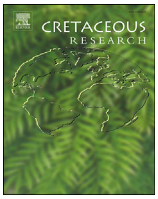
Cretaceous Research 135 (2022) 105176

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes



A new, Late Cretaceous gonorynchiform fish in the genus †*Notogoneus* from drill core of crater-lake deposits in a kimberlite maar, Northwest Territories, Canada

Terry C. Grande [a, *], Mark V.H. Wilson [a, b], Alberto V. Reyes [c], Serhiy D. Buryak [c], Alexander P. Wolfe [b], Peter A. Siver [d]

[a] *Department of Biology, Loyola University Chicago, Chicago, IL 60660, USA*
[b] *Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada*
[c] *Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta T6G 2E3, Canada*
[d] *Department of Botany, Connecticut College, New London, CT 06320, USA*

ARTICLE INFO

Article history:
Received 6 September 2021
Received in revised form
10 February 2022
Accepted in revised form 12 February 2022
Available online 19 February 2022

Keywords:
Gonorynchidae
†*Notogoneus*
Cretaceous
Campanian
Kimberlite maar
Canada

ABSTRACT

The Gonorynchiformes are a group of mostly marine fishes that are the sister group to the Otophysi (e.g., carps, tetras, catfishes). They include milkfishes (family Chanidae) and beaked sandfishes (family Gonorynchidae) among extant taxa. The only freshwater genus is the strictly fossil †*Notogoneus*, which until now contained eight species of Late Cretaceous to early Miocene age. A ninth species, †*Notogoneus* maarvelis, sp. nov., is described here from a single, small specimen found in a diamond-exploration drill core into strata deposited in a kimberlite maar lake in northern Canada. The maar crater was formed by the explosive emplacement of the "Wombat" kimberlite pipe, one of many in the nearby region. The new species is the oldest known member of the genus †*Notogoneus* and is dated by U–Pb geochronology on associated tephras as early Campanian or about 82 Ma. Although very small, the type and only specimen is very similar in morphology, meristics, and body proportions to the type species †*N. osculus*. The most important difference is that the origin of the pelvic fin in the new species is beneath vertebral centrum 26, whereas the origin of the dorsal fin is above vertebral centrum 20. In †*N. osculus*, in contrast, the two fins both originate opposite centrum 22 or 23. The new species is the only one known among those of †*Notogoneus* or the extant *Gonorynchus* in which the pelvic fin origin is well behind that of the dorsal fin. The new species agrees with †*N. osculus* and other congenerics in key attributes of the genus †*Notogoneus*, including subopercular clefts and, in the caudal skeleton, autogenous parhypural plus hypurals 1 and 2. The bones of the new species ossified at a much smaller size than did those of young individuals of †*N. osculus*, suggesting that the new species likely attained a much smaller adult size as well. This small, new species, as well as other unidentified fish fragments, was discovered in a core into maar-lake deposits within otherwise fossil-poor areas of the North American craton. Such discoveries highlight the potential importance of maar lakes and similar crater-lake settings for revealing more about fish diversity in the Late Cretaceous than has been previously known.

1. Introduction

The family Gonorynchidae (Ostariophysi: Gonorynchiformes) is represented by six genera. The only extant genus, *Gonorynchus* Scopoli, 1777, with common names including mousefish, sandfish, sand eel, beaked salmon, or beaked sandfish, is a marine Indo-Pacific genus with five valid species. Fossil genera include †*Charitosomus* von der Mark, 1885, from marine deposits of Syria and Lebanon, along with †*Ramallichthys* and †*Judeichthys* (Gayet 1982, 1985 respectively) from Cenomanian deposits of the West Bank. T. Grande (1996), T. Grande and L. Grande (2008), and Poyato-Ariza et al. (2010) suggested that all three Middle Eastern nominal genera might be synonymized with †*Charitosomus* bearing the valid name. †*Sapperichthys* Amaral et al., 2013, was more recently named as a monotypic genus from the Cenomanian of the Sierra Madre Formation of Chiapas, Mexico. †*Notogoneus* Cope, 1885, the focus of

---

* Corresponding author.
E-mail addresses: tgrande@luc.edu (T.C. Grande), mvwilson@ualberta.ca (M.V.H. Wilson), areyes@ualberta.ca (A.V. Reyes), buryak@ualberta.ca (S.D. Buryak), awolfe@ualberta.ca (A.P. Wolfe), pasiv@conncoll.edu (P.A. Siver).

https://doi.org/10.1016/j.cretres.2022.105176

this study, is a very widely distributed and long-lived genus with species that have been found in Late Cretaceous to early Miocene deposits of North America, Australia, Germany, Asia, and Europe. The family is diagnosed in part by the presence of elongated frontal bones, conical-like tooth patches on the endopterygoids and basibranchial 2, a triangular opercle bone, and a unique, V-shaped dentary.

†*Notogoneus* is represented by eight nominal species, of which †*N. osculus* Cope, 1885, the type species, was redescribed by L. Grande and T. Grande (2008). With the exception of †*N. longiceps*, †*Notogoneus* differs from all other gonorynchid genera by the presence of deep clefts along the posterior margin of its subopercles. Its placement within Gonorynchidae is debatable but it has usually been considered sister to the extant genus *Gonorynchus* or to *Gonorynchus* + [†*Ramallichthys* + †*Judeichthys* + †*Charitosomus*]. It shares with *Gonorynchus* several likely synapomorphic characters, including an enlarged lacrimal (infraorbital 1), a uniquely shaped premaxilla and maxilla, a distinctive scale morphology, and a loose articulation between the dentary and anguloarticular. However, †*Notogoneus* differs from *Gonorynchus* and other gonorynchid species, by exhibiting a more generalized caudal skeleton (i.e., hypurals not fused to the terminal caudal centrum and hypurals one and two autogenous), as well as narrower, non-articulating anterior neural arches and supraneurals (L. Grande and T. Grande, 2008). These more generalized characters suggest that †*Notogoneus* is not the sister group of *Gonorynchus* alone, but rather of the clade that includes *Gonorynchus* plus most fossil gonorynchid genera.

Nonetheless, †*Notogoneus* is a pivotal genus in understanding the phylogeny of the family Gonorynchidae and character evolution within the family. Its suggested basal phylogenetic placement relative to the species of *Gonorynchus* and its closest relatives (T. Grande and Poyato-Ariza, 1999; L. Grande and T. Grande, 2008; T. Grande and L. Grande, 2008; Amaral et al., 2013) also provides important insights into the historical biogeography of the Gonorynchiformes, and the age of the oldest known fossil of †*Notogoneus* is important for providing a minimum age for the split between its lineage and that of *Gonorynchus*.

Here we describe a new species of †*Notogoneus* from a diamond exploration drill core into strata deposited in a maar lake that followed the eruptive emplacement of a kimberlite pipe in the Northwest Territories of Canada. The maar-lake deposits of this kimberlite pipe, called Wombat, and others nearby, including the Giraffe Pipe (Wolfe et al., 2017), have been studied for their geological genesis (Wolfe et al., 2012; Reyes et al., 2019; Buryak et al., 2019; Buryak, 2020) and their paleontological significance, mainly for algae (e.g., Wolfe et al., 2006; Siver, 2013) and palynomorphs (Hu et al., 2011). Parts of small fossil fishes and a patch of scales have been recovered from two cores into the Wombat maar strata, but one specimen represents a complete fish skeleton with unmistakable identification different from the others and is described here as a new species.

The new species is the oldest known member of the genus †*Notogoneus* and dates to the very early Campanian, about 82 Ma. The previous oldest record of the genus was †*N. montanensis* L. Grande and T. Grande, 1999, from deposits of the Two Medicine Formation in Montana, USA; that species was found at a late Campanian site called "Jack's Birthday Site," and is estimated to be about 76–77 Ma in age (D. Trexler, pers. comm. Dec. 2019). The new species is represented herein by a single specimen of a possible juvenile fish, preserved as a nearly complete part and a less complete counterpart.

2. Geologic context

The Wombat kimberlite maar (64.92° N, 110.45° W; paleolatitude ~63°N) is situated in the Slave craton within the Lac de Gras kimberlite field of Northwest Territories, Canada (Fig. 1). Although the Slave craton is largely devoid of Phanerozoic sedimentary cover rocks, studies of sedimentary xenoliths within kimberlite crater fills suggest that the region at various times has been covered by middle Devonian and Cretaceous-Paleogene marine shales and mudstones (Nassichuk and McIntyre, 1995; Cookenboo et al., 1998; Sweet et al., 2003). Notably, xenoliths of Cretaceous marine and Paleogene terrestrial sedimentary cover rocks, together with Paleogene post-eruptive maar lake deposits in the Lac de Gras kimberlite field (e.g., Wolfe et al., 2017), suggest a post-100 Ma transition from a marine to terrestrial environment on the Slave craton (Stasiuk et al., 2002, 2006; Sweet et al., 2003; Ault et al., 2013). The modern surface is dominated by exposed bedrock and lakes (Fig. 1), with local cover by sediments and landforms attributed to advance and retreat of the Laurentide Ice Sheet during the last glaciation (e.g., Dredge et al., 1995; Kelley et al., 2019).

The buried Wombat maar deposits are intersected by three diamond exploration cores, one drilled in each of 1993, 2000, and 2005: CH93-29, DDH00-5, and BHP05-11, respectively (Fig. 1). The specimens described in this paper were collected from core CH93-29, archived at Connecticut College (New London, USA), and core DDH00-5, deposited with the Northwest Territories Geological Survey core archive in Yellowknife, Canada (Fig. 2). A total of ~195 m (vertical equivalent; VE) of crater lake facies was intersected by cores CH93-29 and DDH00-5, which were drilled at angles of 45° and 60°, respectively. The lower ~15 m (VE) of the crater fill comprises grey laminated to massive siltstone with common flattened clay lenses and land plant detritus, and is the interval where the fish fossils described here were recovered (Figs. 2, 3). The upper ~180 m (VE) of the crater fill comprises dark clay-rich laminites with rare lithic and country rock fragments. Two grey-white tephra layers, comprising preserved glass shards and some weathered glass pseudomorphs, were sampled from each core at approximately the same depth intervals near the bottom of the lake sequence (Fig. 2), indicating a likely interval of stratigraphic overlap between the two cores. Samples in the Wombat cores are identified with a three-number code: the first represents the core box number (Fig. 3); the second is the channel in the box (with 1 representing the stratigraphically highest channel); and the third represents the depth of the sample in the channel.

The fish specimens described here were discovered opportunistically during bulk sampling of the cores by Siver and Reyes (CH93-29) and Buryak and Reyes (DDH00-5), due to common fracturing of the core into thin "cookies" along lamination planes (e.g., Fig. 3). The stratigraphically lowest specimen is 40-3-30 in DDH00-5, a partial fish with preserved head in laminated silt at 274.2 m and 237.5 m core and VE depth, respectively (Figs. 2, 3). This specimen is ~4 m stratigraphically beneath a prominent dated tephra bed, described below. Also, in DDH00-5, the part and counterpart of a patch of fish scales were collected from 206.5 m to 178.8 m core and VE depth, respectively. Two fossil fish specimens were recovered from CH93-29. Specimen 56-1-46 is a fish body with no tail and most of the head missing, in laminated silt at 310.0 m and 219.2 m core and VE depth, respectively. The most complete of the four fossil fish specimens from Wombat pipe is specimen 61-2-120, in laminated silt at 343.2 m and 242.7 m core and VE depth, respectively. This last specimen (Fig. 4) is the basis of the new species named in this paper. In a composite stratigraphy

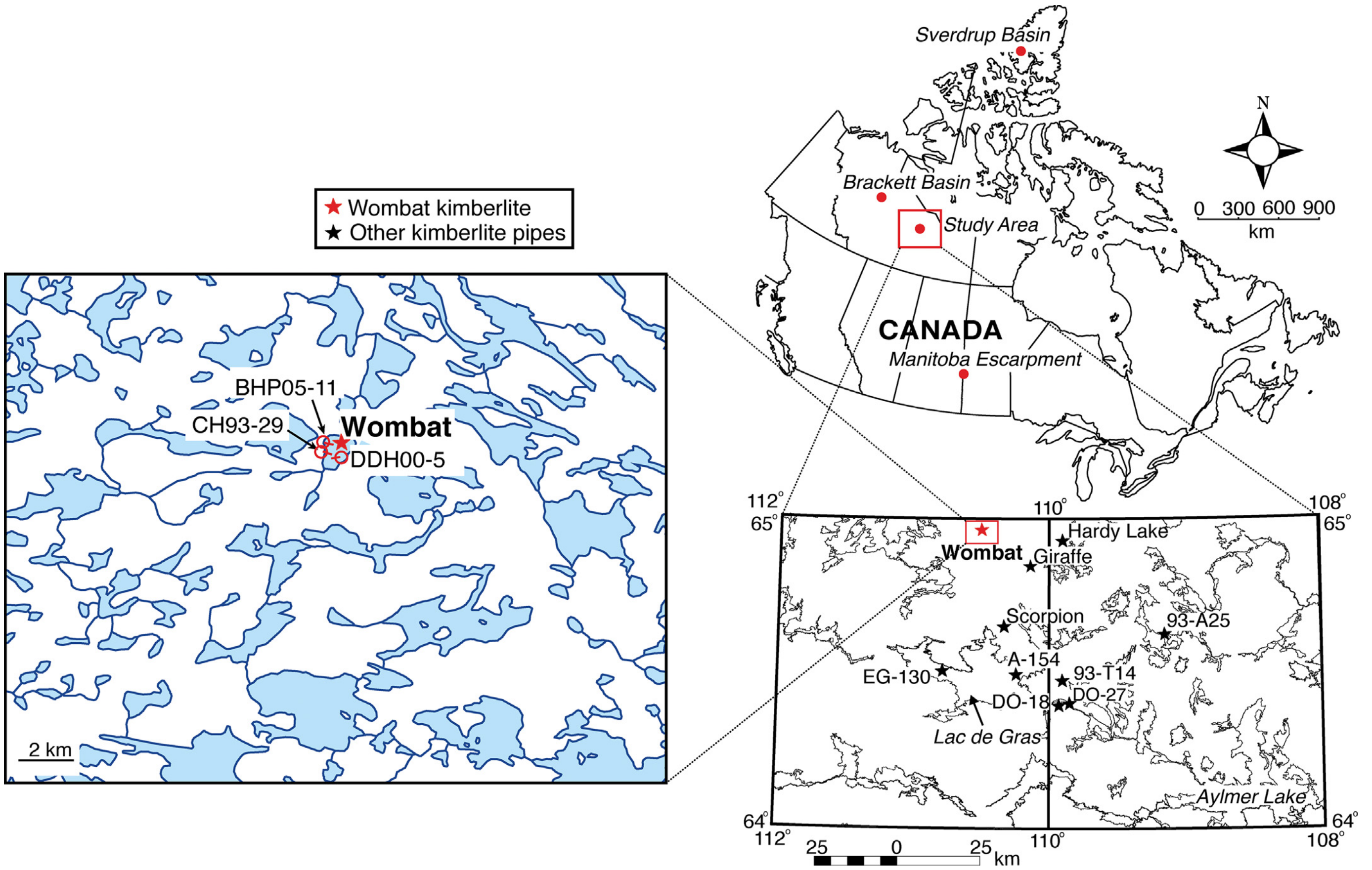


Fig. 1. Map of the Wombat locality and locations of the many other prominent kimberlite pipes in the Lac de Gras kimberlite field, Northwest Territories, Canada (adapted from Stasiuk et al., 2002). Drilling azimuths for the Wombat pipe exploration drill cores are indicated by short dashes on the red location symbols. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

for the Wombat lacustrine fill in both cores, the four fish fossils span ~60 m of massive to laminated lacustrine mud (Fig. 3).

