is an anterior carotid foramen at the apex of the auditory bulla and the carotid foramen is situated medially. The inferior petrous sinus foramen and foramen lacerum posterior, both of which perforate the medial margin of the bulla rather than the basiocciput, are confluent on the right and abut one another on the left side. The carotid foramen is in the immediate vicinity of these two foramina on both right and left sides. The body of the mandible is deep, the coronoid process (and less so the goneal region) is moderately hooked, and the mandibular condyles are oriented slightly outward (figs. 1 and 2).

The vertebral column is essentially complete, but at least one caudal vertebra, of what is obviously a long tail, is missing (fig. 3). The spine of C2 is short and barely bifid (and thus does not cup the spine of C3) and the spines of C3-T2 are only moderately elongate. The transverse processes of the lumbar vertebrae are gracile (fig. 3). All other elements of the



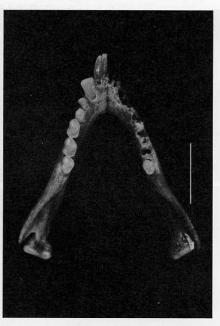
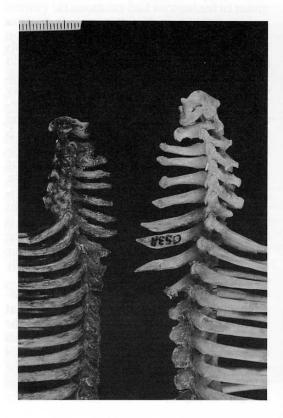
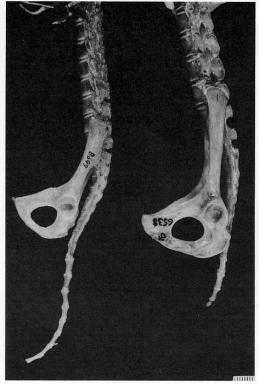


Fig. 2. Basal and occlusal view of skull (left) and occlusal view of mandible (right) of AMZ 6698 (type, *Pseudopotto martini*). Scale bar = 1 cm.





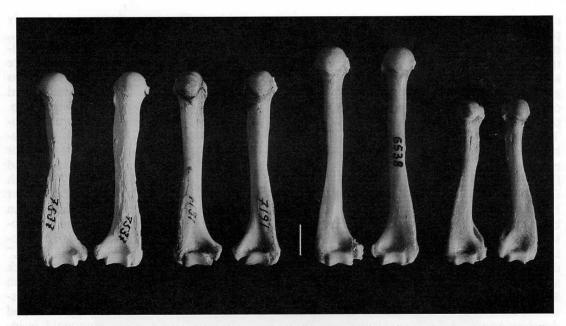


Fig. 4. Posterior view of right and left humeri of different morphs of *Perodicticus potto* (from left to right, AMZ 7537, 7191, and 6538) compared to AMZ 6698 (type specimen of *Pseudopotto martini* (AMZ 6698, far right). Note the bilateral entepicondylar foramina and the more exaggerated curvature on the humeri of AMZ 6698 (see Schwartz and Beutel, in press, for discussion of morphs of *Perodicticus potto*). Scale bar = 1 cm.

axial skeleton (sternum, sacrum, and all ribs) are present. The sternal ends of the clavicles are D-shaped and they and the acromial ends are unexpanded. Right and left scapulae, humeri, radii, and ulnae and the right hand and wrist bones are preserved. The humerus is perforated by a large entepicondylar foramen, it bears a strong deltoid flange, and its S-shaped shaft is noticeably curved mediolaterally (fig. 4). The ulna is also curved, but in the anteroposterior plane; its styloid process is moderately hooked. In the hindlimb, the os coxae, all long bones, both patellae, and the right foot and ankle bones are present. The os coxa is elongate and gracile. The upper half of the long and essentially rodlike ilium is slightly expanded along the posterior margin and the acetabular fossa is deep and constricted; the pubis is also elongate. The head of the talus is neither very knoblike nor laterally expanded. With the notable exception of some thinning of the cortical bone of the scapula, the postcranium is essentially free of any pathology.

