

## First occurrence of a †coccolepidid fish (?Chondrostei: †Coccolepididae) from the Upper Lias (Toarcian, Early Jurassic) of southern Germany

Samuel L.A. Cooper, Adriana López-Arbarello, and Erin E. Maxwell

### ABSTRACT

The non-neopterygian group †Coccolepididae, a moderately diverse predominantly freshwater family, remains an imperfectly known Mesozoic group of actinopterygians, currently classified within Chondrostei based on the presence of several acipenseriform synapomorphies. Coccolepidids first appear during the Early Jurassic in marine sediments, although their fossils are poorly known from this time, and none have yet been described from the Toarcian (Upper Lias). Here, we describe a new genus and species of coccolepidid fish, †*Toarcocephalus morlok* gen. et sp. nov. from the Lower Jurassic (Toarcian) Posidonienschiefer Formation of Holzmaden in southern Germany. †*Toarcocephalus morlok* is diagnosed by a unique combination of characters including a shallow lower jaw with a massive angular, opercle and subopercle equal in size, preopercle that only borders the subopercle but does not reach the opercle; dermal skull bones strongly punctate, with externally smooth upper and lower jaw bones. Discovery of a coccolepidid at Holzmaden represents the first occurrence of the group from a Toarcian deposit, as well as the oldest record of the family in mainland Europe. Both described specimens of †*T. morlok* were victims of successful predation events: one individual was likely decapitated (pabulite) and the other preserved within a regurgitalite (fossilized oral ejecta). The evolution of Coccolepididae is discussed briefly in relation to a marine/freshwater origin.

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## INTRODUCTION

†Coccolepididae (sensu López-Arbarello et al., 2013) is an enigmatic family of early actinopterygians with still debatable phylogenetic relationships. Historically, coccolepidids were lumped within the obsolete polyphyletic ‘palaeoniscoids’ because of their supposed conservative skeletons (e.g., Woodward, 1890a, 1891; Gardiner, 1960, 1967, 1993; Kirkland, 1998). Recent revision of the family Coccolepididae has identified key anatomical synapomorphies with the monophyletic Acipenseriformes (López-Arbarello et al., 2013), thus proposing the placement of the family within the monophyletic Chondrostei, a clade comprising the living sturgeons (Acipenseridae) and paddlefishes (Polyodontidae), as well as extinct relatives, including †Peipiaostidae, †Chondrosteidae, and †Birgeriidae (Grande and Bemis, 1996; Hilton et al., 2004; Hilton and Forey, 2009). This has led many authors to propose the combination of †Coccolepididae within Chondrostei although the close relationship of Birgeriidae to Chondrostei and the assignment of other fossil actinopterygians have been drawn into question (López-Arbarello et al., 2013; Argyriou et al., 2018; Olive et al. 2019; Ebert et al., 2021; López-Arbarello and Ebert, 2021; but see Schultze and Arratia, 2015, Schultze et al., 2021, for alternative hypotheses whereby Coccolepididae is allied with the paraphyletic Palaeoniscimorpha) – however, this hypothesis for Coccolepididae being included with Chondrostei has never been subjected to a phylogenetic analysis (Olive et al., 2019).

†Coccolepididae was erected by Berg (1940) who diagnosed the family simply as including “all non-neopterygian fishes with only a single series of ossified radials supporting the dorsal fin”. Subsequent works regard Berg’s diagnosis as inadequate to differentially diagnose the family (Gardiner, 1960; Hilton et al., 2004; López-Arbarello et al., 2013; Olive et al., 2019) – in part due to the poor post-cranial ossification in these fishes; and because the number of radial supports in the dorsal fin among basal actinopterygians has been poorly surveyed (Hilton et al., 2004). Despite difficulties diagnosing members of the family, taxa currently included in †Coccolepididae range from

the Sinemurian stage of the Early Jurassic to the Barremian–Albian stages of the Early Cretaceous (Forey et al., 2010; Olive et al., 2019). They are predominately found in freshwater environments, although a few rare occurrences in shallow marine deposits are documented (Woodward, 1890a; Gardiner, 1960; Hilton et al., 2004; Ebert et al., 2021; López-Arbarello and Ebert, 2021). The type taxon, †*Coccolepis bucklandi* Agassiz, 1843, is described from the Tithonian Solnhofen Plattenkalk in Bavaria (Germany), with numerous additional species ranging from the Early Jurassic – Early Cretaceous subsequently referred to †*Coccolepis* (see Hilton et al., 2004 and López-Arbarello and Ebert, 2021, for a review). However, many of these species have since been placed into their own genera (e.g., †*Coccolepis macroptera* = †*Barbalepis macroptera*: Olive et al., 2019) or are recognized as being in urgent need of taxonomic revision (e.g., †*Coccolepis’ liassica* Woodward, 1890a); only †*C. bucklandi* and †*C. solnhofensis* López-Arbarello and Ebert, 2021 are regarded as true members of *Coccolepis*. Therefore, †*Coccolepis* is now restricted to the Tithonian stage of the Late Jurassic (López-Arbarello and Ebert, 2021).

Although coccolepidids were a rare faunal component throughout their evolution, their oldest records are already widely distributed in eastern (China and Siberia) and central (England) Laurasia. During the Middle and Late Jurassic, the group expanded geographically into western Laurasia (North America) and southern Gondwana (Argentina, Australia), later being restricted in their occurrences to southern Gondwana and central Laurasia (England) during the Early Cretaceous (Olive et al., 2019). However, little is yet known of the group’s origins, early diversity and distribution during the Early Jurassic. Only two coccolepidids have been described from the Early Jurassic: †*Coccolepis’ liassica* from the Sinemurian of Lyme Regis in England (Woodward, 1890a, 1891; Gardiner, 1960; Forey et al., 2010), and †*Plesiococcolepis hunanensis* Wang, 1977, from Hunan Province in China (Chang and Miao, 2004). Both of these taxa remain inadequately described, and the generic affinity of †*C. liassica* remains ambiguous. Coccolepidids have not previously been described from the Toarcian. A privately-owned specimen



from the Posidonienschiefer Formation of Schandelah (near Braunschweig), Lower Saxony (northern Germany) was figured and labelled as '*Coccolepis* sp.' as part of a regional fossil guide (Hauff et al., 2017); however, no further records of coccolepidid-like fishes have thus far been documented from the formation.

Here we describe the first occurrences of coccolepidid fishes (†Coccolepididae) from the Posidonienschiefer Formation at Holzmaden, based on two partial specimens. The Holzmaden coccolepidid represents the first described from the Toarcian, bridging an outstanding gap in the family's evolutionary history. The cranium of this fish is highly diagnostic, which in addition to its chronostratigraphic isolation from all other coccolepidids strongly supports assignment to a new genus and species.

## GEOLOGICAL SETTING

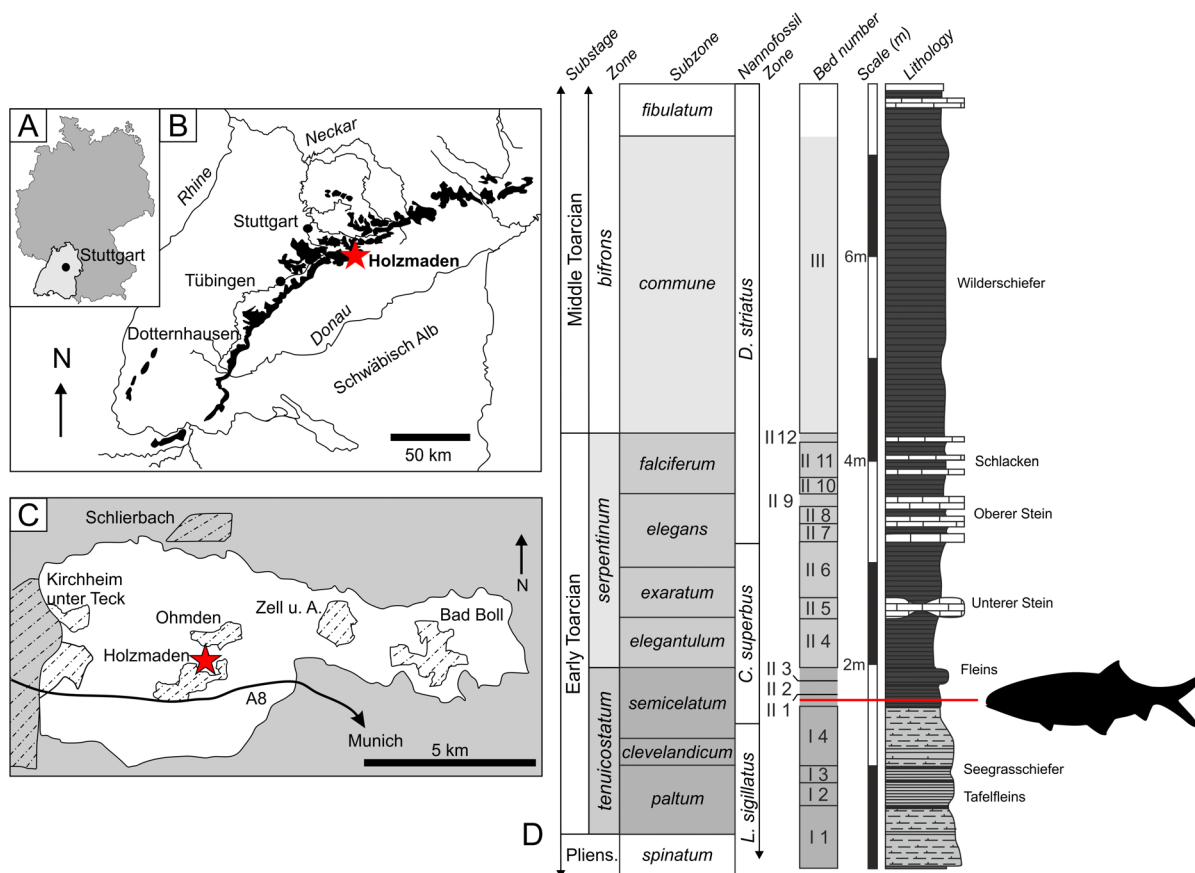
The Lower Jurassic (lower Toarcian) Posidonienschiefer Formation is a marine black shale Konservat-Lagerstätte famed for its exceptionally well-preserved marine fossils. The formation crops out in Germany from Waldshut-Tiengen in the south to Lower Saxony in the northwest, with coeval aged and similar lithostratigraphic deposits in Luxembourg, the Netherlands, France, and the United Kingdom (Riegraf et al., 1984; Röhl and Schmid-Röhl, 2005; Bour et al., 2007; Trabucchi-Alexandre et al., 2012; Mönnig et al., 2018). Of particular interest is the area around Holzmaden (Baden-Württemberg; approximately 30 km SW of Stuttgart) where the majority of historic and modern collecting has taken place. The historic label of 'Holzmaden' is often used anecdotally to denote any number of former or active quarries within the Holzmaden area, particularly between the towns of Kirchheim unter Teck, Holzmaden, Ohmden, Schlierbach, Zell unter Aichelberg, and Bad Boll (Maxwell et al., 2022; Cooper et al., 2022, fig. 1c) (Figure 1A-C). The section at Holzmaden represents a continuous succession of the lower to lower-middle Toarcian Liassic rocks, spanning the *tenuicostatum* – *bifrons* ammonite zones (Hauff, 1921; Riegraf et al., 1984) (Figure 1D). The palaeoenvironment represents a shallow to moderately deep, restricted siliclastic shelf setting within a sub-tropical epicontinental sea (Röhl et al., 2001; Röhl and Schmid-Röhl, 2005; Mönnig et al., 2018). Oxygen levels sporadically fluctuated throughout the Toarcian, with the onset of the global Early Toarcian Anoxic Event (E-TOAE) occurring in the latest *tenuicostatum* Zone (Röhl et al., 2001). The

laminated beds in the lower part of the section (*tenuicostatum* Zone) represent a shallower environment more proximal to the palaeo-shoreline; but becoming progressively deeper and shifting basinward in the upper beds, influenced by a regional marine transgression (Röhl et al., 2001; Mönnig et al., 2018).

