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# The oldest teleosts (Teleosteomorpha): their early taxonomic, phenotypic, and ecological diversification during the Triassic

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# Abstract

As the fossil record reveals, neopterygians had a major diversification after the great mass extinction at the Permian-Triassic boundary, including the appearance of the major clade Teleosteomorpha. Detailed studies of new taxa (*Pseudopholidoctenus germanicus*, *Barschichthys ruedersdorfensis*, and *Ruedersdorfia berlinensis*) from the lower Anisian (middle Muschelkalk) of Germany and their comparisons with other Triassic relatives are presented, including new information concerning size, shape, and diet. Two families, Pholidophoridae and Marcopoloichthyidae, made a modest appearance during the Anisian of Europe and Asia almost simultaneously, with *Pseudopholidoctenus* (and the teleosteomorphs *Barschichthys* and *Ruedersdorfia*) from the Germanic Basin, being the oldest stem teleosts (244 Ma), followed shortly by *Marcopoloichthys ani* from Italy. The early teleostean diversification was fast—already in the late Ladinian three lineages were present: Prohalecitiidae (Europe), Pholidophoridae (Asia, Europe), and Marcopoloichthyidae (Asia, Europe), with ca. 20 species inhabiting the Tethys Ocean during the Middle–Late Triassic. Most Triassic teleosteomorphs were small, ca. 50 mm standard length, and a few as possibly miniature, with torpedo or oblong shapes, and suction feeders—probably a plankton based-diet. These first Triassic radiations were replaced during the early Sinemurian of marine ecosystems of Europe with two major groups: (a) non-monophyletic 'pholidophoriforms' and (b) proleptolepids and leptolepids, having an average size (ca. 100 mm SL) longer than Triassic forms, with oblong and fusiform shapes. A fast dispersion from the Tethys to the Paleo-Pacific followed, as demonstrated by the presence of small (ca. 50 mm SL) suction feeder proleptolepids in the early Sinemurian of Chile.

# Key Words

body shape, ecosystems, feeding, Mesozoic, miniaturization, morphology, radiation, systematics, taxonomy

# Introduction

About two hundred years ago, Agassiz (1832) described two species of his new genus *Pholidophorus (P. latiusculus* and *P. pusillus*) from the upper part of the middle Norian (Upper Triassic) of Seefeld, Austria (Brandner and Poleschinski 1986). In 1843, he added several Jurassic species to *Pholidophorus*, a list that increased considerably by Woodward (1895), who recognized many Jurassic species, disregarding the Triassic ones; Woodward's taxonomy was followed by nearly all researchers because of his prestige. His authoritative opinion was taken to the extreme when an Early Jurassic species from the Lower Lias of Dorsetshire, *Pholidophorus bechei*, was considered by Woodward as the type species, because it was better known, an approach that was followed even by Nybelin (1966) in his review of certain 'pholidophoriforms'. More recently, Arratia (2013) revalidated the Late Triassic species *Pholidophorus latiusculus* as the type species and removed the Early Jurassic *Ph. bechei* from *Pholidophorus* and placed it in a new genus, *Dorsetichthys* (Arratia 2013: p. 118).

In contrast to the speciose Jurassic so-called 'pholidophoriforms' (sensu Arratia 2000), Triassic pholidophorids were described rarely. A Carnian (lower Late Triassic) species was described by Kner (1866), a Norian (Late

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Triassic) species by Gortani (1907), and a Rhaetian (Late Triassic) species by Airaghi (1908). Zambelli (1975, 1977, 1980a, b, c, 1990) revised Triassic pholidophorids related to the holotype Pholidophorus latiusculus that were recovered in fossiliferous sites near Bergamo, Lombardy, northern Italy (e.g., Cene, Ponte Giurino, and Endenna). He erected several pholidophorid genera (e.g., Parapholidophorus, Pholidoctenus, Pholidorhynchodon, and Eopholidophorus) and species from two main Norian localities near Bergamo (Cene and Ponte Giurino). At the same time, Griffith (1977) erected a new pholidophorid genus and species, Pholidophoretes salvus, among other Carnian fishes in the northern Alps (Lunz, Austria). Almost 40 years later, Arratia (2013, 2017) provided detailed taxonomic revisions of previously described Triassic pholidophorids from Europe and erected a few new genera (e.g., Annaichthys, Lombardichthys and Zambellichthys) and species and provided extensive morphological descriptions. Based on these taxa and additional teleosts, Arratia (2013) proposed a phylogenetic hypothesis of these Triassic pholidophorids within Teleosteomorpha or stem-based teleosts. These European Triassic pholidophorids are restricted to the Late Triassic, from the Carnian to the Rhaetian, and to marine deposits in the southern and northern Alps. Research on Middle Triassic (late Ladinian) fishes from southern China has added important information to the knowledge of pholidophorids and early teleosteomorphs, with the discovery of a new genus (Malingichthys) with two species, which were interpreted as the oldest pholidophorids and oldest teleosts (Tintori et al. 2015). The new genus Malingichthys extended not only the paleogeographic area of pholidophorids to East Asia, but also extended the time, back to middle late Ladinian. Currently, the oldest European teleosteomorph is Prohalecites porroi Tintori, 1990, also from the Middle Triassic (late Ladinian; ca. 240 Ma) of Italy. Recently, the range of teleosteomorphs has been enlarged by the description of new taxa: Marcopoloichthys ani from the Anisian of China (Tintori et al. 2007), M. andreetti and M. faccii from the Norian of Italy (Tintori et al. 2007), and Seinstedtia parva Schultze et al. (2022) from the Norian Fuchsberg Quarry near Seinstedt, Lower Saxony (Schultze et al. 2022: fig. 2), which is the first described Triassic teleosteomorph for Germany.

Whereas the finds from Italy, Austria and China are from the open marine Tethys, the teleosteomorph specimens from Rüdersdorf are from the restricted marine basin of the Central European Basin (Germanic Basin). Up to 2021, there was a single mention of basal teleosteomorphs for Germany; a skull roof identified as *Pholidoctenus* sp. from Rüdersdorf was figured by Schultze and Kriwet (2021) outside the Tethys (see below for new taxonomic assignment). Only recently, small teleosteomorph fishes were described from an upper Norian/lower Rhaetian locality in the central European Basin (Seinstedt, Lower Saxony; Schultze et al. 2022).

New findings and/or revision of fossiliferous localities or specimens, or the acquisition of new knowledge sometimes

give unexpected results. A single finding that was previously mentioned as *Pholidoctenus* sp. by Schultze and Kriwet (2021), is restudied herein, plus two other new fishes from the same locality (Rüdersdorf near Berlin, Germany). These fishes indicate an even earlier appearance of stem teleosts or teleosteomorphs in the Anisian (lower Middle Triassic) in a paleogeographic region where no teleosteomorphs were previously reported, the European (Germanic) Triassic basin (lower Muschelkalk) of Rüdersdorf near Berlin. These fishes and all other early teleosts, their sizes and body shapes, geographic distributions, and ecosystems are discussed here in the complex framework of early teleostean diversification during the Triassic.

#### Geological site

The Muschelkalk Quarry Rüdersdorf, 25 km east of the center of Berlin, is a historic source of building stone and cement for the city of Berlin (Schroeder 2015). The quarry has been in operation for hundreds of years. The Muschelkalk (from upper lower to lower upper Muschelkalk) is exposed as an island in between Pleistocene deposits. The Muschelkalk is moved to the surface by movement of the underlying Zechstein salt. Marine fossils (bivalves, crinoids and many others) are known throughout the sequence. The most common and best known vertebrates are nothosaurids (Raab 1907; Schröder 1914; Rieppel and Wild 1996); single bones are common, but also complete specimens have been found. Schröder (1914) described different species of Nothosaurus, but after Rieppel and Wild (1996), only one species, Nothosaurus marchicus, is recognized in the Muschelkalk of Rüdersdorf. Other marine reptiles are rare (in the lower Muschelkalk: Cymatosaurus according to Huene 1944 and Omphalosaurus after Maisch and Lehman 2002), and the black, rounded crushing teeth of Placodus are also known. Shark teeth have been found in the middle Muschelkalk (Acrodus lateralis, Hybodus plicatilis, Palaeobates (Strophodus) angustissimus; see Raab 1907 and Picard 1916) and in the upper Muschelkalk (Acrodus, Palaeobates; see Raab 1907), as well as actinopterygian teeth in the middle Muschelkalk (Gyrolepis tenuistriatus and Colobodus; see Raab 1907 and Picard 1916) and upper Muschelkalk (Colobodus and Saurichthys; see Raab 1907). Additionally, scales broadly assigned to "Semionotus" have been known for a long time. Recently, the private collectors, Mr. W.-W. Tornow and Mr. E. Barsch, have found complete and nearly complete fishes from horizons in the Mittlerer Muschelkalk, but most specimens of teleosteomorphs are represented by isolated skull roofs as described below.

#### Stratigraphy

Zwenger (1993: see fig. 4.1.26 for Mittlerer Muschelkalk) and Kramm and Hagdorn (2020: tab. 2) described the

System	Series	Stage	Rüdersdorf sequence	Stem teleosts
TRIASSIC	201.3	Rhaetian		Parapholidophorus caffii
	Z08.5-	Norian		Seinstedtia parva Marcopoloichthys faccii Pholidoctenus spp. Parapholidophorus nybelini Pholidorhynchodon malzannii Lombardichthys gervasuttii Pholidophorus latiusculus Annaichthys pontegiurinensis Zambellichthys bergamensis
	_ 227-	Carnian		Knerichthys bronni Pholidophoretes salvus
	- 237 -	Ladinian	239.5 a Glaukonitkalk	Malingichthys spp. Prohalecites porroi Marcopoloichthys furreri
	241- JUDDIW	Anisian	Image: Second state of the	Marcopoloichthys ani gen. et sp. nov.: Pseudopholidoctenus germanicus Barschichthys ruedersdorfensis Ruedersdorfia berlinensis
	-246.5-			

Scheme 1. Diagrammatic representation of the Triassic geological system, with special reference to the Rüdersdorf sequence, and a distribution of stem teleosts.

stratigraphic sequence of the Muschelkalk of Rüdersdorf based on earlier accounts. The Muschelkalk of Rüdersdorf reaches from the upper lower Muschelkalk into the lower upper Muschelkalk (Scheme 1). The new fishes described here occur in the lower part of the middle Muschelkalk, in the orbicularis-Schichten (= Unteres Karbonat) and in the above Untere Wechsellagerung. The "Fischmergel" forms the base of the Untere Wechsellagerung and is separated from the underlying orbicularis-Schichten by a 3-m thick bench of dolomite. Few fish remains are known from the Oberer Muschelkalk (Glaukonitkalk). The small specimens described here were collected in the so-called "Fischmergel" near the base of the Untere Wechsellagerung of the middle Muschelkalk, corresponding to middle Anisian (about 244 Ma; Kramm and Hagdorn 2021).