The upper incisors are narrow, moderately procumbent, and subequal in length; their crowns are minimally spatulate but relatively high (figs. 1, 2). The upper canine is tall, trenchant, slightly recurved posteriorly, and somewhat compressed buccolingually. Its crown bears a distinctly raised anterior margin and a modest vertical lingual ridge. The upper P2 is about half the height of the canine but approximately twice as tall as the other

Fig. 3. Left, cervical and thoracic vertebrae of AMZ 6698 (type, *Pseudopotto martini*) (left) and *Perodicticus potto* (AMZ 6538) (right): note disparity in length of vertebral spines of C3–T2. **Right**, lower lumbar and caudal vertebrae of AMZ 6698 (type specimen of *Pseudopotto martini*) (left) and *P. potto* (AMZ 6538) (right): note short tail in *P. potto* and long tail (even with missing terminal caudal vertebrae) of *Pseudopotto martini*. Scales are in mm.

cheekteeth. This tooth is somewhat compressed buccolingually and its anterior and posterior margins are sharp. P2 also bears a moderate vertical swelling along its lingual surface as well as a thin band of lingual cingulum. Viewed from the buccal side, the crown is somewhat triangular in outline; the posterior edge is longer and more vertical. The three-rooted P³ is tiny and triangular in both occlusal and buccal outline. It is oriented obliquely in the jaw and is separated from P² by a slight diastema. The lingual surface of P3 is concave and surrounded at its base by a modest band of cingulum. The P4 bears a large, tall paracone and a smaller protocone; the hypocone region is somewhat distended. The well-developed para- and more developed metastylar regions give the tooth a "waisted" appearance at its midsection. On M¹, the large paracone and even larger metacone are accentuated further by moderately developed para- and metastylar regions. The M¹ paracone lies almost directly opposite the protocone; faint protocristae connect the protocone with the buccal cusps. The posterior displacement of the metacone gives the distal margin of the tooth a "waisted" appearance. The straight, uncingulated lingual margin, in conjunction with a very small hypocone, squares up that side of the tooth; there is a weakly developed prehypocone crista. M² is similar to M¹ in that the paracone lies almost opposite the protocone but the metacone of the latter tooth is smaller and is distended slightly buccally (rather than posteriorly); the tooth is therefore not waisted along its distal margin. The lingual margin of M² is straight and the small, ledgelike hypocone is incorporated into a somewhat ledgelike postcingulum. The upper third molar is rudimentary, comprising only a single cusp. The tooth is triangular in buccal and occlusal outlines and bears a moderately well-developed lingual cingulum and a small but spikelike metastyle.

In the lower jaw, the three preserved teeth of the toothcomb are relatively narrow and long. The P_2 is tall, trenchant, and buccolingually compressed, and the tip of the tooth is slightly recurved posteriorly. The convex anterior edge of the crown terminates in an angled projection, whereas the slightly concave posterior edge ends in a small, com-

pressed heel. The crown bears a moderately well-developed lingual cingulid. The tiny P₃, which bears sharp stylids, is somewhat triangular in buccal outline. Its lingual surface is long and concavely sloped and its margins are adorned with cingulids that course toward the stylids. P₄ is composed of a single cusp. The long axis of this tooth is more anteroposteriorly than obliquely oriented. The posterior edge of P4 is longer than its anterior edge; a vertical ridge delineates a deep and narrow posterior fovea behind it. The tooth bears a thin lingual cingulid. On all lower molars the protoconid is modestly larger than and situated slightly anterior to the metaconid; these cusps are connected by a crest. Anterior to the protoconid is a very small "cusp," from which a thin paracristid courses back toward the base of the metaconid. Again on all lower molars, the buccally positioned cristid obliqua courses toward the protoconid and the small and compressed entoconid is incorporated into the postmetacristid. The lower molar hypoconid is also slightly larger than the entoconid. On M₂ and even more so on M, the trigonid is wider than the shallow talonid primarily because the protoconid is large and swollen buccally. The M₃ is distinguished from the other lower molars by its crown, which tapers posteriorly and also bears a hypoconulid; this cusp is positioned centrally on the posterior margin.

AMZ-AS 1730 is a subadult. It is similar in overall shape and robusticity to juvenile *Perodicticus potto* (fig. 5). In spite of the fact that the specimen is heavily coated in a thick, shiny material, one can locate on the basicranium the anterior carotid foramen, the carotid foramen, the inferior petrous sinus foramen, and the foramen lacerum posterior (fig. 5); these foramina are similar in disposition and configuration to those of AMZ 6698. Even though the orbital rims had not reached adult proportions, the lacrimal fossae are incorporated into the inferior orbital margins.

