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A new 'tapir' from Ellesmere Island, Arctic Canada — Implications for northern high latitude palaeobiogeography and tapir palaeobiology

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Abstract

The oldest and northernmost record of the tapir lineage, *Thuliadanta mayri* gen. et sp. nov. from Ellesmere Island, Arctic Canada (78°50′N) implies that tapiroid evolution was well underway by early Eocene (Wasatchian) time in northern high latitudes, and raises the possibility of a North American origin for the group. Phylogenetic analyses place the new Arctic tapir as the sister group to the later more advanced *Desmatotherium*, *Colodon*, and *Irdinolophus*. A phylogenetically-derived biogeographic reconstruction posed here suggests the tapir lineage may represent a rare instance of counterflow wherein an exotic North American taxon invaded Asia during the early Eocene. Moreover, *Thuliadanta* seems a plausible ancestor to *Desmatotherium* from both continents, suggesting that this branch of the tapir lineage may have originated at high latitudes and subsequently dispersed from there to mid-latitudes. *Thuliadanta*'s occurrence on Ellesmere Island indicates that northern high latitudes should also be evaluated as a potential source area for some of the exotic taxa appearing in mid-latitudes during Eocene time. Using today's tapirs, and specifically the mountain tapir, as analogs, *Thuliadanta* seems a plausible year-round inhabitant in the mild temperate lowland forests of the Eocene High Arctic.
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1. Introduction

Tapirs and their more immediate extinct relatives (i.e., Superfamily Tapiroidea) are an ancient group of perissodactyls or odd-toed ungulates characterized by the presence of an enlarged narial incision that is typically associated with a short, fleshy proboscis (Hooker, 1989; Colbert and Schoch, 1998). Today's tapirs are tropical in distribution (MacDonald, 1987). Here, I document an early Eocene High Arctic 'tapir' from the Eureka Sound Group in the Canadian High Arctic, the oldest and northernmost known record of the lineage. Discovered on expeditions to Ellesmere

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Island in the 1970s–1980s, these fossils initially were tentatively identified on faunal lists as the rhinoceratoid *Hyrachyus* (e.g., Marincovich et al., 1990; Eberle and McKenna, 2002). However, detailed study (See Systematics section below) clearly distinguishes the High Arctic tapiroid from *Hyrachyus* and places it closer to middle Eocene tapiroids from both North America and Asia.

The early Eocene tapiroid-bearing strata of the Eureka Sound Group preserve the northernmost known record of early Tertiary mammals. The first fauna was discovered in 1975 on central Ellesmere Island (Dawson et al., 1976), with subsequent discoveries in the late 1970s–1990s in Eureka Sound Group strata elsewhere on Ellesmere Island and nearby Axel Heiberg Island (Dawson, 1990; Dawson et al., 1993; Eberle and Storer, 1999). In addition to fossil mammals, a diverse lower vertebrate fauna that includes

land tortoises, monitor lizards, snakes, and crocodilians strongly corroborates long-standing paleobotanical evidence for a mild temperate arctic climate during the Eocene (Estes and Hutchison, 1980; McKenna, 1980).

