An Eocene conger eel (Teleostei, Anguilliformes) from the Lillebælt Clay Formation, Denmark

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A conger eel (Anguilliformes, Congridae) is described from the lower Lutetian concretionary nodules of the Lillebælt Clay Formation exposed at Trelde Næs, eastern Jutland, based on two partially complete articulated cranial skeletons. One of the cranial specimens exhibits an otolith void from which a cast was taken, used by Schwarzhans (2007) to describe the extinct *Pseudoxenomystax treldeensis*, which is placed herein within the new genus *Smithconger* gen. nov. *Smithconger treldeensis* (Schwarzhans, 2007) is characterized by well-developed lateral processes on the frontals, supraoccipital crest absent, sphenotic spine rather large, anteriorly pointed and exposed on the flattened surface of the skull roof, otic bullae considerably reduced, maxilla almost straight and distally pointed, maxillary and dentary teeth numerous and arranged in multiple rows, dentary with slightly convex ventral profile, opercle with smooth posterior margin and subopercle short. The otoliths of *Smithconger treldeensis* show high dorsal rim, broad and deep dorsal depression, no ventral furrow, sulcus straight, shallow, centrally positioned with anteriorly reduced colliculum, and ostial channel at anterior tip of colliculum short, not reaching the predorsal rim. The otolith-based species *Bathycongrus waihaoensis* Schwarzhans, 2019 from the Kaiatan (Bartonian/Priabonian) of New Zealand is also assigned to the genus *Smithconger*. *Smithconger* is tentatively referred to the congrid subfamily Congrinae due to the lack of hypohyals in the hyoid bar. This new Eocene genus of conger eel shows a certain degree of similarity with the extant *Bassanago*. The diversity and relationships of other Eocene congrids is also briefly discussed.

Keywords: Anguilliformes, Congridae, *Smithconger* gen. nov., Eocene, Lutetian, Lillebælt Clay Formation, eastern Jutland.

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Eel-like fishes of the order Anguilliformes constitute a distinctive lineage of elopomorph teleosts that comprises more than 900 extant species arranged in 19 families (Anguillidae, Chlopsidae, Congridae, Cyematidae, Derichthyidae, Eurypharyngidae, Heterenchelyidae, Monognatidae, Moringuidae, Muraenesocidae, Muraenidae, Myrocongridae, Nemichthyidae, Nettastomatidae, Ophichthidae, Protanguillidae, Saccopharyngidae, Serrivomeridae, Synaphobranchidae), which occupy a variety of environments from freshwaters to shallow marine biotopes, to abyssal depths (Nelson *et al.* 2016). The extremely elongate anguilliform body

plan is unique within the Teleostei, being characterized, among the other features, by dorsal and anal fins confluent with caudal fin, ethmoid fused with the vomer, palatine absent, gill arches free from the neurocranium and displaced posteriorly, uppermost branchiostegal rays curving dorsally behind the opercle, and a ribbon-like 'leptocephalus' larva (e.g., Regan 1912; Trewavas 1932; Robins 1989; Johnson *et al.* 2012). The appearance of anguilliforms in the fossil record dates back to the late Cenomanian (about 94 Ma; Marramà *et al.* 2016), with several taxa collected from the Sannine Limestone in Lebanon (Hay 1903; Belouze 2002; Belouze et al. 2003a, b; Forey *et al.* 2003). However, the origin of the extant lineages took place primarily at the end of the Cretaceous and during the Palaeogene (e.g., Santini *et al.* 2013), being well documented by the diverse anguilliform assemblage of Monte Bolca (Blot 1978, 1984; Pfaff *et al.* 2016), but also by the fossils from other localities (e.g., Bonde 1966; Casier 1967; Taverne & Nolf 1978; Young 1993; Bannikov & Parin 1997; Belouze 2002). The otolith record of anguilliforms is relatively rich and diverse, especially that of the Congridae (Schwarzhans 2019b), whose members appear to be present since the Campanian (Nolf & Dockery 1990) and are well documented since the Maastrichtian (Schwarzhans 2010). Conversely, the skeletal record of congrids is rather poor and the earliest skeletal remains of conger eels are represented by four species (*Bolcyrus bajai*, *Bolcyrus formosissimus*, *Paracongroides heckeli*, *Voltaconger latispinus*) from the late Ypresian of Monte Bolca (Blot 1978), plus some isolated bones referred to *Paraconger sauvagei* from the Lutetian Sables de Lede (Taverne & Nolf 1978), where otoliths assigned to the same species were reported by Stinton & Nolf (1970). In addition, partially complete articulated skeletons of conger eels are also known from Oligocene of Northern Caucasus, Russia, with the species *Pavelichthys daniltshenkoi*, and from the Oligocene of Apsheron Peninsula, Azerbaijan, with the species *P. perekischylika* (Prokofiev 2007). The goal of this paper is to describe the skeletal remains pertaining to the family Congridae discovered in the concretionary nodules of the Eocene Lillebælt Clay Formation, Denmark. One of these specimens, a partially complete neurocranium, exhibits an otolith void *in situ*, thereby providing a unique opportunity to link the skeletal and otolith records of an Eocene conger eel and to define in much detail its distribution in space and time (Schwarzhans & Carnevale 2017).

Geological setting

The specimens documented herein primarily consist of incomplete and partially articulated skeletal remains embedded into concretions collected along the south-eastern coast of Trelde Næs, a small peninsula in the eastern Jutland, close to the town of Fredericia (Fig. 1). The fossils were collected from the Lillebælt Clay Formation, an Eocene fossiliferous grey-green, non-calcareous clay that commonly includes mixed carbonate and phosphatic concretions (Heilmann-Clausen *et al.* 1985), which is well-exposed along the coastal cliffs at Trelde Næs. Heilmann-Clausen *et al.* (1985) subdivided the Lillebælt Clay Formation into six lithological units, of which the first two are considered of late Ypresian age. According to Schnetler & Heilmann-Clausen (2011), the transition between the second and third lithological units seems to define the boundary between Ypresian and Lutetian. Concretions occur in the third, fourth, fifth and (possibly) sixth lithological cycles (Heilmann-Clausen *et al.* 1985). There is no information about the lithological cycle from which the concretionary nodules containing the fossils described herein were collected (see also Collins & Jakobsen 2003), but it is reasonable to conclude that they date back to the early Lutetian. The fine-grained sediments of the Lillebælt Clay Formation accumulated in the North Sea Basin, about 300 km from the Swedish coasts (Thomsen *et al.* 2012) at depths between 100 and 350 meters (Schnetler & Heilmann-Clausen 2011; Carlsen & Cuny 2014).

The fossiliferous content of the Lillebælt Formation is quite abundant. Bonde (1968) reported the occurrence of brachiopods, echinoderms, annelids, molluscs (e.g., Schnetler & Heilmann-Clausen 2011) and crustaceans (e.g., Collins & Jakobsen 2003) at Trelde Næs. Vertebrates are represented by cartilaginous and bony fishes. Hansen *et al.* (2013) described associated skeletal and dental remains of an odontaspidid shark, while Carlsen & Cuny (2014) provided a detailed analysis of a diverse elasmobranch assemblage, comprising more than 30 taxa. Bony fishes are represented by isolated teeth (Carlsen & Cuny 2014) and bones (Heilmann-Clausen *et al.* 1985), as well as by otolith voids from which casts were taken (Schwarzhans 2007) and rare partially complete articulated skeletal remains (Bonde *et al.* 2008) preserved in the concretionary nodules, including those described in this study.

