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THIERRY SMITH¹, JONATHAN I. BLOCH², SUZANNE G. STRAIT³,
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Abstract — The earliest Eocene of North America (Wa-0) is well sampled but mammals of small body size are still poorly known. Here we describe the upper and lower cheek teeth of a new species of the insectivore *Macrocranium*, *M. junnei*. This is the oldest species of the genus known in North America. *M. junnei* shares many similarities with *M. vandebroeki* from Dormaal in Belgium, a locality close to the Paleocene-Eocene boundary in Europe. Cladistic analysis of *Macrocranium* from North America and Europe suggests that *M. junnei* was slightly more derived than *M. vandebroeki* in having a somewhat reduced metastylar lobe on P⁴ (as does later occurring *M. nitens* from North America). *Macrocranium* may have originated in Europe, with *M. vandebroeki* emigrating west to give rise to *M. junnei* in North America. The latter then gave rise to *M. nitens* and *M. robinsoni* in the early and middle Eocene of North America.

INTRODUCTION

Amphilemuridae is an Eocene radiation of erinaceomorph insectivores with no known modern representatives. *Placentidens* Russell and Savage 1973, *Amphilemur* Heller 1935, *Pholidocercus* von Koenigswald and Storch 1983, and *Gesneropithec* Hürzeler 1946 are amphilemurids from the early through late Eocene of Europe. *Macrocranium* Weitzel 1949 is an amphilemurid from the early through middle Eocene of both Europe and North America (McKenna and Bell, 1997).

Study of virtually complete skeletons of *Macrocranium tupaiodon* Weitzel 1949 and *M. tenerum* (Tobien 1962) from the middle Eocene of Messel (Germany) show that they were slender forest-floor-dwellers with saltatorial specializations (Storch, 1993, 1996). *M. tupaiodon* was about 16 cm in head-to-body length, a specialized cursor, and an omnivore, possibly with a preference for fish. *M. tenerum* was a small and gracile animal of 9 cm head-to-body length, truly bipedal and

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occasionally ricochetel, with an insectivorous diet probably composed of ants (Storch, 1996). *M. tenerum* was a hedgehog-like insectivore and, as in living hedgehogs, its body was covered with spines (Storch, 1993; Storch and Richter, 1994).

The earliest *Macrocranion* known to date, *M. vandebroeki*, is known only from northern Europe (Dormaal, Paleocene-Eocene transition of Belgium), based on upper and lower cheek teeth (Smith and Smith, 1995). Study of the tarsal bones of *M. vandebroeki* (Godinot et al., 1996) indicates that it was cursorial like *M. tenerum*.

The new *Macrocranion* species described here from the Eocene of North America is a virtual contemporary of *M. vandebroeki*. It is the most common small mammal in screen-washed samples. Specimens are from University of Michigan locality SC-67 from northern Bighorn Basin (Gingerich, 1989, 2001) and University of California locality V99019 from southeastern Bighorn Basin (Strait, 2001; Holroyd et al., 2001). Discovery of *M. junnei* is important because it contributes new information about intercontinental migrations of mammals at the Paleocene/Eocene boundary.

INSTITUTIONAL ABBREVIATIONS

AMNH	— American Museum of Natural History, New York (U.S.A.)
HLMD Me	— Hessisches Landmuseum, Darmstadt (Germany)
IRSNB	— Institut Royal des Sciences Naturelles de Belgique, Bruxelles (Belgium)
SMF	— Senckenberg-Museum, Frankfurt am Main (Germany)
UCMP	— University of California Museum of Paleontology, Berkeley (U.S.A.)
UM	— University of Michigan Museum of Paleontology, Ann Arbor (U.S.A.)
USGS	— United States Geological Survey, Denver (U.S.A.)
USNM	— United States National Museum, Washington (U.S.A.)

SYSTEMATIC PALEONTOLOGY

Order LIPOTYPHILA Haeckel, 1866
 Suborder ERINACEOMORPHA Gregory, 1910
 Family AMPHILEMURIDAE Hill, 1953
 Subfamily AMPHILEMURINAE Hill, 1953
Macrocranion Weitzel, 1949

Macrocranion junnei, new species

Figs. 1-3

Holotype.— UM 93378, right maxilla with P⁴-M³.

Type locality and horizon.— Willwood Formation in locality SC-67 at the south end of Polecat Bench, southern part of the NW 1/4, NE 1/4, Section 10, Township 55 North, Range 100 West, Park County, northern Bighorn Basin, Wyoming (Elk Basin SW Quadrangle; see Gingerich, 1989, 2001).

