

Anterior Dentition of *Notharctus* and the Adapid-Anthropoid Hypothesis

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Abstract. We describe the morphology of the first complete incisor-canine complex for *Notharctus tenebrosus*. Gregory's classic description, based on heavily reconstructed and fragmentary material, needs to be amended to include the following points: I¹ occludes simultaneously with I₁₋₂; I² is essentially nonocclusal and staggered behind I¹; RI¹ and LI¹ do not contact interstitially but are separated by a small median diastema; I¹ bears a prominent mesial prong. These five features are distinctly lemuriform in appearance: in general *Notharctus* is phenetically most similar to the pattern found in some lemurids and indriids. We consider an abstraction of the common plesiadapiform-omomyid anterior dental configuration as the primitive primate character state and argue that the adapid (sensu lato) morphology is derived. We further suggest that this predominantly Eocene group is the sister taxon of modern lemuriforms. The incisor-canine morphology of *Adapis* and *Leptadapis* is autapomorphic and less suggestive of the primitive pretoothcomb strepsirhine dentition than the notharctine pattern appears to be. While the morphologically simple lower incisors of notharctines are truly similar to those of anthropoids, the preponderance of anatomical differences within the incisor-canine complex leads us to conclude that these similarities were convergently evolved in adapids and the higher primates. The least refuted hypothesis of anthropoid origins, and the one which appears to make most phenetic as well as cladistic sense, acknowledges the monophyly of the Haplorhini and the likelihood that anthropoids are descendants of an early tarsiiform stock.

Introduction

The morphology of the adapid anterior teeth has figured importantly in assessments of the phylogenetic relationships of this predominantly Eocene family. Following Leidy's [1873] early postulate of a North American notharctine-platyrrhine ancestor-descendant sequence, based largely upon similarities of the molar dentitions of *Notharctus* and *Alouatta*, later workers such as Gregory [1920] drew special attention to the spatulate form of notharctine and platyrrhine incisors. Gregory [1920, 1922] and Gingerich [1975c] also noted that the anterior teeth of some of the European adapines somewhat resembled the tooth-combed lemuroids and lorisooids in that the lower canine is subcaniniform and incorporated into a continuous incisor-canine battery. Le Gros Clark [1959] reemphasized that the anterior teeth of adapids are more primitive overall than modern strepsirhines', indicating that the former group, *sensu lato*, may be the ancestral stock from which the lemuriform taxa evolved. At the same time he cautioned that a lack of specializations also made it possible that notharctines were ancestral to platyrrhines [see also Simpson, 1940]. Finally, Gingerich [1975a, 1977, 1980, 1981a; Gingerich and Schoeninger, 1977], in a series of papers, articulated and developed these arguments. He concluded that adapids are the ancestral stock of both the anthropoids and lemuriforms, citing, among other features, a number of characters of the incisor and canine teeth as evidence for that hypothesis. Others [e.g. Cartmill and Kay, 1978] have promoted the adapid-anthropoid hypothesis as a possibility, citing their skepticism regarding haplorhine monophyly and the presence of some dental similarities shared between them [Kay, 1980].

While the morphology of adapine incisors and canines is known from a fair number of specimens, notharctine anterior teeth are very scarce indeed [for example, see Gregory, 1920; Gingerich, 1979b]. We have recently prepared a *Notharctus* specimen recovered by Jacob Wortman which preserves what appears to be the only complete incisor-canine complex now available for the genus. The purpose of this report is to describe the morphology and occlusion of this specimen, compare it with adapine material and extend our comparisons to anthropoids, particularly with reference to higher primate origins. Our analysis confirms that the incisor-canine complexes of *Notharctus* and *Adapis* differ in several important respects. Both patterns contrast with the most common arrangement found in Anthropoidea and the presumed ancestral anthropoid condition. We conclude that neither of the known adapid morphologies are likely to be ancestral to anthropoid anatomy but instead represent an independently derived system, probably indicative of the close cladistic ties of adapids and living strepsirhines.

Materials and Methods

The Yale Peabody Museum (YPM) specimen 12956 (fig. 1) represents *Notharctus tenebrosus*, a Middle Eocene species, recovered in 1902 from sediments near the mouth of Cottonwood Creek, Bridger Basin, Wyo. It thus presumably derives from the Black's Fork Member and Bridger B faunal association [see Robinson, 1957], now termed middle Bridgerian (early Middle Eocene). It comprises the partial right and left premaxillae and maxillae with RI²-LM³ and a partial mandible with RP₂-LM₃ (the crowns of LP¹ and LP₄ are missing). It should be pointed out that the upper and lower teeth, especially the molars, occlude naturally and are certainly of a single individual. The sizes of this specimen's molars and premolars (table I)

are comparable to those of *N. tenebrosus* as measured by Robinson [1957], and the log of the M_1 area also fits into the range for that taxon as illustrated by Gingerich [1979b, fig. 3]. YPM 12956 is clearly referable to *Notharctus* on the basis of its partially fused symphysis, presence of large mesostyles on upper molars, 'incipient' twinning of the P^4 paracone, protoconid-directed flexure of the cristid obliqua on M_3 and possibly the faint indication of minimal root twinning on P_2 . In this combination of features it is most similar to *N. tenebrosus*, to which we refer it here.

Anteriorly, both the mandible and maxillae were somewhat deformed by lateral crushing and the incisors and canines were displaced. Under our direction, Mr. Otto Simonis of the Department of Vertebrate Paleontology, American Museum of Natural History (DVP/AMNH), repositioned these teeth during cleaning and reconstruction of the jaws. The mandible suffered three major breaks, but preserves nearly the entire planum alveolare, the right corpus and the base of its ramus. The fractures posterior to LM_3 and LP_4 were fairly clean and the pieces aligned well. The third break, at the level of LP_1 , resulted in the loss of some bone and required greater care in restoring the pieces. Comparisons with more complete adapid specimens and a refitting based upon occlusal contacts influenced the final reconstruction. At the symphysis most of the bone had been eroded away externally but for the region at RP_{1-2} . The lingual plates of the alveoli for the incisors and canines were cleaned to allow the repositioning of these teeth. Corroboration for this reconstruction was provided by comparisons with American Museum of Natural History *Notharctus* specimens that preserved intact symphyses with either roots or alveoli for the anterior dentition (e.g., AMNH 1707, 5009, 11457, 11475, 12579, 14568, 93618).

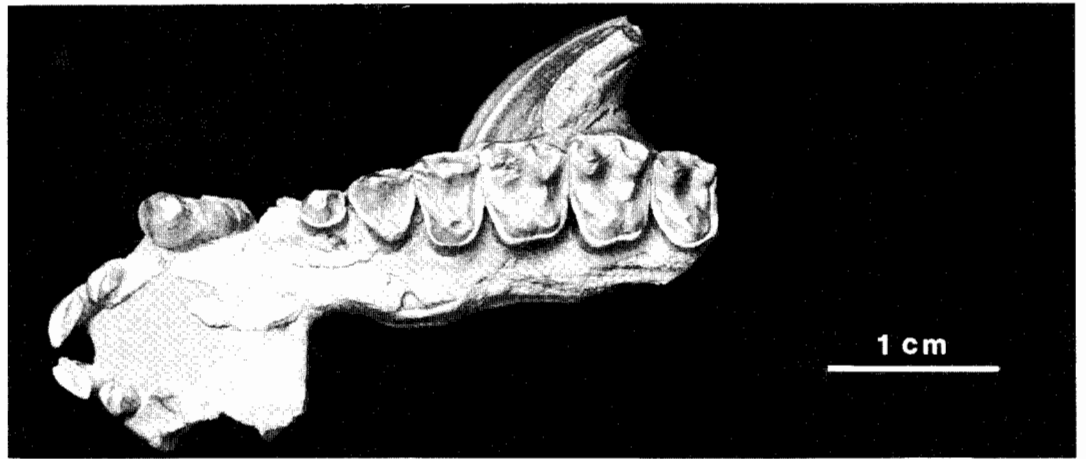
While the Yale maxilla does not present the complete palatal surface, premaxillomaxillary and intermaxillary sutures provide important information about the position of the upper incisors relative to each other and to the canine. The premaxillomaxillary suture is obliquely oriented and extends from I^1 to approximately 3 mm beyond I^2 . This reconstruction agrees with that given by Gregory [1920, p. 128, fig. 35] for AMNH 11466. The left premaxilla preserves the lingual alveolar surfaces for both I^{1-2} into which the respective teeth easily fit. While the left premaxilla preserves its palatal surface, the right premaxilla is represented by facial fragments labial and superior to I^2 . The latter remains attached to the maxilla

anterior to the C^1 . The left maxilla presents more detail than the right, but the latter mirrors it in preserving the maxillary palatal process between the intermaxillary suture and the canine alveolus. With the intermaxillary suture restored and the cheek teeth in occlusion, the left premaxilla was aligned and attached to the maxilla. Irreparable distortion prevented the correct transverse alignment of the upper canine, so that its reconstructed position and orientation was based on reciprocating wear facets and should be considered tentative; it is surely too far lateral (compare fig. 1 and 2). While we are not certain that the rest of the dentition is now 'true to life', this reconstruction seems reasonably accurate, although it differs significantly from that given by Gregory [1920, p. 1231], which was based upon more fragmentary material.

