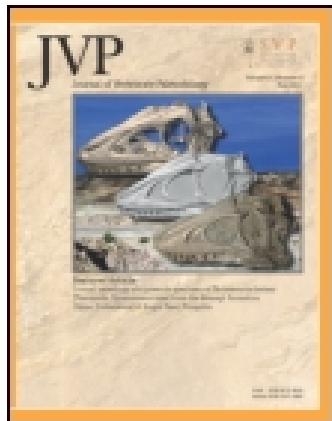


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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

†Zappaichthys harzhauseri, gen. et sp. nov., a new Miocene toadfish (Teleostei, Batrachoidiformes) from the Paratethys (St. Margarethen in Burgenland, Austria), with comments on the fossil record of batrachoidiform fishes

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Published online: 09 Sep 2014.

To cite this article: Giorgio Carnevale & Bruce B. Collette (2014) †Zappaichthys harzhauseri, gen. et sp. nov., a new Miocene toadfish (Teleostei, Batrachoidiformes) from the Paratethys (St. Margarethen in Burgenland, Austria), with comments on the fossil record of batrachoidiform fishes, *Journal of Vertebrate Paleontology*, 34:5, 1005-1017

To link to this article: <http://dx.doi.org/10.1080/02724634.2014.854801>

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†*ZAPPAICHTHYS HARZHAUSERI*, GEN. ET SP. NOV., A NEW MIOCENE TOADFISH
(TELEOSTEI, BATRACHOIDIFORMES) FROM THE PARATETHYS (ST. MARGARETHEN IN
BURGENLAND, AUSTRIA), WITH COMMENTS ON THE FOSSIL RECORD OF
BATRACHOIDIFORM FISHES

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ABSTRACT—Toadfishes (Batrachoidiformes) are benthic fishes often burying in the sand or under rocks that occur worldwide in tropical to temperate marine and brackish waters. The Batrachoididae, the only known family of the order Batrachoidiformes, includes 23 extant genera and about 80 species arranged in four subfamilies. A new genus and species of toadfish, †*Zappaichthys harzhauseri*, gen. et sp. nov., is described from the middle Miocene (upper Badenian) Leitha Limestone of St. Margarethen in Burgenland, Eisenstadt-Sopron Basin, Austria. It is based on three partially complete, well-preserved articulated skeletons plus a neurocranium that display a unique combination of characters [possession of 29 (10 + 19) vertebrae; dorsal fin with three solid spines and 16 rays; anal fin with 11 rays; pectoral fin with 20–25 rays; interorbital region of the neurocranium wide; postorbital sector of the neurocranium longer than the orbital one; four ossified pectoral-fin radials; opercle with a strong pointed spine; subopercle bearing two spines and two short filaments; scales absent] that support its recognition as a new genus of the family Batrachoididae. †*Zappaichthys harzhauseri*, gen. et sp. nov., is the oldest member of the Batrachoidiformes known to date based on articulated skeletal remains. The fossil record of batrachoidiform fishes is discussed in detail.

INTRODUCTION

The Batrachoidiformes, commonly known as toadfishes, are small- to medium-sized fishes characterized by a tapering body and a large and flattened head with eyes on top and often with barbels or flaps around their mouths. These fishes are found worldwide in tropical to temperate marine and brackish waters down to depths of about 350 m (Greenfield et al., 2008) and some species are exclusive of South American freshwaters. Toadfishes are voracious ambush predators feeding on a variety of benthic invertebrates and fishes. These fishes are characterized by a well-developed swimbladder, with some species bearing photophores along their flanks and belly and some others that are characterized by hollow, venomous opercular and dorsal-fin spines. Toadfishes are widely known for their multiharmonic, male vocalizations used in courtship to attract females to male nest sites (see Bass and McKibben, 2003) produced by rapid contraction of paired striated muscles attached to the walls of the swimbladder (e.g., Tower, 1908; Fine et al., 2001). Batrachoidiforms are often used in medical research as experimental animals (e.g., Walsh, 1997; Boyle et al., 2001; Reimschuessel, 2001).

Since the publication of the seminal paper by Regan (1912), the batrachoidiforms have been traditionally aligned with the lophiiforms, placed in the Pediculati, based on skeletal features of the neurocranium and pectoral girdle. Briggs (1955) and McAllister (1968) proposed a close relationship with the gobiociforms, whereas Greenwood et al. (1966) redefined the sister-group relationships of batrachoidiforms and lophiiforms and

allied them with percopsiforms, ophidiiforms, and gadiforms within the Paracanthopterygii. Subsequently, Rosen and Patterson (1969) added some other taxa to the Paracanthopterygii, including the gobiociforms. The limits and composition of the Paracanthopterygii have been discussed by a number of authors in the last four decades (e.g., Gosline, 1970; Lauder and Liem, 1983; Rosen, 1985; Patterson and Rosen, 1989; Johnson and Patterson, 1993), whereas molecular studies demonstrated the non-monophyly of this group (e.g., Wiley et al., 2000; Miya et al., 2005; Smith and Wheeler, 2006) and grouped the batrachoidiforms with different acanthomorph taxa, including the ophidiiforms, mastacembelids, and callionymids. More recently, molecular studies using several markers sampled from a huge number of species concur to indicate that batrachoidiforms occupy a basal position within percomorphs (e.g., Near et al., 2012, 2013; Betancur et al., 2013).

As emphasized by Rice and Bass (2009), little is known about the anatomy, evolutionary history, ecology, and behavior of batrachoidiform fishes outside of some European and North American taxa (see, e.g., Siebenrock, 1901; Gill, 1907; Pankratz, 1928, 1930; Monod, 1960; Le Danois, 1961; Isaacson, 1964; Schwartz, 1974). The main exception is the 1046 papers on the physiology and other aspects of the biology of the oyster toadfish, *Opsanus tau*, listed by Schwartz and White (1996) and three previous bibliographies of this species. The taxonomic composition of the Batrachoidiformes was redefined on a worldwide basis by Greenfield et al. (2008), who recognized 23 genera and placed them in four monophyletic subfamilies. The goal of this paper is to describe a new genus and species of the toadfishes from the Middle Miocene coralline limestone of St. Margarethen in Burgenland, Eisenstadt-Sopron Basin, Austria, and to discuss the fossil record of the Batrachoidiformes.

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STRATIGRAPHY AND PALEOECOLOGY

The fossils documented herein were collected in the Kummer quarry (47°48'01.76"N, 16°37'59.12"E), along the Rust Hills, about 2 km east of the village of St. Margarethen in Burgenland, Eisenstadt-Sopron Basin, eastern Austria. The Kummer quarry mostly exposes Miocene deposits usually referred to as Leitha Limestone in the regional literature (Keferstein, 1828; Riegl and Piller, 2000). The Leitha Limestone is primarily characterized by rhodolite facies or maerl-type deposits (calcarene consisting mainly of branching red algae). The Leitha Limestone exposed in the Kummer quarry originated during the Middle Miocene on the western side of a small carbonate platform, the Fertőrákos Platform, which was located at the western margin of the Central Paratethys, documenting paleobiotopes dominated by carbonate shoals surrounding small depressions (Schmid et al., 2001).

The stratigraphic section exposed in the Kummer quarry was described by Schmid et al. (2001) as a sequence of yellow, poorly cemented and highly porous, bioclast-bearing calcarenites alternated with greenish-whitish laminated (partly fish-bearing) marls. Overall, the section is dominated by thick units of corallinacean debris, rhodolites, bivalves (mostly oysters and pectinids), and fragmented echinoids deposited in a shallow environment with coarse, mobile carbonate sand. These carbonate sands were deposited in large channels that originated as a consequence of storm-triggered debris flow. In this context, the greenish-whitish laminated marls represent the background sedimentation within the channels that took place at depths of about 50–60 m during the calm phases characterized by very reduced water energy and turbulence.

The age of the laminated marls has been established based on the calcareous nannoplankton content (see Schmid et al., 2001), which indicates zone MNN5b of Fornaciari et al. (1996), around the Langhian/Serravallian boundary, approximately between 14.0 and 13.5 Ma, and corresponding to the late Badenian of the Paratethys stratigraphy (*Bulimina-Bolivina* Zone of Papp et al., 1978).

