Early Pliocene fish remains from Arctic Canada support a pre-Pleistocene dispersal of percids (Teleostei: Perciformes)

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Abstract: Percid remains from Pliocene deposits on Ellesmere Island, Arctic Canada, are identified as a species of Sander, similar to the valleye and sauger of North America and the pike–perch of Europe and western Asia. They are named as a new species, Sander teneri. These remains are the most northerly percid elements found to date and suggest the palaeoenvironment was significantly warmer in the Pliocene than it is currently. The fossil remains show the presence in North America of the family Percidae as well as the genus Sander prior to the Pleistocene, indicating a previously proposed Pleistocene immigration from Europe or Asia can be discounted. These fossils contradict an earlier hypothesis that percids, in particular Sander, crossed from Eurasia to North America in the Pleistocene; instead, the fossils show percids were already in the area by the Pliocene.


[Traduit par la Rédaction]

Introduction

A unique locality in the Canadian Arctic has produced a number of fossil remains of a small perciform fish. The locality, south of the head of Strathcona Fiord on Ellesmere Island in Nunavut (Fig. 1), preserves as peat the organic sediment that accumulated in a pond in the early Pliocene (Harington 2001; Tedford and Harington 2003). Named the Beaver Pond site, the sediments are possibly the result of beaver activity, as an accumulation of intertwined beaver-cut sticks, mainly aligned northwest–southeast in a matrix of silty sand and cobbles, might represent part of a beaver dam and beaver remains including a partial skeleton have been recovered from the site (C.R. Harington, field notes, 2001; Tedford and Harington 2003). However, the beaver remains belong to the extinct Dipoides, and further evidence is lacking to indicate this genus was a dam-builder (Rybczynski 2008).

Although it is possible that the small beaver periodically dammed the stream, allowing a small lake or pond to form, the water apparently was occasionally drained by a break in the dam (C.R. Harington, personal observation, 2006). Many specimens are relatively complete and in a fine state of preservation. The perciform fish probably would not have lived in bog conditions but could have been in the body of freshwater that occupied the area for relatively long periods, which are marked by silty stringers between peat layers in the stratigraphy (C.R. Harington, personal observation, 2006).

The Beaver Pond site, currently thought to date between 5 and 4 Ma (Tedford and Harington 2003), preserves remains of mammals that indicate an interchange of fauna between Asia and North America that probably occurred prior to ~5 million years ago (Tedford and Harington 2003; Dawson and Harington 2007). This locality, above 78°N latitude, is the only known North American Pliocene vertebrate site north of 55°N latitude (Dawson and Harington 2007).

Geological setting

The Beaver Pond site at 78°31′N, 82°22′W, at an elevation of 378 m, is located south of the head of Strathcona Fiord. This is one of many late Tertiary fossiliferous sites on Elles-
mere Island referred to as the “high terrace sequence.” Typically found high on valley sides, these unconsolidated deposits unconformably overlie the Late Cretaceous to early Tertiary Eureka Sound Group. They are capped with glacial deposits and were presumably deposited prior to significant landscape downcutting (Mathews and Fyles 2000). The Beaver Pond site occurs within a high terrace deposit that is an ~30–40 m thick unit of mostly sands and gravels. The site itself appears to be a slump block (see Mathews and Ovenden 1990) derived from a peat layer that occurs ~5 m below the capping glacial till. The elevation of the hill crest above the site is ~402 m. The fossil beds and associated beds above and below the locality are all freshwater, as indicated by siliceous microfossils (Harington 2001), with no indication of interbedded marine sequences in the vicinity.

Discovered in 1961, the site was not intensively excavated until 1992. For the following 10 years, most collection efforts were focussed on the northeast end of the site, where the mossy peat unit was originally ~2.4 m thick. The Beaver Pond site as currently excavated (in 2006) is 7 m across section facing towards the southeast. The stratigraphy, as determined in 2006 (Fig. 2A), is variable across section, indicating a complex depositional history. The fish remains reported here were recovered from the peat unit at the northeast end of the site (Fig. 2B).

Material and methods

Fossil material

The perciform elements were collected by C.R. Harington and colleagues in 1992 and 1995. The elements collected in 1992 (CMN 53270), discovered by John Tener, were all associated in a single, small bolus of fibrous peat located within 20 cm of the base of the a peat layer, some 60 cm from the northeastern end of the site, and seemed to represent a small individual fish identified in the field as “Percidae?” (C.R. Harington, field notes, 1992). Other elements collected in 1995 (CMN 52226, 52230, and 53271) are not associated with one another or the 1992 specimen, and at least one (a cleithrum) may be a distinct species from the 1992 individual. However, all the bones recovered belong to perciform fishes.

