A PALEOCENE (DANIAN) MARINE OSTEOGLOSSID (TELEOSTEI, OSTEOGLOSSOMORPHA) FROM THE NUUSSUAQ BASIN OF GREENLAND, WITH A BRIEF REVIEW OF PALAEOGENE MARINE BONYTONGUE FISHES

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Abstract: The early Palaeogene represents a key interval in the evolution of modern marine fish faunas. Together with the first appearances of many familiar fish lineages characteristic of contemporary marine environments, early Palaeogene marine deposits worldwide feature the occurrence of osteoglossid bonytongues. Their presence in marine rocks is surprising, given that these fishes are strictly associated with freshwater environments in modern settings and in other parts of the fossil record. Despite its possible relevance to faunal recovery after the Cretaceous–Palaeogene (K–Pg) extinction, this marine osteoglossid radiation is relatively understudied. Here we describe an osteoglossid specimen from marine Danian deposits of western Greenland (Eqalulik Formation, northern Nuussuaq Peninsula). It consists of disarticulated cranial, pectoral and vertebral material belonging to a relatively large-bodied predator, similar to the widespread †*Brychaetus* but with some distinctive features. This specimen expands the geographical range of extinct osteoglossids to the Arctic and represents one of the earliest records of this group in marine deposits. We review other fossil occurrences of marine osteoglossids, highlighting temporal and biogeographical patterns that characterize their rise, diversification and sudden disappearance in the middle Eocene. It is likely that the transition from freshwater to marine environments occurred around the K–Pg boundary, possibly related to ecological replacement of predatory fish lineages that went extinct at the end of the Cretaceous. Further study of the Eqalulik Formation fauna could yield additional insight into the consequences of the end-Cretaceous extinction with regard to marine fish evolution and the assembly of modern marine faunas.

Key words: Osteoglossidae, Danian, Greenland, K–Pg extinction, early Palaeogene, marine fauna.

FOSSIL and molecular data point to substantial diversification in multiple groups of marine fishes in the wake of the Cretaceous–Palaeogene (K–Pg) mass extinction (Friedman 2010; Miya *et al.* 2013; Guinot & Cavin, 2016; Alfaro *et al.* 2018; Ribeiro *et al.* 2018; Sibert *et al.* 2018). Early Eocene (Ypresian) marine deposits demonstrate that marine fish faunas had a relatively modern phylogenetic composition by 50 Ma, with a dominance of acanthomorphs (Patterson 1993; Friedman *et al.* 2016; Friedman & Carnevale 2018). Among the new groups to appear in the early Palaeogene are multiple lineages of large, predatory acanthomorphs (and, more specifically, percomorphs) that persist to the modern day: billfishes, scombroids (tunas, mackerels and relatives), carangoids and barracudas (Friedman 2009;

Monsch & Bannikov 2011; Miya *et al.* 2013; Alfaro *et al.* 2018; Ribeiro *et al.* 2018). This has been interpreted through the lens of an ecological release model, with extant groups filling ecological roles vacated by the extinction of the dominant clades of large-bodied Late Cretaceous marine predators, such as †ichthyodectiforms, †pachyrhizodontids, †pachycormids and †enchodontids (Cavin & Martin 1995; Cavin 2002; Friedman 2009). The familiar modern predators that first emerge in the early Palaeogene are joined by a parallel, but short-lived, marine radiation of an unlikely group of non-acanthomorph teleosts: the osteoglossomorphs, commonly known as bonytongues. This is particularly striking because all extant osteoglossomorphs are restricted to freshwater environments, with few species occasionally found in

brackish waters (Berra 2007). Similar environmental associations characterize nearly all of the osteoglossomorph fossil record, which extends to the Middle–Late Jurassic (Hilton & Lavoué 2018; Capobianco & Friedman 2019). In contrast to the strong freshwater association that characterizes c. 130 million years of the osteoglossomorph record, the Paleocene–Eocene interval yields several species of marine osteoglossomorphs from sites across the world (Casier 1966; Danilchenko 1968; Bonde 2008; Wilson & Murray 2008; Forey & Hilton 2010; Alvarado-Ortega et al. 2015). Phylogenetic relationships of these marine forms remain unresolved (Wilson & Murray 2008) and it is unclear whether they represent a polyphyletic assemblage arising from multiple freshwater–marine environmental transitions (as proposed by Bonde 2008) or a monophyletic radiation stemming from a single marine invasion. Nonetheless, several marine taxa can be confidently placed within the osteoglossomorph subclade Osteoglossidae (Forey & Hilton 2010). Extant osteoglossids are freshwater but are distributed between Africa, South America, Southeast Asia and northern Oceania. The geographically widespread occurrences of marine osteoglossids in early Palaeogene deposits hint at an intriguing scenario where marine dispersal followed by freshwater invasions played a role in shaping the modern disjunct distribution of this group (Bonde 2008; Forey & Hilton 2010; Hilton & Lavoué 2018; Capobianco & Friedman 2019), which has otherwise been interpreted in a vicariance biogeographical framework.

Here we present new material of a marine osteoglossid from early Paleocene (Danian) deposits of Greenland (Fig. 1). Although not diagnostic at the specific or generic level, this fossil is nevertheless significant on both geographic and stratigraphic grounds. It expands the range of marine bonytongues to high latitudes, and represents a rare example from the early Paleocene, an interval important for constraining patterns of turnover associated with the K–Pg but for which relatively little fossil fish material is known when compared to the Late Cretaceous and Eocene (Patterson 1993). We place this specimen in the broader context of the marine osteoglossomorph radiation(s) by giving an overview of known fossil occurrences. Finally, we outline outstanding questions surrounding this distinctive and unusual feature of early Palaeogene marine ichthyofaunas and compare it to other examples of short-lived lineages that are prominent after the K–Pg mass extinction and which might be interpreted as components of a recovery fauna.

MATERIAL AND METHOD

Specimens examined

Skeletonized specimens of extant taxa and fossil specimens of extinct taxa belonging to Osteoglossomorpha were examined as comparative material. Names of extinct taxa are preceded by a dagger symbol (†).

Hiodontidae. Hiodon tergisus UMMZ 180315.

Mormyridae. Marcusenius macrolepidotus UMMZ 200066; Mormyrus lacerda UMMZ 200084.

Osteoglossidae. Arapaima gigas UMMZ 177540, UMMZ 203831; †Brychaetoides greenwoodi MGUH 28906; †Brychaetus muelleri NHMUK PV 39699, NHMUK PV P641, NHMUK PV P3893, NHMUK PV P66889; cf. †Brychaetus sp. MGUH 28907; †Brychaetus? sp. NHMUK PV P73088; Heterotis niloticus UMMZ 213845; †Heterosteoglossum foreyi MGUH 28904; †Magnigena arabica NHMUK PV OE PAL 2007-1; Osteoglossidae indet. †NHMUK PV P66354; Osteoglossum bicirrhosum UF 189007, UMMZ 203832; †Phareodus testis NHMUK PV P61230; †Ridewoodichthys caheni MRAC RG 9169–70; Scleropages formosus UMMZ 203833, UMMZ 213853; †Xosteoglossid rebeccae MGUH 28905.

Osteoglossomorpha incertae sedis. †Foreyichthys bolcensis NHMUK PV P16821; †Monopteros gigas MNHN F BOL 285, MNHN F BOL 288; †Thrissopterus catullii IGUP 8839–8840.