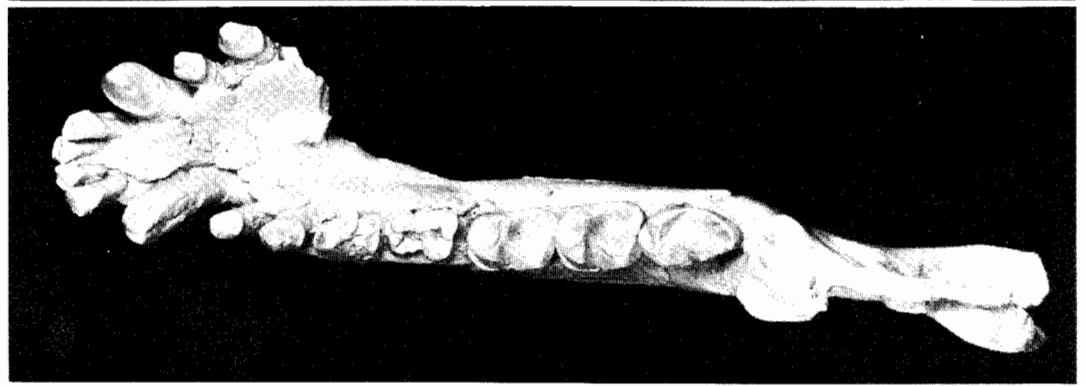
Taxonomic nomenclature follows Szalay and Delson [1978] (e.g., *Adapis* and *Leptadapis* together comprise the Subtribe Adapina [adapinans]; Lemuriformes includes Lemuroidea and Lorisioidea). All observations were confirmed using stereo and some scanning microscopy. All measurements were recorded to the nearest 0.1 mm. The approaches we have followed in inferring polarity and reconstructing morphotypes are outlined by Szalay [1977a], Delson [1977] and others and involved general surveys of the morphologies of the taxa discussed below.

Morphology

In general, YPM 12956 agrees with Gregory's [1920] description of the gnathic and facial morphology of *Notharctus*. While the incisive foramina have not been preserved, the extent of the palatal processes of the maxilla and premaxilla preclude their having extended posteriorly much beyond I^2 . Like other notharctines, the Yale specimen has four premolars; however, the crown of LP^1 was apparently lost during the animal's life. Replacement bone occupies the space between LC^1 and LP^2 and the root of LP^1 remains in its crypt. A palatal fossa is situated posterior to RI^2 to receive the C_1 apex. Remnants of the maxillopalatine suture are



a



b



c



d

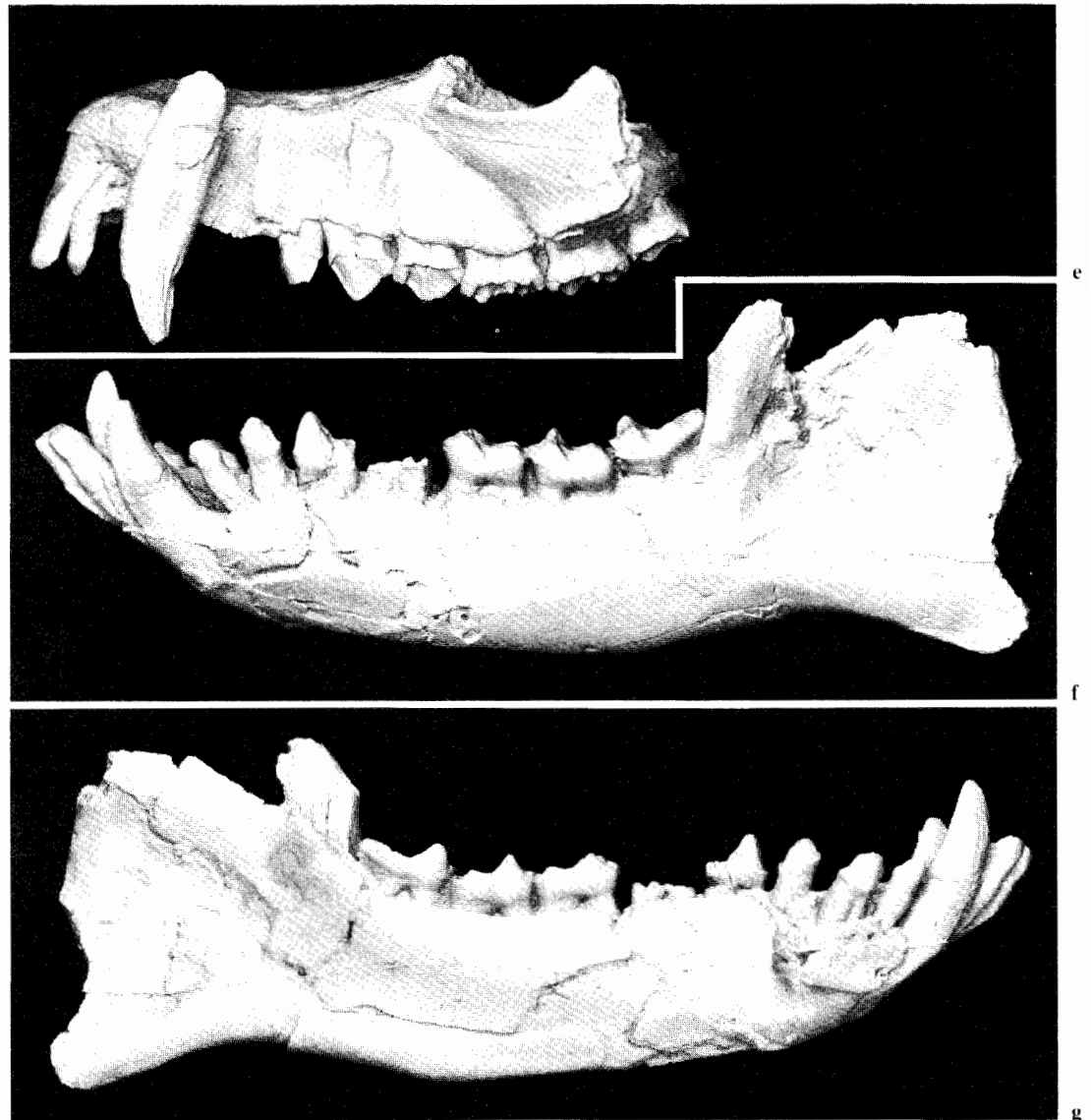


Fig. 1. *Notharctus tenebrosus*, YPM 12956, Middle Eocene of Wyoming. **a** Occlusal view of maxilla (cast). **b** Occlusal view of mandible (cast). **c** Oblique left frontolateral view of maxilla and mandible in incisor occlusion, wax-plaster reconstructive support material emphasized. **d** As **c**, of cast, to emphasize the clarity of detail without loss of accuracy thus obtained. **e** Maxilla in left lateral view (cast). **f** Mandible in left lateral view (cast). **g** Mandible in right lateral view, with lingual surfaces of left dentition and corpus (cast). All views to same scale.

Table I. Measurements (in mm) of YPM 12956 teeth

Jaw	Measurement	I1	I2	C	P1	P2	P3	P4	M1	M2	M3
Upper	M-D	3.3	2.1	4.0	–	2.7	3.8	4.2	5.1	5.3	4.1
	B-L	1.5	1.3	3.0	–	2.1	4.3	5.5	6.2	6.7	5.5
Lower	M-D	1.8	2.0	2.8	1.8	2.4	3.9	–	5.1	5.5	6.0
	B-L	1.4	1.8	3.0	1.6	1.9	2.8	–	3.8	4.2	3.6

M-D = The greatest mesiodistal diameter; B-L = perpendicular buccolingual dimension.

visible at the level of LM²⁻³ and posterior to LM³. While the maxilla is broken exteriorly at the level of LP¹, it does preserve the infraorbital foramen, which is double as in some adapines [Stehlin, 1916; Gingerich and Martin, 1981]. The malar originates low on the maxilla just superior to LM², and its inferior surface is grooved posterior to the tubercle for the anterior tendon of the masseter [Gregory, 1920]. The orbital rim of the malar is not pierced by a foramen as it sometimes is in *Notharctus* [Gregory, 1920]. The orbital mosaic is not discernable although the floor of the orbit preserves the infraorbital canal.

