AN EARLY PLIOCENE HIPPARIONINE HORSE FROM THE CANADIAN ARCTIC

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ABSTRACT. A partial skull of a juvenile hipparionine equid from Ellesmere Island, Canada, is the northernmost fossil record of a horse (78° 33′ N). Biostratigraphical analysis of the associated fossil biota suggests an age of 3·5 to 4 Ma (early Pliocene). Preserved facial characteristics of the equid include a very reduced preorbital fossa located posterior to the infraorbital foramen. The deciduous premolars have low crown heights, complex fossette plications, multiple pli caballins, and oval, isolated protocones. The teeth are quite large, corresponding to an adult with a tooth row length of *c.* 150 mm. This combination of facial and dental characteristics and large size is not observed in any contemporaneous North American hipparionine, but is instead found in some Asiatic hipparionines, most notably *Plesiohipparion*. If the resemblance is not a result of convergence, then this represents the first record of an Old World hipparionine dispersing to North America. Alternatively, the specimen may represent a hitherto unknown, high-latitude hipparionine clade.

FREQUENT intercontinental dispersals of terrestrial mammals occurred during the Cenozoic between North America and Eurasia, and played a major role in faunal evolution in these two regions (Tedford *et al.* 1987; Flynn *et al.* 1991; Webb and Opdyke 1995; Woodburne and Swisher 1995). Interchange across the trans-Beringian route has occurred periodically and at varying intensity since the Paleocene. Equids are one of the best known taxa that participated in this faunal exchange, with the separate dispersals of anchitheres, hipparionines, and *Equus* to the Old World, although other ungulates, carnivores, lagomorphs, and rodents also used this route extensively. The Beringian dispersal route has remained at very high latitudes during the Cenozoic (Woodburne and Swisher 1995). This northerly location has undoubtedly acted as a filter to potential dispersers. Flynn *et al.* (1991) noted that the extreme rarity of pre-Quaternary high-latitude terrestrial mammal localities in the Holarctic makes it impossible to determine whether climate or ecological competition (or some combination of both) was the actual filtering agent.

Field work by the Geological Survey of Canada and the Canadian Museum of Nature has resulted in the discovery of a diverse, high-latitude, Pliocene fossil biota on Ellesmere Island in the Canadian Arctic (Harington 1996, 1997; Dompierre and Harington 1997; Rybczynski and Harington 1997) (Text-fig. 1). The Strathcona Fiord beaver-pond locality has produced fossil plants (both pollen and macrobotanical specimens), invertebrates (insects and molluscs), and vertebrates (fish, frog, bird, and at least 12 mammals). The types of trees found are larch, alder, and birch; in all, 10 bryophytes and 34 vascular plants have been identified. The general palaeoenvironment is interpreted as boreal forest with standing water and extensive grassy patches. The vertebrate fauna includes a number of biogeographical range extensions. We report here on one biogeographically interesting member of the fauna, a hipparionine horse found in 1995. The remaining vertebrate taxa are presently under study by CRH.