# Material and methods

The described fossil material is deposited in the fish paleontological collection of the Museum of Natural History, Berlin, Germany (**MB**). A broad comparison was done with other Triassic teleosteomorphs deposited

in the Geologische Bundesanstadt Wien Abteilung, Paläontologische Sammlungen, Vienna, Austria (GBA); Department of Geology, University of Innsbruck, Innsbruck, Austria (Innsb); Civic Museum of Natural Science Enrico Caffi, Bergamo, Italy (MCSNB); Geowissenschaftliche Sammlungen, Zentralmagazin Naturwisssenschaftlicher Sammlungen, Martin Luther-Universität Halle-Wittenberg, Halle (Saale), Germany (MLU); Geological-Paleontological Section of the Naturhistorical Museum, Vienna, Austria (NHMW); and the Palaeontological Institut and Museum, University of Zurich, Switzerland (PIMUZ).

### Anatomical terminology

The terminology of the skull roof bones is based on homology and ontogeny (Schultze 2008 and Teng et al. 2019 and literature cited therein). The first time that the parietal and postparietal bones are cited in the text, as well as in figures, the traditional terminology is shown in square brackets, e.g., parietal bone [= frontal]: pa [= fr] and postparietal bone [= parietal]: ppa [= pa]. Since most of the fishes studied herein are represented by skull roof plates, the characteristics of the plates, including measurements and proportions (taken with a digital Vernier caliper), were compared with similar plates in other Triassic pholidophorids. Only complete exposed plates, preserved in dorsal view, were considered to make the values comparable. To avoid misunderstanding concerning these measurements, these are explained below (see Fig. 1).



Figure 1. Pholidophorid skull roof illustrating possible measurements. See text for explanation.

The skull roof length (= SRL) is taken from the most anterior to the most posterior margins of the plate. The orbital region is the area of the plate bordering the eyes dorsally; the length of the orbital region or orbital region length (= ORL) is taken from the most anterior margin of the plate to the dorso-posterior margin of the orbit, at the region of the plate corresponding to the autosphenotic or sphenotic corner (it includes the parietal [= frontal] bones). The **postorbital region** is the area of the plate extending between the autosphenotic regions to the posterior margin of the plate (it includes the supratemporotabulars [= dermopterotics] and postparietal [= parietal] bones); the postorbital region length (= PORL) is taken from the level of both autosphenotics to the posterior margin of the plate. The nasal region is the most anterior area of the plate, usually triangular in shape, and articulating laterally with the nasal bones and occasionally, depending on the taxon, with the rostral; the nasal region length (= NRL) is taken from the most anterior tip of the plate to the posterior line forming the triangle. The nasal region width (= NRW) is taken at the base of the triangle corresponding to this region. The mid-orbital region width (= PORW) is measured at the mid-region of this area, and the postorbital region width is taken at the broadest point of the postorbital region or postparietal plus supratemporotabulars [= dermopterotic] area. The postorbital region width (POW) is measured as the broadest point of the region.

For body size analyses of Triassic stem teleosts, we compiled data on their total and standard lengths (= maximum standard length of Romano et al. 2016) at species level. Incomplete taxa (e.g., Zambellichthys Arratia, 2013 known only by the head) were excluded. Most fishes studied here have hemiheterocercal tails; thus, the standard length was measured from the most anterior tip of the head to the last scale carrying the lateral line and ending approximately at the mid-region between the dorsal and ventral posterior body lobes. Thus, sometimes identification of the last scale carrying the lateral line is not possible due to incomplete preservation or the scales are not preserved or displaced, making any identification difficult. The body shape of the stem Triassic pholidophorids was studied, as well certain anatomical complexes, such as the jaws and their position in the head and their dentition, with the aim to identify possible feeding habits. It is noteworthy to mention that the quality of preservation of most Triassic stem teleosts is generally very good to excellent.

#### Illustrations

Illustrations are based directly on the specimens. The drawings were done with the help of a camera lucida attached on a WILD stereomicroscope M5A. Except for the photographs of the new taxa described here, which were taken with a Nikon R9 and 30 mm lens, all others were taken by professional photographers working for the various academic institutions as listed in Acknowledgements.

### Systematic Paleontology

Teleosteomorpha Arratia, 2001 Pholidophoriformes sensu Arratia, 2013 Pholidophoridae Woodward, 1890 sensu Arratia, 2013

#### Pseudopholidoctenus gen. nov.

https://zoobank.org/A3980B26-695C-477E-98E9-1A960AD85DAC

Type species. Pseudopholidoctenus germanicus sp. nov.

#### Pseudopholidoctenus germanicus sp. nov.

https://zoobank.org/CC8072F4-A28E-42EA-91D9-3D45809E1BBD Figs 2–6

2021 Pholidoctenus sp. Schultze and Kriwet: p. 321, fig. 11.

**Diagnosis.** (Based on a unique combination of characters among stem teleosts. Autapomorphies are identified with an asterisk [\*].) Small fish of about 55 mm total length. Skull roof bones covered by small tubercles and ridges of different sizes. The length of the nasal region is about 30% of the midorbital width (Table 1). The length of the postorbital region is about 50% of the orbital region length [\*]. Deep opercle about five times deeper than the subopercle. Suture between opercle and subopercle slightly oblique. Ventral limb of cleithrum straight and narrow, lacking a posterior expansion at the confluence of both limbs. With a series of large scales or scutes, almost square-shaped, preceding the epaxial lobe of the caudal fin [\*]. Less than 18 principal caudal rays present [\*]. No hypaxial procurrent rays present [\*]. Scales covered with a smooth layer of ganoine. Posterior margin of the scales with a few conspicuous acute projections or serrae.

**Derivatio nominis.** The name refers to the similarity of the skull roof and serrations on bones and scales to the genus *Pholidoctenus* from the Norian of Italy.

**Type material.** *Holotype*. MB. f. 18641, a well-preserved skull roof including sensory cephalic cranial system.

**Paratypes.** MB. f. 19904, almost complete specimen (missing the anterior part of the head and distal tips of the caudal fin rays), relatively well preserved considering the hardness of the rock and problems cleaning the surface of bones without destroying them. MB. f. 19905 and 19906, skull roofs.

**Provenience.** Opencast mine in Rüdersdorf, 25 km east of the center of Berlin, Germany.

Age. Lower Middle Triassic, lower Anisian (middle Muschelkalk).

**Description.** This is a small species of about 55 mm total length and about 36 mm SL. Specimen MB. f. 19904, with the body and squamation preserved in situ, is a rare one in a locality where the fishes are usually preserved as disarticulated bones (Fig. 2). The anterior part of the head is missing, and since the body is slightly bent, it is not possible to estimate its body shape accurately; possibly, it was oblong, and the peduncle depth seems to be half of the predorsal depth. The pectoral fins are missing, and the pelvic fins are incompletely preserved. The dorsal fin is placed at about half the length of the fish, and the anal is placed posteriorly, very close to the ventral margin of the caudal fin.

*Skull roof.* The nicely preserved skull roof (8.3 mm long and 7.5 mm wide at the postorbital region) has all dermal bones fused into a large plate (Fig. 3), with the exception of the rostral and nasal bones that are not preserved. The skull roof plate is almost triangular, being narrow anteriorly at the so-called triangular nasal region and expanding

posteriad, reaching its maximum width at the supratemporotabular [= dermopterotic] level and ending in a straight line (Fig. 3). A posterior process is absent in the posterior margin of the supratemporotabular region. The skull roof looks like a flat plate having a straight profile. Most of the skull roof is formed by the orbital region whose length is about 62% of the total length of the skull roof. The small triangular nasal region is short, and its length is about 11% of the skull roof length (Table 1). The lateral margins of the nasal region would articulate with the nasal bones that are not preserved, but considering the oblique position of both sutures for the nasal bones, it is assumed here that the rostral bone had an anterior position in front of the nasals. The orbital region is narrower than the postorbital region, with the width at its mid-region being ca. 33% of the postorbital region width (Table 1).

The skull roof (Fig. 3) does not show obvious sutures, but there is a slight median overgrowth in the region where both parietals [= frontals] would fuse, a tenuous, incomplete suture where both postparietals [= parietals] would meet, and a tenuous suture separating the short and small right supratemporotabular [= dermopterotic]. According to this interpretation, the parietal region would be the largest component of the skull roof, forming the whole orbital region and extending into the postorbital region. There is no process at the lateral margin at the confluence of the nasal and orbital regions of the plate. The lateral margin of the plate, at the supratemporotabular region, shows an invagination that may be occupied by the dorsal margin of the suborbital or an accessory suborbital, as in Pholidoctenus serianus (Zambelli 1977; Arratia 2013) and Ph. sanpellegrinensis (Arratia 2017). There is no evidence of a supraoccipital bone and/or epiotics at the posterior region of the plate.

The preorbital region of the skull roof plate that is formed by the fusion of both parietals occupies a significant part of the plate (Table 1). In contrast, the anteriormost narrow orbital region is about 30% of the postorbital region. This gives the skull roof characteristic proportions and shape (see section "Morphological



**Figure 2.** *Pseudopholidoctenus germanicus* gen. et sp. nov. in lateral view (MB. f. 19904) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Scale bar: 1 cm.



