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Morphology and phylogenetic relationships of fossil snake mackerels and cutlassfishes (Trichiuroidea) from the Eocene (Ypresian) London Clay Formation

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Abstract

'Gempylids' (snake mackerels) and trichiurids (cutlassfishes) are pelagic fishes characterised by slender to eel-like bodies, deep-sea predatory ecologies, and large fang-like teeth. Several hypotheses of relationships between these groups have been proposed, but a consensus remains elusive. Fossils attributed to 'gempylids' and trichiurids consist almost exclusively of highly compressed body fossils and isolated teeth and otoliths. We use micro-computed tomography to redescribe two three-dimensional crania, historically assigned to †*Eutrichiurides winkleri* and †*Progempylus edwardsi*, as well as an isolated braincase (NHMUK PV OR 41318). All from the London Clay Formation (Eocene: Ypresian), these specimens represent some of the oldest fossils identified as trichiuroids. We find that †*Eutrichiurides winkleri* does not show diagnostic characters of †*Eutrichiurides*, and it is assigned to a new genus. In order to investigate the placement of these fossils relative to extant lineages, we combine existing morphological character sets for 'gempylids' and trichiurids along with published mitogenomic data. Our analyses recover a monophyletic Trichiuridae nested within a paraphyletic 'Gempylidae'. The taxon formerly known as †*Eutrichiurides winkleri* is considered Trichiuroidea *incertae sedis*, while †*Progempylus edwardsi* and NHMUK PV OR 41318 are recovered within the 'gempylid' grade. Using previously published descriptions and character optimisations from our phylogenetic analyses we suggest possible placements for laterally compressed body fossils historically associated with Trichiuroidea (†*Argestichthys,* †*Abadzekhia,* †*Chelifichthys,* †*Anenchelum,* †*Eutrichiurides,* †*Musculopedunculus*).

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'GEMPYLIDS' (snake mackerels) and trichiurids (cutlassfishes) are two associated families of pelagic percomorph fishes. Typically they have slender to eel-like bodies, deep-sea predatory ecologies and large fang-like teeth. These nominal families are

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only modestly diverse; 'gempylids' include 23 species in 16 genera, and trichiurids 32 species in 9 genera (Nakamura and Parin 1993). For the past century, 'Gempylidae' and Trichiuridae have been closely associated with Scombridae (tunas and mackerels), and, less consistently, Xiphoidei (billfishes). Regan (1909) recognised the divisions Trichiuriformes and Scombriformes (in addition to Luvariformes and Xiphiiformes, which are now associated with other groups) in a suborder Scombroidei. While a close affinity between 'gempylids' and trichiurids has long been recognised (here referred to as Trichiuroidea *sensu* Nakamura and Parin 1993), the exact relationship between the families remains equivocal in light of both anatomical and molecular evidence. Some morphological (Johnson 1986; Pothoff *et al*. 1986; Carpenter *et al*. 1995) and molecular analyses support trichiuroid monophyly, with trichiurids nested within 'gempylids' (Orrell *et al*. 2006) or with reciprocally monophyletic trichiurids and gempylids (Betancur-R *et al*. 2013; Alfaro *et al*. in press). However, others indicate trichiuroids are paraphyletic to (morphological: Collette *et al*. 1984; molecular: Miya *et al*. 2013), or polyphyletic within (Near *et al*. 2013; Betancur-R *et al*. 2017) a group with variable composition but which always contains scombrids. Despite these differences, two patterns consistently emerge in addition to the close association of trichiurids and 'gempylids'. First, trichiurids always form a clade. Second, 'gempylids' are typically interpreted as paraphyletic, either with respect to trichiurids (Johnson 1986; Pothoff *et al*. 1986; Carpenter *et al*. 1995; Orrell *et al*. 2006) or other groups (Collette *et al*. 1984; Miya *et al*. 2013; Near *et al*. 2013; but see Betancur-R *et al*. 2013, 2017). Unfortunately, many of these molecular studies are limited in their sampling of taxa (Near *et al*. 2013: two 'gempylids' and two trichiurids; Betancur-R *et al*. 2013: four 'gempylids' and six trichiurids; Betancur-R *et al*. 2017: six 'gempylids' and six trichiurids) or sequence data (e.g. mitochondrial genes only; Miya *et al*. 2013). Additionally, the most comprehensive morphological analyses of relationships have enforced monophyly of one group with respect to the other (Russo 1983; Gago 1998) or, when combined, have employed limited character sampling (ontogenetic characters only; Gago 1997).

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Fossils identified as 'gempylids' and trichiurids consist almost exclusively of isolated teeth, otoliths, and highly compressed, effectively two-dimensional body fossils (Miya *et al*. 2013: SI Text S2). The earliest putative remains assigned to each group are problematic. Nolf and Stringer (1996) interpret Late Cretaceous (Campanian) otoliths as belonging to 'gempylids', but this identity has recently been questioned (Stringer *et al*. 2016; Schwarzhans *et al*. 2018). Isolated teeth from the early Paleocene (Danian) of Angola (Dartevelle and Casier 1959) are attributed to the trichiurid †*Eutrichiurides,* but their affinities are also subject to question (see below). More secure evidence for the early history of trichiuroids derives from the body fossil record. The oldest articulated fossils interpreted as 'gempylids' are from early Eocene (early Ypresian) deposits, and include undescribed material from the Fur Formation of Denmark (Bonde 2008). Younger Eocene specimens include a three-dimensionally preserved skull of *Progempylus* and an unnamed braincase from the London Clay Formation of the UK (Casier 1966; Monsch 2005), undescribed material of two taxa from Monte Solane, Italy (Gempylidae gen. indet., Gempylidae gen. indet. cf. *Thrysitoides*; Zorzin *et al*. 2011: figs 8-9; Giusberti *et al*. 2014: figs 5C, 6A-B), and Iranian material assigned to *Epinnula* and *Thrysitoides* (Arambourg 1967; originally interpreted as Oligocene, but see Afsari *et al*. (2014) for a reassessment of age). Post-Eocene 'gempylids' are represented by †*Abadzekhia* (Oligocene of the Caucasus and Germany; Bannikov 1985, 2005, 2010), †*Chelifichthys* (Miocene [Messinian] of Algeria; Carnevale 2006) and †*Hemithyrsites* (Miocene [Messinian] of Italy and Miocene [Burdigalian] of the Caucasus: Sauvage 1873; Daniltshenko 1960). Excluding isolated teeth, the oldest articulated skeletal remains associated with Trichiuridae are an incomplete skull assigned to †*Eutrichiurides* (Casier 1966) from the early Eocene (Ypresian) London Clay Formation of the UK, a fragmentary skull also assigned to †*Eutrichiurides* (Bonde *et al*. 2008) from the Lillebælt Clay of Denmark, and an as-yet undescribed specimen similar to †*Anenchelum* from roughly contemporaneous deposits of Monte Solane, Italy (Zorzin *et al*. 2011). Most other trichiurid body fossils are assigned to either †*Anenchelum* (Blainville 1818) or the extant *Lepidopus* (Blainville 1818) and are middle Eocene-Pliocene in age, but some distinctive fossil

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taxa have been recognised, most notably †*Musculopedunculus micklichi* (Oligocene [Rupelian] of Germany; Parin and Astakhov 2007).

Uncertainty surrounding the relationships of fossil 'gempylids' and trichiurids stems from a number of factors. First, fossil taxa, including those discussed above, have not been included in a formal, published phylogenetic analysis (but see a formal cladogram in an unpublished PhD by Monsch 2000 and informal placement, based on verbal argumentation, in Monsch and Bannikov 2012; fig. 2). Second, morphological datasets for 'Gempylidae' and Trichiuridae rely heavily on soft-tissue and cranial characters (~80%: Russo 1983; ~50%: Gago 1998). The former are almost impossible to obtain from fossils, and the latter challenging due to the prevalence of two-dimensional fossils in which postcranial structure is clear but crania are often badly crushed. Third, available character lists target either 'gempylids' (Russo 1983) or trichiurids (Gago 1998) and the intrarelationships of those individual families, rather than sampling both extensively to explore their mutual relationships. This is particularly problematic given uncertainties in the relationships between these groups, which is amplified in the case of fossils that putatively exhibit unusual mosaics of 'gempylid'- and trichiurid-like characters (e.g. †*Argestichthys*; Prokofiev 2002).

In this study, we combine existing morphological character sets for 'gempylids' and trichiurids along with published molecular sequence data and additional observations of extant taxa in order to infer phylogenetic placements for some of the earliest fossil trichiuroids. Specifically, we investigate a series of fossils from the Eocene (Ypresian) London Clay Formation of the UK: †*Eutrichiurides winkleri*, †*Progempylus edwardsi*, and an isolated braincase previously interpreted as belonging to a 'gempylid' (Fig. 1). These specimens represent nearly all three-dimensionally preserved examples of trichiuroids (Casier 1966; Monsch 2005), with the potential to preserve many of the cranial features that feature prominently in anatomical analyses of living species. We present new descriptions of these specimens, based on a combination of external examination and micro-computed tomography (μCT) scanning. In addition to analytically inferred placements for these three-dimensionally preserved London Clay specimens based on a

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morphological character matrix for Trichiuroidea, we provide possible placements of other fossil taxa associated with the group.

Materials and methods

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Specimens examined

Below we list the specimens used in the course of this study. Both wet and dry specimens were studied for extant taxa, indicated with '[W]' and '[D]' respectively. Wet specimens were studied using radiography and μCT, indicated by '[R]' and '[C]' respectively (see methods section below). Following Patterson and Rosen (1977), the names of extinct taxa are preceded with a dagger symbol ('†').

Trichiuroidea. Additional observations were made of extant Trichiuroidea based on descriptions in Russo (1983), Gago (1998), Nakamura and Parin (1993), Nakamura and Fujii (1983) and Fujita (1990).

'Gempylidae'. NHMUK PV OR 41318 (Fig. 1b) an isolated braincase from the Eocene (Ypresian, 52-49 Ma) London Clay Formation, UK (Friedman *et al*. 2016); *Gempylus serpens* BMNH 44.670[D], FMNH 71423[W,C]; *Hemithyrsites prometheus* BMNH 44.650[D] BMNH 1906.9.8.149[W,R], UMMZ 250143[W,C]; *Lepidocybium flavobrunneum* LACM 36320-1[W,C]; *Nealotus tripes* BMNH 2016.4.14.59[W,R]; *Neoepinnula orientalis* BMNH 1986.9.8.164.5[W,R]; *Nesiarchus nasutus* 1998.8.9.127.37-38[W,R] , FMNH 71422[W,C]; *Paradiplospinus gracilis* BMNH 2009.5.18.74-75[W,R], BMNH 2009.5.18.143[W,C]; †*Progempylus edwardsi* NHMUK PV OR 32388[C] (Fig. 1a) a cranium from the Eocene (Ypresian, 52-49 Ma) London Clay Formation, UK (Friedman *et al*. 2016); *Rexea prometheoides* FMNH 120779[W,C]; *Ruvettus pretiosus* BMNH 44.620[D], BMNH 1997.5.21.40[W,R], BMNH 1938.6.23[W,C]; *Thyrsites prometheus* BMNH 99.1.16.4[W,R]; *Thyrsitoides marleyi* BMNH 1986.9.8.147[W,R,C].

Trichiuridae. NHMUK PV P 26904[C] (Fig. 1c) a cranium from the Eocene (Ypresian, 52-49 Ma) London Clay Formation, UK (Friedman *et al*. 2016); *Aphanopus carbo*

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BMNH 1899-1-16.5 [D], BMNH 1961.6.20.1[W,R], BMNH 2006.6.27.1[W,C]; *Benthodesmus simonyi* BMNH 1972.1.10.64[W,R,C]; *Eupleurogrammus glossodon* BMNH 1955.5.13.3[W,R]; *Lepidopus caudatus* BMNH 44.820[D], BMNH 1864.10.5.7[W,R], BMNH 1903.6.27.22[W,C]; *Lepturacanthus savala* BMNH 51.19.27.14.3[W,R], UMMZ 219522[W,C]; *Tentoriceps cristatus* BMNH 1974.3.5.1-3[W,R], BMNH 1987.1.23:28[W,C]; *Trichiurus lepturus* BMNH 44.850[D], BMNH 1897.12.1.343[W,R], UMMZ 219710[W,C].

Pomatomidae. *Pomatomus saltatrix* studied from the literature (Leapley 1952) and UMMZ 111069[W,C].

Scombridae. *Gasterochisma melampus* studied from the literature (Kohno 1984) and specimen photographs of AMNH 098426SD[D].

X-ray Computed Tomography

Fossil specimens †*Eutrichiurides winkleri* and †*Progempylus edwardsi* were studied using μCT scanning. These specimens had previously been mechanically prepared in order to expose external bones, and μCT presents an effective method of obtaining additional information of the internal anatomy of fossil specimens (Beckett and Friedman 2016). Extant taxa were scanned to obtain details of internal osteological anatomy not available from radiography or the literature.

Fossil specimens and Recent BMNH specimens were scanned using the Metris X-Tek HMX ST μCT scanner in the Imaging and Analysis Centre of the Natural History Museum, London. FMNH and UMMZ specimens were scanned using the Metris X-Tek XT H 225ST μCT scanner at the CTEES facility in the Department of Earth and Environmental Sciences, University of Michigan. Scan settings are provided in Beckett et al. (2018). Tomogram stacks were segmented using Mimics Materialise v.16.0-19.0 x64 (http://biomedical.materialise.com/mimics). High-resolution models produced in Mimics were exported as .ply files, then imported into Blender (blender.org) and rendered as two-dimensional images.

Radiography

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Radiography of extant specimens from the Life Sciences collections of the Natural History Museum, London was undertaken in the Radiography Suite using the Solus Schall X-ray setup. All specimens were imaged at 3 μA with a working distance of 75 cm. Voltages and exposure times are given in Becket et al. (2018, S1).

Dataset Assembly

Morphology. We combined datasets for 'gempylids' (Russo 1983) and trichiurids (Gago 1997, 1998) to create a single morphological character matrix. Russo (1983) provides a character list, but no character-by-taxon matrix is presented in his thesis. However, we were able to reconstruct his character matrix based on his most parsimonious cladogram (Russo, 1983: fig. 47). Characters duplicated in source matrices were amalgamated, and indicated as such in the character list (Beckett et al. 2018). We also excluded characters that we could not interpret in comparative material due to ambiguity in the original character definitions (Gago 1998: 4, 36 and 60; Russo 1983: 2, 7, 10, 27, 30, 32, 37, 55, 62, 69, 71, 72, 77 and 78). We utilised published descriptions by Russo (1983), Gago (1998), Nakamura and Fujii (1983) and Fujita (1990) to code characters for taxa from Russo (1983) not included in Gago (1998) and vice versa. Additional character states for extant taxa were obtained by studying dry specimens, radiographs and μCT data.

We also added five taxa to this combined dataset. In addition to the three fossil specimens described below (†*Eutrichiurides winkleri,* †*Progempylus edwardsi* and NHMUK PV OR 41318), we increased our sampling of outgroup lineages by including the pomatomid (bluefish) *Pomatomus saltatrix* (Leapley 1952) and early diverging scombrid *Gasterochisma melampus* (Kohno 1984) in addition to the scombrolabracid (longfin escolar) *Scombrolabrax heterolepis* used in previous systematic studies. The resulting character matrix has 32 taxa coded for 144 characters. Of these, 103 relate to the skeleton (73 cranial, 38 postcranial), 3 refer to otoliths, 7 concern soft tissues, and 23 are developmental characters.