Referred specimens.— Seventy-six dental specimens described as *Macrocranion* sp. from Castle Gardens (UCMP locality V99019 or USGS locality D2018), Township 46 North, Range 89 West, Washakie County, southeastern Bighorn Basin, Wyoming (see Strait, 2001, p. 133).

Age and distribution.— *Macrocranion junnei* is known only from the earliest Wasatchian (Wa-0), in northwestern Wyoming.

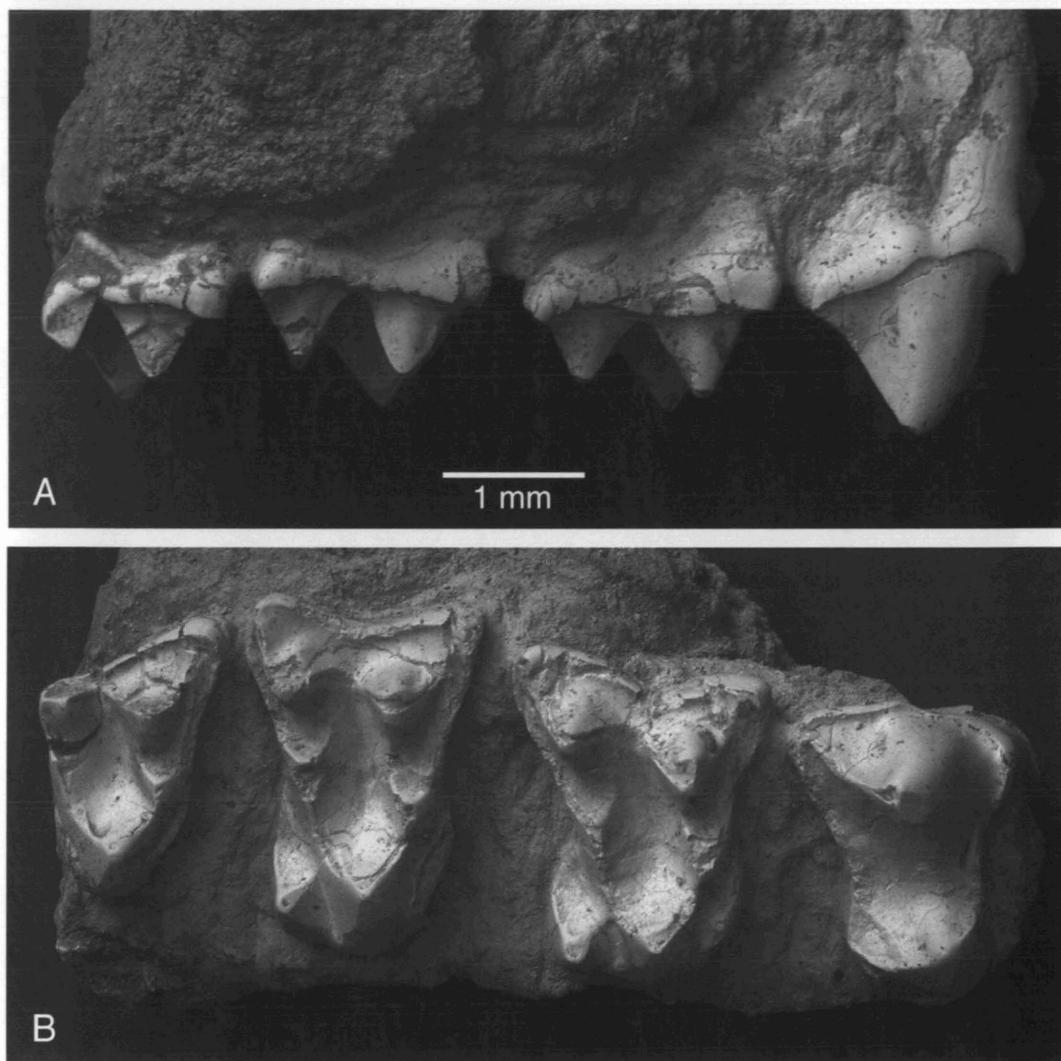


FIG. 1 — *Macrocranion junnei*, new species, scanning electron micrograph of right maxilla with P⁴-M³ (UM 93378, holotype). A, labial; and B, occlusal views. Scale bar equals 1 mm.

