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ARTICLE

New records from Banks Island expand the diversity of Eocene fishes from Canada's western Arctic Greenhouse

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Abstract: Eocene vertebrates from the Canadian Arctic, including sharks, bony fishes, turtles, crocodylians, birds, and mammals, have provided strong evidence for relatively warm ice-free conditions in the Arctic during the Eocene Greenhouse interval. Recent expeditions to Banks Island (Northwest Territories) in the western Arctic have recovered a relatively more marine-influenced Eocene fauna, including sand tiger sharks, bony fishes, turtle shell fragments, and a single crocodylian specimen. We report here on new additions to this fauna, including diagnostic large scales that confirm the presence of *Amia* in the western Arctic. One very large lateral line scale corresponds to a fish approximately 1.4 m in total length, larger than the maximum size for extant *Amia calva*. We also recovered approximately 100 distinctive teeth that we assign to the teleost genus *Eutrichiurides*, which is otherwise known from lower latitude Paleogene sites in the United States, India, Africa, and Europe. The genus is interpreted as an ambush predator in shallow marine environments, consistent with the inferred Eocene paleoenvironment of Banks Island. The presence of *Eutrichiurides* in the Arctic adds a distinctive new element to the Eocene Greenhouse fauna and is intriguing with respect to the biogeography and dispersal capabilities of this taxon.

Key words: Eocene, Arctic, greenhouse, climate optimum, Banks Island, fishes, *Amia*, *Eutrichiurides*.

Résumé : Les vertébrés éocènes de l'Arctique canadien, y compris les requins, les poissons osseux, les tortues, les crocodiliens, les oiseaux et les mammifères, fournissent une preuve solide indiquant des conditions sans glace relativement chaudes dans l'Arctique pendant l'intervalle de « serre éocène ». Les expéditions récentes à l'île Banks aux Territoires du Nord-Ouest dans la région ouest de l'Arctique ont récupéré une faune éocène plutôt d'influence marine, y compris des requins-taureaux, des poissons osseux, des fragments d'écailles de tortue et un seul spécimen crocodilien. Nous faisons rapport ici de nouveaux ajouts à cette faune, y compris des grandes écailles diagnostiques qui confirment la présence d'Amia dans la région ouest de l'Arctique. Une très grande écaille de la ligne latérale correspond à un poisson d'environ 1,4 m de longueur totale, plus grand que la taille maximale pour le genre Amia calva existant. Nous avons aussi récupéré à peu près 100 dents distinctives que nous attribuons au genre téléostéen Eutrichiurides, beaucoup plus connu aux sites de latitude inférieure de Paléogène aux États-Unis, en Inde, en Afrique et en Europe. Le genre est considéré comme un prédateur d'embuscade dans les milieux marins peu

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profonds, ce qui concorde avec le paléoenvironnement éocène déduit de l'île Banks. La présence d'Eutrichiurides en Arctique ajoute un nouvel élément distinctif à la faune de serre éocène et ceci est fascinant du point de vue de la biogéographie et du pouvoir de dispersion de ce taxon. [Traduit par la Rédaction]

Mots-clés : éocène, Arctique, serre, optimum climatique, île Banks, poissons, *Amia*, *Eutrichiurides*.

Introduction

The discovery over the past several decades of a wide range of late early to middle Eocene (approximately 50–53 Ma) vertebrates from the Canadian Arctic has been instrumental to developing the concept of the "Greenhouse Earth" interval during which global temperatures were significantly higher than at present and the Arctic experienced mild temperate conditions with above-freezing winters (Dawson et al. 1976; Estes and Hutchison 1980). A host of vertebrates, including fishes, turtles, lizards, alligators, and a diverse mammalian fauna that includes tapirs, primates, and the hippo-like *Coryphodon*, have been recovered from Ellesmere Island, from nonmarine sediments of the lower–middle Eocene Margaret Formation of the Eureka Sound Group (Eberle and Greenwood 2012 and references therein).