In addition to the material listed here, further observations of osteoglossomorph osteology were made based on Kershaw (1970, 1976), Taverne (1977, 1978) and Hilton (2003).

Micro-computed tomography

The specimen described here (NHMD 72014 A+B) and some of the comparative specimens were studied using micro-computed tomography (µCT) datasets produced using Nikon XT H 225ST industrial µCT scanners at the University of Michigan and the Natural History Museum, London. Individual scanning parameters are given below:

NHMD 72014 A+B (two halves of the specimen scanned independently). Voltage, 210 kV; current, 220 µA; filter, 2.5 mm copper; reflection target, tungsten; effective pixel size, 92 µm; scanning facility, University of Michigan CTEES. Following best practices in the accessibility of tomography data (Davies et al. 2017), we have made tomograms, .mcs files, and .plys of segmented structures available in the Dryad Digital Repository (Capobianco et al. 2019).

†Brychaetus muelleri NHMUK PV P641. Voltage, 190 kV; current, 305 µA; filter, 2.7 mm copper; reflection target, tungsten; effective pixel size, 62.9 µm; scanning facility, University of Michigan CTEES.

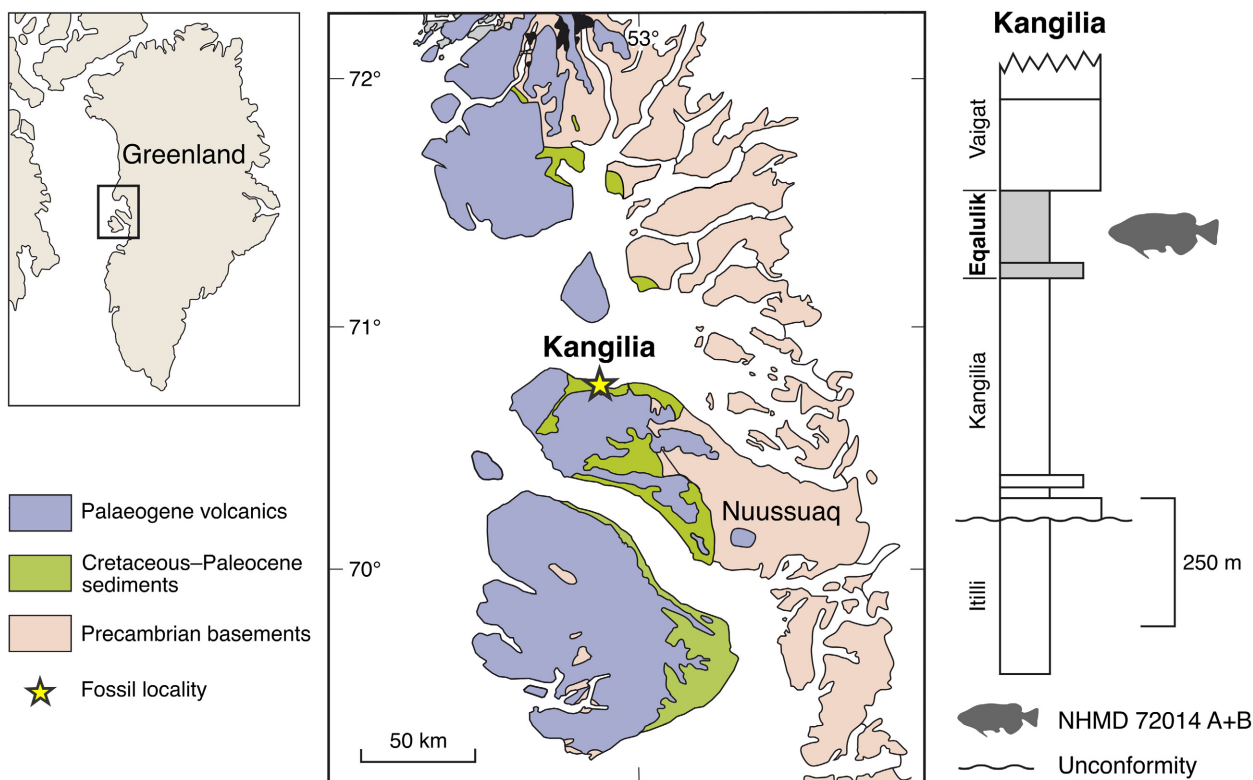†Brychaetus muelleri NHMUK PV 39699. Voltage, 210 kV; current, 200 µA; filter, 1 mm tin; reflection

FIG. 1. Map of the Nuussuaq Peninsula, western Greenland, with simplified stratigraphic log of formations of the Late Creta-ceous – Paleocene Nuussuaq Group outcropping in Kangilia. Modified from Dam *et al.* (2009).

target, tungsten; effective pixel size, 50.6 μm; scanning facility, NHM, Imaging and Analysis Centre.

Scans were acquired using Inspect-X and reconstructed using CT Pro 3-D (Nikon Metrology, USA). Additionally, reconstructed tomograms for *Osteoglossum bicirrhosum* UF 189007 were downloaded from Morphosource (media M26520).

Reconstructed datasets were visualized and segmented using Mimics v. 19.0 (Materialise, Belgium). 3-D models of segmented skeletal elements were exported from Mimics as surface files (.ply). Surface files of elements belong-ing to the two halves of NHMD 72014 A+B were reconstructed together in Blender v. 2.79 (blender.org). Two-dimensional high-resolution renderings of surface files were also acquired in Blender.

Institutional abbreviations. FUM, Fur Museum, Fur, Denmark; IGUP, Istituto Geologico dell'Università di Padova, Padova, Italy; MCSNV, Museo Civico di Storia Naturale, Verona, Italy; MGUH, Geology Museum, University of Copenhagen (stored at Fur Museum), Denmark; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal de l'Afrique Cen-trale, Tervuren, Belgium; NHMD, Natural History Museum of Denmark, Copenhagen, Denmark; NHMUK, Earth Sciences col-lections, Natural History Museum, London, UK; UF, University

of Florida, Gainsville, USA; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, USA; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, Michi-gan, USA.

SYSTEMATIC PALAEONTOLOGY

TELEOSTEI Müller, 1845
OSTEOGLOSSOMORPHA Greenwood *et al.*, 1966
OSTEOGLOSSIFORMES Berg, 1940
OSTEOGLOSSIDAE Berg, 1940
Gen. et sp. indet.
Figures 2–5

Material. NHMD 72014 A+B, two halves of an ellipsoidal con-cretion with disarticulated bones, including maxilla, urohyal, scapula, several vertebral centra and fragments of lepidotrichia and radials (Fig. 2).

