

The origin of the plesiadaplid primates and the nature of *Purgatorius*¹

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The origin of the plesiadapid primates and the nature of *Purgatorius*

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ABSTRACT: Pandemonium dis, new genus and species, bridges the gap between the basal primate Purgatorius and the otherwise basal plesiadapid Pronothodectes. With other evidence, this shows that the Plesiadapidae had no post-Purgatorius phyletic association with non-plesiadapoids, and that therefore their derived resemblances to other groups, such as the Euprimates and the Paromomyidae sensu stricto, are homoplastic. Purgatorius janisae, new species, is based on the specimens which have usually been used as a standard for P. unio.

I discuss all species of Purgatorius and some other plesiadapiforms, and expand a basal family Purgatoriidae. I return Saxonella to the Plesiadapidae after showing its point of divergence. Two palaechthonine specimens retain P1; one even retains a complete anterior dentition, and the other represents a new genus and species, Anasazia williamsoni.

Broad comparisons identify aspects of the dental morphotype of the Euprimates. Purgatorius shares a large proportion of them, and I therefore keep (or return) the Plesiadapiformes in (or to) the Primates as their basal radiation. I evaluate critically some other characters relevant to this conclusion. In a new phylogeny I derive the Plesiopithecidae from the Protoadapini, among other things. A new classification of the Primates introduces a number of heresies, which are not restricted to the Plesiadapiformes; Eosimiae and Altaniinae are new taxa.

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Introduction

The Plesiadapidae is the best-known family of Paleocene primates. *Plesiadapis* was named in 1877 by Gervais, but already in 1854 (Charlesworth, 1855) Charlesworth had erected the genus *Platychoerops* for an early Eocene species. The family now contains six genera in two subfamilies, which are often separated at the family level, and it is ancestral to the family Carpolestidae, which becomes convergent on multituberculates. The phyletic relations of these forms can be seen from Figure 1, which is at the end of the monograph. (The time scale and correlations of this figure, in addition to the phylogeny itself, represent original interpretations, based mostly on the following papers: Aubrey et al., 1988; Berggren, 1993; Buckley, 1993; Butler, Krause, and Gingerich, 1987; Cande and Kent, 1992; Clyde, Stamatakis, and Gingerich, 1993; Hardenbol, 1993; Lucas, 1993; Obradovich, 1993; Odin and Luterbacher, 1992; Swisher, Dingus, and Butler, 1993; and Tauxe et al., 1994.)

Plesiadapis is known from skulls and much postcranial material (e.g., Russell, 1964; Szalay, Tattersall, and Decker, 1975; Gingerich, 1976, 1992; Szalay and Dagosto, 1988), *Nannodectes* from two partial skulls and some postcranial material, and the other genera from jaws and teeth only. Plesiadapids are common in most Paleocene faunas of the Euramerican continent, and they evolved rapidly. As a result, the family has been more important than any other in correlating the middle and late Paleocene faunas of this region since the work of Gingerich (1975).

However, the phyletic relationships of the Plesiadapidae to other primates have been controversial. Initially, some resemblances in the molars to the late Eocene protolemuroid *Adapis* prompted the name (an association advocated as late as 1975 by Szalay), and there was a later association (e.g., Gingerich, 1976) with tarsioids on the basis of enlarged incisors and a fusion of the ectotympanic to the auditory bulla with its extension as a bony external auditory meatus. Bown and Rose (1976) suggested a special relationship to the Paromomyidae (*sensu stricto*), which have a generally similar appearance although differing in major respects. Gunnell (1989) agreed with the latter proposal.

The existence of a special relationship between Paleocene primates (and their immediate relatives) and later primates has been questioned (e.g., Martin, 1968; Wible and Covert, 1987; Gunnell, 1989). As a result, Gingerich (1989) has named an order Proprimates to include them and other possibly related groups. The Proprimates is in principle a natural paraphyletic group (cf. Van Valen, 1978a), and it may be the best approach whether or not undoubted primates originated from the Paleocene forms. I will conclude, however, that retention of the current order Primates is probably desirable.

A new genus from the early Paleocene of Montana shows that the Plesiadapidae came directly from the basal primate genus *Purgatorius*. Because *Purgatorius* lacks, or can be inferred to have lacked, the derived resemblances of plesiadapids to other primates, the latter resemblances must be convergent.

Institutional abbreviations: Halle, Geiseltalmuseum, Halle/Saale, Germany; KU, University of Kansas Museum of Natural History; LACM, Los Angeles County Museum of Natural History; NMMNH, New Mexico Museum of

Natural History; UALP, University of Arizona, Laboratory of Paleontology; UCMP, University of California Museum of Paleontology; UM, University of Minnesota, Department of Geology and Geophysics.

Order Primates Linnaeus, 1758

Suborder Plesiadapiformes (Van Valen, 1969) Simons and Tattersall, 1972
(= Microsyopoidea Van Valen, 1969; = Paromomyiformes Szalay, 1973)

Superfamily Plesiadapoidea (Trouessart, 1897) Bown and Rose, 1976

Family Plesiadapidae Trouessart, 1897

Subfamily Plesiadapinae Trouessart, 1897

Pandemonium, new genus

Type and only known species: *Pandemonium dis*, new species

Diagnosis: As for *P. dis*.

Etymology: Satan's palace, in Milton's Paradise Lost, with reference to Purgatory Hill and analogy to *Purgatorius*.

Pandemonium dis, new species

Plates 1-4

Type: U.M. No. VP 1631, right M₂.

Known distribution: Late Puercan (early Paleocene), Tullock Formation, McCone County, Montana: Purgatory Hill Local Fauna. The Purgatory Hill locality is in the lower part of the Collins Ranch Member of the Tullock Formation, thus being stratigraphically in the middle part of the formation (Rigby and Rigby, 1990).

Etymology: The city of punishment in Dante's Inferno, with reference to Purgatory Hill and euphony.

Referred specimens: U.M. Nos. VP 1635, left P⁴ lacking parastyle; 2201, left M¹ or M²; 1526, mesiolingual two thirds of right upper molar; 1553, lingual half of left upper molar; 1627, lingual three fourths of right upper molar; 1630, right M¹ or M²; 2193, right P₃ lacking apex and lingual part of protocone and lingual part of base; 2190, left P₃; 2189, left P₄; 1519, left M₁; 1620, right M₁; 1639, left M₁; 1648, eroded left M₁; 1532, trigonid of right M₂₂; 1621, left M₂; 1631, right M₂; 1541, talonid of right M₂₂; 2185, left M₃ lacking lingual border of talonid; 2186, right M₃ lacking mesiolabial border of trigonid; 2187, right M₃; 2206, lingual half of molar trigonid; and probably 2194, left I¹, and 2211, right P³.

Diagnosis: A plesiadapid with the following distinctions from generally similar plesiadapoids or from *Purgatorius*: styler shelf wide for a primate; upper molars relatively transverse; conules moderate; hypocone small but differentiated from postcingulum; postcrista weak to absent. P³ and P⁴ without conule; metacrista strong and with trace of metacone on P⁴; postcrista and postcingulum moderate; parastylar lobe small but distinct. Lower molars moderately transverse; trigonid relatively low; cusps rounded; paraconid reduced and not always distinct from paracristid; talonid at least as wide as trigonid; basins broad and moderately shallow; hypoconulid of M₃ expanded into incipient third lobe. P₃ and P₄ simple, transverse, *Pronothodectes*-like; metaconid absent and paraconid barely detectable on P₄ only; talonid small, transverse; weak cristid obliqua and entocristid present in usual

	Labial length	Length at metaconule	Width
2194, I ¹	2.3	—	1.8
2211, P ³	1.9	—	2.8
1635, P ⁴	2.5	—	3.1
1526, M ¹ or 2	—	1.9	—
2201, M ⁷²	2.5	1.9	4.0
1630, M ⁷²	2.6	1.9	4.0
1553, M ^u	—	1.9	—
1627, M ^u	—	2.2	—

Table 1. Measurements (in millimeters) of upper teeth of *Pandemonium dis*.

	Length	Trigonid width	Talonid width
2193, P ₃	1.9	1.3	1.2
2190, P ₃	1.9	1.4	1.2
2189, P ₄	1.9	1.6	1.4
1639, M ₁	2.5	1.8	2.0
1519, M ₁	2.8	1.9	2.1
1648, M ₁	2.6	1.9	2.0
1620, M ₁	2.4	2.1	2.3
1621, M ₂	2.6	2.1	2.3
1631, M ₂	2.7	2.4	2.4
2185, M ₃	3.6 ± 0.1	2.3	—
2186, M ₃	3.8	2.0	2.0
2187, M ₃	3.2 ± 0.1	1.9	1.8
1532, M ₂ or 3	—	2.0	—
1541, M ₂ or 3	—	—	2.3

Table 2. Measurements (in millimeters) of lower teeth of *Pandemonium dis*. Ca. 95 percent measurement bands are given.

positions on P₄. Tables 1 and 2 give measurements.

Comparisons: *Pandemonium* is in almost all respects intermediate between *Purgatorius* and *Pronothodectes* or similar to one or the other of these genera. It is even more primitive than *Purgatorius unio* (but not *P. janisae*, described below) in that the relatively flat part of the stylar shelf is slightly broader, it differs from *Purgatorius janisae* and *Pronothodectes matthewi* in nearly lacking a metacone on P⁴, and it may be more derived than *P. matthewi* in that the paraconid is usually more reduced. The latter character, however, is sufficiently variable that not much reversal of evolution would be required to transform the paraconid of even the known population of *Pandemonium* into that of *Pronothodectes*. I trust that the possibility of sampling error from a variable population is too obvious to require repeated mention in the paper.

Pandemonium has several differences from *Purgatorius* not mentioned in the diagnosis. The characteristic shift of the lingual part of the upper molars, present in *Purgatorius unio* and most other

Plesiadapiformes, is absent in *Pandemonium* as well as in other plesiadapids and carpolestids, and apparently also in the purgatoriid *Torrejonia* Gazin (1968). (It is also absent from the quadrate teeth of microsypids and paromyids *sensu stricto*.) This is to say that in *Pandemonium* the lines joining the paracone with the paraconule and the metacone with the metaconule are nearly parallel to the transverse axis of the tooth, not at about a 30° angle to it; the protocone is nearly in the middle of the space between the extension of these lines, not on or nearer to the metacone-metaconule line; and the lingual half of the mesial and distal borders of the tooth are not angled appreciably distolingually.

For a comparison of *Pandemonium* with *Purgatorius* and *Pronothodectes* I will divide the characters into three groups: those in which *Pandemonium dis* resembles *Purgatorius unio*, those in which it resembles *Pronothodectes matthewi*, and those in which it is intermediate or, rarely, different from both, the latter marked as [O]. The characters are, as usual, not mutually independent functionally, morphologically, or developmentally. *Pandemonium dis* differs from *Purgatorius janisae* in additional characters, as can be seen from the later discussion of *P. janisae*. After giving the character state for *Pandemonium dis* I give, sequentially, the states for *Purgatorius unio*, *Purgatorius janisae*, and *Pronothodectes matthewi*. For P⁴ the comparisons are necessarily with *Purgatorius janisae* rather than with *P. unio*.

Pandemonium dis *Purgatorius unio* *Purg. janisae* *Pron. matthewi*

Resembling *Purgatorius unio*:

Upper molars

- | | | | |
|--|--|------------------|----------------------|
| 1. Relatively transverse as <i>P. dis</i> | | less transverse | less transverse |
| 2. Postcingulum not continuous with metacingulum as <i>P. dis</i> | | as <i>P. dis</i> | continuous |
| 3. Metaconule not larger than paraconule as <i>P. dis</i> | | as <i>P. dis</i> | larger |
| 4. Centrocrista moderately strong as <i>P. dis</i> | | intermediate | weak |
| 5. No transverse valley from protofossa to labial border of tooth as <i>P. dis</i> | | as <i>P. dis</i> | present |
| 6. Parastylar lobe projecting as <i>P. dis</i> | | as <i>P. dis</i> | not projecting |
| 7. Ectoflexus moderately deep as <i>P. dis</i> | | as <i>P. dis</i> | shallow |
| 8. Tooth shortest mesiodistally at level of metaconule as <i>P. dis</i> | | as <i>P. dis</i> | no contraction there |

P⁴

- | | | | |
|---|-----------|------------------|---------------------------|
| 1. Conule absent | [unknown] | as <i>P. dis</i> | present and large |
| 2. Parastylar lobe more projecting than in <i>P. matthewi</i> | [unknown] | as <i>P. dis</i> | (as stated in comparison) |

Lower molars

- | | | | |
|---|------------------|------------------|---------------------------|
| 1. Paraconid not appressed against metaconid | as <i>P. dis</i> | as <i>P. dis</i> | appressed |
| 2. Paraconid appreciably lower than metaconid | as <i>P. dis</i> | as <i>P. dis</i> | not or barely lower |
| 3. Paraconid moderate | moderate | strong | strong |
| 4. Postmetacristid relatively steep | as <i>P. dis</i> | intermediate | relatively low slope |
| 5. Cingulids usually slightly stronger than in <i>P. matthewi</i> | as <i>P. dis</i> | intermediate | (as stated in comparison) |

P₄

- | | | | |
|---|------------------|------------------|--------|
| 1. Hypoconulid present in addition to hypoconid | as <i>P. dis</i> | as <i>P. dis</i> | absent |
| 2. Protoconid not tilted mesially | as <i>P. dis</i> | as <i>P. dis</i> | tilted |

Resembling *Pronothodectes matthewi*.

Upper molars

- | | | | |
|--|-----------|--------------|------------------|
| 1. Protocone twist [see text] absent | present | intermediate | absent |
| 2. Hypocone weakly differentiated from postcingulum | absent | absent | as <i>P. dis</i> |
| 3. Postparaconule wing sometimes bifurcates | not found | not found | as <i>P. dis</i> |
| 4. Conules (except with bifurcation) not closer to protocone than to paracone and metacone | closer | closer | as <i>P. dis</i> |

P⁴

- | | | | |
|--|-----------|--|------------------|
| 1. Protocone lobe about as long mesio-distally as wide | [unknown] | shorter | as <i>P. dis</i> |
| 2. Postcrista strong and merges with postcingulum | [unknown] | relatively weak and abuts postcingulum | as <i>P. dis</i> |

Lower molars

- | | | | |
|---|------------------------|------------------------|------------------|
| 1. Teeth relatively transverse | relatively elongate | relatively elongate | as <i>P. dis</i> |
| 2. Trigonid relatively low | relatively tall | relatively tall | as <i>P. dis</i> |
| 3. Talonid of M ₃ appreciably larger than trigonid | not or slightly larger | not or slightly larger | as <i>P. dis</i> |

4. Hypoconulid lobe present on M ₃	absent	absent	present
5. Mesoconid present on cristid obliqua	absent	absent	present
6. Talonid at least as wide as trigonid on M ₁ and M ₂ , not much if at all narrower on M ₃	narrower	narrower	as <i>P. dis</i>
7. Paracristid weak to moderate, moderately distinct from paraconid	moderate and not to weakly distinct	moderate and not to very distinct	weak to moderate and not to very distinct
8. Talonid basin of M ₁ and M ₂ broader than long	about equal dimensions	about equal dimensions	as <i>P. dis</i>
9. Entoconid of M ₁ and M ₂ distinct from entocristid	not distinct	intermediate	distinct
10. Hypoconulid weaker than entoconid on M ₁ and M ₂	about as strong	intermediate	weaker

P₄

1. Tooth nearly as broad as long	relatively elongate	relatively elongate	as <i>P. dis</i>
2. Talonid very transverse	not transverse	not transverse	very transverse

Intermediate (and other):

Upper molars

1. Cusps moderately blunt	relatively acute	relatively acute	blunt
2. Protocone apex moderately lingual	relatively central	moderately lingual	lingual
3. Conules moderately bulbous	acute	acute	bulbous
4. Metastyle moderate to weak	relatively strong	relatively strong	absent
5. Conules about as separate as paracone and metacone	closer	as <i>P. dis</i>	usually farther apart
6. Protocone moderately low	relatively tall	relatively tall	low
7. Precingulum moderately separate from paracingulum	widely separate	widely separate	nearly or quite meet
8. Styler shelf relatively broad [O]	narrow	relatively broad	narrow

P⁴

1. Protocone only moderately more mesial than paracone	[unknown]	definitely more mesial	not or barely more mesial
2. Cusps only moderately acute	[unknown]	relatively acute	relatively blunt
3. Metacone nearly absent [O]	[unknown]	relatively large	relatively large

Lower molars

1. Talonid of M ₂ somewhat larger than trigonid		not larger	appreciably larger
2. Labial surface of protoconid only moderately steep	steep	steep	relatively low slope
3. Protoconid moderately low on M ₂ and M ₃	relatively tall	relatively tall	low
4. Paraconid somewhat labial	central	somewhat labial	labial
5. Cristid obliqua extends only weakly to the apex of the metaconid of M ₁	not extend to apex	weakly to apex	strongly to apex
6. Labial surface of hypoconid only moderately steep	steep	steep	relatively low slope
7. Paraconid usually more reduced than in <i>Pronothodectes matthewi</i> [?O]	moderate	strong	moderately strong
8. Trigonid somewhat compressed mesiodistally, that of M ₂ and M ₃ slightly shorter than talonid	not compressed	not compressed	appreciably compressed

P₄

1. Labial surface of protoconid only moderately steep	steep	steep	moderately low slope
2. Cristid obliqua present but weak	moderate	moderate	absent
3. Entocristid present but weak	moderate	strong	absent
4. Paraconid nearly absent	distinct but weak	strong	absent
5. Protoconid relatively long mesiodistally near apex	no elongation	no elongation	elongate
6. Paracristid nearly absent	weak	strong	absent

7. Hypoconid slightly more lingual than in <i>Purgatorius unio</i>	(as stated in comparison)	as in <i>P. unio</i>	appreciably more lingual than in <i>P. unio</i>
8. Hypoconid not much higher than hypoconulid	much higher	not much higher	talonid uncusped but highest at site of hypoconulid
9. Talonid basin very weak	moderate	moderately strong	absent

The incisors of *Purgatorius* are unknown, but one specimen (U.M. No. VP 2194, an isolated I¹), probably belongs to *Pandemonium* rather than *Purgatorius*. It is of an appropriate size and has some indications of plesiadapid apomorphies. The apical bifurcation is not yet present, but there is an incipient distobasal cusp and the curvature of the tooth is generally comparable. In plesiadapids, as in plagioulacoid and taeniolabidoid multituberculates but more markedly, the distal cusp probably served, like I² of lagomorphs (function discovered in the latter by S. Avery, personal communication), partly as a stop for the lower incisors (Gingerich, 1976). This function is only incipient, if present at all, in *Pandemonium*.