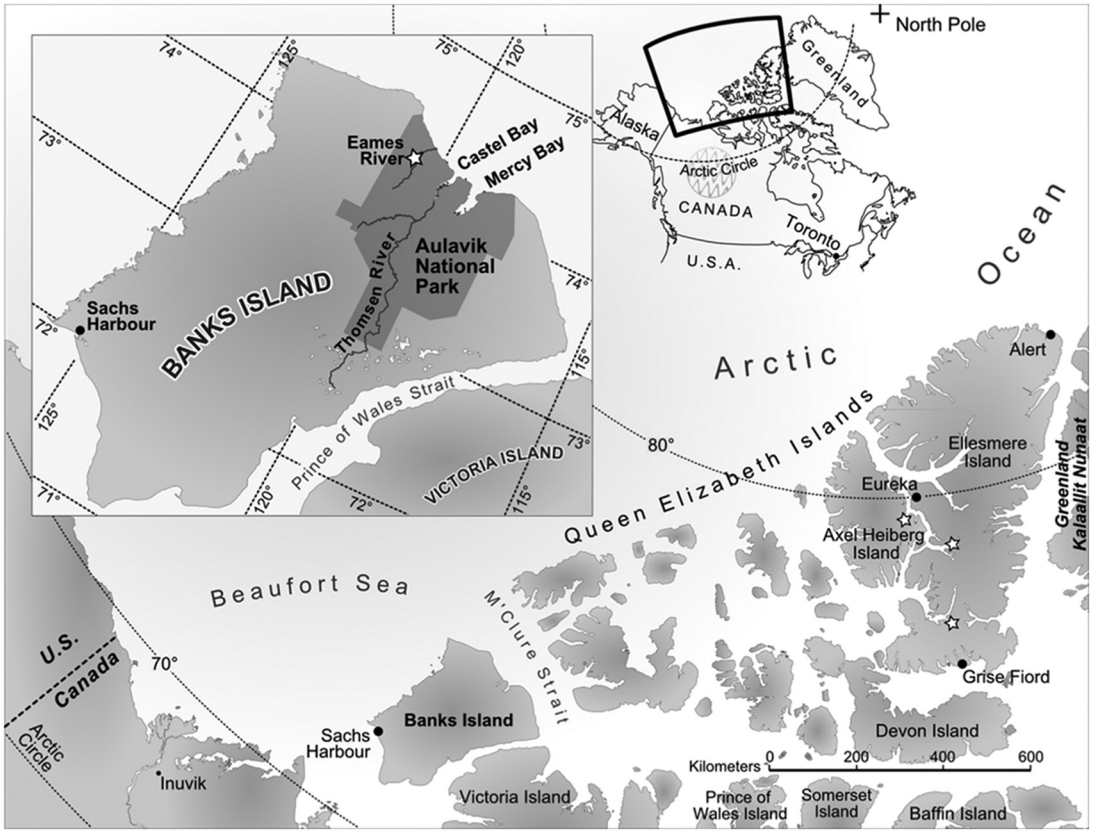
Banks Island, at the far western edge of the Canadian Arctic archipelago approximately 1100 km west of Ellesmere (Fig. 1), also preserves a significant Eocene Greenhouse assemblage, but one that complements and augments the finds from Ellesmere in that it is more marine-influenced and samples a less terrestrial paleoenvironment (Eberle et al. 2014; Padilla et al. 2014). Eberle et al.'s (2014) recent report documented bony fish (the gar *Atractosteus*, possible amiid, esocids, and indeterminate teleosts) and crocodyliform (a single eusuchian centrum) fossils and Padilla et al. (2014) described the chondrichthyan fauna, which is notable for its relatively low diversity but very high numbers of teeth of the sand tiger sharks (*Carcharias* and *Striatolamia macrota*).

