The earliest fossil evidence for sexual dimorphism in primates

(*Notharctus*/paleontology/Eocene/primate evolution)

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ABSTRACT Recently obtained material of the early Eocene primate *Notharctus venticolus*, including two partial skulls from a single stratigraphic horizon, provides the geologically earliest evidence of sexual dimorphism in canine size and shape in primates and the only unequivocal evidence for such dimorphism in strepsirhines. By analogy with living platyrrhines, these data suggest that *Notharctus venticolus* may have lived in polygynous social groups characterized by a relatively high level of intermale competition for mates and other limited resources. The anatomy of the upper incisors and related evidence imply that *Notharctus* is not as closely related to extant lemuriform primates as has been recently proposed. The early Eocene evidence for canine sexual dimorphism reported here, and its occurrence in a nonanthropoid, indicates that in the order Primates such a condition is either primitive or evolved independently more than once.

The fossil record of early Cenozoic primates grows richer each year, providing evidence that bears uniquely on the initial differentiation of the order and the phylogenetic relationships of living and extinct taxa. When the fossil remains are sufficiently complete and well preserved, additional critical paleobiological issues can be studied and inferred, such as mode of locomotion, dietary adaptations, and social organization. Although a number of studies have assessed the mode of locomotion (1–3) and dietary adaptations (3, 4) of early Cenozoic primates, little is known concerning the social organization of these animals. Here, we report recently obtained material, the most complete yet recovered, of the early Eocene primate *Notharctus venticolus*, which sheds light on the probable form of its social organization and the phylogenetic position of the genus with respect to other living and fossil primates.

MATERIALS AND METHODS

The new fossils of *Notharctus* were excavated from Quarry 6 in the Buck Spring area of the Wind River Basin, Natrona County, Wyoming (5). The quarry is one of several extremely fossiliferous concentrations found in the B-2 stratigraphic horizon in the type area of the Lost Cabin Member of the Wind River Formation (5–8). Fossil mammals associated with these specimens include the primate *Shoshonius cooperi*, the perissodactyl *Lambdotherium popoagicum*, and 62 other species that indicate a late early Eocene age (Lostcabinian; late Wasatchian) (see ref. 9). Analyses of quarry and surrounding sediments reveal that the fossils accumulated in a periodically drained freshwater pond adjacent to a major perennial stream (5).

During the time that the strata at the Buck Spring Quarries were deposited, only one large species of notharctine primate is known to have lived (8). Remains of this species, *N.*
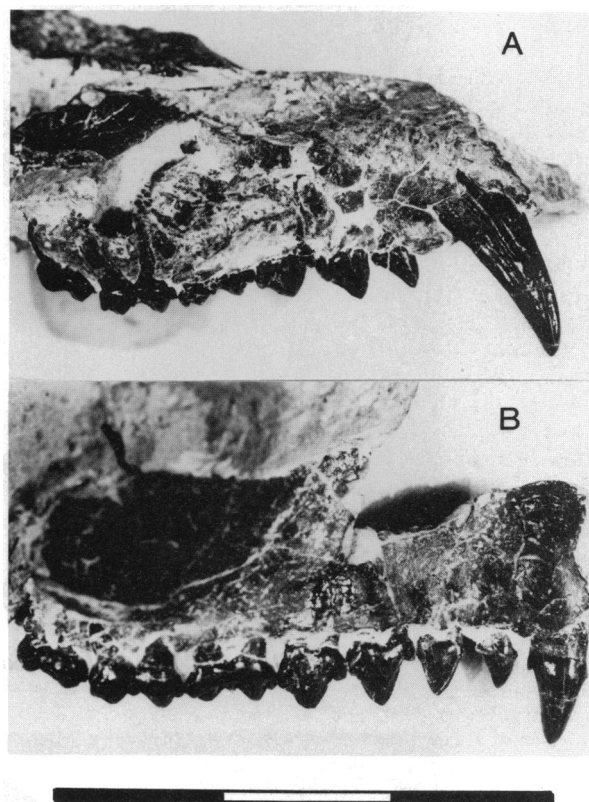
FIG. 1. Lateral view of upper dentitions of *N. venticolus*. (*A*) Male, CM 60497. (*B*) Female, CM 62006. (Scale is in cm units.)

venticolus, are easily distinguished from those of lithosympatric *Notharctus nunienus* on the basis of its larger size and different molar morphology (10–12). Extensive comparisons between the new sample of *Notharctus* from the Buck Spring Quarries and known material of *N. venticolus* and *N. nunienus* (including the type specimens, both of which were also collected from the Lost Cabin Member of the Wind River Formation) leave no doubt that all of the specimens discussed here represent *N. venticolus*.