Pandemonium presumably had 3 upper and lower incisors and 4 premolars at least in the upper jaw, because its descendants the Carpolestidae did so initially (Fox, 1994). At least *Pronothodectes matthewi* had only 2 lower incisors and only 3 premolars in each jaw, the number of upper incisors being unknown (Gingerich, 1976).

Pronothodectes matthewi is generally regarded as the most primitive known plesiadapid and, except for *Pandemonium*, this seems unexceptionable. L.S. Russell (1958) referred an M₁ from the Torrejonian of Locality 2E, Calgary, Alberta, to *Pronothodectes* sp. Krause (1978) transferred it to the Microsyopidae, *sensu lato*, an allocation which seems reasonable although I have not seen the specimen. Fox (1990) returned to Russell's identification; from Russell's photograph the paracristid is looped, which is uncharacteristic of plesiadapids.

The Carpolestidae, on which see Rose (1975), constitute a small North American family derived from early plesiadapids¹ and convergent on multituberculates. It has three known genera; sometimes *Carpolestes* is included in *Carpodaptes*, but *Carpolestes* is adaptively distinct especially by its functional incorporation of the M₁ trigonid into the enlarged crest of P₄ and by its appreciably less transverse P³ and P⁴. *Elphidotarsius*, the ancestral genus of the three, occurs as early as *Pronothodectes* does, but an ancestor of *Elphidotarsius* would perhaps be referable to a species of *Pronothodectes* with more teeth than known species possess. Two unnamed genera referred to the Carpolestidae have recently been reported from approximately the basal Eocene of China

¹Stucky and McKenna (1993) place the Carpolestidae within the haplorhine Euprimates, of all places, for unstated reasons. Possibly they relied on the ambiguous and too restrictive comparisons of Sigé et al. (1990) and, less directly, Rose and Krause (1984), but the origin of carpolestids from a primitive plesiadapid such as *Pronothodectes* is well established (Rose, 1975).

(Beard, Wang, and Tong, 1993); at least one of these seems to be correctly referred to the family. The more common form may, however, be a primitive plesiadapid, pending contrary evidence. Its lack of a central conule on P^3 (although one is present on P^4) suggests a phyletic divergence between *Pandemonium* and *Pronothodectes*.

Saxonella represents a similar adaptive facies to the Carpolestidae, but it was derived separately and does not become as extreme. Although it is often placed in a separate family, I do not see it as distinct enough from plesiadapids for such a rank and return it to the Plesiadapidae as the subfamily Saxonellinae. It is known from the early part of the late Paleocene of the Euramerican continent; see D.E. Russell (1964) and Fox (1991). [The name of the American species, *S. naylori*, dates from an abstract: Fox, 1989a.] Although *Saxonella* is usually associated with the Plesiadapidae, Gingerich (1976) placed it within the Paromyidae *sensu stricto*. Fox (1991) adequately dealt with this placement, but he too was skeptical of a plesiadapid ancestry.

There are indeed several respects in which *Saxonella* is more primitive than *Pronothodectes matthewi*. The protoconid of P_4 is not tilted forward, P_4 has a weak paraconid and entocristid, the paracristid of the molars is stronger, and the molar paraconid is usually more central and separate from the metaconid (but Halle Wa 399, an isolated M_3 , has a paraconid like that of *Pronothodectes*). The crests and cusps are also somewhat sharper, and the precingulum is separated from the paracingulum on M^2 and M^3 , although not on M^1 (the latter resembling *Pronothodectes* in this). All these states, except the stronger paracristid, are characteristic of *Pandemonium.dis*.

However, *Saxonella* is more derived than *Pandemonium*, and resembles *Pronothodectes*, in several other ways. Most strikingly, perhaps, it has the characteristic plesiadapid (and carpolestid) central conule on P^4 . An upper incisor, which D.E. Russell (1964) referred probably correctly to *Saxonella*, is fully plesiadapid-like, with a bifurcated apex and a large basal cusp. The upper molars are not transverse, the postcingulum is continuous with the metacingulum, there is a transverse valley from the profossa to the labial border of the tooth, there is no projecting parastylar lobe, the molars are not shortest at the level of the metaconule, the protocone apex is lingual, and there is no metastyle. Other differences of *Saxonella* from plesiadapines are presumably autapomorphies. I infer that *Saxonella* diverged after *Pandemonium.dis* and before *Pronothodectes matthewi*; perhaps the latest common ancestor of saxonellines and derived plesiadapines would also be referable to *Pronothodectes*.

Pandemonium is similar to various other primitive primates, but these similarities, to the extent that they are derived, are less than to *Pronothodectes* and do not seem to indicate a more special affinity than that all are primitive primates.

Discussion: The Plesiadapidae are among the most useful taxa for Paleocene stratigraphy because of their rapid evolution and abundance. *Pandemonium* extends the period of rapid evolution into the early Paleocene. We do not of course know just when *Pandemonium* originated from *Purgatorius*, but the transition from *Pandemonium* through *Pronothodectes* to *Plesiadapis* was probably not much more than a million years, although *Pronothodectes* does survive contemporaneously with early *Plesiadapis* just as *Purgatorius* does with *Pandemonium*. *Pandemonium* neatly bridges the gap between *Purgatorius* and *Pronothodectes*, and its

placement in a different family from the Purgatoriidae is of course entirely vertical, on the basis of what later plesiadapids became. One could reasonably argue that *Pandemonium* itself should be referred to the Purgatoriidae rather than to the Plesiadapidae, but as plesiadapid adaptations are clearly being evolved in *Pandemonium* I refer it to that family. Biological classification does not, yet, employ fuzzy hierarchies to mirror the natural world; they would probably be too complex anyway.

The connection of *Purgatorius* with the Plesiadapidae raises the question of whether *Purgatorius* should be referred to this family. If there were no other Paleocene primates known, this would be a good allocation. However, in all known respects *Purgatorius* is or, for ambiguous characters, could be, the most primitive known primate. It is therefore morphologically, and perhaps even phyletically (although biogeography makes this unlikely *a priori*), ancestral to all other primates. The Purgatoriidae of my classification includes the primates that are dentally most primitive; other characters, when known, may perhaps compel reallocation of some forms. Because the known teeth of *Purgatorius* generally resemble those of the middle Paleocene genera *Palenochtha*, *Plesiolestes*, *Premnoides*, *Torrejonia*, and *Palaechthon* (see below), I refer *Purgatorius* to the same family. It is entirely plausible that the semimolariform P⁴ of these genera (including *Purgatorius*) is primitive for primates, as many also be the semimolariform P₄ of *Plesiolestes* and *Palaechthon*. I discuss the Micromomyinae below, but note here that gliding adaptations are not regarded as themselves providing family-level distinction for recent mammals.

P. dis has been mentioned, as an unnamed plesiadapid, by Szalay and Delson (1979). Perhaps the unnamed species discussed by Buckley (1988), from the late Puercan of Simpson Quarry, Crazy Mountain Field, Montana, also will prove referable to *Pandemonium*. Hartman et al. (1989) have also cited an undescribed species of *Purgatorius* from this quarry.

Paromomys, *Phenacolemur*, and *Ignacius* are the Paleocene members of the Paromomyidae *sensu stricto*. and have some resemblances to the Plesiadapidae. Gingerich (1976) and Gunnell (1989) have associated these two groups on the basis of several characters. The conules of the upper molars are small, but they aren't in *Pronothodectes*. The cingula are strong and the paracrista is weak, as commonly happens with reduction of cusp height. I¹ is tricuspsate, and there is a bony external auditory meatus. These last two characters are apparently stronger, although the last is common enough. (Because *Microsypops* seems to lack at least an ossified meatus, we may reasonably infer that *Purgatorius* also lacks one.)

However, the I's of at least *Phenacolemur* and the Eocene paromomyid *Arcius* have their anterocone rounded, not acute as in plesiadapids, and the mediocone is appreciably more apical on the crown and may well not even be homologous to that of plesiadapids (Rose, Beard, and Houde, 1993). This suggestion is supported by the simple I¹ of *Pandemonium*; the argument would be unchanged if this tooth is from *Purgatorius*. The incipiently trilobed I¹ which Rose, Beard, and Houde (1993) have tentatively referred to *Palaechthon* is morphologically suitable for an ancestor of paromomyids; I suspect that the small distobasal cusp of this tooth is an incipient laterocone rather than a lateroconule. In addition, *Elpidophorus*, a mixodectid transitional to

the Plagiomenidae, has a trilobed I¹ convergent on that of plesiadapids (Szalay, 1969).

It is not, in any case, reasonable to derive *Paromomys* from *Pandemonium*, much less from *Pronothodectes*. Even *Pandemonium* is more derived than *Paromomys* in having relatively broader lower molars, with the labial slopes of the protoconid and hypoconid less steep. P₄ is nearly as broad as long, its talonid is very transverse, the labial surface of the protoconid is less steep, the cristid obliqua is weaker, and the paracristid is weaker. The upper teeth, however, are in themselves compatible with an ancestry in *Pandemonium*.

Most authors (e.g., Kay and Cartmill, 1977; Szalay and Delson, 1979) have derived *Paromomys* from the vicinity of *Palaechthon* or *Plesiolestes*, and Gunnell (1989) puts his new genus *Premnoides* even closer to *Paromomys* than he does the Plesiadapidae. *Paromomys* is known slightly earlier than *Premnoides* (Tomida and Butler, 1980; Tomida, 1981; Robison, 1986), but again it may well be that an ancestor of *Paromomys* would fit into *Premnoides*. I discuss below a slightly different possibility.

Superfamily *Microsyopoidea* (Osborn and Wortman, 1892) Gunnell, 1989
 Family *Purgatoriidae* (Van Valen and Sloan, 1965) new concept²
 Subfamily *Purgatoriinae* Van Valen and Sloan, 1965
Purgatorius Van Valen and Sloan, 1965

Purgatorius janisae, new species

[The best reproduction of the scanning electron micrograph of the type of *P. janisae* is by Kielan-Jaworowska, Bown, and Lillegraven (1979), who also give the only published figures of upper teeth of *P. janisae*.]

Type: UCMP 107406, right mandible with P₂-M₃.

Type locality: Late Puercan (early Paleocene), Tullock Formation, Garfield County, Montana: Garbani Local Fauna.

²Gunnell (1989) elevated the Purgatoriinae to family rank, but this "family" was monotypic and was so ranked merely because *Purgatorius* didn't fit his (basically noncladistic) classification, it being too primitive. Treatment of putative ancestors is, of course, a general and inherent defect in cladistic classifications. In my treatment here the family is a natural paraphyletic group, like the Insectivora or the Condylarthra, consisting of those Plesiadapiformes which lack sufficient adaptive divergence from the ancestral plesiadapiform to be separated at the family level. Some of its characters are apomorphies (those of the Plesiadapiformes) and some are plesiomorphies (those separating it from other plesiadapiform families), and because they are used for these other taxa they don't require explicit listing here. Together they define a phyletically and adaptively unified group. Such a group is not a grade, contra common rhetoric of cladists, because it has phylogeny as an intrinsic component.

Conversely, the *Microsyopoidea* of the present classification is not conceptually mine, although I had first used the name itself in 1969 when proposing the taxon which is now, more properly, called the Plesiadapiformes.

Known distribution: Type locality and the early Paleocene Ravenscrag W-1 stratum in the Ravenscrag Formation near Ravenscrag, Saskatchewan.

Etymology: For Christine Janis, in recognition of her innovative work on fossil mammals. I follow customary scientific Latin rather than the classical third declension for the ending.

Diagnosis: *P. unio* Van Valen and Sloan (1965) and *P. ceratops* Van Valen and Sloan (1965), the latter known only from an M_2 , are the only other described species of *Purgatorius*. I discuss *P. ceratops* below. *P. janisae* differs from *P. unio* in the following respects, with the samples now available:

The P_4 is wider, its talonid is narrower than the trigonid, the paraconid is larger and so its apex is higher, the cristid obliqua is weak rather than much taller than the entocristid, the hypoconulid (Van Valen, 1994, discusses identification of cusps and crests) is nearly as tall as the hypoconid, the talonid basin is a transverse valley rather than being cup-shaped, the distolabial corner of the talonid is less well developed, and the lingual side of the protoconid is nearly flat longitudinally rather than quite convex. The distolingual corner of the trigonid is angular in cross section rather than rounded, the angle being formed by a crest continuous with the entocristid rather than by the cristid obliqua; a trace of a metaconid is present where this crest more or less meets the extension of the cristid obliqua (the eocristid). In *P. unio* the eocristid (Vandebroek, 1961; Van Valen, 1994) extends up the postvallid to the apex of the protoconid, somewhat lingual of the midline, and lacks any suggestion of a metaconid; the entocristid is low and stops near the base of the protoconid. The differences in P_4 are morphogenetically coherent, being related to a greater development of the lingual part of the tooth relative to the labial part in *P. janisae*.

In the lower molars the paraconid is larger and more separate from the metaconid; the trigonid cusps are less rounded, so the longitudinal valley of the trigon basin is less widely open; the cristid obliqua extends up the postvallid; the postmetacristid is much more pronounced, so the trigonid looks more elongate in lingual view and somewhat broader in distal view; the hypoconulid is better developed and projects more distally; the labial wall of the trigonid is flat rather than rounded in distal view, especially on M_2 and M_3 , and the lingual and labial walls of the trigonid converge considerably toward the apex of the trigonid; the labial surface of the hypoconid is more sharply curved in occlusal view; and the molars are generally more angular. On M_3 there is an incipient development of a cusplet on the lingual side of the hypoconulid.

The upper molars are appreciably less transverse, the styler shelf is broader distally than mesially (and broader distally than in *P. unio*), the deepest part of the ectoflexus is central rather than more distal, the metacone is usually somewhat more lingual relative to the paracone, the paracingulum is stronger, the premetaconule wing is absent, the postparaconule wing is weak rather than stronger than the preparaconule wing, the protofossa is usually shallower, the preprotocrista is stronger than in *P. unio* and is stronger than the postprotocrista, the protocone apex is more mesial, the lingual half of the tooth is less angled distolingually, the lingual slope of the protocone is steeper (the protocone apex is more lingual), the postcingulum extends labially past the apex of the metaconule, and a

	Labial length	Length at metaconule	Width
2213, M ¹	—	1.4	2.9 ± 0.1
1637, M ¹	1.8	1.3	3.0
1652, M ¹	—	1.4	2.9
1597, M ²	—	1.5	2.9 ± 0.1
2212, M ²	1.9	1.5	2.8
2191, M ³	—	1.4	2.9

Table 3. Measurements (in millimeters) of upper teeth of *Purgatorius unio*. Ca. 95 percent measurement bands are given.

	Length	Trigonid width	Talonid width
1616, P ₄	1.6	0.9	1.0
1504, M ₁	2.1	1.5	1.4
2209, M ₂	2.0	1.5	1.4
2214, M ₃	2.2	1.4	1.1
1506, M ₃	2.1	1.5	1.2
1547, M ₁	2.0	1.6	1.4

Table 4. Measurements (in millimeters) of lower teeth of *Purgatorius unio* and *P. ceratops* (1547).

slight hypocone is developed on the postcingulum, which is thereby a bit broader lingually than centrally. A postcrista (Van Valen, 1966; = "pli *Nannopithecus*", etc.) is variably present in both species.

Tables 3 and 4 give measurements of the Montana specimens of *Purgatorius unio*. Some differ slightly from those of Van Valen and Sloan (1965); presumably technique differed.

The best reproduction of the scanning electron micrograph of the type of *P. janisae* is by Kielan-Jaworowska, Bown, and Lillegraven (1979), who also give the only published figures of upper teeth of *P. janisae* (LACM No. 28128). Szalay and Delson (1979) also present good drawings of upper molars of *P. unio* and of the type of *P. ceratops*. Szalay (1969b, Plate 57) gave photographs of *P. ceratops* and several teeth of *P. unio*. I give here (Plates 4-5) photographs of all known Montana specimens (see below) of *P. unio* and *P. ceratops*. I have seen other specimens of *P. janisae* through the courtesy of W.A. Clemens, but as these are undescribed I use only characters which can be seen on the published specimens with respect to that species.

Discussion: Clemens (1974) referred the type of *P. janisae* to *P. unio*, and it has since become the standard of reference for this species. Because of the difference of its P₄ from the premolar (UM No. VP 1616) from Purgatory Hill which Van Valen and Sloan (1965) had called a P₄ of *P. unio*, Clemens (1974) regarded the latter specimen as probably a P₃. I believe that it is in fact a P₄, for the following reasons. The size is appropriate in relation to the molars (the P₃ of *P. janisae* is smaller); the trigonid is relatively tall; the talonid is relatively long in relation to the trigonid, is even broader than the trigonid, is completely basined, and has a tall postcristid and a well-developed

ectoflexid; and the enamel on the labial side of the talonid extends appreciably lower (toward the roots) than that of the trigonid. Both P_3 and P_4 of *Pandemonium dis* are known and differ appreciably from UM No. VP 1616.

There is also an upper premolar, UM No. VP 2211 (Plate 1), from Purgatory Hill, which Van Valen and Sloan (1965) regarded as a P^4 of *P. unio*. Clemens (1974) disputed this allocation because of its large morphological difference from the P^4 of LACM No. 28128, which is in a jaw with molars of *P. janisae*. The Purgatory specimen looks like a P^4 , by the transverse width of its protocone, even if *Pronothodectes matthewi* is used as a standard of comparison. It is exactly intermediate in width between the known P^4 s of *Purgatorius janisae* and *Pandemonium dis*, and is close morphologically to the latter. It could conceivably be a P^3 of *Pandemonium dis*, a P^4 of *Pandemonium dis*, or a P^4 of *Purgatorius unio*, in which case P^4 would differ morphologically between the species of *Purgatorius* more than any other tooth. I suspect that it is a P^3 of *Pandemonium dis* and have mentioned it with that species. Because the tooth cannot be satisfactorily identified I do not use it in comparisons.

Neither *P. janisae* nor *P. unio* has obvious special affinities with any later primates. Gunnell (1989) notes that the high position of the paraconid on the P_4 of *P. janisae* is unusual and is likely to be autapomorphic; however, it is somewhat variable and overlaps with the condition in *Palaeochthon alticuspis*. *P. unio* has no definite autapomorphies and may be an appropriate structural ancestor for all other primates, as is commonly believed (perhaps for *P. janisae*). The polarity of most of the differences between *P. unio* and *P. janisae* are unclear in the context of primitive purgatoriids, although a detailed phyletically-oriented revision of the group and its immediate descendants should give better information. (The Torrejonian species of purgatoriids also need detailed revision with respect to their number and boundaries, considering the usual interspecific differences among comparable Pleistocene [including "Recent"] species.)