Because this specimen's teeth are less worn and not translucent as a result of skeletonization, the details are easier to discern (fig. 6). AMZ-AS 1730 retains right and left dm₃s; the permanent successors (P₃s) are just beginning to erupt. The dm₃s are small, triangular in buccal outline, and somewhat com-

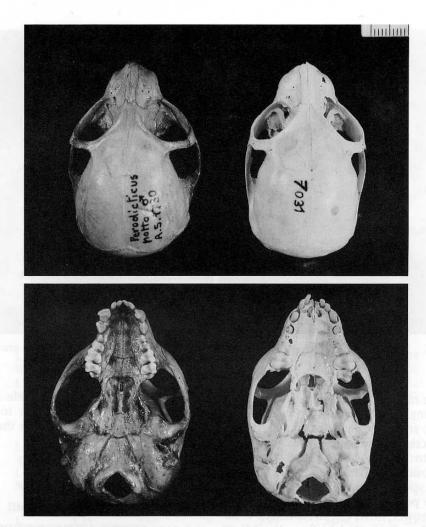


Fig. 5. (Above and below) AMZ-AS 1730 (left) compared to juvenile *Perodicticus potto* (AMZ 7031) (right). Note general similarity in overall skull shape but lacrimal fossa lying at terminus of inferior margin of orbit in AMZ-AS 1730. See text for further discussion. Scale is in mm.

pressed buccolingually; the lingual side of each tooth bears a vertical crest that separates a small anterior fovea from a larger posterior one. The upper posteriormost deciduous molar is unshed on the left side of the jaw whereas, on the right side, the P⁴ is almost completely erupted. Characteristic of posterior deciduous molars, the left dm⁴ is submolariform. Although smaller than M¹, the dm⁴ is morphologically similar in that the paracone lies opposite the protocone and the metacone region is distended, thereby "waisting" the tooth just above (buccally) the small but distinct hypocone. With regard to comparable

permanent teeth, AMZ-AS 1730 is recognizably similar to AMZ 6698 in the relative size and morphology of the upper incisors, the toothcomb teeth, the upper canines, upper and lower P2s, the P³s, the P⁴, and the lower molars. For example, on the unworn P₄s one can clearly see that the lingual surface is concave and bears a vertical ridge that delineates a small posterior fovea from a larger anterior one. Although slightly shorter mesiodistally and more transverse buccolingually than the M¹ of AMZ 6698, the M¹ of AMZ-AS 1730 is similar in, for example, the alignment of the paracone with the protocone, the enlarge-

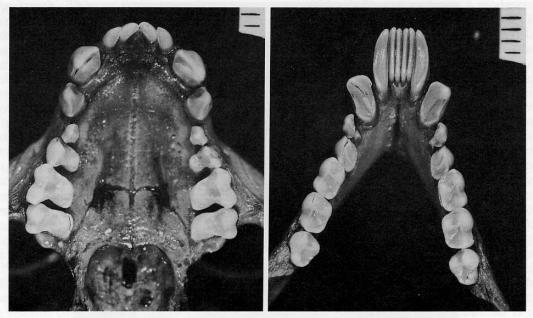


Fig. 6. AMZ-AS 1730: upper dentition (left) and lower dentition (right). Scales are in mm.

ment of the metacone-metastylar region, and the "waisting" of the crown along its distal margin; the small hypocone bears a faint prehypocone crista. The M² of AMZ-AS 1730 is similar to M2 of AMZ 6698 in that is it narrower buccally than M1 and it bears a ledgelike hypocone that is incorporated into a ledgelike postcingulum. This tooth is relatively narrower, however, in AMZ-AS 1730 and is further distinguished from the M2 of AMZ 6698 in having a much smaller metacone and a lingual cingulum that courses from the hypocone around the protocone. Although they are still unerupted, one can see that the M3s are quite reduced in size (especially in that they are mesiodistally very short) but differ from the rudimentary M³s of AMZ 6698 in having a small, spikelike protocone. The lower molars of AMZ-AS 1730 are like those of AMZ 6698 in essentially every detail. The major difference lies in the M₃s: in the AMZ-AS 1730, the metaconid is relatively larger and more buccally swollen and the talonid is smaller relative to the trigonid.

Dental measurements of the two specimens and a representative sample of *Perodicticus potto* are given in table 1 and cranial and humeral measurements for AMZ 6698

and a sample of *P. otto* in table 2. The humerus was measured in order to provide a reflection of size differences in the postcranium.