Diagnosis.— Small species of *Macrocranion* similar in morphology and size to *M. vandebroeki* but differs from this species in having a more reduced metastylar lobe and a less anteriorly projecting parastylar lobe on P⁴ (as in *M. nitens*), and in having the metaconid more posterior on the P₄ and lower molars; *M. junnei* (like *M. vandebroeki*), differs from later species of *Macrocranion* in having a deeper ectoflexus on the upper molars, a shorter M², and a more expanded parastylar lobe on M³.

Etymology.— Named for George H. Junne, who has collected many mammalian specimens from SC-67, including the type specimen of *Macrocranion junnei*.

Description.— The holotype (UM 93378) is represented by a substantial piece of a right maxilla with P⁴-M³ (Fig. 1A-B, 2A-B). P⁴ is premolariform with no metacone. The paracone is large and projects much farther than that of M¹. The labial border is relatively flat and short. The parastylar lobe is relatively short, rounded, with a weak parastylar cusp present. The metastylar lobe is somewhat posteriorly expanded and joined to the top of the paracone by a crest.

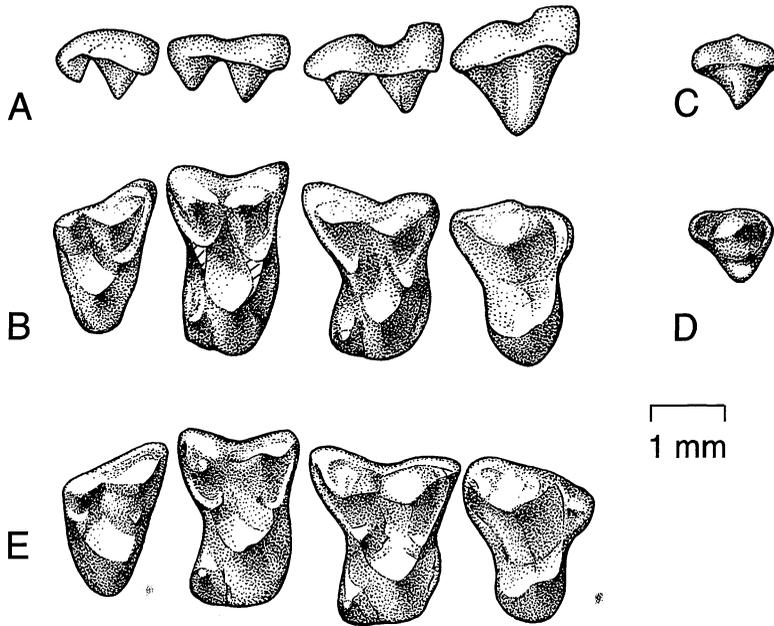


FIG. 2 — Upper teeth of *Macrocranion junnei*, new species, compared to those of *Macrocranion vandebroeki* from Dormaal, Belgium. A-B, *M. junnei* holotype, right maxilla with P⁴-M³ (UM 93378) from Polecat Bench, in labial and occlusal views. C-D, *M. junnei*, right P³ (UCMP 212484) from the earliest Wasatchian (Wa-0) of Castle Gardens in northwestern Wyoming, in labial and occlusal views. E, *Macrocranion vandebroeki*, composite right maxillary dentition with P⁴-M³ (IRSNB M1804, P⁴; M1806, M¹; M1807, M²; M1808, M³, reversed), in occlusal view.

M¹ shows distinct connate cusps, with moderately developed para- and metastylar lobes projecting anterolabially and posterolabially, respectively. The labial shelf is relatively short, with a distinct ectoflexus. The paracone is slightly larger and higher than the metacone. A connate hypocone is completely separated from the protocone.

M² is anteroposteriorly shorter, with a deeper ectoflexus than that on M¹, and it is more or less equal in width to M¹. The para- and metastylar lobes project more labially. As on M¹, a small crest joins the hypocone to the posterior side of the protocone.

M³ has a semitriangular form with a moderately long parastylar lobe. The protocone is somewhat compressed anteroposteriorly, making the labial border to the tooth almost pointed. The metaconule is worn.

Among the referred specimens, a small P³ (UCMP 212484) is present (Fig. 2C-D). The principal cusp has the same aspect as the protocone of P⁴, but it is smaller and lower. The posterior and lingual borders of the tooth are developed in two lobes.

A fragment of lower jaw (UCMP 212532) preserves the left P₄-M₁ (Fig. 3A-B). The P₄ is premolariform, with a dominant protoconid and a very small metaconid. The metaconid is situated posteriorly in comparison to the protoconid. The talonid is short but wide. The talonid basin is very small and positioned lingually relative to the trigonid.