The High Arctic has long been considered as 'en route' for land animals dispersing across Holarctic continents during parts of the Paleogene when intercontinental connections were at high latitudes (McKenna, 1975, 1983, 2003; Marincovich et al., 1990). Moreover, Asia has been hypothesized as a likely source area for many advanced, exotic mammalian taxa that appeared in mid-latitude North America during Eocene time (Beard, 1998). Here, I show via a phylogenetically-derived biogeographic reconstruction that the tapir lineage may well represent a rare instance of 'counterflow,' wherein a North American taxon successfully invaded Asia during the Eocene. Moreover, the new
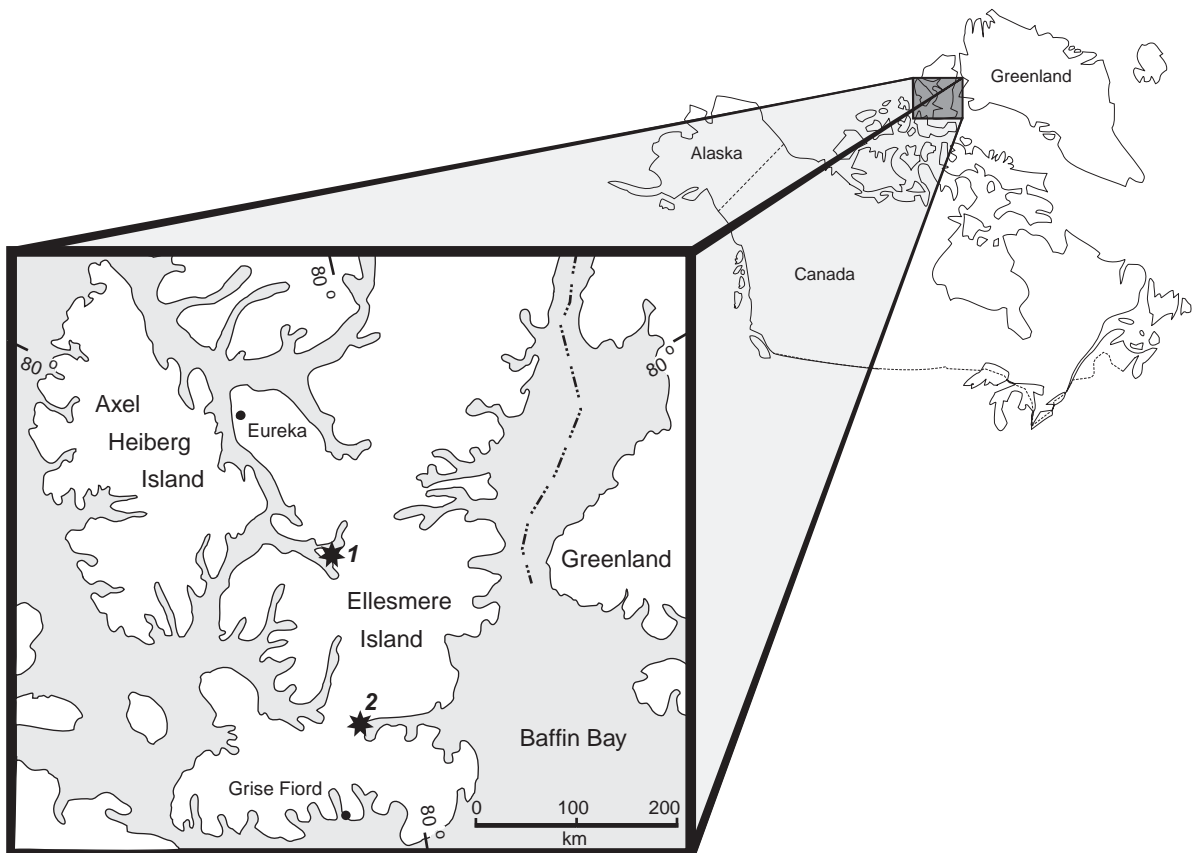

Fig. 1. Map of northernmost North America focusing on Ellesmere Island showing general locations of sites at which the Arctic tapiroid occurs. 1, Bay Fiord; 2, Swinnerton Peninsula.

High Arctic tapir suggests that tapiroid evolution was well underway at northern high latitudes prior to their mid-latitude appearance and raises the possibility of a high latitude origin for some tapir taxa and subsequent dispersal to mid-latitudes.

2. Geologic age and fauna

On central Ellesmere Island, Eocene terrestrial vertebrates occur in two stratigraphic levels in upper parts of the Eureka Sound Group, the lower of which contains the tapiroid. The diverse fauna from the lower level, comprising fish, amphibians, reptiles, birds, and over 20 mammalian taxa, indicates an early Eocene age, equivalent to the younger part of the Wasatchian North American Land Mammal Age (NALMA; West et al., 1981; Dawson et al., 1993; Eberle and McKenna, 2002). Specifically, Perissodactyla, Hyaenodontidae, *Pachyaena*, *Miacis* and cf. *Vulpavus*, all of which first appear at mid-latitudes in the Wasatchian, and *Anacodon*, which last appears in the Wasatchian (Robinson et al., 2004), are known from the lower faunal level in the Eureka Sound Group (Eberle and McKenna, 2002). Additionally, *Pachyaena* — index taxon for the Wasatchian — occurs in the lower faunal level, as do *Coryphodon*, *Paramys*, and *Viverravus* (Eberle and McKenna, 2002), all typical of the Wasatchian at mid-latitudes (Robinson et al., 2004).

The lithology of the terrestrial vertebrate-bearing strata of the Eureka Sound Group, supported by the fossil flora and fauna, indicates a lush proximal delta front to delta plain environment with abundant channels and lowland swamps (Miall, 1986).

3. Materials and methods

The six specimens of the new tapiroid diagnosed here were recovered in the 1970s and 1980s by field parties headed by the Carnegie Museum of Natural History. They reside in fossil collections at the Canadian Museum of Nature (CMN) in Ottawa. Most specimens are from localities in the Wasatchian-aged lower faunal level near Bay Fiord on central Ellesmere Island. However, one specimen is from correlative strata on Swinnerton Peninsula, southern Ellesmere Island (Fig. 1).

In describing the specimens, all of which are jaw fragments and teeth, I follow dental terminology outlined by Van Valen (1966). C, I, M, and P designate canine, incisor, molar, and premolar, respectively. Lower-case letters (e.g., m1) designate teeth from lower jaws, and upper-case letters (e.g., M1) teeth from upper jaws. L refers to a left tooth (e.g., Lm1), while R refers to a right tooth (e.g., Rm1).

Phylogenetic analyses use PAUP 3.1.1 (branch and bound method; see Swofford, 1993). Multistate characters were treated as unordered. Results are discussed below.

4. Systematic palaeontology

Class Mammalia

Order Perissodactyla Owen, 1848
Suborder Ceratomorpha Wood, 1937
Infraorder Tapiromorpha Haeckel, 1866
Superfamily Tapiroidea Burnett, 1830
Thuliadanta mayri gen. et sp. nov.