SYSTEMATICS
ORDER PRIMATES
SUBORDER PROSIMII
SUPERFAMILY LORISOIDEA
FAMILY INCERTAE SEDIS
Pseudopotto, new genus

Type Species: Pseudopotto martini, new. Included Species: Type only. Distribution: Currently known only from

the Cameroons and "Equatorial Africa."

DIAGNOSIS: As for type species.

Discussion: See under type species.

ETYMOLOGY: *Pseudo-*, *potto*; to reflect the superficial resemblances of the specimens to the extant potto (*Perodicticus potto*), the taxon to which they were originally allocated.

Pseudopotto martini, new species

HOLOTYPE: AMZ 6698, skull, mandible, partial dentition, postcranial skeleton (figs. 1–4, 8, 9).

Type Locality: "Equatorial Africa."

DISTRIBUTION: Type locality, especially the Cameroons. Recent.

HYPODIGM: Type plus AMZ-AS 1730, skull and mandible with teeth.

ETYMOLOGY: In honor of Dr. Robert D. Martin, distinguished primatologist and expert on all facets of prosimian biology.

DIAGNOSIS: Similar to extant lorisids in developing a short, tubular petrosal extension,

TABLE 1
AMZ 6698, AMZ-AS 7130, and Perodicticus potto

Length (L) and width (W) and summary statistics of upper and lower first and second molars. P. potto sample combined for male, female, and sex unknown (from Schwartz and Beutel, in press).

Measurements are in millimeters.

LIZE THE		AMZ 6698	AMZ- AS 1730	Perodicticus potto				
				n	Ā	Range	S	CV
12 110		varie.	M	axillary der	tition		N Inne	
Right								
M1	L		4.00	33	4.17	3.6-4.8	.26	6.23
	w		4.00	33	4.95	4.0-5.9	.41	8.27
M2	L		3.00	33	4.00	3.0-4.5	.31	7.79
	W	_	4.00	33	5.37	3.9-6.2	.55	10.17
Left								6
Ml	L	4.30	3.80	34	4.13	3.6-4.8	.04	6.32
****	w	4.05	3.90	34	4.98	4.0-5.7	.06	7.47
M2	L	3.20	3.10	34	3.96	3.0-4.5	.32	8.07
12 47	W	4.15	4.00	34	5.35	4.0-6.2	.47	8.50
			Ma	ındibular de	ntition			
Right								
M1	L		3.60	33	4.01	3.4-4.7	3.4-4.7 .27	6.64
	w		2.40	33	3.32	2.3-3.9	.28	8.48
M2	L	_	3.60	33	4.22	3.4-4.8	.27	6.34
	W	_	2.75	33	3.88	2.6-4.5	.35	8.98
Left								
M1	L	3.75	3.50	34	3.99	3.6-4.7	.22	5.41
	w	2.50	2.60	34	3.38	2.5-4.2	.33	9.67
M2	L	3.70	3.50	32	4.18	3.6-4.8	.26	6.30
	w	2.70	2.75	32	3.92	2.6-4.7	.44	11.10

TABLE 2
AMZ 6698 and Perodicticus potto

Cranial and right humeral measurements and summary statistics. P. potto sample combined for male, female, and sex unknown (from Schwartz and Beutel, in press). Measurements are in millimeters.

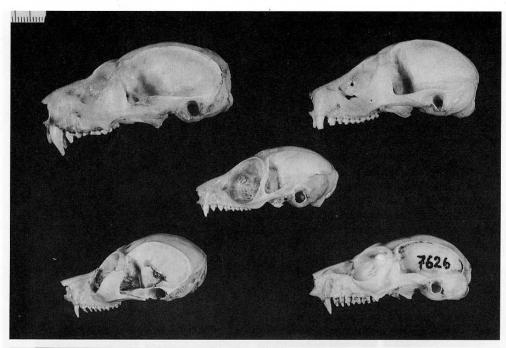
Kalendar Production	Contract I	Perodicticus potto						
	AMZ 6698	n	Ŕ	Range	S	CV		
Right humeral length	57.65	31	71.23	57.6-79.7	4.11	5.77		
Cranial length	59.30	35	63.89	59.3-77.6	2.93	4.59		
Nasal length	12.80	34	16.58	12.8-19.0	1.52	9.18		
Biorbital breadth	36.66	35	39.93	36.7-42.1	1.36	3.41		
Interorbital breadth	7.30	35	9.30	7.3-11.0	.87	9.40		
Biporion breadth	34.40	35	37.57	33.8-43.2	2.03	5.41		
Bicanine breadth	e e la la L a mari	34	17.29	15.1-20.9	1.06	6.14		
Min, temporal line sep.	16.80	35	15.10	10.4-19.3	2.04	13.48		