M₁ (UCMP 212532 and 212595) is somewhat exodaenodont. The trigonid is not much higher than the talonid. The paraconid is low. Prolongation of the paralophid forms a crest that is perpendicular to the lingual border of the tooth. The metaconid is posteriorly positioned in comparison to the protoconid. The talonid is slightly longer and wider than the trigonid. The hypoconulid is small, low, and not very distinct on the posterior border of the tooth.

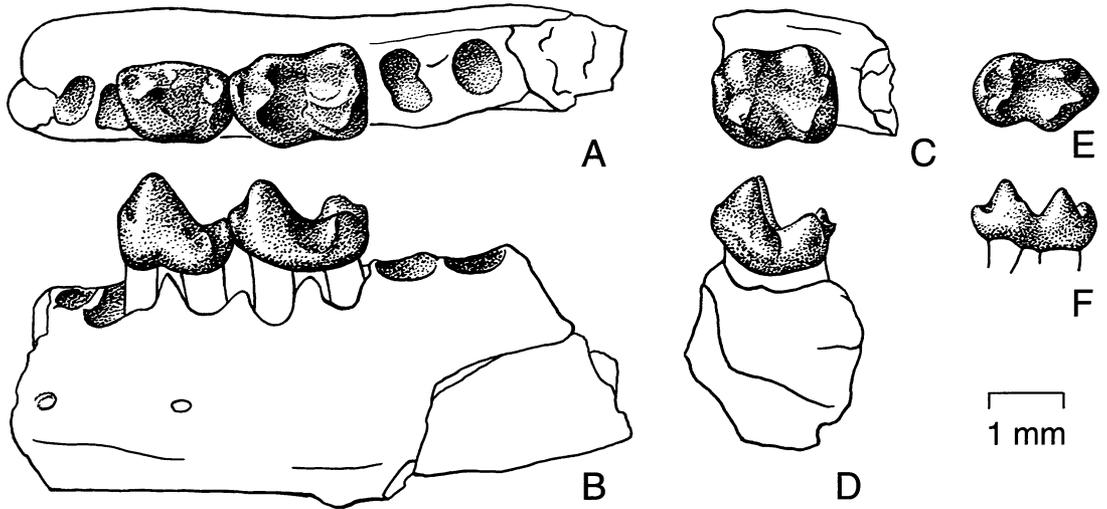


FIG. 3 — Lower teeth of *Macrocranium junnei*, new species, from Castle Gardens. A-B, left dentary with P_4 - M_1 (UCMP 212532), in occlusal and labial views. C-D, fragment of left dentary with M_2 (UCMP 212575), in occlusal and labial views. E-F, left M_3 (UCMP 212811, reversed), in occlusal and labial views.

M_2 (UCMP 212575, Fig. 3C-D) is relatively similar to M_1 , but the crown is more square in occlusal view. The protoconid and metaconid are somewhat more separated than on M_1 . The talonid is approximately equal in width to the trigonid.

M_3 (UCMP 212811, Fig. 3E-F) is narrower than M_{1-2} . The talonid is clearly longer than the trigonid. The hypoconulid is well developed and positioned slightly lingually relative to the trigonid.

Measurements of teeth in the holotype are listed in Table 1. Other measurements of upper and lower teeth are given by Strait (2001: 135, table 5). The weight of *Macrocranium junnei* is estimated to have been about 24 grams based on M^1 size, using an equation developed for prediction of body mass for insectivorous mammals (Bloch et al., 1998, p. 826).

COMPARISONS

Macrocranium junnei has many of the derived erinaceomorph characters mentioned by Novacek et al. (1985), including a premolariform P^4 (lacking a metacone), M^{1-2} with a narrow styler shelf and distinct hypocone, the talonid on M_1 as wide or wider than trigonids, and presence of a small hypoconulid on M_{1-2} . It is attributed to the family Amphilemuridae because it has a weaker hypocone on M^{1-2} and retains a larger M^3 than is seen in Erinaceidae.

Comparison of the Wa-0 taxon with the different genera of the subfamily Amphilemurinae (*Placentidens*, *Amphilemur*, *Pholidocercus*, *Gesneropithex*, and *Macrocranium*) indicates that it belongs to the genus *Macrocranium* because it has unreduced para- and metastylar lobes on M^{1-2} , semirectangular M^{1-2} , and connate or sectorial molar cusps. *Macrocranium* is presently considered to be the most primitive of the Amphilemuridae.