The Garbani locality, which yields *P. janisae*, and Purgatory Hill, with *P. unio*, are penecontemporaneous, and one may expect that some of the differences between the species will be derived in each direction. However, *P. unio* is more similar in its lower molars to the earlier and more primitive *P. ceratops*, and also is overall more suitable as an approximate ancestor for *Pandemonium* and later plesiadapids. Perhaps the populations ancestral to *P. janisae* would even be referable to *P. unio* in a broad sense.

Purgatorius ceratops is even more primitive, with its small talonid, although it is still too poorly known to say much more. Szalay (1969b) and others have questioned its distinctiveness from *P. unio*, but the difference is too great for normal intraspecific variation. In addition, *P. ceratops* comes from the early Mantuan of Harbicht Hill, the second-earliest fauna known from the Paleocene, and is contemporary with surviving dinosaurs. Rigby (1988, 1989) and Rigby and Rigby (1990) give details on these points. Archibald and Lofgren (1990) and Fox (1990a) have questioned the provenance of the unique specimen of this species. Rare though it is, I extracted it myself from a group of supposed condylarth teeth from Harbicht Hill; there was no chance whatever of mixing, at any stage. The species is also unknown elsewhere, and its primitive morphology agrees with its early age.

In fact, *P. ceratops* will probably be referable to a different

genus when better known, as originally noted (Van Valen and Sloan, 1965). In addition to its smaller talonid, which is a strikingly primitive feature, it differs from *P. unio* in having a shallower talonid basin, more bulbous trigonid cusps, the lateral face of the protoconid straight rather than convex in distal view, a more transverse metaconid, the trigonid basin as low lingually as centrally, and the transverse valley of the trigonid basin lower than the longitudinal valley. Not all of these characters distinguish *P. ceratops* from *P. janisae*, although most do and there are strong additional differences from the latter which can be seen from the comparison of *P. janisae* with *P. unio*.

Purgatorius retained the primitive complement of four premolars, but I have not seen direct evidence that it retained more than two incisors. However, the Carpolestidae initially retained their entire dentition in both jaws except for P_1 (Fox, 1994), as does the specimen described below as cf. *Palaechthon woodi* for the lower jaw. Thus *Purgatorius* presumably did have a complete dentition, as is usually stated, because it is known to have retained P_1 (Clemens, 1974).

Purgatorius has been reported from three localities outside the Hell Creek Field. Johnston and Fox (1984) referred to this genus four upper teeth from the Ravenscrag W-1 stratum in the Ravenscrag Formation near Ravenscrag, Saskatchewan. The mammals from this stratum (Johnston and Fox, 1984; Fox, 1990a) indicate an age in the early Paleocene a bit earlier than Purgatory Hill, perhaps even early Puercan (*sensu stricto*). Insofar as I can tell from the published stereophotographs, the Ravenscrag W-1 population resembles *P. unio* rather than *P. janisae*, except probably for the protocristae. As Johnston and Fox (1984) noted, their material does seem specifically distinct from the Garbani specimens (*P. janisae*), which they accepted as *P. unio*.

Wolberg (1978, 1979) described the Olive Local Fauna from the Tongue River Formation, Powder River County, Montana. Although the fauna is late Tiffanian, a single M_3 appeared similar to *Purgatorius* and Wolberg tentatively referred it to this genus. I have not seen this specimen, and the figure in Wolberg (1978) is probably inadequate for identification even without the homogenization produced by the commercial photocopy. The tooth is smaller than those of the known species of *Purgatorius*, but I obviously have no constructive suggestions. Perhaps it should be compared with some of the Litocherinae of Gingerich (1983), although Wolberg did make such comparisons with species then known.

In addition, Hartman et al. (1989) included what was designated as a new species of *Purgatorius* in their faunal list for Simpson Quarry, late Puercan of the Crazy Mountain Field, Montana. These specimens are not yet published.

There are now several primates known from the early Torrejonian, of Dragon age, but only one other primate tooth has been reported from strata known to be earlier. This is an upper molar, UALP No. 11042, from the Wagonroad Local Fauna of central Utah, figured by Tomida and Butler (1980). Adequate determination of the affinities of this tooth will require a detailed comparative and phylogenetic revision of the Torrejonian purgatoriids, which is badly needed but is beyond the scope of this paper. However, I make some comments.

An upper molar from the Dragon, UALP No. 11041, appears congeneric

with "*Talpothenach*" *torrejonius* Kay and Cartmill (1977), although perhaps not conspecific with it. Gunnell (1989) lumped the Wagonroad specimen, UALP No. 11042, with this tooth as the same species and from the same locality, and referred both to "*Plesiolestes*" *nacimienti*, in which he also included "*Talpothenach*" *torrejonius*. However, "*T.*" *torrejonius* is not conspecific with "*P.*" *nacimienti*, at least if KU No. 9557, the well-known skull from the *Deltatherium* Zone (Torrejon) of Big Pocket, Kutz Canyon (= Coots Cañon), San Juan Basin, New Mexico, represents "*P.*" *nacimienti*, as it is supposed to. (The type of "*T.*" *torrejonius* is a maxilla from the same level of the Torrejon in the same area [Taylor, 1981].) Major differences are the presence in "*T.*" *torrejonius* of a protocone on P³, a taller molar protocone, the lack of a lingual hypocone lobe, the front border of the upper molar not forming an angle at the paraconule, the mesiolingual slope of the molar protocone forming a crestlike angle, the unwrinkled enamel, and perhaps the reduced M³. I do not know whether "*T.*" *torrejonius* is referable to *Plesiolestes* or *Palaechthon*, although probably it is referable to one of these genera. The Wagonroad specimen, UALP No. 11042, does not appear to be conspecific with UALP No. 11041 and is not referable to any species for which upper teeth are known, although it too is in the vicinity of *Plesiolestes* and *Palaechthon*. The Wagonroad specimen is worn, but its shallow protofossa is apparently characteristic.

Standhardt (1986) referred three teeth to *Palaechthon nacimienti*, a species which Gunnell (1989) has placed in *Plesiolestes*. These teeth are from the Tom's Top Local Fauna in the upper part of the Javelina Member of the Tornillo Formation, Big Bend National Park, Texas. Standhardt regarded Tom's Top as late Puercan, on the basis of paleomagnetic results which were not presented in detail. This age may well be correct, although the fauna as given (considering the specimens themselves, rather than the identifications) is not closely diagnostic for age and could be early Torrejonian. In particular, despite rather good drawings of the teeth referred to *P. nacimienti* I cannot unambiguously identify the species of any of them, nor is it clear that they are all conspecific. Future comparisons should also consider *Premnoides* Gunnell (1989). The single upper molar, TMM No. 41400-17, could possibly be conspecific with UALP No. 11042, the Wagonroad tooth, but this seems rather unlikely on the basis of Standhardt's drawing.

Purgatorius janisae shows some indications of phyletic approach to the Mixodectidae, although this probably involves convergence because of crossing apomorphies. A critical evaluation of that possibility (and therefore, more generally, of plesiadapiform affinities for the Mixodectidae) is beyond the scope of this paper. I note that the possibility of a mixodectid-primate relationship has been raised, and usually rejected, for the past century, but that some (mostly favorable) evidence now available has not been considered in this context previously, including the existence of *Purgatorius*.

Subfamily Palaechthoninae³ Szalay, 1969*Anasazia*, new genus

Type and only known species: *Anasazia williamsoni*, new species.

Etymology: For the Anasazi Indians, who also formerly inhabited the San Juan Basin, although indeed a bit later. The gender is feminine; some primates are female.

Diagnosis: As for *A. williamsoni*.

Anasazia williamsoni, new species

Plates 6-7

Type: NMMNH No. P-19860, right mandibular fragment with P_1 , P_3 , and P_4 , the base of P_2 , and partial alveoli of the canine and an incisor.

Type locality: Kutz Canyon, San Juan Basin, New Mexico.

Known distribution: Kutz Canyon and the upper part of Kimbeto Wash, San Juan Basin, New Mexico; Torrejon G of Williamson (1993), and perhaps lower.

Etymology: For Thomas E. Williamson, in recognition of his major contributions to our knowledge of the Torrejon.

Referred specimen: NMMNH No. 16191, partial left maxilla with M^{1-2} . Some specimens now referred to other species may possibly belong to *A. williamsoni*.

Diagnosis: A palaechthonine which possesses P_1 and in which both P_2 and the lower canine are relatively large. The lower incisor(?s) is/are not much enlarged. P_4 is unusually broad in the trigonid region; it lacks any trace of a metaconid but has a small and low paraconid. The upper molars are transverse and rather primitive, but the protocone twist is unusually well developed. The protocone apex is lingual and the profossa is less transverse than usual. Dental formula $I_{21}^2, C_{11}^2, P_{41}^2, M_{31}^3$. Tables 5 and 6 give measurements.

Comments: The type specimen of this species preserves evidence of probably all the antemolar dentition of the mandible. It was confiscated from a commercial collector who had obtained it illegally, and details of its original provenance are unavailable. It is, however, from somewhere in the Torrejon of Kutz Canyon, San Juan Basin, New Mexico, and therefore not from the highest Torrejon (Torrejon H of Williamson, 1993, corresponding to the former *Pantolambda* Zone). I describe it and two other Torrejon palaechthonine specimens with the kind permission of Peter Williamson. The type specimen is the same as the one which Williamson and Lucas (1993) compared with *Palaechthon nacimienti* and noted as possibly new, although the number of the specimen had been NMMNH No. P-19650 and they used both numbers in

³Gunnell (1989) proposed family-group names based on both *Palaechthon* and *Plesiolestes*. The former (which I rank as a subfamily, Palaechthoninae), however, dates from Szalay (1969) and has priority when, as in my classification below, both genera are included in the same family-group taxon.

	Length	Width	Labial height
C alveolus	2.1 ± 0.1	—	—
P ₁	1.3	1.0	—
P ₂ base	1.8	1.2	—
P ₃	2.0	1.4	2.7 ± 0.1
P ₄	2.9	1.7	3.0 ± 0.1
P ₁₋₄	8.4	—	—

Table 5. Measurements (in millimeters) of mandible of *Anasazia williamsoni*, NMMNH No. P-19860. Ca. 95 percent measurement bands are given. As elsewhere, measurements are for (or as for) complete teeth; height is oblique enamel height.

	Length	Width
M ¹	3.0 ± 0.2	3.7 ± 0.1
M ²	2.7	4.0

Table 6. Measurements (in millimeters) of upper molars of *Anasazia williamsoni*, NMMNH No. P-16191. Ca. 95 percent measurement bands are given.

different places. Further slight preparation has made identification of the tooth loci unambiguous.

I refer the upper dentition to the same species because it is of a suitable size (unlike any other similar species), it also has a general resemblance to *Palaechthon*, it also represents an undescribed species, and it has a compatible stratigraphic provenance. It lacks the mesiolabial part of M¹. It is from NMMNH Locality 1112, which is in the upper part of Kimbeto Wash and in Torrejon G of Williamson (1993).

Description: The P₄ is two-rooted and relatively long and low in lateral view. The base of the enamel is nearly horizontal from the talonid to the trigonid both labially and lingually. The protoconid is vertical, and its distal face (concave in lateral view) has a gentler slope than the mesial face, which is convex in lateral view. The apex of the protoconid is not elongated longitudinally, but the cusp itself is moderately elongate. There is no trace of a metaconid. The paraconid is a weak but distinct swelling, relatively low on the tooth (at about the height of the hypoconulid). The paracristid is relatively strong; it extends mesially and a bit labially from the apex of the protoconid to a point near the level of the paraconid, where it turns lingually to the apex of the paraconid. The eocristid and entocristid both extend weakly up the postvallid; they meet about two thirds of the way up in the midsagittal plane of the tooth. The eocristid is stronger as it becomes the cristid obliqua, which has almost no transverse component. The postvallid is nearly flat between the eocristid and the entocristid.

The talonid is rather large, being nearly as wide as the trigonid and about two fifths its length. It is somewhat transverse, and meets the trigonid at a relatively sharp angle in lateral view. The main talonid cusp, the hypoconid, is about half the height of the protoconid in labial view; the talonid slopes steeply mesiolingually from the

hypoconid. The eocristid forms an acute angle at the hypoconid and descends mesially (as the cristid obliqua) and lingually (as the postcristid) from it. A small but distinct hypoconulid occurs at the end of the eocristid; it is lower than the hypoconid and is slightly more mesial than the distal part of the hypoconid. A weak entocristid extends mesially from the hypoconulid and forms a slight border to the talonid basin before rising to the eocristid on the postvallid. The tooth lacks any cingulids.

P_3 also has a vertical protoconid, and also is two-rooted. It is generally similar to P_4 , with the following differences. The tooth itself is smaller in size, and the talonid is much smaller, being just a transverse shelf, short mesiodistally and without cusps or crests except for the cristid obliqua. The tooth is more transverse because its length is more reduced than its width. The distolabial corner of the protoconid is moderately sharp from the entocristid extending to the apex of the protoconid but, as noted, this crest does not extend onto the talonid. The paraconid is absent as a distinct cusp, although the paracristid extends to its position and (more weakly) even a bit beyond, as an incipient cingulid.

P_2 is one-rooted; only its base is preserved. This is smaller than that of P_3 and is oriented slightly obliquely.

P_1 , also one-rooted and smaller than P_2 , consists largely of a vertical protoconid on which there is a moderately strong longitudinal eocristid. Distally the eocristid extends down to a nubbin of a talonid (thereby serially homologous to the hypoconid: Van Valen, 1994), from which an entocristid loops mesiolingually and, more weakly, extends up the middle of the lingual face of the protoconid to its apex. The position of the paraconid, which is not developed as such, is distinct, high on the mesial side of the protoconid. At this point the eocristid becomes a weak lingual cingulum which extends distobasally and more or less meets the equally weak entocristid on the lingual side of the protoconid.

The alveolus for the canine is present. It indicates a relatively large (or at least mesiodistally long) tooth, larger than P_1 and perhaps even larger than P_2 . An incisor alveolus is preserved mesial to that for the canine and appears to be only moderate in size, smaller than that for the canine. Only a single incisor appears to have been present, because the preserved alveolus is immediately adjacent to the mandibular symphysis, but conceivably a lateral incisor could have occurred in the missing anterolateral part of the mandible..

The mandibular depth is moderate relative to tooth size. The symphysis extends to a point below the distal part of P_2 .

The upper molars are relatively transverse, especially M^2 . The protocone twist is unusually well developed, especially on M^2 . The paracone and metacone are about equal in size, moderately developed, and conical. The styler shelf is wide for a primate, with a moderate ectoflexus at least on M^2 . The centrocrista is moderate and straight. The paracrista is moderate and extends mesiolabially from the paracone apex to a relatively strong parastyle. The metacrista is weak and extends distolabially from the apex of the metacone; there is no separate metastyle. The conules are moderately developed and are located rather near the paracone and metacone; they are shifted lingually relative to these latter cusps.

The protocone is lingual and is conical in form, and is rather massive. The protocristae are moderate on M^1 and relatively weak on M^2 .

The postprotocrista is directed toward the metacone, while the preparacrista is directed appreciably mesial to the paracone. There is a distinct vertical swelling on the labial surface of the protocone between the protocristae. The protofossa is of moderate depth and is only somewhat elongate labiolingually. The postcrista is strong; it extends from the protocone to the lingual end of a moderately strong postcingulum. The postcingulum does not merge with the metacingulum. The precingulum is also moderately strong throughout. It extends somewhat farther lingual than does the postcingulum; it does not merge with the paracingulum.

M² is appreciably more transverse than M¹. The mesial alveoli of M³ are partly preserved; the tooth seems to have been unreduced, about as wide as M². The upper molars are moderately worn. The major wear is flat, removing much of the protocone, paracone, and metacone from their apices. The parastyle is mostly removed by transverse movement of the trigonid, but the predominantly flat wear indicates an emphasis on crushing or grinding some sort of resistant food which came in packets large enough to minimize tooth-on-tooth contact. Some fruits and gums could do this.

Comparisons: The type of *Anasazia williamsoni* is the second specimen of a palaeochthonine in which P₁ is known to occur, the first being the type of *Palenochtha weissae* Rigby (1980); however, see cf. *Palaechthon woodi*, below. The presence of this tooth shouldn't really be surprising, because it is present in *Purgatorius* and populations polymorphic for its presence should precede those where it is definitively absent. (I predicted such ancestral polymorphism in tooth number for the canid *Otocyon* [Van Valen, 1964] before it was discovered.) Presence and absence of even small teeth is a convenient character which some mammalian systematists like to use to delimit genera, despite the often negligible adaptive significance of the difference. (For example, the recent erinaceid "genera" *Hylomys* and *Neotetracus* differ mainly in this way, and I therefore synonymized them [Van Valen, 1967].) Probably future expansion of knowledge will lead to discovery of actual cases of polymorphism of tooth number in the Plesiadapiformes and elsewhere [Gingerich, Dashzeveg, and Russell (1991) have suggested that *Teilhardina belgica* was polymorphic for the presence of P₁], but there is now no evidence that *A. williamsoni* itself was polymorphic in this way.

The relatively small incisor of *A. williamsoni* is also unique for palaeochthonines, as far as is known (but see cf. *Palaechthon woodi*, below.)

The P₄ of *A. williamsoni* differs from that of *Plesiolestes? wilsoni* in several ways. It is appreciably smaller. The talonid is relatively smaller, with a much weaker hypoconulid. The entocristid is much weaker. The paraconid is lower, and the eocristid does not extend the apex of the protoconid longitudinally as it does in *Plesiolestes wilsoni*. The enamel is not wrinkled.

Differences from *Plesiolestes sirokyi* are as for *P. wilsoni*.

The P₄ differs from that of *Plesiolestes problematicus* in being appreciably larger, lacking a metaconid, having a shorter and narrower talonid with a much weaker entocristid, having a less elongate shape to the tooth, and having a trigonid that is wider than the talonid.

From *Premnoides douglassi* the P₄ of *A. williamsoni* differs as

follows. It is appreciably larger. The trigonid is wider than the talonid, not the reverse. The paraconid is lower and distinct. The talonid is relatively longer and the trigonid is relatively broader. The protoconid is probably lower. The trace of a metaconid is absent but a hypoconulid is present.

The P_4 differs from that of *Palaechthon nacimienti* in being larger, being more elongate, having a somewhat shorter talonid, having a distinct paraconid, and having the cristid obliqua oblique and more labial on the talonid.

From *Palaechthon alticuspis* the P_4 differs as follows. It is appreciably larger as well as more elongate. The paraconid is smaller and lower. The hypoconulid is much lower than the hypoconid. A metaconid is absent.

The P_4 differs from that of *Purgatorius unio* and *P. janisae*, jointly, as follows. The protoconid is much lower. The tooth is much more elongate in lateral view. It is also more transverse, in occlusal view. The trigonid is wider than the talonid rather than the reverse. The distal slope of the protoconid is much gentler.