Here, we further expand the Eocene fish fauna from Banks Island, including an unambiguous and more informative record for amiids (*Amia* sp.) and a large sample of teeth of the "scombroid" teleost *Eutrichiurides*. These discoveries were made from strata of the lower–middle Eocene Cyclic Member of the Eureka Sound Formation at sites near the Eames River within the northern part of Aulavik National Park on northern Banks Island (Fig. 1). The new finds definitively expand the range of amiids to the western edge of the Canadian Arctic during the Greenhouse interval and add a distinctive new predatory teleost to the Arctic that is otherwise known from a range of lower latitude Eocene sites.

Materials and methods

The fossils were collected on Banks Island in 2002, 2010, and 2012. All required permits were obtained from the Parks Canada, Western Arctic Field Unit, the authority for research activities in Aulavik National Park. Fossils are curated in the collections of the Canadian Museum of Nature (CMN) in Ottawa, Canada, and loaned to the University of Colorado Museum of Natural History (UCM) and Michigan State University Museum (MSUM) for study. Identifications were made on the basis of comparisons with specimens at the Natural History Museum (London) (NHM) and the Field Museum of Natural History (FMNH), Chicago, as well as collections held at UCM and MSUM. Terminology for amiid specimens follows Grande and Bemis (1998). We note that additional Eocene fish specimens from Banks Island have been collected that are not included in this report; our focus here is on the diagnostic and most informative material from Banks Island that has not previously been described. Nomenclature and classification follow Betancur-R et al. (2013).

Fig. 1. Canadian Arctic islands and Banks Island (inset). Fossils described here were collected from exposures along the Eames River (starred) in Aulavik National Park. Modified from Eberle and Greenwood (2012).



Geologic setting and age

The fossils described below were collected over the course of three field seasons (2004, 2010, and 2012) from CMN localities (BKS04-15, BKS04-19, and BKS04-22) that sample Eocene strata near the Eames River inside Aulavik National Park on northern Banks Island, Northwest Territories, Canada (approximately 74°10′N, 120°45–46′W, approximately 76°N paleolatitude according to GEOMAR data) (Fig. 1). Precise locality data are not provided here because the localities are within the boundaries of a Canadian national park; that information is available to qualified researchers, on request from the CMN.

The Eocene vertebrate-bearing strata are assigned to the Cyclic Member of the Eureka Sound Formation (Miall 1979; Eberle et al. 2014; Padilla et al. 2014). The Cyclic Member consists of coarsening-upward cycles of shale, silt, unconsolidated sand, paleosol, and lignitic coal, interpreted as a deltaic sequence in a marginal marine setting (Miall 1979). The unit preserves abundant shark teeth, bivalves, the trace fossil *Ophiomorpha* (interpreted as a thalassinidean shrimp burrow and generally indicative of a shallow-water, moderately high-energy coastal marine environment according to Frey et al. (1978)). Rare marine microfossils (foraminiferans and radiolarians) have also been documented from the Cyclic Member (Miall 1979). The fossils described here were recovered as float, alongside hundreds of shark teeth, on unconsolidated sands in the Cyclic Member. This was supplemented by dry screening to recover smaller specimens (primarily small shark teeth).

The Eocene age for these fossil localities is based on pollen samples initially analyzed by Hopkins (1974, 1975) and reported by Miall (1979). Reanalysis of four pollen samples collected near the Eames River by Sweet (2012) (discussed in Padilla et al. 2014) suggests that the localities are late early to middle Eocene in age and spanned the early Eocene Climate Optimum based on species richness and the abundance of *Caryapollenites* spp., *Ericipites*, *Intratriporopollenites* (Tilia), *Nyssapollenites* sp., and *Quercoidites* (oak) pollen. The presence of *Pistillipollenites* suggests a probable minimum age of middle Eocene for the samples, while the absence of *Aquilapollenites tumanganicus* Bolotnikova and closely allied species, infrequent occurrences of *Momipites* spp., and the richness of the angiosperm component of the assemblages precludes an earliest Eocene age (Padilla et al. 2014).