4.1. Etymology

Thule (Latin): farthest north; *danta* (Spanish): tapir; *mayri*: in honour of Ulrich Mayr, geologist for the Geological Survey of Canada (GSC) who led numerous expeditions responsible for mapping much of the Canadian Arctic.

4.2. Holotype

CMN 30804, right maxilla with P1 through M3, base of orbit and anterior part of zygomatic arch.

4.3. Type locality

Locality 76H7-10-3 (field #76-35), Eureka Sound Group, central Ellesmere Island, Nunavut, Canada (Wasatchian).

4.4. Referred specimens

CMN 30812, associated parts of upper and lower dentitions, including LP1, fragments of upper premolars, incomplete R and LM1, fragment of RM2, RM3

and labial fragment of LM3, broken incisor and L canine, right mandibular fragment with p3, p4, anterior base of m1, m2, and part of m3, left mandibular fragment with associated p1 to p4, trigonid of m1, m2, m3, plus associated enamel and bone fragments from Locality 76-60; CMN 30800, maxillary fragment with M1, M2, and incomplete M3 from Locality 76H7-10-1; CMN 32224, maxillary fragment with LM2, and bases of P3, P4, M1, and M3 from Locality Mck7/15/87-1; CMN 30801, juvenile L dentary with dp4, m1, base of m2, and unerupted m3, from Locality 76-49 (all preceding localities near Bay Fiord, Ellesmere Island); and CMN 32222, RP4 from Locality 84-8, Swinnerton Peninsula, Ellesmere Island.

4.5. Diagnosis

Medium-sized tapiroid about the size of *Desmatotherium intermedius* with narial incision comparable to that of *Helaletes nanus*; small canine and large postcanine diastema; differs from other tapiroids in lacking a metaloph on P3 and P4, although metaconule present; incipient hypocone on P4; as in *Colodon*, rectangular M1 and M2 (transverse width > length); upper molars with buccally-flattened, lingually-displaced metacone, although not so lingual as in *Colodon*; differs from other tapiroids in possessing p1; as in *Colodon*, p3 and p4 with relatively large entoconid, and talonid wider than trigonid; lower molars with small, narrow paralophid and reduced metalophid and entocristid; m3 with hypoconulid.

4.6. Description

The holotype (CMN 30804, Fig. 2), a right maxilla, indicates that *T. mayri* was comparable in size to the middle Eocene (Bridgerian) North American mid-latitude tapiroid *D. intermedius*. Although incomplete and damaged, the base of the narial incision seems to be present on CMN 30804 (see dashed line on Fig. 2a), and is comparable to that found in *H. nanus* wherein it extends backward to a point over the P3-P4 juncture, where it meets the ascending portion of the maxilla. While the latter is broken off of CMN 30804, the preserved morphology at its base suggests that the ascending portion of the maxilla would have extended vertically over the infraorbital foramen, as in *H. nanus*. Consequently, it is inferred that *T. mayri*

had an enlarged narial incision comparable to Bridgerian *H. nanus*, a feature that diagnoses Tapiroidea (Colbert and Schoch, 1998). As in other tapiroids, the infraorbital foramen on *T. mayri* is located above the P4-M1 juncture.

Thuliadanta bore a small canine and large postcanine diastema, as in *Helaletes* (see Radinsky, 1963). P1 is simple, with a large central cusp and a posterolingual shelf, whereas P2 is oval, with closely spaced, subequal para- and metacones and no hypocone. As in other tapiroids, the para- and metacones on premolars of *T. mayri* are laterally compressed, contrasting with the more rounded, conical cusps born on premolars of more primitive moropomorphs *Homogalax* and *Heptodon*. However, contrasting with other tapiroids, and more like that of *Homogalax*, *T. mayri* lacks a metaloph on P3 and P4, although a distinct swelling (i.e., metaconule) occurs directly lingual to the metacone. On CMN 32222, an unworn RP4 of *T. mayri* (See Fig. 2), a prominent metaconule occurs lingually, and connected via a short crista, to the base of the metacone, while a long, low, thin crista extends lingually to the apex of the protocone; this seems a plausible precursor to a metaloph. As in *H. nanus*, an incipient hypocone occurs on P4 of *T. mayri*. P3 and P4 of *T. mayri* have an ovate shape (with comparable labial and lingual lengths) as in *Desmatotherium*, *Colodon*, and *Irdinolophus*, and contrasting with *H. nanus,* which bears more triangular-shaped P3 and P4 (i.e., labial length > lingual length). As in *Colodon* (see Radinsky, 1963), M1 and M2 of *T. mayri* are relatively rectangular, with a transverse width noticeably greater than the length. As in other tapiroids, the metacone on upper molars of *T. mayri* is lingually-displaced relative to the paracone, although not so lingual as in *Colodon* and *Irdinolophus*. Contrasting with *Hyrachyus* (see Colbert and Schoch, 1998), but as in tapiroids, the ectocingulum labial to the metacone is well developed on *T. mayri*. As in other tapiroids, the M3 metacone is reduced and crestlike on *T. mayri*.

