Proc. Natl. Acad. Sci. USA
Vol. 96, pp. 2559–2562, March 1999
Anthropology

Canine sexual dimorphism in Egyptian Eocene anthropoid primates: *Catopithecus* and *Proteopithecus*

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Contributed by Elwyn L. Simons, December 29, 1998

ABSTRACT Two very small late Eocene anthropoid primates, *Catopithecus browni* and *Proteopithecus sylviae,* from Fayum, Egypt show evidence of substantial sexual dimorphism in canine teeth. The degree of dimorphism suggests that these early anthropoids lived in social groups with a polygynous mating system and intense male–male competition. *Catopithecus* and *Proteopithecus* are smaller in estimated body size than any living primates showing canine dimorphism. The origin of canine dimorphism and polygyny in anthropoids was not associated with the evolution of large body size.

Sexual dimorphism in canine teeth is widespread among living anthropoid primates (1) but is absent or very weak among living prosimians (2). Among primates, the magnitude of dimorphism is associated with patterns of intrasexual aggression, group size, and demography (1, 3–6). Some studies have argued that the magnitude of sexual dimorphism is also correlated with body size, diet, substrate preferences and phylogenetic inertia (1, 3, 6–10). Although canine dimorphism has been identified in a variety of fossil anthropoids from the Oligocene and Miocene and in several groups of Eocene prosimians, we know very little about canine dimorphism in the earliest anthropoids. In this paper, we present the evidence for canine sexual dimorphism in two of the earliest fossil anthropoids, *Catopithecus browni* and *Proteopithecus silviae*, from the late Eocene of the Fayum, Egypt. They belong in different families: the former in Propliopithecidae and the latter in Proteopithecidae. Hence the development of canine dimorphism was likely not a new feature among anthropoideans at the time of deposition of Quarry L-41. The data reported here not only provide insights into aspects of the social and reproductive behavior of the earliest anthropoids but also offer important evidence about the mechanisms underlying the evolution of dimorphism in primates.

Both *Catopithecus* and *Proteopithecus* come from the late Eocene Quarry L-41 in the lower sequence of the Jebel Qatrani Formation of Fayum, Egypt. The estimated age of the quarry, based on paleomagnetic correlations is 36 Myr (11). Thus far, this quarry has yielded nine primate species, including five early anthropoids belonging in three or more families (12).

Catopithecus browni is the most abundant primate from L-41 and is known from several relatively complete but crushed skulls, numerous mandibular specimens, and a few postcranial elements. Previous analyses indicate that *Catopithecus* had a body mass of 400–800 g, was diurnal, had an insectivorous and frugivorous diet, a catarrhine dental formula of 2.1.2.3 and was an arboreal quadruped (13–16). The phylogenetic affinities of *Catopithecus* are not agreed on. Most authorities consider *Catopithecus* and its relative *Oligopithecus* to be sister taxa of the later propliopithecine catarrhines, and hence a close relative of *Propliopithecus* from the early Oligocene of Africa and Oman (15–18). However, in a phylogenetic analysis of anthropoid evolution that strived to be different, Kay and colleagues (19, 20) placed *Catopithecus* as the sister group of all later anthropoids. This conclusion is belied by the catarrhine dental formula of *Catopithecus* and by its specifically propliopithecine-like dental and postcranial characteristics, which distinctly differ from those of *Proteopithecus*. Although several studies have suggested the presence of canine dimorphism in *Catopithecus*, its presence has never been formally documented (15, 19, 21). The usual difference in size between lower jaws and teeth of two individual male and female *Catopithecus* was figured by Simons and Rasmussen (15).

Proteopithecus sylviae is a tiny anthropoid species from L-41 that is less common than *Catopithecus*, although it is the second most frequently found primate there. To date it is represented by two skulls, over 30 maxillary or mandibular specimens, and a few limb bones (21, 22). Estimated body size for *Proteopithecus* is approximately 250 g. Like *Catopithecus*, *Proteopithecus* was almost certainly diurnal, had a frugivorous–insectivorous diet, and was arboreal with adaptations for both leaping and quadrupedal progression. *Proteopithecus* has a dental formula of 2.1.3.3. and has most commonly been identified as a non-catarrhine basal anthropoid possibly near the origin of platyrrhines (21, 22). In the description of the dentition of *Proteopithecus*, it was suggested that this species showed evidence of canine dimorphism (21).