Occurrence. The specimen was collected by Abraham Løv-strøm of the Geological Survey of Denmark and Green-land (GEUS) in 1957. It comes from the Kangilia Ridge in the north coast of the Nuussuaq Peninsula (western
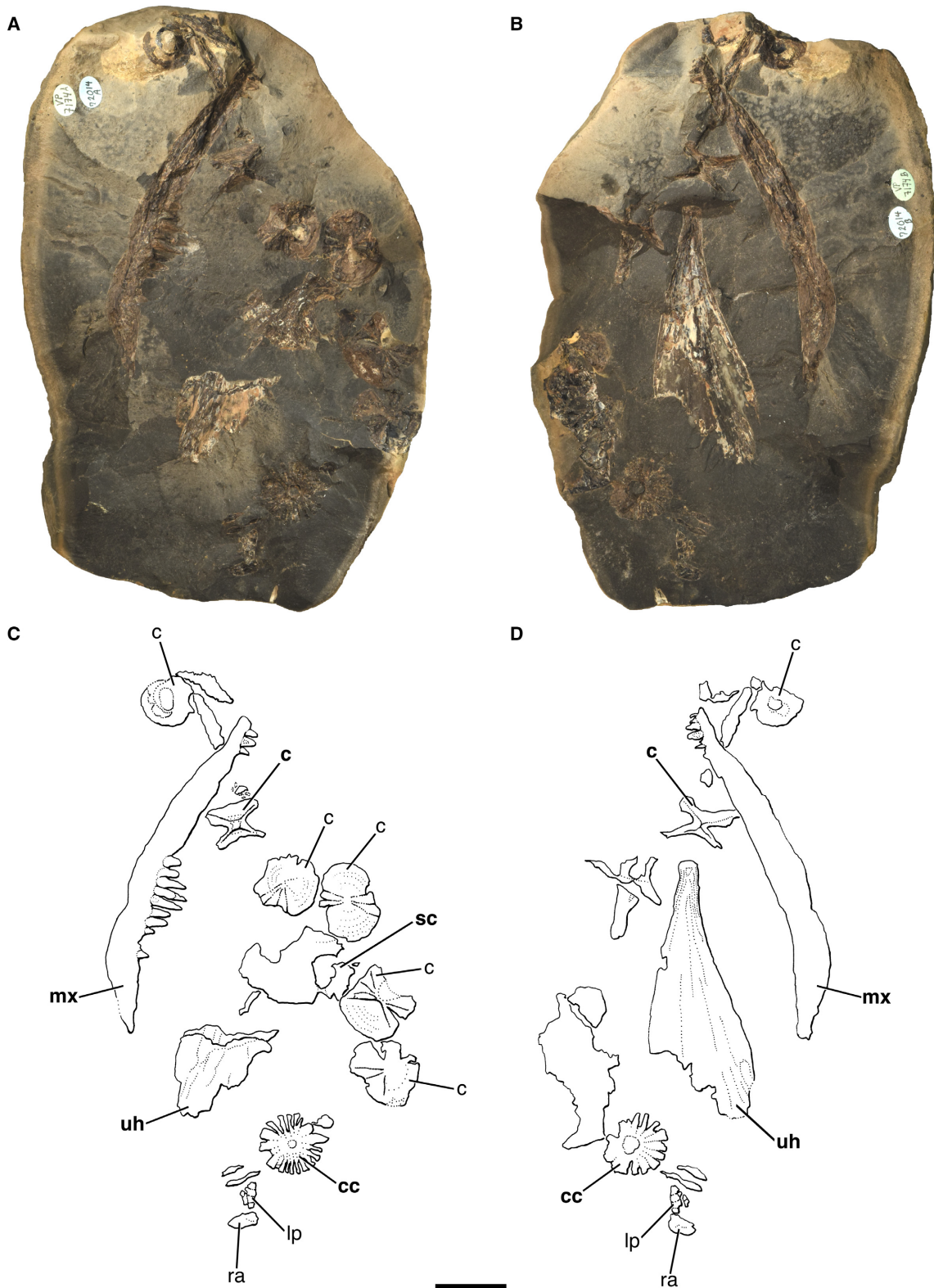
FIG. 2. Photographs of NHMD 72014 A+B (A, B), with interpretative line drawings (C, D). Labels in bold indicate elements rendered in Figs 3–4. Unlabelled elements have uncertain identity. Scale bar represents 20 mm. *Abbreviations*: c, centrum; cc, caudal centrum; lp, lepidotrichia; mx, maxilla; ra, radial; sc, scapula; uh, urohyal.
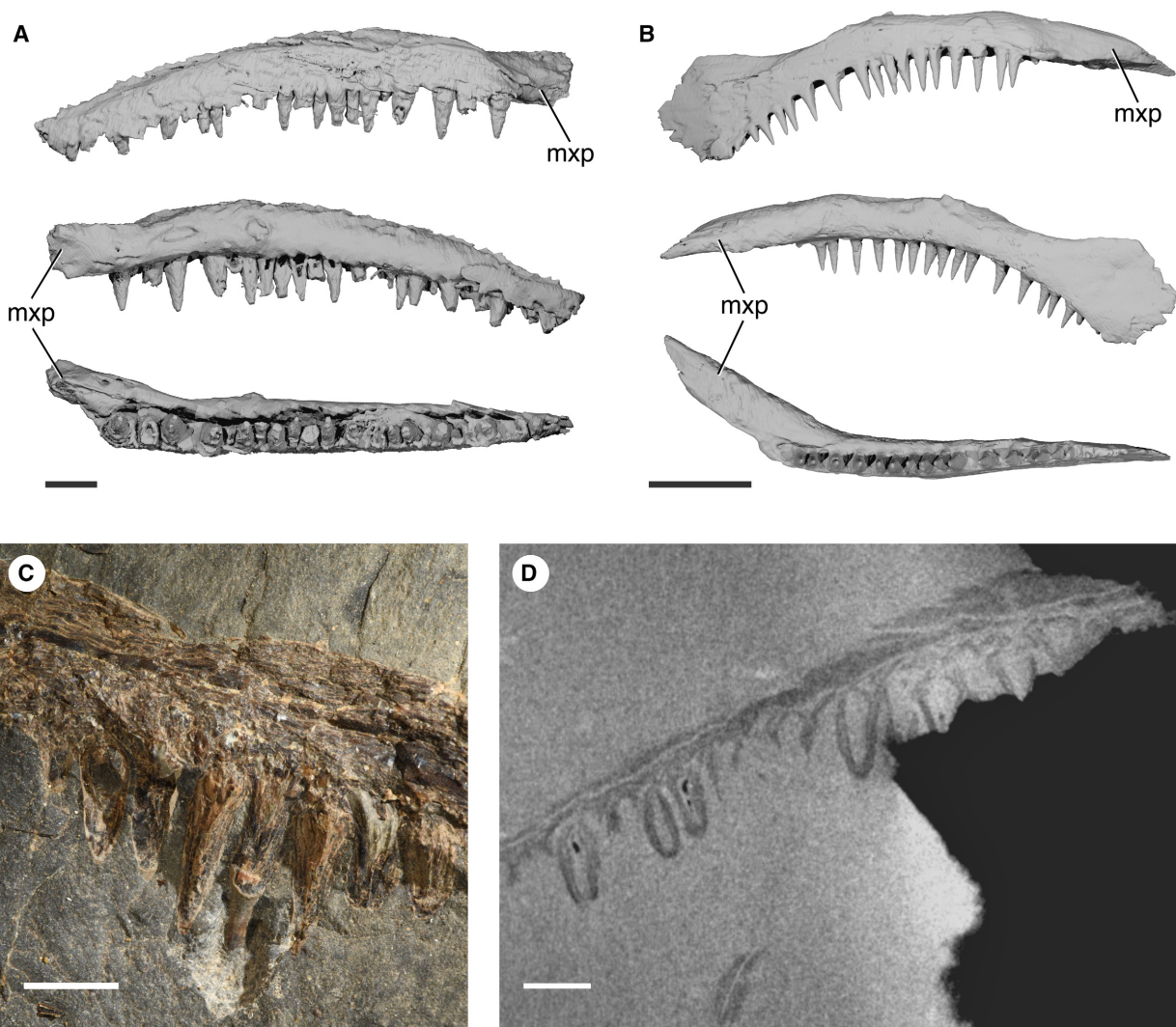
FIG. 3. Maxillary and dental morphology of NHMD 72014 A+B. A–B, renderings comparing the maxilla of NHMD 72014 A+B (A) with the maxilla of †*Brychaetus muelleri* NHMUK PV 39699 (B) in lateral, mesial and ventral views (from top to bottom). C, close-up photograph of maxillary teeth. D, tomogram showing maxillary teeth in sagittal section. Scale bars represent 10 mm (A, B); 5 mm (C, D). *Abbreviation*: mxp, anterior articular process of maxilla.