The symphyseal suture line along the planum alveolare is obliterated. Yet inferiorly an unfused portion of the left symphyseal surface is retained. This may conform to the 'condition 2' specimens of Beecher [1983]. AMNH 5009 is a fairly complete dentary of *N. tenebrosus*, and as in the Yale specimen the internal symphyseal surface is smooth, while externally and inferiorly a suture line is visible. This would most probably have been the condition of YPM 12956 had it not been damaged.

Incisors

As in *Adapis* and indriids [Rosenberger and Szalay, 1980], I¹ is a low-crowned, buccolingually thin tooth with a strong mesial

process. There are delicate traces of a lingual cingulum. The worn apical margin makes it impossible to determine if the fresh I¹ were capped by a naturally sharp or a blunt edge. I² is roughly trapezoidal in outline, and the plane of its crown is oriented essentially parallel to that of I¹. The lack of any I¹⁻² interstitial facets, as well as the respective distance between alveoli, indicates that I² was staggered behind I¹ [see also Gregory, 1920]; therefore, the teeth did not form a compact arcuate unit as in the mandible (fig. 1a, b). This is confirmed by our examination of occlusion.

The apical margins of all lower incisors are extensively worn leaving no precise way of inferring their unworn height. They are rather procumbently implanted, and a continuous broad band of wear-induced dentinal exposure demonstrates that all four incisors were arranged in a close-packed natural arc across the mandibular symphysis. Gracile lingual cingula are also present on I_{1,2} as a lingual buttress on I₂.

Canines

The upper and lower canines are rather similar to one another in size and shape, possibly indicating that the individual is female. We are also aware of other notharctine canines of somewhat different appearance, at-

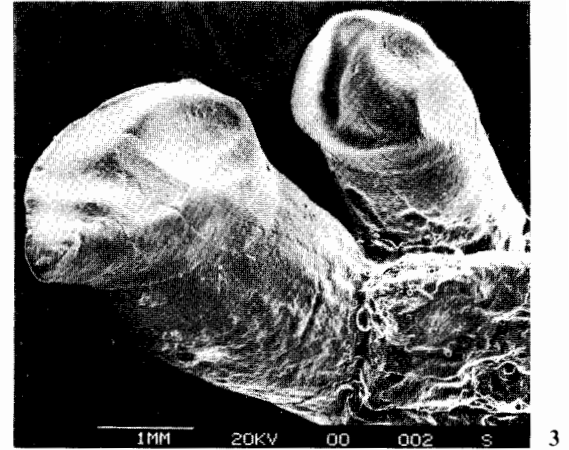
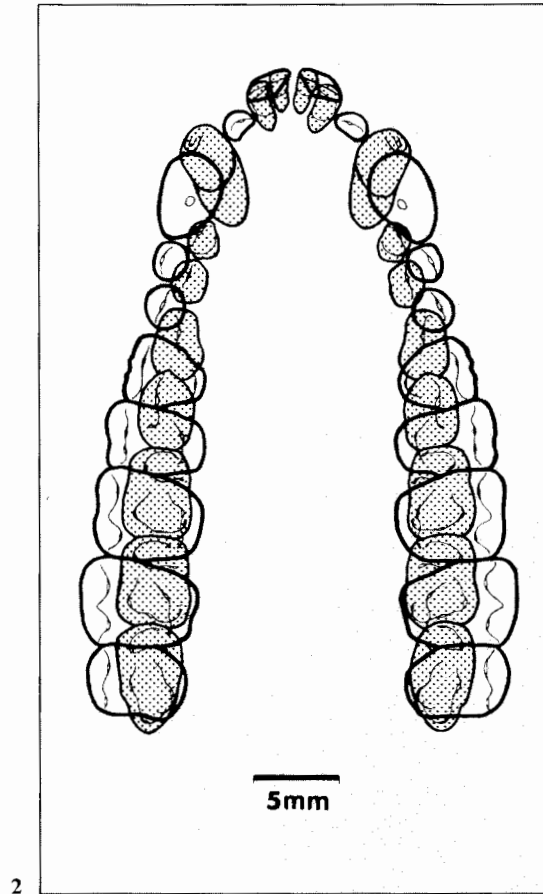


Fig. 2. Illustration of reconstructed lower (stippled) and upper teeth of *N. tenebrosus* in occlusion, based on YPM 12956. Note, in particular, the exclusive occlusion of I_{1-2} with I^1 and the isolation of I^2 .

Fig. 3. Scanning electron micrograph of left I^{1-2} of YPM 12956 (cast), original scale included. Note separate lingual facets on I^1 for $I_{1,2}$, and apical and cervical wear on I^2 .

tributable to *Notharctus* or *Pelycodus* species; thus, the Yale specimen should not be considered morphologically typical for the subfamily. C^1 and C_1 are roughly cylindrical in section, recurved along the root-crown axis and sharply pointed. The crowns, especially of the uppers, are indented by many short vertical grooves buccally and lingually. The C^1 shows a mesial sulcus on the crown, and there are only slight indications of the development of distal cristae on either tooth. Each crown projects vertically well beyond the

apices of adjacent premolar cusps, and are separated from upper and lower lateral incisors by brief diastemata.

Occlusion

The I^1 apical margin and lingual fossa just below the margin are heavily worn and indicate an edge-to-edge as well as overbite occlusion (fig. 2). The combined mesiodistal breadth of I_{1-2} , and their apically worn occlusal facets, correspond with the breadth of I^1 (table I) and its worn apical margin (fig. 1a-c, 3).

Table II. Comparative ratios of primate upper and lower incisors

Taxon	n	I ¹ $\frac{M-D}{B-L}$	I ² $\frac{M-D}{B-L}$	$\frac{I^1 \text{ area}}{I^2 \text{ area}}$	I ₁ $\frac{M-D}{B-L}$	I ₂ $\frac{M-D}{B-L}$
Strepsirhini						
Adapidae						
<i>Notharctus tenebrosus</i> , YPM 12956	1	2.2	1.6	1.8	1.3	1.1
<i>Pelycodus jarrovii</i> ^a	1	2.2	1.1	1.8	–	–
<i>Pelycodus epsi</i>	1	1.9	–	–	–	–
<i>Adapis parisiensis</i>	1–4	2.1	2.0	1.0	1.0	1.1
Lemuriformes						
<i>Lemur catta</i>	3–8	2.6	1.9	1.2	–	–
<i>Haplemur griseus</i>	4	1.7	1.7	1.2	–	–
<i>Propithecus verreauxi</i>	4	1.8	2.5	1.9	–	–
<i>Phaner furcifer</i>	2–3	3.3	2.0	3.7	–	–
Anthropoidea						
Platyrrhini						
<i>Leontopithecus rosalia</i>	19–25	1.1	1.2	1.3	0.8	0.9
<i>Saguinus midas</i>	10	1.1	1.2	1.1	0.9	0.9
<i>Callithrix jacchus</i>	11–13	1.3	1.2	1.4	0.8	0.6
<i>Saimiri sciureus</i>	6–7	1.1	1.0	1.3	0.6	0.7
Catarrhini						
<i>Parapithecus grangeri</i>	1	1.1	–	–	–	–
<i>Propliopithecus chirobates</i> ^b	1	–	–	–	0.9	0.8
<i>Propliopithecus zeuxis</i> ^b	1	–	–	–	0.8	0.8
<i>Dendropithecus macinnesi</i> ^c	1–14	1.1	0.8	1.4	0.7	0.8
<i>Proconsul africanus</i> ^c	4–15	1.3	0.9	1.5	0.8	0.8

n = Sample size; M-D and B-L, as in table I; area = M-D × B-L. Superscripts at taxa refer to published measurement sources: ^aGregory [1920]; ^bKay et al. [1981]; ^cAndrews [1978]. Note especially: the relatively greater mesiodistal length of I¹ in strepsirhines compared to anthropoids; the proportional similarities of I¹ and I² in *A. parisiensis* and of areal ratios between notharctines and *Propithecus*, and the relative buccolingual dominance of I₁₋₂ in anthropoids as compared to adapids.