As emphasized by Schmid et al. (2001), the most striking feature of the laminated marls is the extraordinary preservation of the fauna, which consists of bivalves, bryozoans, brachiopods, crustaceans, regular and irregular echinoids, chondrichthyan teeth, and exquisitely preserved articulated fish skeletons. Such a remarkable preservation of the fossils seems to be related to the concurrent effect of persistent lack of water agitation and episodic events of bottom hypoxia. Phytoplanktonic blooms, possibly triggered by periodically increased input of nutrients deriving from variation in river discharges, resulted in the development of bottom hypoxia that caused the mass mortalities of the benthic fauna, allowing, at the same time, the extraordinary preservation of the fish skeletons.

The fish assemblage includes representatives of more than 35 families with an overall diversity of more than 45 taxa. Only a limited portion of this diverse assemblage has been described (Münster, 1846; Heckel, 1850, 1856; Heckel and Kner, 1861; Kner, 1862; Gorjanović-Kramberger, 1902; Bachmayer, 1980; Bellwood and Schultz, 1991; Schultz, 1993, 2006a, 2006b; Chanet and Schultz, 1994; Carnevale et al., 2012; Carnevale and Harzhauser, 2013). It is clearly dominated by round herrings, sardines, and lanternfishes, followed by scorpionfishes, cods, and seabreams. Overall, the structure and composition of the fish assemblage points to a complex and heterogeneous paleoenvironment with rocky reefs and seagrass beds, which were present in close proximity to the depositional environment.

MATERIALS AND METHODS

The specimens are deposited in the Geologisch-Paläontologische Abteilung, Naturhistorisches Museum, Vienna. The available material consists of three articulated skeletons plus a complete neurocranium preserved on greenish-whitish

laminated marls, with bones that appear dark orange or brown. Some specimens required matrix removal before examination in order to allow investigations of their structure in as much detail as possible; this was achieved using thin entomological needles. The fossils were examined using a Leica MZ6 stereomicroscope equipped with camera lucida drawing arm. Measurements were taken with a dial caliper, to the nearest 0.1 mm. All extinct taxa are marked with a dagger (†) preceding their name.

Institutional Abbreviations—**CMM-V** Vertebrate Paleontology, Calvert Marine Museum, Solomons, Maryland; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **NHMW**, Naturhistorisches Museum, Vienna.

Anatomical Abbreviations—**ach** anterior ceratohyal; **bb**, basibranchial; **ctb**, ceratobranchial; **dhh**, dorsal hypohyal; **ep**, epural; **epi**, epioccipital; **exo**, exoccipital; **f**, frontal; **hyb**, hypobranchial; **hyp**, hypural; **le**, lateral ethmoid; **pch**, posterior ceratohyal; **phy**, parhypural; **pto**, pterotic; **ptt**, posttemporal; **pu**, preural centrum; **soc**, supraoccipital; **spo**, sphenotic; **u**, ural centrum; **v**, vomer; **vhh**, ventral hypohyal.

SYSTEMATIC PALEONTOLOGY

Subdivision TELEOSTEI sensu Patterson and Rosen, 1977
Order BATRACHOIDIFORMES Goodrich, 1909
Family BATRACHOIDIDAE Bonaparte, 1832
Genus †*ZAPPAICHTHYS*, gen. nov.

Diagnosis—Halophrynine batrachoidid with 29 (10 + 19) vertebrae; dorsal fin containing three solid spines plus 16 rays; anal fin containing 11 rays; pectoral fin with 20–25 rays; interorbital region of the neurocranium wide; postorbital sector of the neurocranium longer than the orbital one; four ossified pectoral-fin radials; opercle with a strong pointed spine; subopercle with two spines and two short filaments; scales absent.

Etymology—Genus named in honor of the American musician and composer Frank Vincent Zappa.

Type Species—†*Zappaichthys harzhauseri*, sp. nov.

†*ZAPPAICHTHYS HARZHAUSERI*, sp. nov.
(Figs. 1–8)

Holotype—NHMW 1988/0141/0001a+b, partially complete articulated skeleton in part and counterpart (Fig. 1), 162.3 mm standard length (SL).

Paratypes—NHMW 1976/1812/0044, largely incomplete articulated skeleton lacking most of the head skeleton and with vertebral column mostly preserved as impression only (Fig. 2A); NHMW 1986/0138/0056, partially complete articulated skeleton lacking part of the head and the caudal skeleton (Fig. 2B); NHMW 1986/0138/0028, partially complete neurocranium (Fig. 2C).

Diagnosis—As for the genus.

Etymology—Species named in honor of the distinguished Austrian paleontologist Mathias Harzhauser in recognition of his outstanding contribution to the geology and paleontology of the Paratethys.

Locality and Horizon—St. Margarethen in Burgenland locality; Kummer Quarry; middle Miocene, late Badenian (around the Langhian/Serravallian boundary), *Bolivina-Bulimina* Zone, NN5b zone (see Schmid et al., 2001).

DESCRIPTION

Measurements of the holotype are summarized in Table 1.

The body is cylindrical, with laterally compressed caudal portion. The head is large and depressed; its length is contained slightly less than three times in SL. The snout is moderately developed and bluntly rounded. Based on the structure and configuration of the jaw bones, it is reasonable to hypothesize that the gape of the mouth was nearly horizontal in origin and that

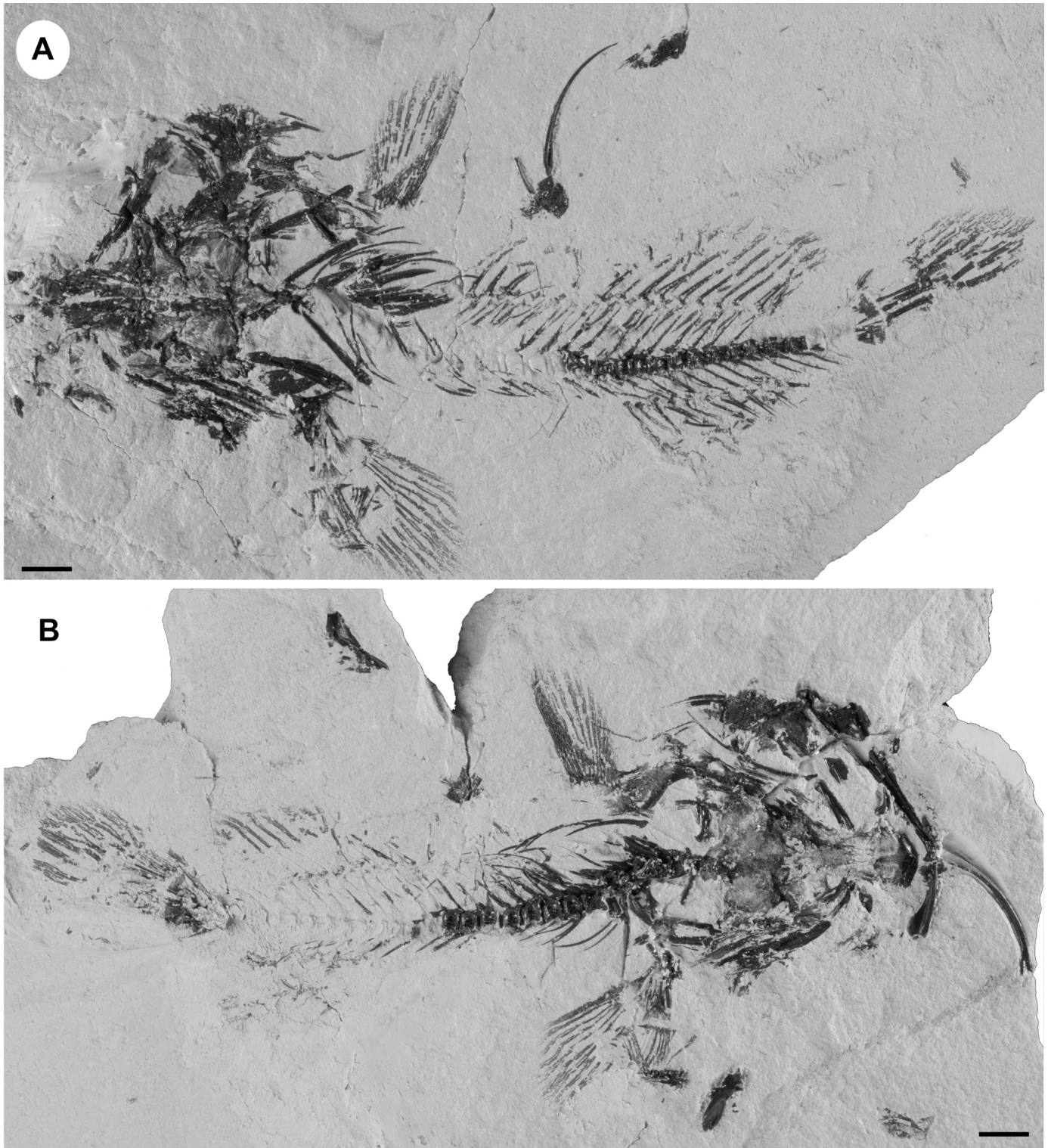


FIGURE 1. †*Zappaichthys harzhauseri*, gen. et sp. nov. **A** and **B**, holotype NHMW 1988/0141/0001a+b. Scale bars equal 10 mm.

the lower jaw protruded beyond the anterior margin of the upper jaw (Fig. 1). The body is naked.

