Proc. Natl. Acad. Sci. USA
Vol. 94, pp. 180–184, January 1997
Evolution

Discovery of the smallest Fayum Egyptian primates (Anchomomyini, Adapidae)

ELWYN L. SIMONS

Department of Biological Anthropology and Anatomy and Primate Center, Duke University, Durham, NC 27705-5000

Contributed by Elwyn L. Simons, October 10, 1996

ABSTRACT **Two new adapiform primate species from locality 41, Jebel Qatrani Formation, Egypt, are described. The first, here named *Wadilemur elegans* genus novum species novum (holotype Cairo Geological Museum 42211), consists of a right mandible with P_3–M_3. The second is assigned to *Anchomomys milleri* species novum, with a holotype Cairo Geological Museum 42842, that includes the right mandible with lower canine to M_3. Both species are allied closely with genera that are known to be from Eocene deposits either in Europe, Tunisia, or the Sultanate of Oman (Arabia), thus enhancing earlier paleomagnetic evidence that locality 41 was deposited in Eocene times.**

Collections made in the last 5 or 6 years have yielded more new information about early anthropoidean evolution than finds of any previous decade of the century, and new descriptions have greatly added to knowledge of Paleogene prosimians in Africa. Most of this information has come from the Fayum, Egypt (1–5). There have been other finds further west in North Africa and in the Sultanate of Oman, Arabian peninsula—a biogeographic part of Africa (6). Godinot and Mahboubi (7–9) also described new primate genera and species from Algeria thought to be earliest anthropoideans. Together with their descriptions, these authors clearly disallowed any affinity between the new Eocene anthropoideans or "near anthropoideans" from Africa and the Chinese *Eosimias* (10)—a point also stressed by Simons (11). *Djebelemur* from Tunesia was figured and analyzed by Hartenberger and Marandat (12). They considered this find to be an adapid, but others thought it may be an anthropoidean (9). Lastly, Ducrocq *et al*. (13) described a new possible anthropoidean relative, *Wailekia*, from the Paleogene of Thailand.

The transition between prosimians and anthropoideans is being narrowed by these new discoveries. There also have been striking advances in understanding other early Tertiary prosimian groups found in the African zoogeographic region. One group of these prosimians, the cercamoniine Adapidae, was first reported from Oman, Arabia, by Gheerbrant *et al*. (14). One year later, Simons and Rasmussen (15) described mandibles and a remarkable cranium of a rather large prosimian, *Plesiopithecus teras*, from the Fayum late Eocene locality 41 (L-41). Subsequently, Simons *et al*. (5) reported on an even larger new genus and species of cercamoniine also from the late Eocene Fayum quarry L-41, *Aframonius dieides*. In this paper, another new genus and species of a diminutive adapoid found in L-41 is reported, *Wadilemur elegans*, as well as a new species of *Anchomomys, Anchomomys milleri*. All of these fossils represent an important addition to understanding the radiations that may have produced the Anthropoidea. The *Anchomomys* group may be considered either a tribe under the subfamily Ceracmoniinae of the Adapidae (as here) or it may prove to be a separate subfamily of its own.

Most of the newly described species from sites in the Afro-Arabian plate are discussed variously by those who named them as being either adapoid or anthropoidean or, in one case, basal omomyid. Nevertheless, with the exception of *Djebelemur*, which consists of a five-toothed, mandibular fragment, the classification of these new Afro-Arabian primates is based on isolated teeth, mostly from the lower dentition. The newly described Paleogene African prosimians mentioned above join an enigmatic, earlier Algerian find, *Azibius trerki*, reported by Sudre (16). In all cases, prosimians found outside the Fayum lack the critical parts of the cranial anatomy that would confirm definite ranking, whether with adapoids or with anthropoideans (3, 17).