Other species for which the P_4 is known are too different to warrant explicit comparison. *Palaechthon torrejonius* (on which see below) is larger than *A. williamsoni*.

The upper molars of *A. williamsoni* differ from those of *Plesiolestes problematicus* and *Plesiolestes wilsoni* as follows. They are larger. There is a greater protocone twist. M^1 is less transverse. The lingual cingula are stronger, except the postcingulum is weaker than that of *P. wilsoni*. The styler shelf is better developed. The protofossa is less transverse. The protocristae are stronger, especially on M^1 .

From *Palaechthon torrejonius* the upper molars of *A. williamsoni* differ as follows. They are larger and also more transverse. The protocone twist is greater. The metacrista is weaker. The marginal conule wings are strong, interrupting the lingual cingula. The enamel is smooth. The postcrista is somewhat weaker and has no indication of the *Paromomys*-like basin with the postcingulum.

The upper molars are distinct from those of *Palaechthon nacimienti* in several ways. They are larger. The protocone twist is much better developed. The conules are larger, and the central conule wings are moderately strong. The styler shelf is wider. M^1 is less transverse. The protocone also is less transverse, as is the protofossa.

From *Palaechthon alticuspis* the upper molars of *A. williamsoni* differ as follows. They are larger. The protocone twist is greater. The styler shelf is better developed. M^1 is less transverse. The postcrista is weaker. The postcrista hardly extends lingually as well as distally from the protocone apex, and it does not produce any trace of bilobation on the lingual margin of the tooth. The protocone apex is more lingual. The protofossa is less transverse.

Upper molars of *Palaechthon woodi* are known, from figured material, only by the provisionally referred tooth from the Bangtail Plateau which Gingerich, Houde, and Krause (1983) illustrated. Their drawing shows no detectable differences from the M^1 of *A. williamsoni*, but the drawing isn't very detailed. Gazin (1971) referred three upper molars to *P. woodi*; his brief description of them also fits *P. williamsoni*. *P. williamsoni* is much larger than *P. woodi*.

The upper molars of *A. williamsoni* differ from those of *Purgatorius*

unio and *P. janisae* as follows. They are ostensibly, and perhaps really (as a population), a bit larger. The protocone twist is greater. The protocristae are closer together, and the conules are closer to the paracone and metacone. The postcrista is better developed. The lingual cingula extend closer to the paracingulum and metacingulum, and the metacrista is weaker.

Other species for which upper molars are known are too different to warrant explicit comparison.

Palaechthon Gidley, 1923

cf. *Palaechthon woodi* Gazin, 1971

Plates 8-9

Another Torrejon specimen of a palaechthonine also preserves evidence of the entire antemolar dentition. It too retains P_1 , and in addition gives evidence of the retention of a complete lower dentition.

The specimen is NMMNH No. P-15684, and comes from NMMNH Locality 1091, on the west flank of Torreon Wash and in the Torrejon H zone of Williamson (1993). It is of suitable morphology for a palaechthonine and not for any other reasonable taxon that I can think of, whether or not now known in the Torrejon. For instance, *Mixodectes* differs notably in having a P_2 that leans mesially, a transverse P_1 , and a large canine. *Palaechthon woodi* is the only palaechthonine known in the Torrejon that is even nearly as small, and it is the most common primate in Torrejon H and is a moderately common species there.

The specimen is an incomplete right mandible with partial P_{1-3} and the base of each of the more anterior teeth. I_1 is enlarged and is adjacent to the symphysis. A tiny I_2 , definitely a tooth, is now located near the tip of the matrix. I_3 is small but larger than I_2 , with a root diameter of 0.7 mm. The canine is of moderate size, its root diameter being 1.1 mm. Its distal part is lingual to P_1 , probably from crowding in the jaw. P_1 is smaller than the canine, with a root diameter of 0.8 mm.

P_2 has a small talonid in a lingual position; the distolingual part of the hypoconid region is worn away apicodistally. A moderate eocristid extends mesially from this area up the distal slope of the protoconid. A weak entocristid is present. P_3 , unlike the more mesial teeth, was apparently two-rooted, but only the mesial root is visible.

Among the Plesiadapiformes, only *Purgatorius* has been thought to have a numerically complete lower dentition. The presence of three incisors as well as P_1 is noteworthy; neither have been known for post-*Purgatorius* microsyooids except for the P_1 of *Palenochtha weissae*. I don't know whether the present specimen represents a real case of some degree of polymorphism for tooth number or whether its species had a late survival of the primitive number overall. If the specimen does represent *P. woodi*, however, as seems likely, the entire configuration of the anterior dentition warrants the establishment of a new genus for this species. Gingerich, Houde, and Krause (1983) had previously suggested such a separation, apparently on the basis of a provisionally referred upper molar which doesn't particularly resemble those of *Palaechthon*. The fragmentary nature of the present specimen

has precluded unambiguous identification, so further speculation (and perhaps even that given) seems unwarranted.

Palaechthon torrejonus (Kay and Cartmill, 1977)

This species, described as the separate genus *Talpohenach*, has usually been regarded as doubtfully separable from *P. nacimienti*. Although only the type specimen is known, or at least designated with the same name, I believe that it is clearly distinct. Some of its distinctions have not been previously noted. It differs from *P. nacimienti* in the following ways: P^2 is larger and P^3 has a well-developed protocone. P^4 is smaller than M^3 , not appreciably larger. A definite hypocone is present on M^1 and M^2 . M^2 , especially, is less transverse. A metastyle occurs on M^2 . The styler shelf is slightly better developed. The enamel is more wrinkled. The postcingulum is stronger, making an incipient *Paromomys*-like basin with the postcingulum on P^4 to M^3 inclusive.

This last feature suggests, and others do not contradict it, that *P. torrejonus* is closely related to *Paromomys*, either as sister taxa or, at the species level, as directly ancestral. (*Paromomys* does occur a bit earlier than *P. torrejonus* is known (Tomida, 1981; Williamson and Lucas, 1993) [and the species of *Paromomys* differ from each other in more than size], but this can of course be the result of incomplete knowledge.)

General discussion

Dental and skeletal characters

It has become a somewhat common practice, implicitly and even explicitly, to regard teeth as more or less valueless in inferring phyletic relationships. This is because teeth are regarded as easily modifiable, by natural selection, in response to changes in diet. Thus dental characters are supposed to be unusually subject to homoplasy. This hypothesis of teeth having an unusual susceptibility to homoplasy has never been tested and I doubt that it is correct. Characters and character complexes do, of course, vary in their susceptibility to homoplasy. Anyone testing the above hypothesis should therefore be careful not to choose characters (even if previously used by others) which are biased samples of the relevant sets. Thus hypsodonty might be regarded as comparable to leg length in ease of homoplasy. Any competent paleomammalogist can find numerous examples of dental homoplasy, but the same is true for characters of the limbs, basicranium, etc. We know more about the evolution of teeth and so we can find more examples of anything for them.

Take the brain, for which Pettigrew (1986; Pettigrew et al., 1989) and others have made a plausible *a priori* argument that it will respond to similar selective pressures in different ways in different lineages. Even Pettigrew's own startling discovery, a similar and unusual modification of visual pathways in primates and the megachiropteran *Pteropus*, now appears to be convergent⁴. [Roth and

⁴Molecular evidence has been regarded as conclusive in this controversy, but Pettigrew (1994) has made a plausible argument that the high proportion of adenine and thymine in the DNA of the Chiroptera

Wake (1985) have noted the convergent evolution of effectively the same morphology in the Bolitoglossini, a group of plethodontid salamanders with binocular vision.] It has actually been found to be absent in another megachiropteran, *Rousettus* (Thiele, Vogelsang, and Hoffmann, 1991). Kaas and Preuss (1993) have demolished the neuroanatomical argument, quite apart from other contrary evidence. The main character is the modified connection of the retinas (morphologically a part of the brain) to the bilaterally paired superior colliculi, or optic tectum, so that the corresponding parts of the visual field of each eye go to the same side of the brain. This helps binocular vision, although it is not required for that function (e.g., *Felis* lacks it.) Thus *Palaechthon* and *Plesiadapis* would be expected to lack the apomorphic state of the character, while there would be no prediction for *Microsyops*. Johnson, Kirsch, Reep, and Switzer (1994) find that *Tupaia* and the Galeopithecidae are intermediate, but Kaas and Preuss (1993) say that *Tupaia* is primitive in this character and the Galeopithecidae probably resemble primates. I don't know the basis for this discrepancy. The most obvious result of the research program of Switzer, Johnson, and Kirsch (1980), Johnson, Kirsch, and Switzer (1982, 1984), Kirsch (1983), Kirsch and Johnson (1983), Kirsch, Johnson, and Switzer (1983), Johnson, Kirsch, and Switzer (1984), Johnson and Kirsch (1993) and Johnson, Kirsch, Reep, and Switzer (1994) is the large degree of homoplasy in the brain traits they have studied, despite their lack of emphasis on this phenomenon.

Teeth have real advantages for use in phyletic inference. They are common and well preserved, usually without distortion. Cheek teeth are usually complicated things, with many partly or entirely independent characters. Fossil species are rarely described without using teeth, and often only teeth are available; there is thus usually little problem of correct taxonomic identification, which creates controversies for unassociated (or even probably associated: cf. Gunnell [1989] and Beard [1993b] for *Tinimomys*) bones. For this reason there is also a much denser record of teeth than for other elements. Teeth are also better known than anything else; even for recent mammals important discoveries are still being made in adult skeletal anatomy. It is the expectation rather than the exception that the taxonomic distribution of skeletal traits changes markedly with increase in knowledge. This has been a particularly severe problem in evidence regarding relationships of plesiadapiforms, and I doubt that we are close to equilibrium yet. Related to this are difficulties in inferring polarities of character states. I don't want to imply that I think that skeletal traits are unimportant (not to mention soft anatomy and molecular evidence), but they aren't a panacea and teeth do have some real advantages.

Nondental characters are necessarily not as widely applicable for taxa that are known mostly or entirely from teeth and jaw fragments. They can, however, be of great value when available, even though they too are subject to large-scale homoplasy. When the proportion of taxa which have such characters available (and accurately associated) is small, the risk of homoplasy increases. This has happened several times in the study of the phylogeny of plesiadapiforms and of their could lead to convergent substitutions and decisively bias the outcome of phyletic inferences which do not take this adequately into account.

relationships to euprimates.

For a recent example, in an overall valuable paper Kay, Thewissen, and Yoder (1992) have based their investigation of plesiadapiform affinities on two genera, *Plesiadapis* and *Ignacius*. These are indeed now the best-known genera, but even for cranial features there is some evidence elsewhere. In particular, it is necessary to consider *Microsyops*, even though this too is a derived genus. It is connected to the plesiolestine purgatoriids by early uintasoricines like *Navajovius*⁴, and it probably shares a post-*Purgatorius* common ancestry with the paromomyids. If we do consider *Microsyops*, as well as the position of *Purgatorius* in the phyletic path between *Plesiadapis* and *Ignacius*, then all the nondental characters used in that paper to group *Plesiadapis* with *Ignacius* (insofar as they can be seen in *Microsyops*) are invalidated.

In particular, the maxilla does not contact the frontal in the orbit, the external auditory meatus is not ossified, the promontory and stapedia arteries are present, there is not a strong mastoid tubercle, the carotid artery does not enter the bulla posterolaterally, and the fenestra cochleae does not have a shelf ventral to it. The presence of a suboptic foramen is unknown for *Microsyops*. These are all characters which, as evolved by *Plesiadapis* and *Ignacius* independently, are more derived than in the euprimate morphotype. Their actual states in the plesiadapiform morphotype therefore do not give evidence against a special relationship of plesiadapiforms with euprimates. The same is true, as has been argued by others, for all other nondental characters I know. Even the hoary postorbital process is still being used, despite its absence in *Plesiadapis* and *Microsyops*.

One such character deserves mention, though, because of its historical importance. This is the composition of the auditory bulla. In *Ignacius* it is apparently formed from an entotympanic (Kay, Thewissen, and Yoder, 1992, but see Szalay and Lucas, 1993), and the same is usually thought to be the case for *Microsyops* (Szalay, 1969b, and later work). In *Plesiadapis*, on the other hand, it seems to be formed from the petrosal (D.E. Russell [1959] and later work, including my own observations; Szalay, Rosenberger, and Dagosto [1987] have described an immature specimen), as in euprimates. The derivation of the Plesiadapidae directly from *Purgatorius* shows that the *Plesiadapis* condition is not homologous to that of euprimates (Van Valen, 1987), and so there is no phyletic importance to whatever the true bullar composition of *Plesiadapis* is. (This is because *Microsyops* was also apparently derived from *Purgatorius*, and its bulla, if any, could not easily be derived from a petrosal bulla.) A small petrosal contribution occurs in the Adapisoricidae, Leptictidae, and Microsyopidae (MacPhee, Novacek, and Storch, 1988), among other groups. Major changes in composition of a pre-existing bulla have nevertheless occurred in diprotodontan marsupials (e.g., Murray, Wells, and Plane, 1987). However, I suspect that *Purgatorius* lacked an ossified bulla.

⁴Unless microsyopines and uintasoricines were derived separately from palaechthonines. In this unlikely case, which would involve much homoplasy, the Uintasoricinae should probably be incorporated into a further expanded Purgatoriidae, and (modifying the assumption) the evidence for a plesiadapiform affinity of microsyopines would be much reduced.

Plesiadapiform systematics

The classification of the Plesiadapiformes is a bit awkward. The Plesiadapoidea is¹ a coherent group, and the Picrodontidae² went off somewhere, by themselves to contemplate their navels (were they also gliders?), but the rest are more difficult. *Microsyops* and *Phenacolemur* are always, I believe correctly, placed in different families. But what to do with the more primitive genera? Most of them have been referred, as a bloc, to either the Paromomyidae or the Microsyopidae in different papers. And there probably isn't enough adaptive differentiation as now known to warrant three families. Yet here I am, using a classification with three families (Table 5). The problem is that the groups are so poorly understood adaptively that any simplification to two families must now be arbitrary.

The Micromomyinae resemble the Paromomyidae in their anterior dentition and their apparent interdigital patagium (see especially Rose, Beard, and Houde, 1993, and Beard, 1993b), but their cheek teeth are divergently derived. Gunnell (1989) has argued for a micromomyine origin from a palaechthonine near *Palenochtha*. Even *Palenochtha* is, however, more derived than the morphotype of the Micromomyinae in several ways: protocone more labial on upper molars, postcrista stronger, a distinct metastylar cusp developed, M³ reduced, M₁ talonid shortened and with reduced hypoconulid, molar hypoconid at least as distal as entoconid, P₂ one-rooted, and P₄ somewhat lower relative to the molars. While the Micromomyinae may have come from an unknown palaechthonine, and these groups do share some apparent synapomorphies, at present *Purgatorius* is the only known genus which lacks appreciable divergent apomorphies from them. The apparent synapomorphies with the Palaechthoninae are mostly or entirely convergently evolved in other plesiadapiforms, so their value is suspect although they nevertheless give positive evidence. Beard and Houde (1989) also derived the Micromomyinae from a more primitive purgatoriid than *Palenochtha*. Because of the apparently nearly basal divergence of the Micromomyinae and Paromomyidae, it seems likely that their special resemblances are homoplastic.

²The names of supraspecific taxa are plural in form, but often it is appropriate to refer to the taxon as such, in the sense of a group, rather than in the sense of its members. In the former case the meaning is as a singular noun, not a plural one, and it is appropriate to use a singular verb form. Thus, the Plesiadapidae *is* a rather small family, but the Plesiadapidae *have* enlarged incisors. Sometimes both meanings are appropriate and either form is suitable. Pedants, who value form over sense, may be satisfied to think of an implied singular noun, such as "taxon" or "family", with which the name is understood to be in apposition.

¹I reinstate *Draconodus* as a valid genus. Williams (1985), who sank it into *Picrodus*, did not in my opinion refute the original argument of Tomida (1982), which I will not repeat.

Why plesiadapiforms are primates

Are the Plesiadapiformes primates? One doesn't need to be a cladist to recognize the importance of phylogeny to classification. If a taxon is to be an adaptively unified part of a phylogeny (Van Valen, 1978a), we first need to estimate the phylogeny. This has not previously been done, except for advocacy of isolated characters without reference to their overall evolution, or scattershot comparisons of a few, mostly derived, genera. Most of the isolated characters have been (or can easily be) shown to be homoplastic or inaccurately delimited taxonomically (e.g., Wible and Covert, 1987; Gunnell, 1989; Kay, Thewissen, and Yoder, 1992; this is even true for a character appearing in an earlier version of the present paper and repeated by Van Valen, in press: a deep fossa at the proximal end of the radius where it articulates to the humerus.)

We don't know what particular group was ancestral to the primates, although proteutherian insectivorans (or possibly their immediate descendants the Adapisoricidae, *sensu latissimo*) presumably encompass it. [Prasad and Godinot (1994) have found that the tarsus of the Indian palaeoryctid *Deccanolestes* has primate-like, or "archontan"-like, features. The significance of this observation is not yet clear.] I therefore use a diversity of primitive genera as a joint pregroup and use only those characters which differ from all of these genera to make comparisons.

For my pregroup I have taken *Kennalestes*, *Asioryctes*, *Cimolestes* spp., *Batodon*, *Leptacodon*, *Mckennatherium*, *Litolestes* (*sensu stricto*), and *Paranyctoides* Fox (1979). For my initial estimate of the euprimate morphotype I have used *Teilhardina* (including the recently described *T. brandti* Gingerich, 1993), *Steinius* (cf. Rose and Bown, 1991), *Donrussellia* spp., *Pelycodus torresi* (Gingerich, 1986a), and *P. eppsi*³. As with the pregroup, only those characters which differ from all these genera are used. I was surprised at the degree of restriction this gave. *Pelycodus* should probably not be used, because it is clearly more derived overall than is *Donrussellia*, as Godinot (1988, 1992, Godinot et al., 1987, as had Savage, Russell, and Waters, 1977, in a different way) has noted, but its inclusion had almost no effect.

I have treated several species separately. *Decoredon anhuiensis*, from about the middle Paleocene of China, is poorly known and is controversial even as to inclusion in the Primates (Van Valen, 1978b; Szalay and Li, 1986; Gingerich, Dashzeveg, and Russell, 1991). *Petrolemur brevirostre* Tong (1979), from the late Paleocene of China, has been referred to its own family (still a *nomen nudum*) by Szalay and Li (1986) and Szalay, Li, and Wang (1986), who suggest a separate origin from what I call the Purgatoriidae with a subsequent Asian radiation. If their suggestion of a special relationship to the Sivaladapinae is correct, the latter name would have priority. However, I remain to be convinced that *Petrolemur* should not be referred to the Anagalida.