Neurocranium—Of the neurocranium only the dorsal surface is exposed in the available specimens and can be properly described (Fig. 3). The neurocranium is remarkably depressed dorsoventrally, relatively elongate and wide, its maximum width

(measured between the two contralateral extensions of the sphenotics) representing slightly more than three-quarters (77.6%) of its length. The orbital portion of the neurocranium is shorter than the postorbital one; the length of the orbital portion reaches about 74% of that of the postorbital one. The postorbital portion of the neurocranium is broadly expanded laterally with respect

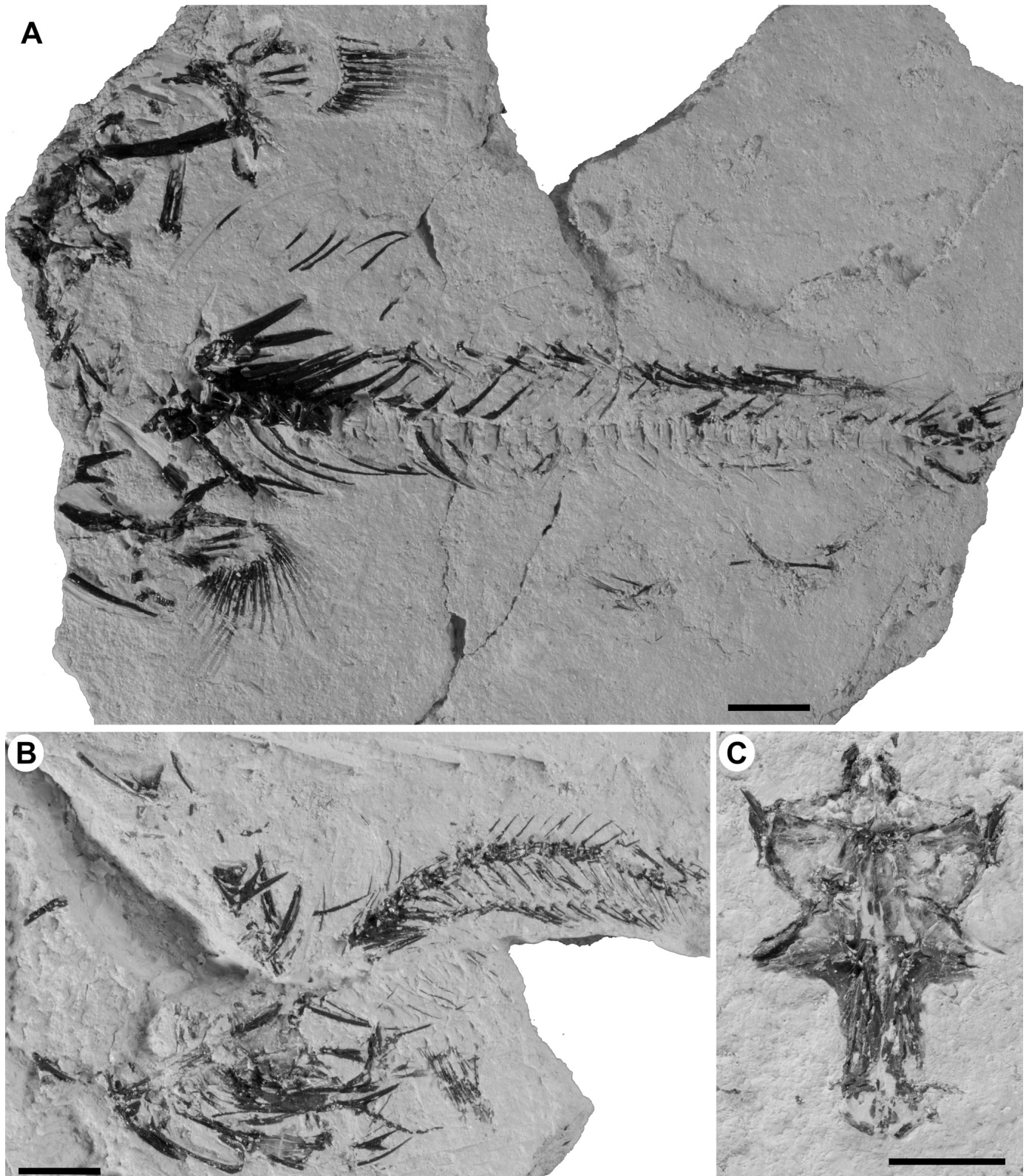


FIGURE 2. †*Zappaichthys harzhauseri*, gen. et sp. nov., paratypes. **A**, NHMW 1976/1812/0044; **B**, NHMW 1986/0138/0056; **C**, NHMW 1986/0138/0028. Scale bars equal 10 mm.

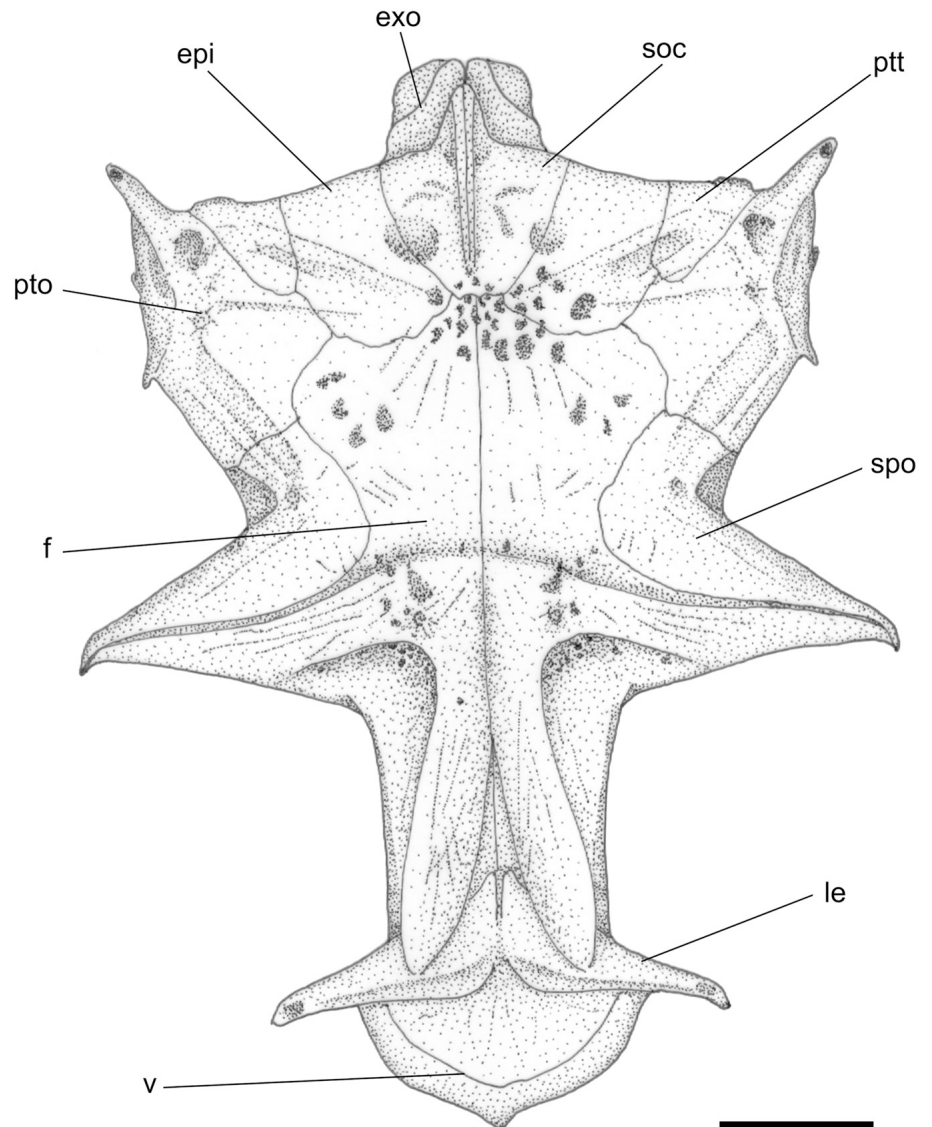


FIGURE 3. †*Zappaichthys harzhauseri*, gen. et sp. nov. Reconstruction of the dorsal view of the neurocranium mainly based on paratype NHMW 1986/0138/0028. Scale bar equals 5 mm.

