

***Arcticanodon dawsonae*, a primitive new palaeanodont from the lower Eocene of Ellesmere Island, Canadian High Arctic**

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Abstract: A new genus and species of palaeanodont, *Arcticanodon dawsonae*, is based on a single lower jaw fragment from lower Eocene (Wasatchian) strata of the Margaret Formation, Eureka Sound Group, on central Ellesmere Island, Nunavut. The new taxon is more derived than early Paleocene Escavadodontidae, but lacks derived traits of Metacheiromyidae. It is therefore most similar to primitive epoicotheriids, although the similarities are essentially in plesiomorphic features. Consequently, *Arcticanodon dawsonae* is classified as Palaeanodonta, incertae sedis, pending discovery of more complete specimens.

Résumé : Un nouveau genre et une nouvelle espèce de Palaeanodonta, *Arcticanodon dawsonae*, est basé sur un seul fragment de mandibule inférieure provenant des strates de la Formation de Margaret (Éocène inférieur - Wasatchien), du Groupe d'Eureka Sound, au centre de l'île d'Ellesmere, au Nunavut. Le nouveau taxon est plus dérivé que Escavadodontidae du Paléocène précoce, mais il ne présente pas les traits dérivés de Metacheiromyidae. Il ressemble donc plus aux époicotheriidés primitifs, bien que les similitudes se présentent surtout dans les caractéristiques plésiomorphiques. Par conséquent, *Arcticanodon dawsonae* est classé en tant que Palaeanodonta, incertae sedis, en attendant la découverte de spécimens plus complets.

[Traduit par la Rédaction]

Introduction

Palaeanodonts are an extinct group of small, fossorial, early Tertiary placental mammals. They are best known from the early Paleocene to late Eocene (Puercan–Chadronian North American land mammal ages (NALMAs)) of western North America and have also been reported from the early Oligocene and questionably from the early Eocene of Europe, as well as from the early Eocene of China. The skeleton of palaeanodonts is specialized for digging, and the dentition is typically reduced in various ways (such as size and (or) number of teeth and cusp pattern). These characteristics make palaeanodonts anatomically similar to extant xenarthrans (especially armadillos) and pholidotans (pangolins or scaly anteaters), to one or both of which they are often considered related. However, palaeanodonts lack the key diagnostic traits of both Xenarthra and Pholidota and have their own specialized features, factors which have contributed to their uncertain phylogenetic position. Nevertheless, it seems probable that palaeanodonts occupied a similar ecological niche to that inhabited broadly by armadillos and pangolins. The more generalized members were terrestrial diggers with omnivorous–insectivorous diets, whereas more derived types had much reduced dentitions and probably fed mainly on ants and

termites. The most derived palaeanodonts were small, subterranean, mole-like forms.

Here we report the northernmost record of palaeanodonts and the first palaeanodont fossil from Eocene strata of the Eureka Sound Group on Ellesmere Island. It represents a new taxon and is based upon a jaw discovered in 2001 at locality (loc.) 76–85 (= CMN loc. P7502), a site near Bay Fiord (Fig. 1). Locality 76–85 was formerly known simply as loc. 85 (see Dawson 2001; Eberle and McKenna 2002). To date, representatives of some 30 vertebrate families are documented from Eureka Sound Group strata in the Bay Fiord area (Eberle and McKenna 2002).

The diverse faunal assemblages of the Eureka Sound Group corroborate long-standing paleobotanical evidence for a mild Arctic climate during Eocene time (Estes and Hutchison 1980; McKenna 1980). Additionally, they support previous hypotheses relating to Eocene paleogeography of the North Atlantic region, specifically the existence of a late Paleocene to earliest Eocene land corridor connecting Europe to North America (Marincovich et al. 1990).

