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SEXUAL DIMORPHISM IN EARLIEST EOCENE *CANTIUS TORRESI* (MAMMALIA, PRIMATES, ADAPOIDEA)

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Abstract—Cantius torresi is a 1,000-1,300 gm adapoid primate from the earliest Wasatchian land-mammal age in North America. Twelve specimens are now known, which preserve most upper and lower cheek teeth and a few fragmentary postcranial remains. Three specimens show *C. torresi* to have been highly dimorphic in canine size, and measurements of mandibular depth in these and four additional specimens show *C. torresi* to have been moderately dimorphic in body size. The presence of sexual dimorphism in *C. torresi* and other Adapoidea distinguishes adapoids from earlier Proprimates, contemporary and later Tarsioidea, and later Lemuroidea and Lorisoidea. Dimorphism is a primitive characteristic of Adapoidea because it is present at the beginning of the adapoid radiation. But, from a comparative point of view, it is a derived feature linking Adapoidea to anthropoid higher primates, supporting the interpretation that anthropoids evolved from earlier adapoids. Sexual dimorphism means *Cantius* and later adapoids lived in social groups with sex-specific behavioral roles. Living primates with this degree of dimorphism are diurnal and polygynous, and adapoids probably were as well.

INTRODUCTION

Cantius torresi from earliest-Wasatchian biochron Wa-0 is the oldest North American species of a genus that ranges through much of the early Eocene in North America and Europe. *Cantius* is the oldest representative of the 'lemur-monkey' Adapoidea (Adapidae and Notharctidae), some of which resemble later simiiform primates and may be ancestral to Anthropoidea (or Simiiformes). Tooth size in *C. torresi* (see below) indicates a primate species ranging from about 1000-1300 gm in body weight (Gingerich et al., 1982, p. 92), like the range of contemporary European *C. eppsi* and smaller than the range of 1300-1800 gm calculated for later North American *C. ralstoni* (Gingerich et al., 1982, p. 94). *C. torresi* was about the size of an extant night monkey (*Aotus*) or a large squirrel monkey (*Saimiri*), and body size and molar morphology taken together indicate that *C. torresi* was predominantly frugivorous like both of these extant ceboids.

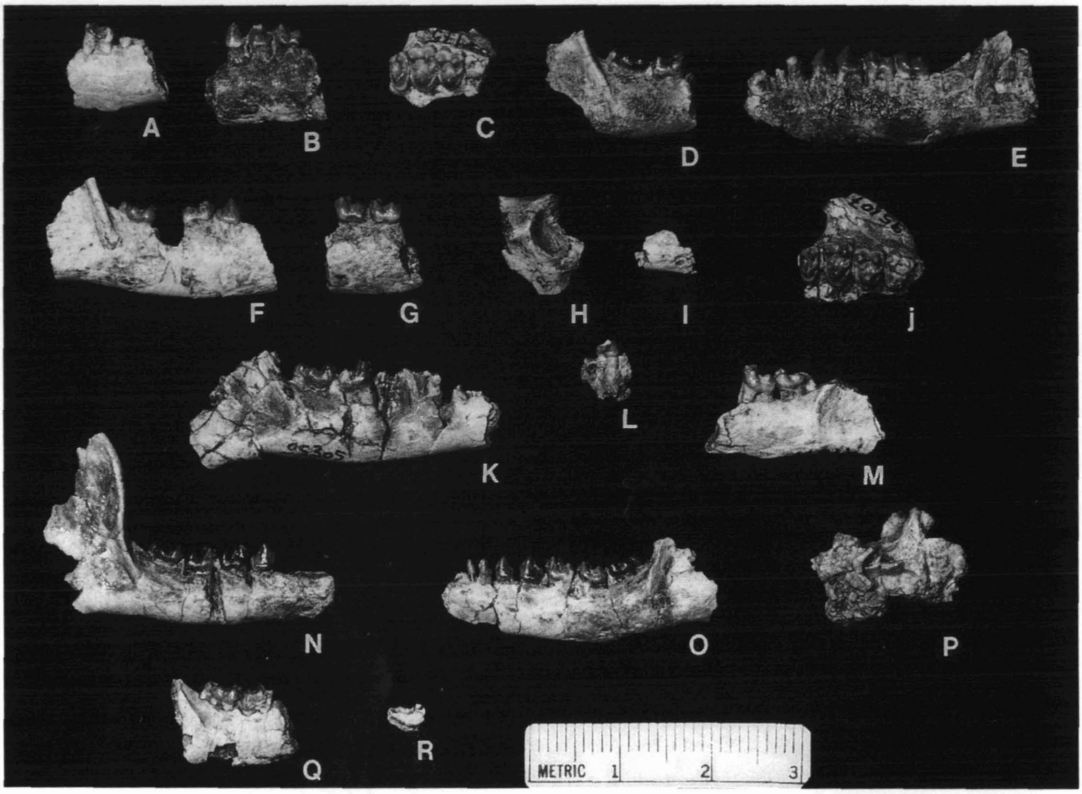

FIG. 1—Specimens of earliest Wasatchian *Cantius torresi* found to date at the type locality, University of Michigan locality SC-67 (A-P), or at SC-69 (Q-R) in the northern Bighorn Basin, Wyoming. All specimens in lateral view unless otherwise noted. A, UM 83467, left dentary with M_2. B, UM 83470 (holotype), left dentary with P_3-M_1. C, UM 83475, right maxilla with M^{1-3} in occlusal view. D, UM 87341, right dentary with M_{2-3}. E, UM 87341, left dentary with C_1-M_2. F, UM 87852, right dentary with P_4, M_1, and M_3. G, UM 87852, left dentary with M_{1-2}. H, UM 87852, part of left pelvis with acetabulum. I, UM 87852, part of right calcaneum. J, UM 95107, right maxilla with P^4-M^3 in occlusal view. K, UM 95305, right dentary with M_{2-3}. L, UM 95796, right maxillary fragment with P^4 in medial view (crown is toward top). M, UM 97899, left dentary with M_{2-3}. N, UM 101958, right dentary with P_4-M_3. O, UM 101958, left dentary with C_1 root and P_1-M_3. P, UM 101958, cranial fragment in uncertain orientation. Q, UM 66143, right dentary with M_{2-3}. R, UM 86132, right M_3. Measurements of teeth in these specimens are listed in Table 1. Scale is in mm.