Of the remarkable vertebrate fossils recovered from the formation – which include ichthyosaurs, plesiosaurs, crocodylomorphs, and pterosaurs – it is the ray-finned fishes that are the most diverse and abundant. Described actinopterygians include the large (ca. 3 m total length (TL)) chondrosteid †*Stronglyosteus*, two species of the †saurichthyid †*Saurorhynchus* (Maxwell and Stumpf, 2017), six genera of †pachycormiforms (Cooper et al., 2022), two ganoid-scaled halecomorphs (†*Holzmadenfuro* and †*Ohmdenfuro*: both Ebert, Thies and Hauff, 2020), the caturid, †*Caturus smithwoodwardi* White, 1925, several deep-bodied semionotiforms (†*Dapedium* spp. + †*Tetragonolepis* spp.) (Thies and Herzog, 1999; Thies and Hauff, 2011), the †ptycholepid, †*Ptycholepis bollensis* Agassiz, 1843; the lepisosteiform †*Lepidotes gigas* Agassiz, 1832 (López-Arbarello, 2012), an abundance of the shoaling teleost †*Lepidolepis* spp. And several taxa currently lumped within the problematic genus †'*Pholidophorus*' (Hauff and Hauff, 1981).

## MATERIAL AND METHODS

Two fossil fishes in the collection of the SMNS represent unique specimens of a hitherto undescribed Toarcian coccolepidid from the Posidonienschiefer Formation. SMNS 59978 comprises an articulated but incomplete skull preserved in right lateral aspect on a small piece of shale, collected in 1993 from bed  $\epsilon_{11}$  ('Koblenzer'; *tenuicostatum* Zone) of the G. Fischer quarry in Holzmaden (located opposite Urwelt Museum Hauff; Figure 1). The second specimen (SMNS 52044) derives from the exact horizon and bed number as SMNS 59978, and was donated to the SMNS in 1982. SMNS 52044 consists of a well-articulated skull in ventro-left-lateral view, with some disarticulated elements of the post-cranial skeleton amalgamated in a confined concentration behind the operculum. The preservation of this specimen is consistent with the typical skeletal accumulation pattern of a regurgitalite, representing the first known coccolepidid preserved as a bromalite inclusion (see Discussion). Both specimens were previously mislabelled in the collection as †pholidophoriforms



**FIGURE 1.** Locality map and stratigraphy of the Posidonienschiefer Formation at Holzmaden, showing the distribution of coccolepids in the formation. **(A)** Simplified map of Germany showing the location of Stuttgart. **(B)** State map of Baden-Württemberg showing regional exposure of the Posidonienschiefer Formation with the Holzmaden area indicated with a star. **(C)** Map of the Holzmaden area with a star indicating the collection locality. **(D)** Stratigraphic log of the Posidonienschiefer Formation at Holzmaden showing the collection horizon for the new coccolepoid fish. Modified from Cooper et al. (2022).

however neither specimen shows any characteristic features of this group.

Anatomical nomenclature and taxonomy of †Coccolepididae follows Hilton et al. (2004) and López-Arbarello et al. (2013). Our definition of the genus †*Coccolepis* follows the revised diagnosis by López-Arbarello and Ebert (2021). Revised nomenclature for the actinopterygian palatoquadrate follows Schultze et al. (2021) after Nielsen (1942, figs. 35a, 36-37). As outlined in the introduction, the interrelationships of †Coccolepididae within Actinopterygii remain unresolved and are outside the scope of this contribution. For the new Holzmaden coccolepoid, we tentatively refer †Coccolepididae to Chondrostei, following the most current diagnosis of the family (López-Arbarello et al., 2013). Standard ichthyological parameters were measured using a digital calliper, and specimens were photographed with a Canon

EOS 200D camera with EFS 55 mm and EF 100 mm macro-lenses. UV photography was attempted for these specimens, however, due to the low fluorescence feedback and high pyrite content in the matrix, the results were not informative.

**Institutional Abbreviations.** **NHMUK** = The Natural History Museum, London, U.K. (formally The British (Natural History) Museum); **SMNS** = Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

### SYSTEMATIC PALAEOLOGY

Class ACTINOPTERYGII Cope, 1887  
 Subclass ?CHONDROSTEI Müller, 1845  
 sensu Grande and Bemis (1996)  
 Family †COCCOLEPIDIDAE Berg, 1940 sensu  
 López-Arbarello et al. (2013)

**Remarks.** Referral to the family †Coccolepididae is based on the following combination of characters (based on revised diagnosis by López-Arbarello et al., 2013): (1) dermal bones of the skull roof ornamented with small and regularly spaced tubercles; (2) maxilla with large postorbital plate; (3) supracleithrum massive, either as large as or larger than the cleithrum. Much of the pre-orbital region is missing in both Holzmaden specimens, creating ambiguity over the possible presence of coccolepidid features in this region of the skull, particularly those pertaining to the contacts between the nasals (Hilton et al., 2004; López-Arbarello et al., 2013). The left nasal is partially exposed in SMNS 52044 although unfortunately the bone contacts are obscured. The new Holzmaden fish is excluded from the Early Jurassic family †Centrolepididae due to the absence of both suborbital bones and complex dermal ornamentation formed by thick enameloid (Gardiner, 1960, p. 248). Likewise, the absence of a broad coronoid process, a large expanded preopercle, an upright suspensorium and variation in dermal ornamentation differentiates the new Holzmaden actinopterygian from the Lower Liassic family †Platysiagidae (Gardiner, 1960, p. 256). It is also excluded from †Ptycholepididae due to the absence of the diagnostic ridged ganoine ornamentation, a large gular plate, an opercle which is significantly larger than the subopercle, and dentition consisting of very small, close-set teeth (Woodward, 1891; Gardiner, 1960, p. 261).

†*Toarcocephalus* gen. nov.

zoobank.org/2BB90CAA-8FAD-45B3-A8D6-685B096F632D

**Diagnosis.** As for the type and so far only known species.

†*Toarcocephalus morlok* gen. et sp. nov.

zoobank.org/09AB0516-607C-4C73-9614-7BEC974045D1

**Diagnosis.** †*Toarcocephalus morlok* gen. et sp. nov. is diagnosed from all other coccolepidid fishes by the following unique combination of characters: upper and lower jaws smooth and unornamented; mandible well elongated and gracile, longer than maxilla and shallow posteriorly; angular large and lenticular; large postorbital expansion of maxilla strongly convex and twice as long as deep with a strongly recurved ventral margin; short premaxilla holding several recurved teeth that are slightly larger than those on the maxilla; skull roof very weakly tuberculated with pronounced striated ridges that are marginally serrated; subopercle trapezoidal and equal in size to opercle; preopercle slender, forming a posteroventral lobular expansion,

only as tall as the subopercle and extending no further than the midpoint of the postorbital plate of the maxilla; operculum and supracleithrum mostly smooth with fine, regularly spaced punctae; supracleithrum massive, accounting for more than 80% of operculum height; large triangular dorsal process on the supracleithrum; nine branchiostegal rays, each thin, lacking distal expansions and confined to the posterior corner of the mandible; gular plate egg-shaped and placed roughly at the midpoint of the lower jaw length; elongated hyomandibula obliquely inclined forward, thin and weakly bow-shaped; ceratohyal well elongated but thin; hypohyals short and robust; sclerotic ring thin and delicate; scales weakly developed; vertebral column aspondylous, composed of simple arcocentral arches with proportionately short spines.

**Etymology.** Generic name chosen for its discovery in Toarcian-aged strata, with suffix *-cephalus* for head, denoting the diagnostic cranium. Species epithet *morlok* named after the savage subterranean antagonists in H.G. Wells' *The Time Machine* (1895), due to their similarly grotesque appearance characterised by large eyes, a blunt face and pointed teeth.

**Holotype.** SMNS 59978, a near-complete and articulated skull, missing the pre-orbital region (Figure 2).

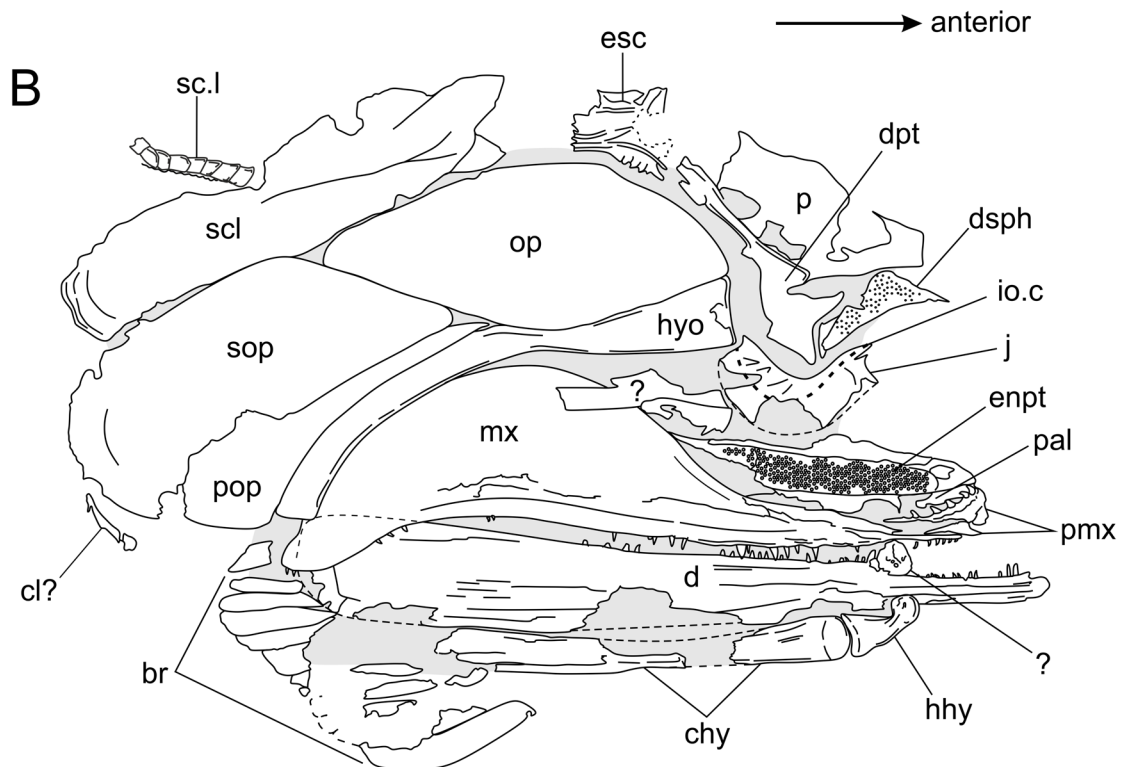
**Paratype.** SMNS 52044, an articulated skull exposed in left ventrolateral view, with associated postcranial fragments preserved as a regurgitalite (Figure 3).