Comparisons with other species

The most diagnostic fossil elements from Strathcona Fiord, particularly the cleithra and anguloarticular bones, were compared with a diversity of perciform species, including those that currently inhabit freshwaters of Canada and the United States, as well as perciforms found in eastern Asia (Siberia) and Europe, and additional marine or fresh water taxa (e.g., *Lates*) that are morphologically similar. Most of the comparative material examined (Appendix A) consists of prepared, dried skeletons with a few exceptions being cleared and stained material or fossil material as noted in Appendix A.

Estimation of body size

To estimate the body size of the fossil specimen, linear regression was performed using the approach of Casteel (1976). We used log-base 10 anterior centrum width regressed against log-base 10 standard length on the second anterior vertebra in 10 specimens of *Sander canadensis* of known size in the collections of the Canadian Museum of Nature.

Institutional abbreviations


Systematic palaeontology

Superorder Acanthopterygii (sensu Johnson and Patterson, 1993)
**Sander teneri** n. sp.

**HOLOTYPE:** CMN 53270, associated but disarticulated cranial and postcranial elements.

**LOCALITY AND HORIZON:** The Beaver Pond site, Strathcona Fiord, Ellesmere Island, Canada; 78°33′N, 82°22′W; 5–4 Ma (Pliocene).

**DIAGNOSIS:** *Sander teneri* is diagnosed by the presence of four or fewer moderately strong spines on the posterodorsal margin of the cleithrum as in most *S. canadensis* and *S. lucius* (*S. vitreus* has 0–6 spines, usually none, which are weaker than in *S. teneri* and *S. canadensis*; and *S. volgensis* has 6–7 spines); the dorsal process of the cleithrum being inclined at a shallower angle rather than more vertically in the other species; the flanges on the posterior edge of the dorsal plate of the cleithrum being placed more dorsally and being more robust than in the other species; the mandibular sensory canal of the anguloarticular long, wide, and of uniform width along its length, not tapered, extending under posterior 0.6 of condyle at a moderately steep angle, surface under canal pore pitted, surface adjoining retroarticular vertical and angular, not gently curved; parasphenoid with a broad mid-ventral keel.

**ETYMOLOGY:** the specific epithet is in honour of Dr. John S. Tener, pioneering Arctic biologist who discovered the speci-
men and spent eight field seasons collecting at the Beaver Pond site.

**Description**

**Jaws, suspensorium, and hyoid bones**

Several partial elements can be identified as jaw or palate elements although they do not seem to be distinctively different from those of other perciforms. This includes the articular head of a left maxilla and a partial left palatine (Fig. 3). About two thirds of the mid-portion of a left ceratohyal and the articular facet of the left quadrate are also in the collection.

Elements of the lower jaw appear to be more distinctive, based on the posterior portion of a left anguloarticular bone, without the retroarticular (Fig. 4). This element measures just under 6 mm long, with the facet being ~3.9 mm long anteroposteriorly. The articular facet is broad and shallow. The angle formed by the dorsal and ventral edges anterior to the facet is ~68°. There is a foramen in the angle between dorsal and ventral edges. In lateral view, there is a deep, open groove for the mandibular sensory canal that extends from almost the posterior end or the bone anteriorly to a point under the anterior third of the articular facet. Such a groove is found in a number of perciforms (e.g., *Perca*, *Sander*, *Ambloplites*, *Micropterus*, *Lepomis*, *Pomoxis*, and *Morone*), but it is most similar to that of *Sander*. The bone in the area where the retroarticular would fit bears a number of deep pits. In medial view, there is an open trough along the anteroventral edge of the specimen.

**Parasphenoid**

There are three portions of a parasphenoid that do not articulate with each other; the total preserved length is ~17.5 mm. The parasphenoid is 2 mm wide along most of the preserved length but widens to 3 mm at the posterior end. The segment anterior to the area for attachment for the branchial apparatus has a broad mid-ventral keel (Fig. 5), somewhat similar to that of *S. volgensis*, which is not present in other *Sander* species (Fig. 6).