The diversity of primates at L-41 rivals any site in the upper sequence of the Fayum, for example Quarry M, where six primate species have been found. The new genus and species here described as well as the new species of *Anchomomys* makes eight primate genera so far described from L-41. Together, these constitute a distinct, much earlier, and different Fayum lower-sequence fauna in which both the prosimians and probably the anthropoideans represent more diversified primate groups than occur in the Fayum upper sequence.

The age of Fayum site recently was reviewed by Kappleman *et al*. (18) and Rasmussen *et al*. (19). In brief, the upper-sequence quarries appear to be about 33 million years ago (Ma) and the L-41 level about 36 Ma, the latter being correlated as Priabonian late Eocene.

Both of the new species described below are clearly related to the *Djebelemur–Anchomomys–Omanodon–Schizarodon* group. It seems, on the other hand, that the idea that the latter two of these genera are distinct from *Anchomomys* is not correct. However, it also seems that the described material of *Schizarodon* is inadequate to sustain a valid generic diagnosis.

As has been noticed by Gheerbrant *et al*. (13), *Schizarodon, Omanodon*, and by inference, *Anchomomys* and *Djebelemur* bear a strong resemblance to the cheirogaleid lemur *Microcebus*, as can be seen in Fig. 1 by comparison with a stereophotograph of a *Microcebus* right mandible. Although the molar resemblances are striking, at least one of the species described below, *A. milleri*, which preserves the canine, shows that these Paleogene prosimians did not have a tooth comb. The origin of the tooth–comb prosimians is still a mystery.

SYSTEMATICS

Order Primates Linnaeus, 1758; Suborder Prosimii, Illiger, 1811; Family Adapidae, Trouessart, 1879; Family Cercamoniinae, Gingerich 1977; Tribe Anchomomyini Szalay and Delson, 1979 (*sensu* Godinot 1988).

Wadilemur, New Genus

Generic diagnosis. Distinctly larger than *Omanodon* and slightly larger than *Shizarodon, Waldilemur* shows typical

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

0027-8424/97/94180-5$2.00/0
PNAS is available online at **http://www.pnas.org**.

Abbreviations: L-41, locality 41; Ma, million years ago; CGM, Cairo Geological Museum; DPC, Duke University Primate Center.

FIG. 1. Stereopair of right dentary of a mouse lemur (*Microcebus murinus*). Duke University Primate Center (DPC) osteo.035, crown view. (×11.) Note caniniform P_2 molars with broad talonids and mesially extended entoconids.

adapoid lower molars with crescentic ridges connecting the cusps. Lower first and second molars are subequal in size and length, with M_3 longer and showing central hypoconulid—no hypoconulid on $M_{1\text{-}2}$. Lower molars differ from those of *O. minor* in that the cristid obliqua does not run up to join the metaconid cusp crown as in both *Omanodon* and *Shizarodon*; also, the entoconid of *O. minor* is shifted further lingually than in *Wadilemur*, and the high point of the paraconid crest (presumably the actual paraconid) in *Omanodon* is shifted more laterally than in *Wadilemur*. Also, in *Wadilemur*, a continuous crest or ridge runs from the tip of the protoconid around to the metaconid encircling the anterior fovea without a break; in *Omanodon*, there is a deep, central notch in this crest. *Wadilemur* differs from *Shizarodon* in being slightly larger, with lower molar metaconid shifted further anteriorly and with a paraconid cusp located more posteriorly in relation to the protoconid so that the trigonid is less open anterolaterally. In both *D. martinezi* and *Algeripithecus minutus*, the cristid obliqua of M_1 runs up into the apex of the metaconid whereas in *Wadilemur*, this cristid runs into the middle of the wall between the protoconid and metaconid. *Algeripithecus* also shows a more crenulate talonid with possible traces of a twinned entoconid—characteristics not seen in *Wadilemur*. Close to *Djebelemur* but much larger and apparently considerably younger, *Wadilemur* has lower molars of subequal length that narrow posteriorly whereas, in contrast, *Djebelemur* has a larger M_1 and a smaller M_3 compared with M_2. In the M_1 and M_2 of *Djebelemur*, the crest running posteriorly from the hypocone is relatively higher above the basin and has a slightly developed cuspule, which may be the analog of the M_3 hypoconulid, whereas in *Wadilemur*, this crest is lower and less well defined and has no cuspule. The latter also differs from *Djebelemur* in having a more mesiodistally compressed trigonid, a comparatively larger M_2 relative to M_1, a relatively smaller M_3 talonid basin, and a more distinctly set off hypoconulid (Fig. 2). In addition, the lower molars of *Wadilemur* are more "notched" externally between the talonid and trigonid, especially in $M_{2\text{-}3}$, whereas in *Djebelemur*, the lateral or buccal outline of these teeth is smoothly rounded.