a reduced second manual digit, somewhat deep mandibular body, and frontally rotated orbits, but differing in having a long tail, laterally compressed lower premolars, buccally emplaced lower molar cristids obliquae, and a less hooked ulnar styloid process. Similar to Perodicticus and Nycticebus in having a bulky skull and mandible, expanded suprameatal shelves, and broad snout, but different in having more hooked mandibular coronoid process and goneal regions. Similar to Perodicticus and Arctocebus in having some elongation of vertebral spines of C3-T2, but different in lacking a bifid spine on C2 and in having taller cheekteeth cusps, more crisply defined cusp apices, crests, and margins, and an entepicondylar foramen. Similar to Nycticebus in having the lacrimal fossa incorporated into the inferior orbital margin, but different in having the fossa more internalized in the orbit in the adult. Distinguished from most lorisiforms (but not Phaner) in having a very diminutive P3, from most extant prosimians (but not Nycticebus) in having the lacrimal fossa incorporated into the inferior orbital margin, and from all extant prosimians in having a diminutive M3.

With more specimens for comparison it may become necessary to remove AMZ-AS 1730 to its own species within *Pseudopotto*. This move may be warranted by the differences between AMZ-AS 1730 and AMZ 6698 in relative size and morphology of M² and M₃. These differences may, however, turn out to represent the extremes of variation within this newly recognized taxon. Since these two specimens are otherwise virtually identical in those very features that distinguish each from any other lorisiform, they both are presented here as examples of *Pseudopotto martini*.

Discussion: The toothcomb in both specimens reflects their phylogenetic relatedness to prosimians (Schwartz and Tattersall, 1985). AMZ 6698 and AMZ-AS 1730 emerge cladistically as lorisiform rather than lemuriform because they possess a prehypocone crista on the first upper molar, an anterior carotid foramen, and inferior petrous sinus and posterior lacerate foramen that are closely approximated and also perforate the medial margin of the auditory bulla (cf. Schwartz, 1986; Szalay, 1975). AMZ 6698 is apomorphically lorisiform in having an elon-

gate and gracile os coxa, with a long and rodlike ilium and long pubis (cf. Jouffroy, 1975). A general relatedness to extant lorisids is indicated by such potential synapomorphies as frontated orbits, a short, tubular extension of the petrosal, thin, high-crowned upper incisors of similar length, and deep mandible with reduced goneal and coronoid hooks (cf. Hill, 1953; Schwartz and Tattersall, 1985) (fig. 7). AMZ 6698 does not, however, possess the lorisid apomorphies of a short tail and distinctly hooked ulnar styloid process, and neither specimen is synapomorphically lorisid in having a lingually directed cristid obliqua that creates a deep hypoflexid notch on the lower molars and ovoid, anteroposteriorly shortened, lower middle and last premolars (Cartmill and Milton, 1977; Mivart, 1864; Schwartz, 1984, 1986; Schwartz and Tattersall, 1985). In spite of being primitive relative to all lorisids in these features, and thus more similar to the reconstructed ancestral morphotype of the lorisiform clade (Schwartz, 1986; Schwartz and Tattersall, 1985), the specimens are most similar to Perodicticus and Nycticebus among known lorisiforms in having such features as a generally bulkier skull and mandible, a broader snout, and more developed suprameatal shelves—features that otherwise would be considered synapomorphic of the latter genera (Schwartz and Beutel, in press; Schwartz and Tattersall, 1985) (fig. 7). AMZ 6698 is reminiscent of Perodicticus and Arctocebus in having some elongation of the vertebral spines on C3-T2 but of Perodicticus alone in having arcuate zygomatic arches and a bizygomatic width that is greater than the maximum biorbital width: both specimens are similar to some, but not all, morphs of Perodicticus in having M₂₋₃ trigonids that are wider than the talonids and that have large and buccally expansive protoconids (Hill, 1953; Mivart, 1865; Schwartz, 1992; Schwartz and Beutel, in press) (figs. 7, 8). AMZ 6698 and AMZ-AS 1730 are, however, more primitive than Perodicticus not only in the degree to which these features are expressed, but also in having an entepicondylar foramen, more noticeably hooked mandibular coronoid and goneal region processes, a short, nonbifid vertebral spine on C2 that does not embrace the spine of C3 from above, a short vertebral spine on