While the holotype CMN 30804 was initially tentatively identified on faunal lists as the rhinocerotoid *Hyrachyus* (e.g., Dawson, 1990; Marincovich et al., 1990), it differs from the latter in the development of its narial incision, more posterior placement of the infraorbital foramen, and more complex premolar morphology — specifically presence of an incipient
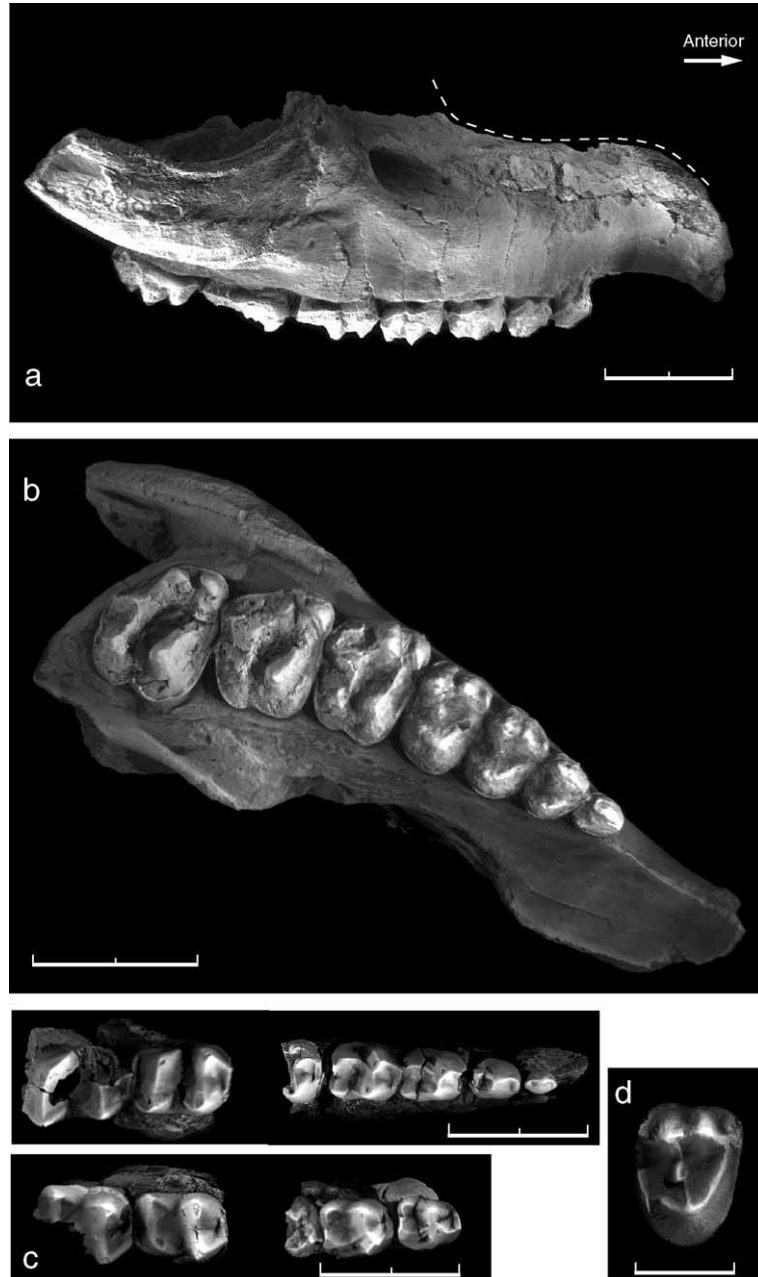
Fig. 2. *Thuliadanta mayri* gen. et sp. nov. (Canadian Museum of Nature). a and b, holotype CMN 30804 labial and occlusal views, respectively, of right maxillary with P1-M3. On a, white dashed line marks the inferred base of narial incision. c, CMN 30812, incomplete left and right lower dentitions with Lp1-p4, Lm1 fragment, Lm2-m3 and Rp3-p4, Rm1 fragment, Rm2, and partial m3. Scale bars for a–c equal 2 cm. d, CMN 32222, RP4; scale bar equals 1 cm.

hypocone on P3-P4 and a large entoconid on p3-p4. On upper molars of *Hyrachyus*, the ectocingulum is absent or narrow labial to the metacone, while on upper molars of *T. mayri* (as in other tapiroids), the ectocingulum is well developed and relatively wide labial to the metacone.