Greenland; Fig. 1). It was briefly mentioned (among other specimens) as indeterminate actinopterygian material from the Danian Kangilia Formation by Bendix-Almgreen (1969) and Rosenkrantz (1970), who further refined its stratigraphic position as belonging to the '*Thyasira* Member'. The same deposits yielded the oldest known gadoid fish, still undescribed and informally known as †'*Protocodus*' (Rosen & Patterson 1969; Cohen 1984). A recent revision of the lithostratigraphy of the Nuusuuaq Basin (Dam *et al.* 2009) assigned some deposits of the Kangilia and Agatdal formations (including the *Thyasira* Member) to the newly named Eqalulik Formation. The Eqalulik Formation was deposited in a relatively deep marine environment, with maximum water depth *c.* 700 m (Dam *et al.* 2009). The age of the Eqalulik

Formation is not well determined, partly because of its diachrony throughout the Nuussuaq Basin (Dam *et al.* 2009). While the macrofauna of the Eqalulik Formation has early Danian affinities (Rosenkrantz, 1970), palyno- and nannostratigraphy suggest a late Danian age (upper NP3 – lower NP4 nannoplankton zone, 63–62 Ma; Nøhr-Hansen & Sheldon 2000; Anthonissen & Ogg 2012).

Description. An almost complete right maxilla (97 mm in length) is preserved in the concretion (mx, Figs 2, 3). It is relatively robust and slightly dorsoventrally bowed. It becomes more laterally compressed posteriorly, although the posterior region of the bone is not complete. Anteriorly, the maxilla extends into a short and deep anteromedial process that would have articulated with the posterior portion of the premaxilla. Posterior to this process, it presents a distinct dorsal thickening, while the medial
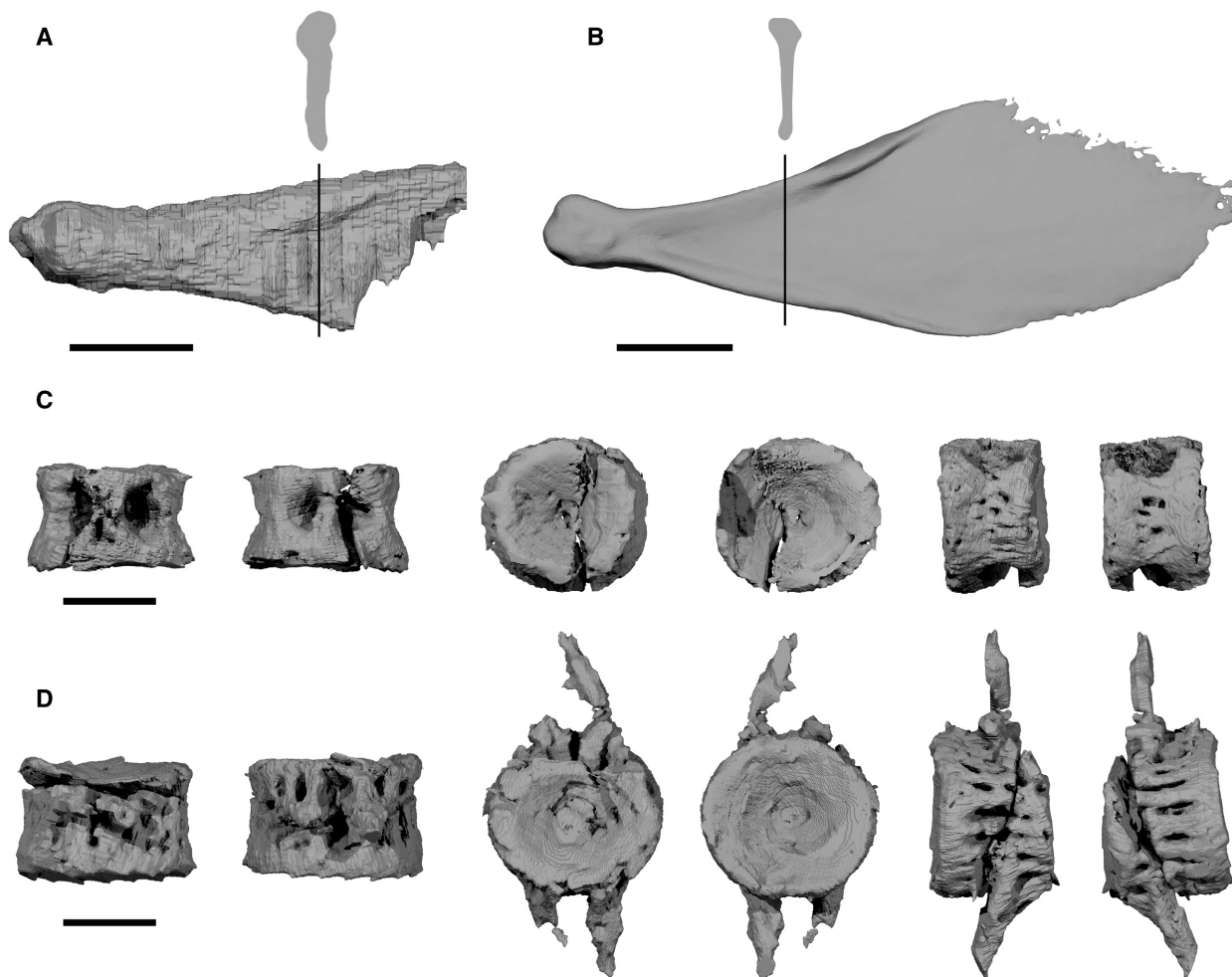
FIG. 4. Isolated skeletal elements of NHMD 72014 A+B. A, rendering of the anterior portion of the urohyal in left lateral view, with silhouette of its cross-section. B, rendering of the urohyal of *Osteoglossum bicirrhosum* (UF 189007) in left lateral view, with silhouette of its cross-section. C–D, renderings of an abdominal vertebral centrum (C) and a caudal vertebra (D) in dorsal, ventral, cranial, caudal, right lateral and left lateral views (from left to right). Scale bars represent: 10 mm (A, C, D); 2 mm (B).

surface of the bone bears a relatively deep elliptical pit. Twenty teeth and six empty tooth sockets are present, arranged in a single row. Teeth increase in size from the posterior to the anterior of the jaw. The teeth are straight, anteroposteriorly compressed at the base and conical at the tip. Each tooth is hollow inside throughout its length (Fig. 3C, D). The tooth base appears to be sheathed in bone for a very short length (less than a third of the length of the tooth).