Individual ossifications are sometimes difficult to identify in fossils, particularly when they are closely sutured (as is often the case in the neurocranium). References to individual ossifications in our descriptions are based

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on visible sutures and positional comparisons with other taxa (both from the literature and first-hand observation).

Molecular Data. 17 taxa from our morphological dataset were matched with mitochondrial sequences from Miya *et al*. (2013; 12n3rRTn dataset, comprising 13596 base pairs, 5 partitions). This molecular dataset represents whole mitogenomic sequences with the ND6 gene excluded. This dataset excludes quickly saturated transitional changes in the third codon positions (see Miya *et al*. 2013).

Phylogenetic Analysis

Parsimony. We analysed the morphology only dataset using maximum parsimony as an optimality criterion in PAUP version 4.0a150 for Mac (Swofford 2003). We performed a heuristic search (addseq=random hold=5 nreps=500) with unweighted and unordered characters and the tree bisection and reconstruction strategy enabled. Nodal support was measured in PAUP by manual calculation of Bremer decay indices and by bootstrap analysis (nreps=100, hold=5, search=heuristic, addseq=random), retaining those clades with a frequency greater than 50%. We rooted our networks on *Pomatomus*.

Bayesian. Both the morphology only and the combined morphological and molecular dataset were analysed in MrBayes v.3.2.6 (Huelsenbeck and Ronquist 2001). A gamma distribution was specified for the morphological-only dataset. The combined dataset was partitioned: the molecular dataset by codon position, and using GTR+gamma distribution (following Miya *et al*. 2013); the morphological partition was assessed using a gamma model. Networks were rooted on *Pomatomus saltatrix* based on topologies presented in past studies (Orrell *et al*. 2006; Betancur-R *et al*. 2013, 2017). Monophyly of the trichiuroid ingroup was enforced. Each analysis ran for two independent runs of four chains, sampling every 500 generations for 15 million generations, and the first quarter of each run was discarded as burn-in. Convergence was indicated by average standard deviation of split frequencies <0.01, effective sample sizes >200 and visual inspection of the marginal probability

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distribution and trace of the analyses in Tracer v 1.6 (Drummond and Rambaut 2007).

Institutional abbreviations: **IRSNB,** Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **FMNH**, Division of Fishes, Field Museum, Chicago, USA; **NHMUK,** Earth Sciences collections, **BMNH**, Life Sciences collections, both Natural History Museum, London, UK; **UMMZ**, Division of Fishes, University of Michigan Museum of Zoology, Ann Arbor, USA.

Systematic Palaeontology

Teleostei Müller, 1845

Percomorpha Rosen, 1973 *sensu* Johnson & Patterson, 1993

Pelagia Miya & Friedman in Miya *et al.* 2013

Trichiuroidea *sensu* Nakamura and Parin, 1993

'Gempylidae' Gill, 1862

Genus †***Progempylus*** Casier, 1966

Type species. †*Progempylus edwarsdi* NHMUK PV OR 32388.

Diagnosis. As for type and only species.

†***Progempylus edwardsi*** Casier, 1966

Figures 2-6

1901 Percidae? cf. *Planesox vorax* Woodward, p. 519.

1966 *Progempylus edwardsi* Casier, p. 250, pl. 40, fig. 2.

2005 *Progempylus edwardsi* Casier; Monsch, p. 449, fig. 4.

Holotype. NHMUK PV OR 32388, an articulated skull preserved in three dimensions.

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Diagnosis. 'Gempylid' fish distinguished by the following combination of characters: braincase narrows above orbit and widens again anteriorly, lower jaw short with point of articulation with quadrate beneath the orbit, pair of vomerine teeth and lateral process on vomer.

Material. Type and only specimen, NHMUK PV OR 32388, a historically prepared specimen that visibly preserves an articulated braincase, jaws, supsensoria and opercular series.

Occurrence. London Clay Formation, Isle of Sheppey, UK. Specimens from this locality are Ypresian in age and dated at 52-49Ma (Friedman *et al*. 2016). The depositional setting is outlined in greater detail in Friedman *et al*. (2016).

Remarks. After being figured and described by Casier (1966), this specimen was revisited by Monsch (2005) who described the specimen briefly and associated it with 'gempylids'.

Description

†*Progempylus edwardsi* (NHMUK PV OR 32388) preserves the skull including the braincase, lower jaw, suspensorium, hyoid arch, gill-arch skeleton and opercular series.

Braincase. In dorsal view the neurocranium is narrow and long, approximately half as wide anteriorly as posteriorly. The paired frontals (Figs 2a & 3a) form the majority of the anterior portion of the skull roof. They are constricted above the orbit, but broken anteromedially such that it is not possible to discern the medial suture of the frontals with the mesethmoid. Narrow ridges ornament the frontals, and radiate from a point above the orbit. The supraorbital sensory canal extends through the frontal in an enclosed tube, branching twice and exiting the frontals via three branches. The first branch is directed medially in the posterior portion of the frontals and is visible as a large pore in the pineal region. The second offshoot exits

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the bone in a pore close to the medial suture of the frontals above the orbit. The main line continues anteriorly and exits the frontals in a small pore anterior to the orbit that is aligned with a groove that extends to the anterior margin of the frontal (Fig. 2a). The frontals are bordered posteriorly by the supraoccipital, parietals, pterotics and sphenotics. An elongate supraoccipital is bordered by the epiotics posteromedially and the parietals anteromedially. The supraoccipital ridge bifurcates, extending anteriorly to the level of the orbit. The parietals suture with the frontals anteriorly, and form part of the epiotic ridge, suturing with the pterotic laterally. The pterotic is elongate with a large ridge. The suture between the parietals and the pterotic can be traced posteriorly to the mid-point of the pterotic shelf. Laterally the pterotic sutures with the sphenotic, which forms the posterior margin of the orbit. The epiotic meets the posteromedial margin of the parietals and the lateral margin of the supraoccipital. A clear suture is visible posteriorly between the epiotic and the exoccipitals. The small intercalar is visible dorsally. It has a curved anterior margin that meets the exoccipitals anteromedially and the posterior margin of the pterotic anterolaterally.

In lateral view (Figs 2b, 3b) the neurocranium is deepest posteriorly, the parasphenoid curves dorsally to suture with the posterior margin of the vomer. The vomer is widest anteriorly where it meets the mesethmoid. Wings on either side of the vomer extend dorsolaterally from behind the vomerine teeth to the point of articulation with the parasphenoid. The vomer bears two pairs of teeth, which are small and posteriorly recurved. The anterior tooth is smaller than the posterior. Posteriorly the parasphenoid overlaps and sutures to the basioccipital. At the posterior margin of the orbit, the strut-like lateral commissure defines the margin of a large trigeminal facial chamber (Fig. 3b). Also visible in lateral view is the foramen for the internal carotid, posterior to the lateral commissure beneath the sphenotics and pterotics.

Jaws. The lower jaw is short and deep, even accounting for missing bone at the anterior and posterior margins (Fig. 4a-b). The dentary exclusively forms the dorsal margin and contributes to the ventral margin of the jaw, with the articular inserted

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into the notch-like excavation in the posterior margin of the dentary. A series of small teeth are borne on the dorsal margin, with three preserved on the right dentary and the base of three or four on the left. These teeth are relatively similar in size and evenly spaced along the jaw. The ventral-posterior margin of the lower jaw and its articulation with the quadrate appear to be missing, as the metapterygoid and fragmentary quadrate are preserved posterior to the preserved portion of the lower jaw. No components of the dermal upper jaw are preserved.

Suspensorium. The suspensorium comprises the palatine, endopterygoid, metapterygoid, quadrate, hyomandibula and symplectic (Fig. 4c-d). In lateral view the palatine consists of an elongate dorsal ridge and a ventral plate-like expansion. The ventral margin of the ventral ridge is jagged but no obvious teeth are visible. The anterior process of the dorsal ridge is hooked and expanded medially, articulating posteriorly with the anterior margin of the endopterygoid, which is oval in shape, pointed anteriorly and concave dorsally. The ectopterygoid is poorly preserved and highly pyritised. A thin lamina of bone on the internal surface of the quadrate on the left side of the specimen may also represent a fragment of ectopterygoid. A broad, flat metapterygoid with a posterodorsal extension sits anterior to the hyomandibular shaft, although the nature of the contact between the two bones is obscured by pyrite. The ventral margin of the metapterygoid articulates with the dorsal margin of the quadrate. The hyomandibula is fragmentary on the right side of the specimen, with only the anterodorsal head and a small ventral extension that articulates with the metapterygoid preserved. More complete on the left side, the hyomandibula has a flat dorsal head and long slender ventral shaft. The dorsal head has two articular areas: an anterior projection that articulates with the sphenotic, and a posterior expansion articulating with the lateral margin of the braincase beneath the pterotic. The opercular process extends directly perpendicular to the ventral shaft of the hyomandibula. It does not articulate with any bones in the fossil, which may indicate that elements of the operculum have moved or are missing. The quadrate is preserved as a fragment on

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both sides and its shape cannot be discerned. The symplectic is small and elongate with an articular head.

Hyoid Arch. The hypohyals are tightly bound. Each hypohyal is rectangular individually, but the dorsal and ventral components are tightly bound to form a square (Fig. 4e-f). The anterior ceratohyal is approximately three times the length of the hypohyals, and bears a narrow, longitudinal groove on its lateral surface. There is no ceratohyal window. The posterior ceratohyal is as deep as the anterior ceratohyal, but shorter in length. It tapers to a posterior point, forming a triangular shape. The anterior and posterior ceratohyals join in an interdigitated suture. Two narrow branchiostegals articulate with the posterior ceratohyal. Additional elements of the branchiostegal series are not apparent.

Gill Skeleton. The gill skeleton is well preserved and largely in articulation, particularly posteriorly (Fig. 5). It preserves the urohyal, hypobranchials 1-3, ceratobranchials 1-5, 4 epibranchials 1-4 and pharyngobranchial 3. Pharyngobranchial 1 is preserved only on the left side.

Hypobranchial 1 is preserved on both sides of the specimen, although both elements have been rotated out of life position. It is elongate with a large laterally-directed anterior head. Hypobranchial 2 is preserved most completely on the left side and has been rotated posteriorly. It is long and straight with an anteriorly expanded head of a similar size to hypobranchial 1. A fragment of bone on the right side correlates with the expected position of hypobranchial 2. Hypobranchial 3 is well preserved on the left side, with a broad posterior expansion that is triangular in shape and extends anteriorly. The right hypobranchial 3 has been rotated posteriorly and is missing the elongate anterior expansion.

Ceratobranchials 1-5 are elongate and straight with a groove extending the length of the ventral surface. Ceratobranchials 1-4 are of approximately equal length but ceratobranchial 5 is only two-thirds the length of the other ceratobranchials and meets its antimere anteriorly. Ceratobranchial 5 is also slightly wider than

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ceratobranchials 1-4, expanding ventrally so the groove faces medially. No teeth are visible on the ceratobranchials.

Epibranchials 1-4 are elongate, curve medially and become progressively smaller from epibranchial 1 to epibranchial 4. Each epibranchial bears a groove on its dorsal surface. Epibranchial 1 widens into a dorsolateral process one-third along its length from the anterior margin. Epibranchial 2 lacks a process but is expanded anteriorly to form a flat triangular shaped head, and epibranchials 3 and 4 are also expanded slightly anteriorly. Epibranchial 3 has no associated processes, while the left epibranchial 4 shows a dorsal process.

Pharyngobranchial 1 is small and rod like with a small anterior head. It is preserved only on the left side shifted anteriorly from its presumed life position. Pharyngobranchial 3 is equal in length to hypobranchial 2 but wider posteriorly, forming a shallow concavity in dorsal view. The ventral surface of the right pharyngobranchial 3 is rough, suggesting the possible presence of a sutured toothplate, although this is not clearly preserved. The urohyal is plate-like, triangular in lateral view, and anteriorly tapers to a trapezoid head. The ventral margin of the urohyal has a small lateral expansion about the midline.

Opercular Series. The opercular series consists of the preoperculum, operculum and suboperculum (Fig. 6). The preoperculum curves antero-ventrally and is widest at the angle of the bone, with a weakly convex posterodorsal margin. The operculum and suboperculum are approximately triangular in shape, with the suboperculum smaller and positioned medio-ventrally to the operculum. A circular facet for articulation with the hyomandibula is preserved on the medial surface of the right operculum, and completely covered by a plate-like lateral process in lateral view. The operculum has a large notch at the posterior of the dorsal margin of the operculum. The ventral posterior margin of the notch forms a point at the posterodorsal corner of the operculum.

'GEMPYLIDAE' incertae sedis

Figsures 7-8

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1966 cf. *Eutrichiurides* Casier, p. 249, text fig. 56, pl. 24, fig. 3.

2005 Gempylinae? *incertae sedis* Monsch, p. 449, fig. 5.

Material. NHMUK PV OR 41318, three-dimensionally preserved braincase.

Occurrence. London Clay Formation, Isle of Sheppey, UK. Specimens from this locality are Ypresian in age and dated at 52-49Ma. The depositional setting is outlined in greater detail in Friedman *et al*. (2016).

Remarks. A historically prepared braincase referred to †*Eutrichiurides* by Casier (1966) and then to 'Gempylidae' by Monsch (2005), this specimen is incomplete anteriorly but is otherwise well-preserved. Comparisons with NHMUK PV P26904 are limited by the small amount of overlap in the regions of the braincase preserved in the specimens. Characters differentiating NHMUK PV OR 41318 from NHMUK PV P26904 are: vomer does not extend markedly posterior to the lateral ethmoids (vomer in NHMUK PV P26904 extends over half the length of the neurocranium to the midpoint of the orbit); strong ornament not apparent on frontal (compared to the ornament on the right fragmentary frontal in NHMUK PV P26904). NHMUK PV OR 41318 also shows clear differences from †*Progempylus edwardsi*: parasphenoid and vomer are approximately parallel to the frontals in NHMUK PV OR 41318 (the parasphenoid and vomer curve dorsally in lateral view in †*Progempylus edwardsi*); basioccipital and exoccipitals extend beyond the posterior margin of the intercalar and pterotic (in †*Progempylus edwardsi* the basioccipital and exoccipitals do not extend posterior to the posterior margin of the braincase).

Description

Braincase. In dorsal view the paired frontals are elongate, narrowing medially above the orbit (Figs 7a, 8a). In the pineal region of the frontals the pores for the medial

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branch of the supraorbital canal are visible. The frontals suture anteriorly with the mesethmoid which narrows anteriorly and is broken laterally. In lateral view the mesethmoid extends to meet the dorsal surface of the vomer (Figs 7b, 8b). The lateral ethmoids extend laterally beyond the mesethmoid and the frontals in dorsal view, and meet the posterior margin of the vomer and mesethmoid in lateral view. The posterior margin of the frontals sutures to the supraoccipital, which bears the supraoccipital crest (Figs 7a, 8a). Dorsally the supraoccipital crest is broken but is well developed and extends posteriorly over the exoccipitals. The parietals lie lateral to the supraoccipital. Postero-medially the frontals are bordered by the sphenotic. The sphenotic forms the posterior margin of the orbit and sutures with the pterotic posteriorly. The parietals suture to the pterotic laterally and the epiotic posteriorly. The pterotic has a pronounced shelf and a well-developed pterotic ridge, almost the same height as the epiotic ridge in lateral view. In dorsal view the epiotics are approximately round and suture with the intercalar and exoccipitals posteriorly. The intercalar is visible on the dorsal surface but is small, being larger on the ventral surface of the neurocranium, suturing with the sphenotics laterally and the basioccipital medially. The exoccipitals are kidney-shaped in lateral view. The basioccipital sutures to the underside of the exoccipitals and is concave in posterior view. In lateral view the basioccipital sutures to the dorsal side of the parasphenoid antero-ventrally and the posterior side of the prootic anteriorly (Figs 7b, 8b). A ventrally placed foramen marks the exit of the vagus nerve from the exoccipital. In both lateral and ventral view the prootic is visible and connects the parasphenoid to the medial margin of the sphenotics. The lateral margin of the trigeminal facial chamber is defined by the strut-like lateral commissure, which forms the anterior margin of the prootic. At the junction of the parasphenoid and the prootic is the foramen for the internal carotid. The parasphenoid, which meets the basisphenoid posteriorly, extends anteriorly to the posterior margin of the vomer and meets this along a `v'-shaped contact at the posterior point of the lateral ethmoids (Figs 7c, 8c). The anterior tip of the vomer is missing and it is not possible to determine if teeth were present.