The idea that Eocene adapoid primates are sexually dimorphic, with males and females differing in canine size, originated with Stehlin (1912, pp. 1231, 1258), who identified specimens of the European adapines *Leptadapis magnus* and *Adapis parisiensis* as male or female based on relative canine size. Subsequently, Depéret (1917) made passing reference to canine dimorphism in *Adapis magnus*, and Schmidt-Kittler (1971) referred female upper and lower canines to this species. I tested Stehlin's idea with a detailed study of skulls and canine teeth of *Leptadapis magnus* and *Adapis parisiensis*. Analysis and interpretation were complicated by postmortem breakage of the skulls and teeth, and by evident reduction of sexual dimorphism with diminishing body size in the *Leptadapis-Adapis* evolutionary lineage, but quantitative comparison with both non-dimorphic and dimorphic living models supported the idea that these adapids were dimorphic (Gingerich, 1981). Godinot (1992) and Lanèque (1993) questioned this, placing specimens with male and female characteristics in separate species, but recent confirmation of dimorphism in *Notharctus* and other adapoids (see below) strengthens the probability that *Leptadapis* and *Adapis* were sexually dimorphic too.

Gregory (1920, p. 125) recognized specimens of the North American notharctine *Notharctus* as male or female based on relative canine size, as did Gingerich (1979). In recent years, Krishtalka et al. (1990) described skulls of *Notharctus venticolis* with conspicuously dimorphic canines, and Alexander (1994) has also interpreted *Notharctus* as being dimorphic. Gingerich and Sahni (1984) suggested that Miocene *Sivaladapis* had dimorphic canines. Finally, Simons et al., in a paper now in press (1996), describe a new adapoid from Fayum quarry L-41 in Egypt, of late Eocene or early Oligocene age, based on dentaries with conspicuously dimorphic canines. Thus sexual dimorphism was widely distributed temporally and geographically in Adapoidea.

The oldest Adapoidea are known from the earliest Eocene of North America (Gingerich, 1986, 1989, and this report); earliest Eocene of Europe (Cooper, 1932; Simons, 1962; Hooker, 1991); early or middle Eocene of North Africa (Hartenberger and Marandat, 1992; and possibly Godinot and Mahboubi, 1992); and later in the early Eocene in South Asia (Russell and Gingerich, 1987). While some of these early records are based on reasonably complete dental remains, the collection described here is the only one that is as yet adequate to demonstrate sexual dimorphism in earliest Adapoidea.

Specimens with catalogue numbers prefaced UM are in collections of the Museum of Paleontology at the University of Michigan.

DESCRIPTION OF NEW SPECIMENS

Cantius torresi was named on the basis of four specimens found at University of Michigan localities SC-67 and SC-69 at the southwestern end of Polecat Bench in Park County, Wyoming (Gingerich, 1986). Three specimens were added to the species sample by Gingerich (1989), and five new specimens are described here. All of the known specimens of *C. torresi* are illustrated in Figure 1 and listed in Table 1. All jaws and jaw fragments contain permanent teeth, and none have been found that preserve deciduous teeth. Measurements given in Table 1 are all new, and were taken with digital calipers checked for accuracy against a graduated glass standard. The digital calipers provide measurements to the nearest 0.01 mm, as recorded here, although it is obviously not possible to measure the curved surfaces of teeth repeatedly with such precision. A statistical summary of dental and mandibular measurements is given in Table 2. C_1 and P_1 excepted, coefficients of variation in Table 2 are all within the range expected for a single homogeneous species and the statistical summary is consistent with a single species being represented.

Maxilla and maxillary dentition.—UM 83475 and 95107 are maxillary fragments showing that the infraorbital canal in *C. torresi* was small. This measures about 0.9 mm in width in UM 83475, and appears to be 1.1 mm in diameter in UM 95107 (the two measurements are similar, but not directly comparable). Part of the jugal is attached to the maxilla in UM 95107, forming the lower rim of the right orbit, but this is not complete enough to permit estimation of the diameter of the orbital opening. The crowns of P^4 in UM 95107 (Fig. 2) and 95796 are unusually long anteroposteriorly. Both are broken, but UM 95796 has the protocone intact with a distinct postprotocingulum connecting the protocone to the posterior cingulum. There is a slight swelling in the position of a paraconid on P^4, but there is no distinct cusp here. The posterior crest on the protocone of P^4 in UM 95107 does not connect with the posterior cingulum.

Upper molars have well developed protocones, paracones, and metacones (Fig. 2), M^1 and M^2 have well developed paraconules and metaconules, but none of the upper molars have mesostyles or hypocones. There is a *Nannopithex*-like crest or posterior projection from the

TABLE 1—Measurements of all teeth of *Cantius torresi* known from University of Michigan localities SC-67 (type locality) and SC-69, all from the earliest Wasatchian land-mammal age (biochron or zone Wa-0), in the northern Bighorn Basin, Wyoming. Measurements are in mm. Sex interpretation is based on canine size and mandibular depth, where known. Abbreviations for tooth crown measurements: *HycldW*, M_3 hypoconulid width; *Len*, length; *PrdH*, protoconid height (premolars only); *TalW*, talonid width (in the case of lower molars); *TriW*, trigonid width (in the case of lower molars); *Wid*, width (in the case of upper teeth and lower premolars). *MD* is mandibular depth measured as depth of the mandibular ramus at M_1. Estimated measurements are enclosed in parentheses.