**Type Locality.** G. Fischer Quarry, Holzmaden, Baden-Württemberg, Germany.

**Type Horizon.** Bed  $\epsilon$ ll<sub>1</sub> ('Koblenzer'), *semicelatum* Subzone; *tenuicostatum* Zone, Posidonienschiefer Formation, Lower Toarcian, Early Jurassic.

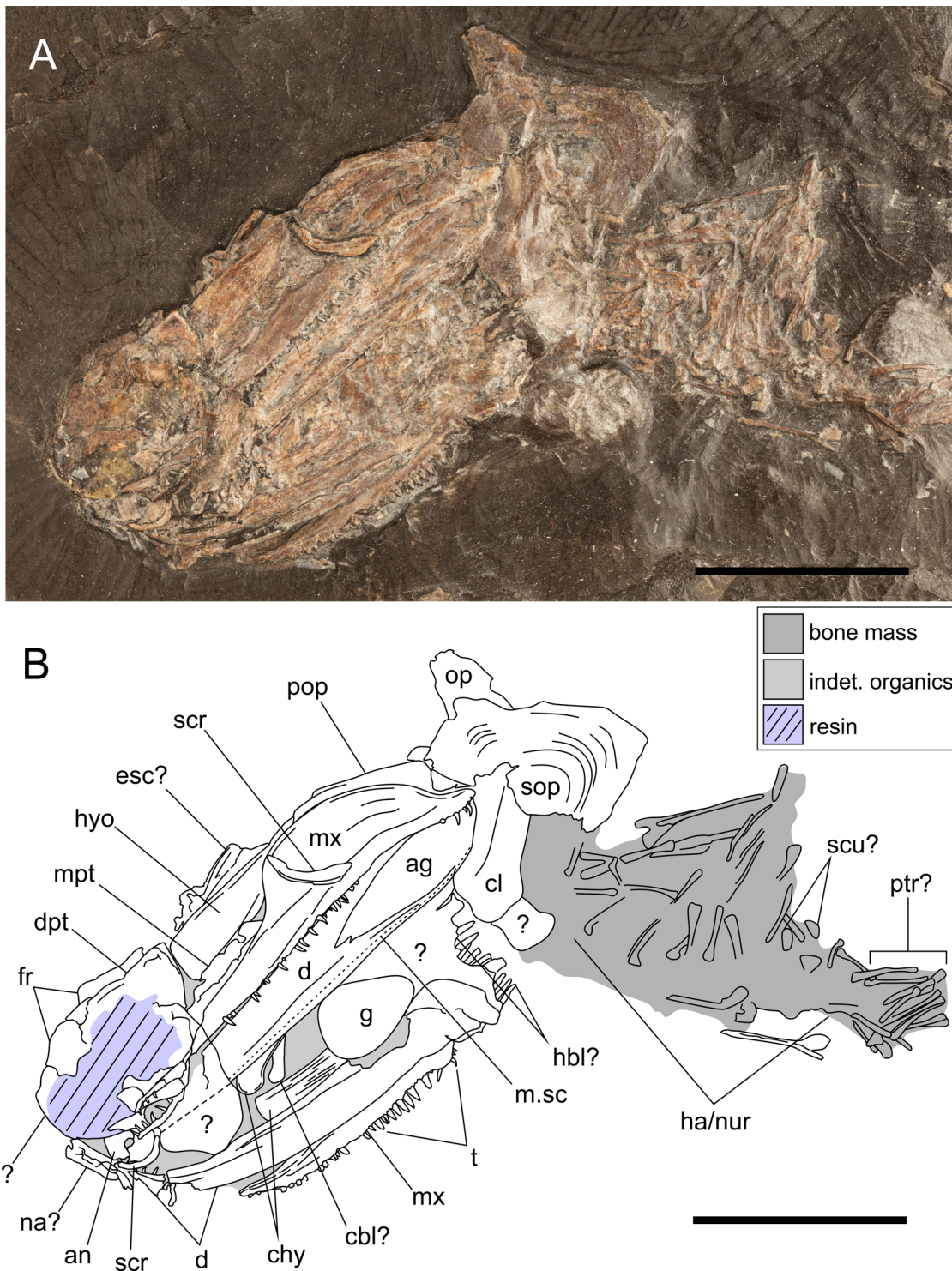
## Description

**General features.** The skull is 44 mm long and 30 mm deep (SMNS 59978), with a maximum known skull length of 73 mm (SMNS 52044). The postorbital region accounts for 60% of the skull length, with a mandible length approximate to 75% of the skull length. The angular measures approximately 35% of the total mandible length. Collectively the operculum is twice as deep as it is long with the massive supracleithrum accounting for 80% of the operculum depth. The skull displays the condition that is shared with both coccolepidids and many other early actinopterygians, notably an anteriorly placed orbit, large postorbital plate on the maxilla, absence of the supramaxilla, jaws extending far behind the orbit and an obliquely inclined suspen-



**FIGURE 2.** SMNS 59978, †*Toarcocephalus morlok* gen. et sp. nov. (holotype), preserved in left internal view. **(A)**, imperfect skull exposed in internal view. **(B)**, line drawing of specimen. Abbreviations: **br** = branchiostegal rays; **chy** = ceratohyal; **cl?** = cleithrum?; **d** = dentary; **dpal** = dermopalatine; **dpt** = dermopterotic; **dsph** = dermosphenotic; **enpt** = endopterygoid; **esc** = extrascalpular; **hhy** = hypohyal; **hyo** = hyomandibula; **io.c** = infraorbital sensory canal; **j** = jugal; **mx** = maxilla; **op** = opercle; **p** = parietal; **pmx** = premaxilla; **pop** = preopercle; **scl** = supracleithrum; **sc.l** = lateral line scales; **sop** = subopercle. Scale bar equals 10 mm.





**FIGURE 3.** SMNS 52044, †*Toarcocephalus morlok* gen. et sp. nov. (paratype), skull and post-cranial elements preserved in ventro-lateral (left) view as a regurgitalite. **(A)**, overview of specimen – skull exposed in left ventrolateral view. Much of the orbital region has been infilled with resin. **(B)**, interpretive line drawing. Abbreviations: **an** = antorbital; **ag** = angular; **cbl?** = ceratobranchial?; **chy** = ceratohyal; **cl** = cleithrum; **d** = dentary; **dpt** = dermopterotic; **esc** = extrascapular; **fr** = frontals; **g** = gular plate; **ha/nur** = haemal/ neural arches and spines; **hbl?** = hypobranchials?; **hyo** = hyomandibula; **ptr?** = pterygiophores; **m.sc** = mandibular sensory canal; **mpt** = metapterygoid; **mx** = maxilla; **na?** = nasal?; **op** = opercle; **pop** = preopercle; **scu?** = preanal scute?; **scr** = sclerotic ring plate; **sop** = subopercle; **t** = teeth. Scale bar is equal to 20 mm.

sorium. Both skulls are incomplete, with the skull roof and rostral portions poorly known in this taxon. The jaws, palate, and suspensorium of the holotype specimen are exposed in internal view, whilst most of the operculum, pectoral girdle, branchiostegal rays, and skull roof are exposed in external view.

### Cranial Skeleton

**Skull roof.** Only the dermopterotic, dermosphenotic and extrascapular of the right side of the skull roof are preserved in SMNS 59978 (Figure 3). Fragments of smooth dermal bone placed antero-dorsally to the orbit in SMNS 52044 likely represent part of the left frontal (Figure 3). The dermosphenotic is asymmetrically semi-lunate, taller than it is wide, and significantly smaller than, but articulating anterior to, the large dermopterotic. The dermosphenotic is confined to the dorsoposterior corner of the orbit and is ornamented externally with weakly developed denticle-like protuberances. Proportionately, the dermosphenotic is smaller than that of †*Coccolepis liassica*.

The dermopterotic is poorly preserved in SMNS 59978. It is more than twice as long as it is wide, is wider at the anterior where it lies just above the dorsal head of the hyomandibula, and becomes progressively narrower towards the posterior (Figure 3). Superficially, the surviving bone is axe-shaped, although the true dimensions of this element are unknown. The ventral bone margin is undamaged, and is obtusely concave such that its shape fits well with the convex dorsal margin of the opercle. The infraorbital sensory canal cannot be observed on account of the poor preservation. A wide and thin expansive bone, partially overlain (in ventral view) by the posterior region of the dermopterotic, most plausibly represents remnants of the broken right parietal. The externa is very weakly ornamented with poorly developed protuberances.

A small pentagonal bone located posterior to dermopterotic is identified as the left extrascapular (Figure 3). The bone is strongly ornamented with deep, longitudinally orientated bony ridges, although is incomplete along the anterior and lateral margins. In relation to the cheek, the extrascapular is situated dorsal to the midpoint of the opercle, with the serrated posterior margin of the bone representing the suture with the missing post-temporal bone.

An incomplete extrascapular from the right side of the skull roof is present posterior to the dermopterotic and parietal in external view. The bone

is damaged anteriorly but is superficially pentagonal. The extrascapular is strongly ornamented with several deep well-developed ridges and grooves aligned longitudinally, as well as a slightly serrated lateral bone margin. In relation to the cheek, the extrascapular is situated roughly at the midpoint of the dorsal margin of the opercle (Figure 3). The empty gap between the extrascapular and the supraclithrum represents the void left from the missing posttemporal.

**Orbital series.** The orbit is placed close to the anterior end of the skull, with the jaws extending well behind it. The majority of the orbital series is mostly obscured or missing in both specimens of †*Toarcocephalus morlok*. The sclerotic ring is incompletely preserved, thin and delicate, lacks ornamentation, and possesses a slightly thickened external ridge (Figure 3). The sclerotic ring is disarticulated in SMNS 52044 with the displaced posterior plate lying on the top of the maxilla. The number of infraorbitals is uncertain as only the incomplete right jugal is preserved, placed posterior to the orbit in SMNS 59978. The jugal is thin and smooth, superficially semi-circular, and holds the infraorbital sensory canal, which passes longitudinally through the midline of the bone (Gardiner, 1960). The anterior surface of the jugal is arch-shaped, indicating its contribution to the posteroventral margin of the orbit (Figure 3). The infraorbital sensory canal passes dorsally towards the overlying dermosphenotic (likely bridged by the missing infraorbitals), similar to †*Coccolepis* (e.g., Hilton et al., 2004).

Much of the orbital region is present in SMNS 52044; however, a combination of rough fossil preparation, repairs using obstructing resin, and the skull's preservation within a regurgitalite all contribute to the difficulty of identifying the individual bones in this region of the skull. A small (1 mm width) hatchet-shaped bone is interpreted as the antorbital as it displays a prominent semi-circular notch on the anterodorsal corner, which (based on †*Coccolepis*) in life would have aligned with a corresponding notch on the nasal to form the narial foramen (Gardiner, 1960). A taller rectangular bone placed dorsal to the antorbital likely corresponds to either the left or right nasal (Figure 3). The naris is therefore placed anteroventral to the orbit, similar to its placement in †*Coccolepis liassica* (Woodward, 1890a; Gardiner, 1960) and in Late Jurassic coccolepidids (López-Arbarelo et al., 2013; Skrzycza, 2014; López-Arbarelo and Ebert, 2021). Sub-orbitals are absent. Supraorbital and rostral bones are not preserved in either specimen.