METHODS

Sexual dimorphism of a population or species is usually estimated as the ratio of the mean male size value over the mean female value. Reliable identification of sex in most fossils is problematic, making it difficult to estimate sexual dimorphism. Several methods have been advanced for identifying sexual dimorphism from isolated dental and gnathic remains of fossil taxa (23). For estimating the level of canine dimorphism in *Catopithecus* and *Proteopithecus*, we have used three of these: extrapolation from the coefficient of variation (CV method), division of the sample into two groups based on the mean (Mean method), and calculating the ratio of the largest and smallest values. The last method obviously overestimates dimorphism but nevertheless provides a cap for the maximum degree of dimorphism that could be present in the sample.

RESULTS

For *Catopithecus* we are able to estimate dimorphism for mesiodistal length, buccolingual length, and crown height dimensions of both the upper and lower canines (Table 1; Fig. 1). The mesiodistal and buccolingual dimensions of both upper and lower canines yield similar estimates of dimorphism using

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Table 1. Estimates of sexual dimorphism in *Catopithecus* and *Proteopithecus*

	Mandibular canine			Maxillary canine			
Method	MD	BL	HT	MD	BL	HT	Jaw depth
Catopithecus		(n = 12)			(n = 4)		(n = 7)
CV	1.22	1.25	1.33	1.18	1.21	1.50	1.13
Mean	1.22	1.22	1.31	1.17	1.21	1.43	1.15
Min/Max	1.38	1.58	1.53	1.22	1.30	1.64	1.17
Proteopithecus		(n = 3)					
Min/Max	1.51	1.28	1.28	—	—	—	—

MD, mesiodistal length; BL, buccolingual breadth; HT, crown height.

the CV and Mean methods (Table 1). The height dimensions, particularly that of the maxillary canine, yield much higher values. The values are comparable to the levels of dimorphism found in New World platyrrhines such as *Saimiri* or *Alouatta* (Fig. 1). In addition, measurements of mandibular depth in *Catopithecus sylviae* suggest that this species also exhibited substantial body size dimorphism (24).

The canine sample for *Proteopithecus* is much smaller than that for *Catopithecus.* Only a single (large) upper canine and three moderately worn lower canines are suitable for measuring. The lower canines suggest considerable sexual dimorphism in both length and breadth (Table 1, Fig. 1). Given the small sample size, the strong magnitude of canine occlusal dimorphism in *Proteopithecus* is likely overestimated. Nevertheless, it is notable that occlusal dimorphism in many anthropoids is usually substantially weaker than that of the crown height (25).

DISCUSSION AND CONCLUSIONS

Because canine dimorphism is correlated with levels of intrasexual aggression in mating competition (1, 3, 6, 24) and with general features of social organization, we can use the dimorphism estimates for *Catopithecus* and *Proteopithecus* to reconstruct features of the social behavior of these Eocene anthro-