Macrocranium junnei differs from the type-species, *M. tupaiodon* Weitzel 1949 from Messel (HLMD Me 11, 515 and 4403, early Lutetian, MP11, early middle Eocene, Germany) and Geiseltal Untere-Mittelkhole (middle Lutetian, MP12, middle Eocene, Germany), in being very much smaller (*M. tupaiodon* is 75% larger) and having molar cusps that are more sectorial and proportionally smaller. The molar cusps of *M. tupaiodon* are much more bulbous. The para- and metastylar lobes

TABLE 1 — Measurements of upper teeth in the type specimen of *Macrocranium junnei*, UM 93378, from Wa-0 locality SC-67. Measurements in mm.

Measurement	P ⁴	M ¹	M ²	M ³
Length	1.45	1.70	1.50	1.25
Width	1.95	2.15	2.25	1.80

are more expanded, and the hypocone is less developed in known American species. These primitive characteristics are more typical of *M. tenerum* (Tobien 1962) from Messel (HLMD Me 1288, early Lutetian, MP11, early middle Eocene, Germany), but the latter is still 30% larger, the hypocone is also more developed, the M¹⁻² are more quadrate because of reduction of labial styler lobes, and the hypoconulid is more lingually situated with the presence of a distinct postcingulum on lower molars.

M. junnei has some primitive similarities with *M. nitens* (Matthew 1918) from the Willwood Formation (e.g., USNM 495248 from McNeil Quarry, Wa-4, early Eocene, Wyoming; see Silcox and Rose, 2001), such as non-reduced styler lobes on the upper molars and anteroposteriorly constricted protocones on M¹⁻². These two species also share a derived characteristic: the P⁴ is somewhat reduced at the level of the labial border. *M. junnei* differs from *M. nitens* (holotype AMNH 15697 and specimen USGS 3676) in having M¹ longer than M², while the talonid on M₁₋₂ is narrower.

M. junnei is similar in morphology and size to *M. vandebroeki* (Quinet 1964) from Dormaal (specimens IRSNB M1804, M1806-1808, Tienen Formation, MP7, Paleocene-Eocene transition, Belgium; see Smith and Smith, 1995). In fact, most of the characteristics shared by *M. junnei* and *M. vandebroeki* that are not present in the other species are primitive: a deeper ectoflexus on the upper molars, a shorter M², and a more expanded parastylar lobe on M³ (Fig. 2B, E). Only one character indicates that *M. junnei* is more derived: the reduced metastylar lobe on P⁴, like those in *M. nitens* and *M. tupaiodon*. Other small differences exist between *M. junnei* and *M. vandebroeki*. For example, the M² is somewhat wider, and the protocone is slightly more anteroposteriorly compressed on M¹⁻² of the holotype of *M. junnei* than it is in *M. vandebroeki*. These differences are minor, like the differences between specimens of *M. junnei* from Polecat Bench and Castle Gardens. Teeth of *M. junnei* from Castle Gardens are somewhat smaller, and the M² is narrower than observed in the holotype. These differences are attributed to intraspecific variability.

M. robinsoni Krishtalka and Setoguchi 1977 from Bad Water Creek area (Wagonbed Formation, late Uintan, late middle Eocene, Wyoming) seems to be related to *M. nitens* because of the presence of wide talonids on lower molars, but it is more derived in having greater reduction of M₃.

In discussing the biochronologic and biogeographic implications of insectivores from the Paleocene-Eocene transition in Belgium, Smith (1997b) suggested that *Macrocranium vandebroeki* from Dormaal might share a close relationship with early Wasatchian *Macrocranium nitens* from western North America. He hypothesized that *M. vandebroeki* might have given rise to middle Eocene *Macrocranium tenerum* in Europe, and *M. nitens* might have given rise to *Macrocranium robinsoni* in the middle Eocene of North America. Together with similar evidence from two other insectivore groups, Smith (1997b) argued that the vertebrate fauna from Dormaal was most similar to that of the Paleocene-Eocene transition in North America.

CLADISTIC ANALYSIS

In order to help resolve the phylogenetic relationships among some species of European and North American *Macrocranium*, we performed a cladistic analysis of 14 characteristics of 7

TABLE 2 — Description of characters used in phylogenetic analyses. Outgroup taxa were *Leptacodon tener* and *Adunator lehmani*. The cladistic analysis used *Leptacodon* to root the preferred cladogram. All characters except characters 3 and 9 were unordered. Autapomorphic characters were excluded from the analysis.