The lower dentition of CMN 30812 is referred to *T. mayri* because associated upper molars are virtually identical to those of the holotype (although the latter is more worn). Whereas other tapiroids lack p1, *T. mayri* has a tiny, simple p1 with a central cusp. The p2 of *T. mayri* bears a small metaconid, large hypoconid, and small entoconid. The p3 of *T. mayri* has a small, low paralophid, large metaconid, and, as in *Colodon* and *Irdinolophus,* a relatively large entoconid. The p4 also bears a large entoconid. Relatively narrower than *Colodon occidentalis*, lower molars of *T. mayri* bear a low, narrow paralophid, reduced metalophid and a low, subtle entocristid, resulting in a relatively open talonid valley (as opposed to the closed basin of *Homogalax*; see Radinsky, 1963). As in *C. occidentalis*, m1 and m2 of *T. mayri* bear a smooth, narrow posterior cingulid with no hypoconulid. The m3 of *T. mayri* appears to have born a hypoconulid, although this region is incomplete on the m3s of CMN 30812. However, an m3 talonid bearing a large hypoconulid was found nearby CMN 30812; its size and morphology suggest that it represents the same taxon.

5. Discussion

5.1. Relationships and palaeobiogeography

Phylogenetic analysis of primarily dental characters using PAUP 3.1.1 (branch and bound method; see Swofford, 1993) produced one maximum parsimony cladogram of 69 steps that places *T. mayri* as the sister group to later, more advanced tapiroids *D. intermedius*, *Irdinolophus mongoliensis*, and *C. occidentalis* (Fig. 3). This tree is also consistent with previous cladistic analyses that place *Irdinolophus* as the sister group to *C. occidentalis* (Colbert, 1999; Dashzeveg and Hooker, 1997).

Based primarily upon cranial characters relating to facial morphology, *C. occidentalis* recently has been placed within the Tapiridae (i.e., the family that includes today's tapirs) and close to extant *Tapirus* (Colbert, 1999, 2003). None of these cranial characters is preserved on *T. mayri*, given the incompleteness of the specimens. However, recent cladistic analyses also suggest that *D. intermedius* and *Irdinolophus* (both known primarily from dental material)
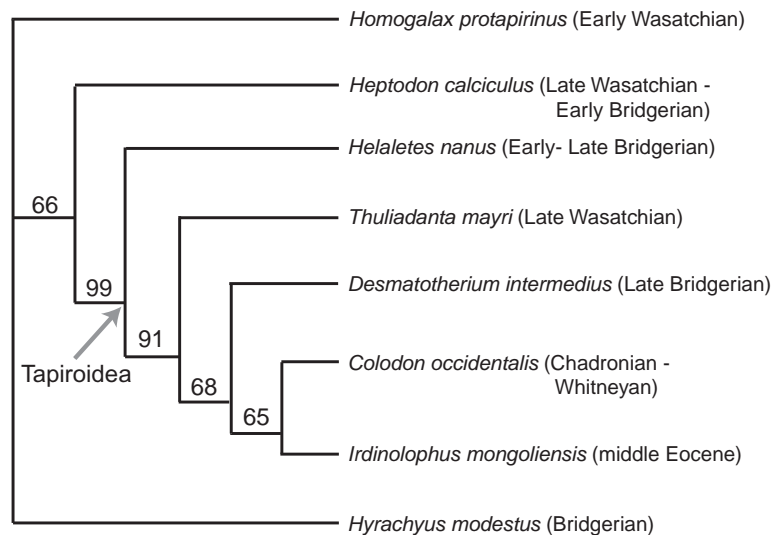

Fig. 3. Phylogenetic analysis of 33 primarily dental characters of eight taxa (see Supplementary Information) produced one maximum parsimony cladogram of 69 steps, with a consistency index of 0.754, homoplasy index of 0.290, and retention index of 0.726. All characters are parsimony informative, and multistate characters were treated as unordered. The basal moropomorph *Homogalax protapirinus* and the basal rhinocerotoid *Hyrachyus modestus* were used as outgroups. The key character uniting Tapiroidea is an enlarged narial incision (Colbert and Schoch, 1998). Numbers on branches represent the percentage of bootstrap values in 1000 bootstrap replicates for a 50% majority rule consensus tree. Geologic ages of taxa compiled from several sources (Dashzeveg and Hooker, 1997; Colbert and Schoch, 1998; Robinson et al., 2004, and references therein; McKenna and Bell, 1997 and references therein) are placed in brackets following the species name.

may also be within Tapiridae (see Colbert, 1999). Consequently, *Thuliadanta* appears to be either a very early tapir or an advanced tapiroid close to the ancestry of true tapirs. While *Heptodon* lacks an enlarged narial incision — the diagnostic character for Tapiroidea, it probably lies close to tapiroid ancestry, given its dental similarities to basal tapiroids such as *Helaletes* (Colbert, 1999; Colbert and Schoch, 1998).