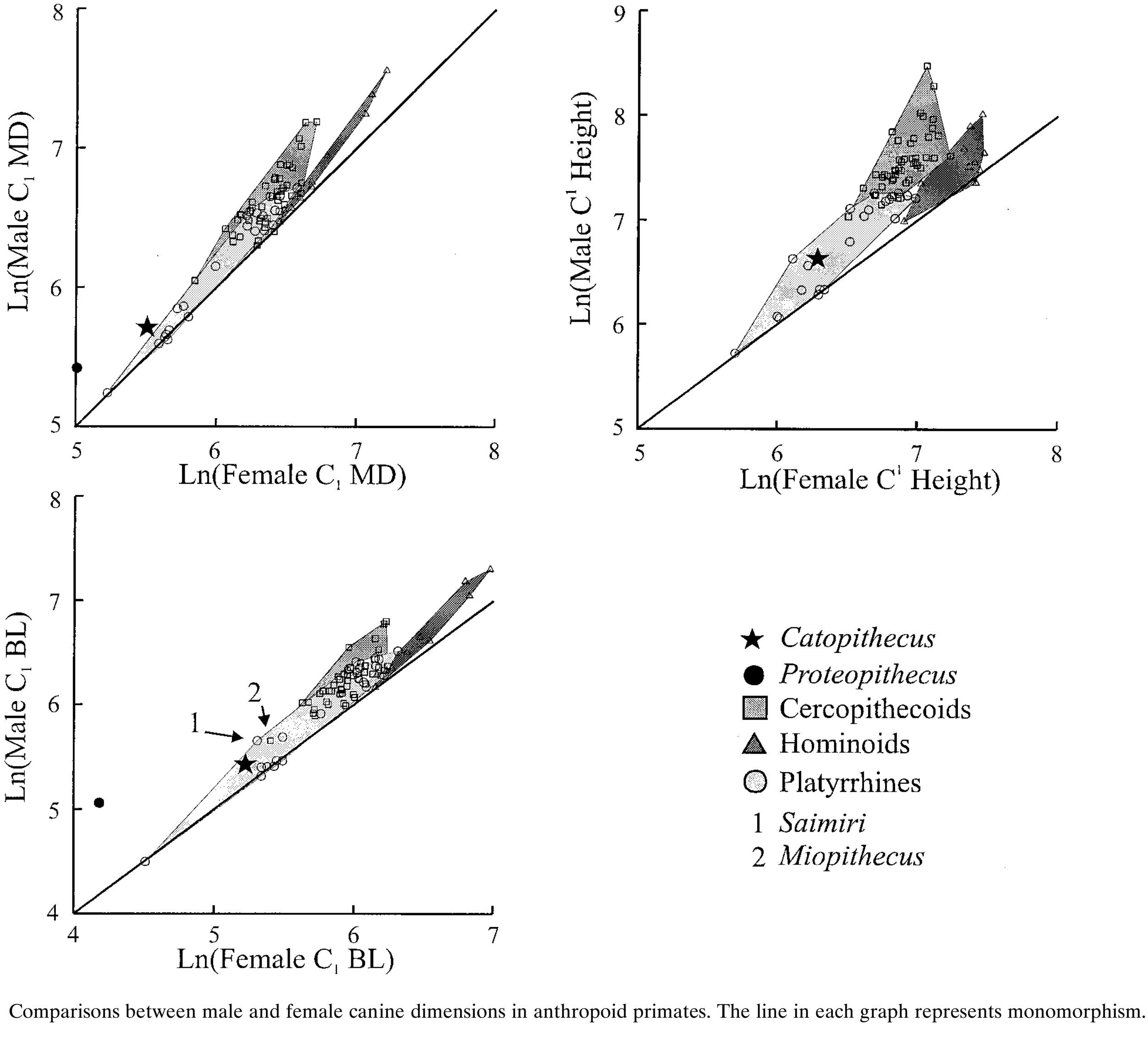

FIG. 1. Comparisons between male and female canine dimensions in anthropoid primates. The line in each graph represents monomorphism.

poids. Canine dimorphism in both *Catopithecus* and *Proteopithecus* exceeds that found in living anthropoids characterized by monogamy, polyandry, or cooperative breeding groups (Fig. 2). Hence, *Catopithecus* and *Proteopithecus* almost certainly had polygynous mating systems. The estimated magnitude of dimorphism for *Catopithecus* and *Proteopithecus* overlap extensively those species characterized by Plavcan and van Schaik (1) as exhibiting "high-intensity" male–male competition (Competition Types 3 and 4). Among modern anthropoids, such groups are usually characterized by several males living with a group of females and establishing a clear dominance hierarchy, or by a single male living with a group of females. Estimates of *Catopithecus* canine dimorphism are lower than those for our small sample of *Proteopithecus* and fall near the median of the range of polgynyous species in which male competition is less frequent. The estimate of jaw depth dimorphism in *Catopithecus* also overlaps high-intensity male–male competition species. Canine and body mass dimorphism are allometrically associated with increasing body mass in primates: larger species tend to be more dimorphic (1, 6). The mechanism underlying this correlation has been widely debated. Leutenegger and Cheverud (7, 8) proposed a quantitative genetic model that suggested that greater magnitudes of dimorphism evolve as a direct consequence of increasing body size. More recently, Mitani and colleagues (26) offered evidence that the correlation between size and dimorphism reflects an underlying correlation between body size and patterns of female dispersal, which ultimately affect operational sex ratios (27). Clearly, the demonstration of substantial canine and mass dimorphism in the earliest anthropoids undermines both models, suggesting that neither dimorphism nor polygyny are necessarily tied to patterns of increasing body mass in primates.