Material and methods

The present study is based on four specimens, a single partially complete neurocranium (Fig. 2) (which includes the impression of an otolith; Fig. 3A), an incomplete articulated skeleton represented by the head and the anterior portion of the abdominal region (Fig. 4), plus two otolith casts housed in the collections of
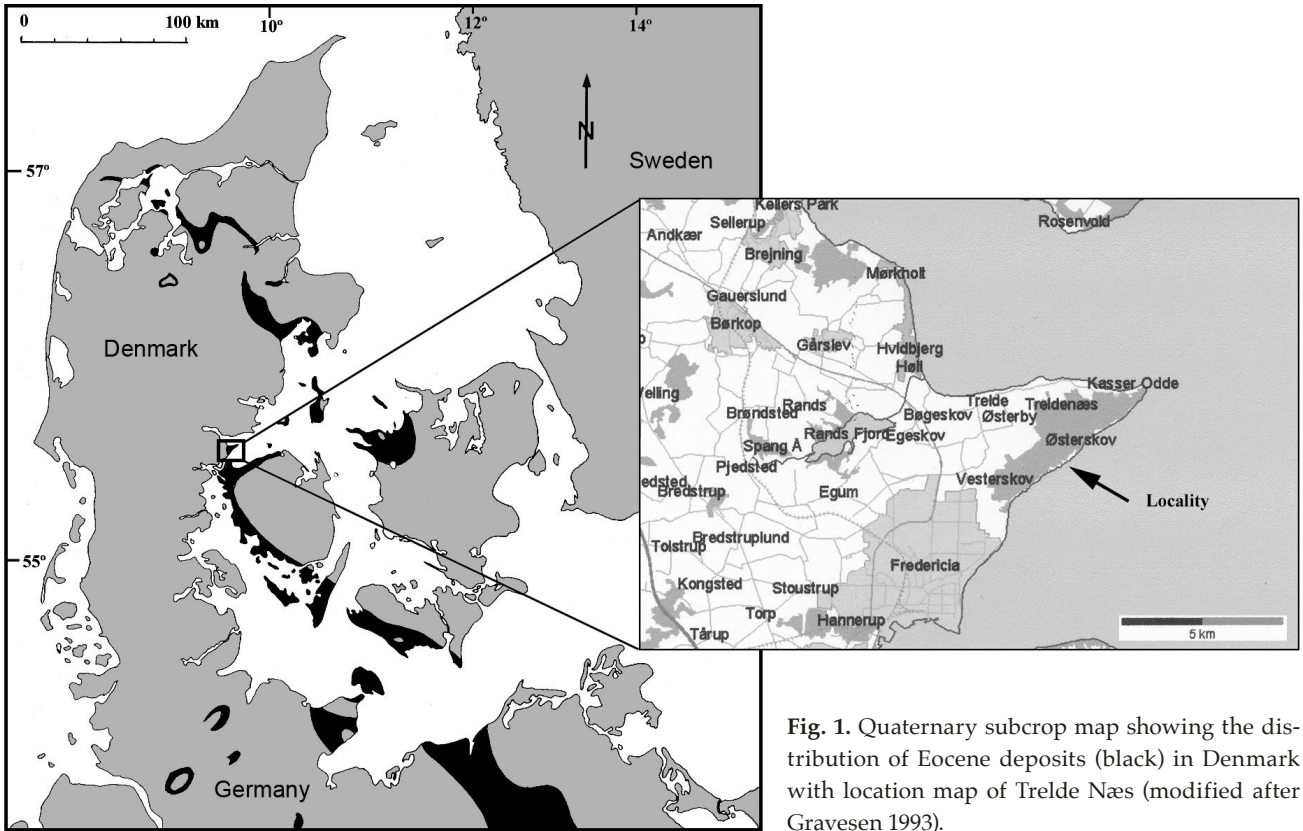
Fig. 1. Quaternary subcrop map showing the distribution of Eocene deposits (black) in Denmark with location map of Trelde Næs (modified after Gravesen 1993).
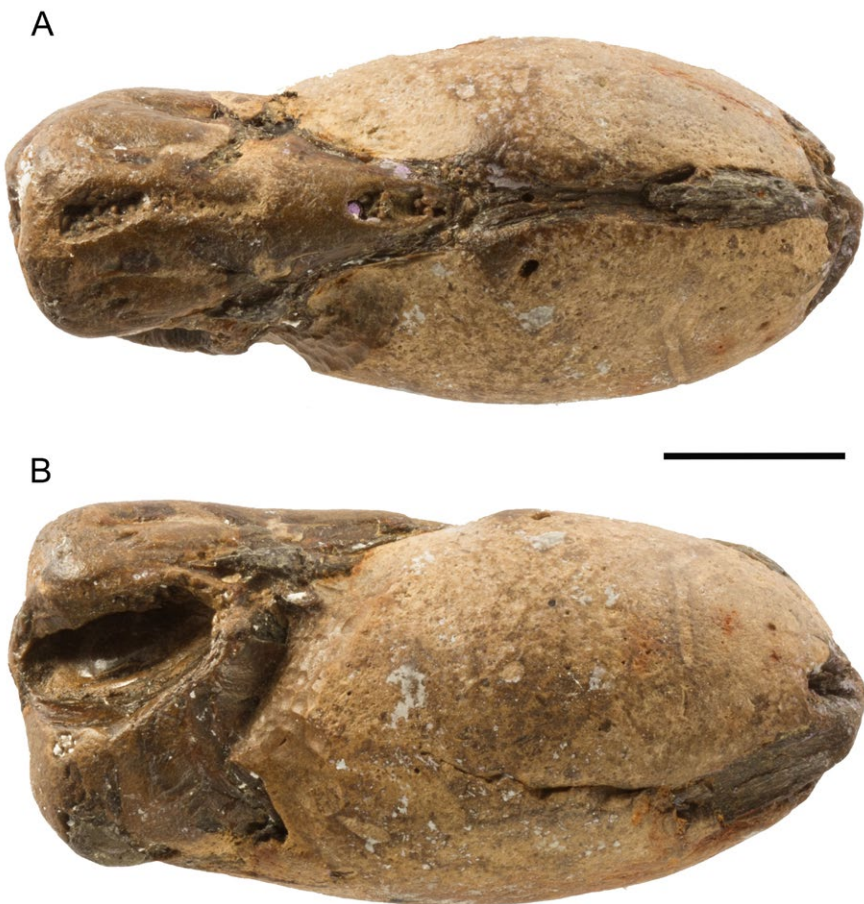

Fig. 2. *Smithconger treldeensis* (Schwarzhans 2007) from the Eocene of Trelde Næs, eastern Jutland, Denmark. Holotype, NHMD-625030. **A**: Neurocranium in dorsal view. **B**: Neurocranium in right lateral view, with a large hollow cavity originally occupied by the saccular otolith. Scale bar 10 mm.

the Natural History Museum of Denmark, Copenhagen. The skeletal material was studied using a WILD Heerbrugg stereomicroscope equipped with a camera lucida drawing arm. The incomplete articulated skeleton required matrix removal before examination to allow investigations of its structure in as much detail as possible; this was achieved using thin entomological needles. During examination, the skeletal remains were moistened with alcohol to enhance some details of their anatomy. Measurements were taken with a dial caliper to the nearest 0.1 mm. Comparative morphological and osteological data were derived mainly from the literature.

Anatomical abbreviations: aa, anguloarticular; ach, anterior ceratohyal; bo, basioccipital; br, branchi-ostegal rays; bsp, basisphenoid; cl, cleithrum; ctb, ceratobranchial; d, dentary; ect, ectopterygoid; epb, epibranchial; epi, epioccipital; etv, ethmovomerine complex; exo, exoccipital; f, frontal; h, hyomandibula; iop, interopercle; lep, lateral ethmoid process; lfp, lateral frontal process; lvp, lateral vomerine process; mx, maxilla; op, opercle; pa, parietal; pas, parasphenoid; pch, posterior ceratohyal; pop, preopercle; pro, prootic; pte, pterosphenoid; pto, pterotic; q, quadrate; soc, supraoccipital; sop, subopercle; sph, sphenotic; uh, urohyal; v, vertebra.