The timing of Wombat kimberlite emplacement is not directly known. Siver et al. (2016), citing unpublished work by Hu et al. (2011), suggested that at least part of the Wombat lacustrine fill is Paleocene in age based on pollen biostratigraphy. However, zircon crystals recovered from a tephra sample in the lower ~15 m of the Wombat lacustrine fill (Buryak, 2020:figs. 2.3, 2.4; Fig. 2 herein) yielded a laser-ablation inductively-coupled-plasma mass-spectrometry (LA-ICP-MS) ^{206}Pb/^{238}U date of 82.36 ± 0.44 Ma (weighted-mean; $n = 18$ of 34 dated zircon crystals; $MSWD = 1.51$). This weighted mean date is based on the youngest cluster of overlapping individual zircon U–Pb dates, some of which were obtained on crystals with adhered glass rims. Accordingly, the weighted mean date is interpreted as a close maximum age for the deposition of the tephra, and in turn implies a Campanian age for the Wombat lacustrine sequence. The dated tephra is near the base of the ~60-m-thick known fish-bearing section of the Wombat. Given a plausible range of sedimentation rates between 0.05 and 0.5 mm yr^{-1}, based on estimated sedimentation rates for Eocene maar lakes in Europe (e.g., Mingram, 1998; Lenz et al., 2011) and Holocene lakes in subarctic Canada (Crann et al., 2015), the 60 m of fish-bearing Wombat pipe lacustrine mud were likely deposited over ~120,000 to, perhaps, 1.2 million years. The estimated age of the single specimen of the new species is thus early Campanian, ~82 Ma.

3. Co-occurring organisms and inferred environmental conditions

The Wombat drill core contains numerous siliceous microfossil remains, including chrysophyte cysts, scales representing synurophytes, chrysophytes and heliozoans, and a variety of pennate and centric diatoms, all indicative of a freshwater lacustrine environment. Two of the most common synurophytes uncovered in the Wombat core include exceptionally large numbers of *Mallomonas porifera* Siver & Wolfe and *Synura cronbergiae* Siver (Siver et al., 2016). Both of these synurophytes were originally described from the Giraffe Pipe locality, a middle Eocene deposit that, like Wombat, represents the remains of a crater lake formed as a result of kimberlite emplacement (Siver and Wolfe, 2010; Siver, 2013; Wolfe et al., 2017). As observed in the Wombat core, both *M. porifera* and *S. cronbergiae* were found co-occurring in Giraffe, implying that these two species thrive in similar habitats. Numerous species belonging to the diatom genera *Eunotia* and *Actinella* (Siver et al., 2015), and extensive concentrations of another synurophyte related to the modern species *Mallomonas lychenensis*, co-occur with *M. porifera* and *S. cronbergiae* in the Giraffe core, suggesting an acidic softwater lake environment. Given that scales belonging to the lineage that includes *M. lychenensis* and specimens of *Eunotia* have also been uncovered in Wombat (Siver et al., 2016), these microfossil remains support an acidic softwater waterbody. In addition to *M. porifera* and *S. cronbergiae*, the Wombat core further

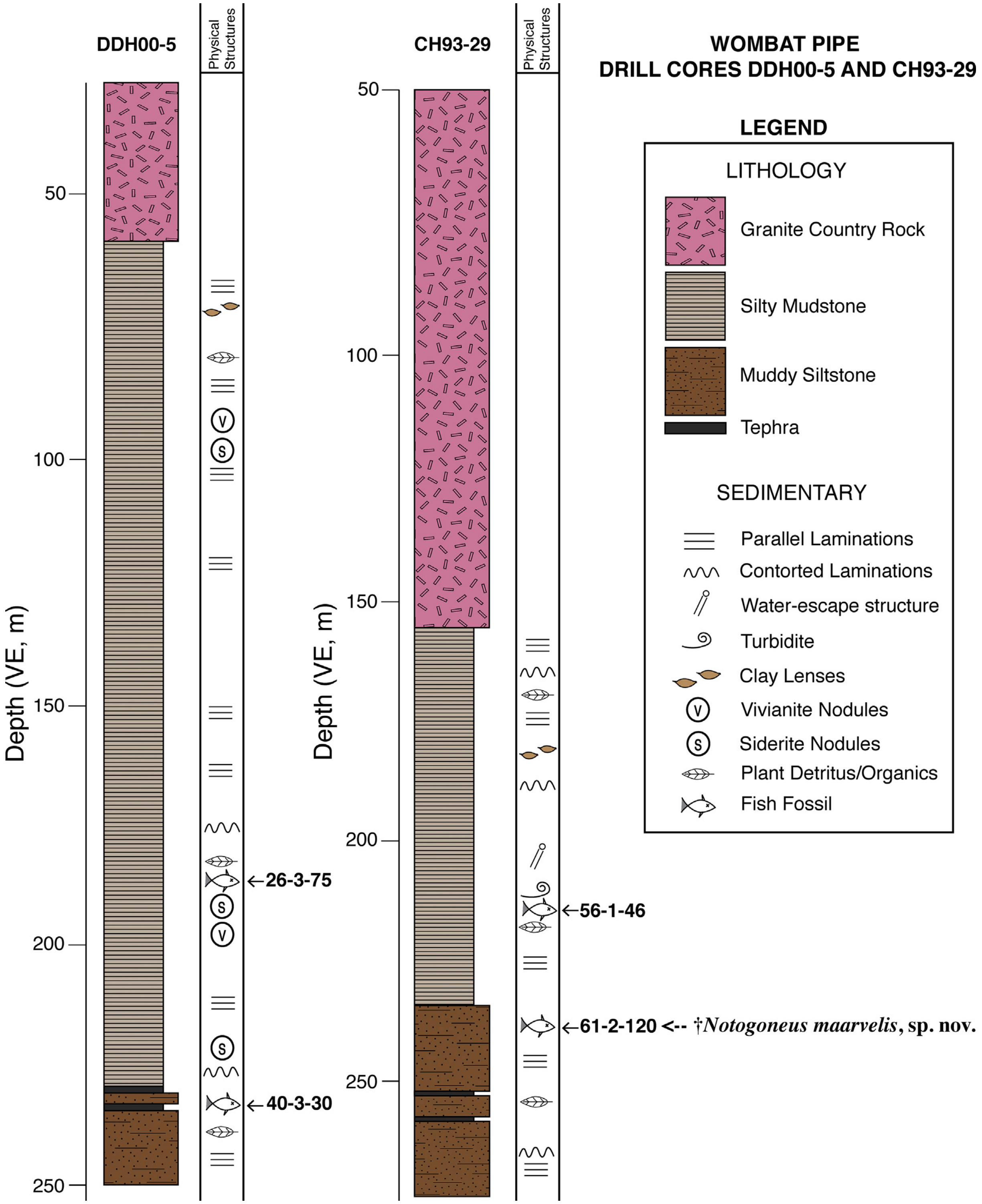


Fig. 2. Summary stratigraphic logs of the Wombat drill cores DDH00-5 and CH93-29. Depth in the dipping cores is expressed as vertical equivalent (VE) depth with respect to the surface elevation at the drilling site. The logs reveal granite country rock at shallow depths in the cores because of the oblique drilling pattern, not because such rocks lie above the crater fill.

contains a large diversity of undescribed synurophyte species. Contemporary lakes that typically harbor the highest diversity of synurophytes are softwater, acidic waterbodies, low in specific conductivity and with moderate levels of dissolved humic substances (Siver, 1995, 2015).

The remains of the extinct diatom *Eoseira* Wolfe & Edlund lends further support to the idea that the Wombat lake was a softwater habitat. *Eoseira* is a diatom genus belonging to the family Aulacoseiraceae originally described from sedimentary rocks of an Eocene lake that covered the Horsefly River Valley in British Columbia,

Fig. 3. Example of a core box containing some of the deeper core of DDH00-5. Depths in the box channels are in meters, measured obliquely along the core. The core has fractured into thin “cookies” and revealed a partial skeleton of a small fish (not the new species named in this paper).

Canada (Wolfe and Edlund, 2005). The freshwater Horsefly waterbody was inferred (Wolfe and Edlund, 2005) to be a warm monomictic lake with a softwater chemistry and abundant nutrients, which supported massive summer blooms of *Eoseira wilsonii*. Other than Horsefly, Wombat is the only known locality harboring *Eoseira* (Siver et al., 2016). In addition, strata in the Wombat core often contain numerous scales of heterotrophic protists representing heliozoans and species belonging to *Paraphysomonas* and *Clathromonas*, further implying ample nutrient concentrations. In summary, based on fossil remains, the Wombat waterbody represented an acidic, freshwater lake with a softwater chemistry, and with moderate nutrient and humic concentrations.

4. Material and methods

4.1. Abbreviations

Anatomical. **1–9**, principal caudal fin rays, branched, upper and lower (9 upper and 8 lower); **aa**, anguloarticular; **ac**, anterior ceratohyal; **afi**, anal fin insertion; **bb**, basibranchials; **br**, branchiostegal rays; **cl**, cleithrum; **den**, dentary; **dfi**, dorsal fin insertion; **dfo**, dorsal fin origin; **en**, endopterygoid; **ep**, epural; **fr**, frontal; **hy1–5**, hypurals 1–5; **iop**, interopercle; **la**, lacrimal; **me**, mesethmoid; **mx**, maxilla; **nspu2**, neural spine of second preural vertebra; **op**, opercle; **pcr**, procurrent caudal rays; **pfo**, pectoral fin origin; **pfr**, pectoral fin rays; **php**, parhypural; **pmx**, premaxilla; **prul**, principal caudal ray unbranched lower; **pruu**, principal caudal ray unbranched upper; **ps**, parasphenoid; **pu1**, centrum of first preural vertebra; **pvb**, pelvic bone; **pvo**, pelvic fin origin; **qu**, quadrate; **r3**, enlarged rib of third vertebral centrum; **sop**, subopercle; **sopc**, subopercular clefts; **u1**, centrum of first ural vertebra; **u2**, centrum of second ural vertebra; **un1**, first uroneural; **un2**, possible second uroneural; **v3**, third vertebral centrum; **v20**, centrum of vertebra 20; **v26**, centrum of vertebra 26.

Institutional. **AMNH**, American Museum of Natural History, New York, New York; **AMS**, Australian Museum, New South Wales, Australia; **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania; **BMNH**, British Museum (Natural History), London, England; **BPBM**, Bernice P. Bishop Museum, Honolulu, Hawaii; **FMNH**, Field Museum of Natural History, Chicago, Illinois (Fossil specimens [PF or P] are in the Geology Department, and Recent specimens are in the Zoology Department, Division of Fishes); **HUJ**, The Hebrew University of Jerusalem, Israel; **MNHN**, Muséum national d'Histoire naturelle (Institut de Paléontologie), Paris, France; **MOR**, Museum of the Rockies, Bozeman, Montana; **NMNZ**, National Museum of New Zealand, Wellington, New Zealand; **NMNH NAS**, National Museum of Natural History, National Academy of Sciences, Ukraine; **PIN**, Paleontological Institute, Russian Academy of Science, Moscow, Russia; **QMC**, Queensland Museum, South Brisbane, Queensland, Australia; **RUSI**, J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa; **UALVP**, Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Canada; **USNM**, National Museum of Natural History, Washington, DC.

Measurements and symbols. TL = total length; SL = standard length (snout to caudal base—the posterior end of the hypural plate). The dagger symbol (†) denotes a taxon that is extinct and known only from fossils.

4.2. Comparative material examined

In addition to the specimens listed here, data taken from other specimens listed by T. Grande (1999) and by L. Grande and T.

Fig. 4. †*Notogoneus maarvelis*, sp. nov., holotype, UALVP 60986a (part), complete fish with SL 29.2 mm and TL 34.6 mm; early Campanian. Scale bar = 5 mm.

Grande (2008) were also used in this paper (e.g., †*Notogoneus parvus* Hills, 1934, Oligocene, Australia; †*N. squamosseus* (de Blainville, 1818), Oligocene, France; †*N. cuvieri* (Agassiz, 1844), Oligocene, France; †*N. janeti* Priem, 1908, Eocene/Oligocene, France) and included in comparative morphometric and meristic ranges. Data from extant taxa were obtained via X-radiographs as well as from cleared & stained and alcohol-fixed specimens. Geologic ages and localities for fossil gonorynchids from the Cretaceous of Lebanon follow Forey et al. (2003). Taxonomic authorities follow Eschmeyer et al. (2010).