The urohyal (uh, Fig. 2) is large (*c.* 80 mm in length) and laterally compressed with a rounded anterior head. It is much deeper posteriorly than anteriorly. Posterior to its rounded head, it bears a thickened dorsal ridge apparent in transverse cross-section (Fig. 4A).

Part of the left pectoral girdle is preserved, including the scapula (sc, Fig. 2) and possible fragments of the cleithrum. The scapula is irregularly shaped with a distinct subcircular scapular foramen (scf, Fig. 5A, B). Details of scapular morphology are difficult to interpret due to its poor preservation and low

contrast in tomograms. A slightly concave facet on the posterior edge of the scapula is interpreted as the articular surface for the first pectoral fin ray (afp, Fig. 5A, B). Marked thickening on the mesoventral edge is probably indicative of articulation with other radials of the pectoral fin and with the coracoid. Fragments of what are probably two lepidotrichia (fin rays) and one radial are present. The lepidotrichia (lp, Fig. 2) appear to be segmented and dorsoventrally flattened. The putative radial (ra, Fig. 2) is subcylindrical in shape.

Seven vertebral centra are preserved in the concretion, ranging from very fragmentary to almost complete (c and cc, Fig. 2). All centra are amphicoelous, subcircular in transverse section and their width and depth is larger than their length. There is substantial morphological variability among the preserved centra. An almost complete abdominal centrum (Fig. 4C) displays oval, deep neural arch pits, probably separated by a shallow and narrow mid-dorsal pit. The neural arch is absent, suggesting that it was an autogenous element in life. A pair of deep ventral pits
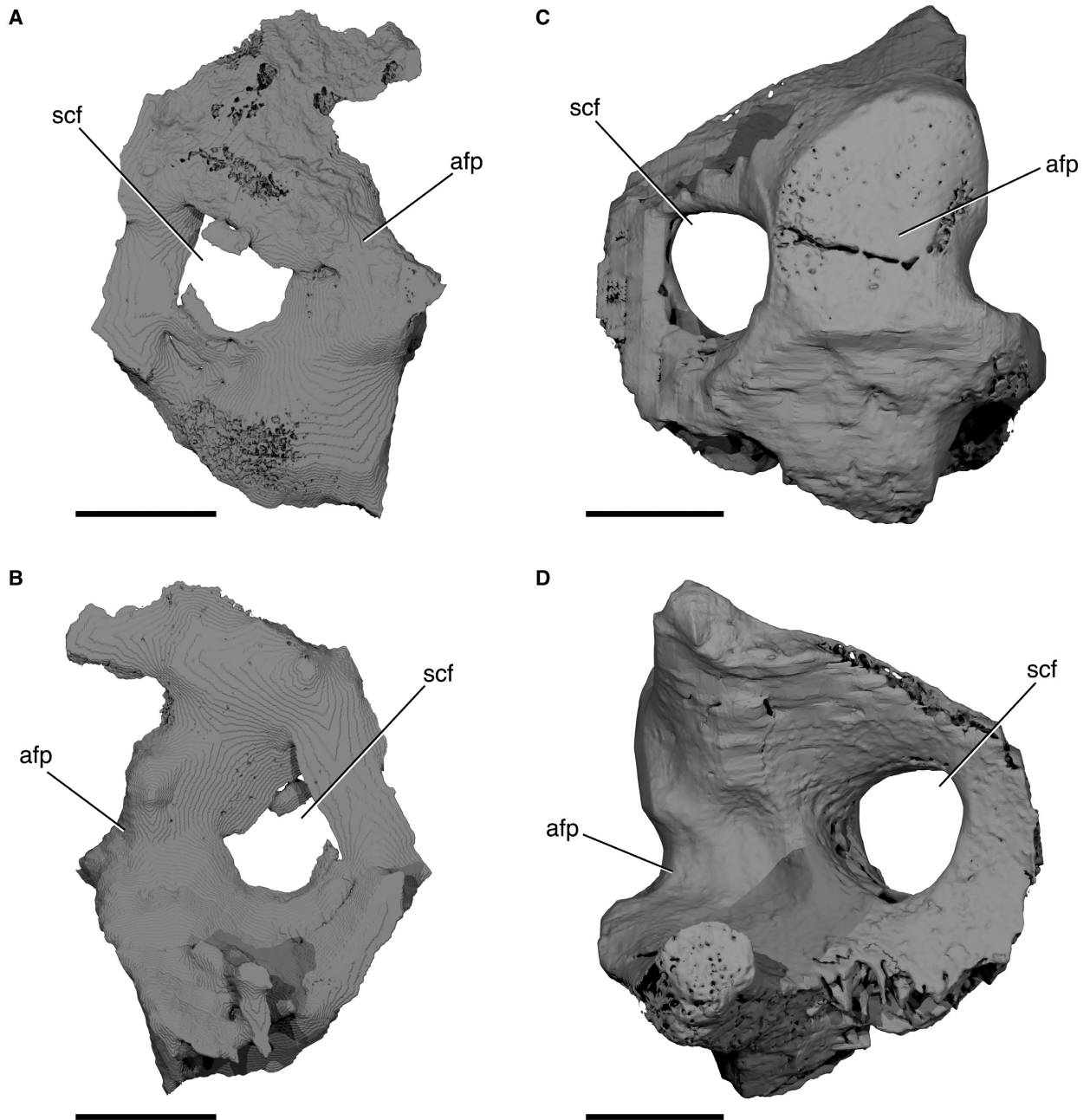
FIG. 5. Left scapula of NHMD 72014 A+B. A–B, renderings of the scapula in lateral (A) and mesial (B) views. C–D, renderings of the left scapula of †*Brychaetus muelleri* (paratype, NHMUK PV P641) in lateral (C) and mesial (D) views. Scale bars represent: 10 mm (A, B); 5 mm (C, D). *Abbreviations*: afp, articular facet for the first pectoral fin ray; scf, scapular foramen.

is also present. The lateral surface of the centrum is pitted by small circular pores. No parapophysis is evident on this centrum. Due to the combination of these features, this centrum could represent one of the anteriormost centra of the vertebral column. An almost complete caudal centrum is preserved in the concretion, together with fragments of its neural and haemal arches (Fig. 4D). Each lateral surface of the centrum presents six or seven longitudinal sulci. A deeper ventral pit is bordered by the haemal arch.

DISCUSSION

Osteoglossid identity of the Greenland specimen and comparison with other osteoglossids

Anteroposteriorly compressed large teeth with a conical tip and a hollow cavity throughout their length are characteristic of some members of Osteoglossidae, especially

of the marine fossil taxon †*Brychaetus* (Casier 1966; Forey & Hilton 2010). Comparable teeth have been found worldwide in several early Palaeogene marine deposits (see section below). The extant osteoglossids *Osteoglossum* and *Scleropages* share a similar tooth morphology, albeit with smaller size relative to the maxilla and with less pronounced anteroposterior compression. The presence of a bony tooth base is a condition found in several fossil osteoglossids, including †*Brychaetus* and †*Phareodus*. The bony base in †*Brychaetus* and †*Phareodus* teeth is usually much deeper than in the Greenland specimen (between one-third and half of the total tooth length for maxillary teeth). A shallow bony tooth base has been described in the marine osteoglossid †*Ridewoodichthys* (Taverne 2009*a*). The size of the Greenland maxilla suggests a relatively large fish, perhaps *c.* 1 m in length assuming body proportions comparable to †*Phareodus*. It apparently differs from the maxillae of †*Brychaetus* and †*Phareodus* in having an anterior articular process that is short and stout rather than elongated and tapering (Fig. 3A, B). Although this feature does not seem to be the result of incomplete preservation of the articular process, the resolution of the scan does not allow us to completely exclude that a longer process was indeed present but taphonomically damaged.