Early–middle Eocene Arctic climate was characterized by warm wet summers and mild winters. Estimates of early–middle Eocene Arctic mean annual temperature range from 8 to 15 °C, summers probably reached 19–25 °C, and winters were above freezing (Eberle et al. 2010; Eberle and Greenwood 2012). Based upon carbon isotope analysis of mummified wood from the Cyclic Member near Muskox River on northern Banks Island, Schubert et al. (2012) concluded that the Eocene forests on Northern Banks experienced three times more precipitation during summer than during winter, a seasonal pattern analogous to today's temperate forests of eastern Asia. Mild coastal marine temperatures are supported by the presence of the sand tiger shark genera *Striatolamia*, *Carcharias*, and *Odontaspis*, whose living relatives inhabit temperate and tropical waters around the world, and the ray *Myliobatis*, whose present-day distribution is restricted to tropical and warm-temperate seas (Padilla et al. 2014 and references therein). In addition to being warm, the shallow coastal waters of the Eocene Arctic Ocean were brackish, as indicated by oxygen isotope analysis of shark teeth from the Cyclic Member (Kim et al. 2014). This is consistent with paleogeographic reconstructions of a largely isolated Arctic Ocean during the early–middle Eocene Greenhouse and an intensified hydrologic cycle with precipitation exceeding evaporation (Pagani et al. 2006). The Banks Island biota would have experienced months of continuous daylight during the summer and continuous darkness during the polar winter, as the Eocene paleolatitude of the Eames River localities was approximately 76°N (Eberle and Greenwood 2012) and well within the Arctic Circle.

Systematic paleontology

Superclass Actinopterygii Cope, 1887
Subclass Neopterygii Regan, 1923
Order Amiiformes Hay, 1929
Family Amiidae Bonaparte, 1838
Amia Linnaeus, 1756
Amia sp.

Referred specimens. CMN 57523 (lateral line scale) (Fig. 2), CMN 57514 (scale).

Locality and horizon. Aulavik National Park, northern Banks Island, NWT, Canada; Cyclic Member, Eureka Sound Formation, late early – middle Eocene.

Description. CMN 57523 (Fig. 2) is a nearly complete large lateral line scale preserved on the internal surface of a small sideritic nodule that has split open to reveal the fossil. The subrectangular scale is slightly rounded at the anterior and posterior corners, slightly deeper anteriorly, and measures 36 mm in anterior–posterior length as preserved and 31 mm where it is deepest from the dorsal to ventral edges of the scale. The lateral line can clearly be seen as an open canal that penetrates the midregion of the scale. The posterior edge of the scale bears a small, ovoid thickened area that is ornamented with raised anastomosing ridges and shallow sunken troughs, representing the free-field area of the scale that would have been externally exposed when the scale was in position along

Fig. 2. Lateral line scale of *Amia* sp. (CMN 57523), anterior to the left, ornamented free field of scale on the right. Scale bar = 1 cm.

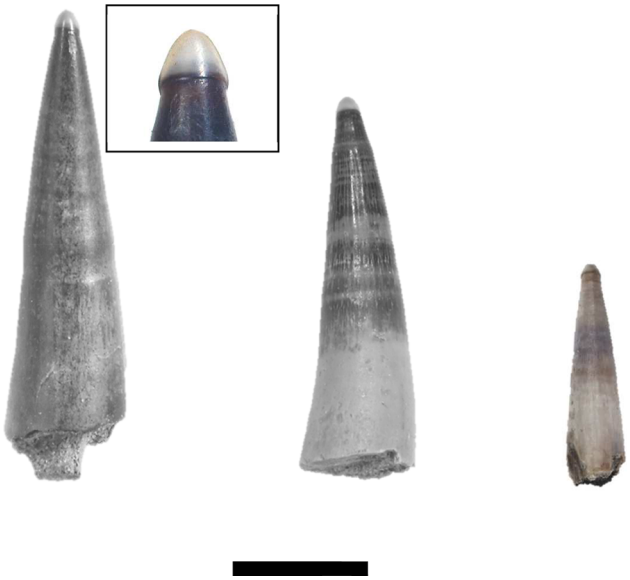
the body. The anterior overlapped area of the scale is extensive and thin and bears very fine subparallel ridges that subtly diverge as they pass along the surface of the scale towards the slightly deeper anterior edge.