†*Notogoneus gracilis* Sytchevskaya, 1986; 4 nearly complete skeletons (52–90 mm SL): PIN 3119/730 (holotype), 3119/736, 3119/752, 3119/753 from upper Paleocene/lower Eocene drill core samples from Boltyshka, Ukraine.

†*Notogoneus longiceps* (von Meyer, 1848); 2 specimens (75–95 mm SL): FMNH PF 14228, 14230, from the lower Miocene near Mainz-Budenheim, Germany.

†*Notogoneus montanensis* L. Grande and T. Grande, 1999; part and counterpart of a skeleton missing part of the skull (~44 mm SL, ~51 mm TL): MOR 1064a and b (holotype). Late Cretaceous (Campanian) Two Medicine Formation of northwestern Montana.

†*Notogoneus osculus* Cope, 1885; 22 specimens (21–470 mm SL): AMNH 3900; FMNH PF9646, 10286, 11954, 11958, 11968, 13043, 14206, 15232, 15320, 15321, 15328, 15319, 15323, 15330, 15331, 15333, 15334, 15335, 15336, 11955 (skull only),11956 (caudal fin). Eocene freshwater deposits of the Fossil Butte Member of the Green River Formation, Fossil, Wyoming.

Gonorynchus abbreviatus Temminck and Schlegel, 1846; 12 specimens (10–300 mm SL): AMNH 3515, 57051, 55562; FMNH 76746, 63856, 57094. Japan and Taiwan.

Gonorynchus forsteri Ogilby, 1911; 14 specimens (60–530 mm SL): AMNH 57121, 57118; MNHN BT028, BT095; NMNZ P.11137, 5341, 1847, P11142, 1145. New Zealand.

Gonorynchus greyi (Richardson, 1845); 35 specimens (7–310 mm SL): AMNH 57121, 32973, 55562, 96053 (dried skeleton), 96057 (dried skeleton); BMNH 1848.3.19.19, BMNH 1855.9.19.967, syntypes; FMNH 103977; MCZ 8841; AMS I.5478, I.43161, I.12852, I.13128, I. 17370816, I.17778001, I.19948004, IA.3830, IB.1437, I.13125, I.13126, I. 13127, I.13226, I.11213, I.28848004, I.28844005, I.30938001, I.33933002, I.33964009, I.19601055, I.33896005, I.33941011. Eastern and western coasts of Australia.

Gonorynchus gonorynchus (Linnaeus, 1766); 21 specimens (50–350 mm SL): AMNH 96050 SD (dried skeleton); AMS I.19808-002, IA.5209; ANSP 53065; BMNH 1853.11.120, holotype; MNHN 3074, 3617, 3619; RUSI 7566–7570, 7784, 8259, 12817, 10596, 15048, A-15759-118, A-18550-139, A-18557-139, 68.05. Southeastern coast of Africa.

Gonorynchus moseleyi Jordan and Snyder, 1923; 15 specimens (56–300 SL): BPBM 3515, 24028, 24054, 24065, 24067, 24077, 25364, 26550, 27759; SU 23239 (holotype). Hawaiian Islands.

†*Charitopsis spinosus* Gayet, 1993; one specimen (80 mm SL): AMNH 3895 (holotype); Cenomanian, marine limestone deposits of Hakel, Lebanon.

†*Charitosomus lineolatus* (Pictet and Humbert, 1866); one specimen (50 mm SL): MNHN SHA 1946; late Santonian, marine limestone deposits of Sahel Alma, Lebanon.

†*Charitosomus major* Woodward, 1901; one nearly complete skeleton (155 mm SL): FMNH UC2019. Upper Cretaceous, late Santonian, marine limestone deposits of Sahel Alma, Lebanon.

†*Charitosomus* ("†*Hakeliosomus*") *hakelensis* (Davis, 1887); 5 specimens: (45–118 mm SL): FMNH PF 13405; MNHN HAK 340, 13d, 112, 113g. Upper Cretaceous, Cenomanian, marine limestone deposits of Hakel, Lebanon.

†*Ramallichthys orientalis* Gayet, 1982; 3 specimens (114–144 mm SL): HUJ EY-386 (holotype), EY 25, EY 381. Upper Cretaceous, lower Cenomanian, marine limestone deposits of Ramallah, West Bank.

†*Judeichthys haasi* Gayet, 1985; one nearly complete skeleton (110 mm SL): HUJ AJ-432 (holotype). Upper Cretaceous, lower Cenomanian, marine limestone deposits of Ramallah, West Bank.

5. Systematic paleontology

Subdivision Teleostei Müller, 1844 (sensu Patterson and Rosen, 1977).
Superorder Ostariophysi Sagemehl, 1885 (sensu Fink and Fink, 1996).
Series Anotophysi Rosen and Greenwood, 1970 (sensu Fink and Fink, 1996).
Order Gonorynchiformes Berg, 1940 (sensu Fink and Fink, 1996).

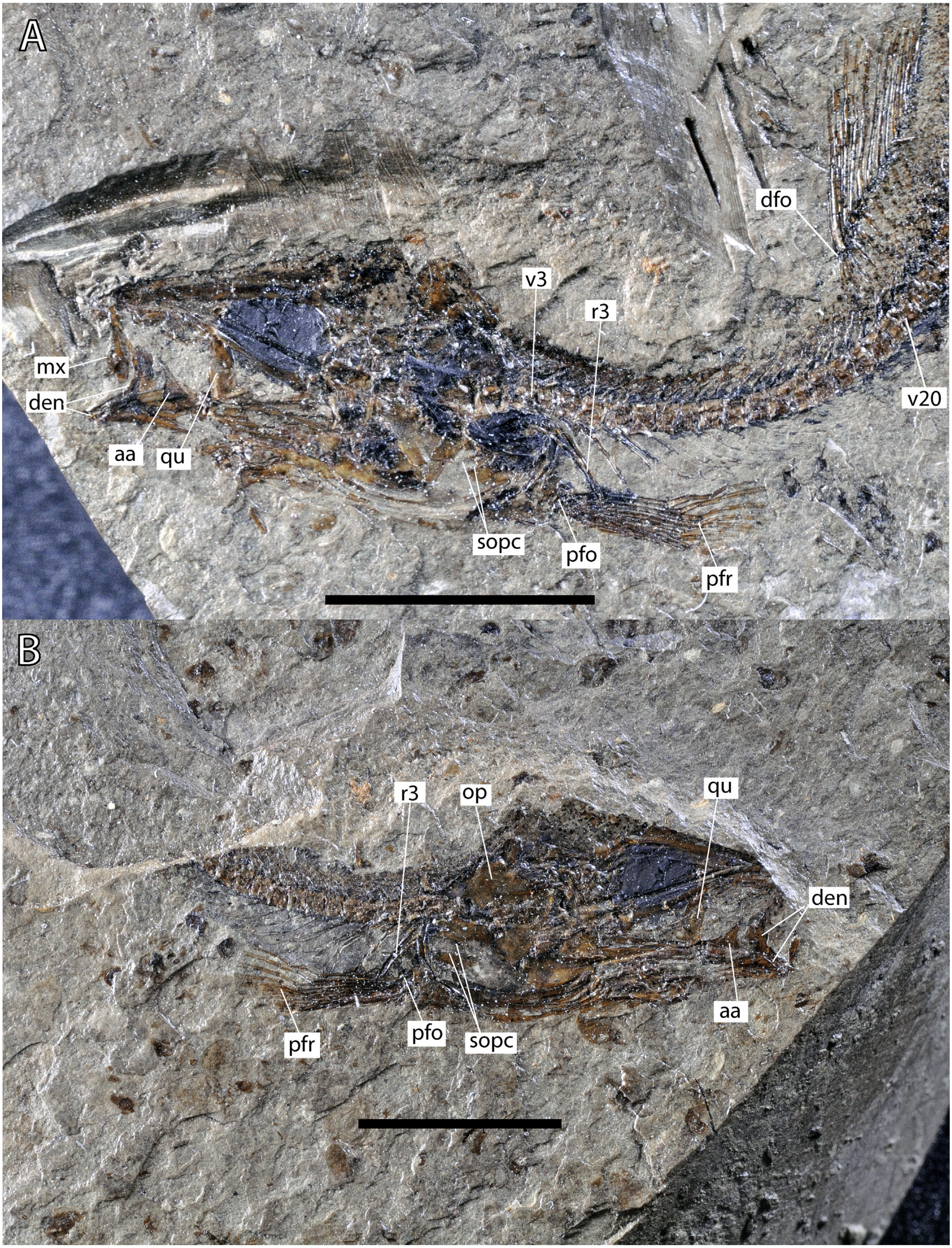
Remarks. See T. Grande (1996) and Eschmeyer et al. (2010) for discussion of nomenclatural issues and synonymies within the Gonorynchiformes.

Family Gonorynchidae Richardson, 1848 (sensu T. Grande, 1996).

Genus †*Notogoneus* Cope, 1885 (junior synonym †*Protocatostomus* Whitfield, 1890).
Type species: †*Notogoneus osculus* Cope, 1885.

†*Notogoneus maarvelis*, sp. nov., T. C. Grande and M. V. H. Wilson, 2022.
Figures 4–8.
ZooBank registration. urn:lsid:zoobank.org:pub:7984DE97-6FF3-4879-8AA5-EF7C4821FF8F

Holotype. UALVP 60986, in part (60986a; Fig. 4) and counterpart (60986b; Fig. 5B). The part is nearly complete with SL 29.2 mm and TL 34.6 mm (Figs. 4, 5A, 6, 7). The counterpart (Fig. 5B) consists of the head, right pectoral fin and girdle, and 15 of the anterior-most vertebrae with associated ribs, neural spines, and intermuscular bones. The preserved portion of the counterpart (Fig. 5B) ends anterior to the origin of the dorsal fin.
Diagnosis. A species of †*Notogoneus* distinguished from all other species in the genus by the following unique characters, which are irrespective of size or age and do not change once established in early development. The origin of the pelvic fin of †*N. maarvelis*, is positioned significantly posterior to the origin of the dorsal fin. This difference is also evident in measurement ratios: the predorsal length is about 52% of SL, whereas the pre-pelvic length (snout to pelvic origin) is about 63%. This differs from all other species in the genus, in which the two values are nearly equal or in some species the pre-pelvic distance is slightly less than the pre-dorsal distance. In the new species, the origin of the dorsal fin is directly above vertebral centrum 20, whereas the pelvic fin origin is directly below vertebral centrum 26. In other species of †*Notogoneus*, the fin rays of the pelvic fins originate directly ventral to the first fin rays of the dorsal fin, or even slightly anterior to them. Additional characters that distinguish †*N. maarvelis* from certain species in the genus are as follows. Total vertebral number (51) is greater than those of †*N. montanensis* (46) and †*N. gracilis* (46–47), fewer than those of †*N. squamosseus* (55 or 56) and †*N. janeti* (55), but similar in number to those of †*N. osculus* (50–52), †*N. longiceps* (52–55), and †*N. cuvieri* (52). The new species resembles all congeners in having


A
dfo
v3
r3
mx
den
aa
qu
v20
sopc
pfo
pfr
B
r3
op
qu
den
aa
pfr
pfo
sopc

subopercle clefts, except for †*N. longiceps*, which differs in lacking them. The number of anal fin rays in †*N. maarvelis* (10) is most similar to that of †*N. osculus* (8–10) but differs from the more common count (9) in the latter species. Anal fin-ray counts reported in other species are fewer, such as counts of 8 in each of †*N. montanensis*, †*N. longiceps*, and †*N. gracilis*.

Etymology. The first part of the specific name *maarvelis* is derived from the word “maar” which is a type of crater created by a volcanic explosion and is often applied to the lake that frequently forms within the crater. The second part of the name, *velis*, is a variant of the word *velum*, meaning covering or vail, which in this case refers to the deposits that filled the maar and concealed the fish within it, prior to discovery. Gender is masculine. This specific name fortuitously also brings to mind the intrepid Captain Marvel, reflecting the first author's passion for Marvel comics.

Locality. Canada, Northwest Territories, near Lac de Gras. It was found in sample 61-2-120 at 213.6 m below the surface, in a 10-cm-diameter mineral-exploration drill core (No. CH93-29) bored into lake deposits in the buried maar crater of the Wombat kimberlite, at 64.92° N, 110.45°W. The locality is within the area known as Mǫwhì Gogha Dè Nııłèe, the traditional territory of the Tłıchǫ people.

Geologic age. Early Campanian, ~82 Ma, estimated from U–Pb zircon geochronology (Buryak et al., 2019; Buryak, 2020).

Preservation. The only known specimen of †*Notogoneus maarvelis* appears to be well ossified but it is a very small fish that likely represents a juvenile. It is preserved in lateral view (Figs. 4, 5), is laterally compressed, and has been split along the bedding plane between the more complete part (left side) and the partial counterpart (right side). The part (Figs. 4, 5A, 6–8) consists of the skull, all median and paired fins, and a well-preserved vertebral column including caudal skeleton. The counterpart (Fig. 5B) consists of the skull, the right pectoral fin and girdle, and the anterior-most 15 vertebrae.

6. Description and comparisons

General. As is characteristic of all members of the order Gonorynchiformes, the orbitosphenoid and basisphenoid appear absent in the new species, the rib of vertebra three is greatly thickened (Figs 5, 6) and is shorter relative to more posterior ribs, and three sets of intermuscular bones are present.

As in most gonorynchids, the pectoral, pelvic, and anal fins are positioned relatively posteriorly on the body, the frontals are elongate and narrow, the opercle is triangular, and the dentary (Fig. 6) has the characteristic gonorynchid V-shape.