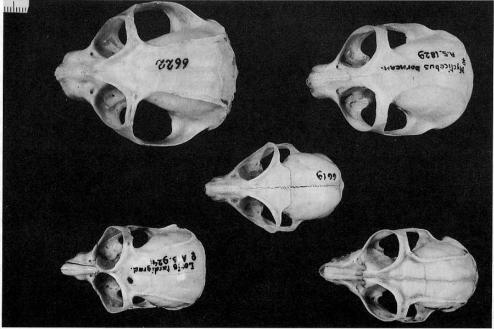


Fig. 7. Lateral (above) and superior (below) views of lorisiform skulls. Upper left, *Perodicticus potto* (AMZ 7537); upper right, *Nycticebus coucang* (AMZ-AS 1829); middle, *Galago senegalensis* (AMZ 6619); lower right, *Arctocebus calabarensis* (AMZ 7765); lower left, *Loris tardigradus* (AMZ-AS 924). Note derived configurations of frontated orbits and short tubular petrosal extension in the four lorisids, bulkier skulls and squared up snouts in *Perodicticus* and *Nycticebus*, and (in *Nycticebus*) the incorporation of the lacrimal fossa into the inferior margin of the orbit. Scales are in mm.



Fig. 8. Lower left permanent dentitions of (from right to left): AMZ 6698 and AMZ 7191, AMZ-AS 1868, and AMZ 6620 [different morphs of *Perodicticus potto* (see Schwartz and Beutel, in press)]. Bar = 0.5 cm.

T3, molars with less puffy cusps and more crisply defined crests, and buccolingually compressed upper canines and P₂₋₃s (figs. 3, 4, 8, 9). More similar to *Nycticebus*, however, is the relation of the lacrimal fossa to the inferior orbital margin: in *Nycticebus* and both specimens the inferior orbital margin terminates at and incorporates the lacrimal fossa (fig. 7).

Metrical comparisons with Perodicticus potto are also revealing. In mesiodistal length and buccolingual breadth of upper and lower first and second molars, both individuals are small compared to a representative sample of P. potto (table 1). Inasmuch as AMZ-AS 1730 is a juvenile individual, its cranial measurements were not included in the analysis. However, various cranial measurements of AMZ 6698, as well as length of its humerus, again demonstrate that the proposed new taxon, Pseudopotto martini, lies at the lowest end of the size range of the Perodicticus sample (table 2). This observation is of particular importance because the "subspecies," batesi (= edwardsi), that is also found in the Cameroons, is the largest form of *Perodicticus potto* (Allen, 1912; Hill, 1953).

Because AMZ 6698 and AMZ-AS 1730 can be identified together as representing a lorisiform primate closely related to lorisids, but one that is not fully lorisid apomorphically, it seems reasonable to allocate these specimens to their own genus and species. This act is not undertaken lightly, especially because this new taxon would be known from only two specimens. Nevertheless, these specimens contribute an array of information that is more complete by orders of magnitude than what is usually provided by the fossils that serve as the type specimens of new taxa.

CONCLUSION

The results of the comparisons summarized above are systematically frustrating in terms of the specific phylogenetic relationships of the new taxon. Although *Pseudopotto martini* is clearly uniquely derived in at least a few features compared not only to lorisi-



Fig. 9. Upper left permanent dentitions of (from right to left): AMZ 6698 and AMZ 7191, AMZ-AS 1868, and AMZ 6620 [different morphs of *Perodicticus potto* (see Schwartz and Beutel, in press)]. Bar = 0.5 cm.

forms, but to prosimians in general, it is not autapomorphy that obscures the phylogenetic relationships of P. martini—as is the case with such systematically vexing taxa as Tarsius, Daubentonia, and Pongo (Schwartz, 1984, 1986; Schwartz and Tattersall, 1985). Rather it is this taxon's confounding association of potential symplesiomorphies and synapomorphies - shared differently with different taxa-that complicates in totally unexpected ways the deciphering of its phylogenetic relationships among lorisiform primates. This is particularly significant when one considers that if a new genus and species had been erected to accommodate a fossil, the specimen (or specimens of the hypodigm collectively) would probably have been less representative of the total animal than the specimens on which the newly proposed taxon, Pseudopotto martini, is based. One wonders, therefore, just how many incomplete specimens, which have ended up being allocated to the hypodigm of a known taxon, are actually distinct taxa waiting to be discovered.