Institutional abbreviations: MCSNV, Museo Civico di Storia Naturale, Verona; MGUH, Museum Geologica Universitas Hafniensis, Copenhagen; MNHN, Museum National d'Histoire Naturelle, Paris; NHMD,
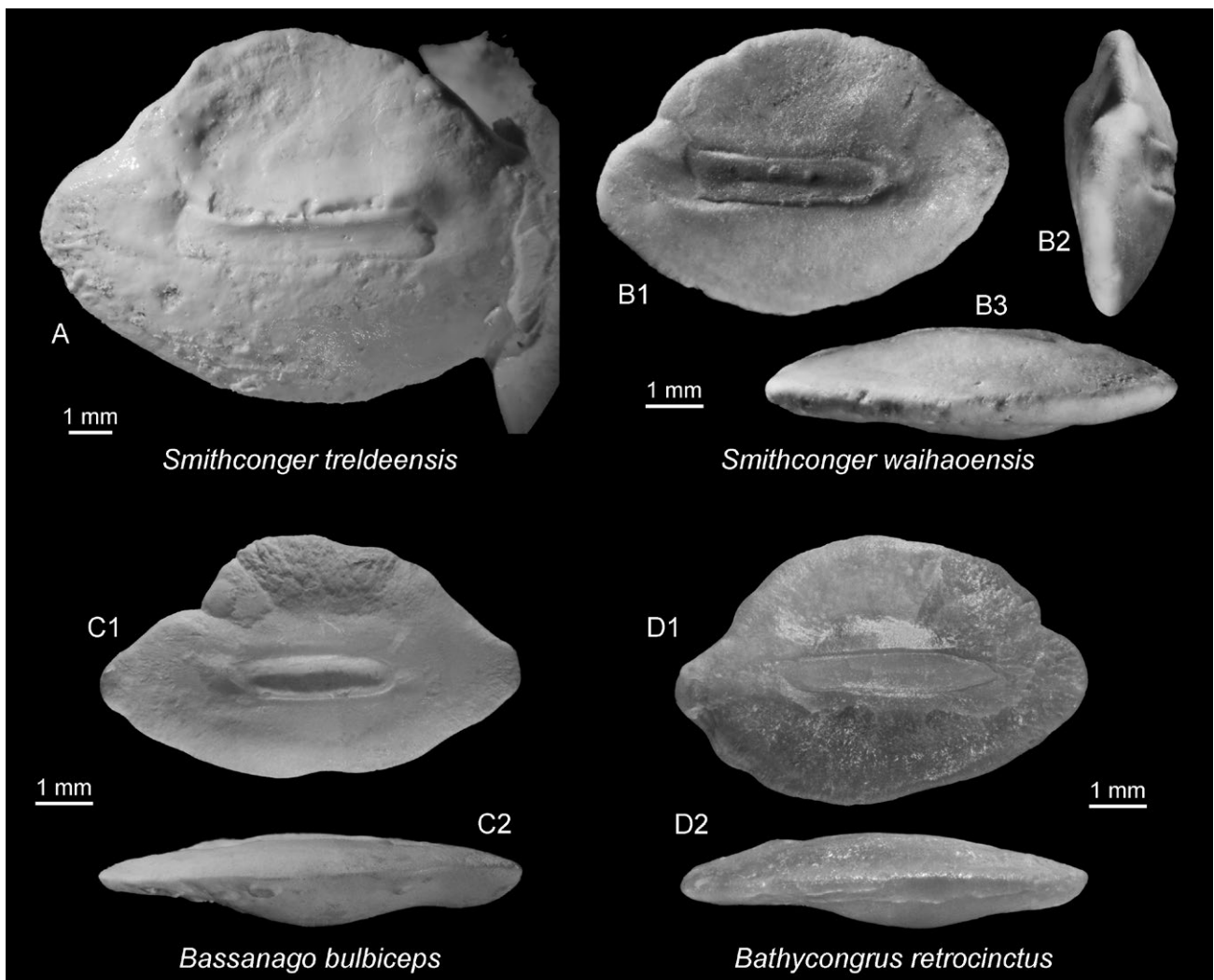

Fig. 3. Otoliths. **A**: *Smithconger treldeensis* (Schwarzhans 2007) from the Eocene of Trelde Næs, eastern Jutland, Denmark, holotype, MGUH 28368. **B**: *Smithconger waihaoensis* (Schwarzhans 2019) from the Kaiatan (Bartonian/Priabonian) of the Waihao River banks, New Zealand South Island, holotype, NMNZ S.46736; B1 inner face, B2 anterior view, B3 ventral view. **C**: *Bassanago bulbiceps* Whitley 1948, Recent, off Wellington, New Zealand, coll. Schwarzhans; C1 inner face, C2 ventral view. **D**: *Bathycongrus retrotinctus* (Jordan & Snyder 1901), Recent, off Dong-gang, Taiwan, ZMUC P2396514, leg. Ho; D1 inner face, D2 ventral view.
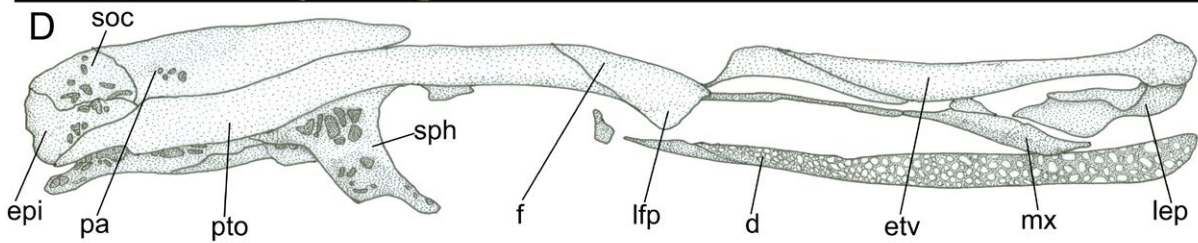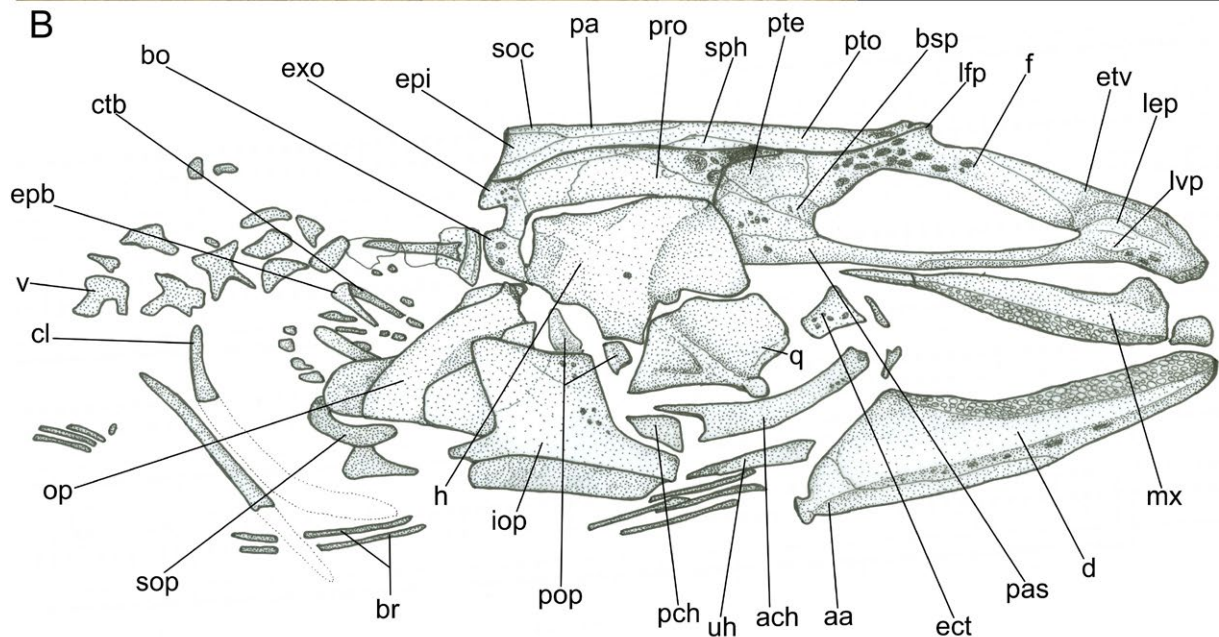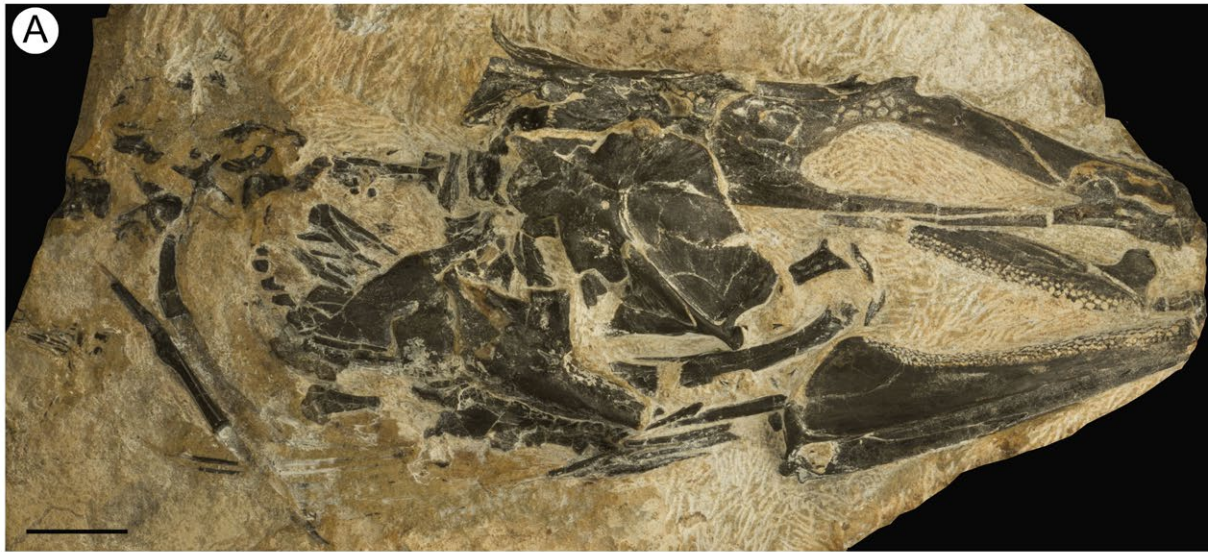
Fig 4. *Smithconger treldeensis* (Schwarzhans 2007) from the Eocene of Trelde Næs, eastern Jutland, Denmark. Paratype, NHMD-625415. **A**: Head and anterior portion of the axial skeleton, right lateral view. **B**: interpretative reconstruction. **C**: Neurocranium in dorsal view. **D**: interpretative reconstruction. Scale bars 10 mm.