**Pectoral girdle**

A partial right posttemporal is preserved (Fig. 7) and similar to those of *Perca* and *Sander*. The preserved dorsal part of a right supracleithrum is also similar to other perciforms and does not seem distinctive. However, the left and right partial cleithra present in the associated material are distinctive to this fish. The dorsal portion of a left cleithrum and about half of the dorsal plate of a right cleithrum are present (Fig. 8). The right cleithrum clearly preserves three flattened spines and the base of a fourth, extending from the posterior edge of the dorsal plate. There are two convex flanges along the posterior edge. The dorsal process of the cleithrum is long and robust.

**Fin spine**

A single, nearly complete fin spine (Fig. 9) is included in the elements of the holotype. It is 10.5 mm long and missing only the distalmost tip. The distal-half of the spine is curved slightly to the left and also posteriorly. The proximal base of the spine at 2 mm wide is about twice as broad as the rest of the element. In anterior view, it has a low, rounded ridge that is positioned centrally on the base but shifts to a slight left lateral position higher on the shaft. On the posterior surface near the base, there are two low, rounded projections medially (the locking processes of Gayet 1987). Broken parts of several other spines are present but lack diagnostic characters.

**Vertebrae**

Six vertebral centra were recovered from the Beaver Pond site, two anterior and four posterior. One is from the anterior part of the vertebral column (Fig. 10), the other two are from a more posterior position. The vertebrae are 3.5–4 mm in diameter. All centra are formed of lacy- or open-strut-type bone, as found in many perciforms. The amphicoelus centra preserve the “notochordal tube” in the dorsal portion of the hollow. The centra are subcircular, with the anterior one being more irregular in shape than the other two.

**Scales**

Approximately 30 scales were recovered, four of them complete. The scales are square in shape, being 4 mm anteroposteriorly and dorsoventrally. There are six strong radii fanning from a posteriorly placed focus to the anterior edge of the scale (Fig. 11). The anterior edge thus bears six deep notches at the points of the radii creating a strongly scalloped border. The scale focus is positioned just anterior to...
the field of ctenii, separated from it by three circuli. The posterior edge of the scales bears a dorsoventrally elongate patch of ctenii, which covers approximately one quarter of the scale (1 mm at deepest point). The posterior edge of this ctenial field is roughly perpendicular to the longitudinal axis of the scale. The ctenii under a dissecting microscope are the transforming ctenii form of Roberts (1993). They are clearly aligned in rows, not randomly distributed, and with 11–12 rows in the middle (deepest) portion of the field. There are ~42 ctenii along the posterior edge of the scale. The ctenii do not bear alae (see Coburn and Gaglione 1992). Circuli are also visible and number ~90. The scales appear to be from a fish at least 7 years old and slow growing.

Size of individual

The body shape of the fossil fish cannot be reconstructed from the elements that are preserved. Similarly, the total number of vertebral centra in the living individual, which would effect its overall length, cannot be determined. However, to estimate the body size of the fossil specimen, we performed a linear regression (see Casteel 1976) on the fossil vertebral elements and compared them with 10 specimens of S. canadensis of known size. The regression equation is log-base 10 standard length = 0.7854 × log-base 10 centrum width + 1.8981 (r² = 0.872, p = 0.000). Using the second anterior vertebral centrum width value of 2.6 mm of the Beaver Pond fossil in this equation resulted in a standard length value of 167.5 mm. As standard length averages ~83.5% of the total length in S. canadensis (personal observation), we estimate a total length of ~200 mm for the fossil specimen, assuming it had roughly the same proportions as S. canadensis.

Unassociated elements

Several additional fish bones were recovered from the Beaver Pond site in 1995 (Fig. 12A–12F). These elements are not associated with each other or with the original 1992 material. They cannot be convincingly assigned to this new species, and some of the elements may not be con-specific. They consist of the following elements:

(1) A partial left opercular bone (CMN 53271) preserves only the horizontal spine with the attached facet for articulation with the hyomandibula. It is likely perciform but has not been identified further.

(2) The posterior portion of a right frontal (Figs. 12A, 12B; CMN 53271), ~8 mm wide at the posterior end, preserves a posterior medial excavation similar to that found in Morone saxatilis (A.M. Murray, personal observation, 2008) The posterior edge of the frontal is straight from the midline, with the lateral edge strongly angled laterally. The lateral edge curves medially in the anterior part of the preserved portion of the frontal. A strong, rounded ridge extends anteriorly across the bone, which is visible in both dorsal and ventral views.