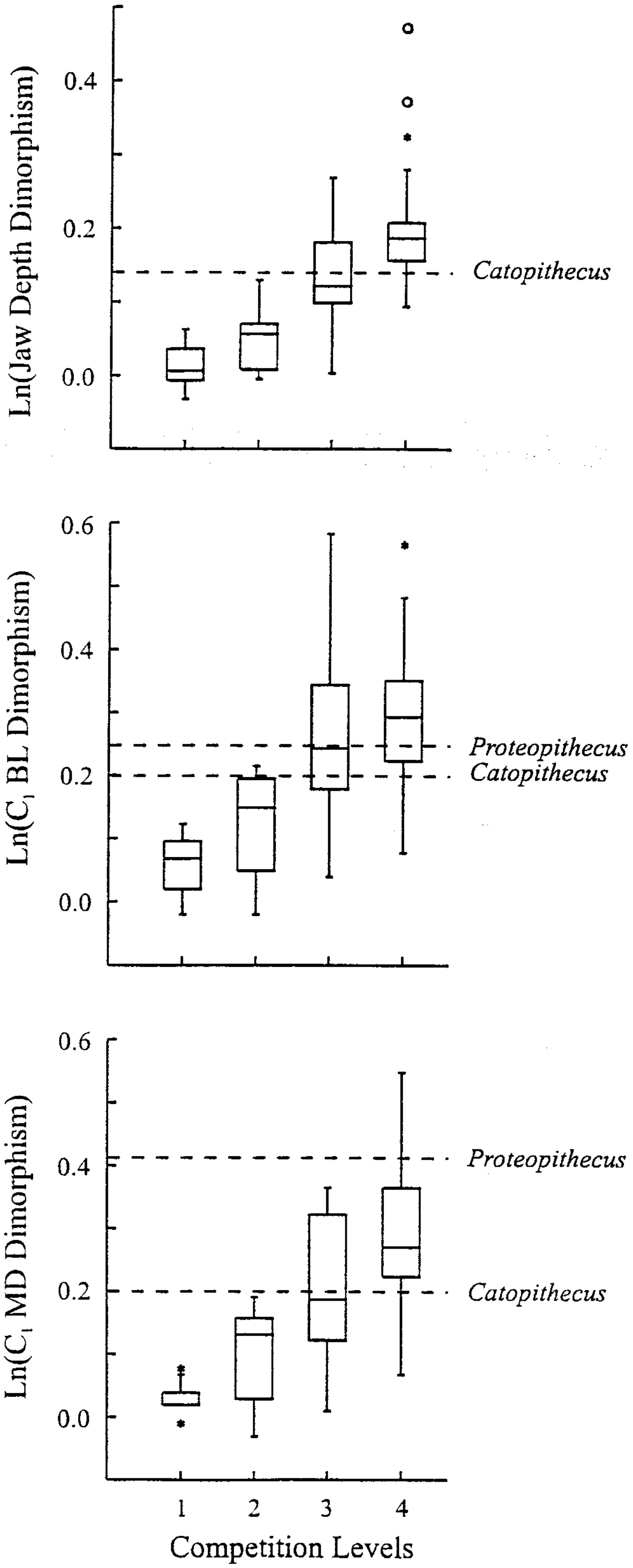

FIG. 2. Box and whisker diagrams of dimorphism among extant anthropoids within "competition levels" from Plavcan and van Schaik (1, 6). The dotted lines illustrate the estimated level of dimorphism in *Catopithecus* and *Proteopithecus*. Asterisks and circles are isolated extant taxa.

Among living primates, canine dimorphism is essentially absent in living strepsirhines and tarsiers. Among New World platyrrhines, canine sexual dimorphism is either weak or absent in about half of the 16 living genera and is absent among the smallest taxa. In Old World catarrhines, canine dimorphism is widespread, being greatly reduced only in hylobatids, *Presbytis potenziani*, and humans. The finding of considerable sexual dimorphism in two of the earliest and most primitive anthropoids along with the presence of dimorphism in the parapithecids documented earlier (24) indicate that canine sexual dimorphism was present very near the base of Anthropoidea and could even have been before the divergence of platyrrhines and catarrhines. This, in turn, might imply that the low levels of dimorphism characteristic of many extant platyrrhines are probably derived.

In view of the near absence of canine dimorphism in all living strepsirrhines and tarsiers and its broad distribution among living and fossil anthropoids, what can we say about the origin of this feature among anthropoids? One of the most surprising discoveries in primate evolution during the past decade has been the diversity and small size of Eocene anthropoids (11, 18). *Catopithecus* and *Proteopithecus* are smaller than any living primate showing canine dimorphism (Fig. 1). The presence of sexual dimorphism in these tiny anthropoids clearly indicates that the initial appearance of canine sexual dimorphism in early anthropoids was not associated with an increase in body size. Likewise, although several studies have found a correlation between canine dimorphism and terrestriality, all postcranial remains indicate that the Eocene and early Oligocene anthropoids from Fayum were arboreal. Perhaps the most distinctive characteristic of anthropoids compared with the majority of living (and probably fossil) prosimians is their diurnality (28). Small, diurnal anthropoids are particularly susceptible to predation, increasing selection for large groups. Hence, we speculate that the origin of polygyny in anthropoid primates was facilitated by a shift to group living necessitated by predation pressure (29, 30) and not necessarily by a shift in female dispersal patterns associated with shifts in diet and resource utilization.