Specimen (Loc.) Collector	Description Tooth	Len	Wid or TriW	TalW	HycldW	PrdH	Sex
UM 66143 (SC-69)	Right dentary with M_{2-3} (MD = 6.20)						♀
K. D. Rose	RM_2:	3.43	–	(3.20)	–	–	
	RM_3:	4.22	2.67	2.40	1.41	–	
UM 83467 (SC-67)	Left dentary with M_2 (MD = 6.56)						♀
B. C. Badgley	LM_2:	(3.20)	–	3.06	–	–	
UM 83470 (SC-67)	Left dentary with P_3-M_1 (holotype; MD = 7.73)						♂
V. Torres	LP_3:	2.35	1.77	–	–	3.13	
	LP_4:	2.80	2.31	–	–	–	
	LM_1:	3.19	2.67	2.87	–	–	
UM 83475 (SC-67)	Right maxilla with M^{1-3}						?
C. E. Badgley	RM^1:	3.29	4.45	–	–	–	
	RM^2:	3.33	5.24	–	–	–	
	RM^3:	2.52	4.35	–	–	–	
UM 86132 (SC-69)	Crown of right M_3						?
P. D. Gingerich	RM_3:	4.22	2.82	2.44	1.56	–	
UM 87341 (SC-67)	Left dentary with C_1-M_2 (MD = 7.76), right dentary with M_{2-3}						♂
B. H. Smith	LC_1:	2.63	1.93	–	–	–	
	LP_1:	–	1.15	–	–	–	
	LP_2:	1.82	1.29	–	–	–	
	LP_3:	2.51	1.84	–	–	2.94	
	LP_4:	2.92	2.48	–	–	3.25	
	LM_1:	3.47	2.74	2.96	–	–	
	LM_2:	3.62	3.30	3.26	–	–	
	RM_2:	3.60	3.28	3.31	–	–	
	RM_3:	4.65	2.91	2.74	1.69	–	
UM 87852 (SC-67)	Left dentary with M_{1-2} (MD = 7.24), right dent. with P_4-M_1, M_3 (MD = 7.11)						♀
B. H. Smith	LM_1:	3.47	2.84	2.97	–	–	
	LM_2:	3.44	3.08	3.16	–	–	
	RP_4:	2.92	2.31	–	–	3.00	
	RM_1:	3.50	2.82	2.89	–	–	
	RM_3:	4.39	2.70	2.53	1.73	–	
UM 95107 (SC-67)	Right maxilla with P^4-M^3						?
B. H. Smith	RP^4:	3.22	4.03	–	–	–	
	RM^1:	3.47	4.89	–	–	–	
	RM^2:	3.33	5.27	–	–	–	
	RM^3:	2.49	4.16	–	–	–	

TABLE 1—continued.

Specimen (Loc.) Collector	Description Tooth	Len	Wid or TriW	TalW	HycldW	PrdH	Sex
UM 95305 (SC-67)	Right dentary with alveoli or roots for C_1-M_1, crowns of $M_{2\text{-}3}$						♂
B. H. Smith	RM_2:	3.80	3.15	3.16	–	–	
	RM_3:	4.67	2.76	2.63	1.70	–	
UM 95796 (SC-67)	Right maxilla with P^4						?
T. W. Churchill	RP^4:	2.78	3.47	–	–	–	
UM 97899 (SC-67)	Left dentary with $M_{2\text{-}3}$						?
G. H. Junne	LM_2:	3.42	3.21	3.28	–	–	
	LM_3:	4.20	2.78	2.56	1.52	–	
UM 101958 (SC-67)	Left dentary with C_1-M_3 (MD = 6.34), right dentary with P_4-M_3 (MD = 6.19)						♀
G. H. Junne	LC_1:	(1.92)	(1.43)	–	–	–	
	LP_1:	0.89	0.88	–	–	1.43	
	LP_2:	1.47	1.14	–	–	2.09	
	LP_3:	2.24	1.67	–	–	2.65	
	LP_4:	2.87	2.15	–	–	3.14	
	LM_1:	3.16	2.55	2.60	–	–	
	LM_2:	3.25	2.95	2.84	–	–	
	LM_3:	3.92	2.59	2.37	1.46	–	
	RP_4:	–	2.04	–	–	3.11	
	RM_1:	3.32	2.55	2.65	–	–	
	RM_2:	3.36	3.00	2.85	–	–	
	RM_3:	4.04	2.60	2.40	1.50	–	

protocone on M^1 and M^2, but this does not join the posterior cingulum of the tooth to form a postprotocingulum as it does in later *Cantius*. M^3 in UM 95107 is the only upper molar to have a complete lingual cingulum: M^1 and M^2 in UM 95107 do not have this, and none of the upper molars in UM 83475 have a lingual cingulum.

Mandible and mandibular dentition.—The most complete dentaries known to date are UM 87341, 95305, and 101958 (Fig. 3). All show the mandibular symphysis to have been open and unfused, with left and right dentaries remaining separate throughout life. Mental foramina can be variable, but there are usually three on the labial surface of the dentary beneath P_1, P_2, and P_3 as shown in Figure 3B. The ascending ramus of the dentary is high and straight (Fig. 1N), with the mandibular condyle positioned well above the level of the tooth row. UM 101958 includes well preserved left and right dentaries, which can be articulated to show the shape of the mandible (Fig. 4).

None of the known mandibles preserves well defined alveoli for incisors. UM 87341 includes the base of the crown of a large canine, and UM 95305 preserves the matrix-filled alveolus of a similarly large canine. UM 101958 preserves the root of a much smaller canine; this is broken obliquely in a way that makes it difficult to measure, and it is broken just below the base of the crown so that measurements of the size of the root in UM 101958 are not directly comparable to those UM 87341. The crown of the lower canine in *Cantius* is normally not much larger than the canine root where this is broken in UM 101958, and addition of some small compensating amount to the measured diameters leaves the projected crown diameters