**Figure 3.** *Pseudopholidoctenus germanicus* gen. et sp. nov. (holotype MB. f. 18641) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). **A.** Photograph of skull roof. **B.** Interpretative drawing. Abbreviations: a.pl, anterior pitline; m.pl, middle pitline; ot.c, otic canal; pa+ppa+asp+stt [= fr+pa+asp+dpt], parietal+postparietal+autosphenotic + supratemporotabular [= frontal+parietal+autosphenotic+dermopterotic]; ppa.b, postparietal branch; p.pl, posterior pitline; sor.c, supraorbital canal; sp, pore of sensory canal. Scale bar: 1 mm (**A**).

 

 Table 1. Approximate skull roof proportions in certain European stem teleosts with well-preserved skull roofs. The measured specimens are identified by their catalogue numbers. Abbreviations: NRL, nasal region; ORL, orbital region; ORW, orbital mid-region width; PORW, postorbital region: SRL, skull roof length.

Species	ORL/SRL	PORL/ORL	NRL/SRL	NRL/PORW	NRW/PORW	PORW/SRL
Barschichthys ruedersdorfensis gen. et sp. nov. (MB f. 19907)	58%	68%	_	—	150%	35%
Parapholidophorus nybelini (MCSNB 3220)	78%	30%	22%	52%	20%	84%
Pholidoctenus serianus (MCSNB 3095)	73%	36%	16%	43%	32%	96%
Pholidoctenus sanpellegrinensis (MCSNB 13207)	63%	58%	15%	46%	32%	80%
Pholidophoretes salvus (NHMW 170/0293)	62%	60%	19%	57%	31%	94%
Pseudopholidoctenus germanicus gen. et sp. nov. (MB f. 18641)	62%	50%	11%	33%	32%	93%
Ruedersdorfia berlinensis gen. et sp. nov. (MB f. 19910)	52%	90%	7.7%	22%	86%	34%
Seinstedtia parva (MLU Sei.2010.76)	61%	63%	16.6%	40%	77%	32.8%

comparisons and taxonomic assignments"). The anterior nasal region of the plate is triangular-shaped, and acting as sutural margins for the nasal bones, an interpretation based on other pholidophorids and teleosteomorphs with the bones in situ. Following such an outline and by comparisons with *Pholidoctenus serianus* and *Ph. sanpellegrinensis*, it is hypothesized here that both nasals were medially sutured in part of their medial contact surfaces. The posterolateral corner of the orbital region is the area corresponding to the autosphenotic or sphenotic, which in this case, is fused to the parietal laterally and supratemporotabular [= dermopterotic] posteriorly.

The surface of the skull roof is covered by a thin layer of smooth ganoine; small tubercles and ridges covering the whole skull roof are observed under high magnification.

The supraorbital sensory canal (Fig. 3B) is visible (on both sides) through the bone, with few small pores, irregularly placed and opening on the surface directly on the trajectory of the canal. The supraorbital sensory canal extends posteriad, ending in the postparietal branch, just anterior to the middle pitline. The supraorbital canal, nicely preserved, shows that there is not a lateral connection with the infraorbital canal, neither with the otic canal whose trajectory (and pores) is partially visible in the right supratemporotabular region of the plate. Three pitlines (Fig. 3B) are clearly visible on the postorbital region. The longest one is the middle pitline that extends from near the mid-region of the plate to the lateral margin of the supratemporotabular region. The short anterior pitline is placed in continuation of the postparietal branch, and the posterior pitline, equally short, extends near the posterior margin of the skull roof plate.

*Circumorbital bones and suborbital region.* Only the posterior part of the circumorbital ring is preserved (Fig. 4) and includes the dermosphenotic and two partially preserved dorsoposterior infraorbitals that probably correspond to infraorbitals 4 and 5. The suborbital region, placed between the dorsoposterior infraorbitals anteriorly and the opercle and preopercle posteriorly, is unclear. It could include one large suborbital or two suborbitals.

**Opercular bones.** The opercle and subopercle, and a small fragment of the preopercle (Fig. 4) are preserved.



**Figure 4.** *Pseudopholidoctenus germanicus* gen. et sp. nov. (MB. f. 19904) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Drawing of cranium and pectoral girdle in lateral view. Hatched areas represent areas that are destroyed or too poorly preserved to allow a description. Arrows point to small serrations. Abbreviations: br.r, branchiostegal rays; b.sob, broken suborbital; b.stt [= dpt], broken supratemporotabular [= dermopterotic]; cl, cleithrum; ?exc, ?extrascapula; op, opercle; pcl, postcleithra; pop, section of preopercle; scl, supracleithrum; sop, subopercle.

The opercle is a large bone, almost five times deeper than the subopercle. It is almost oval-shaped dorsally, expanding slightly at its mid-region and suturing with the subopercle throughout a slightly oblique suture. One small serration is preserved at the posterior margin.

The small subopercle has an oval-shaped ventral contour; its short anterodorsal process is at the confluence of the preopercle, opercle, and subopercle. The three opercular bones have smooth exposed surfaces. The posterior section of three narrow branchiostegal bones are preserved below the subopercle.

**Paired girdles and fins.** A section of a stout, long and narrow lower arm of the cleithrum (Fig. 4) is preserved; the angle of the lower arm is characteristically shaped and implies that the upper section of the cleithrum was short. An elongate and moderately broad supracleithrum is posterior to the opercle and dorsal part of the cleithrum. The trajectory of the lateral line canal is not visible. Three approximately rectangular-shaped elements, scale-like, are positioned posterior to the supracleithrum and cleithrum and are interpreted here as postcleithra. Postcleithra 2 and 3 are slightly displaced and partially

covering each other. There is no information on other pectoral girdle bones or pectoral rays.

The pelvic basipterygium is covered by scales so that information is not available, and the fin is represented by a few, incomplete preserved pelvic rays.

**Dorsal and anal fin.** An incompletely preserved dorsal fin (Fig. 5) is placed slightly anterior to the mid-length of the body trunk, slightly posterior to the incompletely preserved pelvic rays, and it does not oppose the anal fin (Fig. 2). A broad, slightly oval and short scute precedes four paired basal fulcra that are leaf-like and are followed by at least nine dorsal rays, seven with broken bases and two that are displaced. An elongate and broad fringing fulcrum is placed between the last basal fulcrum and the first principal ray, and it is followed by a series of elongated fringing fulcra that decrease in size distally. The first principal ray, only segmented and not branched, has a long base; the following principal rays have also long bases that become thinner posteriad. The bases of the dorsal rays are surrounded by enlarged, thick scales (Fig. 5).

Remains of anal rays (Fig. 6) are preserved posteriorly in the body. Remnants of five anal rays, incompletely



**Figure 5.** *Pseudopholidoctenus germanicus* gen. et sp. nov. (MB. f. 19904) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Dorsal fin and surrounding scales. Abbreviations: b.fu, basal fulcra; f.fr, fringing fulcra; sc, scales; 1st.dr, first principal dorsal ray.



**Figure 6.** *Pseudopholidoctenus germanicus* gen. et sp. nov. (MB. f. 19904) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Posterior part of body illustrating squamation and caudal and anal fins. Arrows point to serrations. Abbreviations: a.fr, anal fin rays; e.bfu, epaxial basal fulcra; f.fr, fringing fulcra; h.bfu, hypaxial basal fulcrum; r.ry, rudimentary ray; L.PR, last principal ray; scu, scutes or enlarged scales; 1st.PR, first principal ray.

preserved, almost reach the anterior margin of the hypaxial lobe of the caudal fin.

*Caudal fin.* The fin lacks its middle-posterior part; it seems to be hemiheterocercal, with an abbreviated dorsal

scaly lobe (Fig. 6). Preceding the dorso-anterior margin of the fin is a series of scutes that apparently were in continuation with the posterior part of the dorsal fin, which is missing. The series of scutes is in continuation with three basal fulcra that are lanceolate in shape with their median posterior margin bifurcated. An incomplete series of elongate fringing fulcra follows. The fin seems to have few principal rays; 14 rays are preserved, and apparently there are not more; their segmentation is mainly straight. The number of principal rays is fewer than in the Italian genus *Pholidoctenus* with 18 to 22 principal rays (Arratia 2013, 2017). Remains of one hypaxial basal fulcrum is preserved; this fulcrum is followed by a series of elongate fringing fulcra. According to the preservation, procurrent rays are absent in the hypaxial lobe of the caudal fin, which is another major difference with species of *Pholidoctenus*.

*Scales and scutes.* Ganoid scales of lepisosteid-type of different sizes and shapes cover the body. Most scales of the dorsal and ventral rows of the flank are rhombic, rectangular or even square-shaped, with a variable number of small serrations at their posterior margin. Apparently, the three main rows of the flank, just posterior to the upper half of the opercle, are deeper and larger than other posterior scales (Fig. 2). The scales decrease in size posteriad and have different shapes, but they are not preserved well enough for a detailed description.

The scales at the posterior region of the dorsal margin anterior to the dorsal fin seem to be enlarged in comparison to dorsolateral scales (Figs 2, 5). The median scales placed posterior to the dorsal fin are incompletely preserved, but there are at least four large, square-shaped scales preceding the epaxial basal fulcra (Fig. 6).