Phylogenetically-derived biogeographic reconstructions to determine the origin of a clade rely on the idea that sister taxa originated in the same geographic area, and ideally should be compatible with other datasets, such as the fossil record and geologic history of an area (Beard, 1998). Following methodology outlined by Beard (1998), I scored each tapiroid taxon for a biogeographic 'character' followed by a posteriori optimization of this character across interior nodes using MacClade. With exception of *Thuliadanta, Irdinolophus*, and possibly *Heptodon* (see discussion below), all of the genera included in the analysis are documented from both North America and Asia and would normally be scored as 'polymorphic', resulting in an ambiguous origin for the tapiroids. However, I scored the continent on which each genus first occurred, thereby making the assumption that the oldest occurrence represented the ancestral state. Results are shown in Fig. 4. While *Heptodon* is scored here as polymorphic based upon initial reports of its occurrence in roughly contempo-
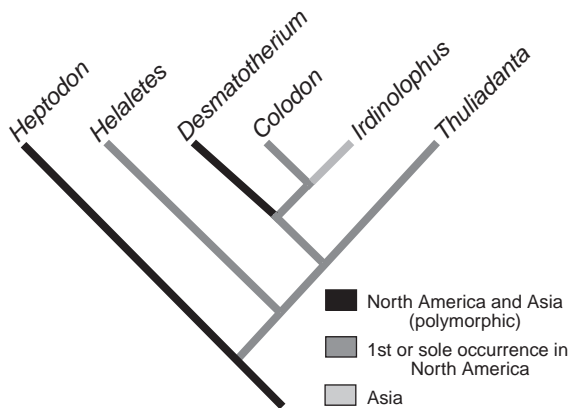

Fig. 4. Phylogenetically-derived paleobiogeographic reconstruction for *Heptodon* and tapiroids included in cladistic analysis. See text for discussion of results.

raneous strata in Asia (Ting, 1998 and references therein) and North America (Colbert and Schoch, 1998), there are ambiguities concerning the identification of the Asian specimens. Specifically, two species of *Heptodon* were reported from Asian Bumbanian-aged faunas (Chow and Li, 1965; Zhai, 1978), alternately correlated with latest Paleocene–earliest Eocene (i.e., late Clarkforkian–early Wasatchian; Beard, 1998) or early Eocene (i.e., late Wasatchian; Ting, 1998). However, their referral to *Heptodon* has been questioned, as they appear dentally more similar to the basal rhinocerotoid *Hyrachyus* (Dashzeveg and Hooker, 1997). If correct, these taxa would represent the earliest Asian occurrence of *Hyrachyus*. Other fragmentary material only tentatively referred to *Heptodon* is documented from Bumbanian faunas (Ting, 1998). Consequently and pending taxonomic revision of the Asian material, *Heptodon* (as based upon the type species *Heptodon calciculus*) may be solely North American.

According to phylogenetic theory, the most recent common ancestors of terminal taxa can be no younger than their descendants (Weishampel, 1996). Consequently, the most recent common ancestor of *Helaletes*, represented best by the early Bridgerian, most basally diverging tapiroid *H. nanus* (see Colbert and Schoch, 1998) and the branch leading to *Thuliadanta* and other tapiroids can be no younger than late Wasatchian (i.e., early Eocene). Since *Thuliadanta* is documented only from North America, while *Helalates* appears to be earlier in North America than Asia (see discussion below), the phylogenetically-derived biogeographic reconstruction posed here suggests that their common ancestor (and consequently the origin of the tapir lineage) also was North American. Wasatchian-aged, mid-latitude *Heptodon* seems too primitive to have given rise to *Thuliadanta*. However, since fossil tapiroids are generally rare, the common ancestor to *Helaletes* and *Thuliadanta* may be a North American ghost lineage whose fossils have yet to be discovered. Wasatchian faunas are well sampled in mid-latitude western North America, yet there are no documented tapiroids in these faunas (Robinson et al., 2004), which may suggest origination outside of this region. Wasatchian occurrence of *Thuliadanta* on Ellesmere Island implies that tapiroid evolution was well underway early on at northern

high latitudes, and raises the possibility of a high latitude origin for the group and subsequent dispersal from there to mid-latitudes.

Other source areas need also be considered. While the Eureka Sound faunal assemblages slightly postdate the land connection between Europe and North America across the North Atlantic, they nevertheless support the existence of such a corridor in that they contain numerous early Eocene genera that still persisted on both sides of the Atlantic (Marincovich et al., 1990; Eberle and McKenna, 2002; McKenna, 2003). However, the oldest documented European tapiroid appears to be *Protapirus* appearing in the early Oligocene (McKenna and Bell, 1997). While *Cymbalophus* from the early Eocene of Europe has been placed by some within Tapiroidea (e.g., McKenna and Bell, 1997), it is most likely a stem equoid (Hooker, 1994). Similarly, the Lophiodontidae, appearing in the early Eocene of Europe, are now considered the sister group to Chalicotheres (Hooker, 1989). Given its lack of early tapiroids, Europe seems an unlikely candidate for the group's origin.