This scale is strikingly similar to lateral line scales of the extant species *Amia calva* (see Grande and Bemis 1998, Fig. 92, p. 147), although the extant species has lateral line scales that are slightly more anterior–posteriorly elongated in proportion. Those authors illustrated (their Fig. 92c) a lateral line scale from a "large individual" that measured 60.8 cm in standard length (SL); the scale measures 17 mm in length, and according to the relation between SL: Total Length (TL) in *Amia calva*, that would correspond to a fish with a TL of approximately 71 cm (in *Amia*, TL = SL(1.169); fishbase.org, accessed 23 January 2017). Assuming similar proportions in the Banks Island *Amia*, a lateral line scale with a length of 36 mm would correspond to a fish of approximately 1.4 m in TL, a length that would exceed the recorded maximum TL of 1.07 m for extant *Amia calva* (Page and Burr 1991).

Superclass Actinopterygii Cope, 1887
Subclass Neopterygii Regan, 1923
Infraclass Teleostei Müller, 1845
Subdivision Percomorphaceae (sensu Betancur-R et al. 2013)
Order Scombriformes (=Stromateoidei sensu Li et al. 2009)
Family Trichiuridae Rafinesque-Schmaltz, 1815
Eutrichiurides sp. Casier, 1944

Referred specimens. CMN 57502 (1 tooth), 57504 (17 teeth), 57505 (6 teeth), 57506 (1 tooth), 57507 (1 tooth), 57509 (14 teeth), 57510 (1 tooth), 57511 (1 tooth), 57524 (5 teeth), 57525 (6 teeth), 57526 (7 teeth), 57528 (10 teeth), 57532 (2 teeth), 57535 (30 teeth).

Fig. 3. Teeth of *Eutrichiurides* sp. from the Eocene of Banks Island. Left to right: CMN 57507 (inset shows the expanded "arrowhead" apex of the tooth), CMN 57505, and CMN 57528. Scale bar = 5 mm.



Locality and horizon. Aulavik National Park, northern Banks Island, NWT, Canada; Cyclic Member, Eureka Sound Formation, late early–middle Eocene.

Description. Approximately 100 teeth recovered from Banks Island (see Fig. 3) very closely match teeth assigned to the "scombroid" teleost *Eutrichiurides* from lower latitude Paleocene and Eocene sites in the United Kingdom, Europe, Angola, Morocco, India, and the United States (North and South Dakota) (see Casier 1944; Arambourg and Bergounioux 1952; Pickford 1987; Kemp et al. 1990; Cvancara and Hoganson 1993; Merle et al. 2002; Monsch 2004; Dutheil et al. 2006; Kumar et al. 2007). Teeth assigned to this taxon from the Eocene of Banks Island range in size from approximately 10 to 25 mm in length, are narrowly elongate and sharply pointed when well preserved, erect to shallowly posteriorly recurved, and conical in cross section. The outer surfaces of the teeth bear very fine longitudinal striations and show subtle lateral banding that gives the teeth the appearance of varying from darker to lighter zones along the length of the teeth. The apices of the teeth characteristically bear a slightly expanded translucent cap that in close view has the appearance of a small expanded spear point or arrowhead positioned on the apex of the tooth (see Fig. 3). Teeth that are well preserved at their base show an expanded area of bone that marks the site of attachment to the jaw. The largest teeth of this taxon are interpreted to be premaxillary fangs (Monsch 2004). The Banks Island teeth are fully consistent with Monsch's (2004) description of *Eutrichiurides* teeth as diagnostic at the generic level based on being comparatively large, semiconical, elongate to stoutly erect, with small slightly expanded caps at their apices, and not as laterally compressed as the otherwise similar teeth of the related trichiurins.