Geologic setting

Although its strata were first recognized in the late 1800s

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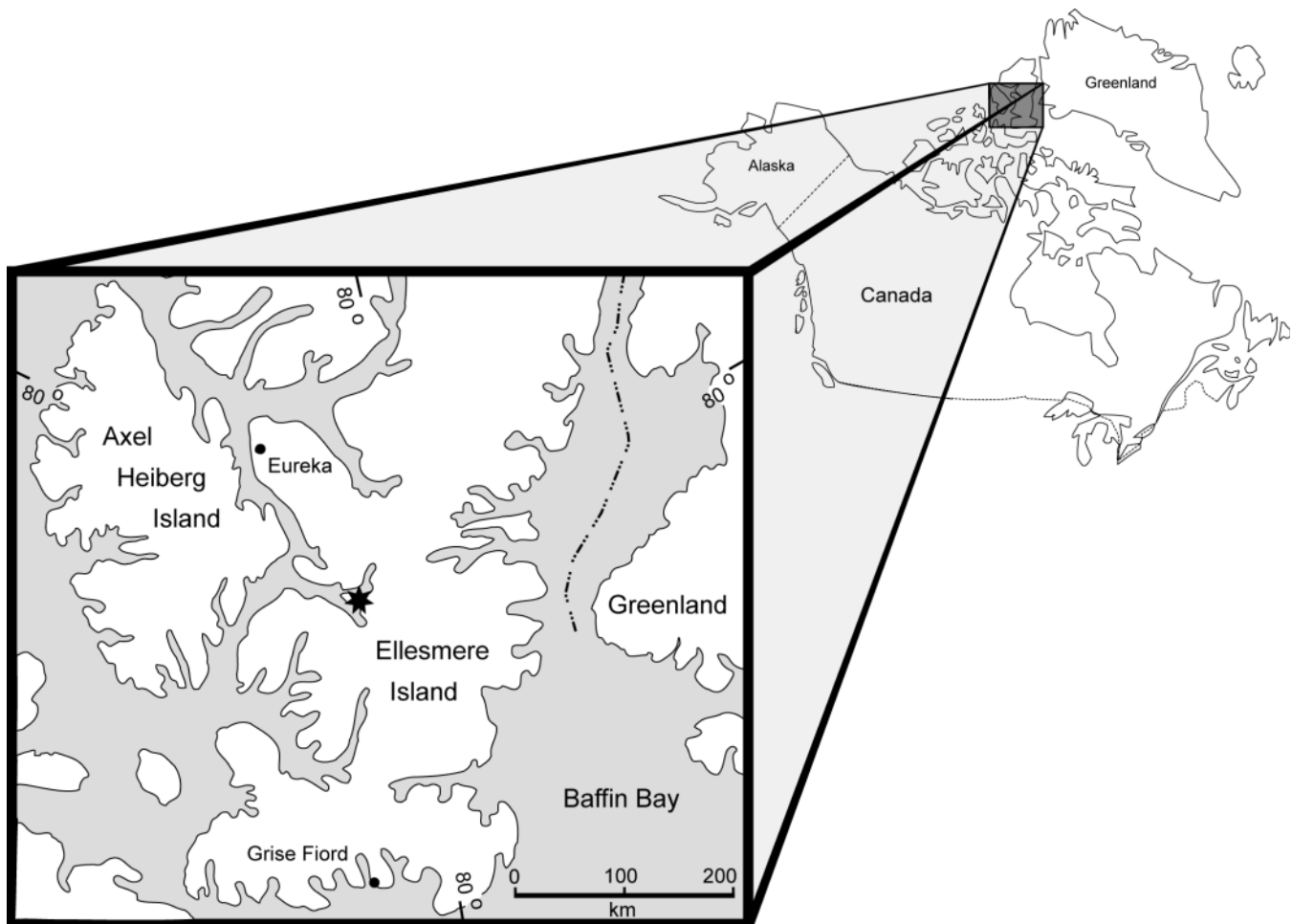
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Fig. 1. Map of Axel Heiberg and Ellesmere Islands, Nunavut territory. Star indicates general location of terrestrial vertebrate-bearing localities of the Margaret Formation, Eureka Sound Group near Bay Fiord.