Type species. W. elegans.

Distribution. The Fayum, Egypt, quarry L-41.

Etymology. From Arabic *Wadi*, meaning a valley or wash, plus *Lemur*/*Lemures* L.

W. elegans, New Species

Holotype. CGM specimen 42211, right mandible with P_3–M_3.

Hypodigm. Type and DPC 13439 left dentary with P_4–M_3 and partial ascending ramus.

Species diagnosis. Same as generic diagnosis.

Etymology. From Latin *elegans*, meaning neat, elegant.

Type species. W. elegans.

Anchomomys, Stehlin 1916

Type species. Anchomomys gaillardi.

Distribution. Middle Eocene site at Lissieu, France.

Etymology. From Greek *anchi*, meaning near, plus *Omomys*, name of a North American Eocene primate. This name is from Greek *omos*, meaning shoulder (many other meanings) combined with Greek *mys*, -mouse.

FIG. 2. Stereopair of *W. elegans* type CGM Cairo Geological Museum (CGM) 42211. (×11.) Right mandibular fragment with P_3–M_3. Note that the large and lingually directed entoconids are broken off on both M_1 and M_2.

A. milleri, New Species

Holotype. CGM 42847, right mandible with complete horizontal ramus, damaged symphysis, and posterior angular and coronoid processes missing. Preserves right canine through M_2.

Species diagnosis. A. milleri is slightly smaller in size than *W. elegans* (Table 1), and the molar metaconids do not seem to project quite as far lingually as in that species. It is slightly larger than *Schizarodon* and much larger than *Omanodon*. The paraconid crest is relatively a little longer and directed more in an anteroposterior line, so the angle between it and the protocristid is much wider—a resemblance to other species of *Anchomomys*. As in *Wadilemur* and *Djeblemur*, the paraconid crests slightly overlap the tooth in front of them at a point where the hypoconulid would be were it present, and both M_1 and M_2 are slightly notched on the distal end where this crest overhangs the tooth. In *A. milleri*, a continuous crest joins the protoconid and paraconid of M_1, which are broken in *Schizarodon*, and in *Omanodon*, there is no distinct paraconid cusp on this tooth. *A. milleri* is morphologically close to *A. gaillardi* from Lisseau, France, with the anteriorly directed paraconid crest (paracristid) also having a similar-sized metaconid. The cristid obliqua of M_1 in these latter two species is directed toward the apex of the metaconid in the same manner, but *A. milleri* is slightly larger overall. *A. milleri* is less close to *Anchomomys stehlini* from Egerkingen, Switzerland. In the latter species, the positions of cristid obliqua and paracristid more closely resemble the condition in *Schizarodon* and *Omanodon*.

Etymology. The species is named for Ellen Miller, who discovered the type and only specimen.