The new species is clearly a member of the genus †*Notogoneus* as it displays the key diagnostic character of the genus: four deep suborbital clefts (Figs. 5, 6). It is probably most closely related to †*N. osculus*, which is the species that is also the best known, and for both reasons most of the comparisons mentioned here are with that species.

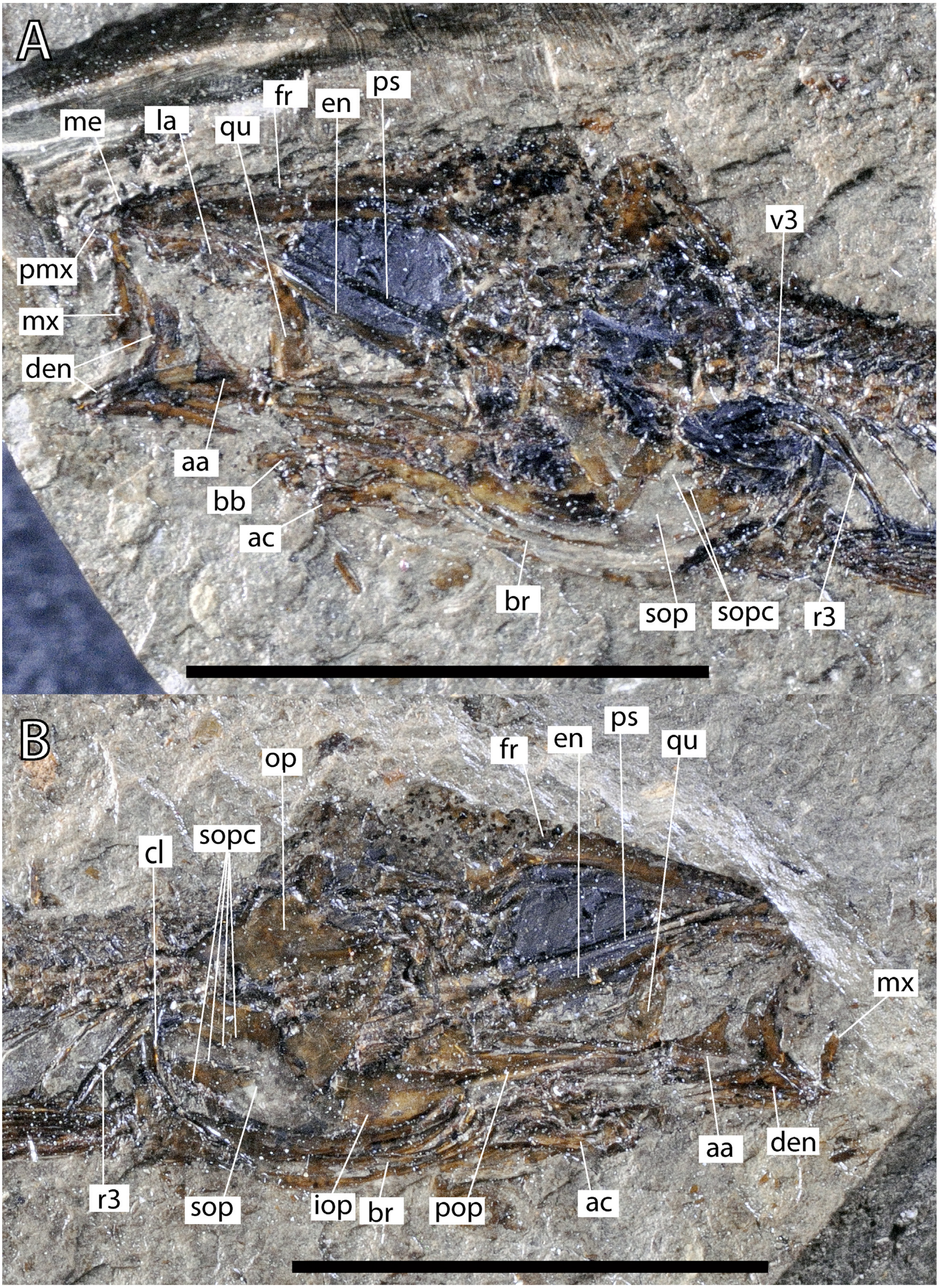
Body. †*Notogoneus maarvelis* is known so far from a small individual, quite possibly a juvenile, of 29.2 mm SL, 34.6 mm TL. Detailed measurements and meristics of the only known specimen of †*Notogoneus maarvelis* are given in Table 1, along with comparisons with relevant species of †*Notogoneus* and related genera. Because of the holotype's probable juvenile life history stage, comparisons are made here not only with adult specimens but also with juvenile specimens of †*Notogoneus osculus*, *Gonorynchus greyi*, and *G. gonorynchus* to ensure that characters reported here are not due to allometric growth. As demonstrated by L. Grande and T. Grande (2008) and by additional measurements made for this study, there are no appreciable differences in fin position between small (27 mm SL) specimens and large (500 mm SL) individuals of the same species in either *Gonorynchus* or †*Notogoneus*. Thus, we are confident that the proportions presented here are not affected by allometry. Moreover, comparisons of †*N. maarvelis* with juvenile †*N. osculus* specimens (FMNH 11958: 27 mm SL, 15319: 31 mm SL) of comparable size clearly shows that the skeleton of †*N. maarvelis* is more developed and more ossified than similar-sized juveniles of the other species. In our comparisons, bones of the suspensorium, pleural ribs, and intermuscular bones are all better ossified in †*N. maarvelis*. This suggests that †*N. maarvelis* might have matured at a much smaller size than did †*N. osculus* (L. Grande and T. Grande, 2008).

In †*N. maarvelis*, the pelvic fins are positioned significantly posterior to the origin of the dorsal fin (Figs. 4, 7). †*Notogoneus maarvelis* has a predorsal length of 15.3 mm SL (52% of SL) and a snout-to-pelvic fin length of 18.4 mm (63% of SL), measured from the snout to the first fin rays of the dorsal fin and to the origin of the fin-ray cluster of the pelvics (Table 1). Correlating these median fin positions with particular vertebral centra, the origin of the dorsal fin in †*N. maarvelis* is directly above centrum 20, while the origin of the pelvic fin is directly below centrum 26. The relative positions are different in the other species, with the two types of fin originating nearly opposite each other or with the pelvic origin in advance of the dorsal origin. The snout-to-pectoral-fin distance is 7.5 mm (23.6% of SL) and the snout-to-anal-fin distance is 24.2 mm (82.9% of SL) (Table 1).

Scales. No scales are preserved in the only known specimen of †*N. maarvelis*, although *Gonorynchus* and other species of †*Notogoneus* have small scales covering the head, including the snout. In †*N. osculus*, however, scales are not seen in specimens smaller than 40 mm (L. Grande and T. Grande, 2008:fig. 3.3). Head scales are not known in other fossil gonorynchid genera, including †*Sapperichthys* (Amaral et al., 2013). The lack of head scales in †*N. maarvelis* might be because of total absence in this species or because of preservation or developmental age. The absence of preserved scales in †*N. maarvelis* means also that the absence of cteni such as those fringing the posterior edge of the “peripheral ctenoid scales” (Roberts, 1993) of *Gonorynchus* and other species of †*Notogoneus* cannot be considered diagnostic of the new species.

Skull roof. Bones of the braincase are difficult to discern due to some crushing of the skull. However, like that of most gonorynchids, the skull is widest in the posterior region and tapers anteriorly (Figs. 5, 6). As seen in both the part and counterpart, the frontals of †*N. maarvelis* taper from posterior to anterior and are very similar to those of other species of †*Notogoneus*. They are comparatively elongated and paired. This is in contrast to the condition in *Gonorynchus*, where the frontals fuse during development (paired frontals were observed in specimens of *Gonorynchus* 75 mm SL and smaller; T. Grande and Arratia, 2010). Among gonorynchiforms, the median frontal condition appears to be unique to *Gonorynchus*. Located at the ventral two-thirds level of the otic region is a well-preserved parasphenoid (Figs. 5, 6). As in all gonorynchiforms, it is devoid of dentition. It articulates with the vomer which is also devoid of teeth in †*Notogoneus*. We were unable to clearly distinguish the vomer and mesethmoid, but in gonorynchids, the mesethmoid extends anteriorly beyond the vomer (T. Grande and L. Grande, 2008; L. Grande and T. Grande,

Fig. 5. †*Notogoneus maarvelis*, sp. nov., holotype. **A**, UALVP 60986a (part), anterior portion of the fish including the skull, pectoral fins, anterior vertebrae, and the anterior part of the dorsal fin. **B**, UALVP 60986b (counterpart), the entire preserved portion including the skull, pectoral fins, and the anterior-most vertebrae. For anatomical abbreviations, see the list in text (above). For additional labeled structures, see Fig. 6. Scale bar = 5 mm.


A
me
la
qu
fr
en
ps
pmx
mx
den
v3
aa
bb
ac
br
sop
sopc
r3
B
op
fr
en
ps
qu
sopc
cl
mx
aa
den
r3
sop
iop
br
pop
ac

2008; T. Grande and Arratia, 2010). The orbitosphenoid and basisphenoid appear to be absent as in congeners. The parietals and supraoccipital are not discernible in either the part or counterpart.

Infraorbitals. Only the lacrimal is preserved in the holotype (Figs. 5, 6). Like that of †*Notogoneus* and *Gonorynchus* it is enlarged longitudinally. The usual characteristic keel along the lower edge is, however, not obvious in †*N. maarvelis*. Excluding the lacrimal, *Gonorynchus* exhibits a reduction of infraorbital number to three autogenous elements. These elements are reduced to thin rods. If the condition in †*Notogoneus* resembles that of *Gonorynchus*, it might explain why these delicate infraorbitals were not preserved and thus not observable in our specimen. The dermosphenotic is a structural part of the cranium but it is also not observable in our specimen.

Opercular series and branchiostegals. The opercular series in †*Notogoneus* consists of four dermal bones, the preopercle, opercle, subopercle and interopercle. A suprapreopercle is a delicate, canal-bearing bone positioned above the preopercle in *Gonorynchus* but not recognizable in †*Notogoneus* including the new species.

The preopercle is a dermal bone that is functionally part of the suspensorium (see below) and is positioned anterior to the opercle, but its details are difficult to discern precisely in our specimen. It consists of two long limbs meeting at a slightly obtuse angle and carries the preopercular sensory canal from the skull roof to the lower jaw. As in gonorynchids, including †*Notogoneus* such as the new species, the anteroventral limb of the preopercle is greatly elongated, correlated with the general reduction in size of the jaws and the elongation of the suspensorium and thus of the skull. As noted by Gayet (1993), the angle made by the intersection of lines drawn through the preopercular limbs is equal to or larger than 90 degrees in gonorynchids, also contributing to the length of the skull. The lower limb of the preopercle also articulates with the posteroventral margin of the quadrate.

As in most gonorynchids (the exception being †*Sapperichthys*: Amaral et al., 2013), the opercle is more or less triangular. It is unornamented and smooth (Fig. 6b). Unlike that of †*Notogoneus osculus* and *Gonorynchus*, the opercle in †*N. maarvelis*, although triangular, does not appear to be excavated along its posterior margin, whereas it is excavated significantly in †*N. osculus* (L. Grande and T. Grande, 2008).

Immediately ventral to the opercle is the subopercle. In all species of †*Notogoneus* except †*N. longiceps* (Perkins, 1970; FMNH 14228), the shape of the subopercle is unique and diagnostic of the genus. It has a series of deep clefts along its posterior margin. In †*N. maarvelis*, four posteriorly directed, deep subopercular clefts are present, thus placing the new species squarely within the genus †*Notogoneus*. The clefts in the new species are particularly visible in the counterpart skull (Figs. 5B, 6B). As illustrated by L. Grande and T. Grande (2008) and in the material examined for this study, the number of subopercular clefts can vary among the †*Notogoneus* specimens examined (the common number is 4 or 5). It is possible that additional specimens of the new species will also demonstrate variation in this character.

The interopercle is mostly covered by the preopercle and subopercle in lateral aspect. It was, however, visible in the counterpart of the new species (Figs. 5B, 6B), in which it does not look unusual. Branchiostegal rays are blade-like or spatulate (Figs. 5, 6) and are four in number, as in †*Notogoneus* and *Gonorynchus*.

Suspensorium. The suspensorium is a functional unit of the fish skull typically including the hyomandibula, symplectic, preopercle, quadrate, metapterygoid, endopterygoid, ectopterygoid, and palatine (the preopercle was dealt with above with the opercular bones). The suspensorium thus combines both dermal and chondral bones. For example, the palatine combines the chondral autopalatine and the dermal dermopalatine. Together with the muscles that originate or insert on them, the bones of the suspensorium function to enclose and control the volume and shape of the upper part of the oral cavity, while also controlling the lateral-to-medial position of the lower jaw articulation (Williams, 1987; Wilson and Williams, 2010). The suspensorium articulates anterodorsally with the ethmoid bones and anteriorly with the maxilla via the autopalatine, posterodorsally with the sphenotic and pterotic (not observable in the holotype) of the cranium via the head of the hyomandibula, posteriorly with the opercle via the opercular arm of the hyomandibula, medially with the branchial arches via the interhyal bone, and anteroventrally with the lower jaw via the quadrate-anguloarticular joint.

The hyomandibula is the largest bone in the suspensorium. It articulates with the sphenotic, pterotic, opercle, interhyal, and symplectic. Both the hyomandibula and symplectic form from the same hyosymplectic cartilage early in development. The hyomandibula can scarcely be seen and its articulations are not clear; the condition in †*Notogoneus* was not discussed by L. Grande and T. Grande (2008). It is uncertain if the hyomandibula in the new species has the two characteristic articulation points that occur in *Gonorynchus* with the sphenotic and pterotic of the cranium.

The quadrate is a large bone of the suspensorium that anteriorly articulates with the lower jaw via the anguloarticular and overlaps with and reinforces the ectopterygoid. In gonorynchids, including the new species, the quadrate shape is diagnostic and can be seen, well preserved, in the new species (Figs. 5, 6). The main body of the quadrate is robust and tall. It has a relatively long posterior process, and between the main body and the process is lodged the symplectic, which articulates with the hyomandibula but cannot be identified in our specimen. The quadrate also attaches along its posteroventral edge to the preopercle.