**Upper jaw.** The upper jaw is composed of a large maxilla, exposed externally in SMNS 52044 (Figures 3, 4A) and internally in SMNS 59978 (Figures 2, 4B-C), and a short premaxilla which is only preserved in SMNS 59978. The maxilla is slender anteriorly but drastically expands and broadens behind the orbit, forming a dorsal plate-like expansion. The postorbital portion of the maxilla is massive with respect to the anterior (infraorbital) portion, accounting for more than 60% of the maxilla length. The postorbital expansion is twice as long as it is deep, is strongly convex with an asymmetrically rounded dorsal margin marked by a roughly medial peak. The dorsal margin obtusely slopes anteriorly, becoming much shallower at the junction below the jugal. From here, the maxilla becomes progressively slenderer, extending only as far forward as the anterior margin of the toothed pterygoid, but terminating short of the proximal end of the dentary. The ventroposterior corner of the maxilla is characterised by a short lobe-like expansion that partially overlies and extends further backwards than the lower jaw. The occlusal surface of this expansion holds several small teeth, which are curved anteriorly. A single row of size-graded teeth extends along the entirety of the oral surface of the maxilla. Teeth comprise of tall, recurved cone-like crowns, each separated by an interval of between 3-4 shorter and more gracile crowns. Tooth morphology and arrangement are comparable to those on the dentary. Similar to the lower jaw, the externa of the maxilla is smooth and lacks any ornamentation (Figure 4A), helping to differentiate this taxon from most other coccolepidid fishes (see discussion).

The premaxilla is short, accounting for only 10% of the upper jaw length. It is well exposed in SMNS 59978 where the bone has flipped orally to expose the external surface (Figures 2, 4B-C). The bone is slender posteriorly, becoming progressively deeper at the anterior to form a stout dorsal expansion. The occlusal surface is gently concave and bears five stout teeth, each with a wide base and evenly spaced with narrow diastemas. These teeth are slightly larger than those on the maxilla.

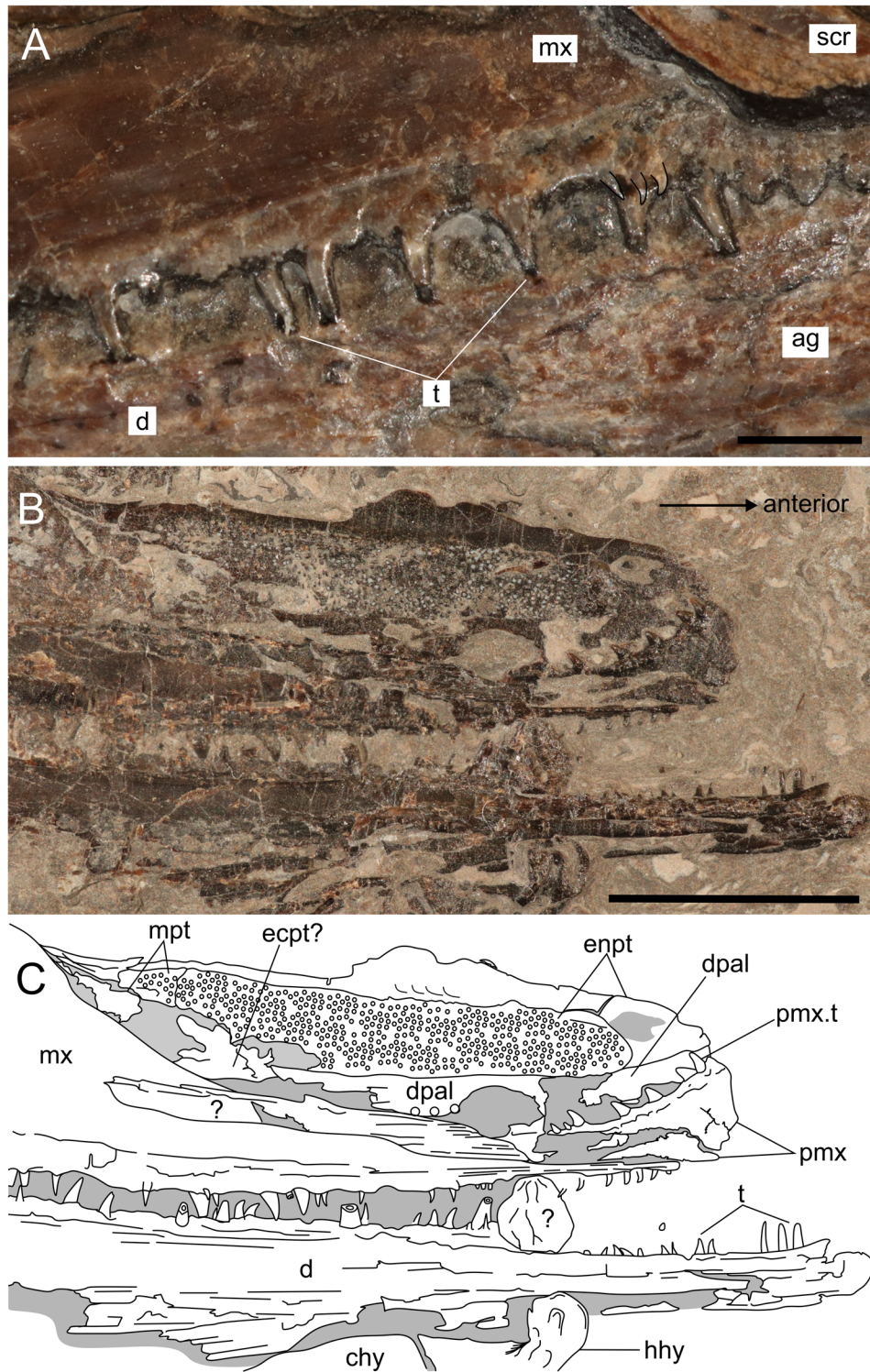
**Lower jaw.** The lower jaw is very elongate with a mandible length equal to approximately 94% of the postorbital length. The left lower jaw is exposed in lateral view in SMNS 52044 but is incomplete anteriorly, whereas SMNS 59978 exposes the entirety of the right lower jaw in internal view. The right ramus of the lower jaw in SMNS 52044 is partly exposed in ventromedial view where it displays an acute, inwards anterior curvature of the rami

towards the mandibular symphysis. The lower jaw is shallow and gracile, with an extremely high length to depth ratio of 16:1. Compared to the maxilla, the lower jaw is longer and extends further where it terminates in a proximal gape level with the premaxilla of the upper jaw. Externally, the lower jaw is composed of an elongate dentary, which bears teeth along its entire occlusal surface, and an elliptical angular which is large and well pronounced: extending for approximately 25% of the total lower jaw length (Figures 2-3). The angular articulates with the dentary via a wedge-shaped suture, with the dentary bone extending both underneath and dorsal to the angular. Externally, the mandible is mostly smooth but becomes weakly ornamented towards the anterior with fine longitudinal striations. Foramina for the mandibular sensory canal are aligned longitudinally along the ventral margin of the lower jaw, extending below the angular bone but not crossing into it; instead, the canal terminates at the ventroposterior corner of the dentary (Figure 3). The medial surface of the lower jaw is imperfectly exposed in SMNS 59978 to reveal to a narrow tube-like Meckelian groove. Unfortunately, the posterior medial surface of the lower jaw, including the dentary contact with the prearticular and articular, and the possible presence of toothed coronoids, are poorly distinguishable due to imperfect preservation in this region.

Teeth are present along the entire length of the dentary, with two prominent size-graded tooth morphologies present, similar in morphology and arrangement pattern to those on the upper jaw. The taller crowns are slender and conical with widened bases and curved apexes. Each of the tall crowns are separated laterally by 2-4 smaller tooth crowns, which are strongly recurved and are less than 1/3 of the height of the larger teeth. All tooth crowns are smooth rather than ornate, with well-developed acrodin caps (Figure 4A).

**Suspensorium.** The left side of the palatoquadrate is nicely exposed in SMNS 59978. The palatoquadrate is a large, lenticular, mostly dentigerous compound structure formed of a large endopterygoid, one or two dermopalatines, and remains of a probable ectopterygoid and dermometapterygoid. The dentigerous surface is armed with a chaotic field of small denticle-like teeth, numbering more than 100; each is roughly identical in morphology and significantly smaller than the marginal dentition. The posterior-most region of the palatoquadrate and its contact with the left suspensorium is partially obscured by the postorbital plate of the right maxilla. The endopterygoid forms the majority





**FIGURE 4.** †*Toarcocephalus morlok* gen. et sp. nov., details of jaws, palatoquadrate, and teeth. (A) maxillary teeth in SMNS 52044 – notice the smooth texture of the bone externa. Please note that some of the smaller damaged teeth on the maxilla are highlighted. (B) close-up of left palate, upper and lower jaws of SMNS 59978. (C), line drawing with surrounding matrix highlighted with false colour. Abbreviations: **ag** = angular; **chy** = ceratohyal; **d** = dentary; **ecpt** = ectopterygoid; **enpt** = endopterygoid; **dpal** = dermopalatine; **hhy** = hypohyal; **mpt** = metapterygoid; **mx** = maxilla; **pmx** = premaxilla; **pmx.t** = toothed region of premaxilla; **scr** = sclerotic ring; **t** = tooth crowns. Scale bars equal 10 mm.



of the palatoquadrate, is lenticular in shape, and mostly dentigerous in occlusal view. The anterior-most end of the endopterygoid pinches out proximally where it becomes abruptly edentulous.

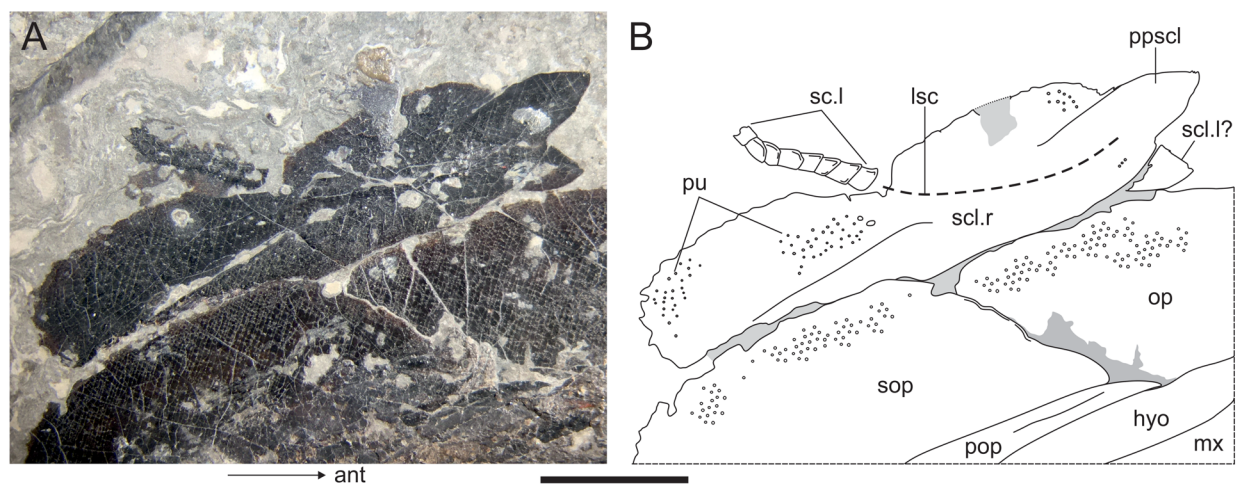
The dermometapterygoid is mostly covered by the right maxilla, with the exposed region being confined to the posterodorsal margin of the endopterygoid where it contributes less than 1/5 of the exposed dentigerous tooth field. The postero-ventral region of the palatoquadrate poorly exposes part of the dentigerous ectopterygoid; albeit the bone is damaged and mostly covered by the right maxilla.