to the interorbital portion; the maximum interorbital width of the neurocranium is 31.3% of that measured between the outermost margin of the sphenotics. The neurocranium is characterized by a considerable lateral constriction at the level of the posterior portion of the sphenotics; the distance between the constricted portion of the sphenotics equals 57.6% of that measured between their outer portion. Part of the dorsocranial surface is sculptured by small and deep irregular pits and strong, thickened ridges. Overall, the outline of the neurocranium is consistent with that of several batrachoidid genera (see, e.g., Greenfield et al., 2008). The frontals are by far the largest bones of the skull roof; these bones are irregular in outline, characterized by a large lateral pointed flange approximately emerging at the half of their length, each forming the anterior edge of the postorbital portion of the neurocranium (Fig. 3). The supraorbital commissure is moderately developed. The anterior interorbital portion of each frontal partially overlaps the lateral ethmoids. The two contralateral frontals articulate with each other through a linear suture. Each frontal articulates posteriorly with the epioccipital and supraoccipital, posterolaterally with the

pterothoracic, laterally with the sphenotic, and anteriorly with the lateral ethmoid. The lateral ethmoid is moderately enlarged, characterized by a gently convex outer surface; the lateral tip of each lateral ethmoid arises perpendicularly from the lateral margins of the interorbital portion of the neurocranium and terminates distally into a blunt and anterolaterally oriented spine (Fig. 3). The vomer is massive and nearly triangular in outline, with a convex anterior margin; the ventral surface of this bone is not exposed in any of the available specimens, thereby preventing the observation of vomerine teeth. There is no evidence of mesethmoid. The supraoccipital is a dome-like bone that bears a thick median crest (Fig. 3). Two contralateral bones medially separated by the supraoccipital are interpreted herein as the epioccipitals (rather than the parietals) following the interpretation of Wiley and Johnson (2010); these bones are relatively large and nearly rectangular in outline; each epioccipital articulates laterally with posttemporal and pterotic and anteriorly with the frontal (Fig. 3). The exoccipital are partially recognizable behind the supraoccipital crest; the outer margin of these bones is convex and nearly smooth. The pterotic is an irregular and medially

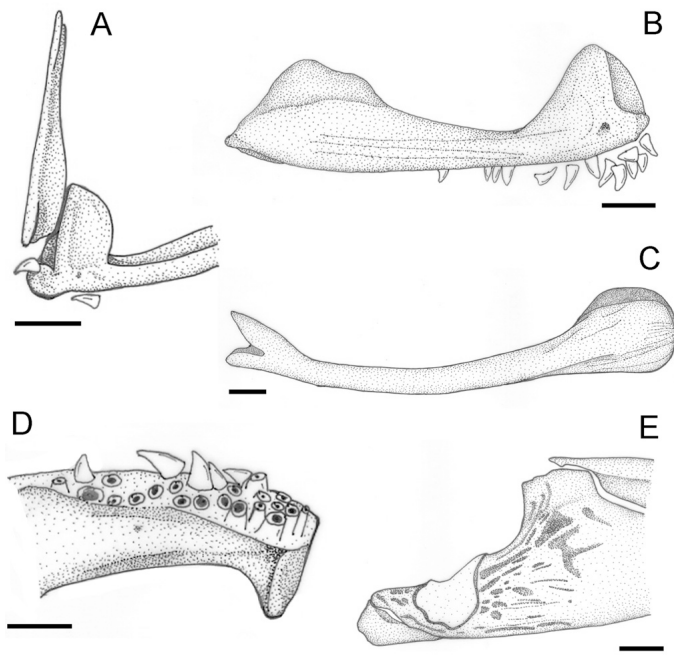


FIGURE 4. †*Zappaichthys harzhauseri*, gen. et sp. nov. **A**, NHMW 1986/0138/0056, paratype, anterior portion of the premaxilla, left lateral view; **B**, NHMW 1988/0141/0001, holotype, premaxilla (autogenous ascending process not preserved), right lateral view; **C**, NHMW 1988/0141/0001, holotype, maxilla, left lateral view; **D**, NHMW 1988/0141/0001, holotype, anterior portion of the dentary, left medial view; **E**, NHMW 1988/0141/0001, holotype, posterior portion of the mandible, left medial view. Scale bars equal 2 mm.

massive bone; a strong and posterolaterally directed spine bearing a lateral-line foramen at its distal end originates from the posterior corner of the pterotic; the lateral portion of this bone is flange-like and characterized by small spiny processes emerging from its outer margin (Fig. 3). The pterotic articulates posteromedially with the posttemporal, medially with the anterolateral corner of the epioccipital and the posterolateral corner of the frontal, and anteriorly with the posterior margin of the sphenotic. The sphenotic is 'L'-shaped, characterized by pointed anterolateral spinous tip (Fig. 3). The sphenotic articulates posteriorly with the pterotic and laterally and anteriorly with the frontal. Thickened ridges connecting short, blunt, and vertically oriented spines run through the whole length of the sphenotic and pterotic. The posttemporal is consolidated with the neurocranium. It is a thick bone characterized by a vertically developed articular condylar surface for the supracleithrum along its posterior margin. Each posttemporal articulates laterally with the pterotic and medially with the epioccipital.

Jaws—The gape of the mouth is rather wide; the maxilla extends posteriorly beyond the posterior margin of the orbit. The premaxilla is greatly elongate, with a slender autogenous ascending process (Fig. 4A); the length of the ascending process equals 67.2% of that of the alveolar process. The articular process has a wide base and a dorsal rounded profile (Fig. 4B). The postmaxillary process is large, with an irregular dorsal margin and a bluntly pointed posterior end. The alveolar process is thick and bears several rows of thick and slightly recurved conical teeth. The maxilla is a large and gently curved bone with a quadrangular posterior end (Fig. 4C). The anterior articular head is characterized by pointed anterolateral and anteromedial processes separated from each other by a moderately developed gap.

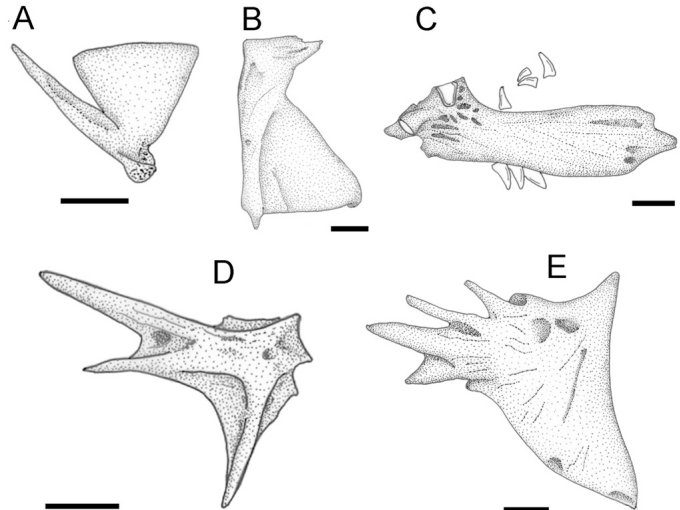


FIGURE 5. †*Zappaichthys harzhauseri*, gen. et sp. nov. **A**, NHMW 1986/0138/0056, paratype, quadrate, right lateral view; **B**, NHMW 1988/0141/0001, holotype, metapterygoid, right lateral view; **C**, NHMW 1988/0141/0001, holotype, right palatine, medial view; **D**, NHMW 1986/0138/0056, paratype, opercle, right lateral view; **E**, NHMW 1988/0141/0001, holotype, subopercle, right lateral view. Scale bars equal 2 mm.