Altanius orlovi Dashzeveg and McKenna (1977), on which see

³I do not accept a genus-level distinction of *Pelycodus* from *Cantius* (Gingerich and Haskin, 1981; Rose and Bown, 1984). All the characters which they give as distinctive are present, to about the extent as in *Pelycodus jarrovii*, in at least some specimens of some species which they refer to *Cantius*, including (for some characters) the type species, "*C.*" *eppsi*. *Copelemur* is, however, distinct.

especially Gingerich, Dashzeveg, and Russell (1991) and Rose and Krause (1984), is from about the Paleocene-Eocene boundary in Mongolia and is perhaps the most primitive definite euprimate known; it lacks the particular synapomorphies of both the Omomyidae and the Adapidae. *Altiatlasius koulchii* Sigé et al. (1990), on which also see Gingerich (1990), from the late Paleocene of Morocco, is more divergent although also primitive. It is the oldest definite euprimate known and may possibly, as Sigé et al. hesitantly suggested, even be cladistically related to anthropoids. Godinot (1993) agrees with this suggestion, more strongly. Without adequate comparative material I would refer it provisionally to the Adapidae, by comparison of *Donrussellia* with *Teilhardina*, but this is not really satisfactory and it does seem a plausible anthropoid precursor.

Eosimias sinensis Beard et al. (1994) is from the middle Eocene of China. It has been placed in a family of its own and referred to the Anthropoidea, but even its primate affinities are controversial (Culotta, 1992). *Afrotarsius chatrathi* Simons and Bown (1985), from about the Eocene-Oligocene boundary in Egypt, has also been referred to its own family and transferred to the Anthropoidea by Ginsburg and Mein (1987); Fleagle and Kay (1988) effectively agreed but Stucky and McKenna (1993) refer it to the Tarsiidae. I suspect that it is part of the basal anthropoid radiation, but the various recently described early genera referred to this group need careful comparative study.

Having found various differences between the euprimate morphotype and the pregroup, as detailed in Table 7, it remains to compare the plesiadapiform morphotype with these characters to see if there are apparent synapomorphies. *Purgatorius* provides an appropriate approximation to this morphotype; I used all three described species jointly. I also made a joint comparison with the Micromomyinae. In addition, because *Purgatorius* has a surprising resemblance to primitive condylarths (Van Valen and Sloan, 1965), I made an additional comparison with *Protungulatum* and *Oxyprimus* jointly, as an estimate of how well the condylarth morphotype agrees with that of euprimates in comparison to the agreement of *Purgatorius*. This provides an approximate estimate of the effects of dental convergence.

Because of their frequent association with the Primates in the Archonta, I also made comparisons with the Tupaiidae and Chiroptera. For the Tupaiidae I used *Tupaia*, *Urogale*, *Dendrogale*, and *Ptilocercus*. For the Chiroptera I used *Ageina*, *Archaeonycteris*, *Australonycteris*, *Hassianycteris*, *Icaronycteris*, *Palaeochiropteryx*, and the unnamed genus from the early Eocene of Fordones, France (Beard, Sigé, and Krishtalka, 1992; Habersetzer and Storch, 1987; Hand et al., 1994; Jepsen, 1970; Marandat, 1991; Revilliod, 1917; Russell, Louis, and Savage, 1973; Russell and Sigé, 1969; Sigé and Russell, 1980).

In all joint comparisons of derived groups, I recognize agreement for a character only if all the compared species in the group have the derived state. "Variable" is added for differences among species when that convention is suspect.

The main entries in Table 7 are differences of the euprimate morphotype from the pregroup, i.e. putative synapomorphies of the Euprimates. The agreement ("yes") or disagreement ("no") of the other genera with these differences then follow sequentially.

Counting the synapomorphies is inappropriate (Why? Think!), contra

Euprimates	<i>Purgatorius</i>	<i>Altanius</i>	<i>Altiatlasius</i>
P ₄			
[None found]	—	—	—
Lower molars			
1. Trigonid lower [also <i>Litolestes</i>]	yes	yes	yes
2. Hypoconid enlarged	no	yes	intermediate
3. Paracristid loops mesially and then distally	yes	yes	intermediate
4. Paraconid distinct from paracristid	some specimens	yes	yes
5. Paraconid cuspidate, not bladelike	some specimens	yes	yes
6. Hypoconulid relatively labial, near hypoconid	no	yes	no
7. M ₃ hypoconulid enlarged, broadened and at least as high as hypoconid	yes	yes	[unknown]
8. Entoconid relatively weak on M ₂ and M ₃ [also <i>Litolestes</i>]	<i>P. unio</i> , not <i>P. janisae</i> or <i>P. ceratops</i>	M ₃ , not M ₂	yes
9. M ₂ relatively transverse	yes	yes	yes
P ₄			
1. Parastylar lobe reduced	yes	yes	[unknown]
2. Metacrista not curving as much labially	yes	yes	[unknown]
3. Postprotocrista absent	Unknown <i>P. unio</i> and <i>P. ceratops</i> , absent <i>Pandemonium</i> , unusually close to preprotocrista <i>P. janisae</i> and perhaps a neomorph	yes	[unknown]
4. Postcrista definitely present, reaching postcingulum	yes	[unknown]	[unknown]

Table 7. Comparisons of the dental morphotypes of various taxa with synapomorphies of the dental morphotype of the Euprimates *sensu stricto* [see text]. For upper molars, see Table 8.

	<i>Eosimias</i>	<i>Afrotarsius</i>	<i>Decoredon</i>	<i>Petrolemur</i>	<i>Micromomyinae</i>
P_4	—	—	—	—	—
Lower molars					
1.	yes	yes	yes	[unknown]	yes
2.	yes	yes	probably no	[unknown]	no
3.	yes	yes	yes	[unknown]	yes
4.	yes	no	yes	[unknown]	yes
5.	yes	no	yes	[unknown]	yes
6.	no	no	probably no	[unknown]	no
7.	[unknown]	yes	yes	[unknown]	yes
8.	yes	yes	no	[unknown]	no
9.	yes	yes	yes	[unknown]	yes
P_4					
1.	[unknown]	[unknown]	yes	[unknown]	no
2.	[unknown]	[unknown]	yes	[unknown]	no
3.	[unknown]	[unknown]	[unknown]	no	no (present <i>Tinimomys</i> and perhaps <i>Micromomys</i> , absent <i>Chalicomomys</i> yes
4.	[unknown]	[unknown]	[unknown]	no	

Table 7 (continued)

	Tupaiaidae	Chiroptera	Galeopithecidae	Mixodectidae	Condylarthra
P ₄					
Lower molars					
1.	yes	no	yes	yes	yes
2.	yes	yes	yes	yes	no
3.	no	no	no	yes (except <i>Elpidophorus</i>)	<i>Protungulatum</i> , not <i>Oxyprimus</i>
4.	intermediate	yes	no	no (except <i>Remiculus</i>)	no
5.	no	no	no	no (except <i>Remiculus</i>)	<i>Protungulatum</i> , not <i>Oxyprimus</i>
6.	no	no	no	no	no
7.	no	no	no	yes	yes
8.	no	no	no	no	no
9.	no	no	yes	yes	yes
P ₄					
1.	no	no	yes	yes	no
2.	no	no	no	intermediate	no
3.	no	no	no	no	no
4.	no	no	no	no	no

Table 7 (continued)

usual cladistic dogma and the usual methods of canned programs. It is nevertheless apparent that *Purgatorius*, and thus the plesiadapiform morphotype, share most of the euprimate synapomorphies found here, and this is even increased if *Altanius* is incorporated into that morphotype, as it should be. *Altiatlasius* is more divergent than the other euprimate genera in the characters used; incorporating it into the morphotype, as is again appropriate, would make little difference. Most of the agreement of *Purgatorius* with the euprimate morphotype is not explained by parallel evolution which is also exhibited by the basal condylarths, the test-group used. It therefore seems likely that the resemblances noted are indicative of phyletic affinity, i.e. are synapomorphies⁴ of the two groups.

Beard (1991a) has summarized in an abstract some postcranial evidence which appears to link the Microsyopidae to the Euprimates. If this proves valid, one may extend it back to the Purgatoriidae, as would be necessary if the traits are homologous rather than convergent. Then the postcranial evidence would corroborate the dental evidence for an origin of the Euprimates from the Purgatoriidae. This argument is strictly phyletic rather than stratophenetic, if one agrees that the Microsyopidae were derived from the Purgatoriidae. The basis for the latter conclusion is morphological (e.g., Gunnell, 1989). In fact most of the traits mentioned are among those which Beard (1993a) later used as synapomorphies of a clade consisting of the Plesiadapiformes, Dermoptera, and Euprimates, and Szalay, Rosenberger, and Dagosto (1987) or Szalay and Lucas (1993) used as synapomorphies for either the Archonta, with or without the Mixodectidae, or a clade of the Plesiadapiformes and Euprimates. (Much of the evidence is unpublished and I am a bit bemused by the rapid changes in its interpretation. I am, though, simply mystified at the first character which Szalay and Lucas [1993] use to support their concept of Archonta. This is the presence of two entotympanics in an auditory bulla. Only the Dermoptera and, possibly, the Chiroptera in their Archonta actually seem to have had this trait at their origin. Some other authors have used canned programs, or similar inference [canned thinking], to put an entotympanic [or two?] in the initiator of the Placentalia, but Szalay, at least, is better than this at phyletic inference.)

The comparisons in Table 7 present dental evidence for a diversity of groups with respect to synapomorphies with the Euprimates. They are suggestive but not definitive with respect to phyletic affinities with the Plesiadapiformes, because the latter have some other dental synapomorphies which are not shared with the Euprimates and therefore don't appear in Table 7. A full evaluation of such possible affinities is beyond the scope of this paper. However, it is apparent that no group in Table 7 outside the Plesiadapiformes has any significant number of the euprimate dental synapomorphies (apart, of course, from those primitive euprimates treated separately) except for the Condylarthra, which are present in the table only to help estimate convergence to a group with similar dental adaptations.

⁴Hennig (1950, 1966) used "synapomorphy" descriptively, referring just to a shared derived character. Its later reinterpretation as equivalent to [historical] "homology" leaves us without a word for Hennig's concept. Is it too late to go back to Hennig in this, so that we would have a simple way to refer to shared derived characters as such?

Euprimates	<i>Purgatorius</i>	<i>Altanius</i>	<i>Altiatlasius</i>
Upper molars			
1. Postcrista present at least M ¹	yes	yes	yes
2. Styolar shelf reduced to narrow ectocingulum	<i>P. unio</i> , not <i>P. janisae</i>	yes	yes
3. Metacrista weaker	yes	yes	yes
4. Metacrista directed more distally than labially	no	no	no
5. Paracrista with little transverse component	no	yes	yes
6. Protocone apex more labial	<i>P. unio</i> , not <i>P. janisae</i>	probably	yes
7. Postprotocrista extends directly distally for a short distance from the protocone apex, so the protocone apex is somewhat elongated mesiodistally	yes	[unknown]	yes
8. Protofossa less transverse	no	yes	yes
9. Protocone twist (see text, <i>Pandemonium</i> comparisons) [lingual borders not angled in <i>Pelycodus</i>]	yes	yes	no

Table 8. Comparisons of the morphotypes of upper molars of various taxa with synapomorphies of the upper-molar morphotype of the Euprimates *sensu stricto* [see text].

Dermoptera

Some cranial and postcranial evidence (Beard, 1990, 1993a, 1993b; Kay, Thorington, and Houde, 1990; Kay, Thewissen, and Yoder, 1992) favors a derivation of the Dermoptera from the Paromomyidae (*sensu stricto*). [D.E. Russell (1964) noted a similarity between the claws of *Plesiadapis* and those of *Cynocephalus*; I do not know whether this is convergent or a synapomorphy present more or less throughout the Plesiadapiformes.] Opposing evidence also exists (Krause, 1991; Kay, Thewissen, and Yoder, 1992), and not all supporting evidence is free of controversy (Szalay and Lucas, 1993). [I note in addition a character advocated in a masterly paper by Beard (1993a) to group the Paromomyidae and Galeopithecidae and exclude the Plesiadapidae and Micromomyinae. This is that the ulnar side of the triquetrum is appreciably constricted relative to the radial side. His own figure shows that the derived state occurs in *Plesiadapis*, and the triquetrum is unknown in the Micromomyinae at least pending preparation of the skeletons of *Tinimomys*.] It is worth explicit mention that the mainland species *Galeopterus variegatus* is easily distinct at the generic level from the Philippine *Cynocephalus volans*, despite the weight of tradition (from external morphology?) that they are congeneric (cf. Thomas, 1908;

	<i>Eosimias</i>	<i>Afrotarsius</i>	<i>Decoredon</i>	<i>Petrolemur</i>	<i>Micromomyinae</i>
Upper molars					
1.	[unknown]	[unknown]	yes	no	yes
2.	[unknown]	[unknown]	yes	no	yes
3.	[unknown]	[unknown]	yes	yes	yes
4.	[unknown]	[unknown]	no	no	no
5.	[unknown]	[unknown]	yes	yes	<i>Tinimomys</i> and <i>Chalicomomys</i> , not <i>Micromomys</i>
6.	[unknown]	[unknown]	yes	no	yes
7.	[unknown]	[unknown]	probably	no	no
8.	[unknown]	[unknown]	no	yes	no
9.	[unknown]	[unknown]	probably	no	yes, except protocone more mesial

Table 8 (continued)

Cabrera, 1925; Szalay, 1969). Just look at their structure! A comparative study would nevertheless be useful with respect to the adaptive significance of the many differences.

Probably the most serious difficulty is the various evidence (Novacek, Wyss, and McKenna, 1988, and earlier work cited there; Wible and Novacek, 1988; Szalay and Lucas, 1993) for a sister-group relationship between the Dermoptera and the Chiroptera. Even *Purgatorius* is too derived dentally to be taken seriously as an ancestor of bats, whose teeth are derived even in the early Eocene in a different way, and the hypothetically ancestral group for the Dermoptera (the Paromomyidae) is appreciably beyond this stage of bat ancestry. It is not reasonable to attach the putative synapomorphies to *Purgatorius*, because other groups derived at least approximately from this genus lack them. The innervation of the patagia is similar in the Dermoptera and Chiroptera (Thewissen and Babcock, 1993). These authors also find the flying squirrel *Glaucomys* to have one of the two relevant nerves restricted to the face, but Gray and Sokoloff (1992) find that nerve extending into the patagium. Thus there may be a constraint on the mode of origin of a patagium, weakening the evidence for its homology. Molecular evidence (Stanhope et al., 1993; Adkins and Honeycutt, 1993; Honeycutt and Adkins, 1993) uniformly and strongly places the Chiroptera far from the Primates, with the Dermoptera probably near the latter but

Tupaiaidae Chiroptera Galeopithecidae Mixodectidae Condylarthra
Upper molars

1.	no	no	no	only <i>Remiculus</i>	no
2.	no	no	no	no	no
3.	no	no	no	no	yes
4.	no	no	no	no	no
5.	no	no	no	no	no
6.	no	no	no	no	yes
7.	intermediate	no	yes	no	yes
8.	intermediate	intermediate	no	only <i>Remiculus</i>	no
9.	no	no	no	no	no

Table 8 (continued)

in any case not close to the Chiroptera. The neural characters of Johnson and Kirsch (1993) give similar results. Clearly there is appreciable convergence somewhere, either between the Paromomyidae and the Dermoptera or between the latter and the Chiroptera. I weakly opt for the second alternative; see also MacPhee, Wible, and Cartmill (1989).

Martin (1990a, 1993) has argued against a relationship of Dermoptera to Primates because of the smaller brain of the former. He himself notes, however, that it is relatively as large as that of the late Eocene euprimate *Adapis*! The same is true for *Plesiadapis* (Gingerich, 1976), as Radinsky (1970) had obliquely suggested. Szalay (1969) described a cranial endocast of *Microsyops* but didn't estimate its volume. Moreover, folivores tend to have smaller brains than do other mammals. Martin also uses a model to infer the time of separation of the major groups of Euprimates as about 80 million years ago, with the *Plesiadapiformes* apparently coming off before 100 million years. A number of such calculations have been done over the years by various people for various groups, including even the Metazoa. All such attempts ignore the effect of a rapid evolutionary rate early in diversification, a common [not universal] phenomenon which entirely vitiates the conclusions, as is the case here.

What then to do with the Dermoptera? One could have them as an

order derived from the Primates, but they don't really seem so greatly distinct adaptively. Consider flying squirrels or flying phalangers. I have put them provisionally as a separate suborder, as Szalay and Lucas (1990 but not 1993) have approximately done, but (if the preferred phylogeny is actually correct) it may be better to reduce them to a superfamily in the Plesiadapiformes⁵.

Primate synapomorphies

I do not regard the Tupaiidae as derived from, or the sister group of, the Primates (e.g., Van Valen, 1965; Luckett, 1980; Martin, 1990; Kay, Thewissen, and Yoder, 1992). I note the unsupported statement by Wible and Covert (1987) that some Microchiroptera have a sheathed penis rather than a pendulous one. The latter state has been used prominently to support the Archonta (e.g., Smith and Madkour, 1980; Novacek and Wyss, 1986). Wible and Covert regarded it as a reversal, but its taxonomic distribution needs study and analytical treatment to test this hypothesis.

With advance acknowledgment of a high risk of error, I suggest the following skeletal characters as putative synapomorphies for the group I here call Primates: brain (and therefore endocranial volume) enlarged in relation to body size, promontorium well separated from basioccipital [Kay, Thewissen, and Yoder (1992) have given a plausible argument for this being nonhomologous between the Plesiadapiformes and Euprimates, and it isn't noticeable in the Dermoptera], deltopectoral crest of humerus lateral in position, lesser tuberosity of humerus strongly developed, and a synovial joint between the distal tibia and fibula. All other characters I know, and there have been many proposed, have proved to have a wider (or occasionally narrower) taxonomic distribution. Perhaps that will be true for these also. They do march with Beard's (1991b) view of the ancestral adaptation of the Primates (*sensu lato*) being vertical climbing and clinging, with a diet predominantly of nonleafy plant products [Beard restricted this to exudates.]

An explicit list of dental synapomorphies can be done only between the Plesiadapiformes and Euprimates. The teeth of the Dermoptera are highly derived and do not support a relationship to the Plesiadapiformes. This has been hypothesized to be a result of the leaf-eating habits of the Dermoptera, but folivorous euprimates are not at all convergent on them (a weak argument). Even *Dermotherium*, from the late Eocene of Thailand (Ducrocq et al., 1992), closely resembles *Galeopterus*.