(3) Specimen CMN 52230 is a partial cleithrum (Fig. 12C) that preserves convex flanges similar to the cleithra of the associated 1992 material (S. teneri holotype, CMN 53270), but no spines are preserved. This cleithrum also differs in that the dorsal edge of the dorsal plate appears straight in the holotype of S. teneri whereas it is slightly convex in CMN 52230. A second unassociated partial cleithrum (CMN 53271, Fig. 12D) seems more similar to that of the holotype of S. teneri, in that there appear to be the remains of spines and the dorsal edge of the dorsal plate is straight. Both cleithra (CMN 52230 and 53271) are believed to be perciform and may well belong to S. teneri, as the postero-dorsal margin of the cleithrum is variable in S. vitreus (Fig. 13) and may have been in the fossil species also.

(4) Specimen CMN 52226 is a first anal pterygiophore (Figs. 12E, 12F). It is missing the proximal tip, part of the left flange and part of the anterior flange. There is a deep groove, oriented antero-dorsally, between the anterior flange and the head of the pterygiophore for the articulation of the anal fin spine. This element is also identified only as perciform.
Relationships of *Sander teneri* n. sp

**Familial identification**

The Beaver Pond fish was first identified as belonging to *Percidae* based on its similarity to both *Perca* and *Sander* in the general morphology of the scales, cleithrum, and anguloarticular. In particular, the cleithra in these genera bear spines of similar shape and size in the same position on the...
posterior part of the dorsal plate. Most of the other material examined either have no spines on the cleithra (e.g., Centrarchidae, Gerreidae) or the spines are very fine and numerous (e.g., Moronidae). The cleithra of other families are of quite different shape, having a dorsal plate that is narrow anteroposteriorly (e.g., Embiotocidae).

The anguloarticular bone of the fossil is also similar to that of Perca and Sander in the shallow facet for the quadrate and the open groove underneath the facet, unlike the deeper facet with no groove found in Embiotocidae and Centrarchidae.

**Generic identification**

Within the Percidae, there are 10 genera with 201 living species, 187 of which are found in North America and the other 14 found in Europe and Asia (Nelson 2006). Relationships among the genera are still a matter of debate. The percids have been grouped into three subfamilies; one of which, the Etheostomatinae (Ammocrypta, Crystallaria, Etheostoma, and Percina), contains predominantly very small individuals (Nelson 2006) and seems to form a monophyletic group (e.g., Sloss et al. 2004). The other two subfamilies are the Percinae and Luciopercinae (e.g., Song et al. 1998). The latter is a group of three genera, Sander, Zingel, and Romanichthys; and the former includes Perca and Gymnocephalus. Percarina has also been placed in Percinae (e.g., Nelson 2006) but has been excluded from most analyses. Most genera of the family Percidae, excluding introductions, are restricted to either North America or Eurasia with only two genera, Perca and Sander, being shared between the two land masses. However, Gymnocephalus is found in Siberia. Based on distribution alone, these three extant genera, Perca, Sander, and Gymnocephalus, are the best candidates for the Beaver Pond site fish.
The identification of the fossil based on general morphology of the bones (as *Perca* or *Sander*) and supported by distribution (as *Perca*, *Sander*, or *Gymnocephalus*) is reinforced by the morphology of the scales. Coburn and Gaglione (1992) determined a number of characters for the scales of percids and related families. The ctenii aligned in rows (as determined a number of characters for the scales of percids and related families. The ctenii aligned in rows (as 1992) indicate the fossil cleithra (Figs. 8, 12C, 12D) show variable posterior spines as is found in *Sander vitreus* (Fig. 13). The posterior fragment of the right cleithrum of *S. teneri* shows four well-defined posterior spines. CMN 52230 (Fig. 12D) possibly represents a different taxon but bears two strong spines. Most recent specimens of *S. vitreus* (*N* = 51) show 0–3 weak posterior spines, but this is variable — several specimens have six or more weak denticulations. Most *S. canadensis* (*N* = 11) and *S. lucioperca* (*N* = 4) show 2–4 posterior spines whereas the single specimen of *S. volgensis* we examined has six (right side) or eight (left side) spines. The presence of spines at the posterior edge of the cleithrum is a widespread character among percids; however, the form of the spine, with confluent weak lateral ridges, appears to be unique to species of *Perca* and *Sander*, including *S. teneri*.