The dermopalatine is placed anterior to the ectopterygoid where the bone is sutured along the entire ventral margin of the endopterygoid. Due to incompleteness and specimen damage, the number of dermopalatine bones in the palatoquadrate is uncertain. The ventral margin of the dermopalatine holds a single row of teeth, larger than those of the dentigerous field carried by the endopterygoid, dermometapterygoid and ectopterygoid; however, only a single dermopalatine tooth is exposed underneath the overlying premaxilla towards the front of the palatoquadrate complex. The dorsal margin of the endopterygoid expands medially to form a tall and wide edentulous flange for anchorage underneath the parasphenoid, which according to Gardiner (1960; although referred to therein as the suprapterygoid), would run the entire dorsal surface of the palatoquadrate.

The hyomandibula is fully exposed in medial view in SMNS 59978, with the dorsal head of the hyomandibula exposed externally in SMNS 52044.

We identify this element as the hyomandibula on the basis that it is exposed in internal view partially underlying the operculum in the holotype, does not hold any dermal ornamentation in SMNS 52044 where the dorsal head is externally exposed, and is overall consistent with the shape and placement of the corresponding hyomandibula in other coccolepidids (e.g. '*Coccolepis*' *liassica*, pers. observ. SC). The hyomandibula is tall and obliquely inclined towards the anterior. The bone is gently arc-shaped, narrow along the midshaft and ventral margin, but gradually widening to form a slightly expanded hatchet-shaped dorsal head. The bone is placed dorsoposterior to the maxilla, extending from the dorsal border of the lower jaw to just anterodorsal of the opercle; extending further forward than the postorbital portion of the maxilla (Figures 2, 5). The quadrate, which should articulate ventrally between the hyomandibula and lower jaw, is not exposed in either specimen.

**Ventral gill skeleton and ventral hyoid arch.** The ventral hyoid arch is fairly well exposed in medial view and is composed of a small robust hypohyal, and an elongate ceratohyal. The hypohyal is located close to the anterior margin of the dentary and contributes only 10% of the ventral axis of the hyoid arch. The right hypohyal is articulated with the right ceratohyal in SMNS 59978, whereas an indeterminate bone located between the dentary and upper jaw in the same specimen may be the displaced left hypohyal (Figure 4B-C). Anteriorly, the bone is narrow and robust, forming a convex head; whereas the bone gradually deepens and becomes thinner towards the posterior, forming a



**FIGURE 5.** †*Toarcocephalus morlok* gen. et sp. nov., details of the pectoral girdle and lateral line. Holotype specimen SMNS 59978, photograph (A) and line drawing (B). Abbreviations: **hyo** = hyomandibula; **lsc** = lateral line sensory canal; **mx** = maxilla; **op** = opercle; **pop** = preopercle; **ppscl** = dorsal process of the supracleithrum; **pu** = punctations; **sc.l** = lateral line scales; **scl** = supracleithrum (**.r** = right; **.l** = left); **sop** = subopercle. Scale bar equals 5 mm.

concave cotyle-like facet for articulation with the ceratohyal. The ceratohyal is well elongated, accounting for just over 90% of the vertical arm of the hyoid arch. The bone is narrow along the medial shaft but expands slightly at the anterior just before it articulates with the hypohyal. The ceratohyal is best exposed in SMNS 59978 except for the damaged posterior region. The anterior ends of both the left and right ceratohyal are also partially exposed in ventral view between the lower jaws in SMNS 52044 (Figure 3). A slightly slimmer bone with a rounded anterior margin is partly exposed between the paired ceratohyals, likely corresponding to the front portion of a ceratobranchial. Exposed towards the posterior margin of the cranium in SMNS 52044 are a transverse series of thin bony rods which are mostly overlain by a large mass of indeterminate bone and soft tissues (Figure 3). The identity of these bones is uncertain, although their placement and arrangement suggest that they may be remnant elements of the branchial arches.

**Gular.** The gular plate is present, albeit poorly preserved in SMNS 52044. The gular is small (gular length equivalent to 15% of total mandible length) weakly pentagonal to ovate, widest at the anterior, very gently convex, and is placed between the lower jaws, roughly mid-way along the dentary. It is uncertain if this position is truly anatomical or if the plate has slipped backwards during the partial decay/digestion process, similar to what has happened to the sclerotic ring in this specimen. The bone is heavily abraded, which has likely destroyed any external ornamentation.

**Branchiostegal rays.** Preserved branchiostegal rays number at least nine and are confined to the posterior-most corner of the ceratohyal. Each ray is very short and flat with a roughly rectangular outline, are of equal breadth and do not overlie one another. Their distal ends are sub-rounded and not expanded as per the condition observed in some Late Jurassic coccolepidid taxa (e.g., †*Condorlepis*; López-Arbarello et al., 2013). The ornamentation is weakly developed, consisting of a patchy leathery texture with weakly pronounced and shallow protuberances.

**Operculum.** The operculum, comprising the opercle, subopercle, and preopercle, is complete in SMNS 59978 (Figure 2). Only the subopercle and fragments of the opercle are preserved in SMNS 52044. As a collective, operculum height is more than twice that of its anteroposterior length, with the subopercle equal in size to the opercle (Figure 2). Similar to the hyomandibula, the operculum is

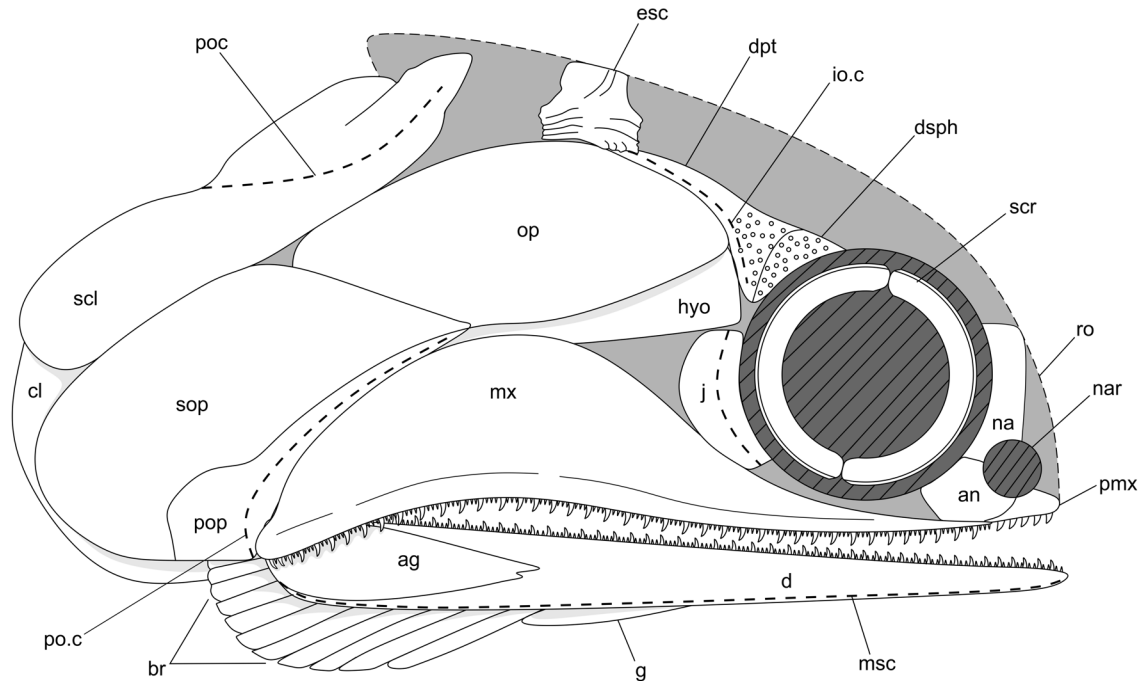
obliquely inclined forward with the long axis oriented approximately 130° to the long axis of the skull. The subopercle is twice as tall as it is deep, is roughly rhombic in shape with a convexly rounded ventral margin, straight anterior margin, and a slightly narrower, albeit straightened dorsal margin where it contacts the ventral plane of the opercle.

The preopercle is slender and narrow, being only as tall as the subopercle; it does not extend dorsally past the subopercle-opercle boundary. Anteriorly, the preopercle is gently concave and narrow dorsomedially. It expands slightly into a rounded ventral fan that extends as far as the ventral margin of the subopercle.

The opercle is equal in size and of a similar shape to the subopercle; it is placed dorsoanteriorly to the two other elements of the operculum with only very brief contact with the dorsoanterior branch of the preopercle. The opercle is oval, slightly asymmetrical, with the dorsal head wider than the ventral; all margins of the bone are either strongly or weakly convex. Dorsoanteriorly, the opercle extends as far as the dorsal margin of the hyomandibula, with the obtusely curved dorsoposterior bone margin bordering the dermopterotic, extrascapular, supracleithrum, and the missing posttemporal. All bones in the operculum appear to be smooth, although under magnification are shown to be very finely punctate (perforated), lack denticles or protuberances, and show an unusual cross-hatching pattern which may be taphonomic in origin.

### Postcranial Skeleton

**Pectoral girdle.** Only the ventral branch of the cleithrum is partially exposed underneath the damaged operculum in SMNS 52044. The bone is too incomplete to draw meaningful anatomical data, however, based on its small size relative to the subopercle, we surmise the cleithrum is proportionately smaller than the supracleithrum. The supracleithrum is massive, occupying almost the entire height of the operculum with the midpoint of the bone aligned roughly perpendicular to the suture between the opercle and subopercle (Figure 5). The supracleithrum is superficially rectangular, somewhat amorphous with equally wide proximal and distal ends. The ventral (distal) end of the bone is sub-oval with strongly convex margins similar to the bones in the operculum. The dorsal (proximal) end is expanded to form an anterodorsal plate-like ridge, terminating at a short triangular projection. The corresponding projection from the underlying left supracleithrum is partially exposed underneath



**FIGURE 6.** Cranial reconstruction of †*Toarcocephalus morlok* gen. et sp. nov. with missing regions based on reconstruction of '*Coccolepis liassica*' in Gardiner (1960). Missing or speculative areas are indicated with a dashed line and coloured in grey. Abbreviations: **ag** = angular; **an** = antorbital; **br** = branchiostegal rays; **cl** = cleithrum; **d** = dentary; **dpt** = dermopterotic; **dsph** = dermosphenotic; **esc** = extrascapular; **g** = gular plate; **hyo** = hyomandibula; **io.c** = infra-orbital sensory canal; **j** = jugal; **msc** = mandibular sensory canal; **mx** = maxilla; **na** = nasal; **nar** = external naris; **op** = opercle; **poc** = postorbital canal; **pop** = preopercle; **ro** = rostral; **scl** = supraclithrum; **scr** = sclerotic ring; **sop** = subopercle.

the ventral margin of the right (external) supraclithrum (Figure 5). A similar process is present in the supraclithrum of *Neslovicella* (Åtamborg, 2007) and likely articulates underneath the missing posttemporal. Foramina for the lateral line canal pass longitudinally through the dorsal half of the supraclithrum in a somewhat obtuse trajectory (Figures 5, 6).