With this qualification, putative dental synapomorphies of the Primates include the following. On P⁴, the parastylar lobe is reduced, the labial curve of the metacrista is reduced, and a postcrista is present, reaching the postcingulum. On the upper molars, the postcrista is present on at least M¹, the metacrista is reduced, the protocone apex is somewhat elongated mesiodistally, and the protocone twist occurs. On the lower molars, the trigonid is lower, the paracristid loops

⁵The name Dermoptera would be inappropriate for such a combined group, despite its being older. It refers to the adaptation of gliding, which most plesiadapiforms lacked. Moreover, the change in meaning would be much less for Plesiadapiformes because that group is already quite diverse and includes putative gliders.

Order Primates**Suborder Plesiadapiformes****Superfamily Microsyopoidea****Family Purgatoriidae****Subfamily Purgatoriinae***Purgatorius***Subfamily Micromomyinae***Chalicomomys, Micromomys, Myrmecomomys, Tinimomys***Subfamily Palaechthoninae***Anasazia, Palaechthon, Palenochtha, Plesiolestes, Premnoides, Torrejonia***Family Paromomyidae***Arcius, Dillerlemur, Elwynella, Ignacius, Paromomys, Phenacolemur, Pulverflumen, Simpsonlemur***Family Microsyopidae****Subfamily Uintasoricinae***Alveojunctus, Avenius, Berruvius, Navajovius, Niptomomys, Uintasorex***Subfamily Microsyopinae***Arctodontomys, Craseops, Megadelphus, Microsyops***Family Picrodontidae***Draconodus, Picrodus, Zanycteris***Superfamily Plesiadapoidea****Family Plesiadapidae****Subfamily Plesiadapinae***Chiromyoides, Nannodectes, Pandemonium, Platychoerops, Plesiadapis***Subfamily Saxonellinae***Saxonella***Family Carpolestidae***Carpodaptes, Carpolestes, Elphidotarsius***?Suborder Dermoptera****Family Galeopithecidae***Cynocephalus [= Galeopithecus], Dermotherium, Galeopterus***Suborder Euprimates****Infraorder Prosimiae****Superfamily Lemuroidea****Adapidae (including Notharctidae)****Plesiopithecidae****Lemuridae (including Cheirogaleidae, Lepilemuridae, Megaladapidae)****Indridae (= Indriidae; including Archaeolemuridae, Palaeopropithecidae)****Daubentoniidae****Lorisidae (including Galagonidae [= Galagidae]),****Superfamily Tarsioidea****Omomyidae (including Anaptomorphidae, Microchoeridae, Necrolemuridae)****Tarsiidae****Infraorder Anthropoidea****Hyporder Eosimiae****Superfamily Parapithecoidea****Afrotarsiidae (or Eosimiidae)****Parapithecidae (including Oligopithecidae)****Superfamily Ceboidea**

- Cebidae (including Aotidae, Atelidae, Branisellidae,
Homunculidae, Pitheciidae, ?Xenothricidae)
Callitrichidae (= Callithricidae; including Callimiconidae)
Hyporder Simiae
Superfamily Cercopithecoidea
Pliopithecidae (including Propliopithecidae)
Pongidae (including Dryopithecidae, Hylobatidae, Oreopithecidae,
Panidae, Proconsulidae, Ramapithecidae, etc.)
Cercopithecidae (including Colobidae, Victoriapithecidae)
Superfamily Hominoidea
Hominidae
Helacidae

Table 9. A classification of the Primates.

mesially and then distally, the paraconid is distinct from the paracristid and is cuspidate rather than bladelike, the hypoconulid of M_2 is enlarged, and M_2 is relatively transverse. A few other possibilities are ambiguous, such as a moderately labial position of the upper molar protocone.

Overall, these dental synapomorphies imply a reduced emphasis on vertical shear and an increased emphasis on holding and dynamically crushing relatively nonabrasive material. They complement the proposed skeletal synapomorphies and corroborate the proposed adaptive shift which was concurrent with, and presumably caused, the origin of the Primates.

Primate classification

Figure 2 (at the end of the monograph) includes my current views on euprimate phylogeny. *Altanius* fits into neither the Omomyidae nor the Adapidae as currently understood, but it is insufficiently distinct to warrant a separate family. Probably the Omomyidae should be extended down to include it, in which case that family would be ancestral to the lemuroids as well as (by an unknown form which would nevertheless fit here) to the tarsiids. Because *Altanius* cannot be referred to an existing subfamily of the Omomyidae (or any other family), including the Decoredontinae of Szalay and Li (1986) [as Gingerich, Dashzeveg, and Russell (1991) note in a different way], I establish a new subfamily for it:

Altaniinae, new subfamily

Type genus: *Altanius* Dashzeveg and McKenna, 1977.

Included genera *Altanius* only.

Diagnosis Size very small; lower incisors small and vertical; upper and lower premolars unreduced; P_4 with moderate paraconid and metaconid; cusps of cheek teeth rather tall, including the entoconid of M_2 ; molar paraconid rather large; M_1 trigonid somewhat elongate; M^3 and M_3 unreduced, with a rather large hypopconulid lobe on M_3 ; metacrista of upper molars with an appreciable labial component.

In my classification of the Primates (Table 9) I have committed some heresies, in addition to lumping some usually recognized families and superfamilies for the sake of adaptive balance. Some of these I have already mentioned, but there are more. In the Prosimiae [the base is Simia, with plural Simiae] there is the recently recognized family

Plesiopithecidae Simons and Rasmussen (1994). As these authors point out, the skull of *Plesiopithecus* shows that it is not an anthropoid, as originally inferred from a mandible. They then compare it with tarsioids and toothcomb-bearing lemuroids, finding the greatest similarity with lorisisids. Oddly, they ignore adapids, although *Plesiopithecus* has enlarged (apparent) canines and no toothcomb, and the same authors have earlier actually derived the Anthropoidea from the Adapidae (e.g., Rasmussen and Simons, 1989). Comparison with adapids indicates a clear affinity with relatively primitive adapines, in particular the Protoadapini of Szalay and Delson (1979). *Plesiopithecus* lacks any evidence of a toothcomb or other specific synapomorphies with the Lemuroidea, as far as known. Its ancestry is similarly presumptively excluded from the Notharctinae and from tribes of the Adapinae other than the Protoadapini. The Protoadapini are adequately primitive and different genera of this group do resemble *Plesiopithecus* in different ways.

Less conventionally, in the Anthropoidea I have a new hyporder⁶ Eosimiae for the noncatarrhine Anthropoidea. The ceboids are indeed moderately derived anthropoids, but the major anthropoid radiation is that of the Simiae. Because both the ceboids and the simians seem to be derived from the natural paraphyletic family Parapithecidae, I include the latter in the Eosimiae. The synapomorphic characters of the Eosimiae are those of the Anthropoidea; their initiator retained the plesiomorphic state for characters for which the Simiae have synapomorphies. The latter characters are quite as good as the former with respect to the classification of the Eosimiae although not, of course, being suitable for phyletic inference at that level. In like manner, the basal family of the Eosimiae is a natural paraphyletic group. Afrotarsiidae is the older name, but *Afrotarsius* is somewhat less likely to belong here than is *Eosimias* although I suspect that both genera do fit here, with others such as *Altiatlasius*.

The suprafamilial separation of the Pongidae from the Hominidae is again a reflection of the apparent magnitude of the adaptive shift. I don't know what to do with the Helacytidae of Van Valen and Maiorana (1991), which is a valid group reflecting real evolution, but I leave them in the Hominoidea *faute de mieux*. Having a formal taxon for the (real) species involved here is unconventional, but, as Ralph Waldo Emerson said, "A foolish consistency is the hobgoblin of little minds. . ." The nature of the independent evolution of HeLa cells is itself severely unconventional and deserves serious scrutiny and study that isn't biased by our preconceptions of how evolution ought to occur.

⁶Hypo-, ?new prefix for the category next below that with the prefix "infra-". Thus hypofamilies are included in infrafamilies. Similarly, "hyper-" might be used for the category next above the one with "supra-", if that is useful somewhere.

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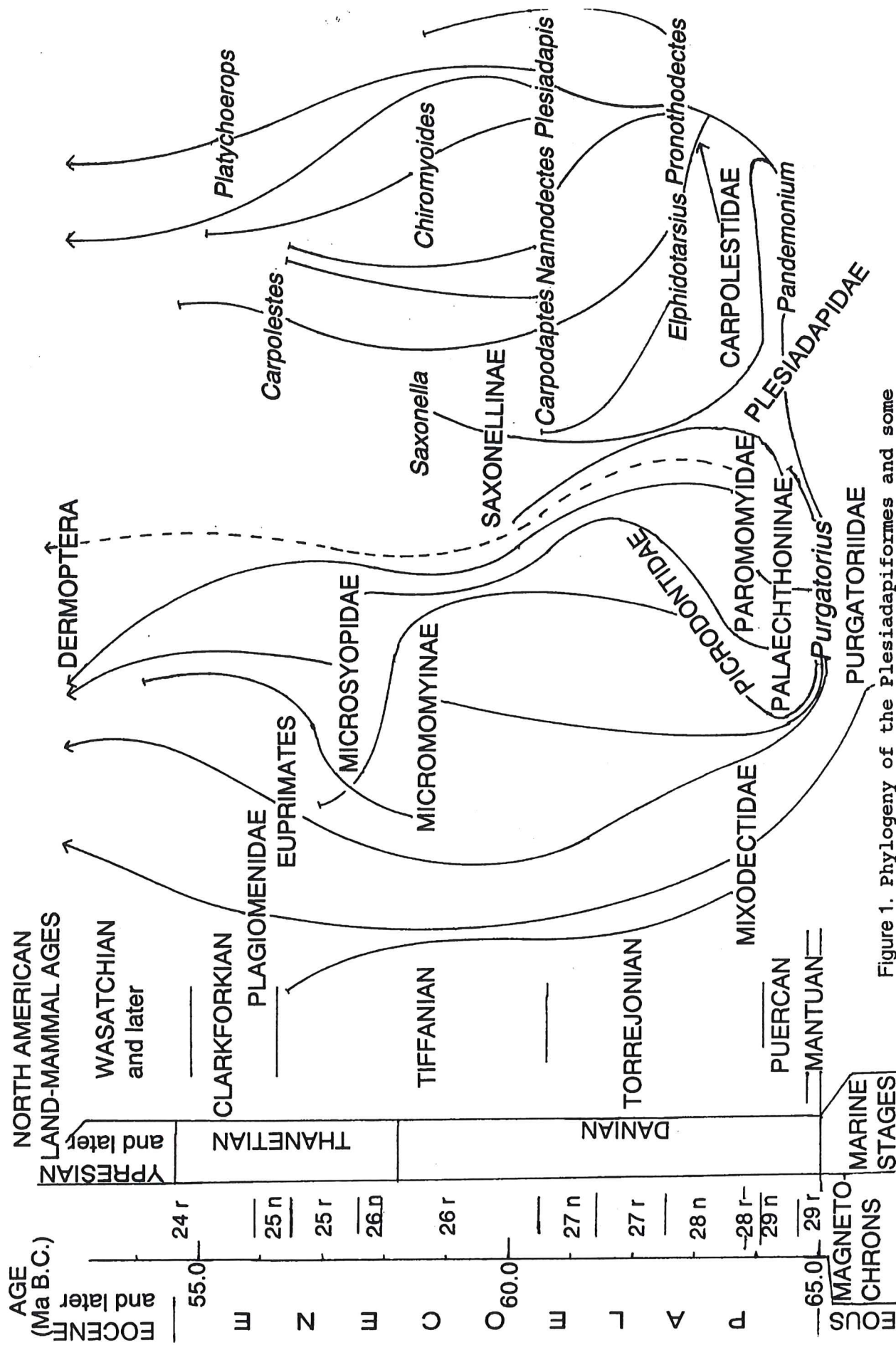


Figure 1. Phylogeny of the Plesiadapiformes and some other taxa. The name of a taxon is at its first known appearance, insofar as possible (except for taxa with genera given); unlabeled lines up from a name indicate later known duration. Incorporation of stratigraphic position does not imply primary use of it in inferring the phylogeny itself.

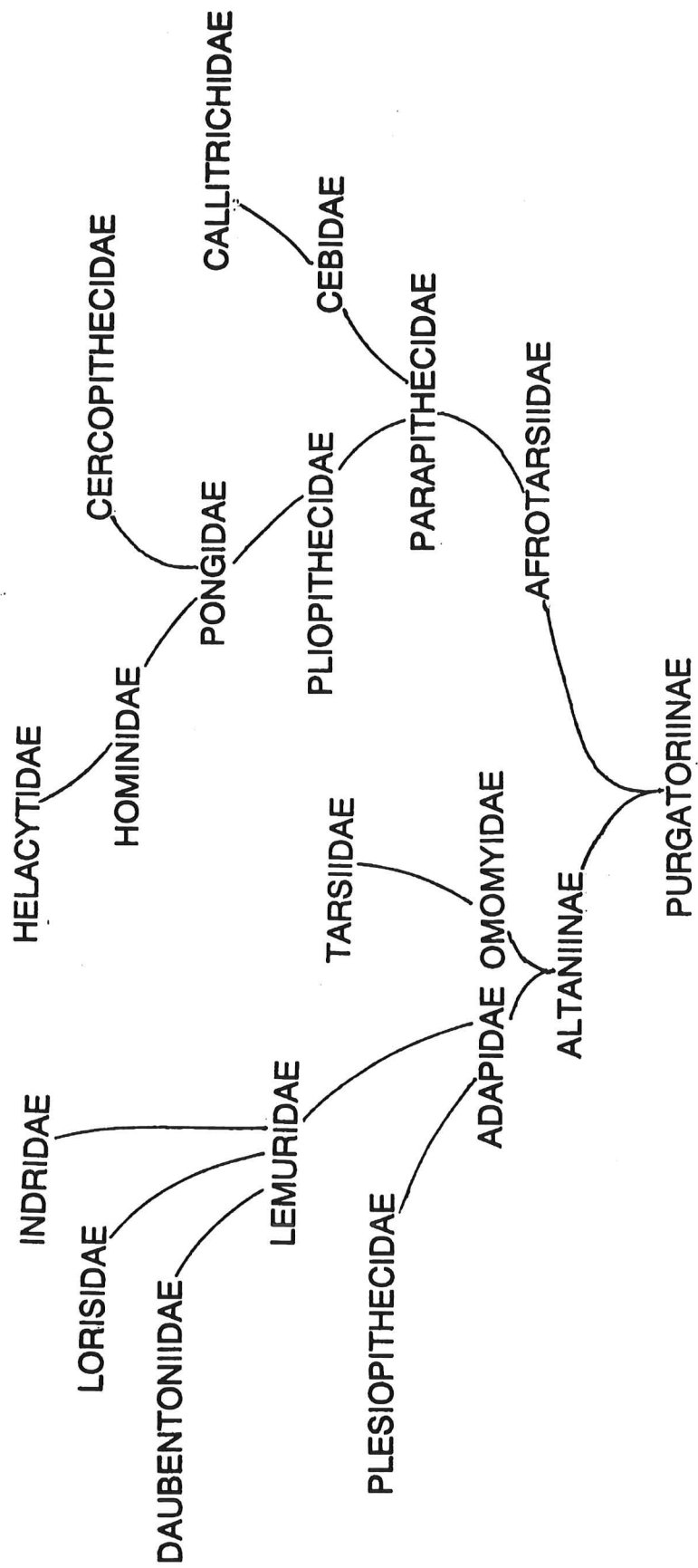


Figure 2. Phylogeny of the Euprimates. There is no time scale.

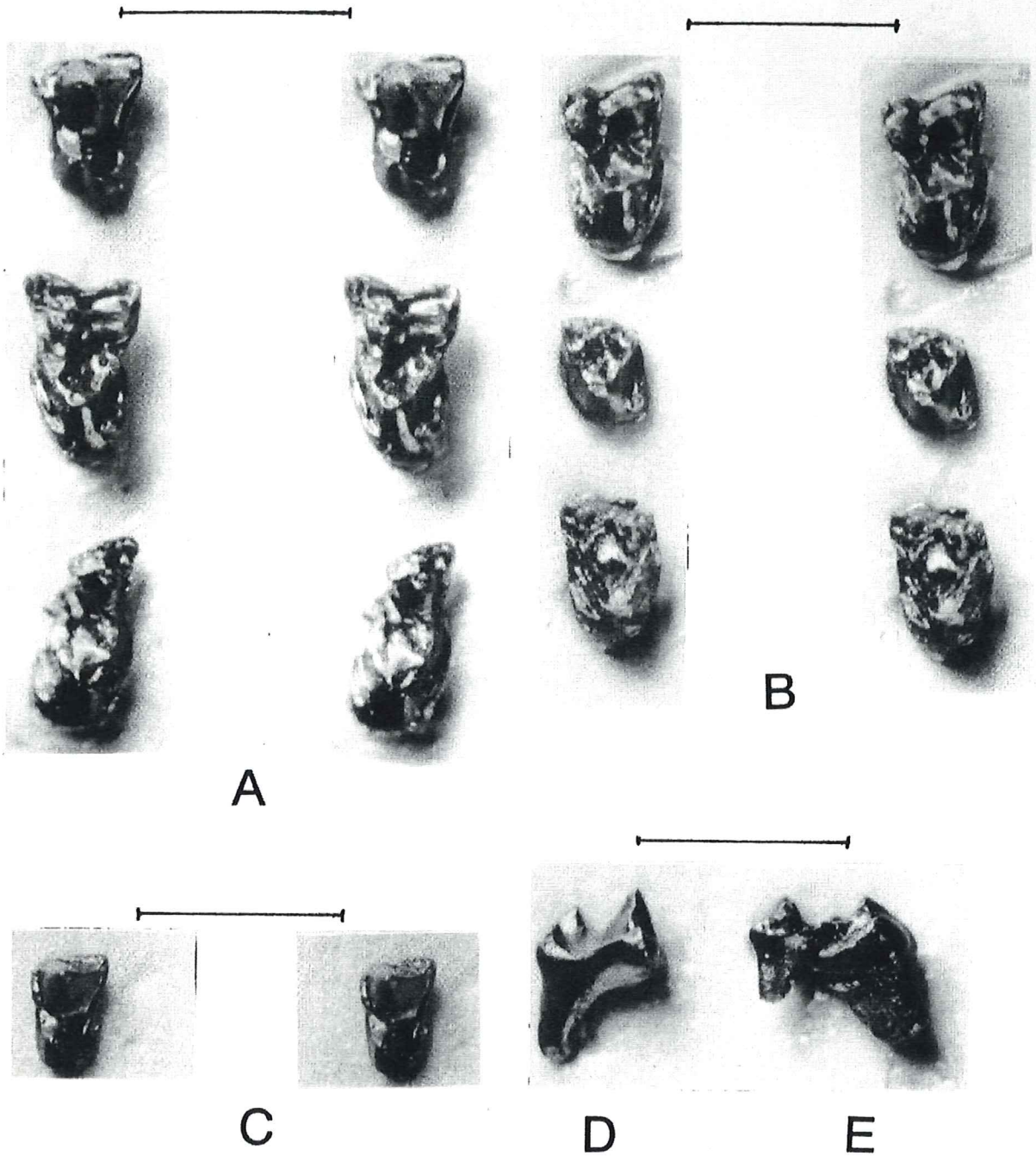


Plate 1. *Pandemonium dis*, UM upper teeth, identified top to bottom. Scale bars are 5 mm.