**Cleithrum:** *Perca flavescens* has 12 or more posterior spines on the cleithrum, and *P. fluviiatilis* has about six spines with distinct confluent ridges extending anterodorsally along the surface of the cleithrum. *Gymnocephalus* has a cluster of two to four long, strong ridges, bound together and terminating in a weak spine-like process. *Morone chrysops* bears about six spines, and *M. saxatilis* about eight spines, at the ends of prominent surface ridges on the ante-

![Fig. 11. Photograph of the two scales of the holotype of *Sander teneri* n. sp. Scale bar equals 2 mm.](image)

rior to posterior edge of the bone. *Mioplosus*, an Eocene percormorph from Wyoming, is similar to all of the species just mentioned but lacks posterior spines or ridges. *Zingel* has one or two very strong spines. Most species of *Sander* have four or fewer spines as in the fossil.

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**Anguloarticular:** Potentially informative characters for this element include the angle of the coronoid (dorsal) process, morphology of the posterior sensory canal pore, and ornamentation and angle of the posterodorsal process. The fossil has a high coronoid angle, similar to that of *P. flavescens*, *P. fluviatilis*, and *S. vitreus*. *Morone, S. canadensis*, *S. volgensis*, and *S. lucioperca* have a lower coronoid angle; and *Gymnocephalus* and *Zingel* have a curved coronoid with low angle.

The posterior sensory canal pore is long in *S. teneri*, extending under the posterior 0.6 of the articulating facet for the quadrate, and is longer, relatively wider, and not tapered as in most percids. The canal lies at a moderately steep angle in the fossil. *Gymnocephalus* and *Zingel* differ from the fossil, *Perca* spp. and living *Sander* spp. in having extremely enlarged canals with the adjacent structures reduced to accommodate the canals and large pores (as is the case for the darters (Etheostominae), which also bear enlarged foramina for the sensory pores in the bones (Wiley 1992; A.M. Murray, personal observation, 2008)). In *Perca flavescens*, the posterior canal pore is attenuate posteriorly. *P. fluviiatilis* is similar, but the anterior-half of the canal pore is narrow and slit-like. *Morone* has a short posterior canal pore, extending only under the last 0.1 of the articulating surface; it is widest in its center and attenuate posterodorsally. *S. volgensis* has a wide canal pore, but the pore is as long or longer than that of the fossil. In *S. vitreus*, the posterior canal is narrower anteriorly, and the ridge between articulation surface and the canal pore is less rounded than the fossil. *S. canadensis* and *S. lucioperca* have a wide canal pore, but it is shorter and more posterior and of variable width. However, the canal pore form in some *S. canadensis* is identical to the fossil.

In the fossil, the surface beneath the sensory canal pore is strongly pitted and the surface adjoining the retroarticular is vertical below, with a sharp angle, a horizontal edge, and a short posterodorsal vertical portion. The posterodorsal process behind the jaw articulation is low and robust but probably abraded.

In *P. flavescens*, the lateral surface below the canal is pitted as in the fossil, and the surface adjoining the retroarticu-
lar is angled and gently concave. In *P. fluviatilis*, the lateral surface of the bone bears fewer pits. The lateral surface of the anguloarticular in *Morone* is not pitted, and the contacts adjoining the retroarticular angle forward 45° and are concave down.

Only a few pits are found on the bone surface below the pore in *Sander volgensis*. In *S. vitreus*, the surface is not pitted but striated. The surface below the canal pore is strongly striated with some pits in both *S. canadensis* and *S. lucioperca*. The external surface adjoining the retroarticular of *S. canadensis* is angular as in *S. vitreus*, but the medial angle projects similarly to the fossil. The angles in this contact are reduced in *S. lucioperca*, more similar to *Perca*.

The fossil is most like *Sander* species in its bone shape, canal pore shape, and surfaces for adjoining the retroarticular. In general, the anguloarticular of *S. teneri* shows a mosaic of characters shared with each of the other species of *Sander* but is most similar to *S. canadensis* and *S. lucioperca*.

**Parasphenoid:** The parasphenoid of *S. teneri* is long and slender with a short, wider gill-arch attachment portion; the palatal surface bears a distinctive broad midventral keel as well as the sharp dorsal keel found in other percids. The
parasphenoid in *Perca* and *Zingel* is shorter with no keel ventrally except for the posterior part near the gill-arch attachment area. *Gymnocephalus* has a short, slender parasphenoid with a rounded double keel midventrally for attachment of eye muscles. The parasphenoid of *Morone* is also shorter with a keel developed posteriorly. Extant species of *Sander* have proportions similar to the fossil, but the ventral keel is not as developed as in *S. teneri*. The fossil bears the proportions of *Sander* spp. but is unique among species of *Sander* in the form of the mid-ventral keel.