#### **Teleosteomorpha Arratia, 2001**

#### Family Barschichthyidae family nov.

#### https://zoobank.org//D155CF4E-8F48-436B-B35F-65D6DCAD8C06

Diagnosis. (Based on a unique combination of characters among stem teleosts. Autapomorphies are identified with an asterisk [\*].) Small fishes about 80 mm total length. The skull roof plate is unique in that its anterior region lacks the triangular nasal region [\*] present in most Triassic teleosteomorphs. The anterior margin of the skull roof plate is expanded [\*] and markedly lobated [\*], giving a unique aspect to the skull roof among teleosteomorphs (Fig. 7). Anterodorsal profile of head gently rounded. Left and right lateral extrascapulars present. One median extrascapular present [\*]. Extrascapulars lacking the anterior 'roll-over' characteristic of pholidophorids. Anterodorsal region of the posttemporal medially positioned. One large, rectangular-shaped suborbital bone. Maxillary blade expanding posteriad [\*]. A tiny supramaxilla 1 contrasts with a large supramaxilla 2 covering most of dorsal margin of maxilla. Lower jaw long, slightly protruding anteriad, with articulation for quadrate placed posterior to posterior margin of orbit. Skull roof covered with tubercles of ganoine of different sizes. Supramaxilla, maxilla and lower jaw covered with longitudinal ridges of ganoine. Ganoid scales of anterior part of body with few serrations on posterior margin. Markedly difference in size between lateral line scale row and dorsal scale rows, and slight decrease in size between lateral line scale row and the next two ventral rows; oval-shaped scales or scute-like below pectoral girdles and fins.

#### Barschichthys gen. nov.

https://zoobank.org/670FBC57-19CF-44C3-B2ED-01181A82FB7E

Type species. Barschichthys ruedersdorfensis sp. nov.

#### Barschichthys ruedersdorfensis sp. nov.

https://zoobank.org/D2B43AEC-EA84-42F9-B4CF-407B96671C23 Figs 7–9

Diagnosis. Same as family diagnosis.

**Derivatio nominis.** The names of the family and of the genus are dedicated to Mr. Enrico Barsch, who from an early age (ca. 15 years old) began to collect in the mine of Rüdersdorf, which is characterized by unique but few fossils in durable, hard-to-work stone. Thus, after years of search and careful work, Mr. Barsch has gathered an important collection studied herein and he also donated part of the collection to the Museum of Natural History (MB) in Berlin.

**Type material.** *Holotype.* MB. f. 19907, a well-preserved skull roof including sensory cephalic cranial system and ornamentation.

**Paratypes.** MB. f. 19908, a well-preserved skull roof including ornamentation. MB. f. 19909, specimen of about 50 mm standard length, preserving the lateral view of the head and part of the trunk, which is interpreted as belonging to the same species due to the orbital region that is expanded anteriorly and broadly expanded posteriorly (though broken), as well as having the same ornamentation as in the holotype and paratype.

**Provenience.** Opencast mine in Rüdersdorf, 25 km east of the center of Berlin, Germany.

Age. Lower Middle Triassic, lower Anisian (middle Muschelkalk).

Description. The head and anterior part of the body of MB. f. 19909 provide information on cranial bones and the pectoral girdle and their relationships and on the scales of the anterior body (Fig. 8). Patchy regions covered with tubercles are badly preserved on some of the lateral head bones and some scales. The head has its anterodorsal profile almost rounded, and the long lower jaw is slightly protruding anteriad (Fig. 9). Although the skull roof of the specimen is partially destroyed showing parts of left and right broken bones, it is evident that the head at the level of the extrascapulars is deeper than long. The diameter of the orbit is small, ca. 25% of the head length. Specimens MB. f. 19907 and MB. f. 19908 differ in the distance between orbits or mid orbital region width (PORW), but they are interpreted here as belonging to the same species because they share some unique features such as lacking the nasal region (NRL) of the skull roof



**Figure 7.** *Barschichthys ruedersdorfensis* gen. et sp. nov. from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). **A.** Photograph of skull roof (holotype MB. f. 19907). **B.** Interpretative drawing. **C.** Photograph of skull roof (MB. f. 19908). **D.** Interpretative drawing. Abbreviations: dsp, dermosphenotic; d.dsp, displaced dermosphenotic; ep, epiotic; fon, anterior cranial fontanel; i.s, incomplete suture; m.exc, median extrascapula; m.pl, middle pitline; ot.c, otic canal; pa+ppa+asp+stt [= fr+pa+asp+dpt], parietal+postparietal+autosphenotic+supratemporotabular [= frontal+parietal+autosphenotic+dermopterotic]; sor.e, supraorbital canal. Scale bars: 5 mm.

plate, having an expanded and undulated anterior margin of the skull roof, and a similar postorbital region structure and proportions and sharing the same characteristic ornamentation. The difference in the mid-orbital region width may indicate sexual differences, a hypothesis that should be tested when more specimens become available.

*Skull roof bones.* Specimen MB. f. 19907 is a nicely preserved skull roof of ca. 19 mm long and 14 mm width at the postorbital region, with all dermal bones fused into a large, characteristically-shaped plate (Fig. 7), with the exception of the rostral and nasal bones that are not preserved. Still, some incomplete suture lines can be observed. Posteriorly, remains of a lateral extrascapula and a median extrascapula are preserved. The skull roof plate is expanded anteriorly, ending on a broadly undulated or lobated margin and expanding posteriad, reaching its maximum width at the supratemporotabular [= dermopterotic] level and ending in a gently curved line. The skull roof looks like a flat plate; however, the first impression is deceptive, because the lateral margins on the

anterior part of the plate are lateroventrally inclined, with the mid-section of the parietal regions of the plate, slightly higher than the lateral orbital margins; the lateral margins of the postorbital region are gently inclined lateroventrally. Most of the skull roof is formed by the orbital region whose length is about 58% of its total length. The small triangular nasal region (Figs 1, 3) present in *Pseudopholidoctenus* gen. nov. is absent here, but the anterior margin is broad; it is ca. 150% of the midregion of the orbital width. Because of the position of the supraorbital sensory canal on the skull roof plate lying closer to the midregion than to the lateral margins, there is the possibility that the nasals were very broad bones, joining at their medial margins and that the rostral bone was anterior to the nasals.

The skull roof (Fig. 7) does not show complete sutures separating bones, but there is a tenuous incomplete suture where both parietals [= frontals] meet, and another tenuous and incomplete suture separating partially the parietal and postparietal regions. Unlike other Triassic teleosteomorphs, a small oval fontanel separates left and right halves of the



Figure 8. *Barschichthys ruedersdorfensis* gen. et sp. nov. (MB. f. 19909) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin) illustrating head and anterior part of trunk in lateral view. Scale bar: 5 mm.

skull plate anteriorly in one skull roof, but it is almost closed in another specimen. As in *Pseudopholidoctenus germanicus* gen. et sp. nov., the parietal region would be the largest component of the skull roof, forming the whole orbital region and extending into the postorbital region. The lateral margins of the plate at the supratemporotabular region are ventrolaterally expanded and carry the otic canal, which is incompletely preserved. There is no evidence of a supraoccipital bone. Suturing with the posterior margin of the plate, there are pieces of the lateral extrascapulae and a median extrascapula preserved (Figs 7, 9). Their anterior margin is smooth and not presenting the so-called thick "roll-over" that characterizes the extrascapulars in pholidophorids, which have only two extrascapulars, not three, as in the case of this fish.

The anterior nasal region of the plate is absent in this fish (compare Fig. 1 and Fig. 7), an interpretation based on other pholidophorids and teleosteomorphs with the region in situ. The broad anterior margin of the skull plate would articulate with the nasal bones, but only one nasal is incompletely preserved, forming an angle of almost 90 degrees with the parasphenoid. The relationship among the anterior margin of the plate, nasals, and rostral (not preserved) is unknown. Due to its size and position, the nasal bone would be part of the anterior region of the circumorbital region. The posterolateral corner of the orbital region is the area corresponding to the autosphenotic or sphenotic, which in this case, is fused to the parietal laterally and supratemporotabular [= dermopterotic] posteriorly.

The surface of most of the skull roof is covered by tubercle-like ornamentation that cannot be described properly due to irregularities in shape and position of the tubercles; however the ornamentation seems to be lacking in the anterior lobated region of the plate. The supraorbital sensory canal (Fig. 7) and otic canal are visible in certain regions where the ornamentation is not preserved. No sensory pores opening on the surface have been observed. Only discontinuous sections of the middle pitline (Fig. 7) are visible on the postparietal plus supratemporotabular region; these are very difficult to observe because of the density of the ornamentation in the isolated skull roof plates, and the surface is damaged in MB. f. 19907 and MB. f. 19909.

**Braincase.** The braincase is covered by bones, and only sections of the interorbital septum and parasphenoid (Fig. 9) are preserved. A posterior section of the interorbital septum covers half the orbit in specimen MB. f. 19909. A section of the ascendent process of the parasphenoid can be observed in this specimen. Teeth or their sockets are not observed, so they are interpreted as absent. Posteriorly, the parasphenoid expands dorsally, but it is laterally covered by the suborbital so that the extension of the ascendent process is unknown. There is another ventrolateral extension that could be an incompletely preserved basipterygoid process.

*Circumorbital bones and suborbital region.* The description is based on MB. f. 19907 with the circumorbital ring partially preserved (Fig. 9) and includes infraorbitals 1 to 3 and the dermosphenotic. There is no evidence of supraorbital bones. Infraorbital 1 is a large, oval-shaped bone, slightly expanded anterodorsally. Infraorbital 2 is short and triangular-shaped. Infraorbital 3 is a large bone slightly rectangular-shaped and extending below the suborbital, reaching the opercular region. Infraorbitals 4 and 5 are not preserved, but remnants of an incomplete dermosphenotic are preserved in MB. f. 19908 and MB. f. 19909. One large, rectangular-shaped suborbital is surrounded by the dorsoposterior infraorbitals anteriorly (not preserved), the opercle posteriorly, and infraorbital 3 ventrally. The



**Figure 9.** *Barschichthys ruedersdorfensis* gen. et sp. nov. from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Drawing of skull roof (MB. f. 19909). Hatched marks represent areas that are destroyed or too poorly preserved to allow a description. Abbreviations: b.dsp, broken dermosphenotic; b.na, broken nasal bone; b.pop, broken preopercle; br.r, branchiostegal rays; br.skr, broken skull roof; cl, cleithrum; ent, entopterygoid; exc, extrascapulae; gu?, gular plates?; io1-3, infraorbitals 1-3; iop, interopercle; lj, lower jaw; op, opercle; orb, incomplete orbital septum; par, parasphenoid; pcl1-3, postcleithra 1-3; pmx, premaxilla; ptt, posttemporal; sc, scale; smx1-2, supramaxillae 1-2; sob, suborbital; sop, subopercle.

trajectory of the infraorbital canal can be seen in infraorbitals 1–3, but no branches or pores are visible.