Discussion

The scales of *Amia* establish that amiid fishes were present at the far western edge of the Canadian Arctic in the Eocene, a further expansion of their previously known range from

the eastern Canadian Arctic (Estes and Hutchison 1980; Eberle and Greenwood 2012) and reassuring given the uncertainty over an earlier account (Eberle et al. 2014) that tentatively identified amiids on Banks Island based on less diagnostic material. The strikingly large lateral line scale indicates that these fish were not only present at this far northern latitude but likely grew to a size significantly larger than extant *Amia calva*. Ray (1960) and Van Voorhies (1996) maintained that ectotherms, including freshwater fishes, follow Bergmann's Rule (Bergmann 1847; Mayr 1956) in which species at higher latitudes exhibit larger body size than their lower latitude close relatives. Belk and Houston (2002), however, convincingly argued against this in their study, which included a large sample size of representatives of 18 relatively large-bodied Northern Hemisphere fish species — they concluded that North American freshwater fishes in general do not follow Bergmann's Rule (although *Amia* was not included in their analysis).

It is not surprising that amiids would thrive in the paleoenvironment interpreted for Banks Island — relatively warm winters above freezing and in a marginal marine setting with low salinity (Kim et al. 2014). Amiids are known to be tolerant of poorly oxygenated conditions and are capable of air-breathing and even aestivation (Grande and Bemis 1998) and so would have been well suited to survive a variety of climatic conditions during the Eocene Greenhouse interval. It can be reasonably assumed that an amiid well in excess of 1 m in length would have been a formidable predator in the Eocene Arctic ecosystem, as living bowfins are voracious predators that consume a variety of prey.

The identification of *Eutrichiurides* in the Arctic Eocene is a bigger surprise, as previous records of this taxon are from much lower latitude sites in the United Kingdom, central Europe, India, Africa, and the United States. The recovery of several dozen teeth of this taxon on Banks Island suggests that it was a regular element of the fauna and not an accidental or sporadic visitor. Eocene paleogeographic reconstructions, e.g., those of Blakey (see Fig. 3 in Eberle and Greenwood 2012), show an open Turgai Strait connecting the Arctic Ocean with the Atlantic and possibly an open Eocene channel between Greenland and Europe. Either or both could have served as dispersal corridors for biotic interchange between the Arctic Ocean and Europe, India, and Africa, although caution is warranted on the basis of this one taxon. *Eutrichiurides* is a distinct new addition to the Arctic Eocene and to date has not been reported from the Eocene of Ellesmere Island, which has gars, amiids, and pikes in common with Banks Island. As such, *Eutrichiurides* may indicate some level of previously unrecognized regional faunal differentiation in Arctic Eocene Greenhouse fishes. Among the fishes now known from the Arctic Eocene, the only recent survivors above the Arctic Circle are the esocids (pikes and their allies), which occur on Banks and Ellesmere islands in the Eocene (see Eberle et al. 2014), and today have a Holarctic distribution at latitudes as high as 74°. Osteoglossomorphs are also known from the North American Arctic but so far have only been reported from Late Cretaceous deposits there (e.g., Grande 1986).

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References

Arambourg, C., and Bergounioux, F.-M., 1952. Les Vertébrés fossiles des gisements de phosphates: (Maroc, Algérie, Tunisie). Division des Mines et de la Géologie, Sevice Géologique Notes et Mémoires. Vol. 92. pp. 1–372.

Belk, M.C., and Houston, D.D. 2002. Bergmann's rule in ectotherms: A test using freshwater fishes. Am. Nat. **160**(6): 803–808. doi: 10.1086/343880. PMID: 18707466.

Bergmann, C. 1847. Über die Verhältnisse der Wärmoekonomie der Thiere zu ihrer Grösse. Göttinger Studien. **1**: 595–708.

Betancur-R, R., Broughton, R.E., Wiley, E.O., Carpenter, K., López, J.A., Li, C., Holcroft, N.I., Arcila, D., Sanciangco, M., Cureton II, J.C., Zhang, F., Buser, T., Campbell, M.A., Ballesteros, J.A., Roa-Varon, A., Willis, S., Borden, W.C., Rowley, T., Reneau, P.C., Hough, D.J., Lu, G., Grande, T., Arratia, G., and Ortí, G. 2013. The tree of life and a new classification of bony fishes. PLoS Curr. doi: 10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288. PMID: 23653398.