The endopterygoids can be identified in the new species, in both part and counterpart (Figs. 5, 6). They are a pair of large, dermal bones that form the floor of the orbit and much of the roof of the oral cavity. An endopterygoid is seen just ventral to the parasphenoid in the holotype. The family Gonorynchidae is diagnosed by the presence of conical teeth on the ventral surface of the posterior end of the endopterygoids (T. Grande and L. Grande, 2008; L. Grande and T. Grande, 2008; Poyato-Ariza et al., 2010). However, in the new species, conical teeth could not be seen. Perhaps this is because the endopterygoid in this specimen is only seen in dorsal aspect. Species of †*Notogoneus* have such teeth, but for many years, †*Notogoneus osculus* was thought to lack them (Perkins, 1970; T. Grande and Poyato-Ariza, 1999; L. Grande and T. Grande, 1999). It is also possible that the specimen of †*N. maarvelis* is too young and that endopterygoid teeth had not yet formed when it died. It was not until many additional specimens of †*N. osculus* were collected and prepared that endopterygoid teeth were observed in a very few specimens larger than 45 mm SL (L. Grande and T. Grande, 1999, 2008). In developmental series of *Gonorynchus greyi*, no teeth are seen in specimens smaller than about 50 mm SL. It appears that endopterygoid teeth begin to form in individuals of *G. greyi* larger than 60 mm SL (e.g., three small teeth were seen on the posterior portion of the endopterygoids in a specimen of *G. greyi*, 75 mm SL, AMS I.5478). Therefore, the presence of endopterygoid teeth in older individuals of the new species is not ruled out, because they might be unobservable in the only specimen possibly due to preservation or young age.

Fig. 6. †*Notogoneus maarvelis*, sp. nov., holotype, showing the skull and pectoral region with important bones labeled. **A**, Holotype part, UALVP 60986a; **B**, Holotype counterpart, UALVP 60986b. For anatomical abbreviations, see the list in the text (above). Scale bar = 5 mm.

Fig. 7. †*Notogoneus maarvelis*, sp. nov., holotype, UALVP 60986a (part). **A**, Body region showing the relative positions of the fins; **B**, Caudal region. Scale bar = 5 mm.

The metapterygoid is usually positioned between with the endopterygoid and the hyomandibula. It is reduced to a slender rod in *Gonorynchus*. L. Grande and T. Grande (2008) were unable to identify the ectopterygoid or metapterygoid in †*Notogoneus osculus* and we also were unable to identify either bone in the new species. The metapterygoid of †*Sapperichthys* and other gonorynchiforms is described as larger, broad, and trapezoidal (Amaral et al., 2013).

Jaws. As with all gonorynchiforms, teeth are absent from the jaws. The jaws of †*N. maarvelis* are typical of gonorynchids and are virtually identical in shape to those of †*Notogoneus* spp. and *Gonorynchus*. As in all gonorynchids, the mouth is sub-terminal although the degree of its downward orientation is variable. The mouth in species of *Gonorynchus* is positioned more ventrally (T. Grande, 1999), while the jaws in †*Notogoneus*, including the new species, have a more terminal position. Possibly the more terminal jaws allowed them to forage with more versatility in the water column and not just from the bottom. The upper jaw consists of a pair of premaxillae and a pair of maxillae, while the lower jaw consists of the paired dentaries, anguloarticulars, and retroarticulars (Figs. 5A, 6). Supramaxillae are absent in gonorynchiforms.

In all gonorynchiforms, the maxilla is excluded from the gape by the premaxilla. In †*Notogoneus*, the premaxilla is a small, thickened, bifurcated bone with limbs forming a right angle, though it is difficult to see its details in the specimen. The bifurcation fits around a process at the anterior end of the maxilla. The maxilla is long and slender with its posterior end forming a rounded margin (Fig. 6). The maxilla articulates with the autopalatine but the articulation cannot be seen in †*N. maarvelis*.

The lower jaw consists of the dentary, anguloarticular, and retroarticular bones (Figs. 5, 6). In gonorynchids, including the new species, the shape of the dentary is unique. The dentary in these taxa has a conspicuous V-shape with one process extending dorsally and the other extending posteriorly. The long process of the anguloarticular articulates with the dentary at the junction between the two dentary processes. In *Gonorynchus*, †*Sapperichthys*, and †*Notogoneus*, including the new species (Figs. 5, 6), the dentary and anguloarticular are loosely connected, thus adding to the delicate appearance and length of the jaws. In the Middle Eastern gonorynchids (e.g., †*Ramallichthys*, †*Charitosomus*), the articulation of the anguloarticular with the dentary is tight and robust. In †*Ramallichthys*, for example, the two elements appear to be one bone and it is difficult to discern the margins of the dentary.

The anguloarticular and retroarticular form the articular facet for the head of the quadrate. The joint between the anguloarticular and quadrate is of particular interest. In the new species, the articular head of the anguloarticular (Figs. 5, 6) resembles that of *Gonorynchus* more so than that of †*Notogoneus*. As described by L. Grande and T. Grande (2008), †*N. osculus* exhibits an elongation of the lower limb of the anguloarticular that articulates with the condyle of the quadrate. This limb was referred to as a retroarticular process in T. Grande and L. Grande (2008), after Gayet (1986, 1993), for comparative purposes. The condition in the new species, however, is more like that of *Gonorynchus*, in which no elongated process is present. A small yet distinct retroarticular is present in the new species, but it is not directly involved in the joint with the quadrate.

Vertebral column. The vertebral column in †*Notogoneus maarvelis* is well preserved. The new species has 51 autogenous centra (Fig. 4), of which 36 or 37 are abdominal centra (Fig. 7A) while 14 or 15 are caudal centra (Fig. 7B). The count in †*N. maarvelis* is more similar to those in †*N. longiceps* (52–55), and †*N. cuvieri* (52), and is overlapped by the range of counts in †*N. osculus* (50–52) (L. Grande and T. Grande, 2008). †*Notogoneus montanensis* and †*N. gracilis* exhibit lower total vertebral numbers of 46–47 respectively, while †*N. squamosseus* and †*N. janeti* both have higher vertebral counts of 55. Vertebral counts in other gonorynchid genera differ more significantly, including 42 or 43 in †*Charitosomus*, †*Ramallichthys*, and †*Judeichthys*. The total vertebral count for *Gonorynchus* varies from 54 to 66 depending upon the species (*G. abbreviatus* has the lowest vertebral count of 54, while *G. forsteri* is a very slender fish that has the smallest vertebrae but the highest number of 66 total centra in the genus; Table 1).

Brinkman (2019) and Divay et al. (2020) described the morphology of isolated centra of †*Notogoneus* based on comparisons with intact material of †*Notogoneus*, *Gonorynchus*, and *Chanos*. In lateral view the centra are at least as tall as or slightly taller than they are long and have a strong, rounded, anteroposterior bar that separates large pits dorsally and ventrally. The centra of the new species closely resemble the morphology described for †*Notogoneus osculus*. *Gonorynchus* lacks the anteroposterior bar and its centra are longer than they are tall.

The anterior neural arches in the new species appear medially expanded but do not come into contact with one another (Fig. 5A, B). The neural arches are fused to their centra and become progressively thinner posteriorly. This condition is very similar to that of †*N. osculus* as reported by L. Grande and T. Grande (2008). Unfortunately, the view of the first two vertebrae in the new species is obstructed by the posterior skull bones so that there is no way to tell if a short neural spine, typical of †*Notogoneus* and *Gonorynchus*, is present on centrum one. The first vertebra in clear view is the third, which carries the greatly expanded first pleural rib (Figs. 5, 6). The ribs articulate with parapophyses that appear fused to the centra. As in †*N. osculus*, the pleural ribs of vertebrae four and five also are expanded and thicker than the posterior ribs, but not to the degree of the first pleural rib, and they are not foreshortened. The pleural ribs become increasingly thin posteriorly. They cannot be seen in the midsection of the fish because of compression of its abdomen, and so an accurate count of pleural rib pairs was not possible. Supraneurals are not discernible in †*N. maarvelis*.

Three sets of intermuscular bones are present but poorly preserved in some regions of the fish. The arrangement of intermuscular bones in the new species resembles the condition in *Gonorynchus* (Patterson and Johnson, 1995).

Dorsal and anal fins. The dorsal and anal fins of †*N. maarvelis* are relatively short, with fin bases of 11% and 7.9% of SL, respectively (Figs. 4, 7). The dorsal fin in †*Notogoneus maarvelis* has 14 principal rays and is supported by 14 proximal radials (Figs. 7, 8A). The first principal fin ray is unbranched. Only one procurrent ray is apparent in the dorsal fin of the new species. In †*N. osculus* there are 13–15 principal rays with up to three procurrents. †*Notogoneus montanensis* has only 8 or 9 principal rays in its dorsal fin.

The anal fin in †*N. maarvelis* contains 10 or 11 principal rays (Fig. 7B). The first is unbranched. The principal rays are preceded by two procurrent rays. The number of anal fin rays in the new species is larger than those of both †*N. osculus* and †*N. montanensis* with each having only 8 principal rays (L. Grande and T. Grande, 1999, 2008). The number of proximal radials in the anal fin of †*N. maarvelis* could not be determined with certainty.

Paired fins. The pectoral fin of †*N. maarvelis* has 10 fin rays (Fig. 5A), while the pelvic fin has 9 fin rays (Fig. 7A). One procurrent ray precedes each first fin ray. In †*Notogoneus* the pectoral ray count is often slightly greater than the pelvic count. †*Notogoneus osculus* exhibits similar fin ray counts (pectoral 9–10, pelvic 8–9). †*Notogoneus montanensis* is the outlier with a pelvic fin ray count of only 7 (L. Grande and T. Grande, 1999); the pectoral fin is not preserved in material of that species. †*Sapperichthys* is aligned more with species of †*Notogoneus* in having pectoral and pelvic fin ray


A
dfo
dfi
v20
v26
pvb
pvo
B
pruu
pu1+u1+u2 +un1
hy3
hy5
ep
hy4
nspu2
un2?
9
8
7
6
5
4
3
2
1
1
2
3
4
5
6
7
8
afi
php
hy1
hy2
pcr
prul

counts of 11 and 8, respectively (Amaral et al., 2013). In contrast, among species of *Gonorynchus*, the pectoral fin-ray count is usually slightly less (8–9 with 9 being the most common) than the pelvic count (10–11, with 10 being the most common).

Caudal skeleton and fin. The caudal fin is like that of †*N. osculus* in having a formula of x,10,9,ix (i.e., 10 procurrent rays and ten principal rays in the upper lobe; 9 principal rays and 9 procurrent rays in the lower lobe; L. Grande and T. Grande, 2008). The outermost principal ray of each lobe is unbranched, so that there are 9 upper and 8 lower branched caudal rays (Fig. 8B). The caudal fin skeleton in †*N. maarvelis* resembles that of other species of †*Notogoneus*, especially that of †*N. osculus*. Both caudal skeletons exhibit five autogenous hypurals, three in the upper lobe and two in the lower (Fig. 8B). The parhypural is autogenous as is one epural (Fig. 8B) and perhaps also uroneural 2, though this is difficult to identify in the specimen. The terminal centrum is compound in †*N. osculus* and it appears so in †*N. maarvelis*. This centrum in species of †*Notogoneus* consists of a fusion of preural centrum 1, ural centra 1 and 2, and uroneural 1. In all other gonorynchids (e.g., *Gonorynchus*, †*Charitosomus*, †*Ramallichthys*) the compound centrum also includes the parhypural and hypurals 1 and 2 (T. Grande and L. Grande, 2008). The condition in the Cenomanian genus †*Sapperichthys* from Mexico is unknown because the caudal fin is missing in both known specimens (Amaral et al., 2013). The condition found in †*Notogoneus* is usually considered primitive for the family. †*Notogoneus* has thus been placed phylogenetically as the sister group to the remainder of the Gonorynchidae (T. Grande and L. Grande, 2008) except perhaps for †*Sapperichthys* (Amaral et al., 2013).

Fin positions. A major difference between the new species and other gonorynchids is the relative position of the dorsal and pelvic fins in relation to the length of the body. In †*N. maarvelis*, the predorsal (snout-to-dorsal origin) distance is 52% of SL and the prepelvic (snout-to-pelvic origin) distance is 63% of SL (Fig. 7A; Table 1). This condition is unique among gonorynchid taxa including any known species of †*Notogoneus*. In †*N. osculus* both the dorsal and pelvic fins are positioned mid-body with a predorsal length of about 56% of SL and a prepelvic length of about 57% of SL. Fin positions in other species of †*Notogoneus* differ only slightly from those of †*N. osculus*. For example, in †*N. gracilis* the pelvic fins begin slightly in advance of the dorsal fin.

In addition to measured distances, fin positions can be evaluated by the particular vertebra opposite which the fin originates. In †*N. maarvelis*, the dorsal fin rays begin directly above vertebral centrum 20 and the pelvic fin rays begin below centrum 26 (Figs. 7A, 8A). In contrast, in †*N. osculus*, the dorsal fin rays begin opposite centrum number 22 or 23, as do the pelvic fin rays. Although a standard length is not available for †*N. montanensis* (the skull of the only specimen is incompletely preserved), we can see that both the dorsal and pelvic fin rays begin opposite vertebral centrum 22.

Among related genera, although not calculated by Amaral et al. (2013), the origins of the dorsal and pelvic fins in the type specimens of the Cenomanian gonorynchid †*Sapperichthys chiapanensis* (Amaral et al., 2013:figs. 2, 3) lie almost directly opposite each other as they do in †*N. osculus*.

The dorsal and pelvic fins in all species of *Gonorynchus* are positioned more posteriorly than in any species of †*Notogoneus*, with an average predorsal length of about 68–70% of SL. The dorsal and pelvic fin origins in *Gonorynchus* are only one or two centra apart, but the dorsal fin is still positioned behind the pelvic fins, unlike in the new species.