Natural History Museum of Denmark, Copenhagen; NHMUK, Natural History Museum, London; NHMW, Naturhistorisches Museum, Vienna; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; ZMUC, Zoological Museum of the University of Copenhagen.

Systematic palaeontology

Order Anguilliformes Regan, 1909
Family Congridae Kaup, 1856

Genus *Smithconger* gen. nov.

Type species. *Smithconger treldeensis* (Schwarzhans 2007), syn. *Pseudoxenomystax treldeensis* Schwarzhans 2007.

Etymology. Named in honour of the American ichthyologist David G. Smith (plus the generic name *Conger*), in recognition of his outstanding contribution to the study of anguilliform fishes.

Diagnosis. A genus of Congridae unique in having the following combination of characters: frontals with well-developed lateral processes; supraoccipital crest absent; sphenotic large and anteriorly pointed, exposed on the flattened surface of skull roof; otic bullae considerably reduced; maxilla elongate, nearly straight, distally pointed, bearing a large paddle-like dorsal process on its anterodorsal extremity; oral jaw teeth numerous, arranged in multiple rows; ventral profile of the dentary convex; mandible not projecting anteriorly beyond the upper jaw; opercle with smooth posterior margin; subopercle short; otoliths oval with high dorsal rim, broad and deep dorsal depression, no ventral furrow; sulcus straight, narrow, shallow, centrally positioned with anteriorly reduced colliculum; ostial channel at anterior tip of colliculum short, not reaching the predorsal rim.

Discussion. Schwarzhans (2007) described the species *Pseudoxenomystax treldeensis* from the Lillebælt Clay based on three otolith casts. One of these otoliths, selected as the holotype (Fig. 3A), was found as a void *in situ* from a partially preserved neurocranium, which was not described nor figured by Schwarzhans (2007). Despite the inadequate preservation of the holotypic neurocranium (Fig. 2), a suite of morphological features reveals a substantial similarity in the overall proportions and general configuration with that of the paratype NHMD-625415. Due to the distinctiveness of these features, especially the relative size and orientation of the sphenotic spine and of the robust

laterally-directed frontal process, these specimens are regarded herein as conspecific.

The extant genus *Pseudoxenomystax* was originally created by Breder (1927) and subsequently discussed by Castle (1960) and is currently not considered as valid with its formerly referred species assigned to the genera *Bassanago* and *Bathycongrus* (e.g., Smith 1989; Castle 1995). The neurocranial morphology of both these genera differs from that of the Eocene fossil from the Lillebælt Clay Formation described herein, thereby supporting its attribution to a new separate genus within the family Congridae.

Composition. Two fossil species are referred to the genus *Smithconger*; the type-species *Smithconger treldeensis* (Schwarzhans, 2007) from the early Lutetian of the Lillebælt Clay Formation of Denmark and *Smithconger waihaoensis* (Schwarzhans 2019), an otolith-based species (Fig. 3B) described by Schwarzhans (2019a) as *Bathycongrus waihaoensis* from the Kaiatan (Bartonian/Priabonian) of the Waihao River, South Island of New Zealand.

Smithconger treldeensis (Schwarzhans, 2007)
(Figs 2–3A, 4–5).

Holotype. NHMD-625030, a partially complete neurocranium exhibiting a large hollow cavity originally occupied by the saccular otolith (Fig. 2), measuring about 44.9 mm in length. The otolith (Fig. 3A) is registered with the number MGUH 28347.

Paratypes. NHMD-625415, a partially complete articulated skeleton represented by the head and a poorly preserved anterior portion of the abdominal region of the body (Fig. 4). Paratypic otoliths are registered with the numbers MGUH 28346 and 28357.

Type locality and horizon. Trelde Næs near Fredericia, eastern Jutland, Denmark, Lillebælt Clay Formation, Middle Eocene, early Lutetian.

Measurements (of the paratype NHMD-625415). Neurocranial length: 76.2 mm; neurocranial depth (measured at midlength of the orbit): 14.8 mm (19.4 % of neurocranial length); preorbital length: 13.6 mm (17.8 % of neurocranial length); orbital length: 28.7 mm (37.6 % of neurocranial length); postorbital length: 34.0 mm (44.6 % of neurocranial length); maxillary length: 33.9 mm (44.4 % of neurocranial length); mandible length: 44.8 mm (58.7 % of neurocranial length); lateral extension of the sphenotic spine: 7.5 mm (9.8% of neurocranial length).

Description. The holotypic neurocranium is inade-

quately preserved to allow an appropriate description of its structure (Fig. 2). Therefore, the descriptive osteology is mostly based on the paratype NHMD-625415 (Fig. 4). Overall, the paratypic specimen NHMD-625415 is largely incomplete, lacking most of the axial skeleton. The head skeleton is partially complete and most of the bones are in some ways displaced from their original position (Figs 4A–B). The axial skeleton is solely represented by at least five incomplete and poorly preserved (abdominal) vertebrae, a partially complete crescent-shaped cleithrum and some fragments of the pectoral-fin rays.

The neurocranium is elongate, slender and somewhat dorsally flattened (Figs 4A–B, 5); its depth measured at the midlength of the orbit reaches about one fifth of the neurocranial length. It is robust anteriorly and projects beyond the lower jaw. The orbit is elongated and occupies more than one third of the entire neurocranial length. Overall, the neurocranium is solidly ossified and some of the bones are ornamented by irregular and deep pits, which are quite abundant on the ventral surface of the frontal in the central and posterior sector of the orbit, but also on the prootic and the ventral surface of the sphenotic; due to the extensive ornamentation of certain neurocranial bones, it is very difficult to recognize the foramina for nerves. The original sutures between the bones are difficult to recognize due to considerable overlapping, as well as of inadequate preservation of the surface of certain bones.