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Trichiuroidea *incertae sedis*

Genus †MACROYNIS nov.

LSID. urn:lsid:zoobank.org:act:28EAA039-9656-40B7-8EE9-0098BBA9FD0E

Derivation of name. *Macro* – long, large, *ynis* – vomer; meaning long vomer in greek.

Type species. *Macroynis casieri* sp. nov.

Diagnosis. As for type and only species.

†***Macroynis casieri*** sp. nov.

Figures 9–11

1966 *Eutrichiurides winkleri* Casier; Casier, p. 244, text-figs 55 & 56, pl. 23, figs 2–5.

2005 *Eutrichiurides winkleri* Casier; Monsch, p. 447, fig. 3.

LSID. urn:lsid:zoobank.org:act:FD07E026-37DF-4A68-ACE7-EB07EB19EF82

Derivation of name. Specific name honours Edgard Casier, who first described the specimen.

Holotype and only specimen. NHMUK PV P26904 is a historically prepared, incomplete isolated skull from the London Clay of Sheppey, UK (for a review of depositional setting and age see Friedman *et al*. 2016). The braincase of this specimen is highly fragmented, particularly the dorsal surface.

Diagnosis. Trichiuroid distinguished from other trichiuroids by the following combination of characters: elongate vomer extending markedly behind the lateral ethmoid, single large premaxillary fang, anterior tooth on dentary in line with other teeth, antero-posteriorly abbreviated hypohyals located greatly anterior to the anterior ceratohyal, presence of a ceratohyal window in anterior ceratohyal, palatine triangular and ventrally extended in lateral view.

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Occurrence. London Clay from the Isle of Sheppey, UK. Specimens from this locality are Ypresian in age and dated at 52-49Ma. The depositional setting is outlined in greater detail in Friedman *et al*. (2016).

Remarks

The holotype of †*Eutrichiurides delheidi*, the type species of †*Eutrichiurides* (Casier 1944), comprises a dentary, premaxilla and series of teeth belonging to a single individual (Leriche 1908; pl. 25, figs 1-2) from the Oligocene (Rupelian) Boom Clay of Belgium. Casier (1944, 1946, 1966) subsequently attributed to †*Eutrichurides* isolated teeth removed from †*Trichiurides*, a genus he re-interpreted as a gadiform. These isolated dentitions have a tortuous taxonomic history, featuring associations with lepisosteids (Woodward 1891) and lophiids (Leriche 1905) in addition to the trichiurid interpretation advocated by Casier and others (Winkler 1876; White 1931). It is from some of these isolated dentitions that Casier (1946) erected †*E. winkleri* (type series: IRSNB P 00320, 00324:00329) from the Eocene (Ypresian) of Forest-lez-Bruxelles, Schaerbeeck, Belgium (Casier 1946: pl. 6, fig. 19a-b). In his review of the London Clay fish fauna, Casier (1966) attributed NHMUK PV P26904 to †*E. winkleri* as the only skeletal (rather than exclusively dental) material of the species.

We question this attribution of NHMUK PV P26904. There are no obvious features shared uniquely between NHMUK PV P26904 and the type material of †*E. winkleri*, and we find no clear evidence that they are conspecific beyond similarity in age. Indeed, the type material of †*E. winkleri* is sufficiently non-diagnostic that we regard identification of these remains at the species level dubious. With respect to generic assignment, more detailed comparisons are possible with the substantially younger type species of the genus, †*E. delheidi*. Similarities with NHMUK PV P26904 are present (e.g. enlarged premaxillary fangs), but these are general features of trichiuroids that provide no evidence for relationships within the group. Pertinently, †*E. delheidi* bears an anteroventral projection at the tip of the dentary, a feature with limited distribution among trichiurids (e.g. *Assurger*, *Evoxymetopon*) but which appears not to be present in NHMUK PV P26904 despite damage to the

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anterior region of the mandibles. We have no confidence that NHMUK PV P26904 and †*E. delheidi* form a monophyletic group relative to other trichiuroids, and therefore erect the new taxon †*Macroynis casieri* to accommodate the London Clay specimen.

Description

Braincase. The braincase is highly fragmented, presumably due to damage during preservation (Fig. 10). The parasphenoid extends the whole length of the neurocranium but is broken midway along its length, and the posterior part of the parasphenoid and braincase is rotated and displaced laterally. In ventral view, the posterior border of the parasphenoid is convex, and bears two raised ridges forming a gutter that extends along the midline. A lateral wing of the parasphenoid contacts the prootic dorsally. Anteriorly, the parasphenoid extends dorsal to the vomer, and the suture between the parasphenoid and vomer is visible in cross section (see Beckett *et al.* 2018). The edentulous vomer is fully half the length of the braincase, tapering to a point markedly posterior to the lateral ethmoids. Anterolaterally, the vomer widens into broad processes. Hourglass-shaped lateral ethmoids are present on either side of the vomer, with their anterior margins level with the widest part of that bone. Posteriorly, the lateral ethmoids are formed of three struts, one of which contacts the frontal.

Jaws. The upper and lower jaws are preserved on both sides of the specimen (Fig. 11a-b). The upper jaws comprise the maxilla and premaxilla; a supramaxilla is not apparent. The maxilla extends along the length of the ethmoid region of the neurocranium, and widens anteriorly to form the premaxillary articular head. At least seven small teeth, of which only the bases are preserved, are borne on the premaxilla. In addition, a single large fang, preserved only on the right side, sits anterior to the smaller teeth. The lower jaw is roughly twice as long as the upper jaw, and extends the full length of the neurocranium. The dentary bears a single row of teeth, which decrease in height posteriorly. Up to four smooth, gently recurved

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teeth are preserved on each dentary, and smaller cusps at the base of some of these may represent extraosseous replacement teeth (Trapani 2001; see .vol files in Beckett *et al*. 2018). The posterior portion of the lower jaw is formed by the articular, which contacts the dentary along a v-shaped margin. A projection of the posterior margin of the articular forms the articulation point with the head of the quadrate.

Suspensorium. Well-preserved components of the suspensorium include the palatine, endopterygoid, quadrate and symplectic (Fig. 11c-d). In lateral view the palatine consists of an elongate rod dorsally, with a ventral plate-like extension. The ventral expansion is triangular in shape and bears a single row of very small teeth on the ventral margin. The anterior margin is concave, and articulates with the posterior margin of the maxillary head. In dorsal view, a median palatine shelf extends approximately half the length of the palatine, narrowing anteriorly and widening posteriorly. The shallow, concave endopterygoid extends from the posteromedial margin of the palatine to the posterior occipital region. The preservation of this bone is compromised by extensive pyritization. A fan-shaped quadrate bears a ventral articular condyle. The symplectic is thin and rod-like, the length of which is approximately two-thirds the height of the quadrate. It is housed in a groove on the medial surface of the quadrate.

A fragment of bone on the right side of the fossil likely represents the ventral extension of the hyomandibula, with a small anterior extension forming an articular head.

Hyoid Arch. The anterior and posterior ceratohyals and dorsal and ventral hypohyals are preserved on both sides of the skull (Fig. 11e-f). They are largely intact, with minor preparation damage to the ventral margin of the right anterior ceratohyal. The triangular posterior ceratohyal is sutured to the anterior ceratohyal via interleaved bone on its medial surface. The anterior ceratohyal is approximately twice the length of the posterior ceratohyal and is constricted at midlength. The lateral surface is grooved for the afferent hyoidean artery. A perforation (the

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ceratohyal window) is present at the narrowest point of the anterior ceratohyal and anteriorly there is a robust tubular extension. The dorsal and ventral components of the trapezoidal hypohyals contact each other at their widest point. The hypohyals are positioned far forward relative to the ceratohyals. The shape of the anterior ceratohyal and position of the hypohyals is mirrored on each side of the specimen, suggesting that the anteriormost portion of the anterior ceratohyal was cartilaginous.

Phylogenetic Results

Parsimony

A maximum parsimony analysis of morphological data yields 40 most parsimonious trees with a length of 434 steps (consistency index [CI]: 0.4097; retention index [RI]: 0.7267; rescaled consistency index [RCI]:0.2977; Fig. 12). Trichiuroidea (Fig. 12 node A) is supported by five characters, two of which have a CI of 1: character 18[1], short ascending process of the premaxilla; c.86[1], elongate dorsal articular process of cleithrum. The parsimony analysis recovers 'gempylids' as a grade with respect to monophyletic trichiurids, and clades within the 'gempylid' grade are largely supported by homoplastic characters. *Diplospinus* + *Paradiplospinus* is resolved as the immediate sister clade to trichiurids, but with very low nodal support (bootstrap support: 0.56, Bremer decay index: 1). (*Diplospinus* + *Paradiplospinus*) + Trichiuridae (Fig. 12 node C) is supported by 13 characters, 3 of which have a CI of 1: c.4[1], concave posterodorsal margin of the preopercle; c.91[1], scale-like external spinous elements of pelvic fin; c.113[1], small hypural notch. Trichiurids are recovered as monophyletic, supported by 33 characters, 12 of which have a CI of 1 (Fig. 12 node D; Becket et al. 2018, S4). Many of the clades within Trichiuridae are also supported by non-homoplastic characters.

†*Progempylus* is resolved as the sister taxon of *Ruvettus.* Eight characters are optimised as supporting this node, but only two of these can be assessed in †*Progempylus*: c.10[1], rounded anterior process of subopercle; c.68[1], bifurcation

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of supraoccipital ridge on the supraoccipital. Together †*Progempylus* and *Ruvettus* form the sister clade to all other 'gempylid' and trichiurid taxa, with the exception of *Lepidocybium*. Monophyly of trichiuroids minus *Lepidocybium* (Fig. 12 node B) is supported by four characters, one of which has a CI of 1 and can be coded for †*Progempylus*: c.53[1], two pairs of teeth on the vomer (also seen in *Ruvettus*, *Thyrsites* and *Neoepinnula*).

NHMUK PV OR 41318 is recovered as the sister taxon of *Rexea.* This placement is supported by a single character: c.61[1], narrowing of the frontals above the orbit before they widen again above the lateral ethmoids. This is a homoplastic character also present in *Progempylus*. Of the characters supporting trichiurids NHMUK PV OR 41318 can be coded for one: c.67[0], pterotic ending before the posterior margin of the neurocranium, a primitive feature excluding it from Trichiuridae.

In a strict consensus, †*Macroynis casieri* is the sister taxon to *Evoxymetopon*, within Trichiuridae. This placement is supported by two characters, both reversals occurring elsewhere in the tree but only co-occurring in these two genera: c.23[0], anterior tooth in line with the remaining dentary teeth; c.33[0], presence of a ceratohyal window. All characters coded for †*Macroynis casieri* show homoplasy.

Bayesian Morphology

As in the parsimony analysis, 'gempylids' are recovered as a grade with respect to a monopyletic Trichiuridae (Fig. 12). In the maximum clade credibility tree (Fig. 12a), nodes within the 'gempylid' grade are poorly supported, with all relationships of 'gempylids' deeper in the tree than *Nesiarchus* collapsing to `gempylid' polytomy in the majority-rule tree (Fig. 12b). In the maximum clade credibility tree, †*Progempylus edwardsi* and NHMUK PV OR 41318 are recovered as sister taxa in a clade with *Neoepinnula* + *Epinnula* and †*Macroynis casieri* is recovered as sister taxon to the grade that includes *Thyrsitoides*, *Gempylus*, *Nesiarchus*, *Diplospinus* + *Paradiplospinus* and Trichiuridae (Fig. 12a). However in the majority-rule tree all fossil taxa lie within the 'gempylid' polytomy. *Diplospinus* + *Paradiplospinus*

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represent the immediate 'gempylid' sister group to the monophyletic trichiurids with a support value of 0.70. The trichiurid clade has a posterior probability of 0.88.

Bayesian Combined Analysis

In agreement with the parsimony and Bayesian morphology only analyses, 'gempylids' are recovered as a grade with respect to trichiurids in the maximum clade credibility tree, albeit with very poor support (Fig. 13a). Trichiurids are resolved as a clade with a posterior probability of 0.87. In the majority-rule consensus tree (Fig. 13b), 'gempylids' form a polytomy at the base of the tree and Trichiuridae are monophyletic, the latter supported by a Bayesian posterior probability of 0.87. Three pairs of 'gempylid'-grade taxa form clades with variable support: *Thyrsitoides* + *Gempylus* (0.73), *Neoepinnula* + *Epinnula* (0.56), and *Tongaichthys* + *Thyrsitops* (0.89). *Diplospinus* and *Paradiplospinus* form a clade with *Nesiarchus* as its sister taxon; the monophyly of this group is supported with a posterior probability of 0.82. In the maximum clade credibility tree †*Progempylus edwardsi* and †*Macroynis casieri* form a clade, with NHMUK PV OR 41318 falling as the sister taxon of *Rexea* + (*Hemithyrsites + Nealotus*). However, all of the fossil taxa are resolved within the basal polytomy in the majority-rule consensus tree.

Removing fossils from the analysis recovers a tree (Becket et al. 2018, S5) with three principal clades, all of which have posterior probabilities above 0.8. Two of these clades contain 'gempylids', and branch as two successively more remote outgroups to a monophyletic Trichiuridae, the latter supported by a posterior probability of 1. The most deeply diverging clade contains *Lepidocybium, Ruvettus, Neoepinnula, Epinnula*, *Tongaichthys* and *Thyrsitops*. The remaining 'gempylids' form a clade that falls as sister to the trichiurids, and this sister relationship has a posterior probability of 1. Trichiurid monophyly is also strongly supported, with a posterior probability of 1.

Discussion

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Relationships within Trichiuroidea

Across all of our analyses, our results consistently recover a monophyletic Trichiuridae nested within poorly supported grade of 'gempylids'. This result is in line with previous morphological (Tucker 1956; Johnson 1986; Pothoff *et al*. 1986; Carpenter *et al*. 1995; Gago 1997) and molecular (Orrell *et al*. 2006; Miya *et al*. 2013; Betancur-R *et al*. 2013, 2017; Near *et al*. 2013) analyses. Within this, relationships among 'gempylids' are highly variable, but *Lepidocybium and Ruvettus* are consistently recovered as the earliest diverging extant taxa. While trichiurids are consistently monophyletic, some relationships within the clade vary compared to previous hypotheses.