Geology and chronology. The fossil-bearing stratum at the Strathcona Fiord beaver-pond locality consists of a 2·4-m-thick (maximum depth recorded) sequence of mossy peat with sand lenses, a few boulders, tree trunks up to 3 m long, and many beaver-cut sticks. This organic-rich sequence is overlain by *c.* 6 m of unconsolidated sand and 12 m of pebble- to boulder-size gravel. The flora is broadly similar to those of the early Pliocene Meighen Island, Canada, and the late Pliocene Kap København, Greenland, localities (Hills and Matthews 1974; Matthews 1977; Funder *et al.* 1985; Matthews and Fyles in press). An age slightly older than the former, based on distinctive seeds of 'Paliurus type,' and much older than the latter is most likely. This estimate is supported by mammalian biochronology, which suggests an early Pliocene (early Blancan) age because of similarities with the Hagerman, Idaho (*c.* 3·5 Ma), and White Bluff, Washington (*c.* 4·3 Ma) faunas.
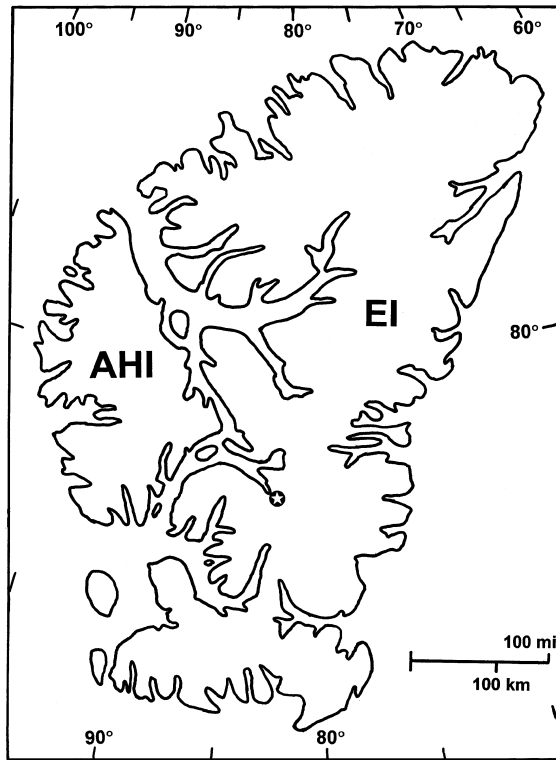
TEXT-FIG. 1. Map of Ellesmere Island (EI) and Axel Heiberg Island (AHI), Nunavut Territory, Canada. Location of the Strathcona Fiord beaver pond locality in central Ellesmere Island is indicated by the star. Western Greenland and northern Devon Island are omitted from the map.

Anatomical abbreviations. IOF, infraorbital foramen; POF, preorbital fossa; DI, upper deciduous incisor; DP, upper deciduous premolar; M, upper molar; P, upper premolar (arabic numerals following dental abbreviations indicate tooth loci).

Institutional abbreviations. CMN, Canadian Museum of Nature, Ottawa; GSC, Geological Survey of Canada, Ottawa; PCSP, Polar Continental Shelf Project, Ottawa.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821
Tribe HIPPARIONINI Quinn, 1955

Genus and species indeterminate

Text-figures 2–3

Material. CMN 51080, associated maxillae and premaxillae of a single individual, with the right DI1 and DP2-DP4 and the left DP1-DP4. The specimen was collected in July, 1995.

Locality. Beaver Pond Locality, head of Strathcona Fiord, west-central Ellesmere Island, Nunavut Territory, Canada (Text-fig. 1); 78°33′ N, 82°22′ W.

Geological age. Early Pliocene, *c*. 3·5 to 4·3 Ma (based on vertebrate and botanical biochronology).

Ontogeny. CMN 51080 is judged to have belonged to a 6- to 10-month-old foal; its deciduous teeth are slightly worn and the M1 had not yet erupted because the posterior surface of the DP4 lacks a compression facet. An alveolus for the M1 had begun to form posterior to the DP4, but the permanent premolars had not started to mineralize dorsal to the deciduous series. The right and left premaxillae are not fused.

Description. The well-formed buccinator fossa located anterior to the DP2 lacks a posterior pocket and is *c*. 43 mm long and 22 mm tall. The IOF is located dorsal to the DP3 (Text-fig. 2A), 33·2 mm above the alveolar margin and 23·3 mm from the maxillary-lacrimal suture. The entire IOF is nearly circular (9·6 mm long and 8·5 mm tall); it contains both anteriorly and posteriorly facing openings. A very shallow depression, *c*. 11 mm long and 15 mm tall, is located anterior to the IOF; it lacks distinct rims. A faint POF is located on the maxilla and lacrimal posterodorsal to the IOF, centred dorsal to the DP4 with its ventral margin *c*. 44 mm dorsal to the alveolar margin. The POF is not strongly rimmed, lacks a posterior pocket, and no portion lies directly dorsal to the IOF. There is no malar fossa.

The DI1 has a short crown, a breadth of 17·0 mm, and a complete infundibulum. The anterior (labial) enamel is finely crenulated but without pronounced grooves. The DP1 has a maximum length of 12·6 mm and a slightly worn occlusal surface formed by lingual and labial lophs connected by a posterior transverse crest. Most of the DP1 is obscured in lateral view by the anterostyle of the DP2 (Text-fig. 2A).