1.	P ³ small to moderate, triangular (0), or very small, peglike or triangular (1)
2.	P ⁴ metacone present (0), or absent (1)
3.	P ⁴ with expanded parastylar lobe(0), somewhat reduced parastylar lobe (1), or parastylar lobe very reduced (2)
4.	P ⁴ metastylar lobe prominent (0), or somewhat reduced (1)
5.	P ⁴ postcingulum present (0), or absent (1)
6.	M ¹ longer than M ² (0), or M ² equal in length to M ¹ (1)
7.	M ¹⁻² protocone anteroposteriorly constricted (0), or enlarged (1)
8.	M ¹⁻² hypocones small (0), or moderate to very large (1)
9.	M ¹⁻² stylar lobes well-developed (0), moderately developed (1), or reduced (2)
10.	M ² deep ectoflexus (0), or shallower ectoflexus (1)
11.	M ³ parastylar lobe prominent (0), somewhat reduced (1), or very reduced (2)
12.	P ₃ double-rooted (0), or single-rooted (1)
13.	M ₁₋₃ trigonid high relative to the talonid (0), or lower relative to the talonid (1)
14.	M ₁₋₂ talonid equal in width to the trigonid (0), or wider than trigonid (1)

TABLE 3 — Character matrix used for phylogenetic analyses. Characters that are not known for a particular taxon or too ambiguous to code are treated as missing ('?')

Taxon	Character number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Leptacodon tener</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Adunator lehmani</i>	0	0	0	0	0	0	1	1	2	0	2	0	0	0
<i>Macrocranium nitens</i>	0	1	1	1	1	1	0	1	1	1	1	1	1	1
<i>Macrocranium junnei</i>	0	1	1	1	1	0	0	1	1	0	0	?	1	0
<i>Macrocranium vandebroeki</i>	?	1	1	0	1	0	0	1	1	0	0	1	1	0
<i>Macrocranium tenerum</i>	1	1	?	?	?	1	1	1	2	1	?	1	1	1
<i>Macrocranium tupaiodon</i>	1	1	2	1	1	1	1	1	2	1	1	1	1	1

lipotyphlan taxa (Tables 2 and 3), using PAUP version 3.1.1 (Swofford, 1993). Our analysis included 5 of the known species of *Macrocranium*, and the primitive erinaceomorph *Adunator lehmani* Russell 1964 from Walbeck (specimens SMF 84/3-13, MP6, late Paleocene, Germany). The primitive soricomorph lipotyphlan *Leptacodon tener* Matthew and Granger 1921 from Mason Pocket (specimen AMNH 17179; Tiffanian, late Paleocene, Colorado; see McKenna, 1968) was used to root the analysis because it is old geologically, it is well known from upper and lower dentitions, and it may have been close to the ancestry of Soricomorpha (Butler, 1988), the sister group to the Erinaceomorpha. Thus, it probably retains many of the characteristics primitive to both groups. *Macrocranium robinsoni* Krishtalka and Setoguchi 1977 and *Macrocranium germonpreae* Smith 1997 were excluded from the analysis because they are known only from lower molars.

Morphology was assessed through a review of the literature (Tobien, 1962; McKenna, 1968; Krishtalka, 1976; Novacek et al., 1985; Smith and Smith, 1995; Silcox and Rose, 2001; Storch and Lister, 1985) and study of casts in the UM, IRSNB, and USGS collections. All characters