The features of the cleithrum, anguloarticular, and parasphenoid bones that we can assess indicate to us that the placement of the new species is within the genus *Sander*.

**Relationships within Sander**

Several molecular analyses have included more than one species of *Sander*. These studies (Billington et al. 1991; Faber and Stepien 1998; Sloss et al. 2004) indicate that the two North American species (*S. vitreus* and *S. canadensis*) form a monophyletic group that is the sister to the group formed by the two Eurasian species (*S. volgensis* and *S. lucioperca* — none of the analyses included *S. marinus*). If these relationships are correct, *S. teneri* might be expected to be most similar to the two North American species of *Sander* unless multiple lineages of the genus are present in North America. A more robust test of the relationships of *S. teneri* is not possible at present, as there are few or no phylogenetic analyses of percids using osteological characters that are relevant to the fossil elements. However, we here suggest that *S. teneri* is indeed closer to the two North American species of *Sander* based on the features described previously.

**Discussion**

**Palaeoenvironment**

The Beaver Pond site preserves the fossil-bearing peat deposits intercalated with sands and gravels. The peat contains fossils that include mostly extant species of mosses and mainly wetland species of vascular plants (Dawson and Harington 2007). The preserved plants (larch (dominant), spruce, pine, alder, and birch) indicate an open woodland habitat (Tedford and Harington 2003). Molluscs have also been recovered (Dawson and Harington 2007). Aquatic vertebrate fossils (frogs, scaup duck, the small beaver *Dipoides*, and the fish reported here) have been collected, as well as other mammals (Dawson and Harington 2007). The mammals from the site (beaver, rabbit, a small canid, shrew, a cricetid rodent, mustelids, horse, deer, and bear) indicate a mixed North American – Asian fauna (Tedford and Harington 2003) and represent genera that are known from Miocene and Pliocene localities further south in North America and Asia (Dawson and Harington 2007). The mammalian fossils for the most part represent extinct species with their...
nearest modern relatives now found considerably farther south (Ballantyne et al. 2006). However, Dawson and Harington (2007) noted that some fossil mammals at the Beaver Pond site also indicate endemism in a region of the High Arctic.

Palaeobotanical evidence shows that the climate was much warmer in the Pliocene than it is today (Mathews and Fyles 2000), and climatic range analysis of the fossil beetle assemblage suggests temperatures 10–15 °C warmer than present with winter lows averaging ~27 °C in the coldest month and summer highs averaging ~12 °C (Elías and Mathews 2002). Ballantyne et al. (2006) obtained similar temperature estimates from fossil wood. Stable oxygen isotopes in combination with annual ring-width of larch from the Beaver Pond site yielded a mean annual temperature at the site of between −7.4 and −3.6 °C, ~14.2 °C warmer than today (Ballantyne et al. 2006). A similar temperature range in North America today is found in mid-latitude areas of Central Canada and mid to northern areas of the Prairies, as well as in southern Yukon Territory.

The pond itself was likely no more than 3 m deep based on analysis of siliceous microfossils (Harington 2003). This shallow, quiet environment would likely increase the water temperature within the pond compared to flowing streams in the surrounding areas. The confined nature and shallow depth would have constrained the diversity of fishes in the pond particularly if winter or summer hypoxia and restricted movement were factors. There is some evidence, based on dropstones, that ice formed on the pond surface in winter. Although there is as yet no further evidence as to whether the pond resulted from the construction of a dam by beavers, the following is worth noting. Keast and Fox (1990) found a beaver pond in Ontario to be occupied only by smaller fishes, including three perciforms: smaller individuals of *P. flavescens* (yellow perch), *Lepomis gibbosus* (pumpkinseed), and a percid of small adult size *Etheostoma exile* (Iowa darter). Large-bodied perciforms such as walleye (*S. vitreus*) were not reported from the beaver pond. However, the Strathcona Fiord fossil represents a fairly small individual.