Alternatively, given that Asia was connected to North America through most of Cenozoic time, was the larger landmass of the two, and is inferred to have had higher taxonomic diversity, Asia was probably the source of many exotic mammals appearing in mid-latitude North America during early and middle Eocene time (Beard, 1998). The hypothesized Asian immigrants, including perissodactyls, artiodactyls, primates, and hyaenodontid creodonts (Beard and Dawson, 1999), would have crossed via Beringia, which acted as a filter because it was considerably closer to the rotational North Pole than today (McKenna, 1983). While early tapiroids are rare in Asia, generic similarities corroborate faunal interchange between Asia and North America. The basal tapiroid *Helaletes* is known from Asia, but it appears to occur later there than in North America, which seems more consistent with the hypothesis that tapiroids originated in North America and subsequently dispersed to Asia, rather than the other way around. Specifically, two species of *Helaletes* were reported from Arshantan-aged strata of Inner Mongolia. While intercontinental biostratigraphic correlations are not all in agreement and more detailed geochronologic data for the Asian faunas are not yet available (Beard, 1998), most correlate the

Arshantan with the 'upper Bridger fauna' of North America or late Bridgerian (i.e., middle Eocene; Qi, 1987; Tong et al., 1995; McKenna and Bell, 1997). While one Arshantan species *Helaletes medius* seems similar to *H. nanus* in size and premolar morphology (Qi, 1987), the other species, *Helaletes fissus*, is more derived. Specifically, *H. fissus* bears premolars whose metalophs bypass the hypocones (Matthew and Granger, 1925; Radinsky, 1965), which is diagnostic for *Desmatotherium* (see Radinsky, 1963; Colbert and Schoch, 1998). Consequently, *H. fissus* is here tentatively transferred back to *Desmatotherium* following its initial identification (Matthew and Granger, 1925), despite others' tentative placement of it within *Colodon* (see Dashzeveg and Hooker, 1997). *Desmatotherium fissum* (=*H. fissus*) in the middle Eocene of Inner Mongolia appears roughly contemporaneous with the first North American appearance of *Desmatotherium*, the late Bridgerian *D. intermedius* (Schoch, 1989; Colbert and Schoch, 1998). *Thuliadanta*, on the basis of its dental anatomy, seems a plausible ancestor for mid-latitude *Desmatotherium* from both continents.

As a cautionary note, tapirs are rare in the fossil record, and it is possible that their absence from early Eocene mid-latitudes may reflect a sampling bias. Future sampling in appropriately-aged strata in North America, Europe, and Asia is needed to shed further light on tapir origins and early dispersal patterns.

5.2. Palaeoclimate, palaeoenvironment, and palaeobiology

Thuliadanta's appearance on central Ellesmere Island, which during Eocene time was well above the Arctic Circle (McKenna, 1980), raises many intriguing questions concerning tapiroid physiology and behavior, including their implied ability to withstand prolonged periods of continuous darkness (i.e., the Arctic winter). Today's tapirs are tropical in distribution (MacDonald, 1987). By analogy, *Thuliadanta*'s occurrence seems consistent with evidence from the fossil flora and lower vertebrate fauna (Estes and Hutchison, 1980; McKenna, 1980) as well as isotope analyses (Jahren and Sternberg, 2003; Fricke and Wing, 2004) for a mild, temperate,

moist arctic climate during the early and middle Eocene. Extensive, lowland forests of large *Metasequoia* (dawn redwood) trees, akin to today's cypress swamps in the southeastern United States, are represented by in situ fossil stumps and peaty litter in correlative Eureka Sound Group strata at nearby Strathcona Fiord (Francis, 1988). $\delta^{18}O$ values from fish vertebrae and tooth enamel of the pantodont *Coryphodon* from early Eocene strata on Ellesmere Island give an estimated atmospheric Mean Annual Temperature (MAT) of 4 °C (Fricke and Wing, 2004). Moreover, paleotemperature and relative humidity conditions predicted from isotope analyses of *Metasequoia* trees in slightly younger (i.e., middle Eocene) Eureka Sound Group strata on nearby Axel Heiberg Island suggest a 'seasonal rainforest' environment, similar to today's Pacific Northwest (Jahren and Sternberg, 2003). Today's closest ecologic analog of the Eureka Sound Group's lower vertebrate fauna is the 'austroriparian' region in the southeastern United States (Estes and Hutchison, 1980).

A plausible living analog to *Thuliadanta* may be the mountain tapir *Tapirus pinchaque*, which lives primarily above 2000 m in the wet cloud forests and paramo of the northern Andes in South America (Downer, 1996a,b). South American tapirs, including the mountain tapir, are thought to have descended from a common tapir ancestor that entered South America from Central America when the Isthmus of Panama formed about 3 Ma (Ashley et al., 1996; Downer, 2001). The high altitude habits of the mountain tapir probably evolved 2–3 Ma, with the rise of the Andes (Downer, 2001). Although equatorial, the Andean forest has a temperature range of 6–12 °C, but receives 2–4 m of precipitation annually, while temperatures on the shrubby paramo range from only 3–6 °C (Downer, 2001). Mountain tapirs prefer moist habitats, maneuver well through dense vegetation, and use their short trunks as an extra 'limb' for gathering food, bathing, defense, and orientation in the dark forest. Based upon the rock lithology and fossil flora, *Thuliadanta* probably lived in (or near) a densely vegetated, lowland forest on a proximal delta front to delta plain (Miall, 1986; Francis, 1988). Given its enlarged narial incision, *Thuliadanta* may have had a short trunk like today's tapirs, although more complete fossils are needed to determine this with certainty.