**Vertebral column and fin support.** With the exception of the pectoral girdle, the postcranial skeleton is very poorly represented. The postcranial skeleton is poorly mineralized in coccolepidids, lacking ossified ribs and centra (Hilton et al., 2004; López-Arbarello et al., 2013; Olive et al., 2019) and thereby hindering their preservation potential in the fossil record. A jumbled mass of fragmented bones from the postcranium are preserved within a regurgitated accumulation behind the skull in SMNS 52044. Due to a combination of anatomical disarticulation, rough fossil preparation, and having been churned up and partially digested in a predator's gut, identifying most of these bones with cer-

tainty is problematic, especially in the absence of articulated comparative materials. Within this regurgitated accumulation though a few bone morphologies are identified.

Several arcocentra in the form of arches and spines are observed, although whether they represent neural or haemal elements is unknown. An isolated element towards the ventral margin of this accumulation is complete, showing the spine to be relatively short and the arch to be a simple bifurcation with a small paired zygapophysis located just dorsal of the arch crest. The majority of the bone accumulation is composed of similar arcocentra elements; however, it is not possible to provide an estimation of their number. Two small rhombic to oval-shaped scale-like ossifications are preserved behind the arcocentra. Their origin is uncertain; however, the shape and size are reminiscent of the preanal scales of some coccolepidid fishes (Hilton et al., 2004; López-Arbarello and Ebert, 2021).

Posterior to these scales are 11 elongate bones seemingly retaining their relative anatomical

arrangement, preserved in the ventral-most region of the regurgitalite. These bones are uniform in length and characterised by a narrow elongate shaft with a single hatchet-like expansion at each end. Their identity is uncertain, although they possibly correspond to either part of an articulated fin support for either for the dorsal or anal fin, or possibly preural arcocentra from the disrupted caudal region of the vertebral column.

**Squamation.** A partial series of articulated lateral line scales are aligned posterior to the supra-cleithrum in SMNS 59978 (Figure 5). The eight surviving scales are exposed in medial view indicating that these scales belong to the left lateral line scale row. The lateral line sensory canal is poorly visible due to a combination of imperfect preservation and the scales exposure in medial rather than lateral view.

**Size estimations.** Both specimens belong to similar sized fishes, with SMNS 52044 representing a slightly larger individual. Skull length is proportionate to four and a half times the total length in †*Coccolepis* *liassica* (Gardiner, 1960), and assuming similar proportions in the new taxon we estimate the largest individual of †*Toarcocephalus morlok* gen. et sp. nov. to be 315 mm TL (SMNS 52044) and the smaller specimen only 207 mm TL (SMNS 59978).

### Comparative Anatomy

†*Toarcocephalus morlok* gen. et sp. nov. is assigned to the family †Coccolepididae based on the following shared characters: (1) dermal bones of the skull roof ornamented with small and regularly spaced tubercles; (2) maxilla with a large postorbital plate; (3) a massive supra-cleithrum, either as large or larger than the cleithrum (López-Arbarello et al., 2013). Absence of postorbital and suborbital bones in †*T. morlok* gen. et sp. nov. is a shared trait of †Coccolepididae and excludes possible referral within the morphologically similar Early Jurassic family †Centrolepididae (see Gardiner, 1960). Absence of an enlarged coronoid process, a vertical suspensorium or a plate-like preopercle placed dorsal to the maxilla additionally excludes assignment to †Platysiagidae (Gardiner, 1960). The weak dermal ornamentation is strikingly dissimilar to the well-developed ganoine ridges on the externa of the dermal bones in †Ptycholepididae. With the exception of †Ptycholepididae, these non-coccolepidid families are presently restricted to the Sinemurian stage of the Early Jurassic (e.g., Forey et al., 2010). The family †Coccolepididae is further diagnosed by a postrostral bone that sepa-

rates only the posterior region of the nasal bones (López-Arbarello et al., 2013; Ebert et al., 2021). The nature of the contacts between the nasals and postrostral bone is unknown in †*T. morlok* gen. et sp. nov.

The genus †*Coccolepis* Agassiz, 1843, was until recently a speciose waste-basket genus encompassing geographically and stratigraphically distant taxa, but is now endemic to the Tithonian of Bavaria with only the type species †*C. bucklandi* and †*C. solnhofensis* considered valid members of the genus (López-Arbarello and Ebert, 2021). †*Coccolepis* differs from †*Toarcocephalus* gen. nov. based on a suite of characters, most notable being the difference in ornamentation. The skull roof and maxilla of †*Coccolepis* spp. are strongly ornamented with sharply pointed, posteriorly directed denticles and strongly developed tubercles (Hilton et al., 2004), whereas the maxilla is smooth and the skull roof very weakly tuberculated in the new Toarcian coccolepidid. The opercle in †*Coccolepis* spp. is larger than the subopercle, although both elements are of equal size in †*Toarcocephalus morlok*. Both taxa possess a slender lower jaw, although it is very short in *Coccolepis* at about half the length of the maxilla (López-Arbarello and Ebert, 2021); whereas in †*Toarcocephalus morlok*, the length of the lower jaw is greater than that of the maxilla. Both genera share few branchiostegal rays which are confined to the posterior region of the lower jaw, a sub-oval gular located roughly at the lower jaw midpoint, and a small trigger-shaped dermosphenotic bone which is likely not fused to the skull roof and contributes to the dorsoposterior margin of the orbit. However, †*Coccolepis* holds two fully developed tooth rows on the upper jaw and one on the lower jaw (Hilton et al., 2004), unlike †*Toarcocephalus morlok* which only holds a single tooth row on both the upper and lower jaws.

†*Coccolepis* *liassica* is the closet taxon to †*Toarcocephalus morlok* in regard to stratigraphy and palaeobiogeography, although it is still spatially and temporally distant, being found exclusively from the Sinemurian stage of Lyme Regis, UK (Woodward, 1891; Forey et al., 2010). The most detailed description and updated diagnosis for this taxon is provided by Gardiner (1960), however, further work on this species is needed to resolve its problematic generic affinities within †Coccolepididae: Hilton et al. (2004) and López-Arbarello and Ebert (2021) supported the assignment of †*C. liassica* to †Coccolepididae, but not to the genus †*Coccolepis*. The skull bones of †*C.*

*liassica* are covered with ganoine, and the ornamentation consists of coarse tubercles that sometimes merge, producing rugae (Gardiner, 1960; López-Arbarello and Ebert, 2021; pers. observ. SC). The ornamentation pattern is much weaker in the new taxon: the maxilla is smooth, with ganoine absent on the external skull bones. The teeth are very small and numerous on the jaws of †*C.* *liassica* but are strikingly larger and fewer in number, with the largest row of teeth being more widely spaced, in †*T. morlok*. †*Coccolepis* *liassica* possesses two tooth rows on the lower jaw (Gardiner, 1960), unlike *T. morlok*. †*Coccolepis* *liassica* is further differentiated from †*T. morlok* by a posterior deepening of the mandible (much shallower in †*T. morlok*); the dorsal margin of the maxilla plate being flat rather than strongly convex; a subopercle larger than the opercle (both equal in †*T. morlok*); and a taller and broader preopercle, encapsulating the entire dorsal margin of the maxillary plate. Branchiostegal rays are also more numerous in †*C.* *liassica* (15 vs. 9; Gardiner, 1960). The stratigraphic isolation and contrasting anatomical landmarks between the two taxa suggest that †*C.* *liassica* most likely represents a unique genus of coccolepidid distinct from both †*Coccolepis* and †*Toarcocephalus morlok*. †*Coccolepis* *liassica*, in addition to the species †*Condorlepis woodwardi* (Waldman, 1971) and †*Sunolepis yumenensis* Liu, 1957, further differ from the two species of †*Coccolepis* and †*T. morlok* on the basis that they all possess an opercle that is smaller than the subopercle (Liu, 1957; López-Arbarello and Ebert, 2021).

†*Condorlepis groeberi* (López-Arbarello et al., 2013) from the Tithonian of Patagonia is similar to †*Toarcocephalus morlok* in the shared presence of an elongated lower jaw which is equal to- or larger than the maxilla; a mandibular sensory canal confined to the ventral margin of the dentary; and branchiostegal rays confined to the posterior half of the mandible. However, unlike in †*T. morlok*, the dorsal margin of the maxillary plate is flat, rather than being obtusely convex, with the slim mandible of †*Co. groeberi* becoming drastically deeper towards the posterior. The supracleithrum and cleithrum are roughly equal in size in †*Co. groeberi*, although the supracleithrum is disproportionately much larger in the new Toarcian species. The branchiostegal rays are noticeably wider and better pronounced with rounded distal margins in †*Co. groeberi*, whereas they are skinnier and placed more posteriorly in †*T. morlok* gen. et sp. nov.

The Upper Jurassic †*Morrolepis aniscowitchi* (Gorizdor-Kulczycka, 1926) of Kazakstan and *M.*

*schaefferi* Kirkland, 1998, from Utah both differ from †*Toarcocephalus morlok* by the presence of a thin splint-like supracleithrum, branchiostegal rays being shorter and wider and originating close to the mandibular symphysis, and the opercle being noticeably taller than the subopercle (see Kirkland, 1998; Skrzycka, 2014).

†*Plesiococcolepis hunanensis* from the Early Jurassic of China is of a similar chronostratigraphic age, although is spatially distant from the new Holzmaden coccolepidid. Both †*P. hunanensis* and †*Toarcocephalus morlok* share the following characteristics (based on diagnosis in Wang, 1977): large teeth evenly spaced on the lower jaw; subopercle taller than long. †*Plesiococcolepis hunanensis* differs from †*T. morlok* by the opercle being larger than the subopercle, and the smaller teeth on the maxilla being tightly packed together (Wang, 1977). The smaller teeth are more spacious with tooth crowns rarely touching one-another in †*T. morlok*. The ornamentation patterns are poorly described in †*P. hunanensis*, although stated as possessing “projecting tuberosities” which are not seen in †*T. morlok*. Both species also possess a highly arched margin of the maxilla, the presence of rounded corners on the opercle, and an elongate supracleithrum that is larger than the cleithrum. Based on Wang’s (1977, fig. 1b) cranial reconstruction, the rostrum is somewhat expanded to form a considerable overbite relative to the anterior margin of the lower jaw in †*P. hunanensis*; a feature not shared with the new Holzmaden coccolepidid.