**Palaeobiogeography**

Although freshwater perciform fishes have been found in Eocene deposits of North America (e.g., Priscacaridae, Mioplosidae; Cavender 1998), the earliest members of the family Percidae in the continent were previously only known from the Pleistocene with remains identified as *Perca, Sander, Etheostoma*, and *Percina* (Cavender 1998); the oldest percids elsewhere are probably those skeletal remains from the Miocene of Siberia (Sytchevskaya 1989; Cavender 1998) or otoliths from the Oligocene of Europe (Weiler 1961). The diversification of North American Percidae, including the strong differentiation of *P. flavescens* and *P. fluviatilis*, suggests that percids have been in North America for much of the Cenozoic.

Cavender (1998) noted that the distribution of fossil and living percids suggested a Tertiary circumpolar distribution of the family with subsequent displacement southwards caused by the glaciations of the Plio-Pleistocene. He supported the idea that much of the North American freshwater fauna was the result of Siberian forms arriving from the west by crossing the northern Pacific. An alternate hypothesis suggests the North American fauna at least in part was derived from the east — invaders crossed the northern Atlantic prior to the Eocene to reach North America (e.g., Collette and Bănărescu 1977; Gaudant 1988).

Three hypotheses of the origin of *Perca* and *Sander* in North America — one Pacific and two Atlantic — have been well summarized by Carney and Dick (2000) although they were specifically referring to the genus *Perca*. In essence, these fish may have arrived via the Bering Isthmus in the Pleistocene (Collette and Bănărescu 1977), which is the Pacific route; they may have arrived from Europe via a North Atlantic land connection during the Oligocene or earlier or have been present in both Europe and North America prior to the loss of connection between the two in the early Tertiary; or they may have traversed the North Atlantic during the late Pleistocene via brackish water at the edge of retreating glaciers (Čihař 1975; Faber and Stepień 1998). These alternate hypotheses for the dispersal of the percid genera shared between North America and Europe (*Perca* and *Sander*) are supported by different evidence.

A barrier to freshwater dispersal via Beringia is assumed to have been present prior to ~1.5 Ma because of the assumed timing of glaciations (during glacial periods, the ice barred these fish from using the Bering Isthmus, whereas during interglacial marine waters barred the route). However, Carney and Dick (2000) noted that the Pleistocene fossils in North America are much farther south than the southern edge of the ice sheets, indicating *Perca* at least was already in North America before the Pleistocene. McPhear and Lindsey (1970) also suggested and considered both *Perca* and *Sander* to have survived glaciation in the Mississippi refugium.

An early Tertiary Laurasian distribution of *Perca* (and similarly, *Sander*) or a dispersal from Europe to North America across the North Atlantic indicates that the genus must be at least early Oligocene in age, prior to the loss of the freshwater connection between the two continents (Carney and Dick 2000). There is an otolith record of *Perca* (*P. hassiaca*) from the early Oligocene of Germany (Weiler 1961), but the fossil skeletal record of *Perca*, with the oldest known skeletal remains in western Europe of Miocene age and the oldest North America *Perca* of Pleistocene age, indicated to Carney and Dick (2000) that the Percidae originated in Europe (which was separated from Siberia by the Obik Sea from the early mid-Cretaceous through to the Oligocene ~30 Ma (Carney and Dick 2000)) and from there dispersed into Siberia and then to North America across the North Atlantic. However, this early dispersal of percids is contradicted by molecular clock evidence, which puts the divergence between Eurasian and North American species of *Sander* much later than this, at ~7–10 Ma (Billington et al. 1990, 1991). This age similarly contraindicates a late Pleistocene northern Atlantic dispersal route proposed by Čihař (1975) but supports a Miocene dispersal (Billington et al. 1991).

Similarly, Faber and Stepień (1998) estimated divergence times from mtDNA genetic distances that supported a dispersal of *Sander* (= *Stizostedion* in their paper) from Eurasia to North America across the North Pacific (Beringian land bridge) ~4 million years ago in the early Pliocene. The ge-
netic differences found in their study indicated that the Eurasian and North American species of *Sander* diverged \( \sim 4.05 \pm 0.50 \) million years BP, the two North American species diverged \( \sim 2.75 \pm 0.40 \) million years BP, and two of the Eurasian species (*S. lucioperca* and *S. volgensis*) diverged \( \sim 1.8 \pm 0.30 \) million years BP, and populations of *S. vitreus* in the Great Lakes and the Ohio River diverged 0.029 \pm 0.005 million years BP. Even with alternate calculations using additional data that supported older divergence times, Faber and Stepien (1998) found the divergence between Eurasian and North American *Sander* was still placed in the early Pliocene. They noted that these divergence times support a Pliocene Beringian (North Pacific) dispersal of *Sander* from Europe to North America and that this route should have been available during low sea levels, which are believed to have occurred in the middle or late Miocene and also in the early Pliocene.