Measurements of the upper and lower canines in the new sample of *N. venticolus*, including maximum mesiodistal length (L) and maximum labiolingual width (W) (measured perpendicular to L), were obtained using Fowler Max-Cal electronic digital calipers. From these data we calculated several indices of canine dimorphism following the method of Kay *et al.* (13).

RESULTS AND DISCUSSION

Four of the new fossils of *N. venticolus* preserve the upper canines. Although the cheek teeth in these specimens are
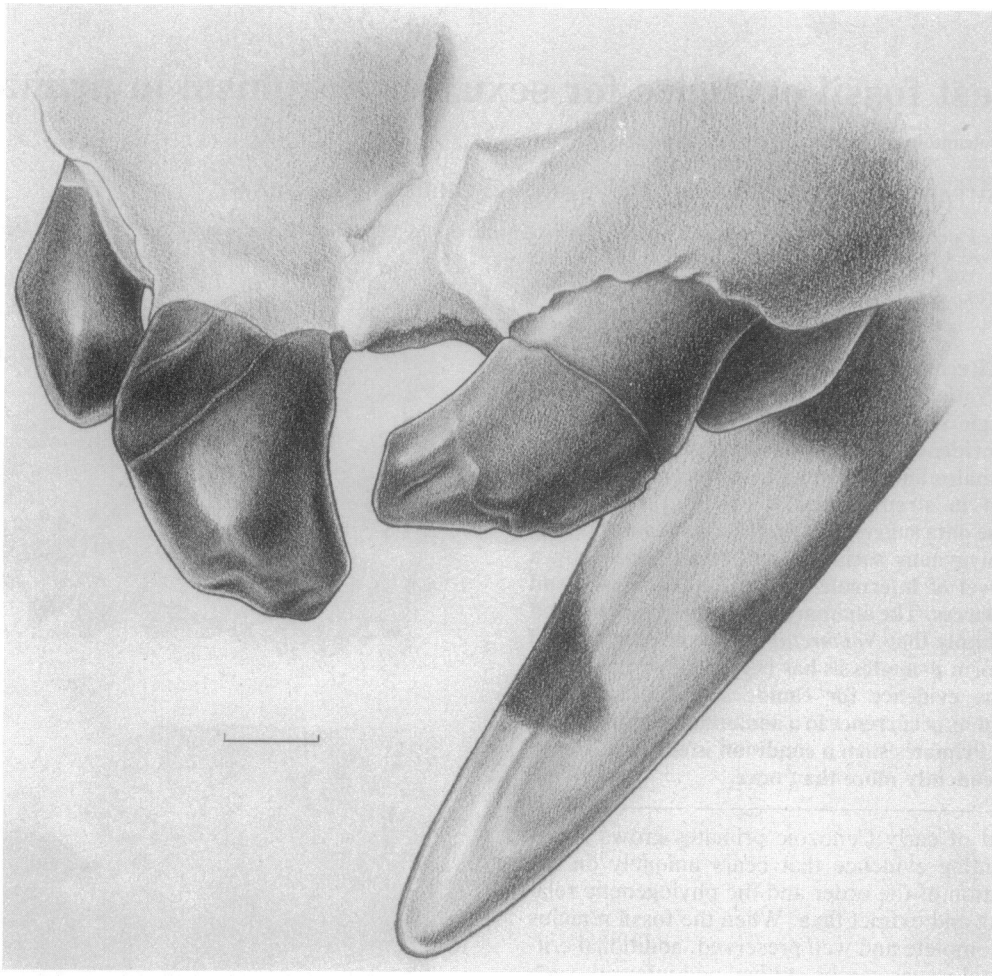
Abbreviation: CM, Carnegie Museum.