In our analyses of morphological characters (under both parsimony and Bayesian frameworks; Figs 12-13), relationships among 'gempylids' agree broadly (and unsurprisingly) with those reported by Russo (1983), a major source of our characters. *Lepidocybium* and *Ruvettus* are recovered in both morphological analyses (Figs 12-13) as successively branching sister taxa to the remaining ingroup. This deep split between *Lepidocybium* and all remaining trichiuroids was argued by Johnson (1986), but is not routinely supported by molecular analyses (Orrell *et al*. 2006; Miya *et al*. 2013) or our combined analysis (Fig. 14). *Paradiplospinus* + *Diplospinus* is recovered in all analyses as the most nested 'gempylid' clade (Russo 1983) and the sister clade to trichiurids in the morphology analyses (Gago 1997, 1998). *Diplospinus* has historically been closely aligned with trichiurids, and was initially placed within the group (Tucker 1956) before its subsequent removal (Parin and Becker 1972). The elongate body plan of *Diplospinus* resembles that of trichiurids, lending support to a close relationship. However, *Paradiplospinus* and *Diplospinus* are rarely included in molecular analyses, so molecular support for this hypothesis is sparse (Orrell *et al*. 2006; Miya *et al*. 2013; Near *et al*. 2013; Betancur-R *et al*. 2017). Addition of molecular data to our analyses results in a different pattern of relationships among 'gempylids'. Rather than comprising numerous successive outgroups to trichiurids, 'gempylids' remain a grade but fall within a more restricted set of clades. However, the monophyly and mutual relationships of these clades are poorly supported in

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analyses that include fossil taxa. Removal of fossils from the combined dataset results in a well-supported pair of 'gempylid' clades (Becket et al. 2018, S5), containing similar constituent taxa to those recovered in previous molecular analyses (Orrell *et al*. 2006; Miya *et al*. 2013), but showing different internal relationships. Other published molecular analyses including multiple 'gempylid' taxa likewise show little agreement between inferred relationships either within the assemblage or to trichiurids (Orrell *et al*. 2006; Miya *et al*. 2013; Betancur-R *et al*. 2013, 2017; Near *et al*. 2013). Satisfactory resolution of 'gempylid' interrelationships remains elusive, and we anticipate that molecular studies targeting additional lineages and increased number of loci might provide increased clarity (see Harrington *et al*. 2016 for a similar case in carangarians).

In contrast to the ambiguity concerning 'gempylid' relationships, we find good support for Trichiuridae (cf. Gago 1998; Betancur-R *et al*. 2013, 2017; Near *et al*. 2013; Miya *et al*. 2013) and broadly consistent patterns of relationships within the group between analyses. Our results provide a test of the division of trichiurids into three "tribes" by Tucker (1956): Aphanopodinae (*Diplospinus, Aphanopus* and *Benthodesmus*), Lepidopodinae (*Assurger*, *Tentoriceps*, *Lepidopus*, *Evoxymetopon* and *Eupleurogrammus*), and Trichiurinae (*Trichiurus* and *Lepturacanthus*). Of these historically recognised "tribes" *sensu* Tucker (1956) only the Trichiurinae are consistently recovered as monophyletic. All of our analyses resolve Lepidopodinae *sensu* Tucker (1956) as paraphyletic with respect to his Trichiurinae. In particular we find that *Eupleurogrammus* and *Tentoriceps* are always successive sister groups of trichiurines. Gago (1998) recovered a similar arrangement and moved *Eupleurogrammus* to the Trichiurinae, to which we also add *Tentoriceps*. This group of four genera is a consistent feature across our analyses. The remaining 'lepidopodines' fall as a grade, in agreement with Gago (1997, 1998). Tucker's (1956) evolutionary tree of trichiurids implies that Aphanopodinae are a grade, with *Diplospinus* being the deepest branch (Tucker 1956: fig. 23). Parin and Becker (1972) removed *Diplospinus* to the 'gempylids', a result supported by Gago (1997, 1998) and our analyses. The core `aphanopodines' are paraphyletic in our morphological analyses as well as those of Gago (1998), but our combined analysis

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supports monophyly of *Aphanopus* + *Benthodesmus,* a result also recovered in previous molecular analyses (Miya *et al*. 2013; Betancur-R *et al*. 2017). In sum, we consistently recover three trichiurid assemblages across our analyses: *Aphanopus* and *Benthodesmus* at the base of Trichiuridae; 'Lepidopodinae', either as the monophyletic sister to trichiurines (in the parsimony analysis) or a paraphyletic grade with respect to trichiurines (in the Bayesian analyses); a monophyletic Trichiurinae (Fig. 12 node E), which falls as the most nested trichiurid clade in the Bayesian analyses. Further morphological and molecular studies should target the relationships of the 'Lepidopodinae', which are particularly unstable.

Placement of London Clay fossils within Trichiuroidea

†*Progempylus* was aligned with 'gempylids' and trichiurids by Casier (1966), who noted its similarity to *Gempylus*. Monsch (2000, 2005) also places †*Progempylus* with 'gempylids' because of its recurved conical teeth. In his unpublished analysis, Monsch (2000: fig. 8.1) recovered †*Progempylus* in a basal polytomy uniting several fossil taxa with Trichiuroidea and a clade containing scombrids and xiphioids. In our analyses, †*Progempylus* is consistently recovered as a 'gempylid'. In the parsimony analysis, †*Progempylus* is recovered near the base of the tree in a clade with *Ruvettus* (supported by: c.10[1], rounded anterior process of subopercle; c.66[1], bifurcation of supraoccipital ridge on the supraoccipital). †*Progempylus* is nested within 'gempylids' in both Bayesian analyses, with no particular relationship to *Ruvettus*. In the morphology analysis, it falls in a clade with *Epinnula*, *Neoepinnula* and NHMUK PV OR 41318. Conversely in the combined analysis maximum clade credibility tree †*Progempylus* is recovered with †*Macroynis*, albeit with very weak support (BPP < 0.5). We consider †*Progempylus* to be a deeply diverging trichiuroid, but can propose no more precise assignment at present.

NHMUK PV OR 41318 has been interpreted as a trichiurid based on association with †*Macroynis* (Casier 1966: 249, fig. 56). Despite this, Casier (1966: 249, fig. 56) describes the morphology of this braincase as intermediate between scombrids (e.g. †*Scombrinus*) and trichiurids (e.g. *Lepidopus*), and Monsch (2005)

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assigned it to 'Gempylidae' *incertae sedis*. In our parsimony analysis (Fig. 12) NHMUK PV OR 41318 is recovered as the sister taxon of *Rexea* (supported by a single homoplastic character: c.61[1], narrowing of frontals above the orbit). NHMUK PV OR 41318 is excluded from the trichiurid crown by character 67[0], as it displays the primitive state of the pterotic ending before the posterior margin of the neurocranium (c. 67[1]: the pterotic extends beyond the posterior margin of the braincase in trichiurids). The braincase shows more general similarities with *Rexea*, including a 'box-like' lateral profile and extension of the supraoccipital crest over the posterior margin of the exoccipitals. NHMUK PV OR 41318 is recovered as sister to †*Progempylus* in our Bayesian morphology analysis (Fig. 13a), and as sister to a clade comprising *Rexea* and other 'gempylids' in our combined analysis (Fig. 14a), although collapses into the 'gempylid' polytomy in the majority-rule consensus tree of both analyses (Figs 13b & 14b). The placement of NHMUK PV OR 41318 outside of the trichiurid clade in phylogenetic analyses supports its historical placement in the paraphyletic 'Gempylidae'. We consider NHMUK PV OR 41318 Trichiuroidea *incertae sedis,* but are confident it can be excluded from Trichiuridae*.*

The specimen renamed here as †*Macroynis* has historically been considered a trichiurid (Leriche 1910; Arambourg and Signeux 1952; Casier 1966; Monsch 2000, 2005), due to its straight serial teeth. Casier (1966) and Monsch (2005) suggested a series of characters tying †*Macroynis* to 'gempylids' and trichiurids more generally: premaxillary fangs (seen elsewhere in *Scombrolabrax* but not scombrids), an elongated skull (typically associated with an elongate body), and a tightly bound maxilla and premaxilla (seen elsewhere in scombrids but not *Scombrolabrax*). Despite this, no formal phylogenetic analyses have been conducted that incorporate either this specimen or †*Eutrichiurides* (with which it was previously associated) more generally. In our parsimony analysis, †*Macroynis* is resolved as highly nested within Trichiuridae as the sister taxon to *Evoxymetopon* (based on the reversal of two highly homoplastic characters). However, this relationship is not upheld in our Bayesian analyses where it is recovered as a 'gempylid' (Bayesian morphology: Fig. 13a; Bayesian combined: Fig. 14a). While this contradicts previous assessments of its placement, this is perhaps unsurprising

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given the limited character information that can be obtained for †*Macroynis.* The highly fragmented braincase of †*Macroynis* results in a large number of uncodeable characters in a morphological matrix that largely targets the braincase, suggesting that its nested position in the parsimony analysis may be due to a "path of least resistance" rather than any meaningful support. However, visual inspection of †*Macroynis* indicates similar jaw proportions to extant trichiurids like *Aphanopus* and *Evoxymetopon,* with the upper jaw extending notably anterior to the braincase and the articulation of the lower jaw behind the midpoint of the orbit. A similar morphology is seen in some elongate 'gempylids' (e.g. *Nesiarchus*, *Diplospinus*, *Paradiplospinus*), in particular those that have previously been either included in (*Diplospinus*: Tucker 1956), or closely associated with, Trichiuridae in the past (Carpenter *et al*. 1995; Gago 1998). †*Macroynis* can be confidently placed in Trichiuroidea, but is of uncertain placement within this group. The morphological analysis suggests a close association with those species with an elongate body plan, either trichiurids or a subset of 'gempylids' sometimes recovered as closely related to trichiurids. However, there is greater uncertainty associated with this placement due to the ambiguities in the relationships of 'gempylids'. As with †*Progempylus*, we consider †*Macroynis* to be *incertae sedis* within Trichiuroidea, but unlike that genus we cannot exclude the possibility of placement within Trichiuridae.

An overview of the fossil record of Trichiuroidea, with comments on the placement of key fossil taxa

Fossil trichiuroids can broadly be categorised in two groups: firstly, those assigned to extant genera; and secondly, those known only from extinct lineages. Extant trichiuroid genera with a fossil record include *Lepidopus* (*L. brevicauda* from the Oligocene of Switzerland, *L. hungaricus* from the Oligocene of Hungary and *L. angustus* from the Oligocene of the Caucasus: Daniltshenko 1980, Dzhafarova, 1988; †*L. lednevi* and †*L. lateralis* from the Miocene of Azerbaijan, †*L. albyi* from the Miocene of Italy and †*L. proargenteus* from the Miocene of Algeria: Arambourg 1927); *Thrysitoides* (†*T. zarathoustrae* from the Eocene of Iran: Arambourg 1943); *Epinnula* (†*E. cancellata* from the Eocene of Iran: Arambourg 1967); and

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Hemithyrsites (†*H. armatus* from the Miocene of Italy: Sauvage 1873; here we follow Monsch and Bannikov 2012 in synonymizing *Hemithyrsites* and *Promethichthys*).

In addition to the taxa described in this paper, trichiuroids assigned to fossil genera include: †*Argestichthys* from the earliest Eocene (Ypresian) of Turkmenistan (Prokofiev 2002); †*Abadzekhia* from the early-late Oligocene (Lower Maikopian-Chattian) of the Caucasus (Bannikov 2005) and Germany (Bannikov 2010); †*Chelifichthys* from the late Miocene (Messinian) of Algeria (Carnevale 2006); †*Anenchelum* from the middle Eocene-early Miocene of Europe; †*Eutrichiurides* from the early Oligocene (Rupelian) of Belgium (we refer to skeletal remains only; isolated teeth attributed to the genus are more widespread but their attributions are questionable) and †*Musculopedunculus* from the early Oligocene (Rupelian) of Germany (Parin and Astakhov 2007). Although several of these genera are represented by near-complete fossils, lateral compression and associated concealment of the braincase and gill arches means that relatively few morphological characters can be scored. Below, we comment on possible placements of these genera based on previously published descriptions and character optimisations (Becket et al. 2018, S4) from our phylogenetic analyses. Several as-yet undescribed Eocene trichiuroids have been figured in the literature (Bonde *et al*. 2008; Zorzin *et al*. 2011; Giusberti *et al*. 2014), but published photographs reveal too little detail to meaningfully comment on their placements.

†*Argestichthys* is the oldest described trichiuroid body fossil (Prokofiev 2002). Prokofiev noted a series of primitive features shared by †*Argestichthys* and gempylids, and argued for a similar insertion pattern of anal-fin pterygiophores in the genus and *Ruvettus* (questioned by Monsch and Bannikov 2012: 264). However, Prokofiev later suggested that †*Argestichthys* shows "proximity to the generalised ancestor of Trichiuridae" (Prokofiev 2002: 233), implying a position on the trichiurid stem. Monsch and Bannikov (2012) classify †*Argestichthys* as Trichiuroidea *incertae sedis*, but tentatively place it as a stem trichiurid in their composite tree. Anteriorly directed symphysial canines on the premaxilla (Johnson 1986) and a short ascending process of the premaxilla (c.18[0]; also present in scombrids) are evidence for a trichiuroid placement of †*Argestichthys*. However the

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postmaxillary process is not well developed (c.21[0]), unlike the condition in trichiuroids but similar to that of outgroups. The reduced supraoccipital crest (c.63[1]) is found in 'gempylids' excluding *Lepidocybium* and *Ruvettus*, however the distribution among trichiurids is more complex, with a reversal in *Assurger*, *Eupleurogrammus*, *Evoxymetopon* and *Lepidopus*. Spine-like external elements of the pelvic-fin spine restrict †*Argestichthys* to outside Trichiuridae + (*Diplospinus* + *Paradiplospinus*)) (c.91[0]; they are scale-like in Trichiuridae + (*Diplospinus* + *Paradiplospinus*)). This combination of primitive characters suggest †*Argestichthys* is a very deeply diverging member of crown Trichiuroidea, or possibly even on the trichiuroid stem.

†*Abadzekhia* has been assigned to 'Gempylidae' (Bannikov 1985; Bannikov and Fedotov 1989), close to *Tongaichthys*, *Thyrsitops*, *Ruvettus* and *Lepidocybium* (Bannikov 2005). It can be placed within Trichiuroidea on the basis of the short ascending process of the premaxilla (c.18[0]; also seen in scombrids), and a low but distinct postmaxillary process (Bannikov 2017) (c.21[0]; a well developed process is a synapomorphy of Trichiuroidea). Within the trichiuroids, †*Abadzekhia* can be further constrained outside of Trichiuridae + (*Diplospinus* + *Paradiplospinus*)) based on the absence of two non-homoplastic characters which support this clade: two radials are reported in the soft dorsal fin pterygiophores by Bannikov (2005) (c.101[0]; three are seen in Trichiuridae although given the size of the additional radial (Johnson 1986: Ch. 30) it is difficult to distinguish genuine absence from taphonomic loss in fossils) and the external elements of the pelvic-fin are spine-like (c.91[0] they are scale like in Trichiuridae + (*Diplospinus* + *Paradiplospinus*)).

†*Chelifichthys* was assigned to 'Gempylidae' by Carnevale (2006), and described as closely related to *Nealotus*, *Hemithyrsites*, *Rexea* and *Rexichthys.* It cannot be evaluated for any of the synapomorphies that support Trichiuroidea, however it has a moderately sized supraoccipital crest (c.63[1]; found in 'gempylids' excluding *Lepidocybium* and *Ruvettus*; trichiurids are characterised by further reduction of the crest, c.63[2]). †*Chelifichthys* also has a preopercle that is widest at the angle of the bone (c.5[0]), which excludes it from the clade comprising *Nesiarchus* + ((*Diplospinus* + *Paradiplospinus*) + Trichiuridae). †*Chelifichthys*

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shows a weakly splintered preopercle (c.1[0]) and two radials in the soft dorsal fin pterygiophores (c.101[0]; Carnevale 2006: fig. 4C; see caveats above for fossils in discussion of †*Abadzekhia*), two primitive features that show derived states in Trichiuridae. Limitations in preserved anatomy preclude precise placement within Trichiuroidea but †*Chelifichthys* can be placed within the 'gempylid'-grade in a position more closely related to trichiurids than *Lepidocybium* and *Ruvettus*, but outside of the clade comprising *Nesiarchus*, *Diplospinus*, *Paradiplospinus*, and Trichiuridae.