Interestingly, but for a small wear facet at the tip of I² (fig. 3), the crown of this tooth is nearly devoid of any obvious occlusal or other abrasive wear. Thus it is quite clear that during incisal centric relation, I_{1,2} occluded entirely with the much broadened I¹ crown, bypassing I² [contra Gregory, 1920, p. 124]. A similar facet is seen on the I² tip of AMNH

55157, an aged *Smilodectes* specimen discussed by Gingerich [1979b]. The presence of such a small facet on both old and young individuals suggests that it may have been formed while some anterior teeth were still erupting and occlusal relationships had not yet reached the adult mode, or that it was produced during nonocclusal behaviors. The

base of I^2 does bear a flat occlusal facet (fig. 3) which corresponds with a small facet along the mesial cristid of C_1 . It is clearly produced as the C_1 moves into occlusion, with its apex resting in the palatal fossa previously described. This faceted surface occupies an area which spans the cervix, lying on both the enamel-covered crown and the root. It is difficult to suggest a selectively advantageous biological role for this occlusal pattern, because action to sharpen the C_1 would lead to gingival abrasion, unless there were local gum retraction. A similar ubiquitous facet appears in *Callithrix*, where Rosenberger [1979] related it to the spatial requirements of incisor staggering, coupled with a vertical C_1 .

The apices of C^1 and C_1 retain a sharp point and are not blunted. Since their roots are closed and other teeth show substantial amounts of occlusal wear, its absence cannot be a function of ontogeny. It may, however, indicate that the individual is female. There are no marked indications of well-developed C^1 - P_1 honing, despite the fact that the canines project sufficiently.

Comparisons, Homologies and Polarities

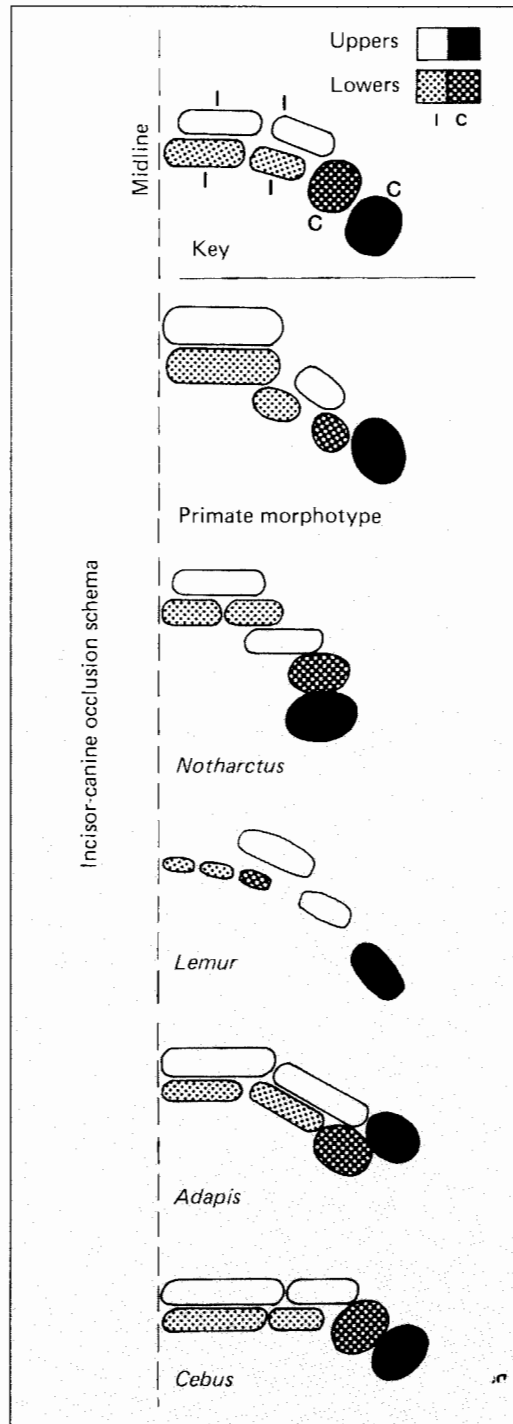
Incisors

The morphological pattern described above for *Notharctus* closely resembles that of *Smilodectes* [Gingerich, 1979a, p. 157, fig. 2] with the exception that I^2 of *Smilodectes* is still more reduced in size and possibly played an even lesser role in occlusion. Our manipulation of epoxy casts and examination of occlusal surfaces suggests that a similar form of I^1 - $I_{1,2}$ occlusion is also found in this notharctine. Upper incisors definitely assignable to *Pelycodus* have not yet been

described. However, one of Gregory's [1920] specimens (AMNH 14656) may represent this genus according to the allocations and synonymy of species stipulated by Szalay and Delson [1979]. It, too, has a mesiodistally expanded crown and mesial prong, and possibly accommodated both lower incisors simultaneously.

The anterior teeth of *Adapis parisiensis* and *Leptadapis magnus* (lowers only) are comparatively well known [e.g. Stehlin, 1916; Gingerich, 1981a]. They exhibit several features which distinguish them from notharctines. The general shape and gracility of I^1 compares well with notharctines but I^2 is relatively broader, lower-crowned and presents a chevron-like crown. Adapinan upper incisors contact interstitially and are arcuately aligned and closely ranked with the canines to form a continuous span of six teeth. Lingual cingula are present on I^{1-2} . The lower incisors are heteromorphic, with lingual cingula and a variably developed lingual buttress; apical margins are peaked on I_2 . As in *Notharctus*, $I_{1,2}$ occlude together into the I^1 lingual fossa. However, the expanded apical margin of I_2 extends beyond the distal edge of I^1 and occludes also with I^2 (fig. 4). Additionally, the lower canine (in both sexes), as noted by Gregory [1920] and Gingerich [1979b], does not project into a pre-canine diastema or a palatal fossa but articulates with the lingual aspect of I^2 . Thus, there is a more or less continuous incisor-canine complex involving the potential occlusion of all anterior teeth simultaneously.

In our sample of the living strepsirhines, indriids most closely resemble the notharctine I^{1-2} morphology [Rosenberger and Szalay, 1980], particularly in the shape of I^1 and the size relationships of I^{1-2} (table II). As in lemurids, I^2 is staggered posterolaterally to



I^1 . Lorisoids are quite different and evidently highly derived. In cases where upper incisors occlude with the toothcomb, as in *Lemur mongoz* and *Propithecus*, I^1 reciprocates the apical aspects of the entire lower battery with the distal margin of C_1 occluding into the I^2 lingual fossa.

Incisor and canine occlusion among anthropoids is quite different from the patterns described above (fig. 4). Although they are not entirely uniform, their morphological and positional relationships appear to be rather standard. We infer the anthropoid morphotype to feature the following: upper incisors moderately high-crowned, robust and spatulate with I^2 somewhat more conical; lowers roughly triangular in labial view and subequal in size; incisors closely ranked but I^2 separated by a diastema from the canine; I^1 lingual fossa reciprocates I_{1-2}

Fig. 4. Schematic diagram of arrangement and occlusion of the right incisors and canine in selected primates, as seen in horizontal view at the occlusal plane. The inferred primate morphotype is based upon a pleiadapoid-omomyid construct and suggests a laterally posted I^2 , exclusive I^1 contact and a spatial situation in which I^2 occludes along the distal aspects of I^1 (and the buccal surface of I^2). Note especially the following conditions: I^2 is aligned frontally in all later forms; the I^1 's may make interstitial contact only if close to the midline; the I^2 of *Notharctus* and *Lemur* is in a staggered position; the close-ranked arrangement of *Adapis* is unique; there is compound I^1_{1-2} occlusion in both *Notharctus* and *Cebus*, but with quite different I^2 relationships. We propose that evolutionary transformation is possible from the inferred morphotype pattern through notharctines to lemuriforms or adapids, or through omomyids (not shown, but essentially as in the morphotype) to anthropoids (illustrated by *Cebus*), but not in any other sequence.

apices, with distoapical edge of I_2 occluding with I^2 . In many living anthropoids the upper lateral incisor may be spiral-shaped lingually, having a modified distal aspect which conforms with the occluding C_1 . In one exception, *Callithrix*, the lower incisors are staggered and grossly modified in form so that I_1 and I_2 occlude apically into separate foveae of the I^1 lingual fossa. Furthermore, like *Notharctus*, the *Callithrix* C_1 occludes palatally to the upper lateral incisors, inscribing a *Notharctus*-like wear facet across the root-crown junction of I^2 .

Notharctines differ from both adapinans and anthropoids in that I_{1-2} occlude solely into I^1 while I^2 is not involved but instead occludes with C_1 . In most anthropoids and in the adapinans I^2 does meet I_2 , but the details of its occlusion with C_1 are different between the two groups. In adapinans, the apical margin of C_1 meets the lingual surface of I^2 , while in anthropoids the C_1 is offset from the I_{1-2} battery and its shaft meets the distal margin of I^2 rather than the full lingual surface.