The mandible is very large and consists of the dentary, anguloarticular, and retroarticular: it is partially recognizable in the holotype NHMW 1988/0141/0001 (Fig. 1). The dentary is slender, slightly bent downward proximally, and characterized by a short and pointed symphyseal process (Fig. 4D). The dentary bears a single row of stout conical teeth with slightly recurved tips for most of its length; the teeth became numerous and arranged in several rows in the symphyseal region (Fig. 4D). The posterior margin of the dentary is bifurcated, with the upper limb dorsally flattened and overlying the coronoid process of the anguloarticular (Fig. 4E). The anguloarticular is very robust and medially sculptured. The articular facet for the articulation with the quadrate is rather large and saddle-shaped. The posterodorsal margin of the coronoid process of the anguloarticular is slant forward with an oblique orientation (Fig. 4E).

Suspensorium—Most of the bones of the suspensorium are inadequately preserved and cannot be properly described. The hyomandibula, symplectic, ectopterygoid, and endopterygoid are badly preserved and extensively fragmented. The quadrate is fan-shaped, with a gently rounded dorsal margin and a strong articular condyle (Fig. 5A). The metapterygoid has a thickened posterior margin and a straight dorsal margin ending anteriorly into a sharp and narrow spine (Fig. 5B). The anterodorsal metapterygoid flange is absent. The palatine is a stout cylindrical bone bearing conical teeth similar to those of the jaws (Fig. 5C).

Opercular Series—The preopercle is partially exposed in the holotype; this bone is moderately elongate and characterized by a smooth posterior margin. The interopercle is roughly quadrangular. The opercle bear a strong pointed spine shorter than that present at the distal end of the horizontal ridge arising from the condyle for the opercular process of the hyomandibula; the main shaft of this bone terminates ventrally into a blunt spine (Fig. 5D). The subopercle bears two thick and pointed spines and two short and robust filaments emerging from its posterodorsal corner (Fig. 5E).

Hyoid Bar and Gill Arches—The hyoid bar is slender and considerably elongate (Fig. 6A, B). The dorsal and ventral hypohyals are thin and irregular. The anterior ceratohyal is expanded posteriorly and characterized by an angular posteroventral

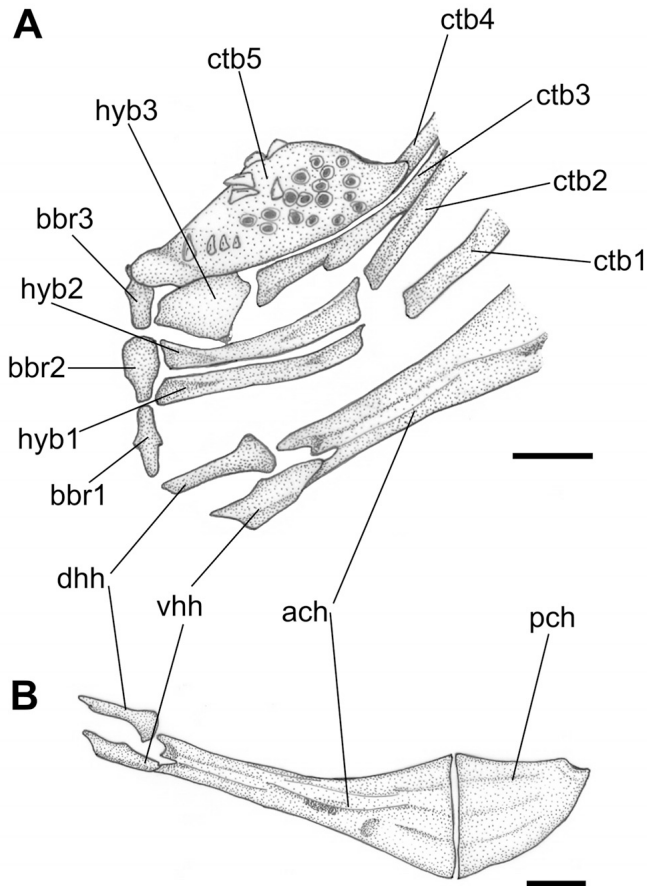


FIGURE 6. †*Zappaichthys harzhauseri*, gen. et sp. nov., NHMW 1986/0138/0056, paratype. **A**, ventral gill arches, left series, medial view; **B**, hyoid bar, right lateral view. Scale bars equal 2 mm.

corner. The posterior ceratohyal is nearly triangular, with a gently convex ventral margin (Fig. 6B). The medial suture between the anterior and posterior ceratohyals seems to be absent (Fig. 6B). The original number of branchiostegal rays cannot be determined.

The ventral gill arches are partially exposed in the paratype NHMW 1986/0138/0056, including what appears to be the dorsal surface of the urohyal and first and second basibranchials (Fig. 6A). The first and second hypobranchials are slender and slightly curved, with a small spine emerging from the posterior corner of their distal ends. The third hypobranchial is fan-shaped, characterized by a single broad posterior articular head and a small and rounded anterior end. The first through fourth ceratobranchials are elongate and nearly cylindrical. The fifth ceratobranchial is subtriangular in outline and bears conical teeth with recurved tips.

Vertebral Column—The vertebral column contains 29 (10 + 19) vertebrae (Table 2). The first centrum is closely associated with the neurocranium. The abdominal centra are rectangular, longer than high. The lateral surfaces of each centrum are extensively sculptured by strong horizontal or slightly oblique ridges and deep irregular pits. The neural prezygapophyses are prominent. The neural spines of the second through seventh vertebrae are strongly ossified and anteroposteriorly enlarged; those of the succeeding vertebrae are slender. The haemal spines are slender, similar to the opposite neural spines. Pleural ribs are absent.

There are 17 pairs of epineural bones; the first epineural is hypertrophied and very robust, inserting along the lateral surface of the first neural arch (Fig. 1A); the following epineurals are slender and slightly curved (e.g., Fig. 2A).

Median Fins and Supports—The caudal skeleton is similar to that of other members of the Batrachoididae, with two large triangular hypural plates and two epurals (Fig. 7); the lower plate is formed by the fusion of parhypural and hypurals 1 and 2 with the first preural and first ural centra, whereas the upper plate results from the fusion of hypurals 3–5 with the second ural centrum. The parhypural consists of a large laminar bone with a nearly angular anteroventral margin. The caudal fin appears to be rounded; unfortunately, it is largely incomplete in all the available specimens, making the evaluation of the original number of caudal-fin rays extremely problematic.

There are two dorsal fins separated by a short gap corresponding to the length of three vertebrae. The spinous dorsal fin appears to originate above the third or fourth abdominal vertebra. It consists of three strong spines, of which the first is preserved as impression only (Fig. 2A). The second dorsal-fin spine is the largest one. The three dorsal-fin spines are supported by three poorly preserved, thick pterygiophores closely associated with the underlying neural spines (Figs. 1A, 2A); the spine-ptyerygiophore complex seems to exhibit the ‘crowded’ configuration typical of batrachoidiforms (see Monod, 1960; Wiley and Johnson, 2010). The second dorsal fin inserts at the level of the ninth abdominal vertebra and consists of 16 soft rays supported by 16 pterygiophores (Table 2). The proximal pterygiophores are relatively slender, with a laminar anterior flange along their main shaft. The medial pterygiophore is nearly cylindrical, with slightly expanded distal end.

The anal fin originates just below the seventh caudal vertebra and contains 11 rays apparently supported by 10 pterygiophores (Table 2). The anal-fin pterygiophores are similar to those of the dorsal fin.

Paired Fins and Supports—The pectoral fin has a rounded profile and consists of 20–25 rays (Table 2). The cleithrum is poorly preserved or inaccessible in all the examined specimens. It appears to be large and crescent-shaped, with a very elongate horizontal limb and a short and spinous process emerging along the posterior margin just above the pectoral fin. The supracleithrum is thick and relatively elongate. Both scapula and coracoids are inadequately preserved and of problematic interpretation. There are four elongate and nearly cylindrical pectoral-fin radials, the lowermost the largest and with a subquadrangular distal end (Fig. 8A).