The oldest body fossil associated with trichiurids is a specimen similar to †*Anenchelum* from the Ypresian of Monte Solane, Italy (Zorzin *et al*. 2011) that shows the elongate body plan associated with trichiurids. †*Anenchelum* itself is known from a number of sites, with nominal species ranging in age from Eocene to Miocene. The taxonomic history of †*Anenchelum* is complicated, largely due to reclassification of species between this genus and the extant *Lepidopus*. Woodward (1901) synonomised these two genera, but Bannikov and Parin (1995) upheld the validity of †*Anenchelum* and recognised the following species: the type †*Anenchelum glarisianum* (Blainville 1818) from several deposits of Oligocene age; †*Anenchelum eocaenicus* (Daniltshenko 1962) from the middle Eocene of Georgia; †*Anenchelum paucivertebrale* from the middle Eocene of the Northern Caucasus (Bannikov and Parin 1995); †*Anenchelum angustum* (Daniltshenko, 1980) from the early Oligocene of the Caucasus and †*Anenchelum lednevi* (Menner 1949) from the early Miocene (Upper Maikopian) of Caucasus. These authors also suggest that the Oligocene *Lepidopus hungaricus* and *L. brevicauda* might belong to †*Anenchelum*. Many of the diagnostic features of †*Anenchelum* are admittedly generalised trichiuirid characters (Bannikov and Parin 1995: 186).

Most species of †*Anenchelum* are poorly known, or descriptions are largely meristic counts with few details of the skull, so here we restrict consideration to the most completely described species: †*A. paucivertebrale* and †*A. glarisianum* (Bannikov and Parin 1995; Gregorova 2010). Bannikov and Parin (1995) consider †*A. paucivertebrale* to be the ancestor of 'Aphanopodinae' and 'Lepidopodinae', effectively suggesting a placement close to the crown trichiurid node. †*A.*

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paucivertebrale can be placed within Trichiurioidea due to the short ascending process of the premaxilla (c.18[1]) and the presence of fangs on the premaxilla (Johnson 1986). As noted by Bannikov and Parin (1995) it shows a differentiated soft and spinous portion of the dorsal fin (c.99[0]; a primitive feature retained by 'gempylids' + *Aphanopus* and *Benthodesmus*). The preopercle is widest opposite the dorsal arm (c.5[1]; observed in trichiurids, *Diplospinus* + *Paradiplospinus*, *Nesiarchus*). No epineurals are observed in the material (Bannikov and Parin 1995; c.98[2]; the absence of epineurals is a trichiurid synapomorphy). The caudal complex is well developed (c.107[0]; seen in 'gempylids', 'Aphanopodinae', and 'Lepidopodinae'). †*A. paucivertebrale* also has a slightly lower vertebral count (c.76: Bannikov and Parin 1995) than extant Trichiuridae (typically around 100: Nakamura and Parin 1993), but higher than even the longest 'gempylids' (*Paradiplospinus*: 60-64). Collectively, these features suggest a position on the trichiurid stem. †*A. glarisianum* has a more typical vertebral count for a trichiurid (110; c.95[2]), and shows three derived features of trichiurids in its opercular series: the opercular series is strongly fimbriate (c.1[1]), the posterior opercular spine is absent (c.6[0]), and the anterior process of the subopercle is rounded (c.10[1]). It can also be excluded from the Trichiurinae + Lepidopodinae based on the presence of a notch between the soft and spinous portions of the dorsal fin (c.99[0]). While it is clear that the affinities of †*Anenchelum* lie with Trichiuridae, it is less clear whether its constituent species form a clade given the meristic variation observed in the putative genus.

†*Musculopedunculus* was previously assigned to Trichiuridae by Parin and Ashakhov (2007). Within the context of the synapomorphy scheme generated by the present study, the genus can be constrained within Trichiuroidea based on the short ascending process of the premaxilla (c.18[0]). An elongate body form with a high number of vertebrae (c.95[2]) and the absence of attached epineurals and epicentrals in the caudal region (c.98[2]) place it in Trichiuridae. The presence of a flexed ultimate centrum forming a urostyle (c.108[0]), observed in †*Musculopedunculus,* is seen in all trichiuroids with the exception of *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps* and *Trichiurus*. Additionally

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†*Musculopedunculus* shows no division between the spinous and soft parts of the fin (c.99[1]), seen in all trichiurids apart from *Aphanopus* and *Benthodesmus.* A well-developed supraoccipital crest (c.63[0]) suggests placement within the Lepidopodinae. †*Musculopedunculus* also shows a well-developed caudal fin, which limits its placement within Trichiuridae to outside of Trichiurinae. †*Musculopedunculus* is therefore considered a crown trichiurid.

†*Eutrichiurides delheidi,* from the Boom Clay of Belgium, is the type species of the genus, and is represented by a premaxilla, dentary and teeth. The premaxilla shows a fang, seen in *Scombrolabrax* and trichiuroids (Johnson 1986), but no other characters exclusive to trichiuroids are apparent. Within trichiuroids, the dentary shows an anteroventral projection at the tip of the jaws as seen in the trichiurids *Assurger* and *Evoxymetopon*. Based on this admittedly scant evidence, we consider †*Eutrichiurides delheidi* Trichiuroidea *incertae sedis*.

These body fossils show that probable 'gempylids' appear in the geological record (†*Argestichthys*) before anatomically primitive trichiurids (†*Anenchelum,* including the undescribed specimen). This pattern is consistent with the sequence of evolutionary origins implied by past morphological and molecular analyses that reconstruct 'gempylids' as a grade (Collette *et al*. 1984; Johnson 1986; Pothoff *et al*. 1986; Carpenter *et al*. 1995; Orrell *et al*. 2006; Miya *et al*. 2013; Near *et al*. 2013), as well as with our own results. Formal assessment of trichiuroid body fossils requires a molecular dataset with broad sampling across the trichiuroids, in addition to an improved morphological dataset, with particular focus on characters not pertaining to the braincase. Lacking new specimens, future work on placing fossil trichiuroid taxa should target well-preserved or geologically older specimens, especially those that are as yet undescribed (e.g. Zorzin *et al*. 2011).

Conclusions

Computed tomography has revealed novel character information for †*Macroynis casieri,* †*Progempylus edwardsi* and NHMUK PV OR 41318, allowing these fossils to be coded into a matrix of Recent taxa and phylogenetically assessed for the first

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time. In these phylogenetic analyses trichiurids are consistently resolved as a monophyletic group nested within a paraphyletic grade of 'gempylids', and we support the term Trichiuroidea for the group as a whole. †*Progempylus edwardsi* is recovered as deeply nested within Trichiuroidea within the 'gempylid'-grade. The isolated braincase previously associated with 'gempylids', NHMUK PV OR 41318, is recovered within the 'gempylid' grade, sometimes in association with *Rexea.* NHMUK PV P26904 is reassigned from †*Eutrichiurides winkleri* to the new genus and species †*Macroynis casieri* and considered Trichiuroidea *incertae sedis.* Laterally compressed body fossils associated with Trichiuroidea are informally placed based on characters within the clade.

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Data Archiving Statement

Data for this study, including a Mimics file, .vol file and .ply files are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.7722q.

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/C034514B-7532-44D0-AA59-D9D687A4CC9F.

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Fig. 1. Photographs of the fossil specimens (**A**) †*Progempylus edwardsi* (NHMUK PV OR 32388), (**B**) NHMUK PV 0R 41318, and (**C**) NHMUK PV P26904. Scale bars: 10 mm.

Fig. 2. The braincase of †*Progempylus edwardsi* (NHMUK PV OR 32388); specimen photograph (**A**) and drawing (**B**) in dorsal view, rendering (**C**) and drawing (**D**) in lateral view, rendering (**E**) and drawing (**F**) in ventral view. Scale bar: 10 mm.

Fig. 3. The braincase of †*Progempylus edwardsi* (NHMUK PV OR 32388), renderings in: (**A**) dorsal view, (**B**) lateral view, and (**C**) ventral view. Scale bar: 10 mm. bas - basisphenoid, boc - basioccipital, epo - epiotic, exo - exoccipitals, f.ic - foramen for internal carotid, fr - frontal, int - intercalar, lat.com - lateral commissure, l.et - lateral ethmoid, mes - mesethmoid, na - nasal, par - parietal, psp - parasphenoid, pto - pterotic, s.c.p.1-3 - supraorbital canal pores 1-3, soc - supraoccipital, spo - sphenotic, tfc - trigeminal facial chamber, vo - vomer.

Fig. 4. †*Progempylus edwardsi* (NHMUK PV OR 32388); rendering (**A**) and drawing (**B**) of the jaws in left lateral view, rendering (**C**) and drawing (**D**) of the suspensorium in left lateral view, rendering (**E**) and drawing (**F**) of the hyoid arch in left lateral view. Scale bars: 10 mm. a.cer - anterior ceratohyal, art - articular, br - branchiostegal, den - dentary, d.hy - dorsal hypohyal, ecp - ectopterygoid, enp - endopterygoid, hyo - hyomandibula, mpt - metapterygoid, pal - palatine, p.cer - posterior ceratohyal, sym - symplectic, qu - quadrate, v.hy - ventral hypohyal.

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Fig. 5. Dorsal view of the gill arches of †*Progempylus edwardsi* (NHMUK PV OR 32388); rendering (**A**) and drawing (**B)**. Scale bar: 10 mm. cb - ceratobranchial, eb - epibranchial, hb - hypobranchial, pb - pharyngobranchial, u - urohyal.

Fig. 6. Left lateral view of the opercular series of †*Progempylus edwardsi* (NHMUK PV OR 32388); rendering (**A**) and drawing (**B**). Scale bar: 10 mm. op - operculum, pop - preoperculum, sop - suboperculum.

Fig. 7. The braincase of NHMUK PV OR 41318 (Gempylidae *incertae sedis*); photographs in; (**A**) dorsal view, (**B**) lateral view, (**C**) ventral view. Scale bar: 10 mm.

Fig. 8. The braincase of NHMUK PV OR 41318 (Gempylidae *incertae sedis*), drawings in; (**A**) dorsal view, (**B**) lateral view, and (**C**) ventral view. Scale bar: 10 mm. boc - basioccipital, epo - epiotic, exo - exoccipitals, f.ic - foramen for internal carotid, f.nX - foramen for the vagus nerve (X), fr - frontal, int - intercalar, lat.com - lateral commissure, l.et - lateral ethmoid, mes - mesethmoid, na - nasal, par - parietal, pro - prootic, psp - parasphenoid, pto - pterotic, s.c.p - supraorbital canal pore, soc - supraoccipital, spo - sphenotic, tfc - trigeminal facial chamber, vo - vomer.

Fig. 9. Photographs of the skull of †*Macroynis casieri* (NHMUK PV P26904) in: (**A**) right lateral view, (**B**) left lateral view, (**C**) dorsal view, (**D**) ventral view. Scale bar: 10 mm.

Fig. 10. The braincase of †*Macroynis casieri* (NHMUK PV P26904); rendering (**A**) and drawing (**B**) in dorsal view, rendering (**C**) and drawing (**D**) in lateral view, rendering (**E**) and drawing (**F**) in ventral view. Scale bar: 10 mm. boc - basioccipital, fr - frontals, l.et - lateral ethmoid, mes - mesethmoid, psp - parasphenoid, vo - vomer.

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Fig. 11. †*Macroynis casieri* (NHMUK PV P26904); rendering (**A**) and drawing (**B**) of the jaws in right lateral view, rendering (**C**) and drawing (**D**) of the suspensorium in right lateral view, rendering (**E**) and drawing (**F**) of the hyoid arch in right lateral view. Scale bars: 10 mm. a.cer - anterior ceratohyal, art - articular, c.w - ceratohyal window, den - dentary, d.hy - dorsal hypohyal, enp - endopterygoid, hyo - hyomandibula, lac - lacrimal, mx - maxilla, pal - palatine, p.cer - posterior ceratohyal, pmx - premaxilla, sym - symplectic, qu - quadrate, v.hy - ventral hypohyal.

Fig. 12. Relationships of Trichiuroidea based on parsimony analysis of morphological data. Strict consensus of 3 most parsimonious trees with tree length = 434 steps. Numbers below nodes represent Bremer Decay Indices. Circles at nodes indicate bootstrap support values. Fossil taxa in bold. 'Ap.' - 'Aphanopodinae'. Trichiurinae as indicated here follows Gago (1998), with the addition of *Tentoriceps* and *Eupleurogrammus*, which are always recovered in this clade. Letters at nodes indicate selected character changes with a CI of 1, for remaining characters see Becket et al. (2018, S4); A –18[1], short ascending process of the premaxilla; 86[1], elongate dorsal articular process of cleithrum; B – 53[1], two pairs of teeth on the vomer; C – 4[1], concave posterodorsal margin of the preopercle; 91[1], scale-like external spinous elements of pelvic fin; 113[1], small hypural notch; D – 1[1] posterior margin of opercular series strongly splintered or fimbriate; 58[1] lateral bony tubular extension of supraorbital lateral-line canal to orbital rim; 67[1] pterotic ends well past the posterior margin of the neurocranium; 83[1] posteroventral plate on coracoid present; 96[1], first neural spine distally bifurcate; 101[1], proximal, middle and distal radials in soft dorsal-fin pterygiophores; 117[1], median caudal cartilage present; E – 30[1], anterodorsal corner of ceratohyal pointed; 36[2], articular head of first basibranchial knob-like and bearing dorsolateral processes; 78[2], anteroventral process of posttemporal separate from poteroventral process; 103[1], foramen at anterioventral corner between the proximal and distal portions of the dorsal-fin proximal radials present; 106[1], anal-fin pterygiophores fused to form a single unit; 108[1], ultimate centrum not flexed.

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Fig. 13. Relationships of Trichiuroidea based on (**A**) the maximum clade credibility tree and (**B**) the majority-rule consensus tree from the Bayesian analysis of the morphological dataset. Circles at nodes indicate Bayesian posterior probabilities above 0.5. Starred nodes are enforced. Fossil taxa in bold.

Fig. 14. Relationships of Trichiuroidea based on (**A**) the maximum clade credibility tree and (**B**) the majority-rule consensus tree from the Bayesian analysis of the combined morphology and molecular dataset (mitochondrial data from Miya et al. 2013). Circles at nodes indicate Bayesian posterior probabilities above 0.5. Starred nodes are enforced. Fossil taxa in bold.