In contrast to the equatorial regions inhabited by today's tapirs, Ellesmere Island was well above the Arctic Circle during the Eocene (McKenna, 1980; Irving and Wynne, 1991). Assuming a spin axis tilt similar to today, the Eureka Sound Group vertebrate flora and fauna must have been adapted to months of continuous sunlight and darkness — the Arctic summer and winter, respectively. Deciduousness and pronounced tree rings indicate that the trees metabolically shut down and became dormant during the months of winter darkness (Axelrod, 1984; Francis, 1988; Basinger, 1991); growth rings on mandibular and limb elements of the salamander *Piceoerpeton* also suggest seasonality (Estes and Hutchison, 1980).

Based upon comparisons with the ungulates living today in the High Arctic, it seems plausible that *Thuliadanta* may have lived there year-round, as do today's muskoxen and caribou. For example, caribou that inhabit the Arctic islands, Boothia Peninsula, and the northeastern mainland do not migrate south to winter in the subarctic forests like their more southern-ranging cousins because the distance is too great (Pielou, 1994) and migrating great distances overland is energetically too costly (Marchand, 1996). Unlike today's high Arctic inhabitants, *Thuliadanta* did not have to contend with the cold. Winter darkness may not have been an obstacle either. By analogy with mountain tapirs which are equally active during daylight and nocturnal hours (Downer, 1996a,b), *Thuliadanta* may also have been adapted to being active in both light and dark environments.

As all living perissodactyls are hindgut fermenters, it is plausible that *Thuliadanta* was as well — an adaptation that seems beneficial to living year-round in the Eocene High Arctic (Eberle and Storer, 1999). Hindgut fermenters, such as today's tapirs, rhinos, and elephants, are at an advantage where food is of limited quality and high in fiber, provided it occurs in large quantities (MacDonald, 1987; Eberle and Storer, 1999). Abundant (and large) tree stumps, thick coals and peaty forest litter layers in the fossil vertebrate-bearing strata of the Eureka Sound Group on Ellesmere Island imply a lush environment with high biomass production that was probably adequate to maintain large hindgut fermenters (such as tapiroids) over the winter months. By

analogy, today's tapirs are browsers, and mountain tapirs feed on a variety of food items that include trees, shrubs, ferns, grasses, fruits, and berries (Downer, 1996a,b). Like extant tapirs, fossil tapirs had brachydont (i.e., low-crowned) molars with transverse lophs or crests, considered by Hooker (2000) to be the optimum browsing adaptation in mild, equable forests. Consequently, despite winter shutdown of High Arctic trees, a 'tapir' adapted to feeding day and night on a broad range of plant materials seems a most credible year-round inhabitant in the dense lowland forests of the Eocene High Arctic.

6. Conclusions

Throughout the Cenozoic, there appear to be numerous instances wherein Asian mammal taxa successfully invaded other landmasses (including North America), but examples wherein mammals from other continents successfully invaded Asia are rare (Beard, 1998). However, animals diffuse in both directions across a land bridge, and some 'counterflow' from the smaller landmass to the larger one should occur. The phylogenetically-derived biogeographic reconstruction posed here suggests that the tapir lineage may have originated in North America (rather than Asia, as others have postulated) and may represent a rare instance of counterflow wherein an exotic North American taxon invaded Asia. Moreover, *Thuliadanta* seems a plausible ancestor to *Desmatotherium* from both continents, suggesting that this branch of the tapir lineage may have originated at high latitudes and subsequently dispersed from there to mid-latitudes. While the High Arctic was most certainly 'en route' for terrestrial animals dispersing across Holarctic continents during parts of the Paleogene, *Thuliadanta*'s occurrence indicates that this region must also be evaluated as a potential source area for some of the exotic taxa appearing in mid-latitudes during Eocene time. Northern high latitudes have been hypothesized as areas of origin for certain Pleistocene mammals (e.g., woolly mammoths; see Lister et al., 2004), but need also be considered for earlier mammalian lineages.

Since today's tapirs are forest-dwellers and tropical in distribution (MacDonald, 1987), *Thuliadanta*, by analogy, supports evidence from the fossil flora,

lower vertebrate fauna, and isotope analyses for a mild, temperate, forested High Arctic during the Eocene. By analogy to today's tapirs, and more specifically the mountain tapir of the wet cloud forests of South America, *Thuliadanta* may have been well adapted to living year-round in the dense lowland forests of the Eocene High Arctic. From a larger standpoint, the Eocene High Arctic environment seems to have favored perissodactyls (odd-toed ungulates) over artiodactyls (even-toed ungulates), as medium- to large-sized perissodactyls (tapiroids and brontotheres) occur at several localities in the Eureka Sound Group on Ellesmere Island, while artiodactyls are conspicuously absent (despite their occurrence at mid-latitudes at this time). The opposite is true of today's Arctic region.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j. palaeo.2005.06.008.

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