The DP2–DP4 (Text-fig. 2B; Table 1) are large but relatively low-crowned (even for deciduous teeth) considering that they have undergone relatively little wear. Pli caballins consist of multiple (3 or 4) folds; fossette plications are complex and numerous. On the DP3 and DP4, the parastyle and mesostyle are very strong, with the parastyle bearing a slight groove, but the metastyle is weak. The protocones are relatively small, isolated from the protoloph, and elongate-oval on the natural occlusal surface. A small protoconal spur is present on the DP2, but lacking on the DP3 and DP4.

The right DP4 was sectioned to determine the enamel pattern in middle to late wear-stage (Text-fig. 3). The enamel forming the pli caballin and fossettes remains very complex (with multiple pli protoloph and pli hypostyle and a very long pli protoconule), but the protocone is much larger (7·5 mm long, 4·0 mm wide) and more oval. It remains isolated from the protoloph. The hypoconal groove is absent by the late wear-stage.

Remarks. The morphology of the IOF, with its dual openings, is quite different from that normally observed on equids. The early ontogenetic stage of the specimen is not a causal factor, since other specimens of equids of similar age have a normal IOF. Determination of whether the IOF morphology is only an odd individual variant, or instead represents a distinctive apomorphy, must wait until additional specimens are recovered.

COMPARISONS WITH OTHER HIPPARIONINES

General size. The length from the anteriormost point of the DP2 to the posterior side of the DP4 of CMN 51080, excluding cement, is 93·7 mm. To allow comparison of its size with those of adults, a least-squares regression was computed between the length of the DP2–DP4 and the P2–M3 length in 35 species of hypsodont equids (Text-fig. 4). Unsurprisingly, the two parameters are strongly correlated, with a correlation coefficient of 0·96. This permits a reliable estimate of what the adult P2–M3 length of CMN 51080 would have been – *c*. 151 mm. Such a value is significantly larger than P2–M3 lengths of almost all North American hipparionines (MacFadden 1984; Webb and Hulbert 1986; Bernor *et al*. 1989). Only *Neohipparion gidleyi* and larger individuals of *Neohipparion affine* and *Cormohipparion occidentale* are of this size. In contrast, numerous Old World hipparionine lineages attained such a large, or even larger, size (Text-fig. 4; Bernor *et al*. 1989).

Comparisons with North American hipparionines. Four genera of North American hipparionines ranged into the Pliocene: *Pseudhipparion*, *Neohipparion*, *Cormohipparion* and *Nannippus* (Hulbert 1993*a*). *Pseudhipparion* and *Neohipparion* became extinct in the very early Pliocene (at the end of the Hemphillian Land Mammal 'Age'), *c*. 4·5 Ma, while *Cormohipparion* and *Nannippus* both persisted into the late