7. Discussion

The genus †*Notogoneus*, with the inclusion of †*N. maarvelis*, is represented by nine species worldwide. Only two species are known from Cretaceous deposits, †*N. montanensis* and †*N. maarvelis*, while all others—†*N. parvus* of southern Queensland, †*N. gracilis* of Ukraine, †*N. longiceps*, †*N. cuvieri*, †*N. janeti*, and †*N. squamosseus* of Germany and France, and †*N. osculus* of North America—are from early Eocene to early Miocene freshwater deposits.

†*Notogoneus maarvelis* is the earliest occurrence of †*Notogoneus*; however, its phylogenetic relationships within †*Notogoneus* are still to be determined. A revision and re-description of the non-North American species are needed and beyond the scope of this paper. Of the North American species, †*N. maarvelis* appears more similar to the type species, †*N. osculus* from the Green River Formation of Wyoming (e.g., fin ray and vertebral centra counts, Table 1). However, it differs from †*N. osculus* most notably in the relative positions of the dorsal and pelvic fins. For †*Notogoneus osculus*, the dorsal and pelvic fins are positioned directly opposite from each other, whereas the dorsal fin of †*N. maarvelis* is positioned considerably more anterior to the pelvics. Six vertebrae separate the dorsal and pelvic fins in †*N. maarvelis*, whereas there are no vertebrae positioned between the dorsal and pelvic fin origins in †*N. osculus*. As discussed, we are confident that the dorsal and pelvic fin positions in the specimen of †*N. maarvelis* would not be different in an adult or larger specimen. Although the older and larger specimens of †*N. osculus* do change considerably in relative body depth and related proportions (L. Grande and T. Grande, 2008), they change little or not at all in antero-posterior proportions. As demonstrated by L. Grande and T. Grande (2008:fig. 3, tables 1–5), allometry does not appear to be an important factor with respect to antero-posterior body proportions in †*N. osculus*.

The phylogenetic placement of †*Notogoneus* within Gonorynchidae has been controversial. For many years †*Notogoneus* was considered to be sister to the extant marine Indo-Pacific genus *Gonorynchus* (e.g., T. Grande, 1996:fig. 3). This relationship was based, in part, on a shared, distinctively V-shaped dentary that is loosely articulated with the anguloarticular, and an enlarged lacrimal (Grande and Poyato-Ariza, 2010; Poyato-Ariza et al., 2010). This apparent relationship, however, was called into question with the examination of additional well-prepared specimens of †*N. osculus*, in which the caudal fin skeleton did not exhibit the derived characteristic gonorynchid caudal fin morphology as previous thought, consisting of a fusion of hypurals 1 and 2 with each other and the terminal centrum, but instead all hypurals are autogenous as are the parhypural and uroneural 2. This generalized caudal-fin skeleton and associated characters placed †*Notogoneus* as the sister to *Gonorynchus* plus a grouping of Late Cretaceous marine genera from Germany, Syria, Lebanon and the West Bank: †*Charitosomus*, †*Charitopsis*, †*Ramallichthys*, and †*Judeichthys* (T. Grande and L. Grande, 2008; L. Grande and T. Grande, 2008; Poyato-Ariza et al., 2010; Amaral et al., 2013).

Amaral et al. (2013) described a new gonorynchid from strata that they suggested were Cenomanian within the Sierra Madre Formation of Chiapas, Mexico. We agree that †*Sapperichthys chiapanensis* represents the oldest gonorynchid known from North and Central America; however, we propose that it is premature to argue for its placement as the most basal gonorynchid. All characters recognizable in †*Sapperichthys* except one are found in †*Notogoneus* or other gonorynchids. The single unique character is the shape of the opercle,

Fig, 8. †*Notogoneus maarvelis*, sp. nov., holotype, UALVP 60986a (part), selected skeletal details labeled and enhanced by ammonium chloride sublimate. **A**, Dorsal and pelvic fins and their positions relative to numbered vertebral centra; **B**, Caudal skeleton with numbered fin rays. For anatomical abbreviations, see the list in the text (above). Scale bar = 5 mm.

Table 1
Measurements and meristics of †*Notogoneus maarvelis*, sp. nov., and comparisons with relevant species of †*Notogoneus*, *Gonorynchus*, and †*Sapperichthys*. Measurements for the holotype of †*N. maarvelis* are in millimeters. Data for †*N. osculus* and *Gonorynchus* are ranges based on multiple specimens and/or species (see Comparative Material Examined).

Character	†*Notogoneus maarvelis,* n. sp.	†*Notogoneus osculus*	†*Notogoneus montanensis*	*Gonorynchus* spp.	†*Sapperichthys chiapanensis*
Total Length	34.6		51		150–200?
Standard Length	29.2	21–470	44	7–530	?
Greatest body depth	2.6 (8.9% of SL)	16–23% of SL		?	
Depth of caudal peduncle	1.7 (5.8% of SL)	10–12% of SL		?	
Head length	6.6 (22% of SL)	23–27% of SL		18–25% of SL	
Head height	4.5 (15% of SL)	?		?	
Length of lower jaw	1.9 (6.5% of SL)	20–24% of SL		?	
Eye diameter	1.7 (5.8% of SL)			3.4–6.5% of SL	
Predorsal length	15.2 (52% of SL)	54–59% of SL		68–74.6% of SL	
Snout to pectoral fin origin	8.6 (29% of SL)	25–29% of SL		18–32% of SL	
Snout to pelvic fin origin	18.4 (63% of SL)	55–61% of SL		67–70% of SL	
Snout to anal fin origin	24.2 (82.9% of SL)	79–87% of SL		90–93% of SL	
Dorsal origin to caudal base	13.3 (45.5% of SL)	41–46% of SL		20–23% of SL	
Pectoral origin to caudal base	17.8 (61% of SL)	71–75% of SL		68–82% of SL	
Pelvic origin to caudal base	11.4 (39% of SL)	39–45% of SL		30–33% of SL	
Anal origin to caudal base	5.0 (17% of SL)			7–10% of SL	
Length of dorsal fin base	3.2 (11% of SL)				
Length of anal fin base	2.3 (7.9% of SL)				
Total centra	51	50–52	46	54–66	at least 40+
Abdominal centra	36 or 37	35–37		42–52	29+
Caudal centra	14 or 15			12–14	11+
Centra smooth or with fossae	fossae	fossae	fossae	smooth	
Proportions of centra in lateral view	square or taller than long	square or taller than long	square or taller than long	longer than tall	square or longer than tall
Compound centrum	pu1+u1+u2+un1	pu1+u1+u2+un1	u2+un1+ ?	pu1+u1+u2+un1+un2+ php+hyp1+hyp2	?
Dorsal fin position	anterior to pelvics	equal to pelvics	equal to pelvics	posterior to pelvics	equal to pelvics
dorsal fin origin above what vertebra	V20 (first ray)	22 or 23	22	36, 42	19 or 20
pelvic fin origin below what vertebra	V26 (first ray)	22 or 23	22	34, 40	19 or 20
anal fin origin below what vertebra	V39 (first ray)	?	36		33
Vertebra centra from anal insertion to end of vertebral column	12	11 or 12	10		?
Dorsal fin rays	i,14 (first unbranched)	13–15	8 or 9	10 to 12	11
Anal fin rays	ii,10 (possibly 11)	8–10	8	7 to 9 (7 rare)	9
Pectoral fin rays	i,10	9–10	?	10 or 11	11
Pelvic fin rays	i,9	8–9	7	8 or 9	8
Caudal fin rays: Procurrents, uppers, lowers	x,1,9,8,1,ix	1,9,8,1	1,9,8,1		?
Branchiostegal rays	4	4	4		?
Subopercle with clefts or not	clefts	clefts	clefts n = 3	not	not
Infraorbitals	lacrimal enlarged	lacrimal enlarged	?	lacrimal enlarged	?
Intermuscular bones	three sets	three sets	three sets	three sets	three sets
Third pleural rib	expanded	expanded	expanded	expanded	expanded

which the authors illustrate as oval with a spiny posterior, instead of the characteristic triangular shape found in gonorynchids. This character might be autapomorphic for †*Sapperichthys*, indicating its difference from †*Notogoneus*, but not necessarily primitive. Unfortunately, the caudal fin skeleton, which distinguishes †*Notogoneus* from *Gonorynchus* and its closest relatives, is not preserved in known specimens of †*Sapperichthys*. We suggest, therefore, pending further information, that both †*Sapperichthys* and †*Notogoneus* be placed in an unresolved trichotomy together with a clade containing *Gonorynchus* and its closest fossil relatives.

Regardless of whether †*Notogoneus* or †*Sapperichthys* constitutes the most basal member of the group, we agree with Amaral et al. (2013) that ancestors of †*Notogoneus*, the only freshwater gonorynchid genus, were likely distributed in the Tethys Seaway during the Cenomanian. By the Campanian, †*Notogoneus* is represented in western and northern North America (L. Grande and T. Grande, 1999; Divay et al., 2020; this paper), but not elsewhere as far as known. Later, in the Paleogene, †*Notogoneus* is found widely distributed among various continents (i.e., Europe, Asia, Australia, and North America) where it was among the cosmopolitan taxa that occur in common among most of those continents (e.g., Chang and Chen, 2000).

An issue raised by L. Grande and T. Grande (1999, 2008) remains: why are there so few deposits of well-preserved Cretaceous freshwater fishes in North America, and why is †*Notogoneus* rare in freshwater deposits despite its known occurrence in North America? One factor undoubtedly is that the interior of North America was occupied for much of the Cretaceous by the Western Interior Seaway, which at times connected the Gulf of Mexico to the Arctic Ocean and extended from the Western Cordillera far to the east (Slattery et al., 2013). The Seaway was home to a remarkable diversity of marine fishes and other animals (e.g., Everhart, 2017), but during its high stands, freshwater habitats were greatly restricted, contributing to the rarity of freshwater deposits noted by L. Grande and T. Grande (1999:612).

Smith et al. (1988) also attempted to explain the low diversity of fossil fishes seen in many fossil deposits not only in the Cretaceous but also in the Paleogene. They pointed out that large river systems (such as the Mississippi/Missouri system and its ancient precursors) are generally long lived and contain abundant species, including long-surviving primitive taxa (e.g., sturgeons, paddlefishes, gars, bowfins, usually having robust bones) as well as a great diversity of smaller fishes. This is in contrast to most lakes, which are of shorter duration in geologic time and often contain lesser fish diversity. However, large river systems generally do not preserve the greatest diversity of fossil fishes because the skeletons of most small species are easily destroyed by predators, scavengers, and fluvial processes. Smith et al. (1988) predicted that greater fish diversity would be discovered by 1) searching for isolated bones using screen washing and similar techniques, and by 2) searching for fishes in fine-grained deposits of overbank ponds and floodplain lakes, including oxbow lakes.

The first of these is essentially what Brinkman et al. (2014, 2017) and Divay et al. (2020) have accomplished, their work yielding an increasing diversity of smaller fishes that also include Campanian specimens of †*Notogoneus*, dating to about 75 Ma, represented by resistant but isolated bones including jaw bones and vertebral centra. The second (floodplain lakes and overbank ponds) is what is illustrated for the Paleocene by the articulated skeletons of fishes such as the esocid †*Esox tiemani*, preserved with an osteoglossiform and a percopsid in the genus †*Lateopisciculus* (Wilson, 1980, 1984; Li and Wilson, 1996; Murray and Wilson, 1996), as well as the Paleocene osmerid †*Speirsaenigma*, found with an osteoglossiform (†*Joffrichthys*) and a different percopsid (†*Massamorichthys*), preserved in another overbank deposit (Wilson and Williams, 1991; Li and Wilson, 1996; Murray, 1996; Wilson, 1996).

A Late Cretaceous example is the discovery of †*Notogoneus montanensis*, of late Campanian age, which was preserved in a freshwater setting west of the Seaway, perhaps also an overbank pond or channel fill (L. Grande and T. Grande, 1999). Maastrichtian examples are the discoveries of the osteoslossiform †*Wilsonichthys aridinsulensis* and the percopsiform †*Lindoeichthys albertensis*, described by Murray et al. (2016, 2019), from quiet-water deposits of a floodplain channel fill such as an oxbow lake. Clearly, the predictions about where increased diversity should be found were largely accurate.

The occurrence of †*Notogoneus maarvelis* represents a very different setting, that of a small lake formed by a volcanic explosion during a kimberlite emplacement within the North American craton. A surprising amount of detailed morphology has been deduced from this very small, juvenile fish, preserved on a single bedding plane in the presumably sheltered environment of a small crater lake and found thanks to the fortuitous placement of a drill bit and the chance split of a drill core.

However, this is not the first time that small fossil fishes such as this have been found in deposits of crater lakes. Such deposits include some famous Lagerstätten with diverse assemblages of fossils, including maar deposits that have also yielded fishes, and an impact crater that has even yielded articulated skeletons of †*Notogoneus*.

A closely similar discovery in South Africa was that of a Late Cretaceous (Maastrichtian) galaxioid fish, †*Stompooria rogersmithi* Anderson, 1998. A complete skeleton was found in a diamond-exploration core drilled into a kimberlite maar deposit. The Stompoor core also yielded ostracods, gastropods, mussels, insects, and a frog (Anderson, 1998). The South African discovery of †*S. rogersmithi* undoubtedly qualifies as highly similar to the present discovery of †*N. maarvelis*.

The famous Eocene Lagerstätte and oil-shale deposit of Messel in Germany is now considered to be a maar, rather than a graben as was previously thought (Mezger et al., 2013; Moshayedi et al., 2020). The Messel maar originated from one or more volcanic, phreatomagmatic explosions, but was not caused by a kimberlite emplacement. An amazing variety of animal fossils has been recovered from Messel, a result of the ancient lake having been meromictic for a long period of time, accumulating and preserving countless dead fishes, amphibians, reptiles, birds, and mammals, many still retaining the last meal in their stomach or the unborn offspring in their uterus (Schaal and Ziegler, 1992). Many fossils have been found because the oil-rich shale was, for many years, mined for its oil in an open-pit excavation, and more recently it has been excavated systematically for scientific study.