Compared to extant osteoglossomorphs, the urohyal closely resembles those of the osteoglossids *Osteoglossum* and *Scleropages* in its marked posterior deepening and laterally compressed cross-section with slight dorsal thickening (Fig. 4A, B). While Taverne (1977) described the urohyal of these two extant genera as having a Y-shaped cross-section, we were not able to observe such a feature. The relatively large size of the urohyal is consistent with an osteoglossid attribution, whereas other osteoglossomorphs (such as *Hiodon* and *Pantodon*) present a much smaller urohyal (besides differing substantially in morphology).

The overall shape of the scapula and the relative size of the subcircular foramen are similar to those of extant osteoglossids with the exception of *Heterotis*, whose scapular foramen is not completely enclosed by bone. While a detailed comparative assessment is prohibitive due to its poor preservation, comparison with the scapula of †*Brychaetus* (Fig. 5C, D) suggests significant differences in shape and proportions. In particular, what we interpret as the articular surface for the first pectoral fin ray appears to be much smaller than in †*Brychaetus*. This feature might relate to the relative size of the first pectoral fin ray, as observed in extant osteoglossid genera. *Osteoglossum* and *Scleropages* (as well as the extinct †*Phareodus*) are characterized by an enlarged and extremely thickened first pectoral fin ray, and in turn present a large articular surface on the scapula. In contrast, the first pectoral fin ray in *Arapaima* and *Heterotis* is only slightly larger than the successive rays and is not particularly thickened, and the relative size of the corresponding articular surface on the scapula of these two genera is substantially smaller than in *Osteoglossum*, *Scleropages* and †*Brychaetus*. Thus, it is possible that the Greenland osteoglossid did not have a greatly enlarged first pectoral fin ray.

An autogenous neural arch in precaudal vertebrae is a plesiomorphic teleost feature and is consistent with an osteoglossid identification (Brinkman & Neuman 2002). The presence of several longitudinal sulci in the lateral surface of the caudal vertebra recalls the vertebral morphology of *Arapaima*. In sum, the Greenland fossil shows clear resemblance to osteoglossids, including specific correspondences to several extinct and modern genera. However, the remains are too incomplete to propose an assignment beyond the family level.

Geographical and stratigraphical distribution of marine osteoglossids

Otoliths referred to osteoglossomorphs have been found in few Mesozoic marine deposits. The otolith genus †*Archaeglossus* from the Middle–Late Jurassic of England could represent the oldest record for this group (Schwarzhans 2018). The presence of early stem osteoglossomorphs in marine deposits would not be completely unexpected, given that the osteoglossomorph lineage probably derives from marine ancestors (Betancur-R *et al.* 2015). Three otolith species originally identified as albuliforms have been recently grouped in the genus †*Kokenichthys* (Schwarzhans 2010) and interpreted as possible osteoglossomorphs (Schwarzhans 2018). These are Aptian–Maastrichtian in age and have been found in lagoonal or marine deposits in Germany, Spain and the USA. In addition to †*Kokenichthys ripleyensis*, the early Maastrichtian Ripley Formation in Mississippi (USA) yielded otoliths with osteoglossid-like morphology (†'*Arapaimina*' *tavernei*; Nolf & Stringer 1996; Nolf 2013). These otolith occurrences should be interpreted with caution because extant osteoglossomorph otoliths show a remarkable morphological variety (Nolf 2013); unique otolith synapomorphies have not been defined for the group; and alternative systematic placements (such as within Albuliformes) are possible. A putative Mesozoic marine osteoglossomorph known from a single articulated specimen is the Cenomanian †*Prognathoglossum kalassyi* from Lebanon, assigned by Taverne & Capasso (2012) to Pantodontidae, an osteoglossomorph lineage with a single extant species: the freshwater African butterflyfish *Pantodon buccholzi*. This bizarre taxon presents a series of peculiar features, including shortened and bulbous braincase, extremely long lower jaw, mouth oriented nearly

vertically, reduced pectoral fins and long dorsal fin extending throughout the length of the body, that challenge its identification as a pantodontid osteoglossomorph. Nonetheless, despite these putative osteoglossomorph occurrences in marine settings before the Palaeogene, definitive marine osteoglossids are found only in sediments ranging from the earliest Paleocene to the middle Eocene (Fig. 6). A possible exception is represented by a single incomplete jaw fragment from the Maastrichtian Ménaka Formation of Mali referred to the genus †*Brychaetus* (O'Leary *et al.* 2019), which is known from early Palaeogene marine deposits worldwide (see following subsections).

Danian. The oldest unambiguous marine osteoglossid fossil is an isolated jaw fragment (probably a premaxilla) from the Fiskeler Member of the Stevns Klint in Denmark (Schwarzhans & Milàn 2017). While this single specimen was described as unidentified osteoglossomorph, the morphology of its teeth (large and columnar in lateral view) is consistent with an osteoglossid attribution. The age of this specimen is remarkable, because the Fiskeler Member immediately overlies the K–Pg boundary in a continuous succession. This demonstrates the presence of osteoglossids in the marine realm in the earliest Danian, shortly after the K–Pg extinction. An almost complete specimen of a marine osteoglossid comes from the Danian Tenejapa Formation of Palenque, Mexico (Alvarado-Ortega *et al.* 2015). It is assigned to the genus †*Phareodus*, which is otherwise known from early–middle Eocene freshwater deposits of the USA, China and Australia (Li 1994; Li *et al.* 1997; Zhang 2003). Thus, this specimen would represent the oldest known †*Phareodus* by at least 5 million years (see following subsections) and the only one from marine deposits. However, the attribution of this specimen to †*Phareodus* has been based on characters (such as opercle shape and absence of teeth on the parasphenoid) that have broader distribution within osteoglossids (including the marine genus †*Brychaetus*; Forey & Hilton 2010). Further study is needed to determine the generic status of this Danian osteoglossid.

Selandian. Fragmentary osteoglossid material is known from marine deposits in the Landana section of the Cabinda enclave of Angola (Taverne 2009*a*, 2016). While these deposits are classically regarded as Danian in age ('Montian' in older literature), a recent reassessment of the regional stratigraphy indicates that the osteoglossid material is most likely Selandian in age (Solé *et al.* 2019). These remains comprise a caudal skeleton and jaw fragments assigned to †*Ridewoodichthys caheni*, which is similar to †*Brychaetus*, and a single caudal skeleton of a slightly younger, unnamed taxon (Taverne 2009*a*, 2016).