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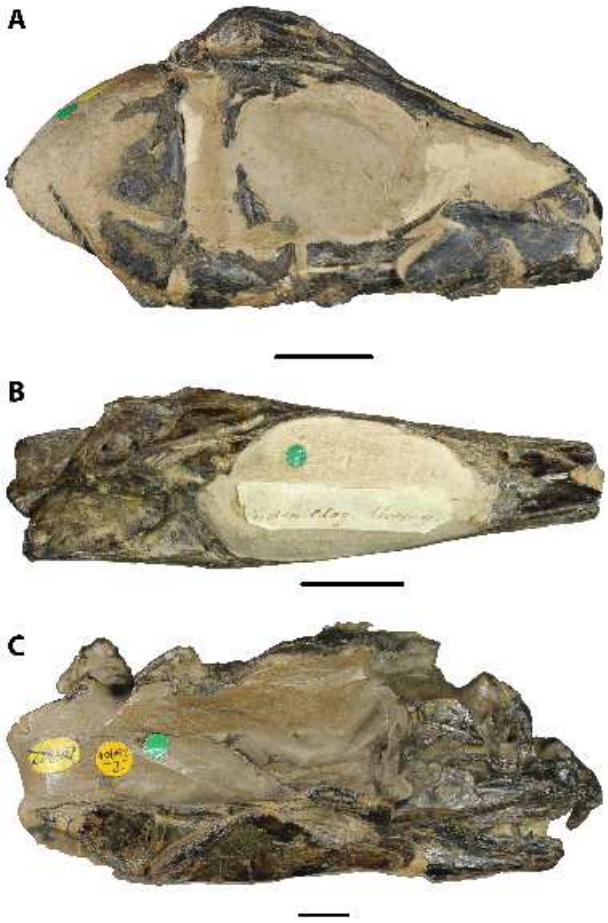

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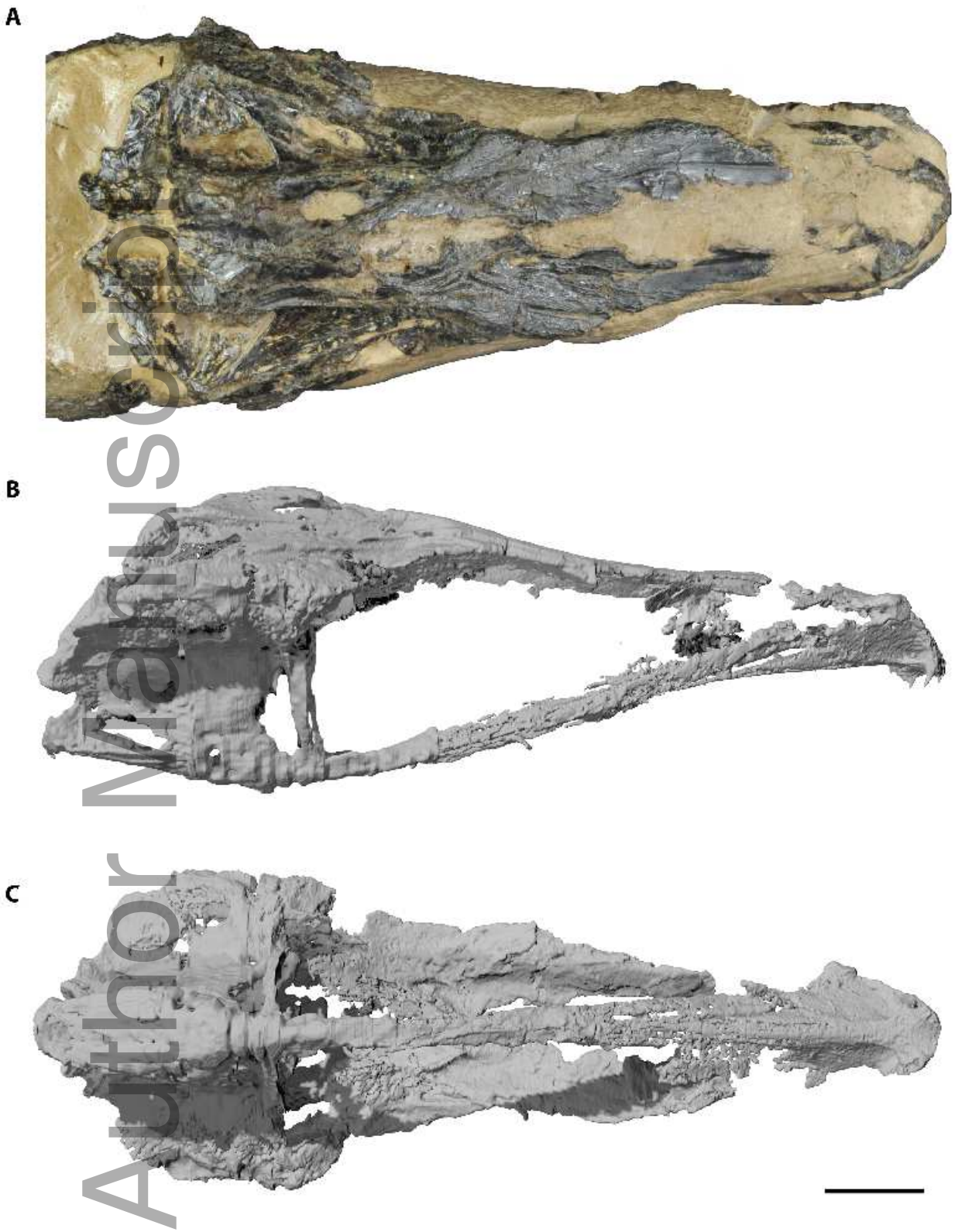

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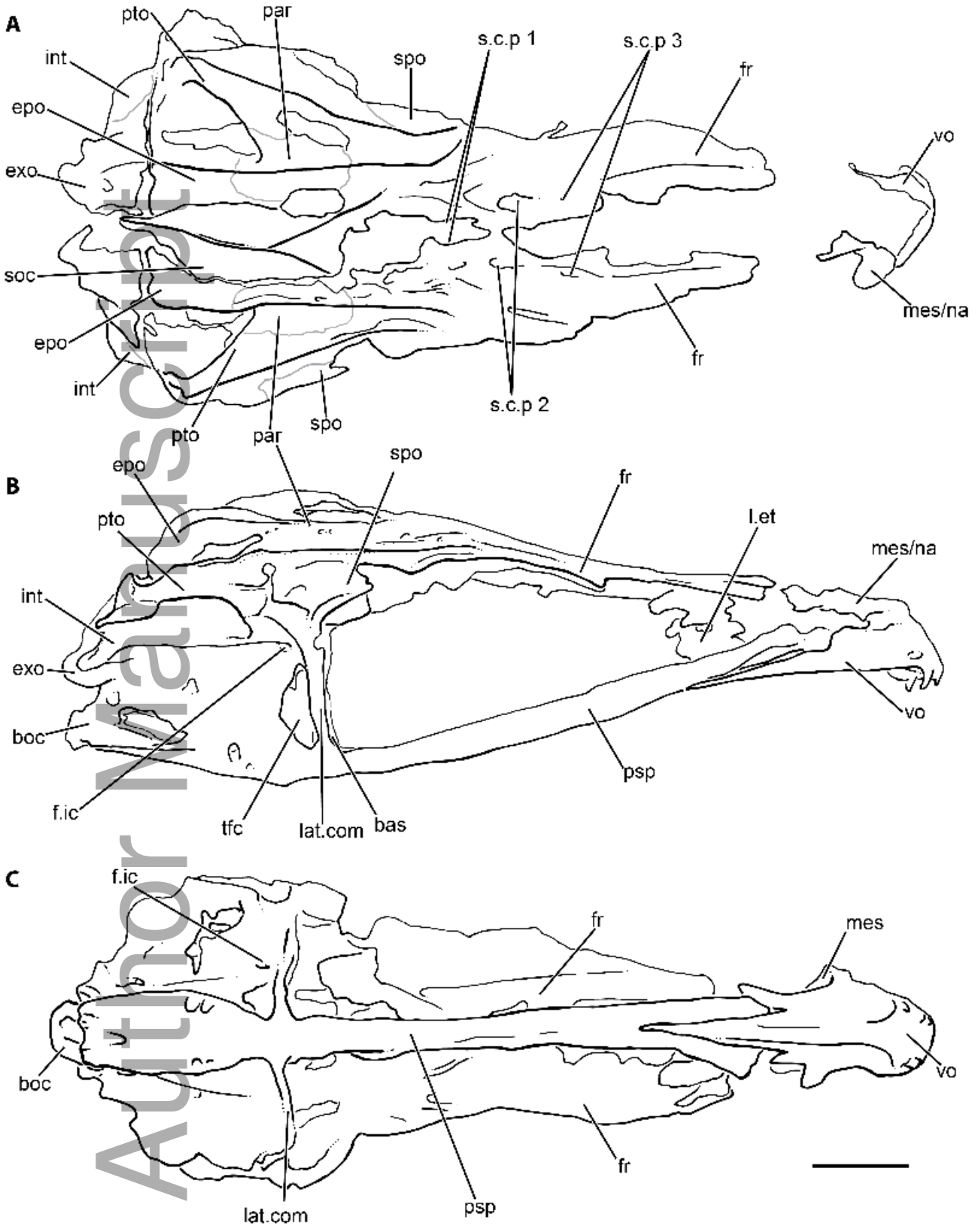

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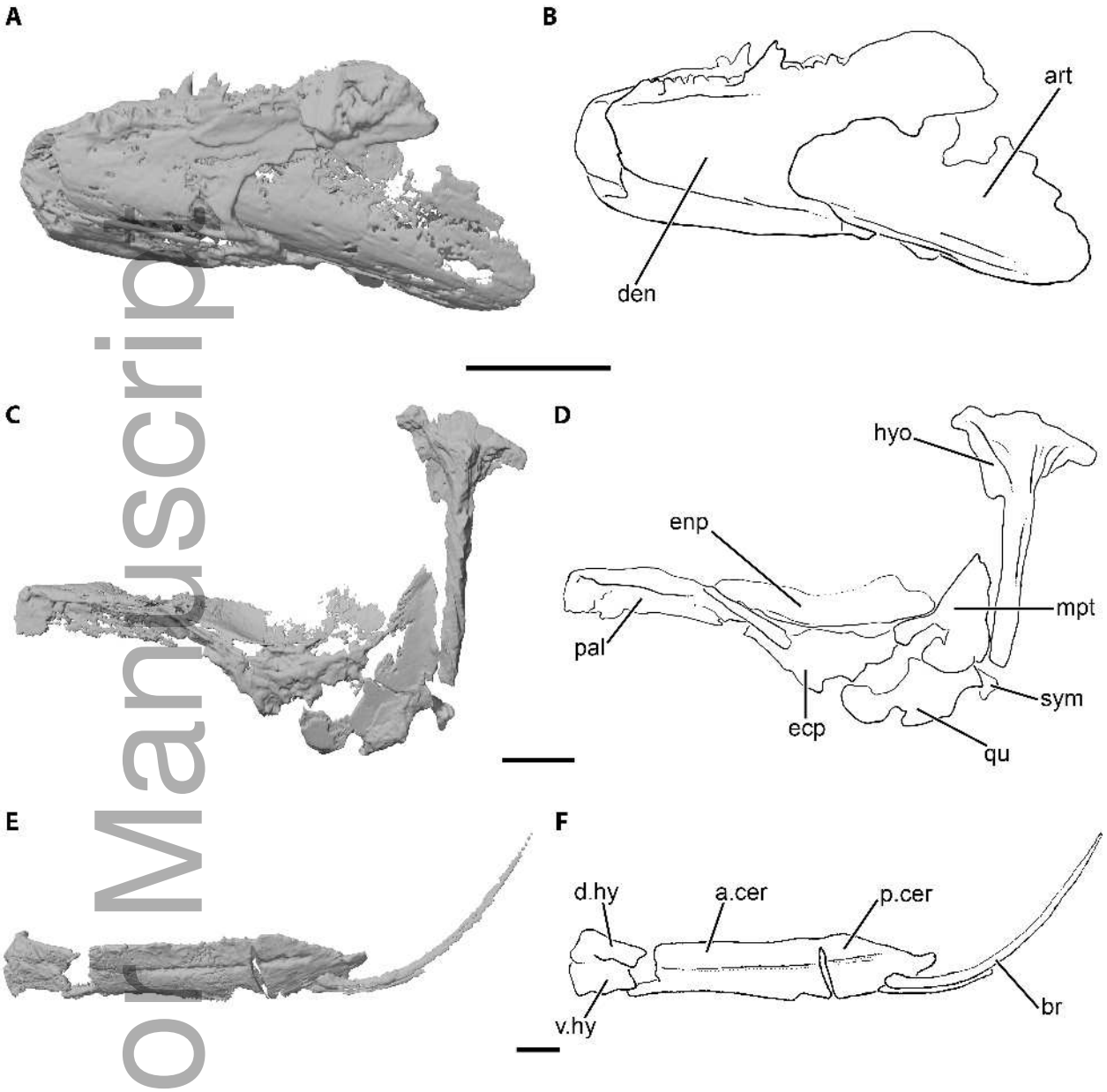

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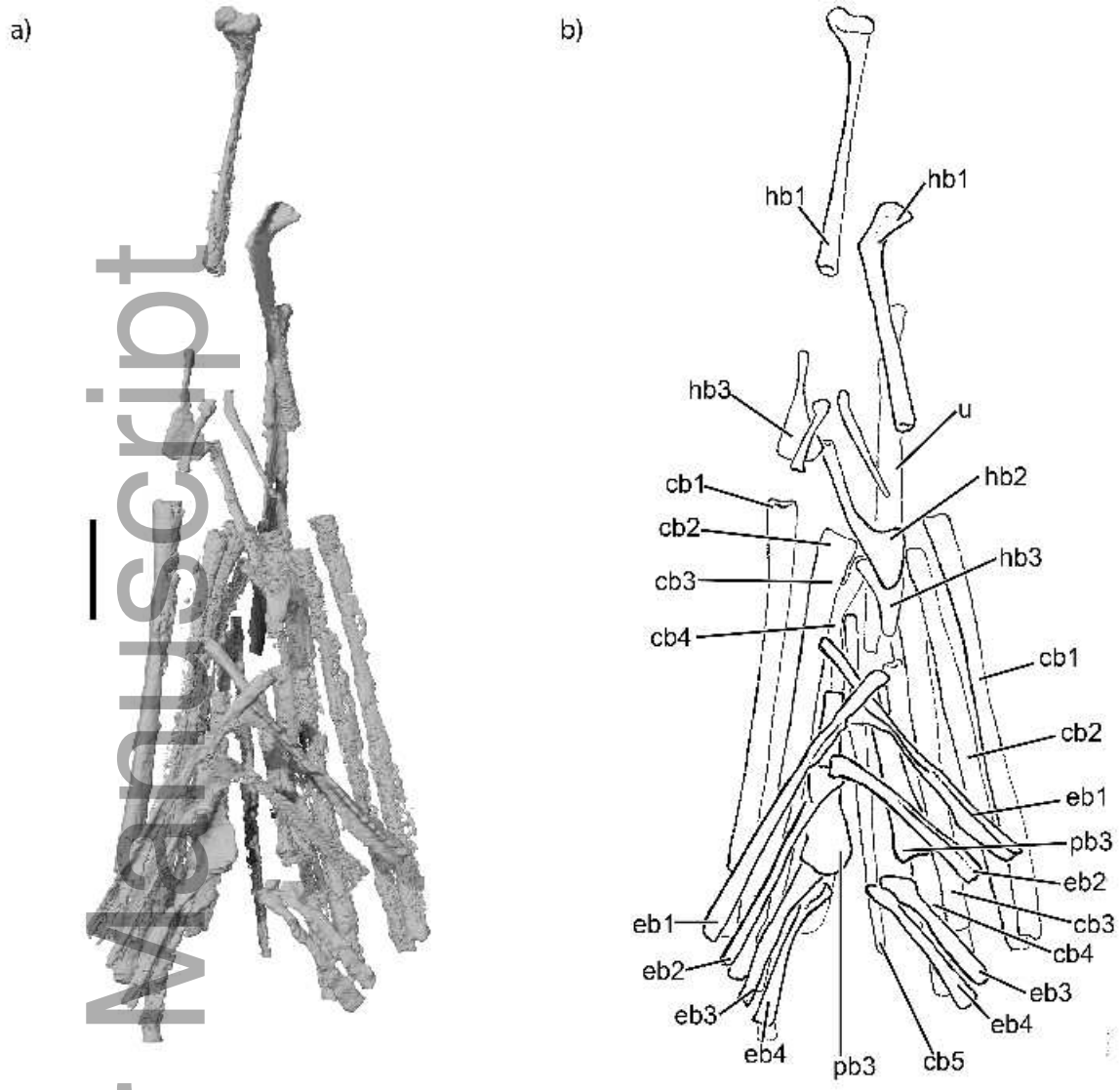