Although similar terms have been used to describe the morphology of adapid and anthropoid anterior dentitions, we question whether the implied traits are homologous. Gregory [1920] referred to the I^1 of *Notharctus* as 'compressed' (transversely broad and labiolingually thin) and I_{1-2} as 'spatulate', descriptors which could equally as well be applied to anthropoids, and indeed both upper and lower incisors of adapids and anthropoids have been described as '... short, nearly vertical incisors with spatulate crowns...' [Gingerich and Schoeninger, 1977, p. 492; Gingerich, 1980, p. 129, table I]. We essentially agree that the lower incisors of notharctines are anthropoid-like in appearance, but view the more complex shapes of *Adapis*-*Leptadapis* as morphologically highly distinct

[Rosenberger and Szalay, 1980; Maier, 1980a].

One can also make an argument for notharctine-anthropoid difference in I_{1-2} -form based upon measurements (table II). Length:breadth ratios suggest that the crowns of adapid lower incisors are essentially square in section, whereas those of our anthropoid sample highlight their typical buccolingual dominance. The phenetic contrasts raise the possibility of homoplastic similarity. Rosenberger and Szalay [1980] have argued that the term 'spatulate' is a poor joint descriptor of the upper incisors of anthropoids and adapids, since their morphologies are distinctly different and probably nonhomologous. In all known adapids (possibly *Pelycodus* and *Leptadapis*, in *Notharctus*, *Smilodectes* and *Adapis*) [Stehlin, 1916; Gregory, 1920; Gingerich, 1979a; Gingerich and Martin, 1981], I^1 is a low-crowned, buccolingually thin tooth having a strongly asymmetrical labial-view outline. This is demonstrable by plotting mesiodistal, buccolingual and apicobasal dimensions which show that adapids are far more similar to living strepsirhines such as indriids than to anthropoids [Rosenberger and Szalay, 1980, p. 145, fig. 1] (table II). Another aspect of I^1 morphology which distinguishes the 'spatulateness' in these two groups is the development of a strong mesial prong in all notharctines and adapinans, which is lacking in anthropoids. The I^1 is dominated by this process, which appears as a localized expansion mesially. The mesial prong is not reinforced by an asymmetrical enamel deposition or by development of a lingual or marginal cingulum (which remains very gracile when it appears in *Adapis*).

The spatial configuration of the upper incisors of anthropoids and adapids also differs substantially. In the latter, the roots and

crowns of the right and left I^1 are broadly spaced apart, effecting a median gap between them [Martin, 1973; Gingerich and Martin, 1981]. This gap is greatly exaggerated in all modern strepsirhines where the I^1 's have entirely lost interstitial contact and a midline diastema appears. The mesial process in adapinans and notharctines can be interpreted as serving a spacing function to close the gap between the medial incisors. YPM 12956, in fact, shows essentially no interstitial contact facets between right and left central incisors. Based on the foregoing we suggest that the presence of a mesial prong in some living indriids may be a vestigial character.

Anthropoids (and many other mammals) may approach an adapid-like pattern in presenting something of a median gap [e.g. Gingerich and Martin, 1981] between I^1 's roots, but in doing so they continue to differ in pattern formation. Usually it is the sheer bulk of the incisal crowns that tends to separate their roots, even when the rostrum is anteriorly narrow (as in *Callithrix*). More importantly, interstitial contact of anthropoid upper median incisors occurs over a relatively large apicobasal height and surface area, often involving cingular development and/or a heavy deposition of enamel in the area of contact. We consider this to be a significant functional advantage in species employing powerful incision, for it allows occlusal loads to be transferred between teeth, reducing stress within them and limiting bending at their alveoli. Judging from these differences in morphology and inferred mechanical constraints, we take the anthropoid complex to be not truly comparable to the adapid in terms of form, function or biological role.

We summarize the above in the context of a hypothesis of incisor evolution in the primates (fig. 4), extending the analysis of Ro-

senberger and Szalay [1980]. The morphology of the anterior teeth of plesiadapiforms and omomyids, particularly in the less bizarre genera like *Plesiolestes*, *Omomys*, *Ou-rayia* and *Anaptomorphus*, is somewhat similar [e.g. Gingerich, 1981b; Rosenberger and Szalay, 1980]. The high-crowned, robust I^1 's dominate the complex, and in all likelihood there is a large degree of interstitial contact between them. In both groups the upper and lower medial incisors occlude in isolation without involving immediately lateral teeth. When they are present, upper laterals tend to be placed parasagittally rather than in the frontal plane parallel to the I^1 's. Thus, the I^1 - I^2 battery cannot form a continuous platform for $I_{1,2}$ occlusion. Correlatively, I^2 's are often reduced and/or morphologically differentiated from I^1 . Given the very common occurrence of this occlusal situation among these two distantly related lineages of the Paleogene radiation [Szalay and Delson, 1979], we believe that this exclusive I^1 - I^1 occlusion and the proportional relations seen in these groups are primitive for primates. Median incisor dominance is also reported for *Purgatorius* [Kielan-Jaworowska et al., 1979], which is regarded as the most primitive primate in all other aspects of the dentition [e.g., Szalay and Delson, 1979; Simons, 1972; Gingerich, 1976].

It follows from this hypothesis that adapids and living strepsirhines modified this primitive arrangement by realigning the upper lateral incisors into the frontal plane. It is noteworthy that notharctines are more similar to the presumed ancestral primate condition in that I^2 occlusion is not fully integrated into the occlusal set, even in its new position. The *Adapis* anterior dentition is thus derived relative to *Notharctus*, while the excessive reduction of *Smilodectes* upper lateral inci-

sors may represent a modified condition within that lineage. The modern tooth-combed strepsirhines such as indriids, which retain reasonably developed upper incisors like those of *Notharctus*, show a tendency to concentrate the occlusion of lower anterior teeth into I¹, with the I² having only peripheral significance. Although in lorises I^{1,2} are differently modified, I_{1,2} and C₁ still wedge lingual to I¹. Thus, the living strepsirhine forms show an extreme version of a *Notharctus*-like system, irrespective of the number of teeth involved in the toothcomb, height of the lower crowns, their caliber, function or biological role. This poses certain problems for those who regard *Adapis* as a more likely ancestral model for toothcombed strepsirhines [Gingerich, 1975c, 1980] for it requires a reversal not only of symphyseal fusion but also of I²-I₂, C₁ occlusion and incisor-canine form to a possibly more primitive state.

Functional inferences add another dimension to this hypothesis and corroborate the morphological interpretations which lead us to deny any phyletic continuity between adapid and anthropoid incisor teeth. For example, the premaxilla of living strepsirhines is highly reduced [Gregory, 1920] as one might expect given the lesser role of incisors in mastication. We think it likely that this is correlated not only with the derived development of the toothcomb but also with an elaboration of the oronasal tissues, accessory olfactory bulb and vomeronasal organ of the lemuriform olfactory mechanism. The latter structures have been described by Maier [1980b] and Stephan et al. [1982] as more highly differentiated than those of a number of insectivorans. *Notharctus* appears to show a more primitive condition than extant strepsirhines in the smaller size of its median diastema, the precocious withdrawal of central

incisor contact, and the gracility of the I¹'s combined with a seemingly comparatively thick premaxillary palatal process. We propose that the transformation that is exemplified by this comparison is associated with a strepsirhine specialization of the olfactory mechanism which in turn is related to the evolutionary shift of the lower incisors' predominant role from harvesting to grooming behaviors [Szalay and Seligsohn, 1977].

The anthropoid mechanism is also derivable from the plesiadapiform and omomyid pattern by frontal realignment of I₂. Unlike the strepsirhines, however, I² appears to have been directly incorporated into the series so that I₂ occludes with it. Additionally, in nearly all the modern forms I² is conical to allow reciprocity with C₁ during occlusion, which appears to be the morphotypic anthropoid condition [Szalay and Delson, 1979; Rosenberger, 1979]. We consider this to reflect a frugivorous specialization of the anterior teeth and rostrum in anthropoids, as it provides the most advantageous dispersion of occlusal-incisivation pressure across the complex. While the premaxillae of modern anthropoids are abbreviated, they are also characteristically robust in order to support the roots of the relatively enlarged and heavily stressed incisors. They give no evidence of a prior reduction in the role of incisor feeding or elaboration of nonmasticatory functions.

Canines

In developing the argument that the Adapidae present a canine complex which is structurally ancestral to anthropoids, Gingerich [1975a et seq.] pointed out several adapid features also characteristic of anthropoids: projecting, interlocking canines (*Mahgarita*); sexually dimorphic canines (*Adapis*, *Lepta-*

dapis), and canine-premolar honing (*Leptadapis*, *Protoadapis*). It appears to us that the absence of all these traits together in any one of the adapids implies just the opposite: that they evolved independently of the ancestral anthropoid pattern!