The Eckfelder Maar, also in Germany, resulted from another eruption in the middle Eocene. It has yielded diatoms, as well as a wide diversity of mostly terrestrial fauna and flora, and is especially well known for its fossil insects (Wappler, 2003).

In addition to being discovered in a maar deposit, †*N. maarvelis* joins a select list of fishes that were discovered in drill cores. For example, the discovery of the Cenomanian clupeomorph fish †*Tycheroichthys dunveganensis* Hay et al., 2007, was extremely fortuitous, since almost the entire fish was preserved in a drill-core sample about the same diameter as the fish.

Another fortuitous drill-core discovery of fishes was in the Boltysh crater in central Ukraine. Boltysh originated as an impact crater with the age of the impact event recently revised to very early Danian, about 0.6 Ma after the K-Pg impact (Pickersgill et al., 2021). Lake deposits of Boltysh were also cored, revealing the fish species †*Notogoneus gracilis* Sytchevskaya, 1986, along with several other fish species (Dykan et al., 2018). The Boltysh fishes apparently date to a later part of the Paleocene. The lake, much larger than the Wombat maar, lasted for millions of years until it was inundated by sea-level rise in the Eocene (Dykan et al., 2018). Though it was not in a maar, the finding of †*Notogoneus* in a core drilled into a crater makes the Boltysh find also very similar to the discovery of †*N. maarvelis*.

These examples of small fishes and other fossils preserved in crater-lake deposits and sometimes discovered in cores drilled into their strata emphasize an important and under-studied source of knowledge about Late Cretaceous biotic diversity. The discovery of kimberlites, their maar craters, and their lake deposits is progressing rapidly and in many regions of the world, but often, access to the drill cores remains restricted unless, as in the case of the Wombat kimberlite, the search for commercially viable diamonds was not successful. When and if such cores become accessible to science, as they have in the cases of the cores into the Wombat maar and the nearby Giraffe Pipe, they provide important windows into life in regions and during spans of geologic time where fossils are otherwise rare. Such important insights are illustrated well by the discoveries reported here and by earlier studies cited above of the paleontology and paleoenvironments of the Wombat and Giraffe craters.

8. Conclusions

A new species of the extinct, freshwater gonorynchiform fish genus †*Notogoneus* is established based on a small, probably juvenile fossil fish from the Northwest Territories of Canada. †*Notogoneus* is the only freshwater genus of the otherwise marine family Gonorynchidae. The fish was found in the crater resulting from the explosive emplacement of the “Wombat” kimberlite pipe. The fossil was found by a diamond-exploration drill core into the deposits of the post-eruptive Wombat maar lake. The age of the fossil is early Campanian, about 82 Ma, based on U—Pb geochronology of an associated tephra layer. The new species is named †*Notogoneus maarvelis* Grande and Wilson, 2022. It is the oldest known member of its genus, establishing a new minimum age for the †*Notogoneus* lineage as well as a minimum age for its establishment in freshwater habitats. All known Cretaceous occurrences of †*Notogoneus* are from North America, but the genus is known from Paleogene and Neogene deposits in Europe, Asia, and Australia. Kimberlites and their fossiliferous maar lake deposits are a valuable source for otherwise rare biota since they occur in thicker parts of the continental crust where fossils of comparable ages are scarce.

Acknowledgements

We are grateful for helpful comments and suggestions by anonymous reviewers and the editor. We thank Loyola University Chicago Foundation Fund (LUC 211155) to TCG and an NSERC Discovery Grant and a Northern Research Supplement Grant to AVR. This project was funded, in part, with grants to PAS from the National Science Foundation (EAR-1725265 and EAR-1940070). We thank Anne Lizarralde for help with sampling core CH93-29 and Barrett Elliott (Northwest Territories Geological Survey) for facilitating access to core DDH00-5. We thank Allan Lindoe for expertly preparing the holotype specimen. We are grateful to W. Simpson, K. Swagel, S. Mochel, and C. McMahan, FMNH, for loans of comparative specimens, and O. Kovalchuk, NMNH, NAS, for photos of †*Notogoneus gracilis* in drill core from Boltysh, Ukraine. We also acknowledge assistance from institutions and persons listed in T. Grande and L. Grande (2008) and L. Grande and T. Grande (2008).

References

Agassiz, L., 1833–1844. Recherches sur les Poissons Fossiles, 5 volumes plus supplement. Published by the author, printed by Petitpierre, Neuchâtel.

Amaral, V.R.L., Alvarado-Ortega, J., Brito, P.M., 2013. *Sapperichthys* gen. nov., a new gonorynchid from the Cenomanian of Chiapas, Mexico. In: Arratia, G., Schultze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic Fishes 5—Global Diversity and Evolution. Pfeil Verlag, München, Germany, pp. 305–323.

Anderson, M.E., 1998. A Late Cretaceous (Maastrichtian) galaxiid fish from South Africa. In: J. L. B. Smith Institute of Ichthyology Special Publication 60, pp. 1–12.

Ault, A.K., Flowers, R.M., Bowring, S.A., 2013. Phanerozoic surface history of the Slave Craton. Tectonics 32, 1066–1083. https://doi.org/10.1002/tect.20069.

Berg, L.S., 1940. Classification of fishes both Recent and fossil. Trudy Zoologicheskogo Instituta Leningrad 5, 87–517 [1965 edition reprinted by the Thai National Document Center, Bangkok, with English translation, 304 pp.].

Brinkman, D.B., 2019. Teleost abdominal centra from the Belly River Group of Alberta, Canada. Paludicola 12, 109–152.

Brinkman, D., Newbrey, M.G., Neuman, A.G., 2014. Diversity and paleoecology of actinopterygian fish from vertebrate microfossil localities in the Maastrichtian Hell Creek Formation of Montana. Geological Society of America Special Papers 503, 247–270.

Brinkman, D.B., Neuman, A.G., Divay, J.D., 2017. Non-marine fishes of the late Santonian Milk River Formation of Alberta, Canada—evidence from vertebrate microfossil localities. Vertebrate Anatomy Morphology Palaeontology 3, 7–46.

Buryak, S.D., 2020. Geochronology and bulk sediment geochemistry of the Late Cretaceous maar lake sedimentary fill of the Wombat kimberlite pipe, subarctic Canada (MSc thesis), Earth and Atmospheric Sciences. University of Alberta, pp. 1–101.

Buryak, S.D., Reyes, A.V., Siver, P.A., Li, L., DuFrane, A., 2019. Bulk organic geochemistry, geochronology, and paleoenvironments of the Late Cretaceous maar lake sedimentary fill of the Wombat kimberlite pipe, subarctic Canada. In: EGU General Assembly Conference Abstracts, 2019EGUGA.2111232B.

Chang, M.-M., Chen, Y.-Y., 2000. Late Mesozoic and Tertiary ichthyofaunas from China and some puzzling patterns of distribution. Vertebrata Palasiatica 38, 161–175.

Cookenboo, H.O., Orchard, M.J., Daoud, D.K., 1998. Remnants of Paleozoic cover on the Archean Canadian Shield: limestone xenoliths from kimberlite in the central Slave craton. Geology 26, 391–394. https://doi.org/10.1130/0091-7613(1998)026<0391:ROPCOT>2.3.CO;2.

Cope, E.D., 1885. Eocene paddlefish and Gonorhynchidae. The American Naturalist 19, 1090–1091.

Crann, C.A., Patterson, R.T., Macumber, A.L., Galloway, J.M., Roe, H.M., Blaauw, M., Swindles, G.T., Falck, H., 2015. Sediment accumulation rates in subarctic lakes: insights into age-depth modeling from 22 dated lake records from the Northwest Territories, Canada. Quaternary Geochronology 27, 131–144. https://doi.org/10.1016/j.quageo.2015.02.001.

Davis, J.W., 1887. The fossil fishes of the chalk of Mount Lebanon, Syria. Scientific Transactions of the Royal Dublin Society 3 (11), 457–632.

de Blainville, H., 1818. Sur les ichthyolites ou les poissons fossiles. Nouveau Dictionnaire d'Histoire Naturelle 27, 310–395. (Deterville, Paris).

Divay, J.D., Brinkman, D.B., Neuman, A.G., 2020. Late Cretaceous *Notogoneus* from microvertebrate assemblages of the Dinosaur Park Formation, Campanian of southern Alberta, Canada, and insight into the ecology and evolution of early gonorynchids. Journal of Vertebrate Paleontology, e1699801, 1–19.

Dredge, L.A., Ward, B.C., Kerr, D.E., 1995. Surficial Geology, Aylmer Lake, District of Mackenzie, Northwest Territories. In: Geological Survey of Canada Map 1867A. https://doi.org/10.4095/207631.

Dykan, N., Kovalchuk, O., Dykan, K., Gurov, E., Dašková, J., Přikryl, T., 2018. New data on Paleocene-Eocene fauna (gastropods, ostracods, fishes) and palynoflora of the Boltysh impact structure (Ukraine) with biostratigraphical and paleoecological inferences. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 287, 213–239.

Eschmeyer, W.N., Grande, T., Grande, L., 2010. A nomenclatural analysis of gonorynchiform taxa. In: Grande, T., Poyato-Ariza, F.-J., Diogo, R. (Eds.), A Comprehensive Review of Gonorynchiformes and of Ostariophysan Relationships. Science Publishers, Enfield, NH, pp. 567–587.

Everhart, M.J., 2017. Oceans of Kansas, Second Edition: A Natural History of the Western Interior Sea. Indiana University Press, Bloomington, Indiana, p. 460.

Fink, S.V., Fink, W.L., 1996. Interrelationships of ostariophysan fishes (Teleostei). In: Stiassny, M., Parenti, L.R., Johnson, G.D. (Eds.), Interrelationships of Fishes. Academic Press, San Diego, USA, pp. 209–249.

Forey, P.L., Yi, L., Patterson, C., Davies, C.E., 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. Journal of Systematic Palaeontology 1, 227–330.

Gayet, M., 1982. Cypriniforme ou Gonorhynchiforme? *Ramallichthys*, nouveau genre du Cénomanien inférieur de Ramallah (monts de Judée). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 295 (11), 405–547.

Gayet, M., 1985. Gonorhynchiforme nouveau du Cénomanien (monts de Judée): *Judeichthys haasi* nov. gen. nov. sp. (Teleostei, Ostariophysi, Judeichthyidae nov. fam.). Bulletin du Muséum national d'Histoire naturelle, Paris 7C(1) (4), 65–85.

Gayet, M., 1986. *Ramallichthys* Gayet du Cénomanien inférieur marin de Ramallah (Judée) une introduction aux relations phylogénétiques des Ostariophysi. In: Mém. Mus. natl. Hist. nat. Paris, n.s. C, Sciences de la Terre, 51, pp. 1–81.

Gayet, M., 1993. Gonorhynchoidei du Crétacé Supérieur marin du Liban et relations phylogénétiques des Charitosomidae nov. fam. In: Documents des Laboratoires de Géologie, Lyon, France, 126, pp. 1–131.

Grande, T., 1996. The interrelationships of fossil and Recent gonorynchid fishes with comments on two Cretaceous taxa from Israel. In: Arratia, G., Viohl, G. (Eds.), Mesozoic Fishes—Systematics and Paleoecology. Pfeil Verlag, München, Germany, pp. 299–318.

Grande, T., 1999. Revision of the genus *Gonorynchus* Scopoli 1777 (Teleostei: Ostariophysi). Copeia 1999, 453–469.

Grande, T., Arratia, G., 2010. Morphological analysis of the gonorynchiform postcranial skeleton. In: Grande, T., Poyato-Ariza, F.-J., Diogo, R. (Eds.), A Comprehensive Review of Gonorynchiformes and of Ostariophysan Relationships. Science Publishers, Enfield, NH, pp. 39–71.

Grande, L., Grande, T., 1999. A new species of †*Notogoneus* (Teleostei: Gonorynchidae) from the Upper Cretaceous Two Medicine Formation of Montana, and the poor Cretaceous record of freshwater fishes from North America. Journal of Vertebrate Paleontology 19, 612–622.

Grande, L., Grande, T., 2008. Redescription of the type species for the genus †*Notogoneus* (Teleostei: Gonorynchidae) based on new, well-preserved material. Journal of Paleontology 28 (5), 1–31.

Grande, T., Grande, L., 2008. Reevaluation of the gonorynchiform genera †*Ramallichthys*, †*Judeichthys* and †*Notogoneus* with comments on the families †Charitosomidae and Gonorynchidae. In: Arratia, G., Schultze, H.-P., Wilson, M.V.H. (Eds.), Mesozoic Fishes 4—Homology and Phylogeny. Pfeil Verlag, München, Germany, pp. 295–310.

Grande, T., Poyato-Ariza, F.-J., 1999. Phylogenetic relationships of fossil and Recent gonorynchiform fishes (Teleostei: Ostariophysi). Zoological Journal of the Linnean Society 125, 197–238.

Grande, T., Poyato-Ariza, F.-J., 2010. Reassessment and comparative morphology of the gonorynchiform head skeleton. In: Grande, T., Poyato-Ariza, F.-J., Diogo, R. (Eds.), A Comprehensive Review of Gonorynchiformes and of Ostariophysan Relationships. Science Publishers, Enfield, NH, pp. 1–37.

Hay, M.J., Cumbaa, S.L., Murray, A.M., Plint, A.G., 2007. A new paraclupeid fish (Clupeomorpha, Ellimmichthyiformes) from a muddy marine pro-delta environment: middle Cenomanian Dunvegan Formation, Alberta, Canada. Canadian Journal of Earth Sciences 44, 775–790.

Hills, E.S., 1934. Tertiary freshwater fishes from Southern Queensland. Memoirs of the Queensland Museum 10, 163–172.