The pelvic fin appears to be characterized by a relatively short spine plus two very large soft rays. The basipterygium is subrectangular, with a relatively large median process (Fig. 8B). The anterior margin of the basipterygium is characterized by a strong spinous process emerging medially as an anterior extension of the median process. Foramina appear to be absent on the medial process of the basipterygium.

DISCUSSION

Taxonomic Remarks

The order Batrachoidiformes solely comprises the family Batrachoididae that consists of 25 extant genera and about 80 species arranged in four subfamilies (Batrachoidinae, Halophryninae, Porichthyinae, Thalassophryninae; Greenfield et al., 2008). The monophyly of this group has been discussed by several authors in the past century. The first attempt to demonstrate the monophyletic status of batrachoidiforms was that of Regan (1912), who recognized several diagnostic features [cited as ‘peculiarities’ by Patterson and Rosen (1989)], some of which actually are unique for this group. Monod (1960) listed several

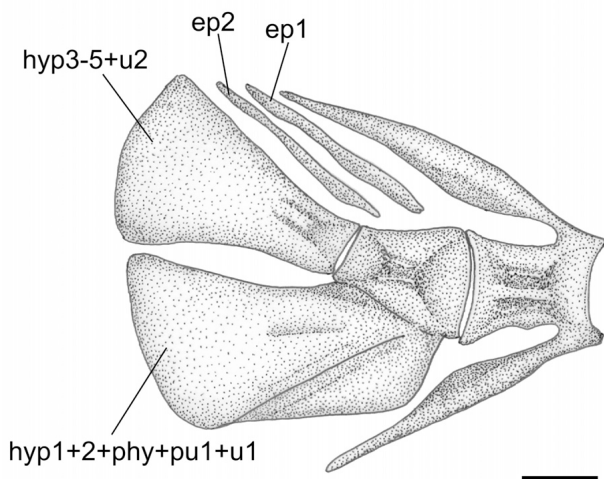


FIGURE 7. †*Zappaichthys harzhauseri*, gen. et sp. nov., NHMW 1988/0141/0001, holotype, reconstruction of the caudal skeleton, right lateral view. Scale bar equals 2 mm.

putative diagnostic features of the batrachoidiforms, and, subsequently, Lauder and Liem (1983) proposed two synapomorphies, endopterygoid unossified and the possession of a dorsal fin with a short spinous portion and a long-based rayed portion, apparently defining the group. More recently, Wiley and Johnson (2010) proposed nine robust synapomorphies for the batrachoidiforms, including larvae with enormous yolk sac bearing an adhesive disc on its ventral surface [see also Breder and Rosen (1966) and Greenfield et al. (2008)]; crowded configuration of dorsal-fin spine-ptyerygiophore complex (see also Monod, 1960); first epineural hypertrophied, robust, and ligamentously bound to the medial surface of the cleithrum; possession of five pectoral-fin radials, the uppermost unossified in some genera, the lowermost the largest and with a condylar association with the coracoid (see also Monod, 1960); supracleithrum with condylar articulation with posttemporal; parietals absent [however, according to Siebenrock (1901), Regan (1912), Monod (1960), Le Danois (1961), Rosen and Patterson (1969), and Lauder and Liem (1983), the parietals are present in batrachoidiform fishes, apparently fused with the epioccipitals and, in certain cases, with the epioccipitals and supraoccipital]; pelvic fin with a very short spine and two rays; mesethmoid unossified (see also Gosline,

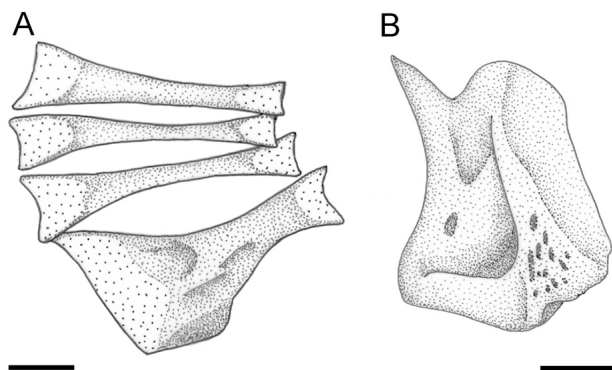


FIGURE 8. †*Zappaichthys harzhauseri*, gen. et sp. nov. A, NHMW 1976/1812/0044, paratype, pectoral-fin radials, right lateral view; B, NHMW 1988/0141/0001, holotype, left basipterygium, ventral view. Scale bars equal 2 mm.

1970); swimbladder with distinctive configuration [see, e.g., Collette and Russo (1981) and Rice and Bass (2009)].

As discussed above, the detailed morphoanatomical analysis of the fossil material documented herein revealed many of the batrachoidiform (and, as a consequence, batrachoidid) synapomorphies recognized by Wiley and Johnson (2010), including the crowded configuration of dorsal-fin spine-ptyerygiophore complex (Fig. 2A), possession of a robust and hypertrophied first epineural (Fig. 1A), posttemporal with articular condylar surface for the supracleithrum (Figs. 1A, 3), parietal and mesethmoid (apparently) absent (Fig. 3), and pelvic fin with one spine and two rays (Fig. 1A).

Within the Batrachoididae, a set of features unquestionably support the assignment of †*Zappaichthys* to the subfamily Halophryinae (see Greenfield et al., 2008), including the possession of three dorsal-fin spines, absence of foramina in the median process of the basipterygium, anterior ceratohyal characterized by an angular posteroventral corner, quadrate fan-shaped and characterized by a gently rounded dorsal margin, and possession of four fully ossified pectoral-fin radials. According to Greenfield et al. (2008), the subfamily Halophryinae includes 12 Old World genera (*Allenbatrachus*, *Austrobatrachus*, *Barchatus*, *Batrachomoeus*, *Batrachichthys*, *Bifax*, *Chatrabus*, *Colletteichthys*, *Halobatrachus*, *Halophryne*, *Perulibatrachus*, and *Riekertia*) plus *Triathalassotia* that occurs along the southeastern coast of South America. Therefore, †*Zappaichthys* represents the 14th genus of this relatively diverse clade of batrachoidid fishes.

†*Zappaichthys* has a peculiar combination of features that clearly justify its recognition as a new, previously unrecognized genus of the Halophryinae clade. It is characterized by a unique combination of features (see Greenfield et al., 2008), including the presence of 29 (10 + 19) vertebrae, presence of 16 dorsal-fin rays, presence of 11 anal-fin rays, presence of 20–25 pectoral-fin rays, overall configuration of the neurocranium (with wide interorbital region and postorbital sector larger than the orbital one), opercle with a single strong spine, subopercle with two spines and two short filaments, medial suture between anterior and posterior ceratohyals absent, rounded anterior end of the third epibranchial, four ossified pectoral-fin radials, and body naked.

The configuration of the distal bones of the opercular series is very useful for generic discrimination of batrachoidiform fishes. At least four halophryine genera, *Barchatus*, *Chatrabus*, *Colletteichthys*, and *Perulibatrachus*, exhibit a general configuration of the opercular bones consistent with that of †*Zappaichthys*, which is characterized by an opercle bearing a single strong spine together with a subopercle with two spines and two filaments arising from its posterodorsal corner. However, all of these genera can be easily separated from †*Zappaichthys* because they are characterized by a different morphology of the anterior end of the third hypobranchial (see Greenfield et al., 2008) and different dorsal- and anal-fin complements (see Table 3). The genera *Barchatus*, *Chatrabus*, and *Colletteichthys* differ from †*Zappaichthys* in having a neurocranium with less laterally developed interorbital region and orbital sector longer than postorbital one (see Greenfield et al., 2008). Moreover, †*Zappaichthys* also differs from *Barchatus*, *Colletteichthys*, and *Perulibatrachus* in lacking a medial suture between the anterior and posterior ceratohyals (see Greenfield et al., 2008), and it further differs from *Perulibatrachus* in lacking a scale covering.