Despite the full attainment of 'large' canine size, all known adapid canines are morphologically different from modern anthropoid canines and our reconstructed anthropoid morphotype. In fact, several different adapid morphologies are evident. Among notharctines, upper and lower canines seem to retain a relatively simple conical shape at a variety of absolute sizes. The enamel cortex generally bears only slight degrees of vertical ridging or lineations, such as the vertical creases seen on YPM 12956 (fig. 1e-g). Lower canines usually project upward and are recurved. While the Yale specimen is only indicative of the genus *Notharctus*, it may be significant that C_1 occludes 'anomalously' with the cervical region of I^2 rather than with the crown. Although the YPM specimen could be interpreted as an individual variant, the genus-wide presence of a similar pattern in *Callithrix* leads us to think that it is not. Among adapines, including the enigmatic North American *Mahgarita* [Wilson and Szalay, 1976], upper canines are characterized by a proliferation of strong vertical sulci along the buccal face of the crown. The crown itself is transversely flattened in cross section. The lower canines of known adapinans, however, are not very high-crowned. In *A. parisiensis* they are low and stout and non-projecting [see Gingerich, 1981a, and above].

It seems to us that the descriptor 'interlocking', for canines in both adapids and anthropoids, is as misleading as 'spatulate' has proven for incisors. We prefer to restrict the

usage of 'interlocking' to the pattern seen in most anthropoids where the canines are widely splayed (in males) and matched so that C^1 - C_1 contact occurs over a broad area, C_1 fits into a precanine diastema, and in centric occlusion there is sequential contact of I^2 , C_1^1 and P_2 or P_3 . Two patterns are evident in adapids. In notharctines, the canines are recurved and oriented vertically (rather than splayed laterally). A consequence of this difference in canine slope is that C_1 in notharctines does not rest during centric occlusion in a precanine diastema but instead contacts I^2 lingually as it passes to the palatal fossa. Wear facets indicating C^1 - P_1 honing are also negligible on YPM 12956 though this may be a function of its gender. The adapinan condition differs from the previous patterns in that C_1 functions with I_{1-2} . While C_1 does occlude lingual to I^2 in adapinans, it does not rest in a palatal fossa as in notharctines. We regard both forms of canine contact in adapids as distinct from the anthropoid pattern and do not consider either interlocking in any manner.

As a principal example of a putative transitional adapid-anthropoid pattern, Gingerich [1975a] noted that (judging by alveoli) *Protoadapis brachyrhynchus* has a large C_1 , obliquely positioned P_3 and C^1 - P_3 honing. It is equally likely, however, that the C_1 was shaped more as in other European adapines and unlike anthropoids. Also, the oblique orientation of P_3 may be a resemblance to the Oligocene *Propithecus zeuxis*, but this does not mean that such a morphology was ancestral for anthropoids generally. In fact, the diminution of P_2 's in parapithecids and platyrrhines such as *Aotus* indicates that the anthropoid morphotype had a small anterior premolar in both sexes [Kay, 1980; Szalay and Delson, 1979; Rosenberger, 1979], that

would not have angled out from the tooth row.

Kay [1980] and Delson and Rosenberger [1980] have pointed out that the development of sexual dimorphism in adapids may also have little significance in linking them to anthropoids. Dimorphic features vary greatly at the species level and are difficult to establish as homologous states across larger taxonomic boundaries. In the case at hand, contrasting morphologies seem to indicate that the state of dimorphism was achieved independently in adapids and anthropoids.

Mandibular Symphysis

As noted above, the symphysis is fused in *Notharctus*. This condition also prevails in some other adapids and indriids [Beecher, 1977] and is universal in anthropoids. At the sheer anatomical level, the morphologies of the symphyseal regions in these animals are not exceptionally similar or uniform. The adapids generally show an enlarged wedge of bone joining each side of the jaw, exposing a large planum alveolare which may stretch as far backward as P_{3,4}. The long axis of the planum is highly oblique, in a sense paralleling the axis of the occlusal plane. On the external surface, the mental region is strongly convex in the frontal plane and there is little or no development of a flattened 'chin'. In contrast, in anthropoids a broad 'chin' is commonly present, even if not inferiorly-everted (or flattened) as in humans, and the mentum is usually nearly vertical in alignment. Except in special cases (e.g., some cercopithecids and *Callithrix*) where the planum alveolare is highly developed, the symphysis is anteroposteriorly compressed.

Some of these differences are brought out by comparing the measured diameters of the elliptical cross section of open and synos-

tosed symphyses (table III). In this example, the long axis of the section is defined as the distance between infradentale and gnathion and the short axis is a maximal length perpendicular to the plane of the outer surface of the mental region dropped to the planum alveolare or superior torus. Our sample suggests that whether or not the symphysis is fused in adapids, the ratio of minor:major axes tends to distinguish *Pelycodus* and *Notharctus* from anthropoids. *Smilodectes* falls nearer the anthropoid dispersion, possibly due to its very shallow jaws. All the values for unfused notharctine and omomyid symphyses fall appreciably above the anthropoid range, even by comparison with such long-symphysis 'specialists' like *Callithrix*. Our morphological observations suggest that the fused symphyses of all adapines are similarly lengthened along the major axis of the joint. Thus, anthropoids appear to have fused the symphysis in another way, correlating this condition with a shortening of its dorsoventral axis.

Given these differences in form, we conclude that the fused symphysis, as a unit character, cannot be homologous in adapids and anthropoids. We speculate that there would be significant functional differences inherent in these alternative patterns and their biomechanical contexts. In *Notharctus*, for example, the horizontally disposed symphysis seems designed to respond to forces transmitted along the nearly parallel axes of the dentaries, as when balancing side force is transmitted to the active side [Hylander, 1979; Beecher, 1977]. The posterior extension of the planum implies an adventitious transferral to the contralateral side [Beecher, 1977; Kiltie, 1981] with the posterior teeth benefitting especially. On the other hand, the vertically disposed anthropoid symphysis,

Table III. Comparative measurements (in mm), ratios and fusion states of the primate mandibular symphysis

Taxon	Major axis			Minor axis			Minor Major	Fusion status
	n	mean	range	n	mean	range		
Strepsirhini								
Notharctinae								
<i>Notharctus tenebrosus</i> , YPM 12956	1	16.00	–	1	5.50	–	0.34	fused
<i>Notharctus tenebrosus</i> , other	6	11.27	10.9–11.5	7	6.50	5.4–6.8	0.58	fused
<i>Smilodectes gracilis</i>	4	9.08	8.5–9.9	4	4.25	4.1–4.5	0.47	unfused
<i>Pelycodus ralstoni</i>	3	6.93	6.6–7.2	2	4.25	4.0–4.3	0.61	unfused
<i>Pelycodus trigonodus</i>	5	8.98	7.4–9.9	5	4.82	3.9–5.6	0.54	unfused
<i>Pelycodus jarrovii</i>	6	12.25	9.9–12.7	7	6.37	5.4–7.7	0.52	unfused
Haplorhini								
Omomyidae								
<i>Anaptomorphus aemulus</i>	1	4.20	–	1	2.40	–	0.57	unfused
<i>Omomys carteri</i>	1	3.90	–	1	2.60	–	0.67	unfused
<i>Hemiacodon gracilis</i>	9	5.46	4.8–6.1	12	3.25	2.5–3.7	0.60	unfused
<i>Microchoerus erinaceus</i>	1	7.00	–	1	3.60	–	0.51	unfused
Platyrrhini								
<i>Callithrix penicillata</i>	6	9.40	9.3–9.8	6	4.07	3.9–4.5	0.43	fused
<i>Leontopithecus rosalia</i>	5	11.20	10.2–11.9	5	5.12	4.8–5.7	0.46	fused
<i>Saguinus midas</i>	6	10.25	9.6–10.8	6	4.53	4.2–4.9	0.44	fused
<i>Saimiri sciureus</i>	3	10.03	9.6–10.5	4	4.25	3.8–4.8	0.42	fused
<i>Aotus trivirgatus</i>	5	11.06	10.2–12.1	5	3.78	3.5–4.3	0.34	fused
<i>Pithecia monachus</i>	6	18.48	15.6–20.4	6	5.42	5.1–5.8	0.29	fused

Given the comparable length of the major axis in the *N. tenebrosus* sample (n = 6) and in these small anthropoids, the difference in minor to major axis ratio is striking.

rather massive mental region, buttressed incisor-canine alveoli, and long moment arm (from the midline) of the large lateral incisors, all indicate that powerful shearing forces are taken up by the symphysis and surrounding bone. We tend to think that this is related to optimizing the efficiency of incision, but this does not devalue the significance of transferring contralateral forces. Incidentally, the reportedly short, deep mandibular corpus in *Protoadapis* also has little bearing on its supposed transitional status,

contrary to what Gingerich [1975a] argued, because the earliest known anthropoids commonly had shallow corpora [Rosenberger, 1981].