Thanetian. The marine osteoglossid †*Magnigena arabica* is known from a partial articulated skull (Fig. 6A) found in the late Paleocene Umm Himar Formation of Saudi Arabia (Forey & Hilton 2010). An isolated premaxilla has been found in marine deposits of similar age from Sessao, the Iullemeden Basin of Niger (Cappetta 1972). Although this specimen was originally described as †*Brychaetus*, Taverne (2009*b*) assigned it to a new extinct species in the modern genus *Scleropages*, which currently occurs in fresh waters of Southeast Asia and northern Oceania. Given the scarcity of the material, we adopt a more cautious approach and consider this premaxilla to belong to an indeterminate osteoglossid. Osteoglossid teeth referred to †*Brychaetus muelleri* have been found in the Thanetian Tuscahoma Formation of Mississippi (USA), which represents either an estuarine or a marine environment (Case 1994).

Ypresian. Early Eocene deposits yield the highest diversity of marine fossil osteoglossids, which are found around the world in the Ypresian. The marine Danata Formation of Turkmenistan yielded three articulated specimens of the relatively large osteoglossid †*Opsithrissops osseus* (Danilchenko 1968). The formation straddles the Paleocene–Eocene boundary, with the fish-bearing horizon lying at the border between Thanetian and Ypresian (Bannikov & Parin 1997). Three osteoglossomorph taxa are known from the coeval Stolle Klint Clay of Denmark, which was deposited in a shallow, landlocked marine basin (Bonde 2008). The Fur Formation directly overlays the Stolle Klint Clay and increases the diversity of early Ypresian marine osteoglossomorphs from Denmark up to six distinct taxa in total (Bonde 2008). Most of these are known from articulated remains. While their systematic affinities are uncertain and require further investigation, at least some of them are recognizable as definitive osteoglossids (including †*Heterosteoglossum*, †*Xosteoglossid* and a †*Brychaetus*-like form; Bonde 2008). Contrary to Bonde (2008), we also regard †*Brychaetoides* from the Fur Formation as an osteoglossid due to shared features with other osteoglossids such as †*Brychaetus* (e.g. the lateral expansion of the anterior portion of the frontals; Fig. 6B). The best known marine osteoglossid is the large predator †*Brychaetus muelleri* from the London Clay Formation of England (Fig. 6D), represented by several articulated specimens (mostly skulls; Casier 1966; Roellig 1974; Taverne 1978). These deposits yield an additional indeterminate osteoglossid, known from a partial neurocranium (Forey & Hilton 2010). Isolated osteoglossid scales have also been found in the London Clay and resemble those of the Danish †*Heterosteoglossum* (Bonde 2008). Osteoglossomorphs have been also reported from the species-rich reef assemblage of the Bolca Lagerstätten in Italy (Taverne 1998), although the interpretation of some of these is

FIG. 6. Photographs of representative fossil osteoglossids found in marine deposits. A, †*Magnigena arabica* (holotype, NHMUK PV OE PAL 2007-1) from the Thanetian Umm Himar Formation of Saudi Arabia. B, †*Brychaetoides greenwoodi* (holotype, MGUH 28906) from the Ypresian Fur Formation of Denmark. C, †*Brychaetus*? sp. (NHMUK PV P73088) from Ypresian phosphates of Morocco. D, †*Brychaetus muelleri* (holotype, NHMUK PV P3893) from the Ypresian London Clay Formation of England. Scale bars represent: 10 mm (A); 20 mm (B, C); 40 mm (D).

questionable. Among them, †*Monopteros* could be an osteoglossid or a more basal osteoglossiform with a peculiar durophagous dentition (Taverne 1998; Bonde 2008). †*Thrissopterus* could represent an osteoglossid with broad pectoral fins and very elongated body (Taverne 1998). †*Foreyichthys* has been alternatively interpreted as closely related to osteoglossids (Taverne 1998; Bonde 2008) or as an indeterminate osteoglossomorph (Forey & Hilton 2010). However, we advise caution in any interpretation of †*Foreyichthys* as an osteoglossomorph. The only known specimen has a very poorly preserved skull and its postcranial skeleton does not present unique osteoglossomorph synapomorphies (pers. obs. of NHMUK PV P.16821). Moreover, †*Brychaetus muelleri* (or a very similar species) is also known from Monte Bolca and is represented by an undescribed articulated specimen (part and counterpart IGUP 26282 and MCSNV IG 24548) that is currently under study by some of the authors of the present paper. Jaw fragments and isolated teeth referred to †*Brychaetus* – based on the anteroposteriorly compressed tooth morphology, with conical enamel cap and hollow bony base – have been found in several Ypresian marine deposits outside of Europe, including the Indian Laki Series (Forey & Hilton 2010), the 'Couches I-0' of Oulad Abdoun, Moroccan Phosphates (Fig. 6C; Arambourg, 1952; Bardet *et al.* 2017), the Tamaguélelt Formation of Mali (Patterson & Longbottom 1989; O'Leary *et al.* 2019) and the Nanjemoy Formation in Maryland and Virginia, USA (Weems & Horman 1983; Weems 1999). Articulated remains of non-Eurasian marine fossil osteoglossids are rare. A 3-D preserved cranial skeleton of a new osteoglossid species from the Ypresian Moroccan phosphates (UMMP 118216) is currently under study by the authors.

Lutetian. The youngest marine osteoglossid remains come from a handful of Lutetian deposits. It is uncertain whether this reflects a decline in diversity or abundance, or instead is a consequence of a more restrictive set of fish-yielding deposits in comparison to the Ypresian. Undescribed cranial material belonging to a new osteoglossid taxon has been recognized in collections from the early Lutetian Habib Rahi Formation from Punjabi Pakistan, which represent a relatively deep marine environment. This specimen (UMMP GSP-UM field no. 1981292) is currently under study by the authors. The same formation yielded another undescribed specimen (UMMP GSP-UM field no. 1981251), preserving the impressions of skull and pectoral fin, that resembles †*Thrissopterus* from Bolca. Putative osteoglossid otoliths have been reported from middle Eocene marine deposits in Europe (Nolf & Cappetta, 1976; Stinton, 1977).

Osteoglossids completely disappear from the marine fossil record after the middle Eocene.

Palaeobiological and palaeobiogeographical significance of marine osteoglossids

The presence of a large-bodied marine osteoglossid in the Danian of Greenland is relevant for a variety of reasons. First, it represents the northernmost known occurrence for this clade, further expanding their geographical distribution in the Palaeogene. While the early Palaeogene was characterized by much warmer temperatures than today (Zachos *et al.* 2001), the Arctic climate at that time was probably temperate with episodic cooling events (Dawson *et al.* 1976; Spielhagen & Tripati 2009; Zhang *et al.* 2019). The presence of a gadoid fish (†'*Protocodus*') in the Eqalulik Formation and of a temperate/warm temperate otolith ichthyofauna known from roughly coeval deposits of central Nuussuaq (Schwarzhans 2004) are further evidence of the environmental conditions of West Greenland in the early Paleocene. This contrasts with modern osteoglossid distribution – limited to tropical environments (Berra 2007) – and hints at a broader temperature tolerance of some early Palaeogene members of the clade.