(Feilden and de Rance 1878; Greely 1888), the Eureka Sound Group was named in 1950 for “deposits of sandstone, shale, and lignite that are younger than the last orogeny” (Troelsen 1950). Tozer (1963) reduced the Eureka Sound Group to formational rank. Since then, three sets of names have been applied to the strata of the Eureka Sound Group. Following discovery of fossil vertebrates in the Bay Fiord region of central Ellesmere Island (West et al. 1975; Dawson et al. 1976), West et al. (1981) proposed four informal members for the Eureka Sound Formation of Ellesmere Island, the uppermost (i.e., Member IV) of which contained Eocene nonmarine vertebrates. Independent of one another, Ricketts (1986) and Miall (1986) each returned the Eureka Sound Formation to group rank, and divided it into numerous formations. Consequently and confusingly, the Eocene, nonmarine vertebrate-bearing rocks near Bay Fiord fall under three different names: Member IV of West et al. (1981), Miall’s (1986) Margaret Formation, and the Iceberg Bay Formation of Ricketts (1986). Based upon recent publications and maps (e.g., Okulitch 1991), the general consensus is that the Eureka Sound is a group that can be divided into numerous formations. Here we adopt Miall’s nomenclature in referring the Eocene nonmarine vertebrate-bearing strata near Bay Fiord to the Margaret Formation.

Eocene terrestrial vertebrates occur in two stratigraphic levels in the Margaret Formation near Bay Fiord (West et al. 1981; Dawson 1990, 2001; Dawson et al. 1993). The diverse vertebrate fauna from the lower faunal level, which includes fish, amphibians, reptiles, birds, and over 20 mammalian genera (see Eberle and McKenna 2002, table 1), indicates an early Eocene age, equivalent to the younger part of the Wasatchian NALMA (West et al. 1981; Dawson et al. 1993). Although the vertebrate fauna from the upper stratigraphic level is considerably less diverse, it has been interpreted as early middle Eocene in age, equivalent to the Bridgerian NALMA (McKenna 1980; West et al. 1981; Dawson 1990; Dawson et al. 1993). Palynology supports an early–middle Eocene age range for the Margaret Formation near Bay Fiord (Norris and Miall 1984).

Many fossil vertebrate localities near Bay Fiord initially and tentatively were tied into Miall’s (1986) stratigraphic section 77-71 (J.H. Hutchison, personal communication to JJE, 2003). However, few of these data have been published (e.g., see Eberle and McKenna 2002). Recent identification in the field of most vertebrate localities, and ongoing correlation to seven detailed stratigraphic sections measured by C. Lee, place nearly all vertebrate localities in the Bay Fiord area within stratigraphic context. Locality 76-85 is within

the lower stratigraphic level and contains a Wasatchian faunal assemblage.

The lithology of the Margaret Formation, supported by the fauna and flora, indicates a lush proximal delta front to delta plain environment, with abundant channels and coal swamps (Miall 1986).

Materials and methods

The specimen described in “Systematic paleontology” was recovered through surface-collecting of loc. 76-85 in 2001, and is housed at the Canadian Museum of Nature in Ottawa, Ontario, Canada. Discovered in 1976, loc. 76-85 is the most productive screening locality in the Margaret Formation near Bay Fiord (M.R. Dawson, personal communication to JJE, 2001). Approximately 500 pounds of matrix from this locality was screen-washed, but no other palaeodont remains have been recovered.

Institutional abbreviations

CMN	Canadian Museum of Nature, Ottawa, Ontario.
NUFV	Fossil vertebrate specimen that is the property of Nunavut Territory, but is currently housed at the CMN
USGS	United States Geological Survey (Denver) collection, now housed at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
YPM-PU	Princeton University collection, housed at Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Dental terminology

i, c, p, m, designate, respectively, incisor, canine, premolar, and molar.

Lower-case letters with numbers (e.g., m1) designate mandibular teeth.

Systematic paleontology

?Order Pholidota Weber, 1904

Suborder Palaeanodonta Matthew, 1918, incertae sedis

Arcticanodon dawsonae, gen. et sp. nov.

HOLOTYPE: NUFV 10 (= CMN 51389), left dentary with canine, root of incisor, and alveoli for p2–p4, m1–m2; collected by J.J. Eberle, July 2001 (only known specimen).

LOCALITY: Locality 76-85 (= CMN loc. P7502), Bay Fiord, central Ellesmere Island, Nunavut, Arctic Canada; Margaret Formation, Eureka Sound Group, lower Eocene (Wasatchian).