Is the symphyseal pattern of the adapids possibly preadaptive to the anthropoid condition? We think not for the following reasons. In one example where a true evolutionary sequence from unfused to fused dentaries is demonstrable, in the *Pelycodus-Notharctus* transition [Beecher, 1983], no other anthropoid-like features evolved simulta-

neously, countering Gingerich's [1977] argument that adapids evince a 'trend' toward anthropoid morphology. Other features of adapid jaws and their dynamics must also have differed considerably from early anthropoids, for the rostrum is long and the glenoid fossa highly modified [Schwartz and Tattersall, 1979; Fleagle and Rosenberger, 1983]. In *Adapis* the insertions for the masseter and medial pterygoid muscles are derivatively enlarged at the mandibular angle [Stehlin, 1916; Beecher, 1983]. This, too, implies that whatever tendency for fusion may have been present in that lineage, it also differed from the situation which influenced the morphology of early anthropoids, which fused their symphyses while the jaws were relatively shallow [Rosenberger, 1981] and the masseters probably less specialized. Further, if Beecher [1983] is correct that the combination of increasing body size and folivory were selectively responsible for symphyseal fusion in notharctines, this trend would not correspond to our predictions of morphology and adaptive patterns of the hypothesized protoanthropoids, for the latter show no signs of a folivorous habit. In fact, it is more likely that the emergence of anthropoids is tied to the evolution of obligate frugivory; large vertical incisors and nonfolivorous cheek teeth are nearly universalities. On the basis of the sum total of morphological differences of the masticatory systems in adapids and anthropoids it appears unlikely that their symphyses are homologously derived or that the anthropoid condition is a derivative of the adapid one. It is worth noting that this interpretation would discount the single dental trait which Kay [1980] thought might be a shared-derived feature linking adapids and anthropoids.

Synopsis

In light of the evidence presented here, we can suggest the following regarding the relationships of adapids to lemuriforms and to anthropoids. There are two different kinds of incisor-canine complexes in adapids and neither are extremely similar to the anthropoid condition. The *Adapis-Leptadapis* condition, which is most similar in incisor occlusion to that of anthropoids, is almost certainly autopomorphic as well. Therefore, the notharctine pattern might prove to be a better model for the antecedent of the strepsirhine toothcomb, contrary to previous opinions. We propose that a relatively robust I¹ is primitive for primates and that adapids and lemuriforms are homologously derived in reducing the size of I¹ and the premaxilla, and in rotating the upper central incisors laterally away from the midline. Anthropoids retain a relatively enlarged I¹ and are autopomorphic in positioning I² into the frontal plane to make contact with I¹ and I₂ and occlude with the C₁ shaft.

So far as we know, these implications are not contradicted by any character analyses of other anatomical systems, i.e. cranial morphology, the brain and special senses, cerebral circulation or postcranial anatomy. This leaves us with one point of similarity between notharctines (primitive adapids) and anthropoids: spatulate lower incisors. While we cannot at this point morphologically demonstrate that they are convergent to our own fullest satisfaction (owing to the lack of biometric data), we have several reasons for believing that they are: the consistently greater thickness of anthropoid I₁₋₂; the occlusal relations with I¹⁻²; the differences in morphology of upper incisors; the more readily envisioned transformation of an anthropoid I¹ set from the plesiadapiform/tarsii-

form pattern than from an adapiform one, and, lastly, the ease with which such simple teeth as lower incisors may be similarly transformed when spatial and occlusal constraints are similar.

The inferred functional properties distinguishing adapid and anthropoid incisors add weight to our argument that they are nonhomologous and nontransformable, if we are correct in interpreting the adapid pattern as a specialization relating to the eventual evolution of the nonmasticatory roles of the toothcomb and the anthropoid condition as a retained dominance of the central incisors for masticatory/incisivation functions. The alternative hypothesis requires complex shifts in natural selection to induce the evolution of 'spatulate', gracile, upper medial incisors (in adapids) from, for example, a more robust primitive condition (as in plesiadapiforms), followed by a secondary thickening of the crown (in early anthropoids) to emulate the more archaic morphology. It seems more parsimonious to theorize directional selection working to modify a simple plesiadapiform-like I^1 into an anthropoid I^1 by reducing its massiveness and still retaining its essential shape and functional significance [following Rosenberger and Szalay, 1980].

The Adapid-Anthropoid Hypothesis

Our major thesis has been that many of the similarities evident in comparing the anterior dentitions of adapids and anthropoids are homoplastic products of convergent or parallel evolution. Hence, they are immaterial to arguments linking these taxa in ancestor-descendant fashion or as sister groups. Why, then, have various authors interpreted these characters otherwise, or advocated

much the same hypothesis for different reasons? It is instructive to examine briefly the history of the adapid-anthropoid idea in light of recent advances in primate systematics. We suggest that the following were especially important in influencing the development of this notion: (1) it emerged during a period when the *scala naturae*, rather than a phylogenetic evolutionary history, was the governing paradigm; (2) it was devised during a period when the morphology, affinities and taxonomy of the Paleogene primates were poorly understood, and (3) it inadvertently incorporated inherent biases pertaining to the processes of paleontological discovery, such as those compounded by the paucity of specimens.

The critical covering principle behind various theories of primate evolution, since such studies originated [e.g., Huxley, 1863], was the *scala naturae*. Since among the living primates, 'prosimians' invariably occupied a lower rung than the anthropoids, it was inevitable, if tarsiers were removed, that lemur-like early Tertiary fossils would be cast as anthropoid ancestors. The adapids, which were structurally similar to lemuroids, fulfilled this expectation. Needless to say, the *scala naturae* is an imprecise guide to the phylogenetic relationships among taxa. By setting lower limits on primitive primate morphology, the *scala naturae* has also influenced the interpretation of character homologies and morphocline polarities. One taxonomic implication of this is that the entire radiation of plesiadapiform primates has been interpreted as collateral offshoots [Le Gros Clark, 1959; Simons, 1972], whose taxonomic affiliation with the euprimates is continually being questioned [Cartmill, 1982; MacPhee et al., 1983]. However, a reevaluation of some of these plesiadapiform traits

[Rosenberger and Szalay, 1980; see also above] by character analysis suggests transformational links between plesiadapiforms, tarsiiiforms and anthropoids. The assumption that adapid and lemuriform morphology is primitive for primates was thus opened to challenge. Two relevant implications emerged: (1) adapid morphology is derived, and suggestive of their exclusive phylogenetic relationships with living lemuriforms, and (2) the omomyids became an increasingly plausible ancestral stock for the anthropoids, even if they did not pass through an adapid-like structural stage of evolution [cf. Szalay and Delson, 1979].

As the Paleogene primate fossil record accumulated, the adapid-anthropoid hypothesis evolved. In its first formulation, Leidy [1873] suggested that the genus *Notharctus* had so much in common with the platyrrhine *Alouatta* that a derivation of South American monkeys from this Eocene genus was likely. As more notharctines became known, without apparent transitional forms between any of them and any higher primate, Leidy's suggestion was modified to encompass the descent of platyrrhines from an unspecified North American notharctine [e.g., Wortman, 1903/04; Gregory, 1920, 1922; Le Gros Clark, 1934, 1959]. During the same period, an origin for the catarrhines was proposed from a different ancestral stock. Neontologists [Hubrecht, 1897; Pocock, 1918; Hill, 1919] were joined by paleontologists [Wortman, 1903/04; Stehlin, 1916; Gregory, 1920] who saw threads of a phyletic relationship between them, *Tarsius*, the predominantly Eocene omomyids and, especially, the European microchoerines. Either as a consequence or a presupposition of this dual hypothesis, Anthropoidea was considered diphyletic with its two branches evolving in

situ in different geographical realms. The spatial division of notharctines and microchoerines satisfied the requirements of the biogeographical complications of that era which were implicit in the disjunct distribution of higher primates and hystricomorph rodents. Simpson [1963] popularized such a view as an exemplary case of the parallel evolution of an advanced grade of organization from a more primitive level. He asserted that two relevant 'prosimian' families (Adapidae and Omomyidae) may have independently spawned the anthropoids. This first-stage hypothesis met opposition on two fronts: adapids and omomyids are now generally accepted as quite distantly related [Simons, 1972; Szalay and Delson, 1979; Gingerich, 1981b] and anthropoids are generally believed by most to have had a monophyletic origin [Delson and Rosenberger, 1980; Luckett and Szalay, 1978; Fleagle and Rosenberger, 1983; Cartmill et al., 1981; but see Cachel, 1979].