COMPARISON OF THE NEW SPECIES

Premolars of the type specimen of *W. elegans* are relatively simple, with a single, principal cusp from which a ridge decends both anteriorly and posteriorly along the anteroposterior axis. Lower P_4 is ~20% larger than P_3, and both show a slightly developed, lingually tilted basin of the heel. Molars increase in length posteriorly ($M_1 < M_2 < M_3$), but because of greater trigonid–talonid breadth, M_2 is the largest tooth ($M_1 < M_3 < M_2$). On all three molars, the metaconids are shifted posteriorly relative to the protoconid, and a cristid obliqua runs forward from the hypoconid toward a line between the protoconid and metaconid. There is no paraconid cusp—only a forward-directed paracristid. The entoconids of the type are broken off in both M_1 and M_2 but are preserved in DPC 13439, where they project lingually with a distinct flare. Hence, in outline viewed from above, all three molars have a distinct notch both lingually and labially between the trigonid and talonid. Neither M_1 nor M_2 of CGM 42211 shows any trace of a hypoconulid, but, in M_3, the hypoconulid is present and well developed and is nearly as large as the hypoconid whereas the entoconid is comparatively much reduced. Although the above features can also be determined in DPC 13439, this particular specimen has considerable damage to the P_3 and some breakage in the trigonid of M_1. In this second specimen also, part of the back of the ramus is preserved and seems rather elongated compared with contemporary primates, inasmuch as the length from in front of P_3 to in back of M_3 is 9.5 mm, and the length from the back of M_3 to the back of the mandible between the articular and angular processes is 10.4 mm. From this specimen, the coronoid process is missing, and the head of the articular process is somewhat damaged. The angular process appears to project sharply backward rather than being rounded off, as in contemporary Fayum anthropoids. Also, unlike these Fayum anthropoids, the depth of the mandible is relatively shallow. For example, under the M_1, this depth is 3.3 mm, and trigonid height is 1.5 mm (or M_1 crown height is 45% of mandibular depth). Comparable measurements in *Catopithecus browni* DPC 15415 are 7.4-mm depth under M_1 compared with 2.4-mm estimated unworn height of the M_1 trigonid; hence, M_1 crown height is 32% of mandibular depth (Fig. 3).

Both specimens of *W. elegans* are broken off in front of the P_3, so little can be said of the more anterior teeth. In the type, there is a socket for P_2, which may indicate a two-rooted P_2. In the type and only specimen of *A. milleri*, the P_2 and lower canine are present, but there is no remaining trace of the incisors. At the base of the symphysis, there is evidence of the inferior transverse torus, which fixes the midline and, in turn, indicates that the incisors were small. The lower canine of the type, CGM 42847 is much taller than the P_2 behind it (there is no trace of a P_1), and, because this canine is not at all directed forward like the lateral component of a tooth comb, the specimen gives no evidence that *A. milleri* was a species having a close ancestral relationship to the strepsirrhines. The numerous and detailed resemblances between the lower postcanine teeth of *Microcebus, Wadilemur*, and *Anchomomys* are consequently hard to evaluate. If there is a close phyletic relationship, it would mean that the prosimian tooth comb arose relatively late in time. If these resemblances are coincidental, the degree of similarity between the lower molars and premolars of the present-day lemur and these Paleogene species is paradoxical.

DISCUSSION

At L-41, the largest prosimian is *A. diedes*, and *P. teras* is somewhat smaller. *W. elegans* and *A. milleri* are both larger than *Djebelemur, Omanodon*, and *Shizarodon*, yet they are the smallest Fayum Egyptian primates. Size comparisons can be drawn as follows from the length of P_3 through M_2 in the types of five of these species:

Aframonius diedes: length of P_3–M_2 is 15.1 mm.
Plesiopithecus teras: length of P_3–M_2 is 11.0 mm.
Wadilemur elegans: length of P_3–M_2 is 8.2 mm.
Achomomys milleri: length of P_3–M_2 is 6.8 mm.
Djebelmur martinezi: length of P_3–M_2 is 6.5 mm.