Casier, E. 1944. Les genres *Trichiurides* et *Eutrichiurides*. Leurs affinités respective. Bull. Musée R. Histoire nat. Belgique. **20**(11): 1–10.

Cvancara, A.M., and Hoganson, J.W., 1993. Vertebrates of the Cannonball Formation (Paleocene) in North and South Dakota. J. Vertebr. Paleontol. **13**(1): 1–23. doi: 10.1080/02724634.1993.10011484.

Dawson, M.R., West, R.M., Langston, W., and Hutchison, J.H. 1976. Paleogene terrestrial vertebrates, northernmost occurrence, Ellesmere Island, Canada. Science. **192**: 781–782. doi: 10.1126/science.192.4241.781.

Dutheil, D.B., Moreau, F., and De Plöeg, G., 2006. Les ichthyofaunes du gisement à ambre de Le Quesnoy (Paléocène et Éocène du bassin de Paris, France). Cossmanniana. **11**(1–4): 1–13.

Eberle, J.J., and Greenwood, D.R. 2012. Life at the top of the greenhouse Eocene world — a review of the Eocene flora and vertebrate fauna from Canada's High Arctic. Geol. Soc. Am. Bull. **124**(1/2): 3–23. doi: 10.1130/B30571.1.

Eberle, J.J., Fricke, H.C., Humphrey, J.D., Newbrey, M.G., and Hutchison, J.H. 2010. Seasonal variability in Arctic temperatures during early Eocene time. Earth Planetary Sci. Lett. **296**: 481–486. doi: 10.1016/j.epsl.2010.06.005.

Eberle, J.J., Gottfried, M.D., Hutchison, J.H., and Brochu, C.A. 2014. First record of Eocene bony fishes and crocodyliforms from Canada's Western Arctic. PLoS ONE. **9**(5): 1–7. doi: 10.1371/journal.pone.0096079. PMID: 24788829.

Estes, R., and Hutchison, J.H. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeogr. Palaeoclimatol. Palaeoecol. **30**: 325–347. doi: 10.1016/0031-0182(80)90064-4.

Frey, R.W., Howard, J.D., and Pryor, W.A. 1978. Ophiomorpha: its morphologic, taxonomic, and environmental significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. **23**: 199–229. doi: 10.1016/0031-0182(78)90094-9.

Grande, L. 1986. The first articulated freshwater fish from the Cretaceous of North America. Palaeontology. **29**: 385–371.

Grande, L., and Bemis, W.E. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Soc. Vertebr. Paleontol. Mem. **4**: iv–690. doi: 10.2307/3889331.

Hopkins, W.S. 1974. Report on 36 field samples from Banks Island, District of Franklin, Northwest Territories. Submitted by A.D. Miall, 1973 (NTS 88C, F, 98D, E). Geological Survey of Canada. Paleontological Report KT-01-WSH-1974.

Hopkins, W.S. 1975. Palynology report on 44 field samples from Banks Island. Submitted by A.D. Miall, 1974 (NTS 88B, C, F, 97H, 98D, E). Geological Survey of Canada. Paleontological Report KT-10-WSH-1975.

Kemp, D., Kemp, L., and Ward, D.J. 1990. An illustrated guide to the British Middle Eocene vertebrates. David Ward, London, UK.

Kim, S.L., Eberle, J.J., Bell, D.M., Fox, D.A., and Padilla, A. 2014. Evidence from shark teeth for a brackish Arctic Ocean in the Eocene greenhouse. Geology. **42**(8): 695–698. doi: 10.1130/G35675.1.

Kumar, K., Rana, R.S., and Singh, H. 2007. Fishes of the Khuiala Formation (early Eocene) of the Jaisalmer Basin, western Rajasthan, India. Curr. Sci. **93**(4): 553–559.