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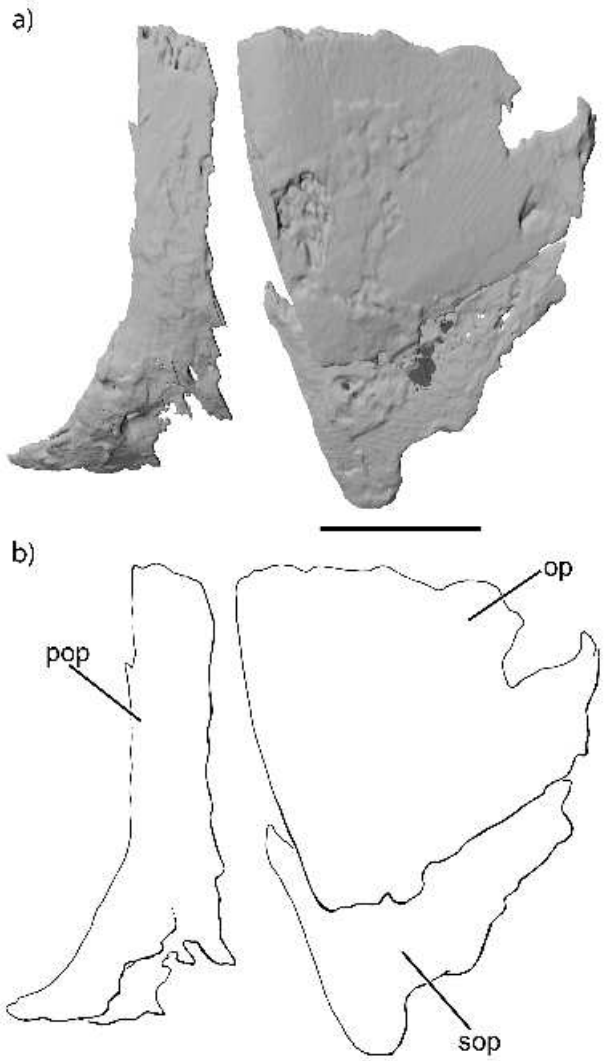

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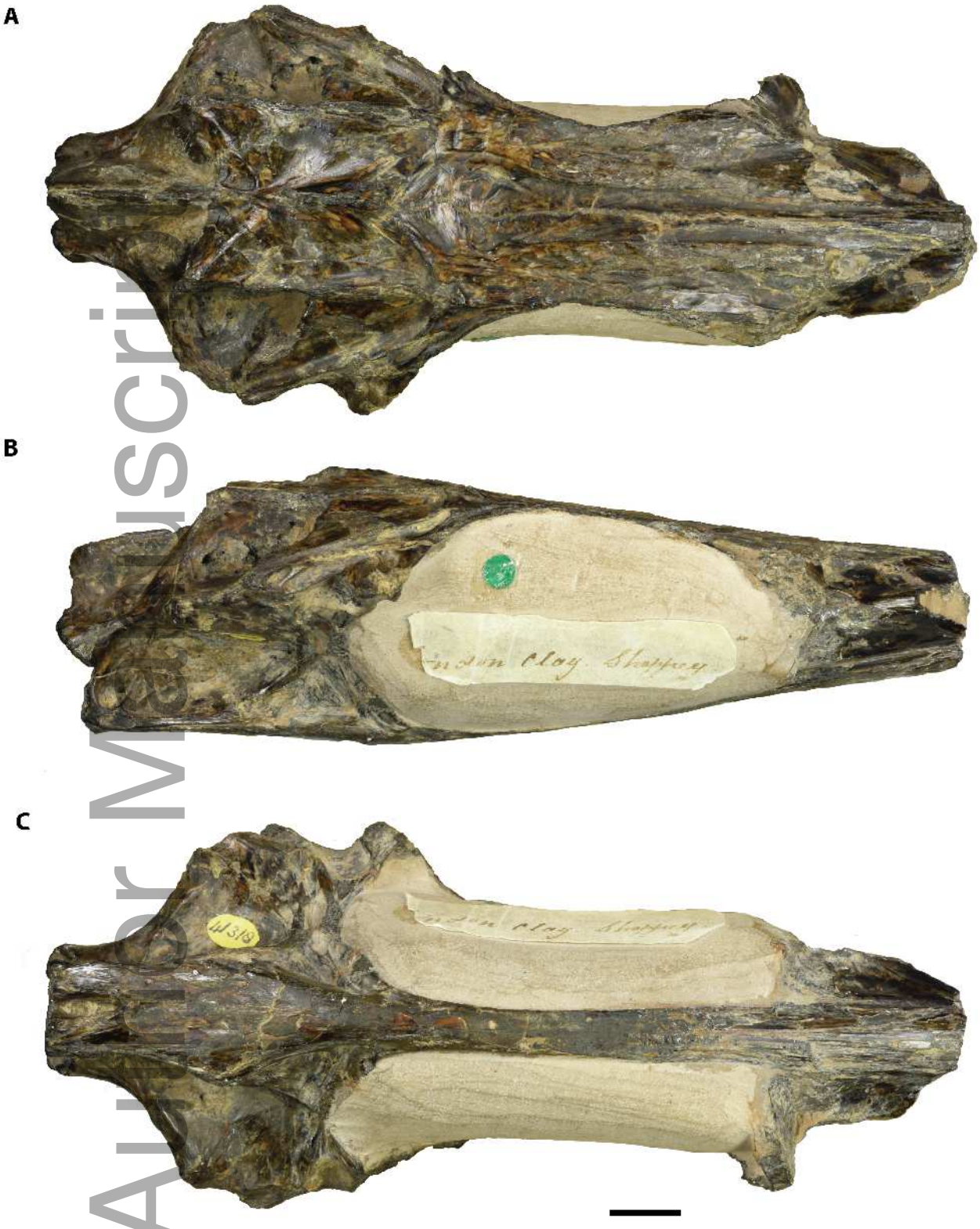

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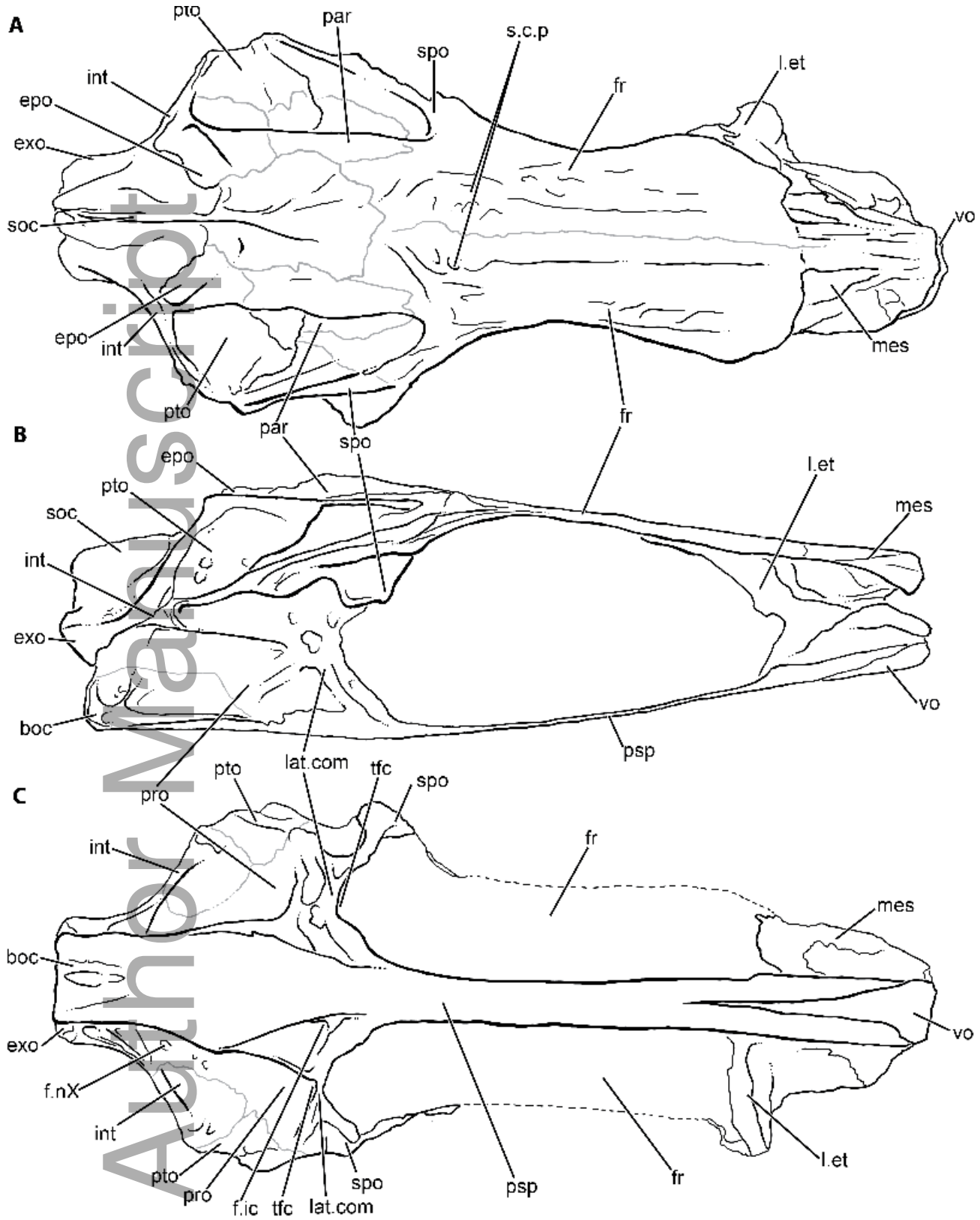

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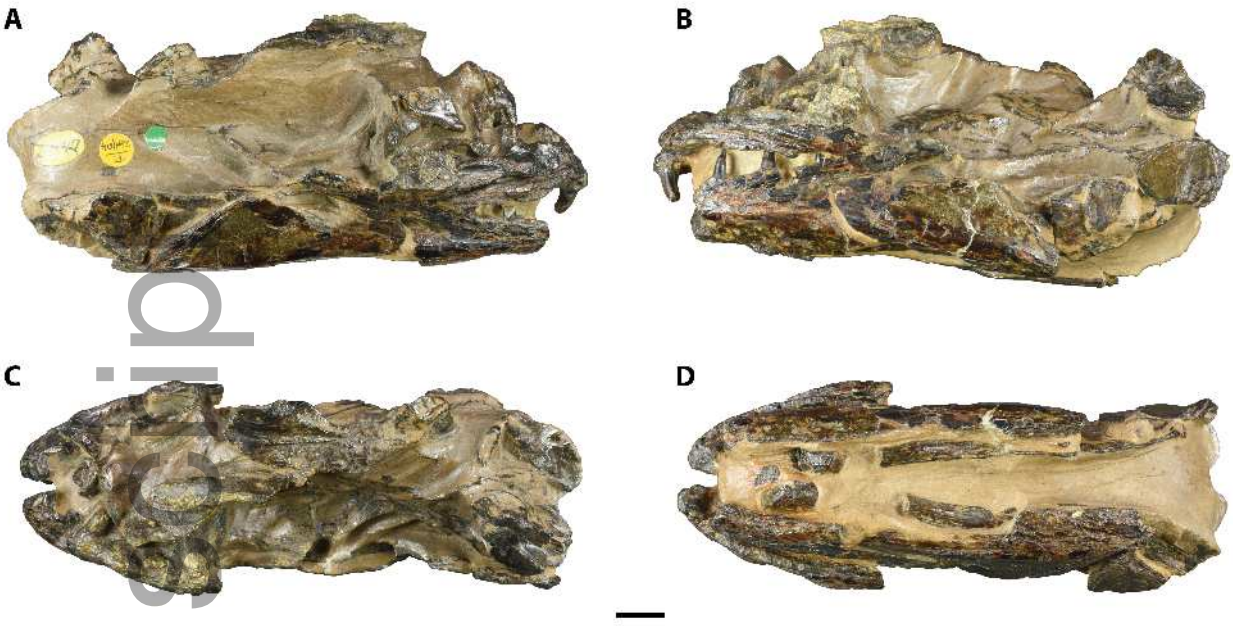

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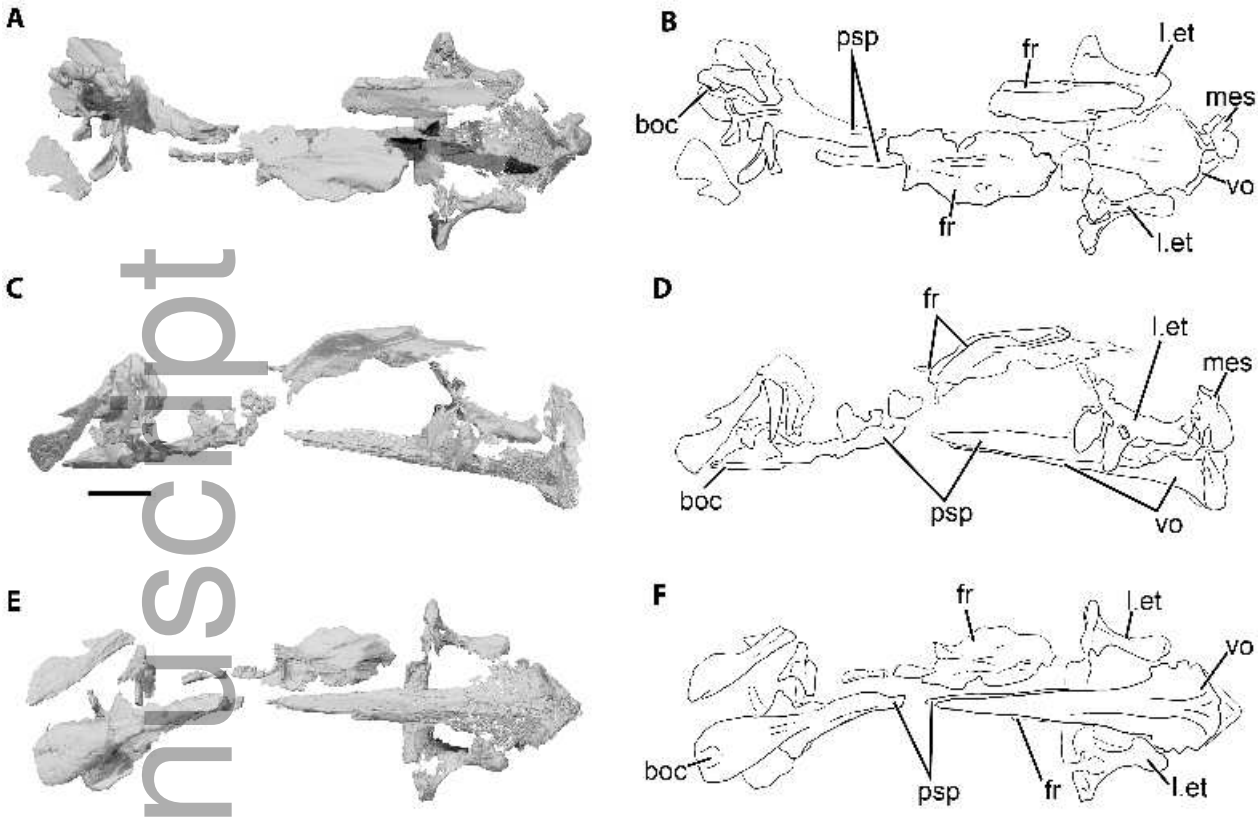