The ethmovomerine complex is thick and bears a broad lateral ethmoid process with almost linear lateral margins emerging just in front of the orbit. The anteroventral portion of the ethmovomerine complex, which apparently comprises the entire dentigerous area, is slightly curved downwards (Figs 4A–B, 5). A small lateral vomerine process can be observed just below the lateral ethmoid process. The frontals are only partially exposed and form most of the dorsal border of the orbit (Figs 4–5). The two frontals are fused to each other into a single bone, which can be easily recognized in the holotype (Fig. 2). A prominent and thick triangular process projects laterally from the dorsal surface of the frontals (Figs 4C–D, 5). As reported above, the ventral surface of the frontals just above the origin of the prominent lateral process is extensively pitted. The parietals are rather large and articulate anteriorly with the fused frontals, laterally with the pterotic and posteriorly with the epioccipital and the small supraoccipital. There is no
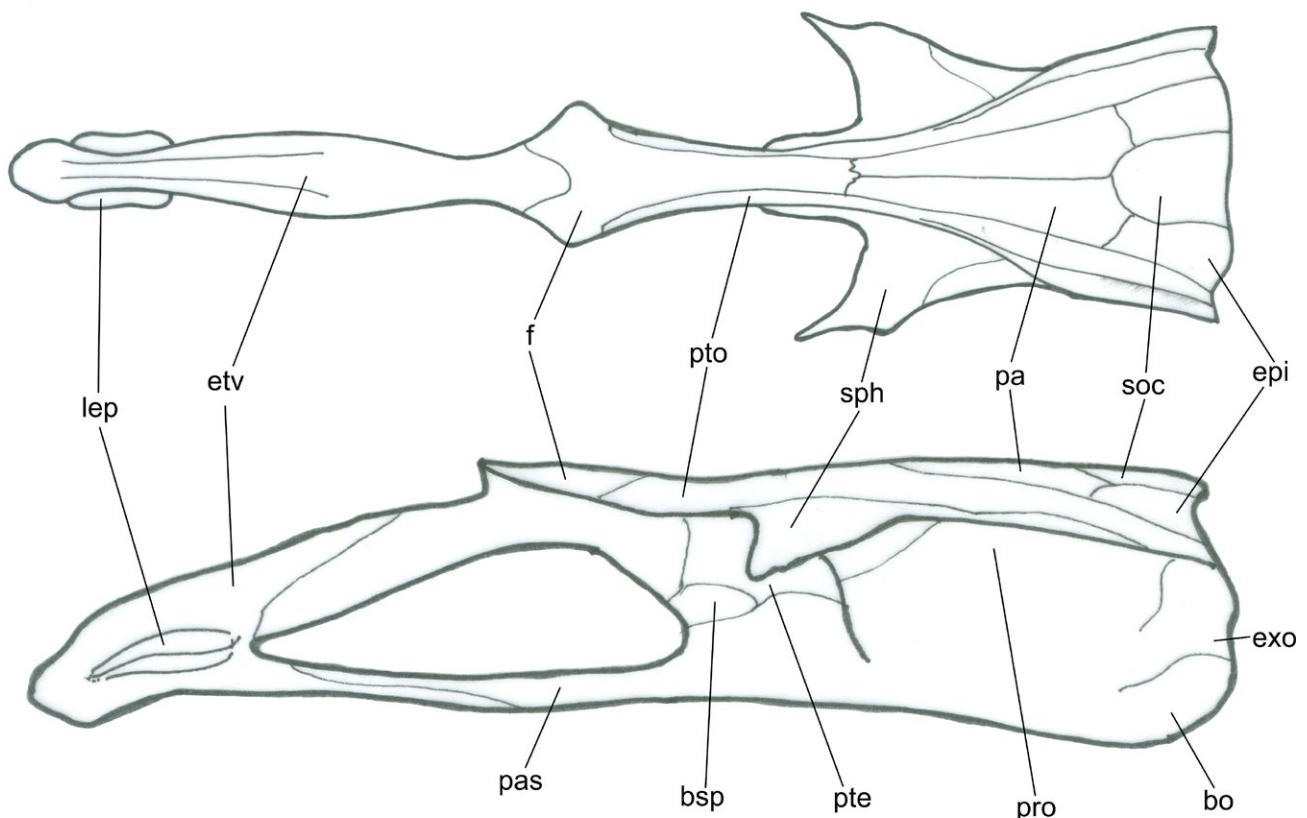

Fig. 5. *Smithconger treldeensis* (Schwarzhans 2007) from the Eocene of Trelde Næs, eastern Jutland, Denmark. Reconstruction of the neurocranium in dorsal (above) and lateral (below) view.

supraoccipital crest. The epioccipital occupies a small triangular surface in the posteriormost portion of the skull roof where it articulates with the parietal and supraoccipital medially and with the pterotic laterally. As in other anguilliform fishes, the pterotic is the major lateral longitudinal bone of the neurocranium; based on its overall morphology, with a smooth and solid outer surface, it is reasonable to hypothesize that the temporal sensory canal was enclosed within this bone. Due to the flattened dorsal aspect of the neurocranium, the sphenotic is clearly exposed on the skull roof (Fig. 5), showing a very high position on the neurocranium compared to most congrid taxa (Fig. 6), in which it contributes to form the lateral wall of the neurocranium (e.g., Smith 1989). The sphenotic is almost triangular in dorsal outline and projects antero-laterally as a pointed blade-like process; it articulates medially and posteriorly with the pterotic and ventrally with the pterosphenoid and prootic. The articular facet for the anterior articular head of the hyomandibula is clearly recognizable in NHMD-625415. The pterosphenoid forms part of the lateral wall of the neurocranium; it articulates with the frontal anteriorly, with the basisphenoid anteroventrally, with the sphenotic and pterotic dorsally, with the prootic posteroventrally, and with the parasphenoid ventrally. The basisphenoid is small and can be easily recognized along the posterior border of the orbit. The parasphenoid is greatly elongate, extending from the basioccipital almost to the anterior tip of the orbit. The prootic is mostly not exposed, covered by the hyomandibula in the paratype NHMD-625415. Although the prootics are only partially exposed in the holotype (Fig. 2), it seems that the otic bullae were consistently reduced in size in origin, resembling the condition observed in *Conger* (e.g., Takai 1959; Asano 1962; Smith 1989). The stout basioccipital forms the posteroventral corner of the neurocranium. The basioccipital articulates dorsally with the large exoccipital.

While the otolith is not preserved in the holotype, its outline is impressed in the cavity allowing the production of a cast (Fig. 3A) that was described by Schwarzhans (2007) as follows: "Large oval otoliths up to about 14 mm length. Ventral rim gently curving, smooth, deepest at its middle; dorsal rim more strongly curving, highest, most expanded just anterior of the middle, this portion sometimes slightly undulated. Anterior tip moderately pointed at its middle; posterior tip symmetrical, not completely preserved. Inner face markedly convex. Sulcus medial, narrow, straight, with well-marked, anteriorly reduced colliculum. Anterior part of ostium indistinctly outlined, without colliculum and thus colliculum centrally positioned on inner face. Ostial canal short, indistinct, beginning near anterior tip of colliculum, not reaching dorsal rim.

Dorsal depression wide, deep; no ventral furrow. Outer face nearly flat to slightly convex, smooth".

Based on the relative size of the jaw bones and the limited forward inclination of the suspensorium, it is reasonable to conclude that the mouth gape was moderately large (Figs 4A–B). The upper border of the mouth gape is formed by the thick and robust maxilla. The maxilla is elongate, nearly straight, distally pointed and bears a large paddle-like dorsal process on its anterodorsal extremity that comprises the maxilla-ethmovomeral facet on its medial surface. The alveolar surface of the maxilla is fully covered by relatively small circular tooth sockets arranged in multiple rows. The mandible is solid, almost linear and nearly triangular in outline, and does not project anteriorly beyond the upper jaw. It is constituted by the dentary and the anguloarticular. The dentary is very large and bears a well-developed coronoid process posterodorsally. The alveolar surface of the dentary is completely covered by tooth sockets arranged in multiple rows identical to those of the maxilla (Fig. 4).