*Upperjaw.* The maxilla and supramaxillae are preserved. An enlarged, narrow premaxilla is preserved as an imprint. The maxilla (Fig. 9) is moderately long, reaching just below the posterior margin of the orbit. However, it is unclear how the posterior margin of the maxilla ended, because the maxilla is broken at its posterior margin. Its anterior articular process is short and narrow in comparison to the maxillary blade that is narrow anteriorly and expands posteriad, with the posterior margin being almost double the depth of the anterior blade. The oral margin (at least at its posterior half) carries small conical teeth; some of these teeth are covered by the oral margin of the bone, but they are seen throughout the bone. The posterior supramaxilla (Fig. 9) is a large, oblong bone that covers about half of the posterior part of the dorsal margin of the maxilla. Below

the anterior end of the supramaxilla, there is a tiny bone that is interpreted here as the anterior supramaxilla. The maxilla and supramaxillae are covered with elongate lines of ganoine, giving both bones a striated aspect.

*Lower jaw.* The lower jaw (Fig. 9) is an elongate bone, with a curved ventral margin, partially exposed below the maxilla, with its posterior region poorly preserved and extending posterior to the maxilla. Consequently, the articulation between lower jaw and suspensorium was posterior to the posterior margin of the orbit. The limit between the dentary and angular is not preserved as well as the trajectory of the mandibular canal. At least, in the posterior part of the jaw, some ridges covered with ganoine are preserved.

*Opercular bones.* The opercle, subopercle, fragment of the preopercle, and an interopercle (Fig. 9) are preserved. The opercle is slightly larger than the subopercle (with its dorsal margin broken; Fig. 9) and characteristically

shaped. Its suture with the subopercle is oblique. The broad subopercle has an almost oblique ventral margin, which becomes slightly rounded posteriorly; its small anterodorsal process is broken and is anteriad directed. The preopercle is represented by some pieces so that a description is not possible, except to propose that the bone was short dorsally because of the position and relationships between the suborbital and opercle. The interopercle is preserved below the preopercle and interopercle, so that it is possible to assume that it was an elongate bone.

**Branchiostegal rays and gular plate.** Remnants of a few, narrow branchiostegal rays are preserved below the interopercle (Fig. 9). Below the posterior part of the lower jaw and opercular region, two elongate bones are preserved, and because of their position, they can be interpreted as being median bones. Thus, these are interpreted here as possibly two gular plates (Fig. 9).

*Pectoral girdle and fin.* It is unclear if one of the scalelike bones that is broken posterior to the extrascapular

bones could be interpreted as a large posttemporal, having a medial position to the supracleithrum (Fig. 9). The dorsal part of the supracleithrum is partially exposed posterodorsal to the opercle. The cleithrum is a long bone whose ventral part is preserved, but the surface of its dorsal, narrower section is partially destroyed. The bone lacks a well-pronounced curvature and extends ventrally below the interopercle and branchiostegal rays, so that it is not possible to observe whether a clavicle was present anteriorly. Remains of the serrated appendage are preserved along the medial, ventral section of the bone. Three scaly types of postcleithra (Figs 9, 10) are present. The first one is the longest of the series and the second one is somewhat oval shaped. Postcleithrum 2 has serrations at its posterior border, but since postcleithra 1 and 3 have their posterior margin poorly preserved, it is unknown whether more serrations were present. There are remains of ornamentation on the lower part of postcleithrum 3 that are shown in Fig. 10.



**Figure 10.** *Barschichthys ruedersdorfensis* gen. et sp. nov. from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Drawing of a section of the lateral trunk illustrating mainly scales and postcleithral bones (MB. f. 19909). Abbreviations: or, ornamentation (tubercles); pcl1-3, postcleithra 1-3; pec.r, broken pectoral rays; sc, scales; scl, supracleithrum. Arrows point to large oval scales or scutes.

Posterior to the posteroventral curvature of the cleithrum, a few broken rays (Fig. 10) are present, but their poor preservation does not allow a description.

*Scales.* The ganoid type of scales covering the body seem to be thick. There is not a distinct row of scales (Fig. 10) carrying the lateral line that can be described as significantly deeper than the next ventral body scale row; however, there is a significant difference between the lateral line scales and the dorsal series of scales that are smaller. The scales carrying the lateral line and those just above and below are rectangular, with short serrations at their posterior margin that are mostly destroyed. Ventrally, the series of scales become smaller and oval. In the ventral midline, or close to it, below the pectoral girdle and pectoral fin, some larger and oval-shaped scales or scutes are present (Fig. 10). Some of them still have preserved rounded or elongate tubercles of ganoine on their surface.

#### Teleosteomorpha Arratia, 2001 Family incertae sedis

#### Ruedersdorfia gen. nov.

https://zoobank.org/94004D17-F2D9-4962-937E-ADB3724C4C5A

Type species. Ruedersdorfia berlinensis sp. nov.

#### Ruedersdorfia berlinensis sp. nov.

https://zoobank.org/F3FFD837-0DBF-4650-AD87-B223884B53C6 Fig. 11

**Diagnosis.** (Based on a unique combination of characters among stem teleosts. Autapomorphies are identified with an asterisk [\*].) The skull roof plate resulting from the fusion of parietal, postparietal, autosphenotic, and supratemporotabular is characteristic in that the orbital region is almost as long as the postorbital region, and the width of the midorbital region is about half the width of the postorbital region ([\*]; Table 1). The length of nasal region is less than 10% of the cranial plate [\*], being a small one among Triassic teleosteomorphs. Middle pitline short, not reaching the lateral margin of the supratemporotabular region [\*]. Skull roof plate covered by a characteristic ornamentation (Fig. 11).

**Derivatio nominis.** The genus name is dedicated to the place of origin (Rüdersdorf) plus the ending "ichthys", for fish. The species name refers to the town of Berlin, indicating the geographic position of the quarry, that is located 25 km east of the center of Berlin (Germany).

**Type material.** *Holotype.* MB. f. 19910, a well-preserved skull roof including characteristic ornamentation.

*Paratypes.* MB. f. 14888, a skull roof plate preserved as impression. MB. f. 19911, a well-preserved skull roof including sensory canal system.

**Provenience.** Opencast mine in Rüdersdorf, 25 km east of the center of Berlin, Germany.

Age. Lower Middle Triassic, lower Anisian (middle Muschelkalk).

**Description.** This taxon is represented by three nicely preserved skull roofs of ca. 18 mm length and 11 mm width at the postorbital region, with all skull dermal bones fused into a plate, with the exception of the rostral and nasal bones that are not preserved. The skull roof plate (Fig. 11) is narrow anteriorly at the so-called triangular nasal region and slightly expands posteriad, reaching its maximum width at the supratemporotabular [= dermopterotic] region; the skull roof plate ends in almost a straight line, with a small process that is exposed at the posterolateral corner of the supratemporotabulars in the paratypes. The skull roof differs from all other taxa studied here and other teleosteomorphs in that the orbital region is as long as the postorbital region (Table 1). The small triangular nasal region is short and its length is about 8% of the skull roof length. Considering the oblique position of both sutural surfaces for the nasal bones and the lateral exits of the supraorbital canal, it is assumed here that nasal bones were placed laterally to the median rostral bone. The orbital region is slightly narrower than the postorbital region, with the width at its mid-region ca. 33% of the postorbital region width (Table 1).

The skull roof (Fig. 11) does not show sutures or incomplete ones. The anteriormost, narrow orbital region is the smallest among the skull roofs studied here, and in addition, its anterior margin is slightly rounded, unlike other preorbital regions that commonly are triangular-shaped. This gives the skull roof characteristic proportions and shape (see Table 1 and section on Morphological comparisons and taxonomic assignments). There is no evidence of a supraoccipital bone. The exposed portion of the epiotics at the posteroventral region of the plate are well developed and conic in shape. The surface of the skull roof is covered by a layer of ganoine, characteristically ornamented (Fig. 11).

The supraorbital sensory canal is visible through the bone, with a characteristic trajectory, with few small pores, irregularly placed and opening directly on the surface. The supraorbital sensory canal extends posteriad, ending in the postparietal, just anterior to the middle pitline. Thus, the last section of the canal can be interpreted as its postparietal branch. The supraorbital canal, nicely preserved, shows that there is not a lateral connection with the infraorbital canal, neither with the otic canal whose trajectory (and pores) is not visible in the supratemporotabular region of the plate. Two pitlines are clearly visible on the postorbital region. One is the middle pitline that is placed posterior to the anterior pitline, and is short, not extending to the lateral surface of the supratemporotabular region. The short anterior pitline is placed in continuation with the postparietal branch of the supraorbital canal, and apparently it does not contact the middle pitline.

# Morphological comparisons and taxonomic assignments

#### Pseudopholidoctenus germanicus gen. et sp. nov.

A broad comparison of the skull roof plate (Fig. 3) of *Pseudopholidoctenus germanicus* gen. et sp. nov., its



**Figure 11.** *Ruedersdorfia berlinensis* gen. et sp. nov. (holotype MB. f. 19910) from Rüdersdorf, near Berlin, Germany (central European Basin; Germanic Basin). Small arrrows point to the epiotics. **A.** Photograph of skull roof plate. **B.** Drawing illustrating details of ornamentation. Sensory canals and pit lines are not observed due to the thickness of the ornamentation. Abbreviation: lp.pr, latero-posterior process of the supratemporotabular area of the skull roof. Scale bar: 5 mm (**A**).

characteristic triangular shape, proportions and fusion of all bones was performed, including pholidophorids (with the characteristic skull roof, triangular in shape), other stem teleosts from the same locality, and other Triassic teleosteomorphs.