Although not currently included in †Coccolepididae, the enigmatic Sinemurian species †*Cosmolepis ornatus* (Egerton, 1853) from Dorset is somewhat comparable to the new Toarcian coccolepidid fish, and thus is relevant to compare and contrast here. Both taxa share the presence of size differentiated teeth in the external jaws with the tallest crowns being well pronounced; skull roof finely tuberculated; and the operculum and jaw bones being somewhat smooth and without tubercles (Woodward, 1890a; Forey et al., 2010). †*Toarcocephalus morlok* differs from †*Cos. ornatus* in the presence of a shallow lower jaw which is proportionately more elongate; a massive angular; teeth which project backwards as opposed to slightly forwards (Forey et al., 2010); and a subopercle in †*Cos. ornatus* that is disproportionate in size relative to the opercle. †*Cosmolepis ornatus* is salient for its well mineralized squamation comprising a full body covering of small to medium palaeoniscoid scales that are weakly ornate with ridged gan-

oine. Egerton (1853) describes the presence of “surface ornament [on the cheek and jaws] composed of fine vermicular plaits of enamel, arranged for the most part in a longitudinal direction”. This feature is well developed in the holotype of †*Cosmolepis ornatus* (NHMUK PV P. 557) but absent in †*Toarcocephalus morlok*. †*Cosmolepis* also possesses numerous branchiostegal rays, which extend along almost the entire length of the lower jaw, and according to Woodward (1890a) are strongly striated, without a gular plate. Branchiostegals number far fewer and are strictly confined to the posterior corner of the mandible in †*T. morlok* (Figure 2).

†*Toarcocephalus morlok* is therefore diagnosable from all other coccolepidid fishes by the following combination of characters: opercle and subopercle equal in size; maxilla shorter than the lower jaw with a strongly convex postorbital plate; single row of teeth on the upper and lower jaw composed of tall crowns which are each separated by several smaller crowns; angular massive; maxilla unornamented; lower jaw extremely narrow and elongate, shallow posteriorly; skull roof weakly tuberculated; opercular and supracleithrum bones weakly punctate; branchiostegal rays short, narrow and confined to the posterior margin of the mandible; premaxilla deeper than anterior region of the maxilla; premaxillary teeth larger than the maxillary teeth; preopercle short, extending as high as the subopercle; opercle with rounded margins; supracleithrum larger than cleithrum and externally punctate (Figure 6).

Like other coccolepidids, †*Toarcocephalus morlok* shares with †*Birgeria*, Polyodontidae and several acipenserids the very large supracleithrum, which is larger than cleithrum (López-Arbarello et al., 2013). Although less pronounced than in †*Condorlepis*, the subopercle of †*T. morlok* also forms an anteriorly directed anterodorsal process, which is similar to the process observed in acipenserids (Hilton et al., 2011: appendix III, character 27). Similarly, the absence of supraorbital bones is another feature shared between †*T. morlok* and other coccolepidids, which is a synapomorphy of Acipenseriformes according to Hilton et al. (2011: appendix III, character 9).

**Range.** Confined to the type locality of Holzmaden, *tenuicostatum* Zone, Toarcian, Early Jurassic.

## DISCUSSION

### Evidence for SMNS 59978 Being a Regurgitalite

Regurgitalites are an ethological class ofomalite traces representing fossilized vomit (oral ejecta) that has been regurgitated by a consumer (Seilacher, 2002; Hunt, 1992; Hoffman et al., 2019; Gordon et al., 2020; Cooper et al., 2021; Serafini et al., 2022). They are characterized by a tight compaction of skeletal remains usually retaining a degree of articulation, often show evidence of acid etching produced by the consumer’s stomach acids, and lack any associated coprolitic material (Myhrvold, 2012; Hoffmann et al., 2019; Qvarnström et al., 2019; Gordon et al., 2020; Freimuth et al., 2021; Serafini et al., 2021).

Regurgitalites (syn. speiballen) are scarcely documented from the Posidonienschiefer: Keller (1977) described a juvenile ichthyosaur with a tightly coiled vertebral column interpreted as the regurgitated meal of a larger ichthyosaur; a second probable regurgitalite containing ichthyosaur bones from Dotternhausen was figured by Jäger (2005, fig. 43). Thies and Hauff (2012) described a multitaxon regurgitalite allegedly containing remains of five fishes (four †*Dapedium* sp. and jaw fragments of †*Lepidotes* sp.). Cooper et al. (2021) figured three additional fish-bearing regurgitalites with single inclusions of †*Dapedium* sp., †*Pholidophorus* sp., and a juvenile †*Pachycormus macropterus*. Most recently, Cooper and Maxwell (2022, fig. 3b-c) figured a large accumulation of disarticulated and brecciated bones containing the anterior portion of the pachycormid fish †*Saurostomus esocinus*, and remains referable to †*Saurorhynchus* sp. and †*Leptolepis* sp. interpreted to be the remains of a regurgitated slurry. Regurgitalites are therefore rare in the Posidonienschiefer despite being deposited under conditions favouring exceptional fossil preservation.

SMNS 52044 consists of a mostly articulated skull and the disrupted portion of the axial skeleton. The surviving portion of the postcranium is mostly disarticulated with the bones densely clustered together behind the skull. The central bone mass is tightly packed with individual elements accumulated together and disarticulated; thereby providing a key indicator for the presence of a regurgitalite (Serafini et al., 2022). Scavenging or abiotic disarticulating factors like water currents would cause bones to become scattered across a wide periphery, resulting in bones becoming isolated, displaced, or hydrodynamically grouped by size (Beardmore and Furrer, 2016; Serafini et al.,

2022). The sclerotic ring has disarticulated; however, the displaced bones are confined to the skeletal mass rather than being displaced away from the skeleton as one would expect to see from an abiotic disarticulation event. Upon ejection from the consumer's alimentary canal, the bones were likely held together by a mucus-like adhesive, which prevented them from dispersing and becoming scattered on the sea floor. The low energy, soupy-substrate, and oxygen-depleted sea floor of the Posidonia Shale Sea (Seilacher, 1982; Riegraf et al., 1984; Martill, 1993; Röhl et al., 2001) further assisted in the excellent preservation potential of the regurgitalite. We can therefore rule out an abiotic or scavenging event as causation for the type of bone accumulation in SMNS 52044. The fish preserved within the regurgitalite is incomplete, as some areas of the postcranium are missing. This indicates that either the fish was incompletely consumed, or that some parts of the fish were not regurgitated. Alternatively, the partially digested fish may have been fully regurgitated into several separate masses distributed apart from one another.

Regurgitated bones and teeth may preserve delicate etching traces, the severity of which is generally governed by the length of time for which the prey was exposed to stomach acids whilst inside the consumer's gut (digestion window) before being regurgitated (Keller, 1977; Hoffmann et al., 2019; Cooper et al., 2021). Unfortunately, SMNS 52044 has undergone rough mechanical preparation that has abraded large areas of the external bone surfaces; therefore, any delicate etching traces have likely been destroyed. Overall, the close compaction of the bones within a confined central bone mass, good articulation of the skull, absence of visible phosphatic material (an indicator of coprolites), or bones displaced away from the central mass, strongly supports the identification of SMNS 52044 as a regurgitalite.

The digestion window was evidently short, being halted by regurgitation within likely only a few hours of ingestion. We conclude this on the basis that the mechanical damage to the prey fish was only prolonged enough to collapse the weakly ossified vertebral column, but not enough to disarticulate the denser cranial bones. The coccolepoid was therefore likely preyed on within the Holzmaden area, implying that the fish was autochthonous to the Posidonienschiefer Formation, rather than having been preyed on elsewhere and transported for a long distance inside of the predator's gut.

In contrast, SMNS 59978 only preserves the skull with no indication of any post-cranial elements in the surrounding matrix. The bones of the skull are mostly perfectly articulated with the exception of the pre-orbital region, which is incomplete due to specimen damage. This unusual degree of incompleteness is unlikely to result from normal decay on the sea floor, especially given the good articulation quality of the remaining skull bones. Likewise, the specimen does not show any biological evidence for having had been regurgitated. There is a possibility that the fish was decapitated in a predation event with the severed head representing the leftovers (pabulite – Klug et al., 2021) of the predator's meal. This hypothesis would explain why the skull is almost fully articulated whilst the body of the fish is entirely absent. The incomplete but articulated lateral line scales also abruptly end within the vicinity of the pectoral girdle, thereby supporting a decapitation explanation rather than a decay-related disarticulation scenario.

SMNS 52044 is significant because it represents the first coccolepoid fish to be preserved as a regurgitalite. This reveals that coccolepidids contributed to the diet of an unknown piscivorous predator in the Posidonia biotope. The producer of the regurgitalite is unknown, but see Thies and Hauff (2012) for a review of likely regurgitate-producing candidates in the formation. Marine crocodylomorphs (†*Thalattosuchia*) are identified as the most plausible candidates for the †*Dapedium* regurgitalite described in Thies and Hauff (2012); however, thalattosuchians are extremely rare in the *tenuicostatum* Zone (Figure 1D) with only a single find having been documented (Hauff, 1921). A small ichthyosaur, a hybodontiform shark, or even a large coleoid cephalopod, are more plausible candidates on account of their varied diets, moderate body size, and co-occurrence with coccolepidids in the *tenuicostatum* Zone of the Holzmaden area (Hauff and Hauff, 1981; Thies and Hauff, 2012) (Figure 7).

### Coccolepidids in Marine Environments

The Posidonienschiefer Formation offers a rare combination of a shallow to moderately deep continental marine basin, in which oxygen became depleted numerous times during the Toarcian (Röhl et al., 2001; Klug et al., 2021). For the section at Holzmaden, sea level is interpreted as being lowest towards the base of the formation within the *tenuicostatum* Zone (Riegraf et al., 1984; Röhl et al., 2001; Schmid-Röhl et al., 2002). The progres-





**FIGURE 7.** Palaeoart depiction of †*Toarcocephalus morlok* gen. et sp. nov. swimming in the twilight of the Posidonia Shale Sea. The post-cranium is based on †*Coccolepis liassica* and †*Coccolepis bucklandi*. Artwork by S. Cooper.

sive marine transgression up-sequence is associated to a progressively receding regional shoreline, with Holzmaden representing a more proximal, shallow water near-shore environment only in the lower beds (*tenuicostatum* Zone) where the coccolepidid specimens were found (bed  $\epsilon$ II<sub>1</sub>). Coccolepidid material is not observed above bed  $\epsilon$ II<sub>1</sub>, with their disappearance in the assemblage likely correlating with the rising sea level and shallow-water habitat loss in the area; and/or decreasing water column oxygenation.