DIAGNOSIS: Small palaeodont with six postcanine teeth: p2–p3 one-rooted, p4, and m1–m2 clearly double-rooted (m3 root number unknown); teeth closely spaced except for short diastema between canine and p2. Slightly larger than half the size of *Tubulodon* (= *Alocodontulum* and *Pentapassalus*). Differs from *Tubulodon* in having relatively larger p2–p3, no diastema around p3, and distinctly double-rooted m2. Differs from *Escavadodon*, *Amelotabes*, and *Auroratherium* in lacking p1, and in root configuration of postcanines. Further differs

Table 1. Measurements (mm) of holotype dentary of *Arcticanodon dawsonae*, NUFV 10.

Dentary:	Length from anterior border of incisor to posterior edge of m2 alveolus) = 11.0
	Depth below m1 (buccal) = 2.65
Breadth:	At p3 = 1.7
	At back of p4 = 2.0
	At back of m1 = 2.3
	At back of m2 = 2.6
Incisor root:	Anteroposterior (AP) diameter = 0.8
	Mediolateral (ML) diameter = 0.6
Canine base	AP × ML = 1.8 × 1.2
p2 alveolus	AP × ML = 0.9 × 0.75
p3 alveolus	AP × ML = 1.0 × 0.7
p4:	Total alveolar length = 1.7
	Anterior alveolus AP × ML = 0.8 × 0.65
	Posterior alveolus AP × ML = 0.85 × 0.8
m1:	Total alveolar length = 1.55
	Anterior alveolus AP × ML = 0.65 × 0.95
	Posterior alveolus AP × ML = 0.85 × 1.0
m2:	Total alveolar length = 1.55
	Anterior alveolus AP × ML = 0.7 × 1.0
	Posterior alveolus AP × ML = 0.8 × 1.0

from *Escavadodon* in having relatively more robust dentary and from *Amelotabes* in having teeth behind p2 more closely spaced. Differs from metacheiromyids in having closely spaced, relatively larger postcanines, presumably with more complex crowns.

ETYMOLOGY: Greek *arktikos*, northern; *an-*, without; and *odous*, *odon*, tooth; in reference to occurrence and in analogy with other palaeodont generic names. Species name honors Mary R. Dawson, pioneer of exploration in the Eureka Sound Group, eminent paleontologist, and esteemed friend and colleague.

DESCRIPTION: NUFV 10, the holotype dentary (Figs. 2, 3, Table 1), although edentulous except for the canine, unequivocally represents a palaeodont, as indicated by the shape of the canine and the shallow, robust ramus, which broadens posteriorly. It resembles primitive epiocotheriids in having relatively unreduced postcanine teeth and ovoid postcanine alveoli. The dentary of *Arcticanodon* is most similar to that of *Tubulodon* (which includes the genera *Pentapassalus* and *Alocodontulum*; see Rose in press), but is only about half the size of representatives of that genus from the Western Interior.

The most distinctive aspect of the dentary is the gradual thickening posteriorly, with the posterior alveoli shifted slightly lingual to the mid-longitudinal axis, such that the buccal alveolar border is thicker than the lingual border. This alveolar arrangement most closely approaches that in the holotype (and only known specimen, YPM-PU 14855) of *Amelotabes simpsoni*, which has been considered to be the most primitive epiocotheriid. As a result of this arrangement, the medial buttress is not very evident on the preserved section of the jaw and probably was less pronounced than in *Tubulodon*, in which it is smaller and more anterior than in *Palaeanodon*.

Nevertheless, the posterior broadening of the jaw indicates that a medial buttress was present. As in other palaeonodonts, the plane of the alveoli exhibits gentle torsion, associated with torsion of the dentary itself, so that when the posterior alveoli face dorsally the anterior alveoli flare somewhat laterally. Torsion of the dentary is more conspicuous in *Arcticanodon* than in other palaeonodonts. As the dentary is missing behind m2, it is impossible to determine if teeth were present more or less all the way to the coronoid process, as in most epoicotheriids, but this seems highly probable. A single mental foramen is present below the anterior root of p4. In *Tubulodon*, there are two mental foramina: a small foramen below p4 and a larger one below the front of p3.