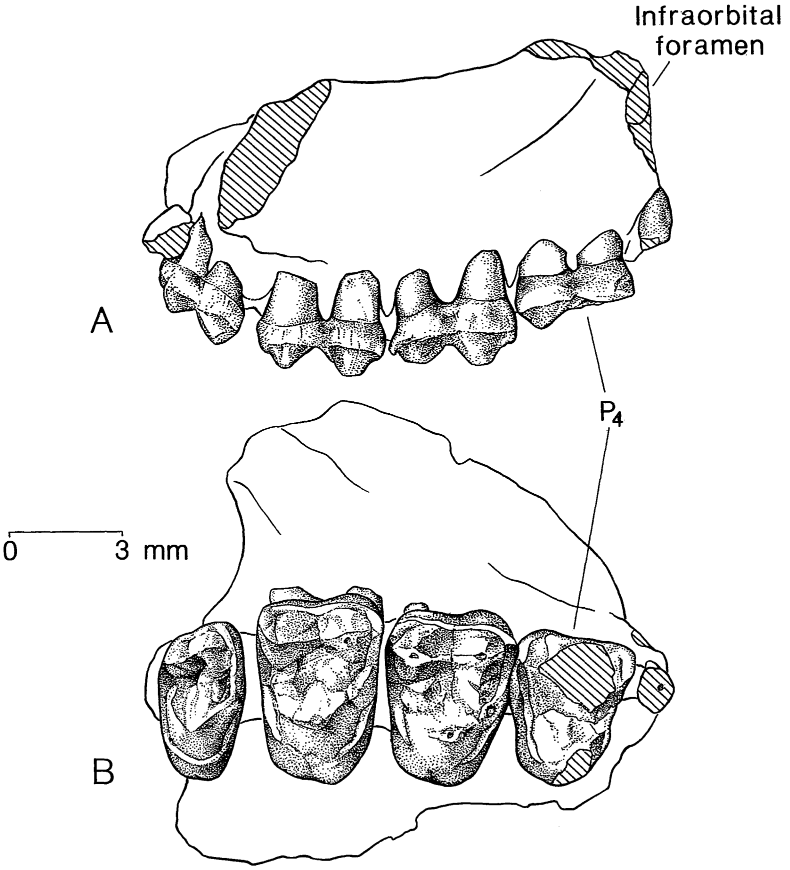

FIG. 2—Right maxilla of *Cantius torresi*, UM 95107, with alveolus for P^3 and crowns of P^4 and M^{1-3}. A, right lateral view. B, occlusal view. Note small infraorbital foramen, large and anteroposteriorly long crown of P^4, and weakly developed *Nannopithex*-like crest posterior to the protoconid on M^1 and M^2. Scale is in mm.

of UM 101958 much smaller than those measured in UM 87341. Canine size is compared in the following section on sexual dimorphism.

All four lower premolars are well preserved in UM 101958 (Figs. 3, 4). P_1 is a small, single-rooted, pin-like tooth with a simple, straight, pointed crown. It has a single protoconid cusp, with weakly developed pre- and postprotocristae. There is no wear evident on the anterolabial surface of the crown, and thus no indication that this tooth functioned as a hone for the upper canine as it sometimes does in later adapoids. UM 87341 preserves the base of the crown of P_1, which was evidently much larger in a putative male (see below), but the crown itself is not preserved and it is consequently not clear whether this functioned as a hone for the upper canine.

P_{2-3} are double-rooted, with simple, anteroposteriorly-elongated, premolariform crowns, each with a single high protoconid and distinct pre- and postprotocristae. P_4 resembles P_2 and P_3, but differs in having a larger and relatively broader crown, with a small anteriorly-positioned paraconid and a distinct metaconid medial to the protoconid. P_4 also has a short,

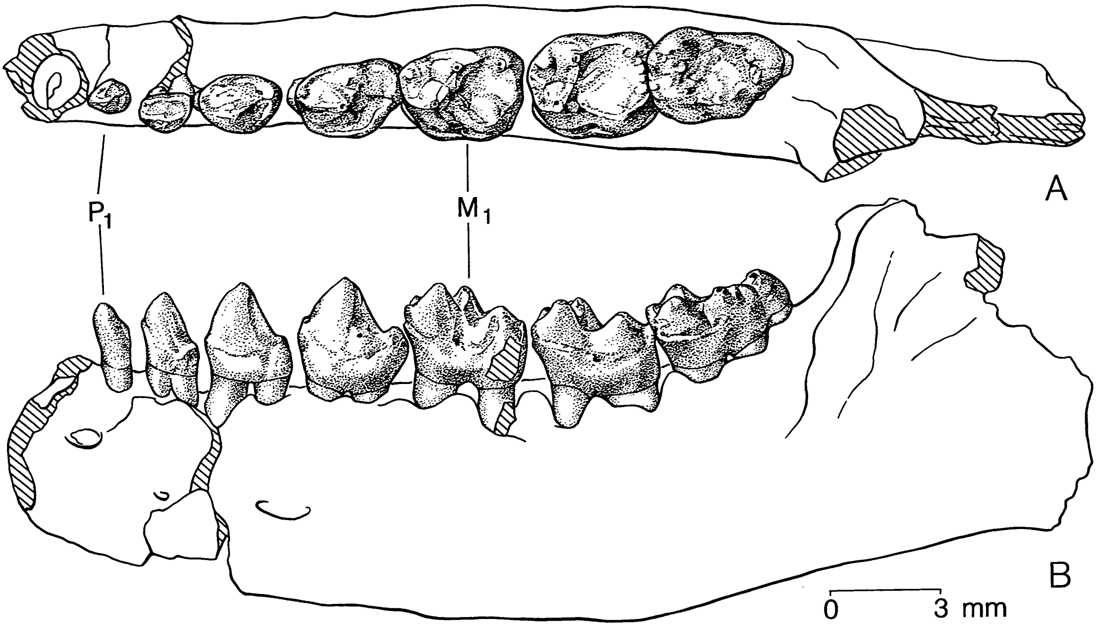

FIG. 3—Left dentary of *Cantius torresi*, UM 101958, with root of C_1, and crowns of $P_{1\text{-}4}$ and $M_{1\text{-}3}$. A, occlusal view. B, left lateral view. Note small size of canine root, small straight P_1, relatively short and broad P_4, and rounded cusps and occlusal outline of lower molars. Scale is in mm.

broad talonid with a weak anteroposteriorly-oriented cristid obliqua. New measurements of P_4 (Table 1) show the crown shape index (length divided by width) of P_4 to be 1.18 in UM 87341, 1.21 in UM 83471 (holotype), 1.26 in UM 87852, and 1.33 in UM 101958. Some specimens have P_4 shorter and broader than the proportions in later Adapoidea, which was interpreted as a primitive omomyid- or tarsioid-like characteristic of *C. torresi* (Gingerich, 1986, 1989), but this is not true of all specimens in the sample at hand.