infra-orbital foramen

A

B
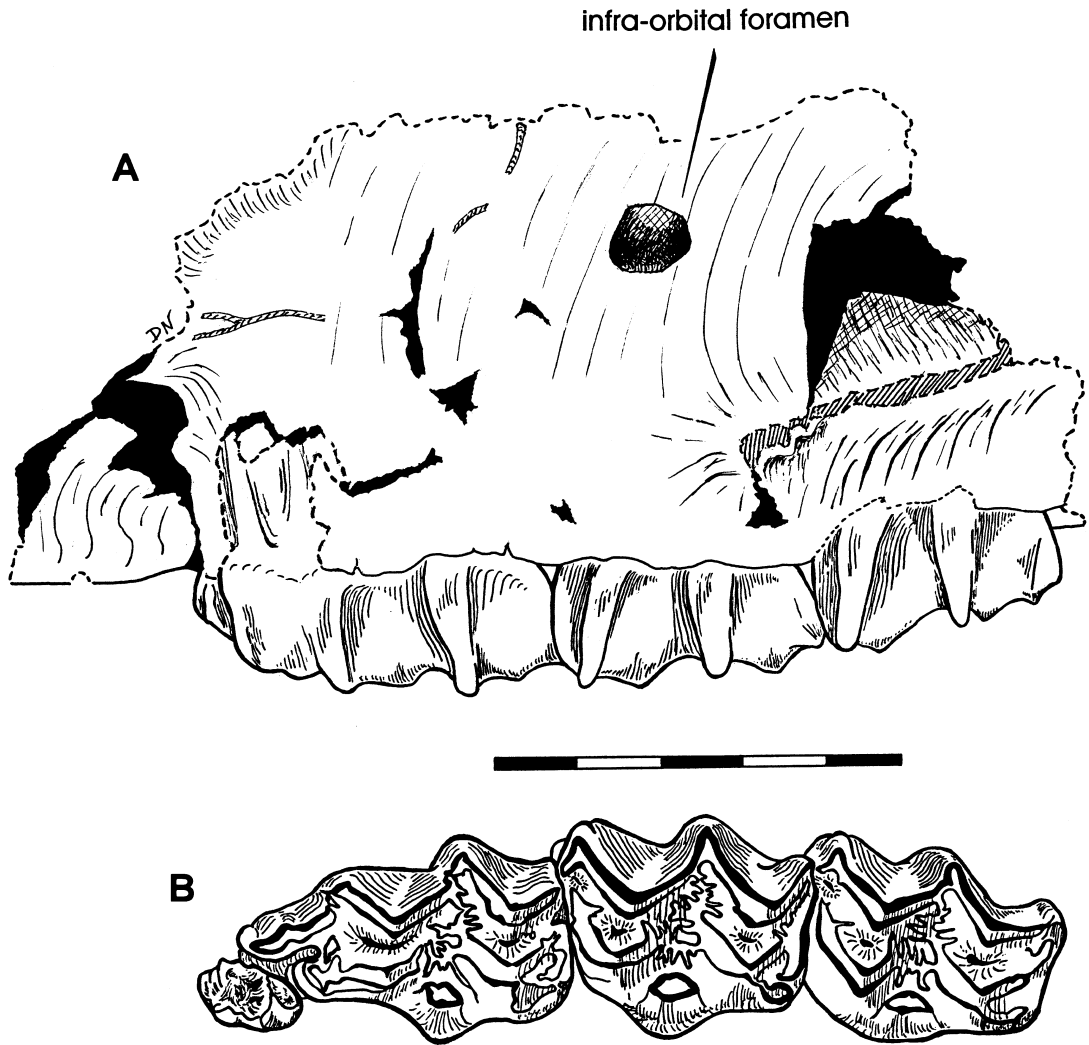
TEXT-FIG. 2. Hipparionini, genus and species indeterminate, from the Strathcona Fiord beaver-pond locality, Ellesmere Island, Canada; CMN 51080: A, left maxilla in lateral view; B, left DP1–DP4 in occlusal view. Scale bar represents 50 mm.

Pliocene (late Blancan, *c.* 2 Ma). Since their origin from a common ancestor in the early Miocene, members of these four genera evolved distinct combinations of derived dental and cranial character states. These allow fairly definitive generic identification of most Pliocene hipparionine specimens, even isolated teeth, despite convergent evolution of some features.

Both *Pseudhipparion* and *Nannippus* are highly unlikely sources of the Strathcona Fiord hipparionine. Their late Miocene and Pliocene species are characterized by much smaller size, more hypsodont teeth, and relatively simple fossette margins and pli caballins (MacFadden 1984; Webb and Hulbert 1986; Hulbert 1993*b*). Their only similarity with the Canadian horse is a reduced POF, but this state evolved convergently numerous times within the hipparionines and by itself is not strong evidence of a close phylogenetic relationship.

Large species are present in *Neohipparion*, most notably *N. affine* and *N. gidleyi*, which were about the

TABLE 1. Measurements (in mm) taken on the occlusal surfaces of the deciduous premolars of CMN 51080, Hipparionini genus and species indeterminate, from the Strathcona Fiord beaver-pond locality, Ellesmere Island, Canada (Text-fig. 1). APL, anteroposterior length; TRW, transverse width; PRL, protocone length; PRW, protocone width; MSCH, mesostyle crown height; PLI CAB, number of folds making up the pli caballin.

| Tooth Locus	APL	TRW	PRL	PRW	MSCH	PLI CAB
Left DP2	37·4	18·5	4·2	3·3	15·3	3
Left DP3	26·9	19·7	4·9	3·6	13·6	4
Left DP4	28·4	18·6	5·5	3·1	–	3
Right DP2	36·9	18·3	4·6	3·2	15·4	3
Right DP3	26·6	19·5	5·2	3·5	13·2	4
Right DP4	28·5	18·3	5·8	3·3	18·4	3

same size as the Strathcona Fiord hipparionine. Late Miocene and Pliocene species of *Neohipparion* (including *N. gidleyi*) share a number of derived dental features, most notably very elongated protocones, curved parastyles and metastyles, pinched mesostyles, and very tall crown height that are not observed on the Canadian equid. They also have a very reduced POF (often completely absent) that does not extend onto the lacrimal (Hulbert 1987). The middle Miocene *N. affine* has a POF located in approximately the same location and with a similar relative depth as CMN 51080, and lacks many of the apomorphic dental states of younger species of the genus. However, *N. affine* has much simpler fossette plications and pli caballins, and larger, more elongate protocones than does CMN 51080 (MacFadden 1984; Hulbert 1987). Therefore, *Neohipparion* is also an unlikely source for the Canadian hipparionine.