The lower dental formula is i1.c1.p3.m3. Just in front of the canine is a root for a small, relatively vertical incisor, presumably the only incisor, as in other palaeonodonts. The canine is short and stout and roughly triangular in cross-section. The anterolateral surface is somewhat rounded, the anteromedial surface flatter, and the posterior surface worn flat by honing against the front of the upper canine. This canine morphology is characteristic of palaeonodonts. The bone at the base of the dentary is broken away behind the canine, revealing the root of this tooth, which bends sharply (at about a right angle) within the jaw. Lower canines of *Palaeonodon* (e.g., USGS 5896 and USGS 21876) are sharply bent in the same way. A short diastema separates the canine and p2 and is the only gap in the dental series.

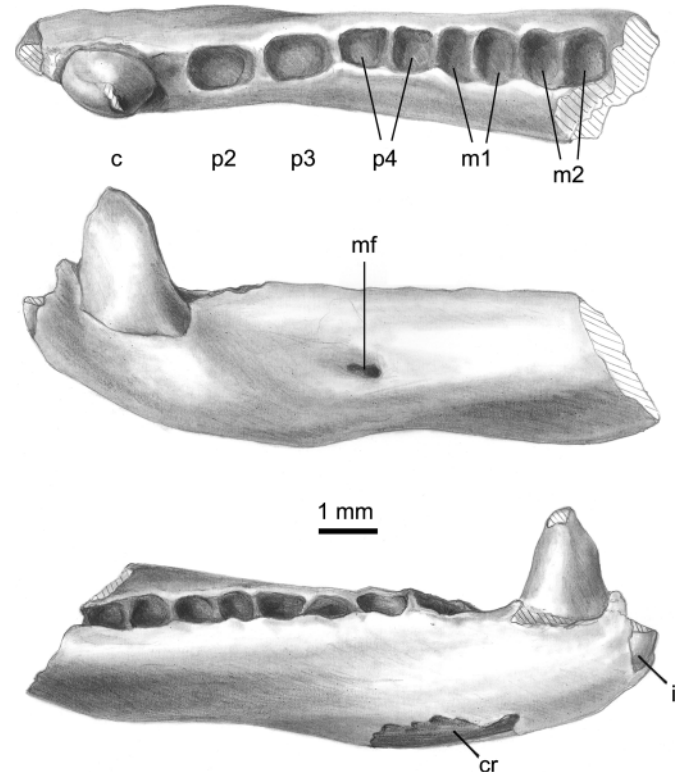
Behind the canine there are alveoli for six postcanine teeth. The first two are ovoid sockets of approximately equal size, which, by analogy with *Tubulodon*, held p2 and p3. They are larger than the anterior alveolus of p4 and longer in mesiodistal diameter than the posterior alveolus of p4 (although slightly narrower). This contrasts with *Tubulodon*, in which the root of p2 is distinctly smaller than either of those for p4, and the root of p3 is about the calibre of the smaller, anterior root of p4. The p4 was two-rooted, and its alveoli are slightly longer but narrower than those for the molars, as in some specimens of *Tubulodon*. The anterior alveolus is smaller than the posterior one. The alveoli for m1 and m2 are ovoid and of similar size. A septum within the alveolus divides each into roughly equal anterior and posterior compartments, as in m1 of *Tubulodon*. The roots of m2 seem to be more completely divided than those of *Tubulodon*. Although the dentary is broken behind m2, the mesial border of the m3 alveolus can be discerned, thus demonstrating the presence of six postcanines.

Discussion

Because of their dental reduction, palaeonodont postcanine teeth evidently were not strongly rooted in the jaw; consequently their dentaries are commonly found with postcanines missing. Nonetheless, palaeonodont dentaries, including that of *Arcticanodon*, present several distinctive features discussed in the description that allow confident identification. Foremost of these, with respect to palaeonodont affinity, is the short, robust canine in association with a shallow dentary, which thickens posteriorly and exhibits slight torsion.

In number and relative size of postcanine alveoli, *Arcticanodon* resembles the Wasatchian epoicotheriid *Tubulodon* more closely than any other palaeonodont, although much of the resemblance is plesiomorphic. They are the only palae-

Fig. 2. Holotype dentary of *Arcticanodon dawsonae*, gen. et sp. nov., NUFV 10, in dorsal, lateral, and medial views. Lower canine and alveoli for premolars and molars are indicated. See "Dental terminology" for abbreviations. Also cr, canine root; i, incisor root; mf, mental foramen.