Lower molars of *C. torresi* are similar to those of later *Cantius* but differ in being smaller and somewhat less angular or more rounded. The smaller size is seen in the values of $\log_e$ (L×W) of M_1, which are (or average) 2.21, 2.33, 2.32, and 2.14 in UM 83470 (holotype), 87341, 87852, and 101958, respectively. For comparison, large samples of early Wasatchian *Cantius ralstoni* have $\log_e$ (L×W) averaging about 2.40 (Gingerich, 1989, fig. 14). The rounded appearance of lower molars is seen in their occlusal outlines (Fig. 3A); in a tendency for their talonid widths to be less than trigonid widths on M_2 (and M_3; Table 1); and in the presence of low, blunt trigonid cusps and a weak metacristid on M_3 (Fig. 3). Further, the hypoconulid lobe on M_3 is short, narrow, and smoothly curved in occlusal outline.

Cranial and postcranial remains.—There is a fragment of cranium, possibly a portion of the left or right temporal, associated with UM 101958, but no informative anatomical characteristics are recognizable in this. UM 87852 includes part of a left pelvis and part of a right calcaneum. The acetabulum of the pelvis measures about 6 mm in diameter, and the pubic ramus measures 3.32 × 1.42 mm where it is broken near the anterior corner of the dorsolateral margin of the obturator foramen. The calcaneum preserves a lateral astragalar facet 3.7 mm long and 2.3 mm wide, with the top of the facet being 4.0 mm above the base of the calcaneal body. The calcaneal tuber, sustentacular facet, and much of the distal part of the body of the calcaneum are missing.

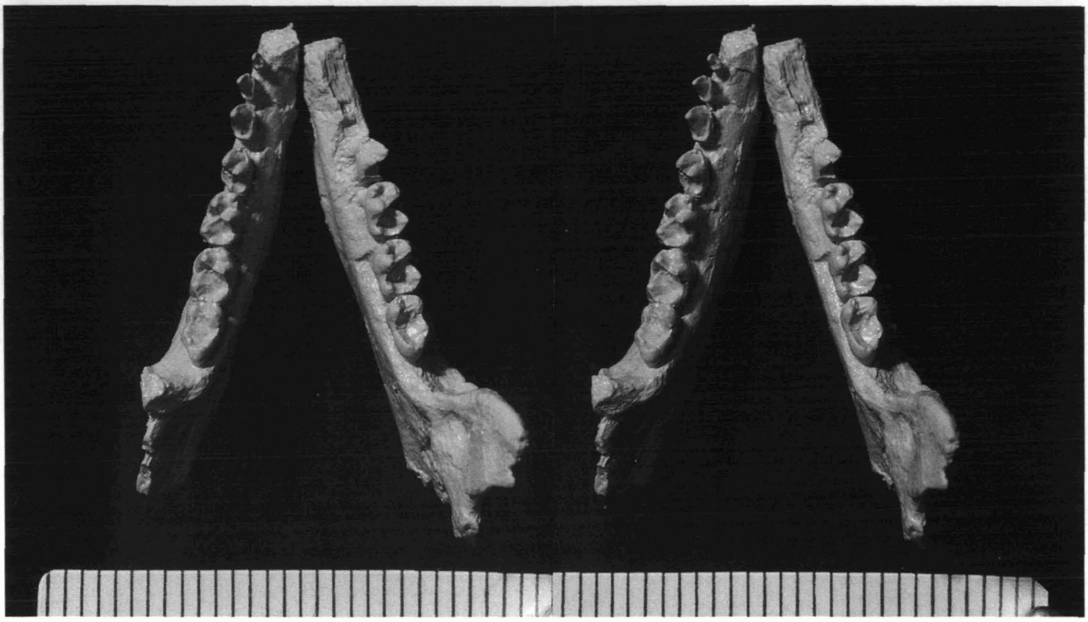

FIG. 4—Left and right dentaries of *Cantius torresi*, UM 101958, in articulation. Stereophotographs are of light-colored casts, in occlusal view. Dental arcade was ∩-shaped at the front in life (incisors are missing here), while mandibular rami were more ∧-shaped as they diverged posteriorly. Scale is in mm.

SEXUAL DIMORPHISM

Sexual dimorphism here refers to dimorphism in secondary sexual characteristics not directly involved in reproduction. Such dimorphism in primates is often expressed as canine tooth size dimorphism, but it may also be expressed as a gross body size dimorphism. Correcting the former for the latter, when known, yields an expression of relative canine dimorphism. Primates of different sex sometimes differ in body shape or pelage coloration, but these obviously cannot be studied in fossils. Dimorphism expressed as a quantitative difference between the mean values of the sexes can only be studied directly when the sexes of individuals are known in advance. However, differences between sexes within a species necessarily imply that the variabilities of dimorphic characteristics in dimorphic species are generally greater than those of the same characteristics in non-dimorphic species. Consequently, it is often possible to recognize dimorphism by unusually high variability even when the sexes of individuals are not known in advance.

Canine dimorphism.—Upper canine teeth are not yet known in *Cantius torresi*. The size of lower canines can be estimated in three specimens: in UM 87341 where the top of the root and part of the base of the crown are preserved; in UM 95305 where the canine alveolus is partially preserved, filled with sediment; and in UM 101958 where the top of the canine root is preserved. Measurements of canine size in UM 87341 and 101958 are listed in Table 1, and taken together these have unusually high coefficients of variation (Table 2). Canine sizes in the two specimens are compared visually in the stereophotographs of Figure 5. Here the lower canine of UM 101958 (Fig. 5A) is clearly much smaller in occlusal cross-section than that of UM 87341 (Fig. 5B). Females in dimorphic primate species have smaller canines than males have, and it is thus natural to expect that UM 101958 was a female in life, while UM 87341

TABLE 2—Statistical summary of tooth size and mandibular depth in *Cantius torresi* based on measurements of the Wa-0 sample given in Table 1 (measurements in mm). N is sample size (number of individuals), SD is standard deviation, and V is coefficient of variation representing standard deviation normalized as a percentage of mean.