Although only partially complete, the suspensorium appears to be wider than deep, inclined forward and characterized by a very large hyomandibula (Figs 4A–B). The hyomandibula has an irregular trapezoid outline and possesses two prominent condyles for the cranial articulation. What appears to be a foramen can be observed on the main vertical shaft of the hyomandibula. The opercular process of the hyomandibula is extremely short and thick. The quadrate is large, fan-shaped, with an irregular dorsal margin. The dorsal margin of the quadrate fits well with the ventral margin of the hyomandibula, suggesting that these bones were remarkably consolidated into a strong functional complex. Only a fragment of the ectopterygoid, probably representing a disarticulated posterior extremity can be observed in the fossil.

The bones of the opercular apparatus are displaced from their original position and overlapped to each other (Figs 4A–B). Of the preopercle only some fragments can be recognized. The interopercle is plate-like, roughly trapezoid in outline. The opercle is only partially exposed; it appears to be fan-shaped, with a gently convex dorsal margin and a rounded and continuous posterior margin. The subopercle is sickle-shaped.

Of the hyoid arch (Figs 4A–B), a partially preserved hyoid bar with anterior and posterior ceratohyals, a largely incomplete urohyal and at least six incomplete branchiostegal rays can be recognized. There are no hypohyals.

Gill arches are represented by fragments of the ventral and dorsal portions, including what appear to be incomplete epibranchials and ceratobranchials (Figs 4A–B).

The affinities of Smithconger treldeensis (Schwarzhans, 2007)

In his fundamental study on the classification of eel-like fishes, Regan (1912) emphasized the diagnostic role of separated vs fused frontals in the subdivision of modern anguilliforms into well-defined groups. The shared possession of fused frontals allowed the recognition of a speciose and morphologically diverse lineage traditionally referred to as the Congroidei (Robins 1989), which includes, among the others, the families Congridae, Derichthyidae, Muraenesocidae, Nettastomatidae and Ophichthidae (Nelson *et al.* 2016). Within this group, the family Congridae is one of the largest and most diverse, currently comprising 194 species arranged in 30 extant genera (Fig. 6). A definition of the Congridae is problematic to provide because of the generalized morphology and substantial uniformity of the overall appearance of most of its members (Smith 1989). Although this family has been considered as non-monophyletic by molecular studies (e.g., Inoue *et al.* 2010; Johnson *et al.* 2012; Santini *et al.* 2013), the co-occurrence of certain morphological traits is almost exclusive of these fishes, making it possible to refer fossil taxa to this family. Therefore, despite the incompleteness of the available material, both the skeletal structure and otolith morphology concur to support the attribution to the anguilliform family Congridae. In particular, the combination of laterally compressed and massive ethmovomer, fused frontals, large sphenotics, otoliths with shallow sulcus, anteriorly reduced colliculum and broad dorsal depression, and forward inclined suspensorium substantially support the placement of the fossils described herein within the family Congridae (e.g., Asano 1962; Smith 1989; Ramon-Castro *et al.* 2021). Primarily based on the criteria proposed by Asano (1962), Smith (1989) subdivided the Congridae into three subfamilies, the Bathymyrinae, Congrinae and Heterocongrinae (the latter recognized as a subfamily by Böhlke 1957). The subfamily Bathymyrinae consists of seven genera (*Ariosoma, Bathymyrus, Chiloconger, Kenyaconger, Parabathymyrus, Paraconger, Rostroconger*; Smith & Karmovskaya 2003; Smith 2018), the subfamily Heterocongrinae contains two genera (*Gorgasia, Heteroconger*; Böhlke 1957), while at least 21 genera (*Acromycter, Bassanago, Bathycongrus, Bathyuroconger, Castleichthys, Conger, Congrhynchus, Congriscus, Congrosoma, Diploconger, Gnathophis, Japonoconger, Lumiconger, Macrocephenchelys, Poeciloconger, Promyllantor, Pseudophichthys, Rhynchoconger, Scalanago, Uroconger, Xenomystax*; Table 1) are implicitly referred to the subfamily Congrinae, considering that Karrer & Smith (1980) suggested that the genus *Blachea* might deserve a separate subfamilial

status. According to Smith (1989), the Bathymyrinae and Heterocongrinae form a sister pair, supported by at least two synapomorphies, possession of a strut-like lateral ethmoid process (lost in *Heteroconger*; Fig. 6L) and unsegmented fin rays. This sister-group relationship has also been confirmed by a comparative study of their otoliths (Schwarzhans, 2019b).

As discussed above, there is no evidence of a strut-like lateral ethmoid process in *Smithconger* (Fig. 5), thereby excluding it from any possible attribution to the Bathymyrinae and Heterocongrinae. Moreover, *Smithconger* differs from the members of the Bathymyrinae by having a supraoccipital, which is reduced but present in the bathymyrine genera *Chiloconger* and *Paraconger* (Fig. 6Q; Table 1). The heterocongrines, commonly known as garden eels, are a specialized clade with a slender and greatly elongate body, a shortened head and a caudal fin stiffened for burrowing on sandy bottoms. These fishes are characterized by unique suite of features that clearly separate them from the other congrids, including a short and oblique mouth and lower jaw projecting beyond the upper one (Böhlke 1957; Rosenblatt 1967; Smith 1989); all of these features have not been observed in *Smithconger*. The Congrinae is the largest of the currently recognized subfamilies. Smith (1989) suggested the loss of hypohyals as a possible synapomorphy for the congrines. As described above, there is no evidence of hypohyals in *Smithconger*, thereby supporting its attribution to this subfamily, which can be also justified by the possession of a moderately large mouth gape and absence of a strut-like lateral ethmoid process. Within the congrines, *Smithconger* resembles in many ways *Bassanago* (see Fig. 6C, Table 1), especially in the well-developed laterally directed frontal processes, absence of a supraoccipital crest, convex ventral profile of the dentary, smooth posterior margin of the opercle, short subopercle and, more generally, in the overall proportions of the neurocranium (e.g., Smith *et al.* 2020). The otoliths of *Smithconger* resemble those of *Bassanago* (Fig. 3C) and, to a lesser extent, those of *Bathycongrus* (Fig. 3D) in having a horizontally positioned and anteriorly reduced sulcus with a single, centrally positioned colliculum, as well as for the presence of a distinctive and wide dorsal depression. However, *Smithconger* clearly differs from *Bassanago* in having considerably reduced (vs large) otic bullae, nearly straight and distally pointed (vs slightly curved and distally expanded) maxilla, basisphenoid with anterior smooth margin (vs with a distinct process) (see Smith *et al.* 2020). The otoliths of *Smithconger* show an indistinct and short ostial channel that is interpreted as plesiomorphic compared to the otoliths of the extant *Bassanago* (and *Bathycongrus*) in which the ostial channel is completely atrophied.
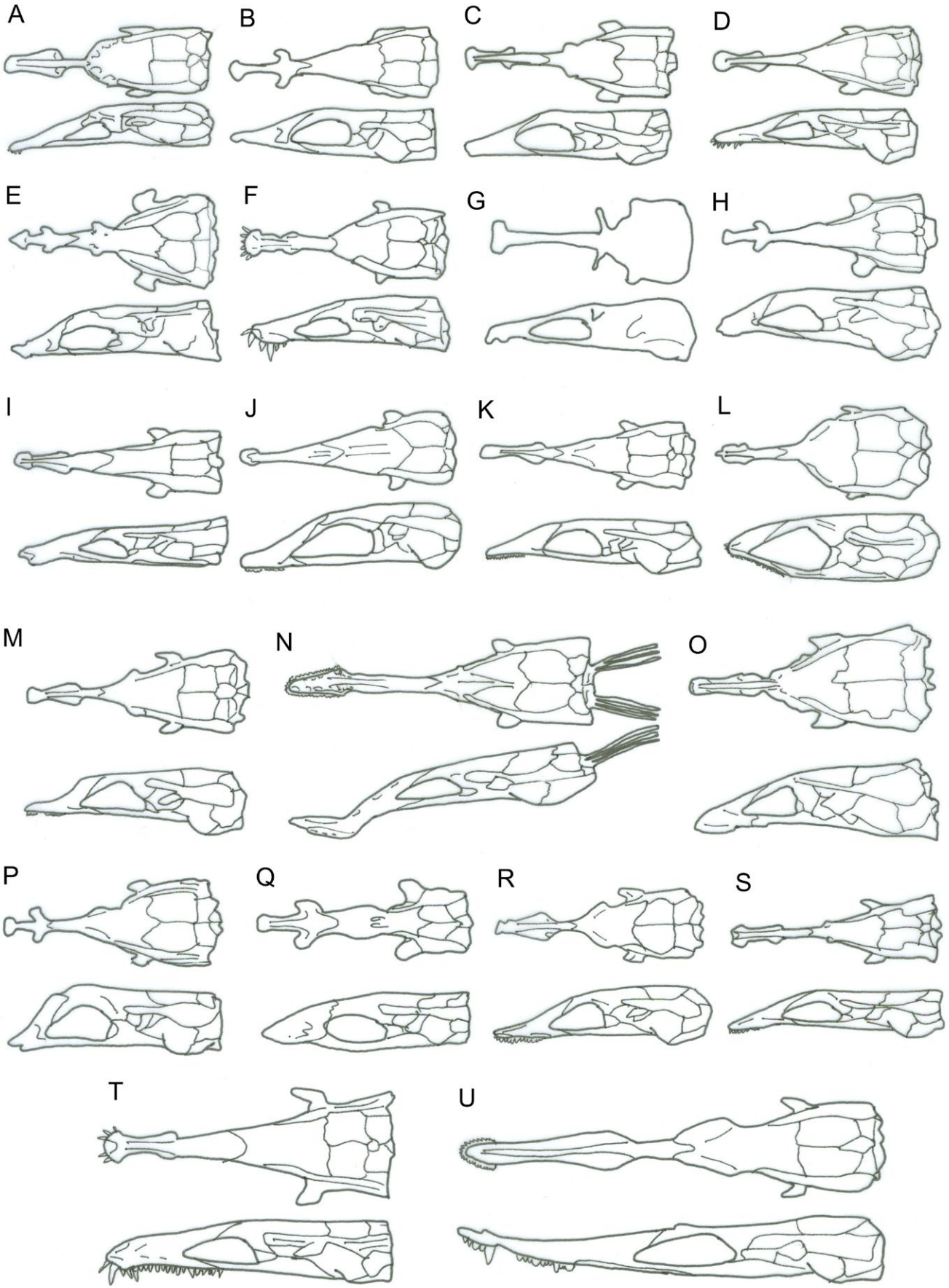
Table 1. Synopsis of selected morphological characters for fossil and extant genera of the family Congridae