Triassic pholidophorids may have the skull roof plate covered with a smooth layer of ganoine or with a layer of ganoine ornamented with ridges and tubercles of different sizes (e.g., in *Lombardichthys* [*Pholidophorus*] gervasuttii, Annaichthys pontegiurinensis, Pholidorhynchodon malzannii, and Knerichthys [*Pholidophorus*] bronni; Arratia 2013). European pholidophorids with a thin ganoine cover and lacking ornamentation on the skull plate as in *Pseudopholidoctenus germanicus* gen. et sp. nov. are the genera *Pholidoctenus*, *Parapholidophorus*, and the Carnian *Pholidophoretes* (Arratia 2013). The three genera have slight differences in proportions of their skull roofs (compare Fig. 3 and Fig. 12B; Table 1): (1) *Parapholidophorus* has the longest and narrowest nasal region (Table 1) in contrast to other Triassic European pholidophorids; (2) *Pholidophoretes* has the shortest and broadest nasal region; and (3) *Parapholidophorus* has an irregular region and/or process at the lateral margin of the parietal region where the supraorbital 1 and nasal bone articulate (see Arratia 2013: figs 59, 61).

In all these European pholidophorids, all bones forming the skull roof are fused (although some specimens still retain incomplete sutures, especially in younger individuals). In contrast, the Chinese pholidophorid Malingichthys nimaiguensis (Fig. 12A) has fused parietals medially, while the supratemporotabulars [= dermopterotics] are separated and the postparietals are fused into one element (Tintori et al. 2015: fig. 4); furthermore, the separation of bones is complete in Malingichthys wanfenglinensis (Tintori et al. 2015: fig. 7). Although, as in the European pholidophorids, the skull roof is longer than broad, the length of the orbital region is ca. 59% of the total length of the skull roof so that the postorbital region is slightly longer than in European pholidophorids. In parallel, the midsection of the orbital region is comparatively broader (ca. 50%) than the postorbital region width in most European pholidophorids, except Pholidophoretes (see Table 1).

While the trajectory of the supraorbital sensory canal (Fig. 3) is clearly visible and showing a long canal in continuation with the parietal branch, ending just in front of the anterior pitline in *Pseudopholidoctenus germanicus* gen. et sp. nov., the canal is shorter in *Pholidoctenus serianus* and *Ph. sanpellegrinensis* (Arratia 2013: figs 78, 79; Arratia 2017). The number of pores in *Pseudopholidoctenus germanicus* is slightly variable between the left and right sides of the skull roof plate (Fig. 3), and it is also variable in *Pholidoctenus serianus* and *Ph. sanpellegrinensis* (Zambelli 1978; Arratia 2013: figs 78A, 79; Arratia 2017: figs 3, 4A). All mentioned pholidophorids, as well as *Pseudopholidoctenus germanicus*, have small sensory pores, lacking sensory tubules, just opening directly above the canal.

The only other known Triassic teleosteomorphs are *Prohalecites* from Ca' del Frate, northern Italy (Tintori 1990; Tintori and Lombardo 1999; Arratia 2013: fig. 95; Arratia 2017: fig. 9; Arratia 2022; Gouiric-Caballi and Arratia 2022: fig. 14), *Marcopoloichthys* from China, Italy and Switzerland (Tintori et al. 2007; Arratia 2022), and the recently described *Seinstedtia* (Schultze et al. 2022) from Germany. The skull roofs of *Prohalecites* (Fig. 12C) and *Marcopoloichthys* (Arratia 2022: figs 4, 5, 7) are not comparable with that of *Pseudopholidoctenus germanicus* from Rüdersdorf, Germany, because their skull roofs lack the characteristic triangular shape of pholidophorids, with the postorbital region significantly broader than the mid-orbital region. The skull roofs of *Prohalecites* and *Marcopoloichthys* are slightly broader at the postorbital

region in comparison to the orbital region (see Fig. 12C). Additionally, the skull roof of *Prohalecites* has a gently curved profile anteriorly, and most bones are independent. Although the skull roof of *Seinstedtia* has an overall shape similar to that in pholidophorids, its postorbital region is considerably broader than the orbital region (Fig. 12D). Additionally, *Seinstedtia* has several other morphological characters that separate the genus from pholidophorids, so it was interpreted as a teleosteomorph, family undetermined by Schultze et al. (2022).

Thus, the skull roof of *Pseudopholidoctenus germanicus* gen. et sp. nov. from Rüdersdorf, Germany has the characteristic shape found in members of Pholidophoridae sensu Arratia (2013), and in particular it has an overall similarity to those of the Italian *Pholidoctenus serianus* and *Pholidoctenus sanpellegrinensis*, although slight differences in proportions are present in the three species (Table 1). Because of the characteristics of the skull roof in different pholidophorids, we currently interpret the skull roof of MB. f. 18641, previously described as *Pholidoctenus* sp. by Schultze and Kriwet (2021) from the lower Anisian of Rüdersdorf, Germany as belonging to a new genus and species, *Pseudopholidoctenus germanicus*.

#### Barschichthys ruedersdorfensis gen. et sp. nov.

The other two new stem teleosts, Barschichthys ruedersdorfensis and Ruedersdorfia berlinensis, described above were recovered together with Pseudopholidoctenus germanicus in the same geological site in the middle Anisian (Middle Triassic) of the Germanic Basin (Scheme 1). The two new fishes represented by isolated skull roof plates (and one lateral view of the head and anterior part of the body) are so characteristic that they can be easily separated from each other and also from Pseudopholidoctenus germanicus. Although the three taxa share the fusion or incomplete fusion of cranial bones into one plate and the narrowing of the orbital region versus an expanded postorbital region, they have major differences in the nasal region, anterior margin of the skull roof and the trajectory of the supraorbital sensory canal when this canal is observed (compare Figs 3, 7 and Fig. 11).

The lateral view of the head of Barschichthys ruedersdorfensis gen. et sp. nov. has some overall similarities with that of members of the Late Jurassic family Archaeomaenidae from Gondwanan continents (e.g., Antarctica, Australia). One of the diagnostic features of archaeomaenids is a "broad cranial roof, with a ventral gently curvature of the antero-dorsal portion of the skull" (Bean 2021: p. 218); however, such apparent similarity is misleading, because the skull roof is also broad, but its shape is completely different from that in archaeomaenids, which lack the expanded anterior margin of the cranial roof plate present in Barschichthys ruedersdorfensis. In addition, the anterior margin of the parietal bones in archaeomaenids is straight, while it is irregular in Barschichthys ruedersdorfensis. Another diagnostic feature of archaeomaenids is "an almost horizontal suture between opercle and subopercle", whereas the



**Figure 12.** Schematic skull roof plates of Triassic teleosteomorphs illustrating variation in shape, proportions and fusion of bones. **A.** Chinese pholidophorid *Malingichthys nimaiguensis*. **B.** Italian pholidophorid *Pholidoctenus serianus*. **C.** Italian prohalecitid *Prohalecites porroi*. **D.** German indeterminate teleosteomorph *Seinstedtia parva*. Abbreviations: pa+asp [= fr+asp], parietal+autosphenotic [= frontal+autosphenotic]; ppa [= pa], postparietal [= parietal]; pa+ppa+asp+stt [= fr+pa+asp+dpt], parietal+postparietal+autosphenotic+supratemporotabular [= frontal+parietal+autosphenotic+dermopterotic]; stt [= dpt], supratemporotabular [= dermopterotic].

Table 2. Size, body shape, and paleoenvironments in Triassic pholidophorids.

Taxon	Body size	Body shape	Geographical	Environment	Age
	(SL in mm)		distribution		
BARSCHICHTHYIDAE family nov.					
Barschichthys ruedersdorfensis gen. et sp. nov.	?	oblong?	Germany	marine	middle Anisian
PHOLIDOPHORIDAE					
Annaichthys	$\pm 60$	oblong	Italy	marine	Norian
Knerichthys	±130	oblong	Italy	marine	Carnian
Lombardichthys	±72	oblong	Italy	marine	Norian
Malingichthys maiguensis	±65	fusiform	Asia	marine	late Ladinian
M. wanfenglinenssi	$\pm 48$	fusiform	Asia	marine	late Ladinian
Parapholidophorus caffii	$\pm 49$	oblong	Italy	marine	Rhaetian
P. nybelini	$\pm 60$	oblong	Italy	marine	Norian
Pholidoctenus serianus	±55	fusiform/oblong	Italy	marine	Norian
Ph. sanpellegrinensis	±55	fusiform/oblong	Italy	marine	Norian
Pholidophoretes	±72	?	Italy	marine	Carnian
Pholidophorus	±75	oblong	Italy	marine	middle Norian
Pholidorhynchodon	$\pm 140$	oblong	Italy	marine	Norian
Pseudopholidoctenus germanicus gen. et sp. nov.	±36	oblong	Germany	marine	middle Anisian
MARCOPOLOICHTHYIDAE					
Marcopoloichthys ani	35-37	torpedo-like	China	marine	middle Anisian
M. faccii	±37	torpedo-like	Italy	marine	early Carnian
M. furreri	±45	torpedo-like	Switzerland	marine	Ladinian
M. andreetti	±36	torpedo-like	Italy	marine	early Ladinian
PROHALECITIDAE					
Prohalecites	30-36	torpedo-like	Italy	marine	late Ladinian
TELEOSTEOMORPHA INCERTAE SEDIS					
Ruedersdorfia berlinensis gen. et sp. nov.	?	?	Germany	marine	middle Anisian
Seinstedtia parva	38	fusiform	Germany	coastal	Norian

suture is oblique in the Triassic *Barschichthys ruedersdorfensis*, and the shape and size of these bones are also different from those in archaeomaenids. Archaeomaenids have supraorbital bones, whereas they are absent in *Barschichthys ruedersdorfensis*. Thus, the circumorbital ring is closed in archmaeomaenids; in contrast, it is open dorsally in *Barschichthys ruedersdorfensis*. The maxilla is comparatively smaller in archaeomaenids than in the German Triassic fish which, in addition, has a unique maxilla among teleosteomorphs, which expands posteriad. The lower jaw of archaeomaenids is short with the quadrate-lower jaw articulation about the middle of the orbit, whereas the lower jaw of the German Triassic fish is long, extending well posteriad to the orbit, and its articulation with the quadrate is placed posterior to the orbit.