		N	Range	Mean	SD	V
Upper dentition						
P^4	L	2	2.78 - 3.22	3.00	0.31	10.37
	W	2	3.47 - 4.03	3.75	0.40	10.56
M^1	L	2	3.29 - 3.47	3.38	0.13	3.77
	W	2	4.45 - 4.89	4.67	0.31	6.66
M^2	L	2	3.33	3.33	–	–
	W	2	5.24 - 5.27	5.26	0.02	0.40
M^3	L	2	2.49 - 2.52	2.51	0.02	0.85
	W	2	4.16 - 4.35	4.26	0.13	3.16
Lower dentition						
C_1	L	2	1.92 - 2.63	2.28	0.50	22.07
	W	2	1.43 - 1.93	1.68	0.35	21.04
P_1	L	1	0.89	0.89	–	–
	W	2	0.88 - 1.15	1.01	0.19	18.81
P_2	L	2	1.47 - 1.82	1.64	0.25	15.04
	W	2	1.14 - 1.29	1.21	0.11	8.73
P_3	L	3	2.24 - 2.51	2.37	0.14	5.74
	W	3	1.67 - 1.84	1.76	0.09	4.85
P_4	L	4	2.80 - 2.92	2.88	0.06	1.97
	W	4	2.10 - 2.48	2.30	0.16	6.76
M_1	L	4	3.19 - 3.49	3.35	0.15	4.62
	W	4	2.63 - 2.96	2.85	0.15	5.26
M_2	L	6	3.31 - 3.80	3.50	0.17	5.00
	W	6	2.98 - 3.31	3.16	0.13	3.99
M_3	L	7	3.98 - 4.67	4.33	0.25	5.85
	W	7	2.60 - 2.91	2.75	0.10	3.72
Mandibular depth		6	6.20 - 7.76	6.95	0.71	10.16

was a male. The canine alveolus of UM 95305 is large like that of UM 87341, suggesting that it too represents a male.

One common index of canine dimorphism is the male/female length ratio or MFL, the ratio of mean anteroposterior canine crown length in males divided by that in females. In *Cantius torresi* this ratio is 2.63 / 1.92 = 1.37, which falls within the range expected of dimorphic primate species (Gingerich, 1981, fig. 7). A better general index for comparing primates of

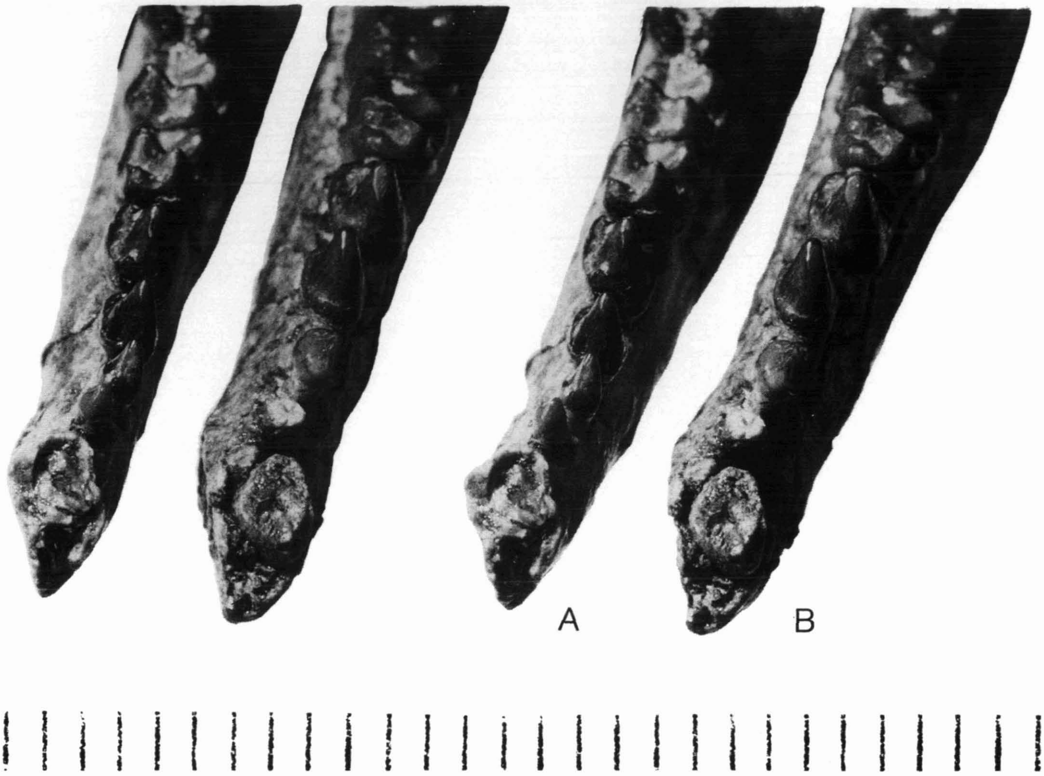

FIG. 5—Stereophotograph showing comparison of roots and teeth of female (A) and male (B) *Cantius torresi*, UM 101958 and 87341, respectively, photographed in oblique anterior view to show differing cross-sections of canine root at base of tooth crown. Scale is in mm.

different body sizes is the (natural) logarithm of the MFL ratio, LnMFL, or, equivalently, the difference between the logarithms of the two measurements (LnML − LnFL). If we use natural logarithms, the logarithm of the MFL ratio, LnMFL, is 0.31, which again falls within the range of dimorphic primate species (non-dimorphic species generally have an LnMFL ratio less than 0.10).