The Fossil Record of Batrachoidiform Fishes

The evolutionary history of batrachoidiform fishes is scarcely documented in the fossil record, which primarily consists of otoliths and of very rare skeletal remains. Unfortunately, the origin and early phases of the evolutionary history of the group remain elusive. What appears to be the earliest representative of the group, †*Batrachoidiformis trapezoidalis*, was described by Nolf

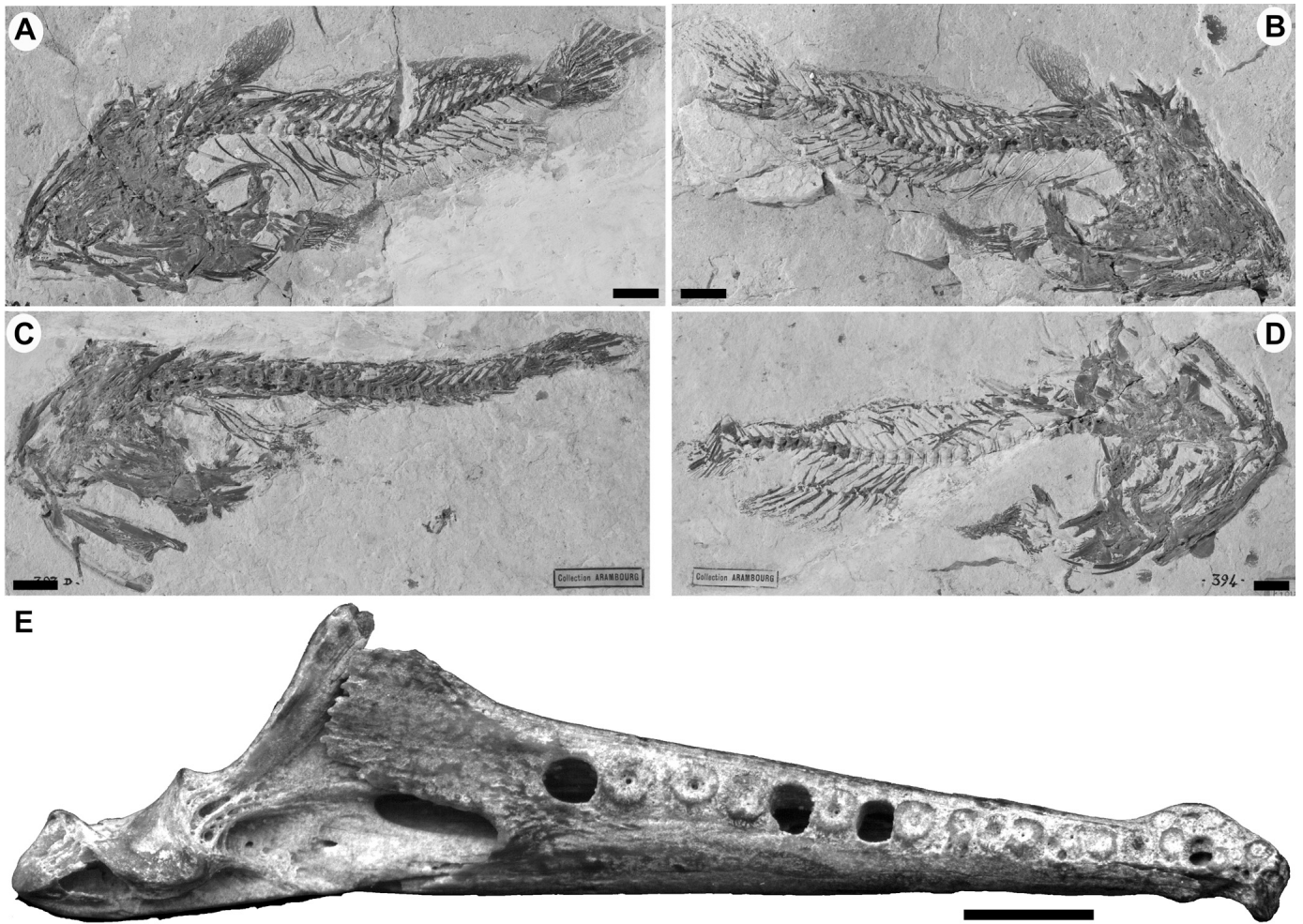


FIGURE 9. **A**, Halophryne batrachoidid from the Miocene diatomites of Raz-el-Ain, Chelif Basin, Algeria, MNHN ORA41d; **B**, Halophryne batrachoidid from the Miocene diatomites of Raz-el-Ain, Chelif Basin, Algeria, MNHN ORA41g; **C**, Halophryne batrachoidid from the Miocene diatomites of Raz-el-Ain, Chelif Basin, Algeria, MNHN ORA393d; **D**, Halophryne batrachoidid from the Miocene diatomites of Raz-el-Ain, Chelif Basin, Algeria, MNHN ORA394d; **E**, *Opsanus* sp. from the Miocene Choptank Formation, Chesapeake Group, Maryland, mandible, left medial view. Scale bars equal 10 mm.

(1988) from the lower Eocene (Ypresian) Gan Clay, Aquitaine, France, based on more than 50 well-preserved otoliths. The Eocene existence of this clade is also testified by the otolith-based taxon †*Batrachoidiformis canovae* from the upper Eocene (Priabonian) Marne di Possagno, northeastern Italy, which was formerly interpreted as an indeterminate lophiiform (Girone and Nolf, 2009; Nolf, 2013). The Oligocene record of toadfishes is extremely scarce, apparently represented by a single taxon from the Rupelian ‘Falun de Gaas’, Aquitaine, France (Nolf, 2013), which was originally assigned to the Apogonidae by Steurbaut (1984). Representatives of extant genera appeared during the early and middle Miocene in Europe, South America, and the Caribbean, including members of the Halophryinae (*Batrachthys*, *Halobatrachus*, *Perulibatrachus*; e.g., Nolf, and Smith, 1983; Radwanska, 1992; Reichenbacher, 1998; Nolf, 2013) and Porichthyinae (*Porichthys*; e.g., Nolf, 1976; Nolf and Stringer, 1992; Nolf and Aguilera, 1998), and it seems that some of the extant species appeared during the Pliocene (e.g., Fitch, 1964; Landini et al., 2002a, 2002b; Carnevale et al., 2011). Finally, otoliths assigned to indeterminate batrachoidid taxa have been reported from Miocene deposits of the Mediterranean region (e.g., Carnevale et al., 2006, 2008).

The only known articulated skeletal remains of batrachoidiform fishes other than those of †*Zappaichthys harzhauseri* described herein are six specimens (MNHN ORA41d+g; MNHN ORA393; MNHN ORA394; MNHN ORA1092d+g; MNHN ORA1103; MNHN ORA1199) from the upper Miocene (Messinian) diatomites of Raz-el-Ain, in the surroundings of the city of Oran, Chelif Basin, Algeria (see Fig. 9A–D). These specimens were listed by Camille Arambourg in a short note (Arambourg, 1921) and subsequently described in detail in his monumental monograph ‘Les Poissons Fossiles d’Oran’ (Arambourg, 1927). According to Arambourg (1927), these specimens are indistinguishable from the extant Lusitanian toadfish *Halobatrachus* (= *Batrachoides*) *didactylus* to which they were referred. This Miocene record of what was interpreted as the earliest record of *Halobatrachus didactylus* was reported in a number of studies (e.g., Rosen and Patterson, 1969; Landini and Menesini, 1984; Patterson and Rosen, 1989; Landini and Sorbini, 1992; Patterson, 1993; Gaudant, 2002; Carnevale, 2004). During a July 2013 visit at the Muséum National d’Histoire Naturelle, Paris, the batrachoidid material from Raz-el-Ain formerly described by Arambourg (1927) was reexamined, revealing a combination of features clearly indicative of totally different taxonomic assignment. The

TABLE 1. Measurements of †*Zappaichthys harzahuseri*, gen. et sp. nov., holotype, NHMW 1988/0141/0001.

Dimension	Measurement (% SL)
Standard length	162.3 mm
Total length	199.6 mm
Head length	34.9
Snout length	10.5
Orbit diameter	9.2
Neurocranial length	28.2
Neurocranial width	20.8
Interorbital width	8.5
Predorsal (1st dorsal) length	42.6
Predorsal (2nd dorsal) length	51.8
3rd dorsal-fin spine length	9.8
2nd dorsal-fin base length	39.3
Preanal length	74.9
Anal-fin base length	18.8
Prepectoral length	42.8
Pectoral-fin length	20.0

Standard and total length in mm. All other measurements are expressed as a percentage of SL.