The new family described here, Barschichthyidae, differs from members of the Triassic family Pholidophoridae sensu Arratia (2013, 2017) in the same characters cited above for archaeomaenids. And the same can be said if a comparison is done with the Triassic Prohalecitidae and Marcopoloichthyidae, all with very characteristic crania (Tintori 1990; Tintori et al. 2015; Arratia 2022). Thus, the diagnosis of the new family is supported by several anatomical and morphological features (see Diagnosis) that are unique to this new taxon, as well as its combination of diagnostic characters.

Finally, the diagnosis of the new genus and species, *Ruedersdorfia berlinensis* (Fig. 11), is characterized by a few autapomorphies and a unique combination of characters that justify its creation as a new taxon. However, due to its combination of characters, its position among stem teleosts is unknown and is interpreted here as Teleosteomorpha incertae sedis.

### Discussion

# Size and body shape and oldest teleosteomorphs or stem teleosts

With very few exceptions, Triassic stem teleosts are small-bodied in comparison to some contemporaneous non-teleost fishes, such as *Birgeria* and *Saurichthys*. Except for marcopoloichthyids, other stem teleosts, such as *Prohalecites* and pholidophorids, including *Pseudopholidoctenus germanicus* gen. and sp. nov., have hemiheterocercal tails so that both the maximum body length or total length and the standard length were measured for most taxa studied here. Interpretation as small body size versus an intermediate or large body size fish is somewhat subjective, because of personal differences in taking measurements so that the comparison below is restricted to what can be understood as a 'small body-sized' or 'miniature' fish in Triassic teleosteomorphs.

Miniaturization, as defined for extant Neotropical fishes by Weitzmann and Vari (1988) and extended thereafter to other fish taxa (e.g., Kottelat et al. 2006) and extant amphibians and reptiles (e.g., Janken 1993; Janken and Wake 1993; Zimkus et al. 2012), involves individuals reaching sexual maturity at 20 mm SL or less and not growing longer than 26 mm SL, and usually exhibiting paedomorphic characters. However, such views are being challenged, because it is considered that after the limitations established by Weitzman and Vari (1988), the threshold is arbitrary. To be considered a miniature, the species needs to present a reduction in body size in comparison with close relatives/sister lineages and the common patterns that follow the miniaturization process, such as reductions and losses of structures (P. Braganca, written comm. November 21, 2022).

Among Permian neopterygians (e.g., the European holosteans Acentrophorus altus and A. glaphyrus, ca. 40-90 mm total length; Gill 1933; Brandt 2021) and Triassic fossil neopterygians, there are some that are so small that they are candidates to be considered as miniature, such as the European neopterygians Habroichthys minimus (ca. 32 mm TL; Bürgin 1992), Peltopleurus notocephalus (ca. 45 mm TL), Peltoperleidus macrodontus (50 mm TL) (Bürgin 1992), and Prosantichthys buergeni (60 mm total length; Arratia and Herzog 2007) and the Asian neopterygians Frodoichthys luipingensis and Gimlichthys dawaziensis (ca. 40 mm TL; Sun et al. 2016a, b), the thoracopterid Wushaichthys exquisitus (ca. 55 mm TL; Xu et al. 2015; Chen and Arratia 2022), the louwoichthyiform Peltoperleidus asiaticus (46 mm TL; Yuan et al. 2022) and the ginglymodian Diandongichthys ocellatus (ca. 45 mm TL and ca. 35 mm SL; Xu and Ma 2023). Among European teleosteomorphs, Pseudopholidoctenus germanicus gen. et sp. nov. (ca. 36 mm SL), according to current information, would be the smallest pholidophorid (see Table 2). Interestingly, paedomorphic characters have not been mentioned for these fishes.

So far as is known, a few of the oldest stem teleosts can be considered as candidates for miniaturization, because the smallest ones have standard lengths of about 30-36 mm (Prohalecites porroi), 35-37 mm SL (Chinese Marcopoloichthys ani; Tintori et al. 2007), and 38 mm SL (Seinstedtia parva; Schultze et al. 2022). With standard lengths of about 48 and 49 mm Malingichthys wanfenglinensis from China and Parapholidophorus caffii from Italy are respectively the smallest species among pholidophorids, whereas the Italian Pholidorhynchodon malzannii (ca. 140 mm SL) and Knerichthys bronni (ca. 130 mm SL) are the longest. Other pholidophorids such as the Italian Pholidoctenus serianus and Ph. sanpellegrinensis, the Chinese Malingichthys nimaiguensis (ca. 55 mm SL), the Italian Annaichthys pontegiurinensis (ca. 59 mm SL), the Austrian Pholidophorus latiusculus (ca. 75 mm SL), the Italian Lombardichthys gervasvasuttii (ca. 72 mm SL) and the Austrian Pholidophoretes salvus (ca. 72 mm SL) form a group of intermediate small-sized fishes that according to the current information would represent the average length among pholidophorids (Table 2). A comparison among families reveals that Pholidophoridae had the broader size diversification of 36-140 mm SL, whereas the diversity within the family Marcopoloichthyidae was narrower, ranging from 35-55 mm SL. A comparison is difficult, because these fishes, as part of their phylogenetic position (e.g., Arratia 2013, 2017, 2022), possess several characters that place them among the most primitive teleosts, but according to our results and a survey of the available literature, they do not exhibit features that could be interpreted as paedomorphic.

Comparisons of species lengths of teleosteomorphs versus their geographical distribution point to the fact that the smallest known taxa were living in Europe (*Prohalecites porroi, Pseudopholidoctenus germanicus* gen. et sp. nov., and *Seinstedtia parva*) and in Asia (*Marcopoloichthys ani*), but they were not co-existing in a temporal dimension (Table 2). More teleosteomorphs of intermediate and long lengths have been found in Europe, and a few in Asia (Table 1), but this could be biased because Triassic stem teleosts have been explored and studied in Europe for longer periods than in Asia.

Evaluating body shapes of stem teleosteomorphs has also been a difficult task because of differences in interpretation that although subtle, still could be significant. Thus, Fig. 13 illustrates the three shapes that we distinguish here. While there is no conflict separating a fusiform or a torpedo-like fish, sometimes it is difficult to distinguish an oblong fish from a fusiform one. All species of marcopoloichthyids are characterized by a torpedo-like form (Tintori et. al. 2007; Arratia 2022); we observe a similar body shape in Prohalecites, with its head considerably large compared to its narrow, elongate body. In contrast, Seinstedtia parva has a beautiful fusiform body, with its middle body region considerably deeper than the head and the caudal peduncle. Although not as clear as in Seinstedtia, the body shape of Malingichthys imaiguensis and M. wanfenglinensis can be also interpreted as fusiform. The body shape of Pholidophorus latiusculus, Pholidoctenus serianus, P. sanpellegriniensis, and others (see Table 1) is better described as oblong, with the body axis longer than its depth.

Among the studied fishes, the body of the German stem teleost *Ruedersdorfia berlinensis* gen. et sp. nov. remains unknown, whereas the body of *Pseudopholidoctenus* germanicus gen. et sp. nov. and *Barschichthys ruedersdorfensis* gen. et sp. nov. is interpreted as probably oblong, and it is covered with ganoid scales. The body of the Eurasian pholidophorids and *Seinstedtia parva* is covered with ganoid scales, adding protection to the inner organs (and body weight); in contrast, *Prohalecites* and *Marcopoloichthys* have naked bodies (Tintori 1990; Tintori et al. 2007; Arratia 2022), but differ in that a series of ganoid scales (= urodermals) is present in the caudal fin of *Prohalecites* (Arratia and Tintori 1999), and that *Marcopoloichthys* has a few large scales around the urogenital region (Tintori et al. 2007; Arratia 2022).

# Buccal morphology and feeding in early teleosteomorphs

The jaws of teleosteomorphs or stem teleosts, either upper or lower jaw, are formed consistently by the same bones: upper jaw comprising a small, mobile premaxilla, a maxilla, and two supramaxillae, which may be absent in some taxa, and a lower jaw formed laterally by a dentary or dentalosplenial, angular, and surangular. Despite such similarities in bone composition, the jaws of these fishes show some major variations that are outlined below, reflecting differences in feeding mechanisms.

The lower jaw (Fig. 14A) of *Prohalecites* (late Ladinian) is moderate in size, with the coronoid process posteriorly placed, the anterior part of the dentary or dentalosplenial markedly narrower than the posterior half of the jaw, and with its articular region for the quadrate at the level of the posterior margin of the large orbit. The lower and upper jaws are armed with many long, conical teeth. Another interesting character is the absence of a supramaxilla in this fish.

The configuration of the jaw (Fig. 14B) of *Marcopoloichthys* (China, Italy, and Switzerland; Anisian to Ladinian; Tintori et al. 2015; Arratia 2022) is quite different from all other Triassic stem teleosts, especially in its articulation of the quadrate at about the mid-region of the orbit when the fish was not feeding, but at the anterior margin of the orbit when the fish was suction feeding (Arratia 2022: fig. 7). The lower jaw has a characteristic shape, with the high coronoid process placed closer to the mandibular symphysis than posteriorly. Both jaws are edentulous, which is a unique feature among Triassic stem teleosts. *Marcopoloichthys* also lacks a supramaxilla, as in *Prohalecites*.