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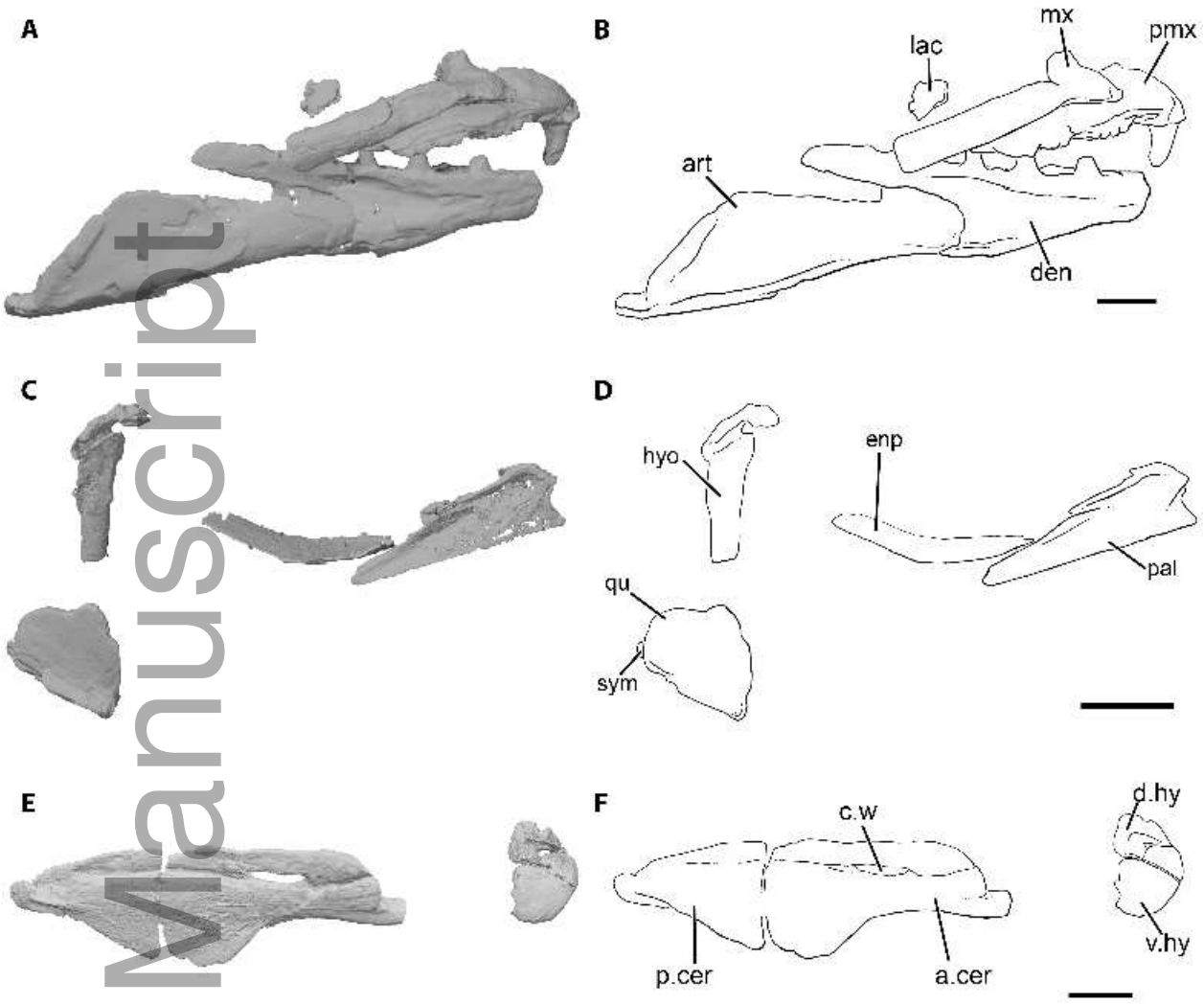

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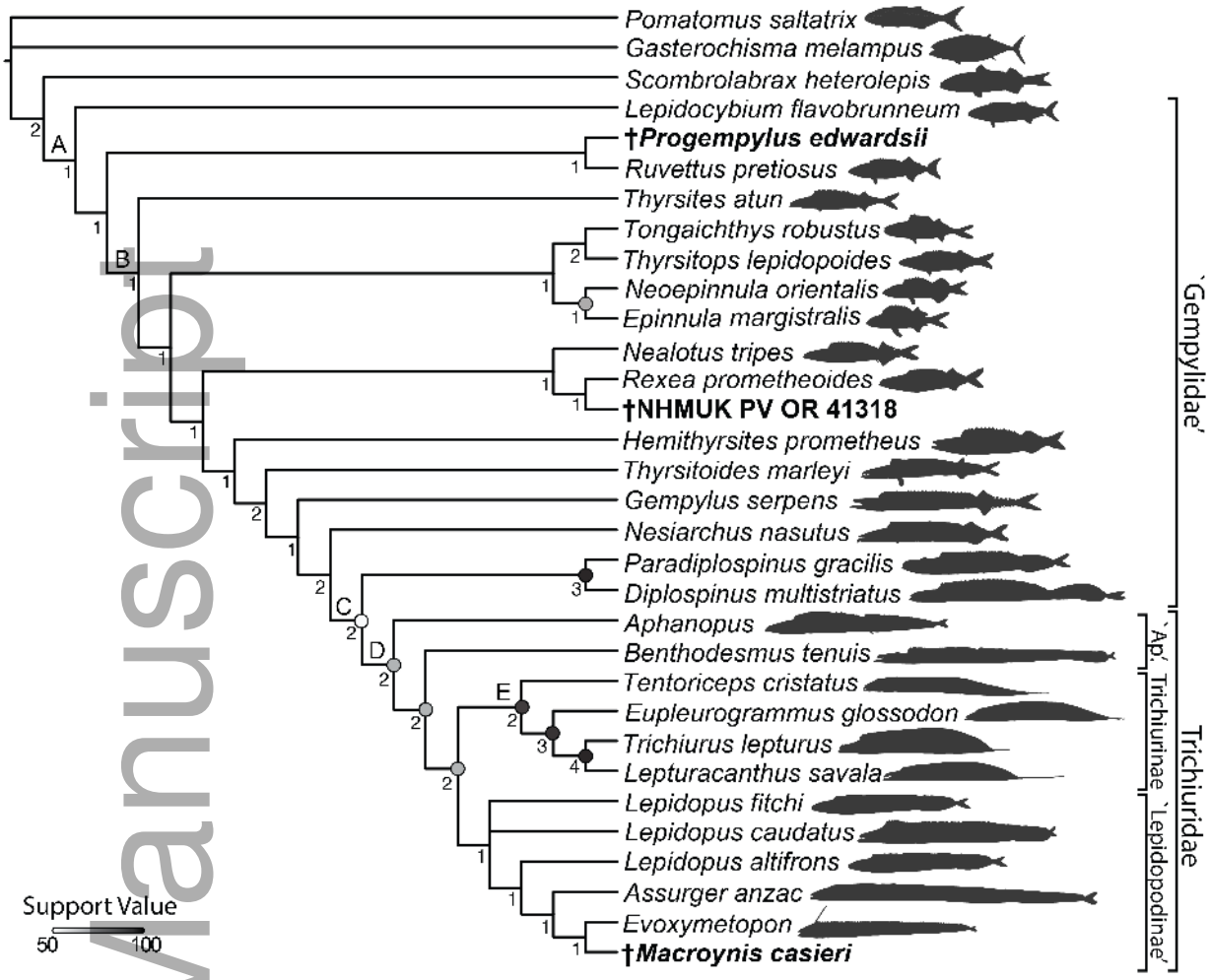

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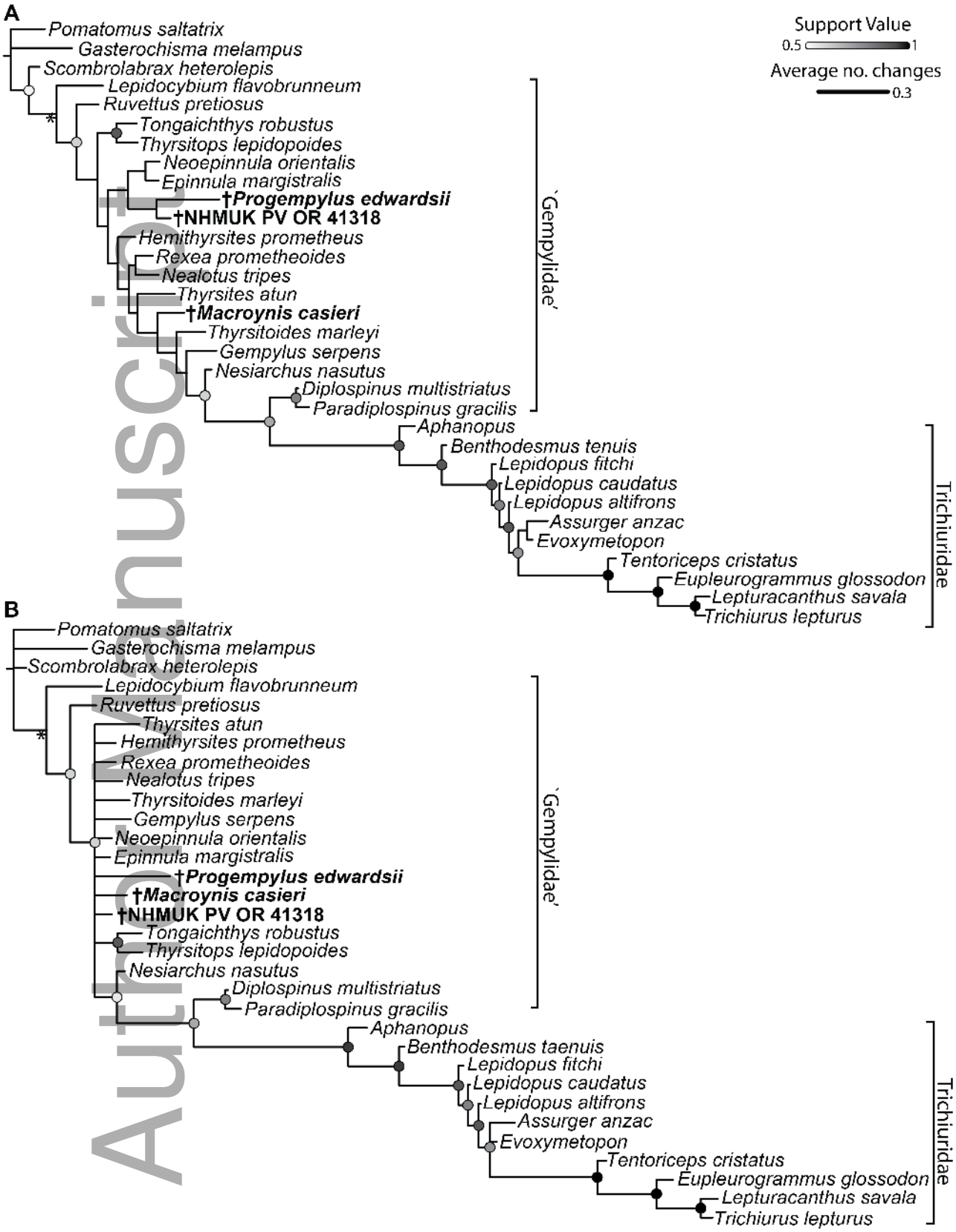

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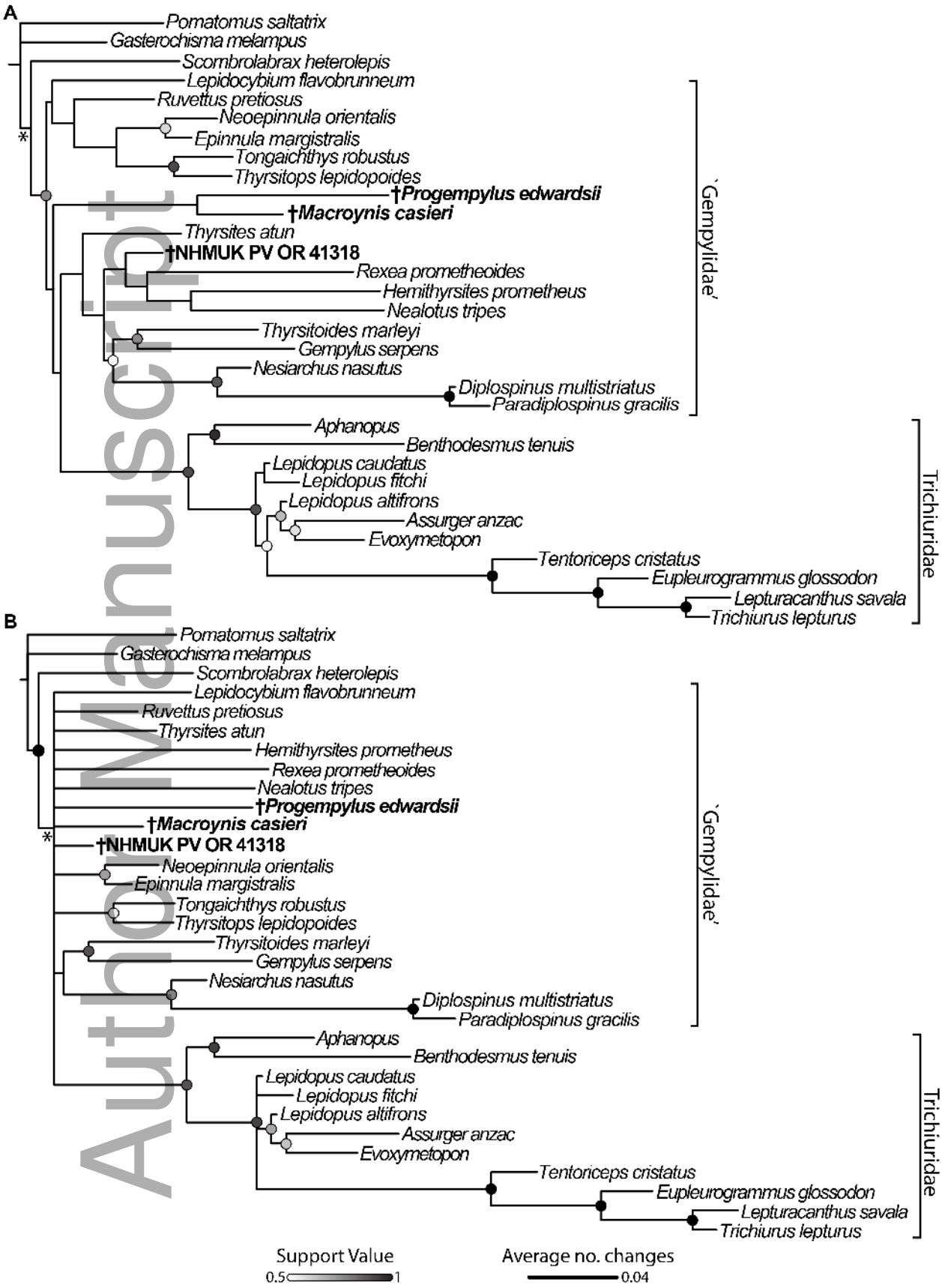

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