Miocene toadfish from Raz-el-Aïn differs from the Lusitanian toadfish in having two spines and three filaments in the subopercle, as well as a different fin-ray and vertebral counts (D: III, 18 or 19 vs. III, 19–21; A: 12 vs. 15–17; vertebrae: 11 or 12 + 17 vs. 11 + 19; see Collette et al., 2006). The number of subopercular spines and filaments and the possession of three dorsal-fin spines unquestionably indicate that the Miocene toadfish from Raz-el-Aïn is a member of the subfamily Halophryinae. Such assignment is further corroborated by the absence of canine teeth and the squared posteroventral margin of the anterior ceratohyal (Greenfield et al., 2008). The subopercular configuration exhibited by the Miocene toadfish from Raz-el-Aïn is also characteristic of the halophryine genera *Chatrabus* and *Riekertia*; both *Chatrabus* and *Riekertia* differ from the Miocene toadfish from Algeria in having a higher number of anal-fin rays, and *Riekertia* also differs from it in having a totally ossified accessory (fifth) pectoral-fin radial (see Greenfield et al., 2008). The combination of peculiar subopercular configuration and meristic features exhibited by the Miocene toadfish material from Raz-el-Aïn might justify the creation of a new genus, because these represent reasonable criteria currently used to discriminate within the Batrachoididae at the generic level (see, e.g., Collette, 1995; Greenfield, 1997, 2006; Greenfield et al., 2008). In some cases (e.g., *Chatrabus*; see Greenfield et al., 2008), however, considerable intrageneric variation of salient morphological and meristic features has been reported, making it very difficult to evaluate the real taxonomic weight of certain potentially diagnostic characters. Therefore, additional comparative information concerning certain extant batrachoidid genera (including *Chatrabus*) would be necessary to properly interpret the taxonomic status of the Miocene toadfish material from Raz-el-Aïn.

Isolated bones belonging to the batrachoidine genus *Opsanus* are known from at least three localities of the Middle Atlantic Coastal Plain. Ray et al. (1968) assigned to *Opsanus* sp. a single neurocranium plus a right lower jaw from the Pleistocene Kempsville Formation, Virginia, and, subsequently, Purdy et al. (2001) extended the record of this genus to the early Pliocene

documenting the presence of two partially complete dentaries from the Yorktown Formation (Lee Creek Mine, North Carolina) referred to *Opsanus tau*. More recently, however, Carnevale and Godfrey (in press) extended further back the record of the genus *Opsanus* with the description of a partially complete left mandible from the Serravallian Choptank Formation, Chesapeake Group, Maryland (Fig. 9E).

In summary, the earliest evidence of batrachoidiform fishes in the record dates back to the early Eocene, whereas modern forms apparently flourished in the Miocene when at least three of the four main lineages (Batrachoidinae, Halophryinae, and Porichthyinae) were in existence. Anyway, considering the basal position of the batrachoidiform lineage within the percomorphs (see, e.g., Near et al., 2012, 2013; Betancur et al., 2013), the origin of this group probably occurred in the Cretaceous, thereby implying the existence of a wide gap in the fossil record. It is interesting to note, however, that a Cretaceous fossil, †*Bacchiaichthys zucchini* from the Campanian-Maastrichtian paralic deposits of Trebiciano, northeastern Italy (Bannikov and Sorbini, 2000), exhibits several batrachoidiform features. In particular, the overall physiognomy of †*Bacchiaichthys* is very similar to that of toadfishes, and it also shows a similar structure of the caudal skeleton, with the epaxial plate fused to the second ural centrum and the hypaxial plate fused to the first ural centrum plus first preural centrum and parhypural, a similar configuration of the first dorsal fin, absence of supraneural, spineless anal fin, and caudal fin rounded and containing a reduced number of rays. †*Bacchiaichthys* shows a number of features that concur to exclude any possible attribution to the Batrachoidiformes as currently defined (see Wiley and Johnson, 2010). However, a much more detailed comparative study of the available material of this putative percomorph fish would be desirable in order to conclusively demonstrate its phylogenetic affinities.

ACKNOWLEDGMENTS

We are grateful to W. Landini (Dipartimento di Scienze della Terra, Università di Pisa) and D. Nolf (Institut Royal des Sciences Naturelles de Belgique, Bruxelles) for useful discussion and precious suggestions and to F. Giudice for technical support during the preparation of the manuscript. M. Harzhauser and T. Nichterl (NHMW), G. Clement and M. Vèran (MNHN), and D. Bohaska (Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.) are thanked for permission to examine material under their care and logistic support. Thanks are also due to A. Schumacher (NHMW), P. Loubry (MNHN), S. J. Godfrey (CMM), and D. Bohaska for the photographs and to S. Raredon (Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.) for the radiographs. Not least our special thanks go to N. Levi and B. Levi, A. Brugnolli, and A. Forchielli for their kindness and wonderful hospitality. For reviewing the manuscript and providing constructive suggestions for its improvement, we are particularly grateful to D. W. Greenfield (Department of Biology, University of Hawaii at Manoa, Manoa) and B. Reichenbacher (Department für Geo- und Umweltwissenschaften, Ludwig-Maximilians-Universität, Munich). The research of the senior author was supported by the SYNTHESYS grants of the Naturhistorisches Museum, Vienna (AT-TAF-304 and AT-TAF-1692), and Muséum National

TABLE 2. Counts for †*Zappaichthys harzahuseri*, gen. et sp. nov.

Specimen	Vertebrae	Dorsal-fin formula	Anal-fin formula	Pectoral-fin rays
NHMW 1988/0141/0001	29 (10 + 19)	III+16	11	25
NHMW 1986/0138/0056	?	III+16	?	16+?
NHMW 1976/1812/0044	27? (10 + 17?)	III+?	?	20

TABLE 3. Synopsis of meristic values of batrachoidiform genera.

Subfamily	Genus	Dorsal-fin formula	Anal-fin formula	Pectoral-fin rays
Porchthyinae	<i>Aphos</i>	II, 32–33	30–32	19–20
	<i>Porichthys</i>	II, 29–41	26–39	14–20
Thalassophryinae	<i>Thalassophryne</i>	II, 17–21	16–20	13–17
	<i>Daector</i>	II, 22–33	21–30	15–18
Batrachoidinae	<i>Amphichthys</i>	III, 28–29	23–26	21–22
	<i>Batrachoides</i>	III, 21–30	19–27	19–20
	<i>Opsanus</i>	III, 23–27	19–23	17–21
	<i>Potamobatrachus</i>	III, 18–19	15–16	18–20
	<i>Sanopus</i>	III, 29–34	24–28	19–23
	<i>Vladichthys</i>	III, 20–21	15–17	18–20
	Halophryinae	<i>Allenbatrachus</i>	III, 18–22	16–19
<i>Austrobatrachus</i>		III, 20–23	15–18	18–21
<i>Barchatus</i>		III, 18	13–14	25
<i>Batrachomoeus</i>		III, 19–24	15–20	21–23
<i>Batrachthys</i>		III, 18–22	14–18	16–23
<i>Bifax</i>		III, 23–24	15–18	20–21
<i>Chatrabus</i>		III, 18–23	13–18	19–25
<i>Colletteichthys</i>		III, 19–22	14–17	21–24
<i>Halobatrachus</i>		III, 19–21	15–17	24–25
<i>Halophryne</i>		III, 17–20	14–17	19–24
<i>Perulibatrachus</i>		III, 16–21	13–17	19–26
<i>Riekertia</i>		III, 19–20	15–17	24–25
<i>Triathalassothia</i>		III, 14–17	11–13	23–24
<i>Zappaichthys</i>		III, 16	11	20–25

Data from Collette (1966, 1968, 1973, 1974, 1983, 1995, 2001), Collette et al. (2006), Collette and Russo (1981), Evermann and Radcliffe (1917), Gilbert (1968), Greenfield (1996, 1997, 1998, 2005, 2006, 2012a, 2012b), Greenfield and Greenfield (1973), Greenfield et al. (1994, 2008), Greenfield and Smith (2004), Hubbs and Schultz (1939), Hutchins (1976, 1986), Penrith and Penrith (1971), Roux (1970), Smith (1952), Walker and Rosenblatt (1988).

d'Histoire Naturelle, Paris (FR-TAF-2507); visits to Calvert Marine Museum, Solomons, Maryland, and National Museum of Natural History, Washington, D.C., were supported by the Clarissa and Lincoln Dryden Endowment for Paleontology and a Smithsonian Short-term Fellowship.

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Submitted August 31, 2013; revisions received October 8, 2013; accepted October 9, 2013.

Handling editor: Charlie Underwood.