The LnMFL ratio for *C. torresi* is presently based on only two canine crown lengths, but these are so different in size and these fall so far outside the range expected for non-dimorphic primates that there is little question that they indicate canine dimorphism. The two canines are so different in size that, without correction, they exceed male-female differences in canine size expected in many dimorphic living primate models (Fig. 6). A canine length of 1.92 mm in female UM 101958 might be suspect because the diameter of the root certainly underestimates the diameter of the crown to some degree, but addition of an arbitrary 10% to the length of the female crown would yield a new estimated length of 2.11 mm and a new LnMFL estimate of 0.22. This is closer to the indices of sexual dimorphism found in extant Ceboidea, but it is by no means certain that 10% should be added to the length of UM 101958. The canines of male and female *Notharctus* described by Krishtalka et al. (1990) and by Alexander (1994) yield LnMFL values even greater than that calculated here for *Cantius* (Fig. 6). Great canine dimorphism is evidently characteristic of notharctine Adapoidea.

Mandibular depth.—Fleagle et al. (1980) considered the coefficient of variation of mandibular depth to be a good indicator of sexual dimorphism in primates because they found

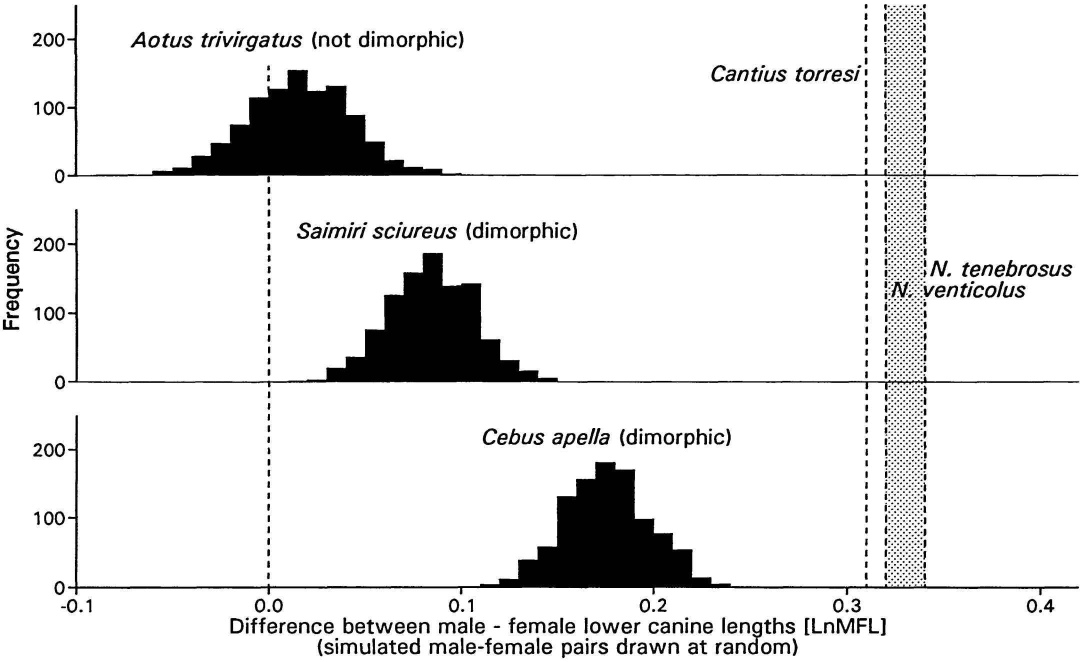

FIG. 6—Graphical demonstration of great lower canine dimorphism in notharctid Adapoidea compared to dimorphism in Ceboidea. Abscissa is log of difference between male and female anteroposterior canine length (LnMFL) in *Cantius torresi* (single dashed line at right) and *Notharctus* spp. (pair of dashed lines with shading at right), compared to LnMFL differences expected in extant non-dimorphic (*Aotus trivirgatus*) and dimorphic species (*Saimiri sciureus* and *Cebus apella*). Histograms for each extant species show LnMFL indices calculated for 1000 male-female specimen pairs drawn at random from geometric-normal male and female distributions with means and standard deviations observed in empirical samples. Calculated values for *Cantius* and *Notharctus* are much greater than those observed in any of the simulations based on extant species, indicating that from the beginning of their diversification notharctids had great dimorphism. LnMFL indices for *Notharctus* are calculated from male and female mean canine lengths given by Krishtalka et al. (1990) for *N. venticolus* and by Alexander (1994) for *N. tenebrosus*.

a high positive correlation between the degree of sexual dimorphism in body weight and the variability of mandibular depth measured below the first lower molar. The coefficient of variation of mandibular depth observed in six individuals of *C. torresi* is 10.16 (Table 2), which lies within the range of dimorphic species and above the range of non-dimorphic species reported by Fleagle et al. (1980: table 1). Ranked, the mean mandibular depths in the six individuals of *C. torresi* are 6.20, 6.27, 6.56, 7.18, 7.73, and 7.76 mm, respectively (Table 1). These cluster naturally into a group of three smaller individuals of mean MD = 6.34 mm, presumed to be females (UM 66143, 101958, and 83467), and a group of three larger individuals of mean MD = 7.56 mm, presumed to be males (UM 87852, 83470, and 87341), and this interpretation of sexes is consistent with interpretation based on canine size where canines or canine alveoli are preserved. It is also consistent with an expected 1:1 ratio of males to females in the species as a whole.

The ratio of male mandibular depth to female mandibular depth is 7.56 / 6.34 = 1.19, and the natural logarithm of this ratio, 0.18, give some indication of body size dimorphism in *Cantius torresi*. The LnMFL indices of dimorphism in canine length calculated above for

Cantius, 0.31 (consistent with values for *Notharctus* graphed in Fig. 6) is much larger than 0.18, suggesting that *C. torresi* probably exhibited considerable canine dimorphism over and above what can be explained by body size dimorphism alone. I am not aware of published measurements or published means and standard deviations for males and females of primate species known to be non-dimorphic or dimorphic (Fleagle et al., 1980, published coefficients of variation for mixed-sex samples) that would permit inter-individual differences in mandibular depth of *C. torresi* to be assessed in the context of living primate models, as was done for canine size in Figure 6.