	supraoccipital	strut-like lateral ethmoid process	lateral process of the frontal	teeth in jaws	lower jaw projecting beyond upper	posterior opercular margin
Acromycter	present	absent	present or absent	multiple rows	no	lobate/fimbriated
Ariosoma	absent	present	present or absent	multiple rows	no	smooth
Bathymyrus	absent	present	present	single row	no	smooth
Bassanago	present	absent	present	multiple rows	no	smooth
Bathycongrus	present	absent	absent	multiple rows	no	serrated
Bathyuroconger	present	absent	absent	two or three rows	no	with strong spines
Blachea	present	absent	present	single row	no	smooth
Bolcyrus	present	absent	absent	multiple rows	yes	smooth
Castleichthys	?	?	?	single row	no	?
Chiloconger	present	present	absent	two or three rows	no	smooth
Conger	present	absent	present or absent	one or two rows	no	smooth
Congrhynchus	?	?	?	multiple rows	no	?
Congriscus	absent	absent	absent	one or two rows	no	smooth
Congrosoma	?	?	?	?	no	?
Diploconger	?	?	?	one to three rows	no	?
Gnathophis	present	absent	absent	multiple rows	no	smooth
Gorgasia	present	present	absent	multiple rows	yes	smooth
Heteroconger	present	absent	absent	multiple rows	yes	smooth
Japonoconger	present	absent	present, very short	multiple rows	no	weakly serrated
Kenyaconger	?	?	?	one or two rows	yes	?
Lumiconger	present	absent	present, very short	multiple rows	no	smooth
Macrocephenchelys	absent	absent	absent	multiple rows	no	with strong spines
Parabathymyrus	absent	present	present	one or two rows	no	smooth
Paraconger	present	present	present	one or two rows	no	smooth
Paracongroides	?	?	?	?single row	no	smooth
Pavelichthys	present	present	absent	multiple rows	yes	?smooth
Poeciloconger	?	?	?	multiple rows	no	?
Promyllantor	?	?	?	multiple rows	no	?
Pseudophichthys	absent	absent	present	multiple rows	no	with strong spines
Rhynchoconger	present	absent	present	multiple rows	no	serrated
Rostroconger	?	?	?	one or tow rows	no	?smooth
Scalanago	?	?	?	?	no	?smooth
Smithconger	present	absent	present	multiple rows	no	smooth
Uroconger	present	absent	absent	two rows	no	smooth
Voltaconger	present	absent	absent	single row	yes	smooth
Xenomystax	present	absent	present	three rows	no	smooth

Includes new data and data from Asano (1962), Blot (1978), Böhlke (1957), Castle (1960, 1963, 1968, 1988, 1995), Castle & Paxton (1984), Eagderi & Adriaens (2014), Ho et al. (2018), Kanazawa (1958, 1961), Karmovskaya (2006, 2011), Karmovskaya & Smith (2008), Karrer & Smith (1980), Prokofiev (2007), Ramos-Castro et al. (2021), Robins & Robins (1971), Rosenblatt (1967), Smith (1989, 2004, 2018), Smith & Kanazawa (1977), Smith et al. (2018, 2020), Smith & Karmovskaya (2003), Takai (1959).

◄ **Fig. 6.** Neurocranium of selected conger eel species in dorsal (above) and left lateral (below) view. **A**: *Acromycter perturbator* (Parr, 1932), redrawn from Smith (1989); **B**: *Ariosoma balearicum* (Delaroche, 1809), redrawn from Smith (1989); **C**: *Bassanago albescens* (Barnard, 1923), redrawn from Smith *et al.* (2020); **D**: *Bathycongrus thysanochilus* (Reid, 1934), redrawn from Smith (1989); **E**: *Bathymyrus smithi* Castle, 1968, redrawn from Castle (1968); **F**: *Bathyuroconger vicinus* (Vaillant, 1888), redrawn from Smith (1989); **G**: *Blachea xenobranchialis* Karrer & Smith, 1980, redrawn from Karrer & Smith (1980); **H**: *Chiloconger dentatus* (Garman, 1899), redrawn from Smith & Karmovskaya (2003); **I**: *Conger oceanicus* (Mitchill, 1818), redrawn from Smith (1989); **J**: *Congriscus megastoma* (Günther, 1877), redrawn from Asano (1962); *K*: *Gnathophis bathytopos* Smith & Kanazawa, 1977, redrawn from Smith (1989); **L**: *Heteroconger halis* (Böhlke, 1957), redrawn from Smith (1989); **M**: *Japonoconger carribeus* Smith & Kanazawa, 1977, redrawn from Smith (1989); **N**: *Lumiconger arafura* Castle & Paxton, 1984, redrawn from Castle & Paxton (1984); **O**: *Macrocephenchelys branchialis* Fowler, 1934, redrawn from Smith (1989); **Q**: *Paraconger caudilimbatus* (Poey, 1867), redrawn from Smith (1989); **R**: *Pseudophichthys splendens* (Lea, 1913), redrawn from Smith (1989); **S**: *Rhynchoconger gracilior* (Ginsburg, 1951(, redrawn from Smith (1989); **T**: *Uroconger syringinus* Ginsburg, 1954, redrawn from Smith (1989); **U**: *Xenomystax bidentatus* (Reid, 1940), redrawn from Smith (1989).