The vast majority of coccolepidids are found exclusively in fresh water or occasionally brackish terrestrial environments (see Olive et al., 2019: table 2; Table 1), although there are a few rare exceptions to this rule. Coccolepidids found from marine environments include †*Coccolepis liassica* from the Lower Lias of England, and the two true species of †*Coccolepis* (†*C. bucklandi* + †*C. solnhofensis* – see López-Arbarello and Ebert, 2021) from the Solnhofen Plattenkalk, but are a rare faunal component of their respective faunal assemblages, with each species only being known by a handful of specimens (e.g., Gardiner, 1960; Hilton et al., 2004; Ebert et al., 2021; López-Arbarello and Ebert, 2021). *Coccolepis* spp. likely inhabited nearby reefs in the Solnhofen Archipelago, hence their rarity in the lagoonal deposits. A similar model is proposed for non-gyrodontid pycnodontiforms

(†Pycnodontiformes), which despite their high diversity are noticeably rare in the lagoonal faunas of the Solnhofen Plattenkalks (Ebert, 2016; Capasso, 2021; Cawley et al., 2021). Described materials of †*Coccolepis liassica*, †*Coccolepis bucklandi*, and †*C. solnhofensis* mostly comprise of complete and fully articulated fishes, which in the absence of regular terrestrial input into the Solnhofen Plattenkalk (e.g., Wellnhofer, 2009; Arratia et al., 2015) rules out the possibility that they were transported from a freshwater terrestrial setting. These coccolepidid taxa were evidently adapted to survive in fully-marine conditions, although their distribution does appear to have been controlled by water depth, with the Lias of Lyme Regis, the lower beds of the Posidonienschiefer Formation in Holzmaden, and the Solnhofen Plattenkalk each representing fairly shallow and near-shore coastal environments (Riegraf et al., 1984; Röhl et al., 2001; Hilton et al., 2004; Lord and Davis, 2010).

#### Coccolepidid Evolution in the Early Jurassic

†Coccolepididae first appears in the fossil record in the lowest Jurassic, with the oldest probable species, †*Coccolepis liassica*, described from the Lower Lias of Lyme Regis (Woodward, 1895; Gardiner, 1960). The precise collection horizon is unspecified for †*C. liassica*, with the cliff exposure at Lyme Regis composed of Lower Jurassic rocks



**TABLE 1.** Jurassic coccolepidids and their inferred palaeoenvironments.

Taxon	Locality	Age	Environment	Reference
' <i>Coccolepis</i> ' <i>liassica</i> Woodward, 1890	Lyme Regis, Dorset, UK	'Lower Lias' (Hettangian – Pliensbachian)	Shallow marine platform	Woodward, 1890; Forey et al., 2010
<i>Toarcocephalus mortlok</i> gen. et sp. nov.	Holzmaden, Baden- Württemberg, Germany	tenuicostatum Subzone, early Toarcian	Marine epipelagic	This study
<i>Plesiococcolepis</i> <i>hunanensis</i> Wang, 1977	Yumushan, Zhoushi mining region, Hunan Province, China	"Early Jurassic"	"Freshwater"	Wang, 1977; Skrzycka, 2014
<i>Morrolepis schaefferi</i> Kirkland, 1998	Utah, USA	Kimmeridgian – Tithonian	Freshwater floodplain	Kirkland, 1998
<i>Morrolepis andrewsi</i> (Woodward, 1891)	Purbeck, Dorset, UK	Late Jurassic - Early Cretaceous	Freshwater/ brackish lagoon	Woodward, 1891; Hilton et al., 2004
<i>Morrolepis aniscowitchi</i> (Gorizdor-Kulczycka, 1926)	Kazakhstan	Callovian/Oxfordian	Freshwater paleolake	Skrzycka, 2014
<i>Iyalepis rohani</i> (Sytchevskaya and Yakovlev, 1985)	Vladimirovka, Baikal Region, Siberia	Early-Middle Jurassic	Freshwater	Sytchevskaya, 2006
<i>Condorlepis groeberi</i> (Bordas, 1943)	Chubut, Argentina	Oxfordian – Tithonian	Freshwater lacustrine	López-Arbarello et al., 2013
<i>Coccolepis bucklandi</i> Agassiz, 1843	Bavaria, Germany	Tithonian	Proximal marginal lagoon	Hilton et al., 2004; López-Arbarello and Ebert, 2021
<i>Coccolepis solnhofensis</i> López-Arbarello and Ebert, 2021	Bavaria, Germany	Tithonian	Proximal marginal lagoon	López-Arbarello and Ebert, 2021
' <i>Coccolepis</i> ' <i>australis</i> Woodward, 1895	Talbragar, New South Wales, Australia	Late Jurassic	Freshwater	Woodward, 1895; Hilton et al., 2004
<i>Sunolepis yumenensis</i> Liu, 1957	Yumen, Gansu Province, China	Late Jurassic or Early Cretaceous	Freshwater	Liu, 1957; Hilton et al., 2004

dating between the Hettangian – Pliensbachian (Lord, 2019). Forey et al. (2010) attributes all known specimens of this species to the Sinemurian-aged beds based on their similar matrix. The only other described Early Jurassic coccolepidid, †*Plesiococcolepis hunanensis*, was recovered from a freshwater deposit in Hunan Province (China), although precise stratigraphic data is also lacking for this species. Both †*C. liassica* and †*P. hunanensis* are considered to be morphologically plesiomorphic members of †Coccolepididae on the basis that they both retain pelvic bones – a feature which is secondarily lost in younger coccolepidids, including †*Coccolepis* (Hilton et al., 2004; Skrzycka, 2014). The private Schandelah coccolepidid specimen apparently lacks ossified pelvic bones (Hauff et al., 2017), indicating that the loss of these elements in coccolepidid evolution occurred prior to the Toarcian. The pelvic region is unknown in the Holzmaden material.

According to Skrzycka (2014), coccolepidids most likely evolved in Europe during the earliest Jurassic, where they underwent a rapid palaeobiogeographic radiation, reaching as far as northeast Russia and central China by the beginning of the Middle Jurassic. Precise stratigraphic data for †*Plesiococcolepis* is unknown, so it is uncertain as to which point during the Early Jurassic coccolepidids first appeared in southern China. If this hypothesis is correct, then it would imply that coccolepidids first evolved in the marine realm, and later colonized freshwater habitats, something that has been proposed for many other fish lineages (Cavin et al., 2008; Cavin, 2017; Cavin et al., 2020). This hypothesis also fits with the results of Betancur-R et al. (2015), which demonstrated colonization and diversification dynamics in extinct actinopterygians to be asymmetrical between habitats, with marine lineages transitioning more frequently into freshwater habitats than the reverse. The Middle – Late Jurassic saw the highest diversity and

richest global distribution of Coccolepididae, with species described from Australia (†*Coccolepis australis* Woodward, 1895), Patagonia (†*Condorlepis groeberi* López-Arbarello et al., 2013), Siberia (†*Iyalepis rohani* (Sytychevskaya and Yakovlev, 1985)), Kazakhstan (†*Morrolepis aniscowitchi* (Gorizdro-Kulczycka, 1926)), the central United States (†*Morrolepis schaefferi* Kirkland, 1998), southern England (†*Morrolepis andrewsi* [Woodward, 1891]), and SE Germany (†*Coccolepis bucklandi* and †*Coccolepis solnhofensis* López-Arbarello and Ebert, 2021) (see Table 1). Coccolepidid diversity drastically declined after the Jurassic-Cretaceous boundary, with a few freshwater species persisting into the Early Cretaceous of southern England (†*Coccolepis* sp., Wealden Supergroup – Forey and Sweetman, 2011), Belgium (†*Barbalepis macroptera* (Traquair, 1911); Olive et al., 2019), southeast Australia (†*Condorlepis woodwardi* (Waldman, 1971); López-Arbarello et al., 2013), and possibly Yumen (Gansu Province), China (†*Sunolepis yumenensis* Liu, 1957; López-Arbarello and Ebert, 2021). This tendency of freshwater environments to serve as evolutionary refugia is a common pattern that is broadly documented in the Mesozoic fish record (Cavin, 2017) and is supported by analysis of ancestral states in Actinopterygii (Betancur-R et al., 2015); it remains an actively researched hypothesis that was first proposed by Charles Darwin (Cavin et al., 2008). The cause of the extinction of †Coccolepididae is unknown; the group entirely vanished by the Albian – Cenomanian stages of the Cretaceous (Olive et al., 2019).

### Unresolved Interrelationships of Coccolepididae

The placement of Coccolepididae within Actinopterygii has changed several times and remains controversial (e.g., Woodward, 1891; Gardiner, 1960) with some recent authors proposing its inclusion within Chondrostei (Hilton et al. 2004; López-Arbarello et al., 2013; Olive et al., 2019) based on some shared characters with Acipenseriformes. Some authors disagree with this grouping (Schultze and Arratia, 2015), with Schultze et al. (2021) proposing possible referral of †Coccolepididae to a non-monophyletic grouping Palaeoniscimorpha on the basis that two of the unique characters of Chondrostei (symphysis between endochondral upper jaw bones, and absence of premaxilla and maxilla) are absent in coccolepidids. However, Schultze et al. (2021) does not discuss the synapomorphies shared between †*Condorlepis groeberi*

and the Acipenseriformes: a parasphenoid with a median anterior process; an opercle smaller than the subopercle; the anterior margin of the subopercle with an anteriorly directed anterodorsal process; a single ventral caudal fulcrum; presence of a pectoral fin spine (Hilton et al., 2011: appendix III, characters 17, 22, 27, 52, 53); and the lateral line bending upwards and continuing in the body lobe following the bases of the caudal fin rays. Furthermore, †*Condorlepis* shares with †*Birgeria* and the Polyodontidae a very long and narrow supra-cleithrum, and along with several acipenserids, a supra-cleithrum which is as large or larger than the cleithrum (López-Arbarello et al., 2013). In †*Condorlepis* the antorbital bone is peculiarly shaped, resembling an inverted ‘Y’, as is the case with the most anterior lateral bone in the infraorbital series of *Acipenser* or †*Peipiaosteus* (López-Arbarello et al., 2013). The presence of an opercle that is smaller than the subopercle (Hilton et al. 2004) is irregularly distributed across †Coccolepididae, seen in †*Condorlepis* but not †*Coccolepis* and †*Morrolepis* (Skrycka, 2014; Schultze et al., 2021). Until rigorously tested with a phylogenetic analysis surveying characters across both Chondrostei and the taxa grouped in the non-monophyletic Palaeoniscimorpha, the true interrelationships of †Coccolepididae within Actinopterygii will remain debatable.

### CONCLUSIONS

A new genus and species of coccolepidid fish, †*Toarcocephalus morlok* gen. et sp. nov., is described from the Lower Jurassic Posidonien-schiefer Formation of southern Germany. Coccolepididae is reported for the first time from the Toarcian stage of the Early Jurassic, thereby bridging an outstanding gap in the fossil record. †*Toarcocephalus morlok* is diagnosed by the following characters: a large postorbital expansion of the maxilla that is strongly convex and unornamented; the lower jaw is longer than maxilla and is shallow posteriorly; the opercle is equal in size to the subopercle, with a short preopercle that only extends as high as the subopercle; a single row of teeth on the upper and lower jaw which are size graded (1 tall: 2-4 short: 1 tall); teeth well-spaced and recurved; few brachiostegeal rays restricted to the posterior end of the lower jaw; skull roof very weakly tuberculated; operculum and pectoral girdle smooth with fine punctae. Based on its patchy fossil record, †Coccolepididae originated in the earliest Jurassic, likely in the marine setting of the Western Tethys, but quickly dispersed into terres-

trial settings to become a predominately freshwater group from the Middle Jurassic onwards. The Holzmaden coccolepidid was easy prey for an unknown piscivore(s) in the assemblage, as both known specimens of this species show evidence of being predated on: one is preserved as a regurgitalite and the other as a decapitated pabulite.

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