*Seinstedtia* (Germany; Norian; Schultze et al. 2022) has a characteristic lower jaw (Fig. 14C) with a deeper symphysis than in other Triassic stem teleosts and with its articular region for the quadrate placed below the posterior half of the orbit, so that when the fish has its mouth closed, the anterior profile of the head is almost triangular. At least the premaxilla and dentary carry minuscule, conical teeth. Contrary to other stem teleosts, *Seinstedtia* has only one supramaxilla in its upper jaw.

Among pholidophorids, Annaichthys pontegiurinensis (Norian of Italy; Fig. 14D) is unique in having the maxillary blade almost parallel to the anterior border of the head that is mainly formed by the lower jaw and the most anterior branchiostegal rays; the articulation of the lower jaw with the quadrate is placed almost at the level of the anterior margin of the orbit when the mouth is closed. This configuration corresponds to a protractile lower jaw. Although most specimens of Pholidophoretes are not very well preserved, the lower jaw of the holotype also has a position similar to that in Annaichthys. In Pholidoctenus sanpellegrinensis (Arratia 2017: figs 4, 7C; Fig. 14E), the articulation between lower jaw and quadrate is placed below the anterior half of the orbit when the mouth is closed, giving the lower jaw definite protractility. As in Annaichthys, the upper jaw of P. sanpellegrinensis has two supramaxillary bones, and both jaws have minuscule conical teeth. The condition is slightly different in Pholidoctenus serianus with the articulation between the lower jaw and quadrate placed at the level of the posterior margin of the jaw, which is longer and



**Figure 13.** Types of body shapes in Triassic teleosteomorphs. **A.** *Marcopoloichthys furreri* (BNM 201166, reversed to the left) illustrating a torpedo-like fish. **B.** *Seinstedtia parva* (MLU Sei.2010.76, reversed to the left) illustrating a fusiform fish. **C.** *Pholidoctenus serianus* (MCSNB 3067) illustrating an oblong fish. Scale bars: 5 mm.

not protractile. In contrast to all other Triassic stem teleosts, *Pholidorhynchodon malzannii* has a long lower jaw, with its articulation with the quadrate lying posterior to the posterior margin of the orbit (Fig. 14F). The long maxilla and long dentary are armed with many small, conical teeth, but in addition, the rostrodermethmoid and lateral dermethmoid carry powerful, larger conical teeth (Arratia 2013: figs 45, 47A; Arratia 2017: fig. 8). The structure of the jaws and dentition point to carnivorous feeding, a fact that is supported by a few specimens with a small pholidophorid in the mouth. *Pholidorhynchodon*, as far as is known, would be the only carnivorous stem teleost living



**Figure 14.** Diagram of Triassic teleosteomorph heads in lateral view illustrating the position of the upper and lower jaws with respect to other cranial bones. **A.** *Prohalecites porroi*. **B.** *Marcopoloichthys furreri*. **C.** *Seinstedtia parva*. **D.** *Annaichthys pontegiurinensis*. **E.** *Pholidoctenus sanpellegrinensis*. **F.** *Pholidorhynchodon malzannii*. Note the posterior extension of the lower jaw (articulation with quadrate) in relation to the orbit. Abbreviations: a.na, accessory nasal; ang, angular; ant?, antorbital?; asp, autosphenotic; br, branchiostegal rays; de, dentalosplenial or dentary; dsp, dermosphenotic; ent, entopterygoid; exc, extrascapula; gu, gular plate; io1, 3, infraorbitals 1, 3; lat.e, lateral ethmoid; ldet, lateral dermethmoid; mx, maxilla; op, opercle; pa [= fr], parietal [= frontal]; na, nasal; par, parasphenoid; pmx, premaxilla; ppa [= pa], postparietal [= parietal]; qu, quadrate; sang, surangular; smx, supramaxilla; smx 1-2, supramaxilla 1–2; sob, suborbital; stt [= dpt], supratemporotabular [= dermopterotic]; sy, symplectic.

in the Late Triassic. The potential food of other species that seem to have protractile mouths is unknown, and considering the structure of the jaws and dentition, we suppose that they were planktivorous, including a variety of small prey; a similar assumption is proposed for the suctionfeeding marcopoloichthyids, who could be also feeding on phytoplankton. Because of its well-developed dentition, *Prohalecites* is proposed here to have had a carnivorous diet, including small prey. Thus, although there is information concerning the possible feeding mechanisms present in Triassic stem teleosts, except for *Pholidorhynchodon*, specific kinds of prey involved are unknown. Apparently,

a suction-feeding mechanism was widespread among these fishes, including the oldest marcopoloichthyid (*Marcopoloichthys ani*), but a small carnivorous fish (*Prohalecites*) is also among the oldest teleosteomorphs.

# Marine versus freshwater environments and the oldest teleosteomorphs

While marcopoloichthyids and pholidophorids inhabited marine waters in Europe and Asia during the Middle-Late Triassic, *Prohalecites* is only known from marine waters of the Middle Triassic of Italy. The stem teleosts from Italy, Austria and China were inhabitants of the Tethys Ocean, whereas Pseudopholidoctenus germanicus gen. et sp. nov. from Rüdersdorf is from the central European Basin (Germanic Basin), and as far is known, all of these fishes were living in a marine environment. In contrast, the recently described Seinstedtia (Schultze et al. 2022) is known from an environment with connection to the sea in the Norian of Germany. The marine aquatic environment (Tethys Ocean) is interpreted here as playing a significant role in the diversification and distribution of stem teleosteomorphs in Eurasia during the Middle-Late Triassic, Europe in the Early Jurassic, and in their dispersion to other latitudes.

The youngest known Triassic teleosteomorph or stem teleost (*Parapholidophorus caffii*) is from the Rhaetian (ca. 208–201 Ma) of Europe, and in the Sinemurian of the Early Jurassic (ca. 199–190 Ma), they are known worldwide, leaving a 2 Ma gap (Hettangian Age) in their history where no teleosteomorphs have been reported, not even other pholidophorids. After this short, apparent gap, there are at least two new radiations of marine stem teleosts in the Sinemurian of Europe represented by:

- Dorsetichthys bechei and other 'pholidophoriforms', especially from marine environments of the Lower Lias of England and France (Nybelin 1966; Woodward 1985; Arratia 2000, 2004), and
- 2) *Proleptolepis*, with at least four species known from the Lower Lias of England (e.g., Lymes Regis, Dorset, and Charmouth; Nybelin 1974), which, contrary to the Triassic teleosteomorphs, have among their characters a well-developed postero-dorsal process in the quadrate, a well-developed series of uroneurals, and cycloid scales.

Almost simultaneously another radiation of proleptolepids is reported outside Europe, and for this, the Tethys Ocean and its connection with the Paleo-Pacific through the Spanish Corridor (Hallam 1977, 1983) played a major role. The fishes involved are the early to middle Sinemurian proleptolepid-like fishes from northern Chile (Quebrada Vaquillas Altas; Covacevich and Escobar 1979; Naranjo and Covacevich 1979), inhabiting the Paleo-Pacific about 199 to 190 million years ago (Arratia and Schultze 1999). These are represented by at least two small species of about 50 mm of maximum length, lacking teeth on their jaws (Arratia and Schultze 1999: figs 5, 7, 8) and are assumed here to have been suction feeders.

The Tethys Ocean continued playing a major role during the Upper Lias of Europe with the appearance and diversification of teleosts:

- 1) *Leptolepis* and *Longileptolepis* had about eight species from the Upper Lias of England, France and Germany (Nybelin 1974; Arratia and Thies 2001; Arratia 2003; Konwert and Stumpf 2017), representing another radiation of fishes that are an important landmark in the evolution of teleosts in which many synapomorphies appeared, as for instance the loss of the surangular, prearticular, and coronoid bones in the lower jaw; presence of an autocentrum forming the vertebral centra; 10/9 principal rays in the caudal skeleton; and the first and last segmented and not branched principal ray forming the leading margins of the caudal fin (Arratia 1999, 2013, 2017).
- 2) At the same time (Upper Lias), numerous species previously identified as *Pholidophorus* (Agassiz 1833–1843; Woodward 1895; Nybelin 1966) were present in marine environments of England, France and Germany. All these species should be re-studied, because they belong to the non-monophyletic genus '*Pholidophorus*' sensu Arratia (2000).

It is noteworthy to mention that by the Early to Middle Jurassic (ca. 170–161 Ma), a few stem teleosts reached distant latitudes and occupied other habitats, such *Oreochima ellioti* living in lacustrine freshwater environments from Victoria Land, Antarctica (Schaeffer 1972; Sepkoski 2002; Bean 2021). This fish was first interpreted as an archaeomaenid pholidophoriform by Schaeffer (1972) and more recently archaeomaenids were interpreted as non-pholidophoriform stem teleosts by Bean (2021).

### Age and oldest teleosteomorphs

The interpretation concerning the oldest stem teleost has changed a few times recently due to new findings and/or new interpretation of the fishes. For instance, *Prohalecites porroi* from the Middle Triassic (late Ladinian, ca. 240–237 Ma) of Italy was interpreted as the oldest teleosteomorph by Arratia (2015). However, at the same time two new pholidophorids (*Malingichthys nimaiguensis* and *M. wanfenglinensis* from the Late Ladinian of China were proposed as the oldest teleosts by Tintori et al. (2015). The new data presented here challenge such interpretations, because the age of *Barschichthys*, *Pseudopholidoctenus* and *Ruedersdorfia* from Rüdersdorf, central European Basin (Germanic Basin) is about 244 Ma, as well as *Marcolopoichthys ani* from Italy, ca. 7 Ma from the Paleozoic/Mesozoic boundary. A few molecular studies placed the origin of crown teleosts in the Paleozoic (e.g., Near et al. 2012; Broughton et al. 2013; Hughes et al. 2018), many years prior to the earliest fossil record known at that time; however, the new fossil evidence presented here shortens the time difference between the Anisian and Paleozoic (Permian) for the teleosteomorphs. Additionally, the results presented above contradict Tintori and other's claim (2015) that China is the center of origin of teleosteomorphs. The new information supports Europe in such a role, but we can expect that new discoveries of Triassic fishes in Eurasia may change today's interpretations.

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