Li, B., Dettai, A., Cruaud, C., Couloux, A., Desoutter-Meniger, M., and Lecointre, G. 2009. RNF213, a new nuclear marker for acamthomorph phylogeny. Mol. Phylogenet. Evol. **50**(2): 345–363.

Mayr, E. 1956. Geographical character gradients and climatic adaptation. Evolution. **10**: 105–108. doi: 10.1111/j.1558-5646.1956.tb02836.x.

Merle, D., Baut, J.P., Ginsburg, L., Sagne, C., Hervet, S., Carriol, R.P., Vénec-Peyré, M.T., Blanc-Valleron, M.M., Mourer-Chauviré, C., Arambol, D., and Viette, P. 2002. Découverte d'une faune de vertébrés dans l'Oligocène inférieur de Vayres-sur-Essonne (bassin de Paris, France) : Biodiversité et paléoenvironnement. C. R. Palevol. **1**(2): 111–116. doi: 10.1016/S1631-0683(02)00018-0.

Miall, A.D. 1979. Mesozoic and tertiary geology of Banks Island, Arctic Canada. Geol. Surv. Can. Mem. **387**: 1–235. doi: 10.1017/S0016756800032726.

Monsch, K.A. 2004. Revision of the scombroid fishes from the Cenozoic of England. Earth Environ. Sci. Trans. R Soc. Edinb. **95**: 445–489. doi: 10.1017/S0263593300001164.

Padilla, A., Eberle, J.J., Gottfrieed, M.D., Sweet, A.R., and Hutchison, J.H. 2014. A sand tiger shark-dominated fauna from the Eocene Arctic greenhouse. J. Vertebr. Paleontol. **34**(6): 1307–1316. doi: 10.1080/02724634.2014.880446.

Pagani, M., Pedentchouk, N., Huber, M., Sluijs, A., Schouten, S., Brinkhuis, H., Sinninghe Damsté, J.S., Dickens, G.R., Backman, J., Clemens, S., Cronin, T., Eynaud, F., Gattacceca, J., Jakobsson, M., Jordan, R., Kaminski, M., King, J., Koc, N., Martinez, N.C., McInroy, D., Moore, T.C. Jr., O'Regan, M., Onodera, J., Pälike, H., Rea, B., Rio, D., Sakamoto, T., Smith, D.C., St John, K.E.K., Suto, I., Suzuki, N., Takahashi, K., Watanabe, M., and Yamamoto, M., for Expedition 302 Scientists. 2006. Arctic hydrology during global warming at the Palaeocene/Eocene thermal maximum. Nature. **442**: 671–675. doi: 10.1038/nature05043.

Page, L.M., and Burr, B.M. 1991. A field guide to freshwater fishes of North America north of Mexico. Houghton Mifflin Harcourt, Boston, Mass.
Pickford, M. 1987. Recognition of an early Oligocene or late Eocene mammal fauna from Cabinda, Angola. Rapp. Ann. Dép. Géol. Minéral. Mus. R. Afr. Cent. **1985**–**1986**: 89–92.
Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. J. Morphol. **106**: 85–108. doi: 10.1002/jmor.1051060104. PMID: 14436612.
Schubert, B.A., Jahren, A.H., Eberle, J.J., Sternberg, L.S.L., and Eberth, D.A. 2012. A summertime rainy season in the Arctic forests of the Eocene. Geology. **40**: 523–526. doi: 10.1130/G32856.1.
Sweet, A.R. 2012. Applied research report on five outcrop samples collected by Andrew Miall from northern Banks Island, NWT (NTS Map Sheets 098E/01, 08, 09). Geological Survey of Canada, Paleontological Report ARS-2012-01.
Van Voorhies, W.A. 1996. Bergmann size clines: a simple explanation for their occurrence in ectotherms. Evolution. **50**: 1259–1264. doi:10.1111/j.1558-5646.1996.tb02366.x. PMID: 28565268.