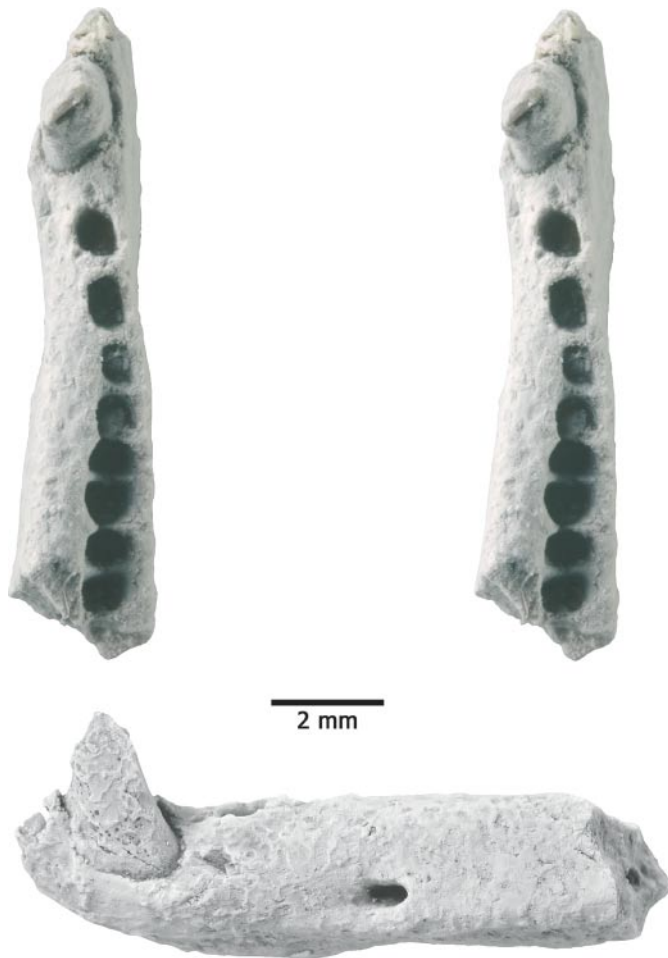


anodonts known to have had six relatively unreduced lower postcanines. Reduction to six postcanines is derived relative to Paleocene *Escavadodon* and *Amelotabes* from western North America, each of which has seven unreduced postcanines. The early Eocene epoicotheriid *Auroratherium* from China, with seven relatively unreduced postcanines (primitive compared with *Arcticanodon*), is more derived than the two Paleocene genera in its degenerate crown morphology, and may be derived compared with *Arcticanodon* in having the molar roots fused (Tong and Wang 1997). Tiffanian *Propalaeonodon*, the most primitive metacheiromyid, is plesiomorphic in retaining seven postcanines. However, it is more derived than *Arcticanodon* in having smaller, simpler postcanines separated by short diastemata — a synapomorphy of metacheiromyids, indicating that Metacheiromyidae had diverged from epoicotheriids by late in the Tiffanian (Rose 1979).

Like *Arcticanodon*, the recently described Tiffanian metacheiromyid *Mylanodon* also had six postcanine teeth. However, the teeth of *Mylanodon*, like those of *Propalaeonodon*, are relatively smaller and separated by short diastemata, and there is an edentulous region behind the last tooth, suggesting that m3 has been lost (Secord et al. 2002). Only p4 and m1 of *Mylanodon* are two-rooted. Like *Palaeonodon*, *Mylanodon* has a well developed medial buttress, a metacheiromyid characteristic.

Arcticanodon is clearly more primitive than the derived epoicotheriids *Tetrapassalus*, *Epoicotherium*, *Xenocranium*, and *Molaetherium* (as well as the more problematic *Dipassalus*

Fig. 3. Holotype of *Arcticanodon dawsonae*, gen. et sp. nov., NUFV 10, in dorsal (stereophotographs) and lateral views.



and *Brachianodon*) in retaining more and relatively larger postcanines. Epoicotheriids were dentally more conservative than contemporary metacheiromyids, retaining more postcanines that were often larger and more complex than those of metacheiromyids. At the same time, epoicotheriids whose postcranial skeletons are known have more fossorially specialized skeletons than do contemporary metacheiromyids.