We thank Friderun Ankel-Simons, P. D. Gingerich, J. Hunter, W. S. McGraw, S. Sampson, C. F. Ross, S. Fleagle, and especially W. Jungers for suggestions and comments on this work. P. S. Chatrath and F. A. Ankel-Simons carried out most of the arduous preparation on the delicate specimens from L-41. We thank the staff of the Egyptian Geological Survey and the Cairo Geological Museum for assisting and supporting our field work. The research reported here was supported by research grants from the National Science Foundation (to E.L.S., J.M.P., and J.G.F), and the L. S. B. Leakey Foundation (to E.L.S. and J.G.F.). This is Duke Primate Center publication no. 666.

1. Plavcan, J. M. & van Schaik, C. P. (1992) *Am. J. Phys. Anthropol.* **87,** 461–477.
2. Kappeler, P. M. (1996) *J. Evol. Biol.* **9,** 43–65.
3. Leutenegger, W. & Kelley, J. T. (1977) *Primates* **8,** 117–136.
4. Gaulin, S. J. C. & Sailer, S. D. (1984) *Int. J. Primatol.* **5,** 515–535.
5. Ely, J. & Kurland, J. A. (1989) *Int. J. Primatol.* **10,** 151–171.
6. Plavcan, J. M. & van Schaik, C. P. (1997) *Am. J. Phys. Anthropol.* **103,** 1–27.
7. Leutenegger, W. & Cheverud, J. M. (1982) *Int. J. Primatol.* **3,** 387–402.
8. Cheverud, J. M, Dow, M. M. & Leutenegger, W. (1985) in *Size and Scaling in Primate Biology*, ed. Jungers, W. L. (Plenum, New York), pp. 51–60.
9. Greenfield, L. O. (1992) *J. Hum. Evol.* **23,** 469–480.
10. Martin, R. D., Willner, L. A. & Dettling, A. (1994) in *The Differences Between the Sexes*, eds. Short, R. V. & Balaban, E. (Cambridge Univ. Press, Cambridge, U.K.), pp. 159–200.
11. Simons, E. L. & Rasmussen, D. T. (1994) *Evol. Anthropol.* **3,** 128–138.
12. Simons, E. L. & Chatrath, P. S. (1998) *Proc. Geol. Soc Egypt Special Publ.* **75,** 775–783.
13. Simons, E. L. (1990) *Science* **247,** 1507–1509.
14. Simons, E. L. (1995) *Science* **268,** 1885–1888.
15. Simons, E. L. & Rasmussen, D. T. (1996) *Am. J. Phys. Anthropol.* **100,** 261–292.
16. Gebo, D. L., Simons, E. L., Rasmussen, D. T. & Dagosto, M. (1994) in *Anthropoid Origins*, eds. Fleagle, J. G. & Kay, R. F. (Plenum, New York), pp. 203–233.
17. Ankel-Simons, F., Fleagle, J. G. & Chatrath, P. (1998) *Am. J. Phys. Anthropol.* **106,** 413–424.
18. Fleagle, J. G. (1999) *Primate Adaptation and Evolution* (Academic, San Diego), 2nd Ed.
19. Kay, R. F., Ross, C. F. & Williams, B. A. (1997) *Science* **275,** 797–804.
20. Ross, C., Williams, B. A. & Kay, R. F. (1998) *J. Hum. Evol.* **35,** 221–306.
21. Miller, E. R. & Simons, E. L. (1997) *Proc. Natl. Acad. Sci. USA* **94,** 13760–13764.
22. Simons, E. L. (1997) *Proc. Natl. Acad. Sci. USA* **94,** 14970–14975.
23. Plavcan, J. M. (1994) *Am. J. Phys. Anthropol.* **94,** 465–476.
24. Fleagle, J. G., Kay, R. F. & Simons, E. L. (1980) *Nature (London)* **287,** 328–330.
25. Plavcan, J. M. (1993) *Am. J. Phys. Anthropol.* **92,** 201–216.
26. Mitani, J. C., Gros-Louis, J. & Richards, A. F. (1996) *Am. Nat.* **147,** 966–980.
27. Emlen, S. & Oring, L. (1977) *Science* **197,** 215–223.
28. Ross, C. (1996) *Am. J. Primatol.* **40,** 205–230.
29. van Schaik, C. P. (1983) *Behavior* **87,** 120–144.
30. Terborgh, J. W. (1983) *Five New World Primates* (Princeton Univ. Press, Princeton).