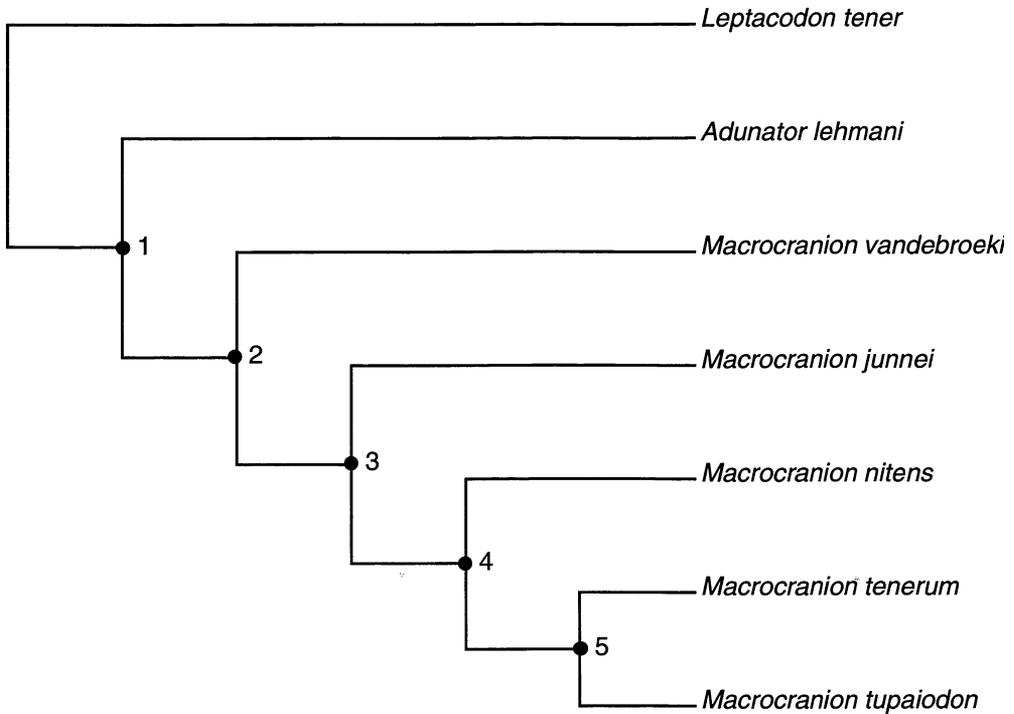


FIG. 4—Hypotheses of phylogenetic relationship among select European and North American *Macrocranium* based on dental characteristics (Tables 2 and 3). Cladistic analysis using a branch-and-bound algorithm (Swofford, 1993) rooted with *Leptacodon* yields a single most-parsimonious cladogram with tree length = 19, consistency index = 0.90, and retention index = 0.90. All characters except 3 and 9 were unordered. Unambiguous synapomorphies supporting each node are as follows (change is from 0 to 1 for binary characters; state indicated for multistate characters): node 1 (Erinaceomorpha)—8; node 2 (*Macrocranium*)—2, 3(1), 5, 9(1), 12, 13; node 3—4; node 4—6, 10, 11(1), 14; node 5—1, 7, 9(2).

analyzed are dental because cranial and postcranial remains are rare or unknown for most of the relevant taxa (although see Storch, 1993, 1996). Some multistate characters (Tables 2 and 3; characters 3 and 9) are ordered, on the assumption that these characters changed in a stepwise manner; all other characters are unordered. Autapomorphic characters known to be present in only one taxon are excluded from the analysis, except in the case of some multistate characters.

An exhaustive search involving all 14 morphological characteristics yielded a single most-parsimonious cladogram (tree length = 19, consistency index = 0.90, retention index = 0.90). This cladogram (Fig. 4) has the five *Macrocranium* species in a monophyletic clade, with *Adunator* as its sister group. Belgian *M. vandebroeki* is the sister taxon to the clade of remaining *Macrocranium* species. New species *M. junnei* from the earliest Wasatchian of North America is the sister group to the *M. nitens* (*M. tenerum* (*M. tupaiodon*)) clade. *Macrocranium nitens* is the sister taxon to the European *M. tenerum* (*M. tupaiodon*) clade. In this analysis, the clade that includes all the species of *Macrocranium* is supported by the following six synapomorphies: 2(1), P⁴ metacone absent; 3(1), P⁴ with a somewhat reduced parastylar lobe; 5(1), P⁴ with no postcingulum; 9(1), M¹⁻² stylar lobes moderately developed; 12(1), P₃ single-rooted; 13(1), M₁₋₃ trigonid low relative to the talonid. A somewhat reduced metastylar lobe on P⁴ (character 4, state 1) suggests that the new species *M. junnei* is slightly more derived than *M. vandebroeki*.