The second stage in the development of the adapid-anthropoid hypothesis took into account these phylogenetic objections by framing it in less narrow terms, with an emphasis on anthropoid monophyly. The *Notharctus*-platyrrhine and microchoerine-catarrhine elements were replaced by a higher taxon phylogeny: the family Adapidae was cast as ancestors of protoanthropoids. Gingerich [e.g., 1980] developed this position by proposing an elaborate list of anatomical traits shared by adapids and anthropoids (see above). In a parallel hypothesis which he has recently revised [MacPhee et al., 1983], Gingerich [1975b et seq.] interpreted all tarsiiiform primates as only distantly related to anthropoids and viewed the latter as the monophyletic descendants of an adapid stock. The alternative to the adapid-anthro-

pooid hypothesis as currently conceived is that tarsiiiforms and anthropoids are monophyletically linked by synapomorphies [Pocock, 1918; Szalay and Delson, 1979; Hill, 1955] and, as we have attempted to illustrate above, the resemblances in anterior dentitions of adapids and anthropoids are largely nonhomologous. The same applies to theorized postcanine tooth homologies dating to the earlier part of this century. For example, the hypothesis that *Notharctus* and *Alouatta* share homologous 'pseudohypocones' [e.g., Gregory, 1920] has not endured empirical ontogenetic tests [Tarrant and Swindler, 1973], which show that the hypocone of *Alouatta* does not split ontogenetically from the protocone as it seems to in the *Pelycodus-Notharctus* transition. Even if it did, as Gregory [1920, 1951] realized, the morphology of *Alouatta* is not the ancestral platyrrhine condition [Rosenberger, 1977, 1979], making this comparison essentially irrelevant.

A number of other theoretical problems are tethered to the adapid-anthropoid hypothesis. Arguing that adapids progressively exhibit trends bearing on the anthropoid condition [Gingerich, 1977] can hardly be taken as evidence that adapids actually are anthropoid ancestors. It may just as easily signal their descent from a more remote common ancestor and/or subsequent subjection to similar selective pressures. Arguing that 'These forms (*Oligopithecus*, *Hoanthonius*, *Amphipithecus*, *Protoadapis brachyrhynchus*) all share some combination of molar morphology, symphyseal fusion, canine honing, premolar crowding, and deep mandibular rami that make some advanced Adapidae virtually indistinguishable from primitive anthropoids' [Gingerich, 1977, p. 177] is open to criticism for a number of reasons. The morphology and systematic position of

all of these fossil forms, actually known by very few specimens, have been variously interpreted by several students [e.g., Conroy, 1978; Szalay and Delson, 1979; Kay, 1980]. Some have been assigned to different taxa above the family level. Additionally, the sharing of a combination of similarities may be an important reason for grouping taxa, but ancestral-descendant hypotheses [Szalay, 1977b] should include statements of homologies and morphocline polarities. If, on the other hand, the veracity of the adapid-anthropoid hypothesis relies upon a family-level framework, lumping some characters of notharctines and others of adapines, the resulting compromise hypothesis becomes so ill-defined as to be essentially untestable with current methods. Arguing that stratophenetically intermediate forms such as those listed above exist [Gingerich, 1977, 1980] is not especially convincing either, since they are epochs and continents apart from each other [Szalay and Delson, 1979].

Is the adapid-anthropoid hypothesis a phylogenetic fallacy? We have attempted to show that the very best presented cases in support of it are not predicated upon a very secure morphological foundation. We have also attempted to illustrate that its development has been influenced by the historical baggage of a previous era, when earlier workers attempted to anchor the question of anthropoid origins against such beautifully preserved fossils as *Notharctus* and worked within another conceptual framework. As an alternative to this, the tarsiiiform ancestry hypothesis stands somewhat damaged [Cartmill, 1982] but unrefuted. The neontological links between tarsiers and anthropoids have endured and been augmented since the turn of the century [Lockett and Szalay, 1978], though fresh arguments have questioned the

cladistic reliability of characters associating tarsiers with fossil omomyids. It seems to us that both the phenetic and cladistic evidence continue to justify the hypothesis that adapids are the sister group of the lemuriforms and tarsiiforms are the sister group of the anthropoids. Until each of these postulates is refuted, the advocacy of yet a third mutually exclusive theory, the adapid-anthropoid hypothesis, appears to be untenable.

Conclusions

The morphology of the incisor-canine complex of *Notharctus* is known from fragmentary remains discussed by Gregory [1920] and from a basically complete specimen described here for the first time. This evidence holds important clues concerning the affinities of the adapid, lemuriform and anthropoid primates. In the spacing, occlusion and size-shape relationship of the upper incisor teeth, *Notharctus* and the other known notharctines (*Pelycodus*, *Smilodectes*) are characteristically lemuriform, albeit of a much more primitive status since the lower teeth had not yet become modified into a comb-like system. This common pattern includes the development of a median interincisal diastema, low-crowned I^1 bearing a strong mesial prong, a structurally gracile $I^{1,2}$ and an I^2 that is staggered, having little or no occlusal interaction with $I_{1,2}$. In the *Adapis-Leptadapis* clade, the conformation of the incisor-canine complex seems to be generally similar but differs in a number of traits. Its median diastema is absent, the transverse diameters of I^2 and $I_{1,2}$ are enhanced, C_1 is subcaniniform, I^2 is fully occlusal and the precanine diastema is absent. These differences represent a derived adapinan occlusal

pattern wherein all the incisors operate as a unitary 'cropping' mechanism, together with a functionally integrated lower canine tooth. Aspects of the adapinan complex are contrary to expectations of a protolemuriform dentition, particularly in the expansion of $I_{1,2}$ crowns and the integration of I^2 into the occlusal set. Here, notharctines resemble lemuriforms and most other primates more than *Adapis* does. We propose that the notharctine morphology is a better model for the pretoothcomb prototype. Further, since we think the ancestral primate anterior dentition resembled a plesiadapoid-omomyid-anthropoid construct and not a strepsirhine pattern of organization, the shared similarities of the upper incisors of adapids and lemuriforms are interpreted as homologously derived and indicative of their sister group affinities.

Comparisons of the adapid anterior dentition with those of living and fossil anthropoids, and with traits of the reconstructed anthropoid morphotype, suggest that many of their shared similarities reflect convergent evolution. Adapids differ in several important respects. Broadly speaking, they have low-crowned rather than moderately to high-crowned upper incisors; $I^{1,2}$ which are buccolingually thin rather than thick, and a distinctly broadened I^1 bearing a strongly defined mesial process. Based upon these structural features, we prefer not to use the term 'spatulate' as a descriptive element in comparisons of adapid and anthropoid incisors for it implies that their shapes are genetically linked as homologues. We consider their similarities superficial and phylogenetically homoplastic. Importantly, notharctine and adapinan anterior dentitions are also quite different themselves, thus devaluing the characterization of an 'adapid' pattern and its

comparison with that of anthropoids. In fact, it is likely that notharctine adapids are more primitive in their anterior tooth morphology than adapinan adapids. This again constrains the form of phyletic comparisons and requires that they be made in the context of morphotypes. We also question the proposal that similarities of adapid and anthropoid canine teeth, especially those related to their degrees of sexual dimorphism, are truly shared homologous conditions; different degrees and different expressions of dimorphism occur in various adapids as they do in anthropoids. Our examination of the morphology of the mandibular symphysis leads us to similar conclusions. In cases where adapids resemble anthropoids in having co-ossified dentaries, the morphological substrates contrast markedly. Since the mechanics of adapid and anthropoid jaws were probably different, dissimilar selective pressures could have channeled a superficially similar result.

We conclude that essentially all of the characters of the anterior dentition and mandible that have been advanced as evidence of a phylogenetic link between adapids and anthropoids are probably derived nonhomologies. Such traits are invalid as cladistic markers. The adapid-anthropoid hypothesis was one of the earliest schemes linking fossil and living primates and has continued to influence our thinking on higher primate phylogeny for more than 100 years. As the systematics of plesiadapiform, adapid and tarsiid primates have been extensively reconsidered, the application of the monophyletic concept of the Haplorhini to the fossil record makes a derivation of the Anthropoidea from an omomyid stock eminently plausible. Similarly, a rethinking of character transformations suggests that adapids are

collaterally related to living lemuriforms, removing them from a more recent common ancestry with anthropoids. In light of our attempted refutation of the morphological basis of the adapid-anthropoid hypothesis, we consider the omomyid-anthropoid hypothesis to be the best working theory.

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