Hu, S., Hickey, L., Siver, P.A., Wolfe, A.P., 2011. Palynology and age of post-eruptive lake sediments from the Wombat kimberlite locality, Northwest Territories, Canada. Geological Society of America Abstracts with Programs 43 (5), 157.

Jordan, D.S., Snyder, J.O., 1923. *Gonorynchus moseleyi*. A new species of herring-like fish from Honolulu. Journal of the Washington Academy of Science 13, 347–350.

Kelley, S.E., Ross, M., Elliott, B., Normandeau, P.X., 2019. Effect of shifting ice flow and basal topography in shaping three-dimensional dispersal patterns, Lac de Gras region, Northwest Territories, Canada. Journal of Geochemical Exploration 199, 105–127. https://doi.org/10.1016/j.gexplo.2019.01.012.

Lenz, O.K., Wilde, V., Riegel, W., 2011. Short-term fluctuations in vegetation and phytoplankton during the Middle Eocene greenhouse climate: a 640-kyr record from the Messel oil shale (Germany). International Journal of Earth Sciences 100, 1851–1874.

Li, G.-Q., Wilson, M.V.H., 1996. The discovery of Heterotidinidae (Teleostei: Osteoglossidae) from the Paleocene Paskapoo Formation of Alberta, Canada. Journal of Vertebrate Paleontology 16, 198–209.

Linnaeus, C., 1766. Systema Naturae. Editio Duodecima, Reformata, 1. Impensis Direct Laurentii Salvii, Holmiae, pp. 1–532.

Mezger, J.E., Felder, M., Harms, F.-J., 2013. Crystalline rocks in the maar deposits of Messel: key to understand the geometries of the Messel Fault Zone and diatreme and the post-eruptional development of the basin fill. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 164, 639–662.

Mingram, J., 1998. Laminated Eocene maar-lake sediments from Eckfeld (Eifel region, Germany) and their short-term periodicities. Palaeogeography, Palaeoclimatology, Palaeoecology 140, 289–305.

Moshayedi, M., Lenz, O.K., Wilde, V., Hinderer, M., 2020. The recolonization of volcanically disturbed Eocene habitats of Central Europe: the maar lakes of Messel and Offenthal (SW Germany) compared. Palaeobiodiversity and Palaeoenvironments 100, 951–973.

Müller, J., 1844. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Akademie der Wissenschaften zu Berlin 1846, pp. 117–216.

Murray, A.M., 1996. A new Paleocene genus and species of percopsid, †*Massamorichthys wilsoni* (Paracanthopterygii) from Joffre Bridge, Alberta, Canada. Journal of Vertebrate Paleontology 16, 642–652.

Murray, A.M., Wilson, M.V.H., 1996. A new Palaeocene genus and species of percopsiform (Teleostei: Paracanthopterygii) from the Paskapoo Formation, Smoky Tower, Alberta. Canadian Journal of Earth Science 33, 429–438.

Murray, A.M., Newbrey, M.G., Neuman, A.G., Brinkman, D.B., 2016. New articulated osteoglossomorph from Late Cretaceous freshwater dpeosits (Maastrichtian, Scollard Formation) of Alberta, Canada. Journal of Vertebrate Paleontology 36, e1120737, 1–14.

Murray, A.M., Brinkman, D.B., Newbrey, M.G., Neuman, A.G., 2019. Earliest North American articulated freshwater acanthomorph fish (Teleostei: Percopsiformes) from Upper Cretaceous deposits of Alberta, Canada. Geological Magazine 157, 1087–1096.

Nassichuk, W.W., McIntyre, D.J., 1995. Cretaceous and Tertiary fossils discovered in kimberlites at Lac de Gras in the Slave Province, Northwest Territories. Geological Survey of Canada Current Research 1995, 109–114.

Ogilby, J.D., 1911. On the genus "*Gonorrynchus*" (Gronovius). Annals of the Queensland Museum 10, 30–35.

Patterson, C., Johnson, G.D., 1995. The intermuscular bones and ligaments of teleostean fishes. Smithsonian Contributions to Zoology 559, 1–85.

Patterson, C., Rosen, D.E., 1977. A review of ichthyodectiform and other Mesozoic teleost fishes, and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158, 81–172.

Perkins, P.L., 1970. *Notogoneus osculus* Cope, an Eocene fish from Wyoming (Gonorynchiformes, Gonorynchidae). Postilla 147, 1–18.

Pickersgill, A.E., Mark, D.F., Lee, M.R., Kelley, S.P., Jolley, D.W., 2021. The Boltysh impact structure: an early Danian impact event during recovery from the K-Pg mass extinction. Science Advances 7, 25, eabe6530. https://doi.org/10.1126/sciadv.abe6530.

Pictet, F.J., Humbert, A., 1866. Nouvelles recherches sur les poissons fossiles du Mont Liban. Chez Georg, Geneva, Switzerland.

Poyato-Ariza, J.F., Grande, T., Diogo, R., 2010. Gonorynchiform interrelationships: historic overview, analysis and revised systematics of the group. In: Grande, T., Poyato-Ariza, F.-J., Diogo, R. (Eds.), A Comprehensive Review of Gonorynchiformes and of Ostariophysan Relationships. Science Publishers, Enfield, NH, pp. 229–337.

Priem, M.E., 1908. Étude des poissons fossiles du bassin Parisien. In: Publications des Annales de Paléontologie, Paris, p. 144.

Reyes, A.V., Buryak, S., Tierney, J., Siver, P.A., Royer, D., Davies, J., Wolfe, A.P., 2019. Post-eruptive maar lake sediments in kimberlite pipes: progress and prospects for reconstructing "greenhouse" paleoenvironments in subarctic Canada. Geophysical Research Abstracts 21, EGU2019-17164.

Richardson, J., 1844–1848. The zoology of the voyage of H.M.S. Erebus and Terror, under the command of Captain Sir James Clark Ross, R.N., ER.S., during the years 1839 to 1843. In: Richardson, J., Gray, J.E. (Eds.), Reptiles, Fishes, Crustacea, Insects, Mollusca, 2. Lords Commission of the Admiralty, London.

Roberts, C.D., 1993. Comparative morphology of spined scales and their phylogenetic significance. Bulletin of Marine Science 52, 60–113.

Rosen, D.E., Greenwood, P.H., 1970. Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. American Museum Novitates 2428, 1–25.

Sagemehl, M., 1885. Beiträge zur vergleichenden Anatomie der Fische. III. Das Cranium der Characiniden, nebst allgemeinen Bemerkungen über die mit einen Weber'schen Apparat versehenen Physostomenfamilien. Gegenbauers Morphologisches Jahrbuch 10, 1–119.

Schaal, S., Ziegler, W. (Eds.), 1992. Messel: an Insight into the History of Life and of the Earth. Clarendon Press, Oxford, p. 322.

Scopoli, G.A., 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde at leges naturae. Gerle, Prag, p. 506. https://doi.org/10.5962/bhl.title.10827.

Siver, P.A., 1995. The distribution of chrysophytes along environmental gradients: their use as biological indicators. In: Sandgren, C., Smol, J., Kristiansen, J. (Eds.), Chrysophyte Algae: Ecology, Phylogeny and Development. Cambridge University Press, pp. 232–268.

Siver, P.A., 2013. *Synura cronbergiae* sp. nov., a new species described from two Paleogene maar lakes in northern Canada. Nova Hedwigia 97, 179–187.

Siver, P.A., 2015. The Synurophyceae. In: Wehr, J.D., Sheath, R.G., Kociolek, J.P. (Eds.), Freshwater Algae of North America: Ecology and Classification, second ed. Academic Press, San Diego, USA, pp. 605–650.

Siver, P.A., Wolfe, A.P., 2010. A whole-cell reconstruction of *Mallomonas porifera* Siver and Wolfe from the Eocene: implications for the evolution of chrysophyte cell architecture. Nova Hedwigia, Beiheft 136, 117–127.

Siver, P.A., Bishop, J., Lott, A.M., Wolfe, A.P., 2015. Heteropolar eunotioid diatoms (Bacillariophyceae) were common in the North American Arctic during the middle Eocene. Journal of Micropalaeontology 34, 151–163.

Siver, P.A., Wolfe, A.P., Edlund, M.B., 2016. *Fideliacyclus wombatiensis* gen. et sp. nov. a Paleocene non-marine centric diatom from northern Canada with complex frustule architecture. Diatom Research 31, 397–408. https://doi.org/10.1080/0269249X.2016.1256351.

Slattery, J.S., Cobban, W.A., McKinney, K.C., Harries, P.J., Sandness, A.L., 2013. Early Cretaceous to Paleocene paleogeography of the Western Interior Seaway: thee interaction of eustasy and tectonism. In: Wyoming Geological Association 68th Annual Field Conference Guidebook, 68, pp. 22–60.

Smith, G.R., Stearley, R.F., Badgley, C.E., 1988. Taphonomic bias in fish diversity from Cenozoic floodplain environments. Palaeogeography, Palaeoclimatology, Palaeoecology 63, 263–273.

Stasiuk, L.D., Sweet, A.R., Issler, D.R., 2002. Organic petrology, organic geochemistry, palynology and petrophysics data from Lac de Gras kimberlites and associated sedimentary rocks and xenoliths. In: Geological Survey of Canada, Open-File Report 4272.

Stasiuk, L.D., Sweet, A.R., Issler, D.R., 2006. Reconstruction of burial history of eroded Mesozoic strata using kimberlite shale xenoliths, volcaniclastic and crater facies, Northwest Territories, Canada. International Journal of Coal Geology 65, 129–145. https://doi.org/10.1016/j.coal.2005.04.011.

Sweet, A.R., Stasiuk, L.D., Nassichuk, W.W., Catunneau, O., McIntyre, D.J., 2003. Paleontology and diamonds: geological environments associated with kimberlite emplacement, Lac de Gras, Northwest Territories, Canada. In: International Kimberlite Conference: Extended Abstracts, 8. https://doi.org/10.29173/ikc3040.

Sytchevskaya, E.K., 1986. Presnovodnaya paleogenovaya ikhtiofauna SSSR i Mongolii (Paleogene freshwater fish fauna of the USSR and Mongolia). In: Trudy-Sovmestnaya Sovetsko-Mongol'skaya Nauchno-Issledovatel'skaya Nauchno-Issledovatel'stov "Nauka", 29, pp. 1–154. [Russian with English summary].

Temminck, C.J., Schlegel, H., 1846. Pisces, parts 10–14. In: Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823–30 collegit, notis observationibus et adumbrationibus illustravit PE de Siebold.

von der Mark, W., 1885. Fische der Oberen Kreide Westfalen. Palaeontographica 31, 32–35.

von Meyer, H., 1848. *Myliobates pressidens, Cobitis longiceps* und *Pycnodus faba*, drei Tertiairfische. Palaeontographica 1, 149–152.

Wappler, T., 2003. Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel. Mainzer Naturwissenschaftliches Archiv Beiheft 27, 1–234 pls. 1–18.

Whitfield, R.P., 1890. Observations on a fossil fish from the Eocene beds of Wyoming. Bulletin of the American Museum of Natural History III, 117–120.

Williams, R.R.G., 1987. The phylogenetic relationships of the salmoniform fishes based on the suspensorium and its muscles (Unpubl. PhD thesis). University of Alberta, p. 752.

Wilson, M.V.H., 1980. Oldest known *Esox* (Pisces: Esocidae), part of a new Paleocene teleost fauna from western Canada. Canadian Journal of Earth Science 17, 307–312.

Wilson, M.V.H., 1984. Osteology of the Palaeocene teleost *Esox tiemani*. Palaeontology 27, 597–608.

Wilson, M.V.H., 1996. Taphonomy of a mass-death layer of fishes in the Paleocene Paskapoo Formation at Joffre Bridge, Alberta, Canada. Canadian Journal of Earth Science 33, 1487–1498.

Wilson, M.V.H., Williams, R.R.G., 1991. New Paleocene genus and species of smelt (Teleostei: Osmeridae) from freshwater deposits of the Paskapoo Formation, Alberta, Canada, and comments on osmerid phylogeny. Journal of Vertebrate Paleontology 11, 434–451.

Wilson, M.V.H., Williams, R.R.G., 2010. Salmoniform fishes: key fossils, supertree, and possible morphological synapomorphies. In: Nelson, J.S., Schultze, H.-P., Wilson, M.V.H. (Eds.), Origin and Phylogenetic Relationships of Teleosts. Verlag Pfeil, München, Germany, pp. 379–409.

Wolfe, A.P., Edlund, M.B., 2005. Taxonomy, phylogeny, and paleoecology of *Eoseira wilsonii* gen. et sp. nov., a middle Eocene diatom (Bacillariophyceae: Aulacoseiraceae) from lake sediments at Horsefly, British Columbia, Canada. Canadian Journal of Earth Sciences 42, 243–257.

Wolfe, A.P., Edlund, M.B., Sweet, A.R., Creighton, S.D., 2006. A first account of organelle preservation in Eocene nonmarine diatoms: observations and paleobiological implications. Palaios 21, 298–304.

Wolfe, A.P., Csank, A.Z., Reyes, A.V., McKellar, R.C., Tappert, R., Muehlenbachs, K., 2012. Pristine early Eocene wood buried deeply in kimberlite from northern Canada. PLoS One 7, e45537. https://doi.org/10.1371/journal.pone.0045537.

Wolfe, A.P., Reyes, A.V., Royer, D.L., Greenwood, D.R., Doria, G., Gagen, M.H., Siver, P.A., Westgate, J.A., 2017. Middle Eocene CO2 and climate reconstructed from the sediment fill of a subarctic kimberlite maar. Geology 45, 619–622.

Woodward, A.S., 1901. Catalogue of the fossil fishes in the British Museum, Vol. 4. Containing the actinopterygian Teleostomi of the suborders Isospondyli (in part), Ostariophysi, Apodes, Percesoces, Hemibranchii, Acanthopterygii and Anacanthini. Taylor & Francis, London, pp. 1–636.