Compared to the Eocene congrid genera from Monte Bolca *Bolcyrus*, *Paracongroides* and *Voltaconger* and to the Oligocene *Pavelichthys*, *Smithconger* exhibits a substantially different neurocranial morphology (Fig. 7; Table 1), mandible not projecting beyond the upper jaw (Table 1), and different oral jaw teeth arrangement (Table 1). In particular, the neurocranium of *Smithconger* clearly differs from that of *Bolcyrus* (Figs 7A–B) by having a different outline and general proportions, well-developed (vs absent) laterally-directed frontal process, skull roof flattened (vs not flattened) bearing a large and acute sphenotic spine, and supraoccipital crest absent (vs present). In addition, *Bolcyrus* is characterized by mandible projecting anteriorly beyond the upper jaw (Fig. 7C; Table 1) and by a single hypohyal in the hyoid bar (Blot 1978). As far as *Paracongroides* is concerned (Fig. 7F), it clearly differs from *Smithconger* by having jaw teeth arranged in a single row (Table 1; see also Blot 1978). *Pavelichthys* differs from *Smithconger* in having a strut-like lateral ethmoid process and mandible projecting beyond the upper jaw and by lacking laterally-directed frontal processes (Table 1; see also Prokofiev 2007). Finally, *Voltaconger* is characterized by a different neurocranial morphology,
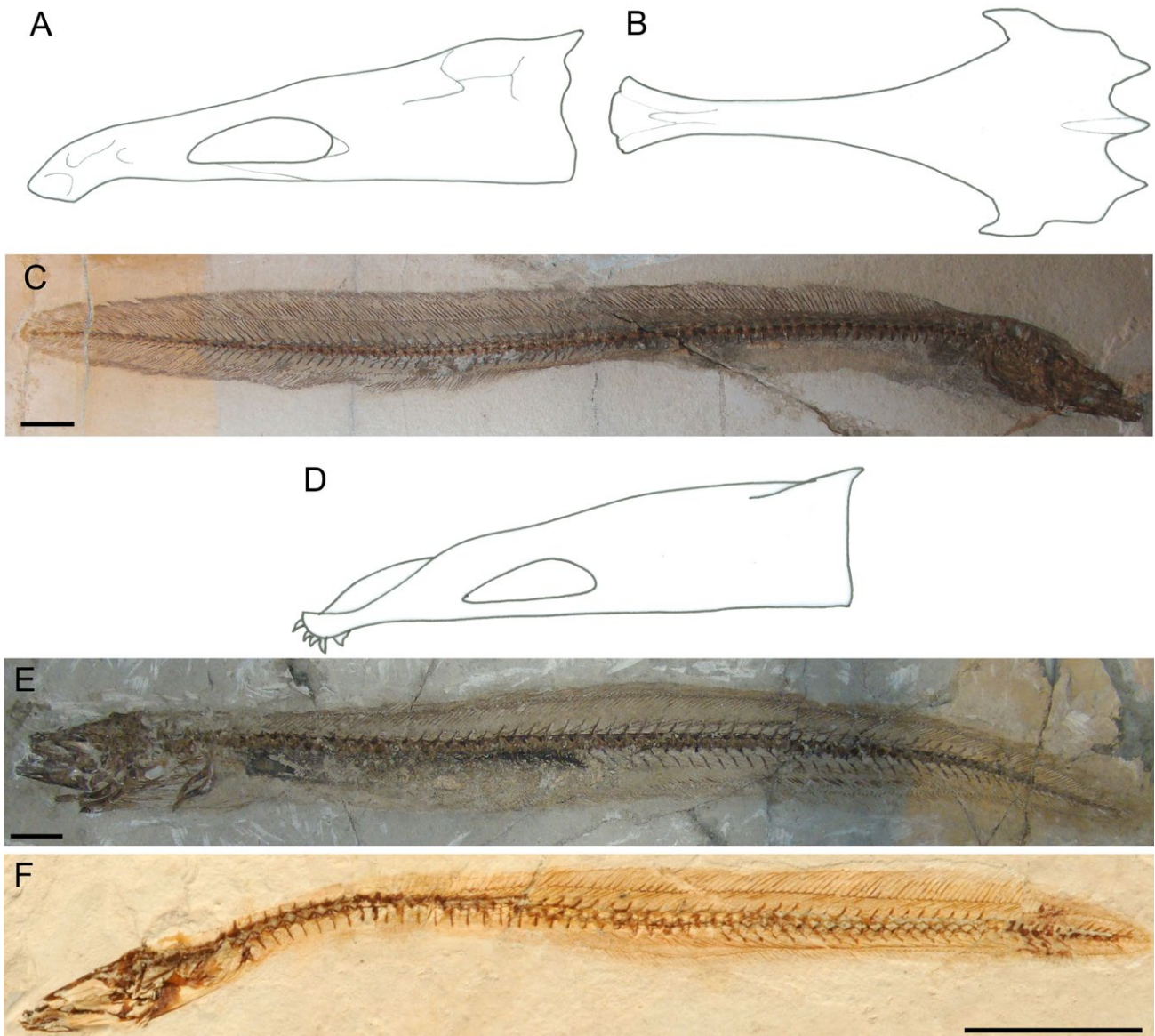

Fig 7. Eocene conger eels from Monte Bolca, Italy. **A–C**: *Bolcyrus formosissimus* (Eastman, 1905), reconstruction of the neurocranium in left lateral (A, based on MNHN 109609) and dorsal view (B, based on MCSNV IG24496); C: MCSNV T.442, right lateral view. **D–E**, *Voltaconger latispinus* (Agassiz, 1839); **D**: reconstruction of the neurocranium in left lateral view; **E**: NHMUK P17024, left lateral view. **F**: *Paracongroides heckeli* Blot, 1978, NHMW 1855/VI/70 – A3382, left lateral view. Scale bars 20 mm

which includes the lack of laterally-directed frontal processes and the presence of a supraoccipital crest (Fig. 7D), and by lower jaw projecting anteriorly beyond the upper one (Fig. 7E; Table 1).

The possible subfamilial attribution of these Palaeogene congrid genera was cursorily discussed by Prokofiev (2007), who concluded that *Bolcyrus* and *Voltaconger* may pertain to the Congrinae, whereas *Paracongroides* and *Pavelichthys* belong to the Bathymyrinae. However, while the attribution of *Paracongroides* and *Pavelichthys* to the Bathymyrinae seems to be reasonably supported by morphological evidence (preanal length of the body exceeding 40% of TL, fin rays not segmented, caudal fin reduced and apparently stiffened, and strut-like lateral ethmoid process in *Pavelichthys*; Blot 1978, Prokofiev 2007), the attribution of *Bolcyrus* and *Voltaconger* to the Congrinae appears to be much elusive. Both these genera are characterized by mandible projecting anteriorly beyond the upper jaw, plus a suite of generalized features commonly considered as diagnostic of the Congrinae (Smith 1989), including ectopterygoid stout, abdominal vertebrae representing less than 40% of the entire vertebral column, myorhabdoi absent, dorsal- and anal-fin rays segmented, caudal fin not reduced, and pectoral fin well-developed (Blot 1978). Moreover, *Voltaconger* lacks hypohyals in the hyoid bar, while *Bolcyrus* has a single hypohyal (Blot 1978). As discussed above, Smith (1989) considered the loss of hypohyals as a synapomorphic feature of the congrines, thereby suggesting that *Bolcyrus* cannot be confidently placed within the Congrinae; according to Johnson *et al.* (2012), however, hypohyals can probably be present in certain congrids. In summary, based on the available data, the subfamilial placement of *Bolcyrus* and *Voltaconger* appears to be not fully resolved. In this context, it is interesting to note that these two genera were placed outside the Congridae, associated with the genera of the extinct family Anguilloididae (*Anguilloides*, *Veronanguilla*), in the phylogenetic analysis published by Belouze (2002).

Acknowledgements

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