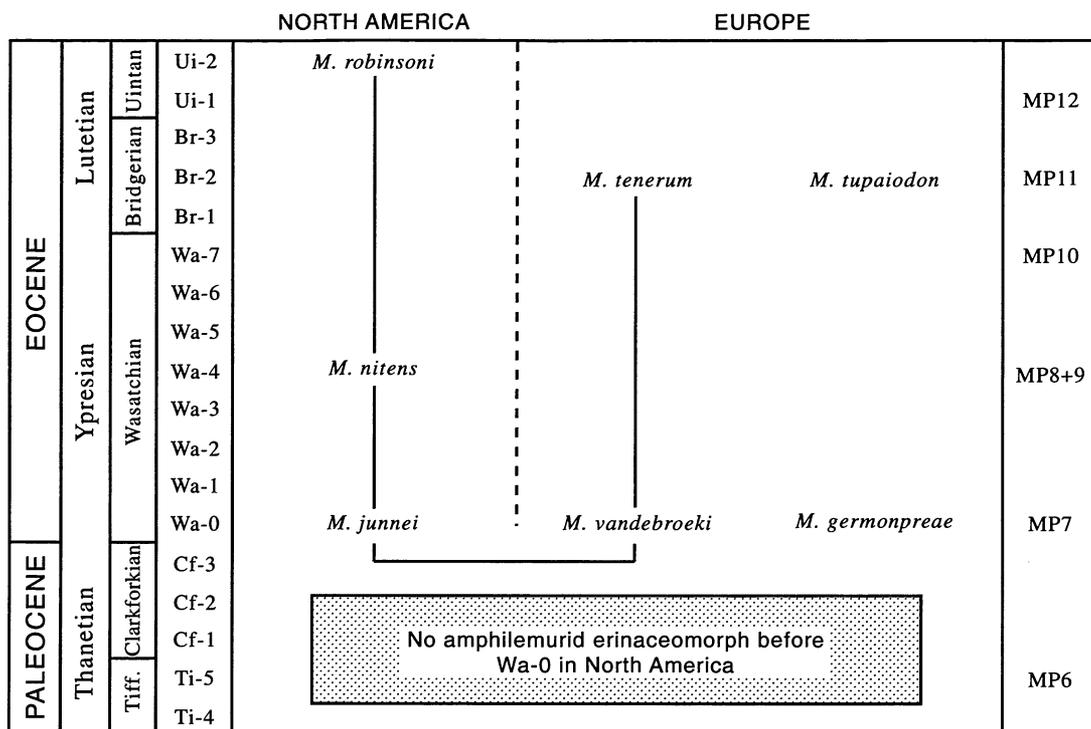


FIG. 5 — Spatial and temporal distribution of *Macrocranium* species in North America and Europe that appear to have phylogenetic relationships with the new species *M. junnei*. Lines connect closely related species. MP intervals are reference levels in the European Paleogene mammalian biochronology (see Schmidt-Kittler, 1987).

DISCUSSION

Of the five known genera of Amphilemuridae, four are restricted to northern Europe. None is present in southern Europe, and only *Macrocranium* is found in both North America and northern Europe. *Macrocranium* is present in many Wasatchian localities but its specific diversity seems to have been low. Until now, only *M. nitens* and *M. robinsoni* were known from North America and the relationships between the different species of *Macrocranium* have been difficult to resolve, particularly at the paleobiogeographic level.

The presence of common genera in America, Europe and Asia early in the Cenozoic has inspired several authors to formulate hypothesis of intercontinental dispersal (Depéret, 1905, 1908; Osborn, 1910; Simpson, 1947; Russell, 1968; McKenna, 1972; Gingerich, 1976, 1980, 1982, 1986; Godinot, 1982, 1996; Smith, 2000; Smith and Smith, 2002). Discovery of *M. junnei* in the earliest Wasatchian of Wyoming, closely related to *M. vandebroeki* from Belgium but slightly more derived, suggests that *Macrocranium* may have originated in Europe, with *M. vandebroeki* possibly dispersing westward across a land bridge via Greenland to give rise to *M. junnei* in the earliest Eocene of North America (Fig. 5).

The idea that some North American modern mammalian groups could have come from Europe at the Paleocene/Eocene boundary (see Gingerich, 1976; Godinot, 1982) was put to the test by the discovery of the Wa-0 fauna from North America, which seemed to show that some forms must have migrated from North America to Europe (Gingerich, 1989). Recent excavations in Dormaal have allowed for the recovery of more than 7000 specimens (mostly isolated teeth) of mammals

(see Smith and Smith, 1996; Steurbaut et al., 1999). Many of these are closely related to North American Wa-0 specimens (Smith, 1999, 2000, 2002). The soricomorph insectivores *Leptacodon* and *Wyonycteris* described first in North America are also present in Dormaal (Smith, 1995, 1996, 1997b). However, these taxa are known from the Paleocene in North America and they are also present in southern Europe. *Macrocranion* is unknown in the Paleocene of North America and Europe, and is unknown in the Paleocene and Eocene of southern Europe. It seems to have arrived in both Europe and North America as part of the wave of immigration at the Paleocene-Eocene boundary that included artiodactyls, perissodactyls, primates and hyaenodontid creodonts.

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