Land connections between Siberia and North America are believed to have been present during the Pliocene at 4.8, 3.7, 2.5, and 2 million years ago; and marine waters are believed to have connected the Arctic and Pacific oceans and therefore barred migration of freshwater organisms from 4.2–3.0, 2.5, 2.2 Ma (Ogasawara 1998). The proposed connection at 4.8 Ma is the youngest potential time when the Ellesmere Island perchid could have invaded North America. However, Dawson and Harington (2007) indicated that interbasin exchange between the two areas and subsequent differentiation of organisms occurred prior to this time, likely before the 5.5–4.8 Ma opening (now revised to 5.4–5.5 Ma by Gladenkov et al. 2002) of the Bering Strait.

The most pertinent argument against the Bering Isthmus route for percids has been the modern distribution of these fishes in Eurasia and North America. Both *Perca* and *Sander* are distributed only in the western part of Siberia and east of the Rockies in North America, with no modern populations occurring naturally in the Pacific regions (McPhail and Lindsey 1970; Čihař 1975). However, the discovery of the Ellesmere Island fossils reported here at the very least demonstrates that some of these fishes had a much expanded range in the past.

The find of a fossil *Sander* from Ellesmere Island deposits \( \sim 4–5 \) Ma indicates that migration from Eurasia to North America may have occurred in the Late Tertiary via the Bering Isthmus. This small fish clearly indicates that percids were present in North America by \( \sim 4 \) Ma and living in the High Arctic.

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Appendix A

List of Comparative Material Examined

Centrarchidae
Ambloplites rupestris CMN 78-0143
Archoplites interruptus UMMZ 179981
Lepomis cyanellus FMNH 60009
L. gulosus FMNH 10108
L. macrochirus CMN 78-0194
Micropterus dolomieui CMN 81-0825
Pomoxis nigromaculatus CMN Z4176
P. sparoides (= P. nigrumaculatus) FMNH 83733

Centropomidae
Centropomus undecimalis ROM 1599

Embiotocidae
Cymatogaster aggregata CMN Z4210
Embiotoca lateralis CMN 77-0272

Gerreidae
Gerres nigri CMN 83-0271
Diapterus auratus CMN 87-0348

Gobiidae
Rhinogobiops nicholsii CMN 69-2435

Latidae
Lates microlepis UMMZ 199757

Mioplosidae
Mioplosus labracoides (fossil material) UALVP 24234

Moronidae
Morone americana FMNH 50206; CMN 76-0054
M. chrysopterus FMNH 63703
M. saxatilis FMNH 10120 (as Morone lineatus); UAMZ uncataloged

Mugilidae
Mugil cephalus UAMZ uncataloged; CMN Z-617

Percidae
Etheostoma caeruleum UAMZ uncataloged

Gymnocephalus cernuus

Published by NRC Research Press
Perca flavescens FMNH 62324; UAMZ 4821; CMN 87-0018; various UMMZ assessed for cleithrum spine counts

Perca fluviatilis UAMZ 6962 cleared and stained; various UMMZ assessed for cleithrum spine counts

Percina caprodes CMN 87-0364

Romanichthys valsanicola UAMZ 6785 and 6865, Romania, both cleared and stained

Sander vitreus FMNH 72205, John G. Shedd Aquarium; CMN 73-0231b, Ontario, Canada; 81-0828, Ontario, Canada; 81-0847, Manitoba, Canada; CMN Z4184; UAMZ uncatalogued, Alberta, Canada; various UMMZ assessed for cleithrum spine counts

Sander canadensis UAMZ 6992 and 6993, Alberta, Canada, both cleared and stained; CMN 77-0338, 78-0178, 78-0181, 78-0182, all from Ontario, Canada; various UMMZ assessed for cleithrum spine counts

Sander lucioperca UAMZ 6921 and 6922, Tulcea County, Sulina, Romania, both cleared and stained; various UMMZ assessed for cleithrum spine counts

Sander volgensis UAMZ CS 164, Belaton, Tihany

Zingel zingel UAMZ 58.18.1

Sciaenidae

Aplodinotus grunniens CMN 76-198 and 60-462a