These comparisons suggest that *Arcticanodon* could be a primitive epoicothere. However, as aforementioned, the resemblances to primitive epoicotheres generally, and *Tubulodon* in particular, are for the most part primitive traits that appeared early in palaeanodont evolution (but subsequent to *Escavadodon*). The dental characters were further modified in Metacheiromyidae, excluding *Arcticanodon* from that family. *Arcticanodon* is similar to *Tubulodon* in lacking p1, but this is not a very compelling character, as it is well known that tooth loss is often a homoplasy. Its importance would be enhanced if it were to be confirmed (as evidence suggests) that metacheiromyids lost teeth at the back of the tooth row, while epoicotheriids lost teeth at the front of the postcanine series. Even so, this would not rule out independent loss of p1 in a separate lineage of primitive palaeanodonts. Parsimony analyses (using Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.1; Swofford 1993) were undertaken on 38 dental, gnathic, and postcranial characters of *Arcticanodon*, 12 genera

of palaeanodonts (excluding *Molaetherium* and *Mylanodon*), and two outgroups (Pantolestidae and Leptictidae). Another analysis was run using only the 15 dental and gnathic features, 12 of which could be scored in *Arcticanodon*. In both instances, the 50% majority rule consensus of equally most parsimonious trees left *Arcticanodon* unresolved among all taxa in the sample. For these reasons, we conservatively leave *Arcticanodon* as incertae sedis within Palaeanodonta.

Paleobiogeographic implications

Until twenty years ago, palaeanodonts appeared to be an endemic North American radiation. Heissig (1982) described the first Old World palaeanodont, which he referred to the North American genus *Epoicotherium*, based on an edentulous dentary fragment from the lower Oligocene of Germany. More recently, Storch and Rummel (1999) described another jaw and a humerus of the same taxon, for which they proposed the new name *Molaetherium heissigi*. Like Heissig's specimen, the new fossils came from lower Oligocene beds just above the "Grande Coupure." The new specimens, while reinforcing the striking similarity to *Epoicotherium*, underscore the biogeographic dilemma posed by these fossils. It is difficult in any case to imagine dispersal of such a highly specialized subterranean mammal from western North America to Europe, but the situation is complicated by the fact that the appearance of both taxa postdates the disruption of the North Atlantic land bridge (McKenna 1983; Marincovich et al. 1990).

In 1997, Tong and Wang described *Auroratherium*, based on a skull and mandible from the lower Eocene of Wutu, China. This primitive epoicotheriid is structurally intermediate between *Amelotabes* and *Tubulodon*. Based in part on this discovery, Storch and Rummel (1999) postulated that palaeanodonts probably originated in Asia rather than North America, and dispersed to North America and Europe from there. Specifically, they proposed that *Molaetherium* and *Epoicotherium* "were part of an extensive interchange of Holarctic faunas when very similar groups of mammals appeared both on the North American and European continent; most of them must have been derived from Asian sources". (Storch and Rummel 1999, p. 184).

This scenario would be possible, perhaps even likely, if European palaeanodonts were restricted to the early Oligocene; however, other possible European palaeanodonts and close relatives of palaeanodonts are known from older strata. The middle Eocene genera *Eomanis* (considered a basal pholidotan; Storch 1978) and *Eurotamandua* (described as an anteater; Storch 1981) bear closer resemblance to North American palaeanodonts, such as *Metacheiromys*, than to either pholidotes or anteaters, suggesting that they might actually be derived palaeanodonts (Rose and Emry 1993; Rose 1999). Recently Nel et al. (1999) reported the presence of "cf. Edentata, gen., sp. indet." from the lower Eocene of France. This, too, seems likely to be a palaeanodont.

That palaeanodonts with probable North American affinity were present in Europe in the Eocene and early Oligocene, together with the presence of a new, primitive epoicotheriid on Ellesmere Island, revives the plausibility of either a North American or an Asian source for European palaeanodonts. China may be east of Eden (Beard 1998), but North America is east of China.

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