A. Stereophotographs, occlusal view: left P⁴, 1635; left M²², 2201; right M^{1 or 2}, 1526.

B. Stereophotographs, occlusal view: right M²², 1630; left M¹, 1553; right M¹, 1627.

C. Stereophotographs, occlusal view: left P³, 2211.

D. Distal view left P⁴, 1635.

E. Distal view right M²², 1630.

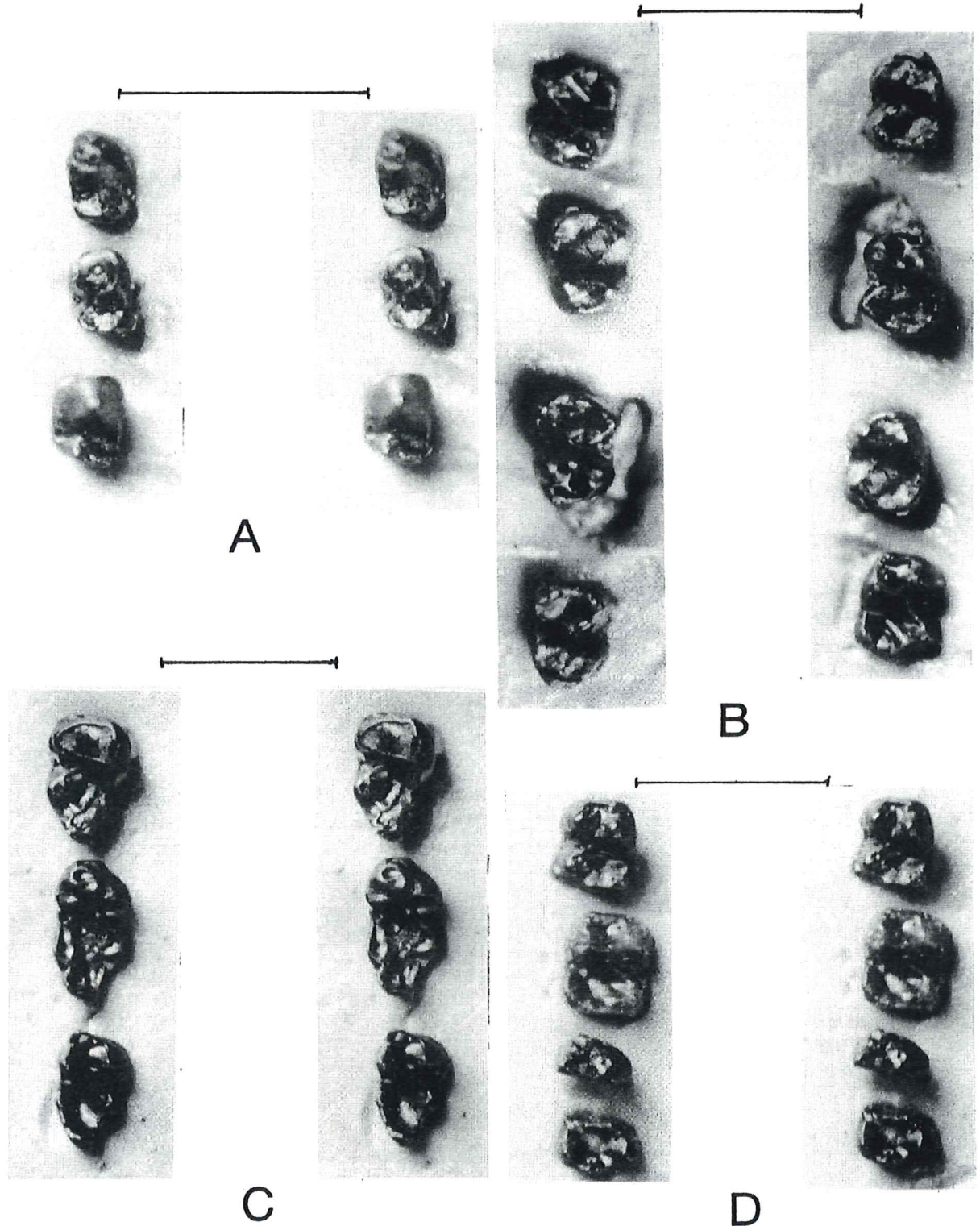


Plate 2. *Pandemonium dis*, UM lower teeth, stereophotographs, occlusal view. Identified top to bottom. Scale bars are 5 mm.

A. Right P_3 , 2193; left P_3 , 2190; left P_4 , 2189.

B. Left M_1 , 1639; left M_1 , 1519; left M_1 , 1648; right M_1 , 1620.

C. Left M_3 , 2185; right M_3 , 2186; right M_3 , 2187.

D. Left M_2 , 1621; right M_2 , 1631 (type); right M_2 or 3 , 1532; right M_1 or 2 , 1541.

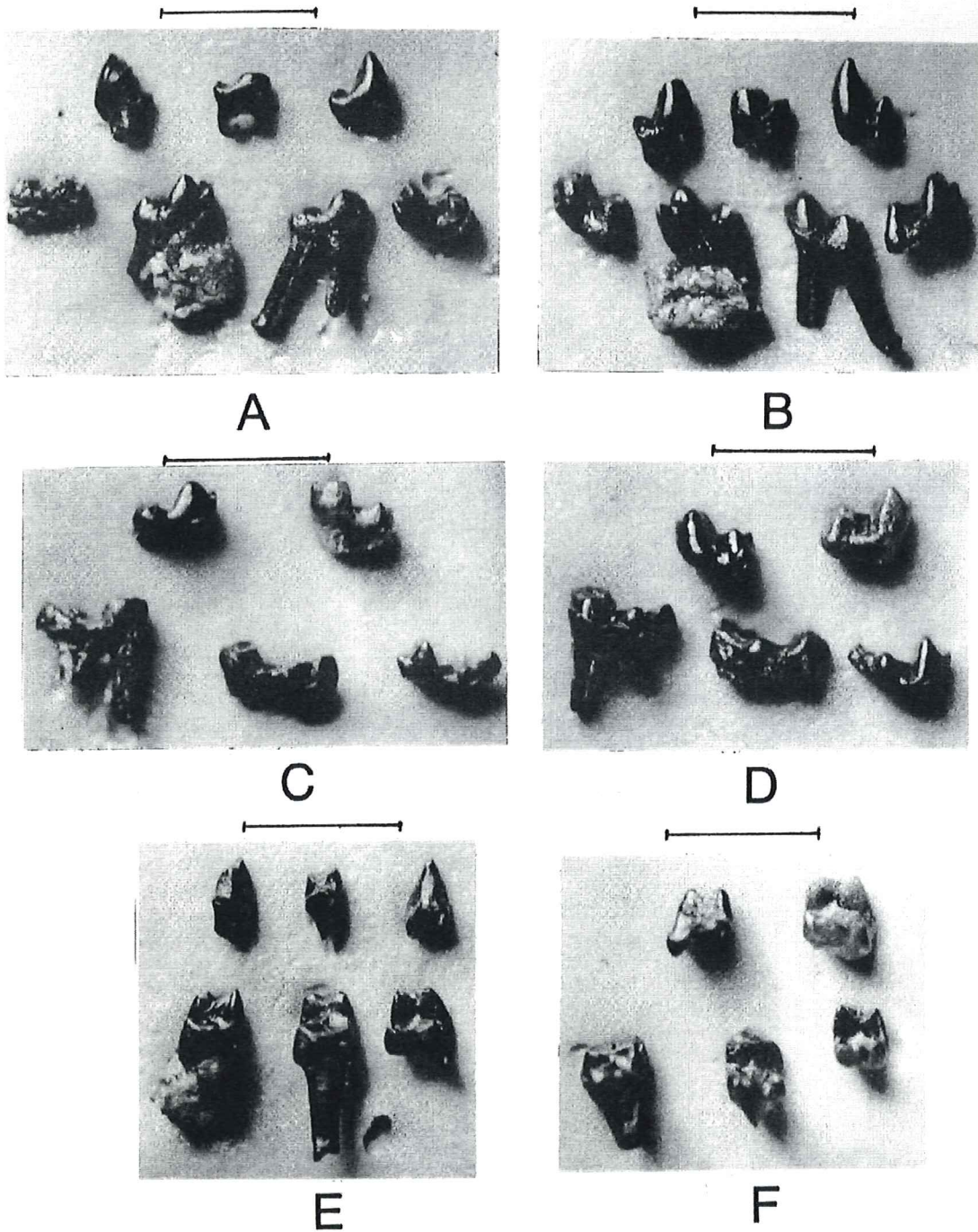


Plate 3. *Pandemonium dis*, UM lower teeth, identified left to right for each row. Scale bars are 5 mm.

A. Lingual views: right P_3 , 2193; left P_3 , 2190; left P_4 , 2189; — left M_1 , 1639; left M_1 , 1519; left M_1 , 1648; right M_1 , 1620.

B. Labial view of specimens in A.

C. Lingual views: left M_2 , 1621; right M_2 , 1631 (type); — left M_3 , 2185; right M_3 , 2186; right M_3 , 2187.

D. Labial view of specimens in C.

E. Distal view of specimens in A except for 1639.

F. Distal view of specimens in C.

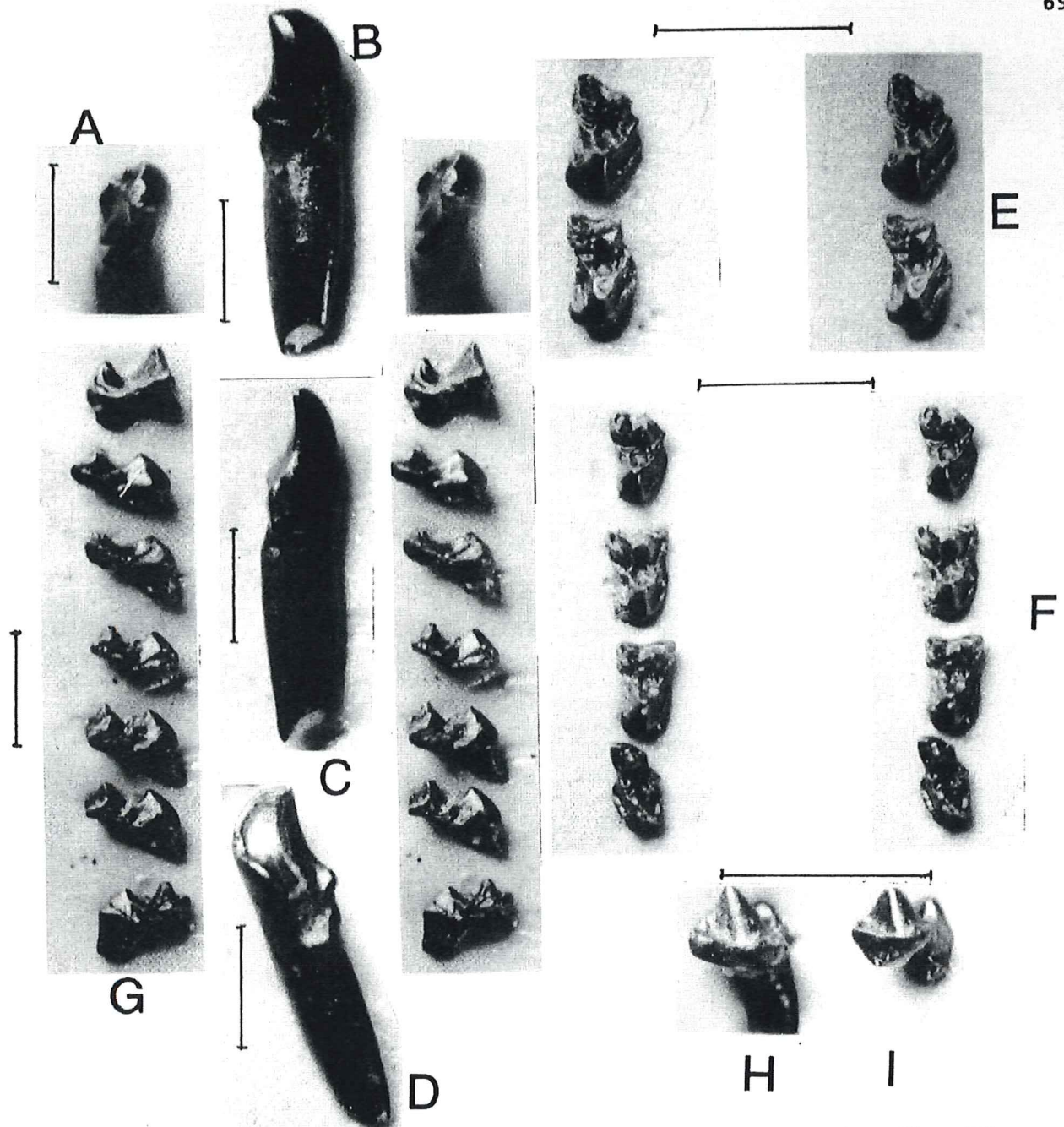
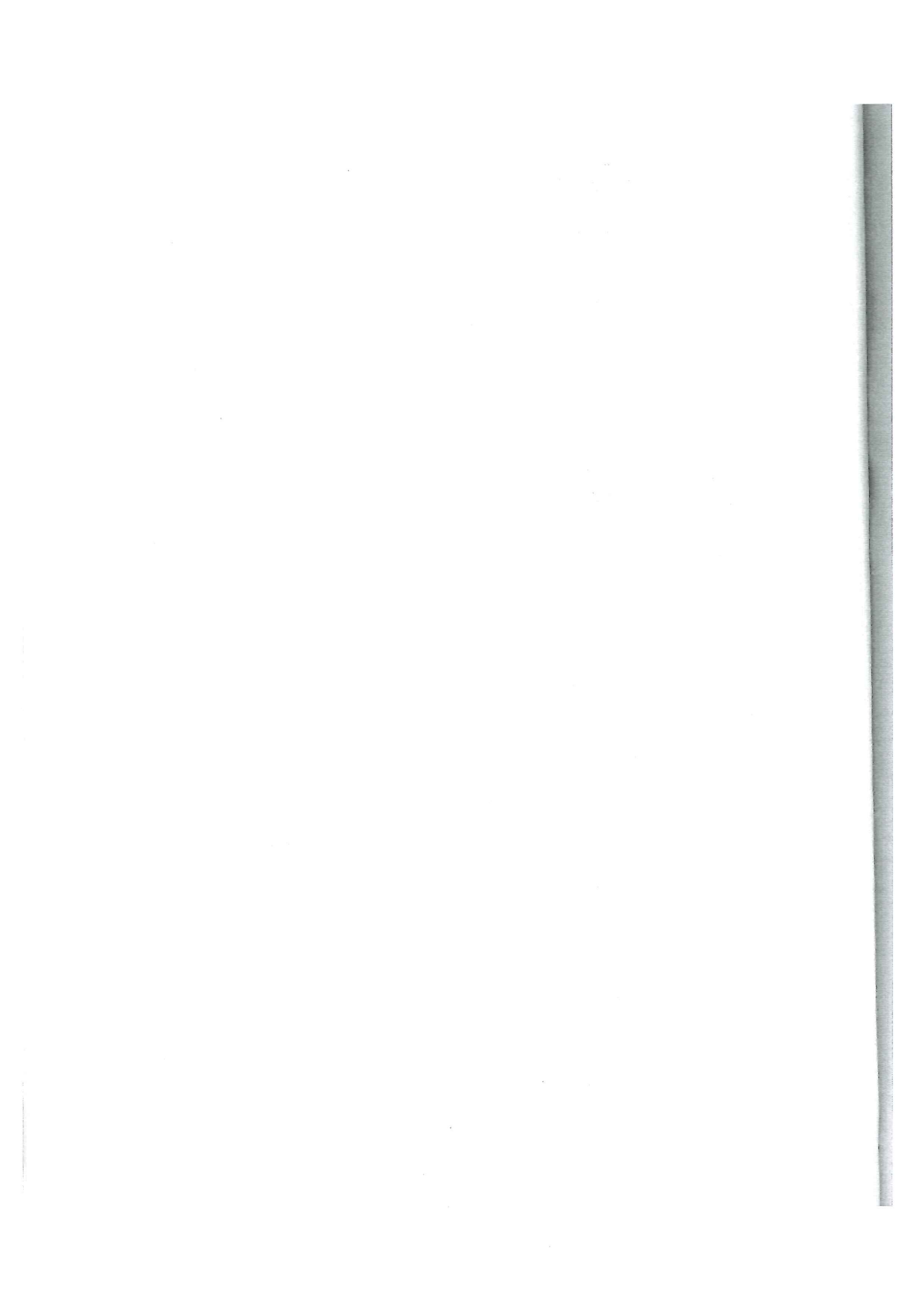


Plate 4. Upper teeth of *Purgatorius unio* and *Pandemonium dis*, UM specimens, identified top to bottom. Scale bars are 5 mm., except 3 mm. for the incisor.

- A-D. cf. *Pandemonium dis*, right I^1 , 2194: occlusal (stereophotographs), labial, distal, and lingual views.
 E. *Purgatorius unio*, stereophotographs, occlusal view: right M^2 , 1597 (type); right M^1 , 1652.
 F. *Purgatorius unio*, stereophotographs, occlusal view: right M^1 , 2213; right M^2 , 2212; right M^1 , 1637; left M^3 , 2191.
 G. Distal views: cf. *Pandemonium dis*, left P^{23} , 2211; *Purgatorius unio*, right M^2 , 1597 (type); right M^1 , 1652; right M^1 , 2213; right M^2 , 2212; right M^1 , 1637; left M^3 , 2191.
 H. *Pandemonium dis*, distal view left P^4 , 1635.
 I. Cf. *Pandemonium dis*, distal view left P^{23} , 2211.