Dentally, members of *Cormohipparion* are the closest match to CMN 51080 among North American hipparionines. They have multiple pli caballins, complex fossette margins, and lack the high degree of hypsodonty observed in other Pliocene hipparionine genera (MacFadden 1984; Hulbert 1988*a*, 1988*b*). Despite these similarities, the teeth of *Cormohipparion* (*Notiocradohipparion*) *emsliei*, the only described Pliocene species in the genus, have several apomorphic traits relative to CMN 51080, including a stronger metastyle and a straight to concave lingual protocone border. *C. emsliei* and its sister taxon *Cormohipparion ingenuum* are also much smaller than CMN 51080 and have better developed POFs (Hulbert 1988*b*). Derivation of CMN 51080 from a member of the *Cormohipparion occidentale*-group is more likely on the basis of size, but would require considerable reduction in the size and depth of the POF. Also, the youngest known members of the *C. occidentale*-group are late Miocene (Hulbert 1993*a*). Therefore, CMN 51080 is not closely related to Pliocene *Cormohipparion*, but could represent a Miocene derivation of this genus.

Comparisons with Old World hipparionines. Hipparionine equids first dispersed from North America to the Old World at about the mid Miocene-late Miocene boundary (*c*. 11 Ma; Garcés *et al.* 1997), and there radiated into a number of speciose clades whose phylogenetic relationships remain uncertain. The pioneering taxon was evidently a member of *Cormohipparion*, most likely part of the *C. occidentale*-group (Hulbert 1988*b*; Bernor *et al.* 1996). Whether there was a subsequent dispersal (or dispersals) of North American hipparionines to the Old World remains a contentious issue among specialists (MacFadden 1984; Alberdi 1989; Bernor *et al.* 1989, 1996; Woodburne 1989). However, no modern author has seriously suggested the dispersal of an Old World hipparionine to North America.

TEXT-FIG. 3. Hipparionini, genus and species indeterminate; CMN 51080; Strathcona Fiord beaver-pond locality, Ellesmere Island, Canada; occlusal view of sectioned surface of right DP4 (reversed); × 1·5.
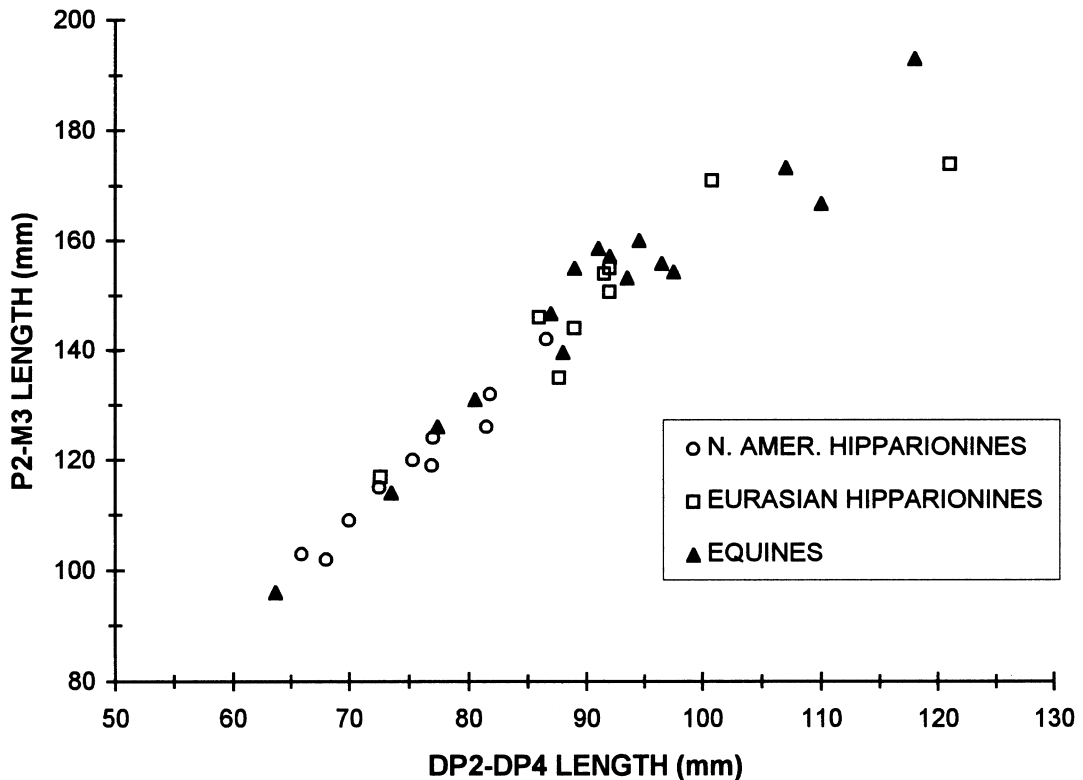
TEXT-FIG. 4. Bivariate scatter plot of DP2–DP4 length versus P2–M3 length in 35 species of hypsodont horses. A least-squares regression of the data produced the following relationship between these two parameters: $Y = 1 \cdot 624X - 1 \cdot 09$. When available, DP2–DP4 lengths were taken from individuals with slightly worn teeth.