Second, the specimen described here is also one of the oldest osteoglossid fossils known from marine deposits. This highlights that, although marine forms are best known from Ypresian deposits, osteoglossids transitioned from freshwater to the sea well before then. Due to the scarcity of osteoglossid remains in Campanian–Paleocene deposits, it remains unclear when and where this environmental transition happened. Campanian–Maastrichtian osteoglossid fossils are known only from freshwater or brackish deposits. They include †*Cretophareodus alberticus* from the Campanian Oldman Formation (Li, 1996) of Canada and a possible indeterminate osteoglossid from the Maastrichtian Tremp Formation in Catalonia, Spain (Blanco *et al.* 2017), in addition to several jaw fragments, teeth and scales from Bolivia and India (Sahni & Bajpai 1988; Prasad 1989; Gayet & Meunier 1998). More complete osteoglossid remains are known from freshwater early Palaeogene deposits, roughly contemporary with the marine occurrences described in the previous section. Among these, the fossil taxa †*Phareodus* (including †*P. encaustus* and †*P. testis* from the early–middle Eocene Green River and Bridger formations of western USA, †*P. songziensis* from the Ypresian Yangxi Formation of China and †*P. queenslandicus* from the late Paleocene – early Eocene Redbank Plains Formation of Australia) and †*Taverneichthys* from the Paleocene Palana Formation of India (Kumar *et al.* 2005; Taverne *et al.* 2009) share osteological features (including a broad supraorbital shelf formed by the frontals and aspects of tooth morphology) with at least some marine osteoglossids (Forey & Hilton 2010). The age of these taxa, their wide geographical distribution and their putative affinities

with widespread marine taxa such as †*Brychaetus* raise the possibility that marine dispersal followed by multiple freshwater invasions might have played a role in the early Palaeogene biogeographical history of Osteoglossidae (Capobianco & Friedman 2019).

It has been hypothesized that the invasion of marine environments by osteoglossomorphs (and specifically osteoglossids) in the early Palaeogene could result from the opportunistic replacement of large-bodied predatory taxa that went extinct at the end of the Cretaceous (Friedman 2009; Friedman & Sallan 2012). These include some large lamniform sharks, stem teleosts such as †aspidorhynchids, †pachycormiforms and †ichthyodectiforms, and crown teleosts such as †enchodontids (Friedman & Sallan 2012; Guinot & Cavin 2016). It is now clear that by the end of the Danian (*c.* 4 million years after the extinction event) osteoglossids evolved large predatory forms in the marine realm, following a transition from freshwater to marine environments that probably occurred across the K–Pg boundary. Danian marine deposits record the presence of giant megalopids as another group of macropredatory fishes (Khalloufi *et al.* 2019). Significantly, large megalopids are known only from freshwater deposits in the latest Cretaceous (Bardack 1970) and from marine deposits during the Palaeogene (Fur Formation, London Clay Formation, and Moroccan phosphates; Bonde 1997; Friedman *et al.* 2016; Khalloufi *et al.* 2019), hinting at a comparable environmental transition before the early Paleocene. Other predatory marine fish taxa that survive up to the present day (such as scombrids, xiphioids, sphyraenids and carangoids) are currently unknown from Danian deposits and appear in the fossil record by the late Paleocene – early Eocene (Fierstine 2006; Monsch & Bannikov 2011; Carnevale *et al.* 2014). However, this pattern may result from the rarity of Danian marine deposits that have yielded fish body fossils. It is unclear whether competition with this modern suite of marine predators or other unknown factors led to the disappearance of osteoglossids from marine environments during or after the middle Eocene.

We suggest that marine osteoglossids represent a striking example of a short-lived recovery fauna, diversifying and dispersing shortly after the end-Cretaceous mass extinction (presumably due to ecological opportunity) and going extinct after a relatively short amount of geological time. Among marine vertebrates, an analogous pattern could have characterized the evolutionary history of †dyrosaurid crocodylians (Hastings *et al.* 2011; Martin *et al.* 2019) and †palaeophiid snakes (Rage *et al.* 2003). Similar examples of early Palaeogene recovery faunas are better known in the terrestrial realm, particularly in the context of the North American mammal fossil record (Rose 1981; Longrich *et al.* 2016).

CONCLUSIONS

NHMD 72014 A+B represents a large-bodied marine osteoglossid from the early Paleocene (Danian) of Greenland. Although the specimen is too fragmentary to suggest a specific or even generic attribution, it presents both similarities (tooth morphology and size) and contrasts (morphology of maxilla and scapula) with the widespread early Palaeogene genus †*Brychaetus*. It is one of the oldest known osteoglossid occurrences in marine deposits and the most northerly occurrence for the family in any environmental setting, adding relevant temporal and biogeographical information to reconstruct a poorly known marine radiation of an ancient teleost lineage that is currently restricted to freshwater. At present, the fossil record suggests that osteoglossids invaded marine environments in close temporal proximity to the K–Pg mass extinction. Marine osteoglossids are rare and show little morphological diversity in the Paleocene, although it is possible that this might stem in part from a relatively meagre fossil record combined with the fragmentary nature of known material of this age. What is clear, however, is that early Eocene deposits yield a range of marine osteoglossids that show some diversity in body form and dentition, and are widely distributed geographically. While several of these occurrences are based upon fragmentary isolated remains, representing an obstacle to the attempt of reconstructing the osteoglossid expansion in marine environments at fine temporal and geographical scale, most named species are known from (at least partially) articulated specimens. Few of these taxa have been described in detail, and none has been subjected to μCT investigation despite relatively 3-D preservation in some examples (e.g. †*Brychaetus muelleri*, †*Brychaetoides greenwoodi*, †*Magnigena arabica*). The marine Palaeogene radiation of osteoglossids represents an unusual episode in the history of this otherwise freshwater group, and demands more detailed investigation than has been undertaken previously. In particular, several outstanding questions about these taxa remain unanswered, most notably whether or not they form a clade to the exclusion of other osteoglossids. Different systematic hypotheses have been offered in the literature (e.g. Taverne 1998, Bonde 2008, Forey & Hilton 2010), but we are confident that available material is of sufficient quality and quantity to make significant inroads on this problem.

Beyond the specific issues surrounding marine osteoglossids, the Greenland specimen suggests an important new source of information bearing on fish evolution in the early Cenozoic. The Danian represents a critical interval for constraining the impacts of the end-Cretaceous extinction on marine fishes, but is poorly sampled. Only a handful of informative body-fossil assemblages are known from this interval, the most prominent of which

are Limhamn Quarry, Sweden (Adolfssen *et al.* 2017) and Palenque, Mexico (Alvarado-Ortega *et al.* 2015). These sites yield relatively few taxa and have received less attention than younger Palaeogene assemblages. In light of the limitations of the existing Danian body-fossil record, further examination of the Eqalulik Formation fauna could make important contributions as a unit that is both palaeogeographically remote and palaeoenvironmentally distinct from existing sites. In addition to the yet undescribed †'*Protocodus*' and the osteoglossid reported here, several concretions from the Eqalulik Formation in the collections of the NHMD contain teleost remains (e.g. NHMD VP-7131 A-C (possible cranial material), NHMD VP-7140 A-B (parasphenoid), NHMD VP-7147 A-D (skull and pectoral fin), NHMD VP-7164 A-C (articulated postcranium covered in scales)). This study shows that such concretions are amenable to study through μCT, and that the remains they preserve (although often disrupted) are largely uncrushed. Although it is probable that known specimens will not be identifiable at the finest taxonomic levels, they still may be sufficiently diagnostic to help better illuminate a poorly understood interval with a significant bearing on the evolution of modern fish diversity.

DATA ARCHIVING STATEMENT

Data for this study, including μCT data for the specimen NHMD 72014 A+B and 3-D models of individual bones segmented from the

μCT data, are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.nh74kg8

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