Table 1. Measurement of *W. elegans* and *A. milleri*

	C	P_2	P_3	P_4	M_1tri	M_1tal	M_2tri	M_2tal	M_3tri	M_3tal
Breadth (bucco-lingual)										
W. elegans										
CGM 42211			0.8	0.9	1.3	1.4e	1.4	1.5e	1.3	1.2
DPC 13439			0.9	1.1	1.2	1.2	1.2	1.1	0.9	0.9
A. milleri										
CGM 42847	0.85	0.7	0.7	0.85	0.9	1.0	1.1	1.1		
Length (mesio-distal)										
W. elegans										
CGM 42211			1.4	1.4	1.7		1.8		1.9	
DPC 13439			1.1	1.2	1.5		1.7		2.0	
A. milleri										
CGM 42847	1.5	1.0	1.0	1.2	1.4		1.5			

FIG. 3. Stereopair of right dentary of *A. milleri* type CGM 42847. (×12.) Note the relatively large canine and the anteriorly directed paraconid crest on the molars, which forms a wider angle with the crest between protoconid and metaconid than in *W. elegans*.

The L-41 primates are perhaps considerably younger than *Djebelemur* but are likely to be older than *Omanodon* and *Shizarodon*. Hartenberger and Marandat (12) remarked that the type mandible of *Djebelemur* is very similar to that of *Pseudoloris* from the Eocene of France but did not mention comparisons with living lemurs. The canine they associated with this type specimen is premolar-like and gracile with an apex located in front of the anterior side of the root, so, from the side, the crown looks somewhat like the letter "P." In addition to the type jaw of *Djebelemur* and the isolated lower tooth thought to be a canine, there are two referred upper molars from Chambi, Tunisia. If the canine belongs with this species, it is much more gracile, comparatively, than the canine of *A. milleri* from L-41. Godinot (20) judged that *Djebelemur* should be ranked with the anthropoideans. The two referred upper teeth of *Djebelemur* look anthropoidean-like, but there is no real proof that they actually belong to the same species as the type mandible. Also, these isolated molars are not unlike the molars of *Plesiopithecus*, an undoubted prosimian. These authors (12) interpreted two small alveolae in front of P_3 as being for a two-rooted P_2, which also may be the case in *Wadilemur*. Whatever other resemblances may eventually be demonstrated, Hartenberger and Marandat (12) concluded that *Djebelemur* is a cercamoniine adapid with some characters "reminiscent of anthropoids."

In 1993, Gheerbrant *et al*. (14) published a description of two new genera and species that they ranked taxonomically in the tribe Anchomomyini. The first of these, *O. minor*, they declared the smallest adapid. Although these authors were not certain of the meaning of the similarities, they cited over a dozen dental characters held in common between *Omanodon* and the cheirogaleid lemur *Microcebus*. (14, pp. 179–180). These authors stated further that, except for the similarities they itemized between these two Omani genera and the cheirogaleids (as well as some with *Djebelemur*), the two Oman primates belonged with the adapids and suggested a strong connection with the European species of the genus *Anchomomys*. They regarded the relationship as close enough to imply a trans-Tethyean dispersion to Afro-Arabia. Finally, Gheerbrant *et al*. (14) stressed that *Omanodon* and *Shizarodon* were among the latest known Paleogene adapids perhaps of Priabonian age. This differs from the range of the anchomomyines in Europe, which do not survive beyond the base of the Priabonian age. They suggested that this seemingly late survival, if real, may be due to less extreme climatic variations in the more southerly regions.

Godinot (20) commented on the paper of Gheerbrant *et al*. (14) and questioned their view that the reduced metaconid and anteriorly extended paracristed on M_1 could be derived from an *Anchomomys*-like morphology, challenging that the anteriorly extended paracristid of *Omanadon* could be derived from the shorter anchomomyine M_1 paracristid. Godinot stated that "reduction of the metaconid [of *Omanodon* and *Shizarodon*] is not found in adapiformes," and he urged that the two Oman genera, on the basis of the referred P_4 (Taqah, Oman) 260, showed similarities to both *Microcebus* and some anthropoideans—"simiiformes" in his usage. He considered the low and reduced metaconid more typical of omomyids, lemuriformes, or anthropoideans. Although admitting that *Shizarodon* and *Omanodon* are difficult to interpret, Godinot favored ranking them with the anthropoideans. However, I do not see the resemblance in the upper molars of *Omanodon* with those oligopithecines. Also, it does not seem that the metaconids of these two Omani prosimians are particularly reduced nor do they seem to be particularly small in *Wadilemur* or *A. milleri*. Fig. 4, a lateral view of the type of *W. elegans*, shows well developed, *Anchomomys*-like metaconids.