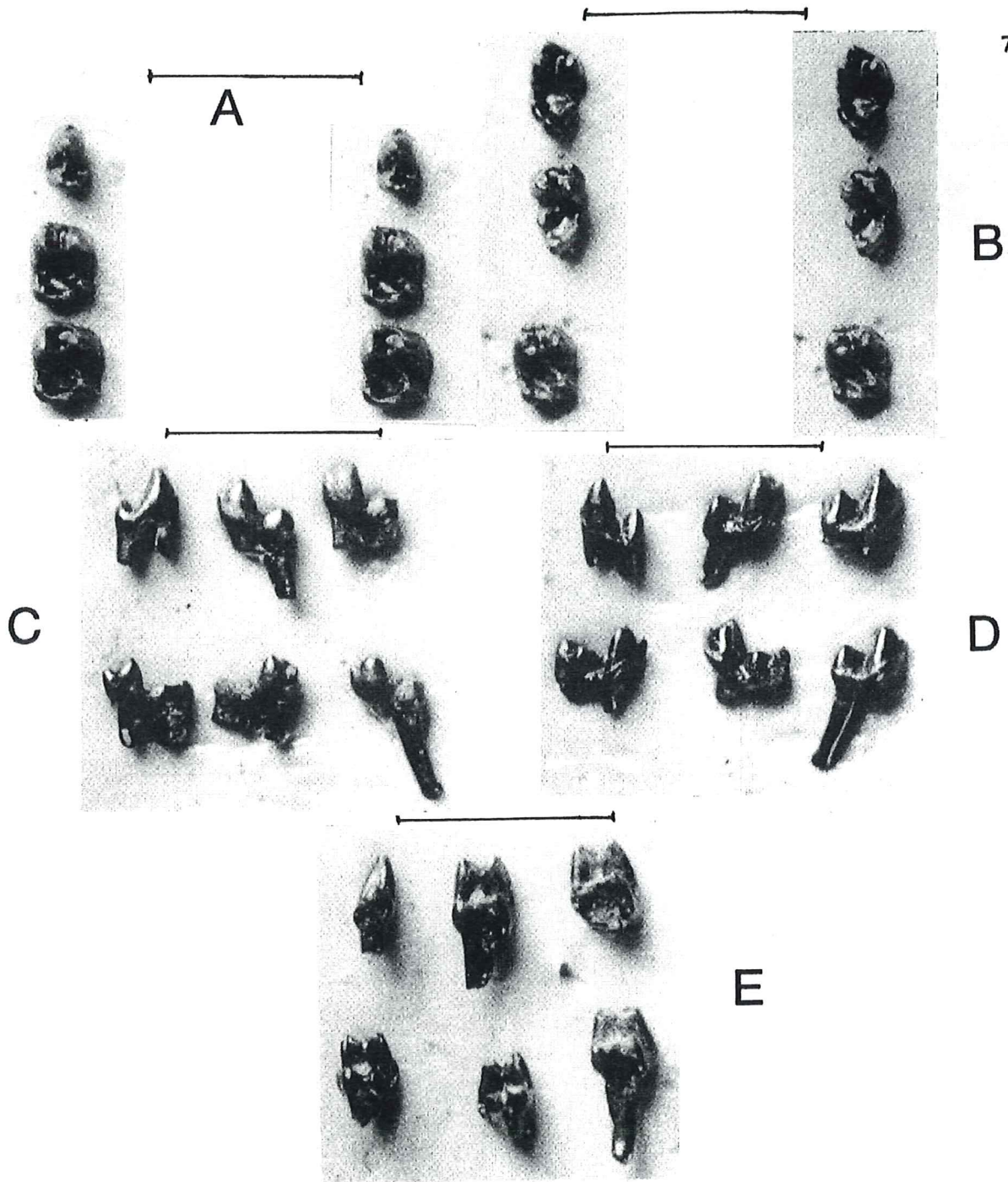


Plate 5. *Purgatorius unio* and *P. ceratops*, UM lower teeth, identified top to bottom (A,B) or left to right for each row (C-E). Scale bars are 5 mm.

A. Stereophotographs, *P. unio*, occlusal view: left P_4 , 1616; right M_1 , 1504; right M_2 , 2209.

B. Stereophotographs, occlusal view: *P. unio*, right M_3 , 2214; left M_3 , 1506; *P. ceratops*, right M_2 , 1547 (type).

C. Lingual views, *P. unio*, left P_4 , 1616; right M_1 , 1504; right M_2 , 2209; - right M_3 , 2214; left M_3 , 1506; *P. ceratops*, right M_2 , 1547 (type).

D. Labial views of specimens in C.

E. Distal views of specimens in C.

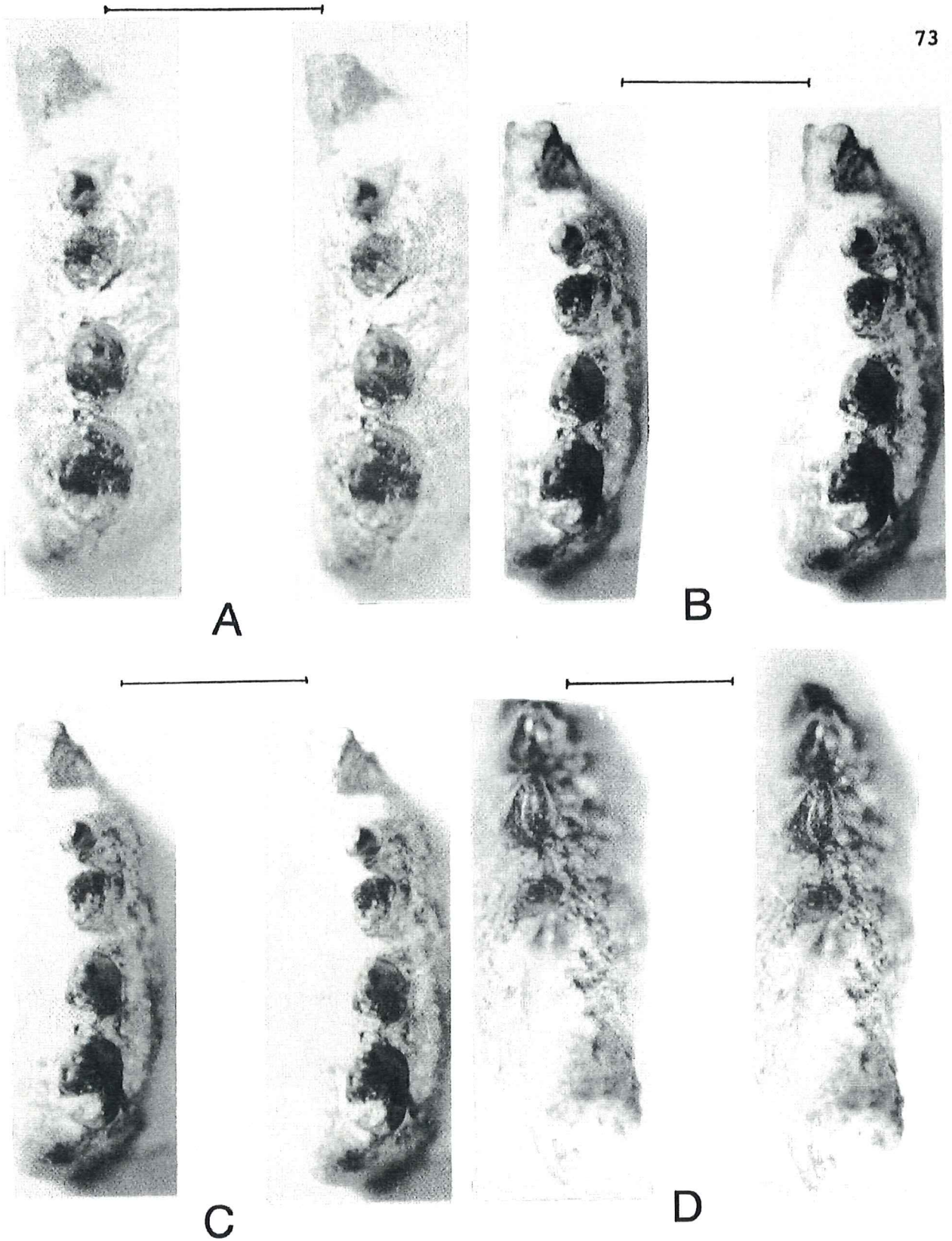
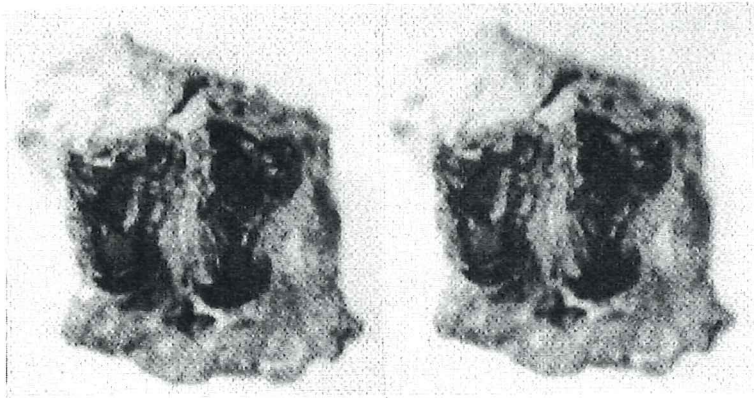
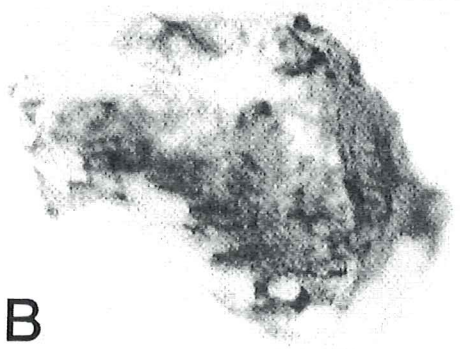


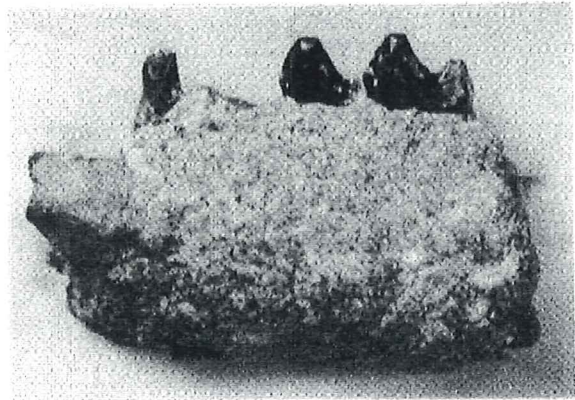
Plate 6. *Anasazia williamsoni*, stereophotographs of NMMNH No. P-19860 (type), right mandible fragment with $P_{1,3-4}$. Scale bars are 5 mm.
 A-C. Occlusal views.
 D. Mesial view of P_3 .



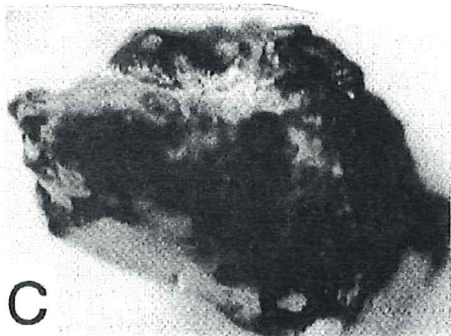
A



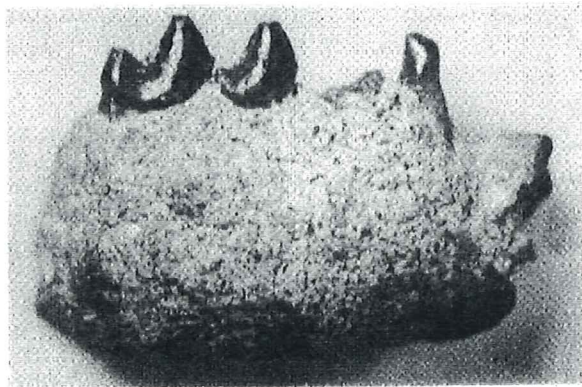
B



D

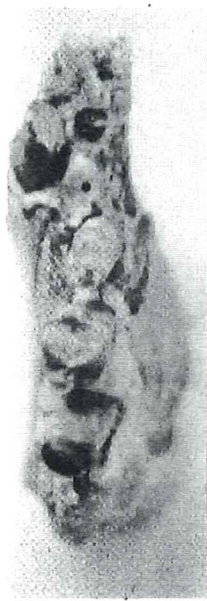


C

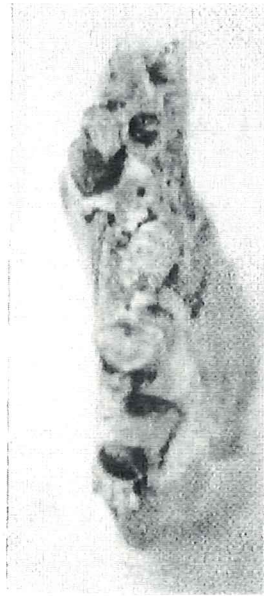


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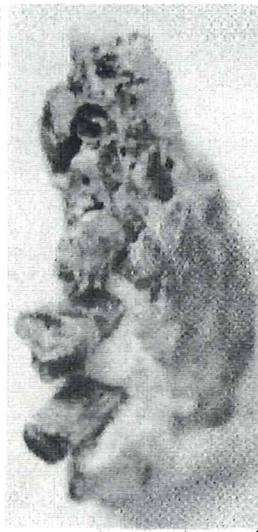
Plate 7. *Anasazia williamsoni*, NMMNH specimens. Scale bars are 5 mm.
 A. Stereophotographs of P-16191, left M^{1-2} , occlusal view.
 B,C: Distal views of M^2 of P-16191.
 D. Lingual view of P-19860, right mandible fragment with $P_{1,3-4}$.
 E. Labial view of P-19860.



A



B



C



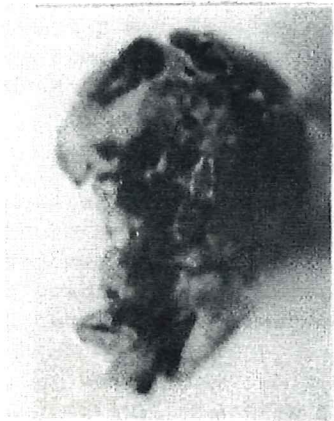
D

Plate 8. Cf. *Palaechthon woodi*, stereophotographs of NMMNH No. P-15684, anterior part of right mandible. Scale bars are 5 mm.
A,B. Occlusal views.
C,D. Oblique labial views.



A

C



B

D

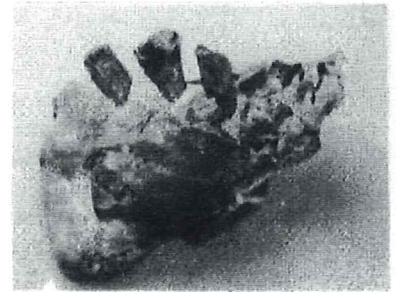
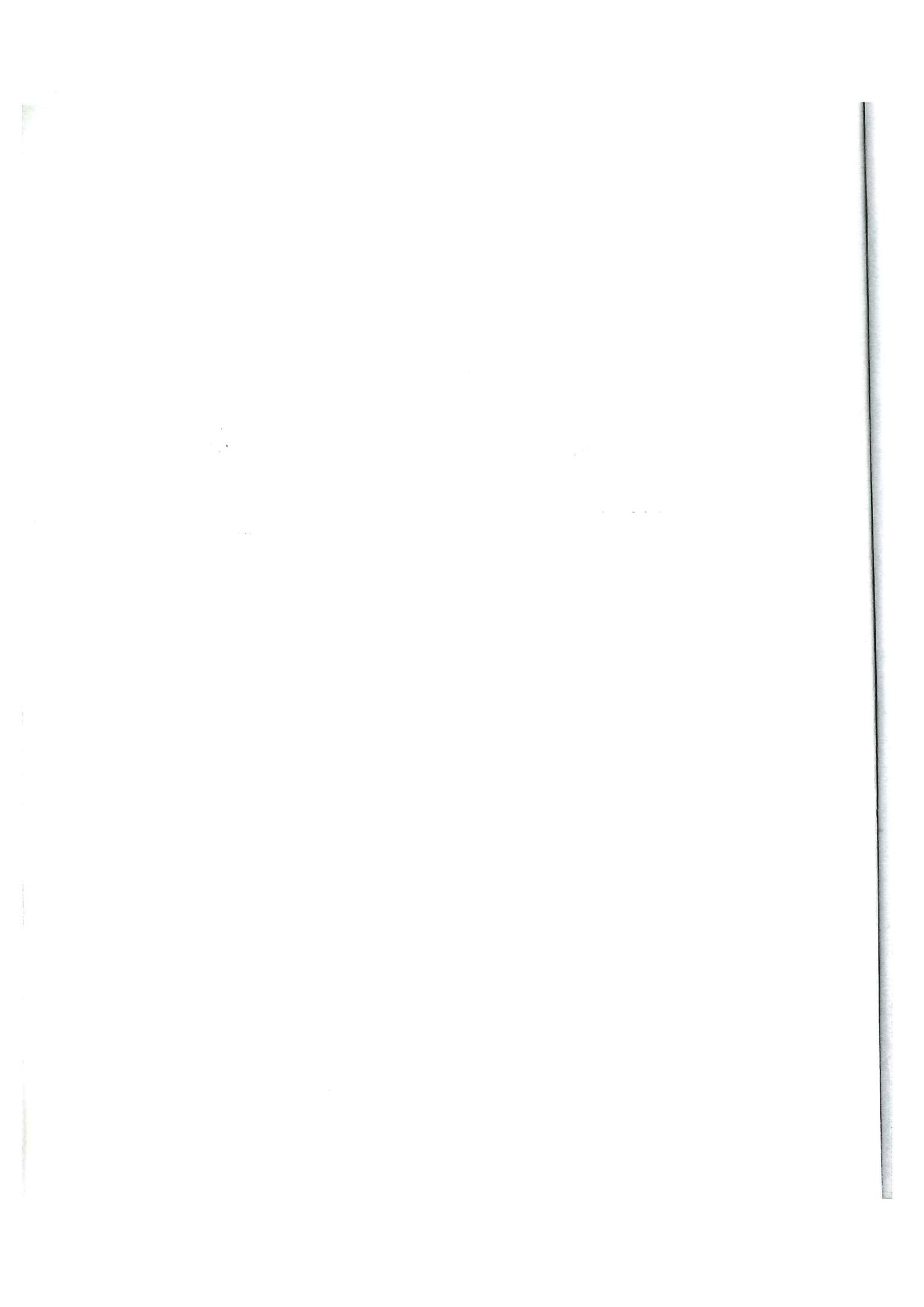


Plate 9. Cf. *Palaechthon woodi*, NMMNH No. P-15684, anterior part of right mandible. Scale bars are 5 mm.
A, B. Stereophotographs of oblique mesiolabial views.
C. Lingual view.
D. Labial view.



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