ACKNOWLEDGMENTS

I thank Dr. R. D. Martin, Professor and Director, Anthropological Institute and Museum, University of Zürich-Irchel, Switzerland, for his generosity and support in allowing me to study the collection of prosimians in his charge and to the faculty and staff for their kind assistance. Other specimens were made available by Drs. Guy Musser (American Museum of Natural History), Richard Thorington (National Museum of Natural History), and Paula Jenkins (Natural History Museum, London). Thanks also go to Dr. Brigit Senut for discussion of AMZ 6698, Dr. Ian Tattersall for advice on the genus name, and to him and Drs. Peter Andrews, Glenn Conroy, and Susan Ford for helpful comments on an earlier draft of this paper. This research was supported by the Provost's Research Fund (University of Pittsburgh), the American Philosophical Society, and the Adolph Schultz Research Fund (Anthropological Institute and Museum, University of Zürich-Irchel).

REFERENCES

Allen, D. G.

1912. A review of the primates, vol. 1. Monogr. Am. Mus. Nat. Hist. 1: 1-317.

Booth, A. H.

1958. The zoogeography of West African primates: a review. Bull. Inst. Français Afrique Noire 20: 587-622.

Cartmill, M., and K. Milton

1977. The lorisiform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. Am. J. Phys. Anthrop. 47: 249–272.

Gray, J. E.

1821. On the natural arrangement of vertebrose animals. London Med. Repos. 15: 296–310.

Groves, C. P.

1974. Taxonomy and phylogeny of prosimians. *In* R. D. Martin, G. A. Doyle, and A. C. Walker (eds.), Prosimian biology, pp. 449–473. London: Duckworth Press.

Hill, W. C. Osman

1953. Primates: comparative anatomy and taxonomy, Vol. I.—Strepsirhini. Edinburgh: Edinburgh Univ. Press.

Jenkins, P. D.

1987. Catalogue of Primates in the British Museum (Natural History). Part IV: Suborder Strepsirhini, including the subfossil Madagascan lemurs and Family Tarsiidae. London: British Museum (Natural History).

Jouffroy, F. K.

1975. Osteology and myology of the lemuriform postcranial skeleton. *In* I. Tattersall and R. W. Sussman (eds.), Lemur biology, pp. 149–192. New York: Plenum Press.

Mivart, St. G.

1864. Notes on the crania and dentition of the Lemuridae. Proc. Zool. Soc. London 1864: 611–648.

1865. Contributions towards a more complete knowledge of the axial skeleton in the primates. Ibid. 1865: 545–592.

Napier, J. R., and P. H. Napier

1967. A handbook of living primates. New York: Academic Press.

Schwartz, J. H.

1984. What is a tarsier? In N. Eldredge and S. Stanley (eds.), Living fossils, pp. 38–49. New York: Springer-Verlag.

1986. Primate systematics and a classification of the order. In D. Swindler and J. Erwin (eds.), Comparative primate biology, vol. 1, systematics, evolution and anatomy, pp. 1–41. New York: Alan R. Liss.

1992. Phylogenetic relationships of African and Asian lorisids. *In* S. Matano, R. H. Tuttle, H. Ishida, and M. Goodman (eds.), Topics in primatology, vol. 3, evolutionary biology, reproductive endocrinology, and virology, pp. 65–81. Tokyo: Univ. Tokyo Press.

Schwartz, J. H., and I. Tattersall

1985. Evolutionary relationships of the living lemurs and lorises and their potential affinities with the European Eocene Adapidae. Anthrop. Pap. Am. Mus. Nat. Hist. 60: 1–100.

Schwartz, J. H., and J. C. Beutel

In press. Species diversity in lorisids: a preliminary analysis of Arctocebus, Perodicticus, and Nycticebus. In L. Alterman and K. Izard (eds.), Creatures of the dark: the nocturnal prosimians. New York: Plenum Press.

Schwarz, E.

1931. On the African short-tailed lemurs or pottos. Ann. Mag. Nat. Hist. 8: 249–256.

Szalay, F. S.

1975. Phylogeny of primate higher taxa: the basicranial evidence. *In* W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the primates: a multidisciplinary approach, pp. 91–125. New York: Plenum Press.