All of the differences of opinion discussed above raise two important points about these small primates. The first is that when taxa are based only on single teeth, small groups of isolated teeth, or even on mandibles having fewer than five teeth, the very incompleteness of the material weakens the scientist's ability to achieve a correct taxonomic allocation. The best of modern practice in paleontology mandates that fossils documented by only one to five isolated teeth should not be named at all. This stricture definitely applies to the type and only species of: *Biretia, Tabelia*, and *Shizarodon*, for instance. The situation is not much better with the type species of *Algeripithecus* and *Omanodon*. Simons *et al*. (21) dealt with this same issue more appropriately when they reported a few omomyid teeth and a lorisid tooth from the Fayum but did not name them. The assignment of isolated teeth to the hypodigm

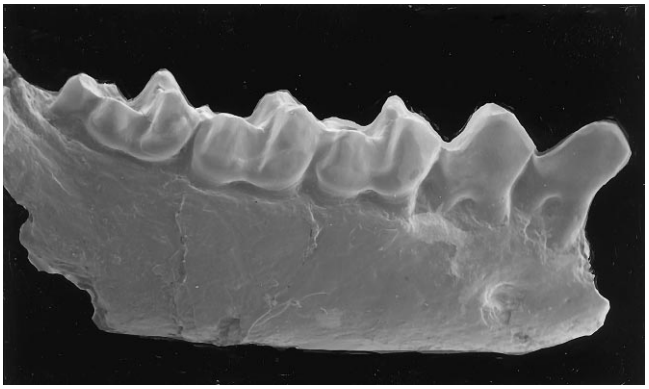

FIG. 4. Lateral view of the type mandible of *W. elegans* CGM 42211. (×5.6.) Right mandibular fragment with P_3–M_3. Note the well developed metaconids.

of a species is an act of judgment by the scientists concerned. Paleontologists well know that, in the past, there have been a number of cases in which even upper and lower jaws were assigned to different genera. At L-41, for instance, at least eight species of small primates exist. The same could be the case for any of the other Afro-Arabian sites discussed here. Assuming a collection of five upper and five lower isolated teeth from L-41, it would be impossible to make a determination, and any grouping one might arrive at would most likely be fictitious. The full extent of this situation for Afro-Arabian Paleogene primates is shown in Table 2. Taking a particular case as an example, *Omanodon* is supposed to stand as a genus separate from *Anchomomys* on the basis of upper molar characteristics detected in the referred, isolated upper teeth from Oman. For the reasons stated, it can be very risky to associate such scattered elements in one taxon.

The second point worth stressing is that, taken altogether, the uncertainty of the various authors discussed above as to whether particular primates are adapiformes or anthropoideans may simply be an indication that, with such fragmentary material, it is not easy to distinguish between those groups we know as adapiformes and early anthropoideans. These similarities, if correct, may of course mean that the two groups are closely related. Authorities have less difficulty separating tarsiids and omomyids and distinguishing them from such forms as *Catopithecus* and *Oligopithecus*, about which a wide range of paleontologists have said that they look like adapids. In any case, it is through the "window" of the whole range of Fayum anthropoideans that we must look to see the correct picture of what the relatives and ancestors of early anthropoideans should look like.