FIG. 2.   Anterior dentition of *N. venticolus* (CM 46507), anterior view. (Scale is 1 mm.)
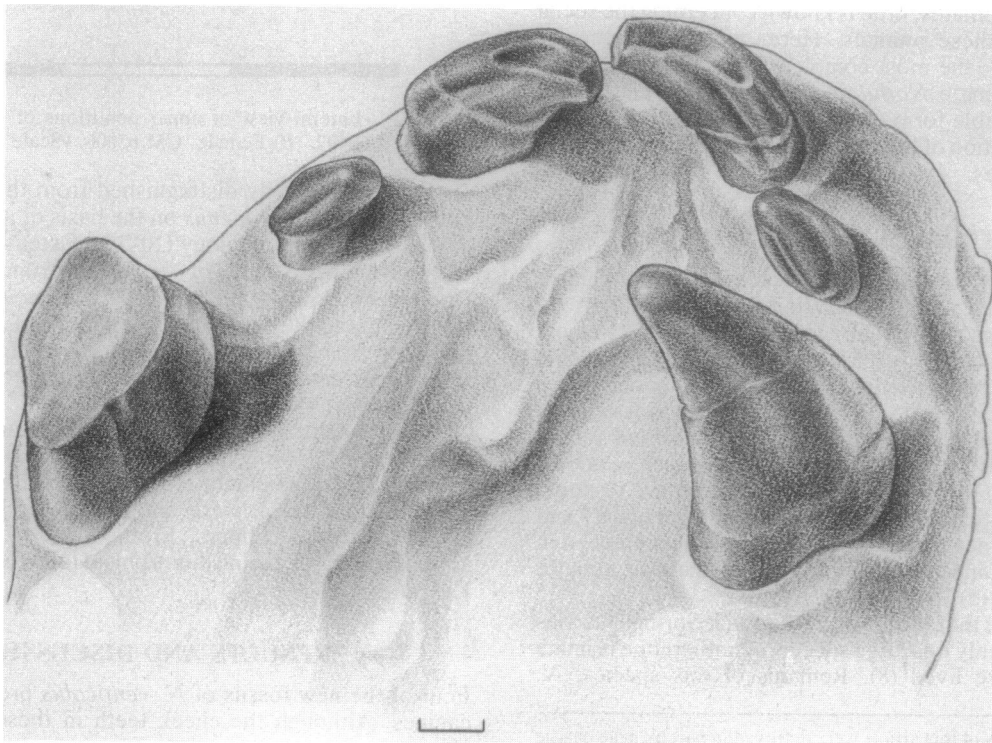

FIG. 3.   Anterior dentition of *N. venticolus* (CM 46507), palatal view. (Scale is 1 mm.)

virtually identical, the upper canines differ markedly in size and shape (Fig. 1). For example, in Carnegie Museum (CM) 46507 (Figs. 2 and 3) and CM 60497 (Fig. 1A), the upper canine is extremely long and tear-drop shaped in cross section due to the presence of a well-developed crest on the distal edge of the crown. The apex of the canine is missing in University of Colorado Museum 47674, but the rest of the crown closely resembles in size and shape the complete upper canines in CM 46507 and CM 60497.

In contrast, in CM 62006 (Fig. 1B), the upper canine is much shorter, more nearly circular in cross section, and bears a much weaker distal crest. We interpret the observed dimorphism in canine size and shape as evidence of substantial sexual dimorphism in *N. venticolus*. By analogy with living primate species that exhibit canine sexual dimorphism, CM 46507 and CM 60497 represent male individuals, whereas CM 62006 is a female. Measurements of the upper and lower canines for all available specimens of *N. venticolus* from the Buck Spring Quarries and the immediate vicinity are provided in Table 1.

The canine dimorphism observed in these specimens cannot be attributed to differences in ontogenetic development. The female specimen (CM 62006), with more heavily worn cheek teeth and a fully erupted canine (its dentoenamel border is clearly visible), unquestionably represents an older individual than one of the males (CM 60497), in which the cheek teeth show little wear and the canine is incompletely erupted. Conversely, the difference in canine crown height between two of the male specimens (CM 46507, CM 60497; see Table 1) can be attributed to different stages of canine eruption.

The lower canines of *N. venticolus* also appear to be sexually dimorphic, although the evidence is less clear than for the upper canines. The only complete lower canine in a jaw (CM 34723) is short and nearly circular in cross section (see Table 1). We interpret this specimen and CM 60496, which shows similar proportions but is less complete, as female individuals. In contrast, a possible male specimen of *N. venticolus*, CM 43168, which lacks the lower canine crown, has a root that is more robust and tear-drop shaped in cross section than in the putative females (Table 1).

The degree of canine sexual dimorphism exhibited by the available sample of *N. venticolus* is assessed quantitatively in Table 1, following the method of Kay *et al.* (13). The canine dimorphism index for this sample is 1.29; however, the relatively small sample size of *N. venticolus* canines requires that this value be treated as an approximation. Taphonomic biases in the fossil record have resulted in the rare preservation of anterior dentitions of early Cenozoic primates (and other small mammals); the sample reported here is unique in

Table 1. Canine measurements, ratios, and canine dimorphism index for *N. venticolus*