It is not surprising that earliest Eocene *Cantius torresi* is sexually dimorphic, given that members of each of the families and subfamilies thought to be derived from it appear to be dimorphic: Notharctinae (Gregory, 1920; Gingerich, 1979; Krishtalka et al., 1990; and Alexander, 1994), Cercamoniinae (Simons et al., 1996), Adapinae (Stehlin, 1912; Depèret, 1917; Schmidt-Kittler, 1971; Gingerich, 1981), and Sivaladapinae (Gingerich and Sahni, 1984). This indirect evidence suggesting that sexual dimorphism might be expected in earliest *Cantius* is now corroborated by direct evidence of dimorphism in *C. torresi* fossils.

DISCUSSION

Godinot (1992) interpreted the broad P_{3-4} and relative squareness of upper molars in North American earliest Wasatchian Wa-0 *Cantius torresi* as indicating a species advanced over later *C. ralstoni* from subsequent biochron Wa-1, and he inferred that two *Cantius* lineages must have coexisted during Wa-0 time. There is nothing in the known sample of Wa-0 *Cantius* to suggest the presence of more than one lineage, and measurements of the known specimens (Table 2) are consistent with presence of a single species. In view of the great similarity of *C. torresi* and *C. ralstoni*, including overlapping distributions in all characteristics that can be quantified, it seems more plausible to regard Wa-0 *C. torresi* and Wa-1 *C. ralstoni* as stages in a single North American lineage, with *C. ralstoni* being a direct though possibly not unique descendent of the earlier species. (*C. torresi*-to-*C. ralstoni* in North America and *C. eppsi* in Europe are geographically-separated sister species, and represent contemporary, recently-separated, and closely-related lineages evolving independently on different continents.)

Discovery that *Cantius torresi* was dimorphic like other adapoids has implications for the origin of primates, for systematic interpretation of adapoid fossils, for our understanding of the probable behavior of earliest adapoids, and for the origin of anthropoid higher primates. *Cantius torresi* and the tarsioid omomyid *Teilhardina brandti* (Gingerich, 1993) are the earliest primates known from North America, and among the earliest known anywhere in the world. Sexual dimorphism in earliest *Cantius* and the lack of dimorphism in any Paleocene proprimate or Eocene omomyid sets adapoids apart from proprimates and omomyids (and all later prosimians), and shows how poorly we understand the origin and early diversification of primates. Dimorphism is clearly associated with the presence of monkey-like spatulate incisors and projecting interlocking canines in adapoids, as a lack of dimorphism is associated with pointed incisors in proprimates, tarsioids, lorisoids, and lemuroids, but the phylogenetic relationships of all of these groups remain mysterious.

All species-level studies of adapoid systematics should consider the effect of dimorphism on species variability (cf. Godinot, 1992, and Lanèque, 1993, on *Adapis*). We must use dimorphic anthropoids as well as non-dimorphic lemuroids and lorisoids as models for interpreting Eocene species or we risk placing males and females of dimorphic forms in different species.

The presence of marked canine dimorphism and significant body size dimorphism in *Cantius torresi* indicates sex-specific behavioral roles. Comparison with living primates suggests that *C. torresi* was neither monogamous nor polyandrous, but rather lived in polygynous single-male or multi-male groups with significant intermale competition (Fleagle, 1988; Kay et al., 1988).

This inference is based on correlations of sexual dimorphism and behavior observed in living anthropoid primates, principally extant diurnal ceboids. Dimorphism is partly a visual display, which explains why it is best developed in diurnal primates. Given the stem phyletic position of *C. torresi* relative to later adapoids, and the wide distribution of dimorphism throughout Adapoidea, it is reasonable to infer that adapoids were diurnal and that a single-male or multi-male social organization with male-male competition was characteristic of all Adapoidea.

Finally, sexual dimorphism with its associated behavioral traits is an important difference distinguishing adapoids from contemporary tarsioids (omomyids and tarsiids), and an important resemblance linking adapoids to anthropoid higher primates: adapoids are, anatomically and behaviorally, the higher primates of the Eocene. This does not mean that adapoids are anthropoids. Many of the known Eocene adapoids retain some primitive mammalian and primitive primate characteristics (e.g., in the frontal bone, orbit, middle ear, and foot), but adapoids also share numerous dental and other resemblances with Oligocene and later Anthropoidea that make them probable ancestors of Anthropoidea (Gingerich, 1975, 1980, 1984; Franzen, 1994; Rasmussen, 1994).

The question is not whether dimorphism and other traits can appear or disappear in evolution, but rather whether these *did* appear or disappear, and, if so, *when* it happened. Dimorphism is important in linking Eocene adapoids and Oligocene anthropoids because it is a characteristic of resemblance in similar taxa that are known to have overlapped in geological time and geographic space. As a counter example, lack of canine and body size dimorphism in the Lemuroidea of Madagascar may be primitive, or lemurs may have evolved from a dimorphic ancestor (losing dimorphism when the ancestor or ancestors became isolated on Madagascar): we have no evidence of overlap linking lemuroids to any other group of primates, non-dimorphic or dimorphic, and hence we do not know what happened when lemuroids became isolated from other primates.

The origin of Anthropoidea is a longstanding problem with a large literature favoring living *Tarsius* as the closest 'sister' taxon to living Anthropoidea, which it may well be. However, an historical problem of evolutionary origin cannot be solved by comparison of the anatomy of living animals nor of the molecular sequences of living animals, however comprehensive and detailed these may be, unless all of the relevant groups are living and can be sampled in similar ways. Adapoidea as a group of geologically older and more primitive anthropoid-like primates are relevant to the problem of the origin of Anthropoidea, but they are extinct and cannot be studied anatomically nor molecularly like living animals are studied. Hence it can never be ruled out that Adapoidea, were they living, would lie between *Tarsius* and Anthropoidea on a cladogram of extant taxa. Historical evidence is not only relevant but crucial to an historical inquiry. It is a simple fact that the more we learn from fossils about the morphology of primitive anthropoids, the more they resemble Eocene adapoids (Simons, 1995), and the more we learn from fossils about adapoids, the more they resemble Oligocene anthropoids. Sexual dimorphism is another resemblance of Adapoidea to Anthropoidea.

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