Bernor and co-authors presently recognize four major species-groups of Old World hipparionines: the *Hippotherium*-group with a chronological range of *c.* 11 to 6 Ma; the *Hipparion sensu stricto*-group, *c.* 9 to 7 Ma; the *Cremohipparion*-group, *c.* 9 to 3 Ma; and the '*Sivalhippus*'-group, *c.* 9 to 0·5 Ma (Bernor *et al.* 1989, 1996; Bernor and Lipscomb 1995). The two chronologically older clades, the *Hippotherium* and *Hipparion sensu stricto* species-groups, share no unique apomorphies with the Strathcona Fiord hipparionine.

Within the *Cremohipparion*-group there is a clade of four species, several from Asia, that have a well-formed caninus fossa, an apomorphy for hipparionines (Bernor *et al.* 1989). Although CMN 51080 lacks a distinct caninus fossa, the shallow depression anterior to the IOF is located in the position of the caninus fossa of *Cremohipparion*. Compared with other late Miocene and Pliocene hipparionines, the cheek teeth in the *Cremohipparion*-group are relatively low-crowned. A juvenile Chinese specimen referred to *Cremohipparion forstenae* by Bernor *et al.* (1990, text-fig. 16Q) in the same wear-stage as CMN 51080 has a slightly less complex enamel pattern in its DP2–DP4 and a relatively smaller DP1, but otherwise the morphology of the two is similar. *C. forstenae* has the most reduced POF of any member of *Cremohipparion* (Bernor *et al.* 1989, 1990), but its fossa differs from that of CMN 51080 in being larger and deeper, and in having a distinct posterior rim. Asiatic *Cremohipparion* are of moderate to small size, with P2–M3 lengths of 120–140 mm, and have a posteriorly located IOF. The only known Pliocene species of *Cremohipparion, C. licenti,* is very different from CMN 51080 in both its facial morphology, with a very deep, posteriorly pocketed POF, a malar fossa, and a pocketed buccinator fossa, and its dental morphology, with simple fossette plications, single pli caballins, and round protocones (Qiu *et al.* 1987; Bernor *et al.* 1989). *Cremohipparion* therefore is unlikely to be the source of the Canadian hipparionine.