Specimen	H	L	W	C_1L	C_1W	C^1L	C^1W	CDI
CM 46507 (m, u)	10.4	4.8	3.0	—	—	—	—	—
CM 60497 (m, u)	8.9	5.0	2.9	—	—	—	—	—
UCM 47674 (m, u)	—	4.8	3.3	—	—	—	—	—
CM 62006 (f, u)	5.1	3.3	2.6	—	—	1.47	1.18	—
CM 43168 (m, l)	—	4.4	3.1	—	—	—	—	—
CM 34723 (f, l)	5.4	3.4	2.8	—	—	—	—	—
CM 60496 (f, l)	—	3.0	2.7	1.38	1.13	—	—	1.29

UCM, University of Colorado Museum; m, male; f, female; u, upper canine; l, lower canine; H, crown height; L, maximum mesiodistal length; W, maximum buccolingual width; C_1L, ratio of mean mesiodistal length of lower canine (male/female); C_1W, ratio of mean buccolingual width of lower canine (male/female); C^1L, same as C_1L, but for upper canine; C^1W, same as C_1W, but for upper canine; CDI, canine dimorphism index (see ref. 13).

preserving anterior dentitions of several individuals of the same species from a single quarry horizon.

Despite the less than ideal sample, it is instructive to compare the degree of canine sexual dimorphism in *N. venticolus* with that documented for extant platyrrhine primates (13). This comparison indicates that the degree of canine sexual dimorphism in *N. venticolus* was similar to that in the most highly dimorphic species of extant platyrrhines (13). The social organization among these dimorphic species (which include *Cebus apella* and all species of *Alouatta* for which behavioral information is available) is distinguished by an extremely high level of intermale competition for estrous females and other limited resources, with an established male dominance hierarchy being maintained throughout the year (13).

Other workers (14–16) have suggested that a high degree of canine dimorphism in higher primates may be the result of factors other than intraspecific male competition, such as: phyletic inertia; natural selection favoring increased body size or increased body size dimorphism; and natural selection for resource partitioning and/or different roles for the sexes in defense against predation. However, the degree of intraspecific male competition remains the most consistently significant correlate of canine sexual dimorphism, at least among platyrrhines (13). If this correlation holds more generally, the social organization of *N. venticolus* may have been characterized by a polygynous breeding strategy with a high level of intermale competition for mates, as occurs in extant platyrrhine species showing marked canine dimorphism (13).

Previous workers have suggested that the canines of notharctines were sexually dimorphic (17, 18), but in all instances these interpretations have been based on isolated specimens from different stratigraphic horizons, on specimens that represent different species, or both. Similar suggestions have also been advanced for the late Eocene primate *Adapis* from Europe (19), but again the fossil dentitions on which these interpretations were based lack precise stratigraphic control and may represent different species of *Adapis* (20, 21) rather than evidence of sexual dimorphism. Thus, the new material of *N. venticolus* provides the geologically earliest evidence for canine sexual dimorphism in primates and the only unequivocal evidence for such dimorphism in strepsirhines. Similar sexual dimorphism is known in Oligocene (22), Miocene (23), and many extant higher primates (13–16) but is not found in extant lemuriforms (24).

One of the new *Notharctus* skulls (CM 46507) has also yielded important phylogenetic information in that it preserves, for the first time, the complete and virtually unworn anterior dentition in place. Specifically, a recent cladistic analysis (25), based on a fragmentary and reconstructed anterior dentition of *Notharctus*, erred in citing the absence of interstitial contact between left and right I^1 as a synapomorphy uniting the "predominantly Eocene adapid (sensu lato) group" (including *Notharctus*) with lemuriforms. Further, these authors presumed that *Notharctus* could be used as a phylogenetic stand-in for "adapids (sensu lato)", without establishing that the latter group is a clade.

The pincer-like shape of left and right I^1 in CM 46507 (Figs. 2 and 3) and their well-developed mesial interstitial facets clearly demonstrate that these incisors did occlude interstitially during life (they are not now in contact due only to postmortem distortion of the snout). Interstitial contact between the upper central incisors is almost certainly the primitive condition for strepsirhine primates, as it also characterizes all European adapids for which the relevant anatomy is known (26, 27). Conversely, the lack of interstitial contact and the presence of a wide median diastema between the upper central incisors appears to be a lemuriform synapomorphy that is functionally correlated with the development of the mandibular toothcomb. In sum, the morphology

of the CM 46507 skull of *Notharctus* implies that this taxon and lemuriforms do not share derived features of phylogenetic significance in their anterior dentition.

To conclude, the anatomy of the anterior upper dentition of *N. venticolus* is consistent with the view (28, 29) that *Notharctus* is a very primitive strepsirhine primate, lying outside the clade that includes all living lemuriforms. As such, the early Eocene evidence for marked canine dimorphism in a primitive strepsirhine reported here suggests that this anatomical feature and its behavioral correlates are either primitive for the order Primates or have evolved independently more than once within the order.

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