Table 2. Numbers of teeth described to date that document seven genera of small Paleogene primates from either North Africa or Arabia

Genus	Description
Beritea pivoti	One tooth
Algeripithecus minutis	Several isolated upper and lower teeth
Tabelia hammadae	Apparently three upper teeth and one lower tooth
Azibius trerki	Lower jaw with three teeth
Diebelemur martinezi	Left mandible with P_3–P_3 and isolated teeth including two uppers
Omanodon minor	Two lower teeth, parts of five upper teeth, and possibly seven other teeth (some not referred with certainty)
Shizarodon dhofarensis	One and a half lower molars

I thank F. A. Ankel-Simons, E. R. Miller, and D. T. Rasmussen for reviewing the manuscript and providing useful comments. I also acknowledge the support and help of many colleagues of the staff of the Egyptian Geological Survey and Mining Authority and of CGM. The specimens described here were developed from the matrix by P. S. Chatrath and F. A. Ankel-Simons. Scanning electron micrographs for the figures were prepared at Duke Univ. by L. M. Eivest. The research reported here was supported by grants from the National Science Foundation (BNS-91-08445 and SBR-95-07770).

1. Simons, E. L. (1989) *Proc. Natl. Acad. Sci. USA* **86,** 9965–9960.
2. Simons, E. L. (1992) *Proc. Natl. Acad. Sci. USA* **89,** 10743–10747.
3. Simons, E. L. (1995) *Science* **268,** 1885–1888.
4. Simons, E. L. (1995) *Am. Mus. Nov.* **3124,** 1–10.
5. Simons, E. L., Rasmussen, D. T. & Gingerich, P. D. (1995) *J. Hum. Evol.* **29,** 577–589.
6. Thomas, H., Roger, J., Sen, S. & Al-Sulaimani, Z. (1988) *C. R. Acad. Sci.* **306,** 823–829.
7. Godinot, M. & Mahboubi, M. (1992) *Nature (London)* **357,** 324–326.
8. Godinot, M. & Mahboubi, M. (1992) *J. Hum. Evol.* **7,** 9–16.
9. Godinot, M. & Mahboubi, M. (1994) *C. R. Acad. Sci.* **319,** 357–364.
10. Beard, K. C., Tao, Q., Dawson, M. R., Wang, B. & Li, C. (1994) *Nature (London)* **368,** 604–609.
11. Simons, E. L. (1995) *Science* **268,** 1885–1888.
12. Hartenberger, J. L. & Marandat, B. (1992) *J. Hum. Evol.* **7,** 9–16.
13. Ducrocq, S., Jaeger, J.-J., Chaimanee, Y. & Suteethorn, V. (1995) *J. Hum. Evol.* **28,** 477–485.
14. Gheerbrant, E., Thomas, H., Roger, J., Sen, S. & Al-Sulaimani, Z. (1993) *Paleovertebrata* **22,** 141–196.
15. Simons, E. L. & Rasmussen, D. T. (1994) *Proc. Natl. Acad. Sci. USA* **91,** 9946–9950.
16. Sudre, J. (1975) *C. R. Acad. Sci.* **280,** 1539–1542.
17. Fleagle, J. G. (1994) in *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark*, eds. Corruccini, R. S. & Ciochon, R. L. (Prentice Hall, Englewood Cliffs, NJ), pp. 17–35.
18. Kappleman, J., Simons, E. L. & Swisher, C. C. (1992) *J. Geol.* **100,** 647–668.
19. Rasmussen, D. T., Bown, T. M. & Simons, E. L. (1992) in *Eocene-Oligocene Climatic and Biotic Evolution*, eds. Prothero, D. R. & Bergren, W. A. (Princeton Univ. Press, Princeton), pp. 548–566.
20. Godinot, M. (1994) in *Anthropoid Origins*, eds. Fleagle, J. G. & Kay, R. F. (Plenum, New York), pp. 235–296.
21. Simons, E. L., Bown, T. M. & Rasmussen, E. L. (1987) *J. Hum. Evol.* **15,** 431–437.