The 'Sivalhippus'-group had its origins in the early late Miocene of Asia, and was the most successful and highly dispersed Old World hipparionine clade of the latest Miocene and Pliocene (Bernor and Lipscomb 1995; Bernor *et al.* 1996). It contains several named genera (or subgenera, depending on the classification one uses) including *Proboscidipparion* (Asia), *Plesiohipparion* (Asia, Europe, and Africa), and *Eurygnathohippus* (= *Stylohipparion*) (Africa). Evolutionary trends observed within this species-group include increased size and reduction of the POF, both compatible with the morphology of CMN 51080. Multiple pli caballins and complex fossette plications are present in various Pliocene species of the 'Sivalhippus'-group as well (Bernor *et al.* 1989, 1996). There are few reported deciduous upper dentitions for this group. Qiu *et al.* (1987, text-fig. 16.3) illustrated a deciduous dentition of *Proboscidipparion pater* from the lower Pliocene of China that greatly resembles that of CMN 51080 in terms of size, enamel complexity, and protocone shape. However, CMN 51080 preserves a sufficient amount of the maxilla dorsal to the IOF to demonstrate that it lacked the highly retracted nasals of *Proboscidipparion*. The similarities in the deciduous dental morphology of *P. pater* and CMN 51080 are probably symplesiomorphies, but indicate that large-bodied hipparionines with greatly reduced POFs and suitably complex tooth enamel to give rise to CMN 51080 were present in the late Neogene of Asia. Unfortunately, many of the most diagnostic dental character states of the 'Sivalhippus'-group, especially those of *Plesiohipparion*, are present on the lower dentition (Bernor *et al.* 1989, 1996), and so cannot be observed on CMN 51080.

CONCLUSIONS

Lack of knowledge about what constituted the high-latitude Holarctic biota during the Neogene prior to 3 Ma hinders analysis of intercontinental dispersals between North America and Asia (Flynn *et al.* 1991). Ellesmere Island in the Canadian Arctic is well known for its Eocene terrestrial vertebrates, which have had important ramifications for understanding Paleogene paleoclimatology, biogeography and inter-continental dispersals (Dawson *et al.* 1976, 1993; McKenna 1980; Dawson 1990). Field work conducted since the late 1980s at Strathcona Fiord on Ellesmere Island has produced a rich Pliocene (Blancan) flora and fauna that potentially could do the same for the late Neogene.

Among the vertebrate fossils recovered from the Strathcona Fiord beaver-pond locality is a partial cranium of a young foal. It represents the northernmost record of a hipparionine equid from North America; indeed it is likely the northernmost fossil record of the Equidae in the world. Dental microwear analysis of DP3 from CMN 51080 indicates a browsing diet (Dompierre and Harington 1997); the low crown height and protocone shape support this assessment. However, since the individual represented is such a young juvenile (probably not even weaned), it is difficult to securely extrapolate this diet to adults. The most salient features of the Strathcona Fiord hipparionine are large size, greatly reduced POF, relatively low crown height, oval protocones, and highly complex enamel pattern. Neither of the hipparionine lineages known to have been present at middle to low latitudes of North America during the Blancan, *Nannippus* or *Cormohipparion* (*Notiocradohipparion*), are morphologically close to the Strathcona Fiord hipparionine and both have apomorphies that prevent them from being ancestral to it.

Given the differences with contemporaneous middle- to low-latitude North American hipparionines, the geographical and phylogenetic origin of the Strathcona Fiord hipparionine has two likely scenarios. First, it could represent an autochthonous lineage of previously unknown high-latitude hipparionines whose ancestry lies with mid Miocene North American hipparionines, most likely *Cormohipparion*. Second, it could represent an allochthonous lineage that resulted from a latest Miocene or earliest Pliocene dispersal from Asia to the high latitudes of North America – one that did not subsequently range southward into middle latitudes. Of the late Neogene hipparionine species-groups known from Asia, the 'Sivalhippus'-group of Bernor *et al.* (1989; 1996), in particular species assigned to *Plesiohipparion*, most resemble the Strathcona Fiord hipparionine and most probably contain its closest sister taxon. The long-range dispersal capabilities of *Plesiohipparion* were emphasized by Bernor and Lipscomb (1995), who also noted an interval of major intercontinental extension (within the Old World) for this clade at 5 Ma. This could have also been the time when it dispersed to the Nearctic.

These two hypotheses can be tested with recovery of additional fossils. More specimens from the

Strathcona Fiord locality, in particular adult upper and lower dentitions, would show whether the Strathcona Fiord hipparionine's resemblance to *Plesiohipparion* is based on apomorphies, plesiomorphies or homoplasies. Discovery of mid to late Miocene, high-latitude fossil localities lacking hipparionines would favour the allochthon hypothesis, whereas recovery of hipparionines from such sites (unless morphologically distinct from the Strathcona Fiord horse) would favour the autochthon hypothesis.

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