



# BAJAICHTHYS ELEGANS FROM THE EOCENE OF BOLCA (ITALY) AND THE OVERLOOKED MORPHOLOGICAL DIVERSITY OF ZEIFORMES (TELEOSTEI, ACANTHOMORPHA)

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**Abstract:** The Eocene (Ypresian) fauna of Bolca, Italy yields a famous assemblage of marine tropical teleosts. One of the most anatomically distinctive teleosts from Bolca is the enigmatic †*Bajaichthys elegans*, generally interpreted as a member of Lampridiformes (oarfishes and their allies). Re-examination of the type and only specimen of †*Bajaichthys* contradicts this attribution, and we propose that its original description as a member of Zeiformes (dories) was in fact correct. †*Bajaichthys* bears numerous derived features of zeiforms not found in lampridiforms, including: a pelvic spine, a first vertebra closely associated with the neurocranium, and a reduced metapterygoid not contacting the quadrate. Lampridiform-like attributes, including a greatly elongated ascending process of the premaxilla, are known to be convergent between this group and Zeiformes. Using a combination of morphological and molecular data, we confirm this revised interpretation and resolve the position of

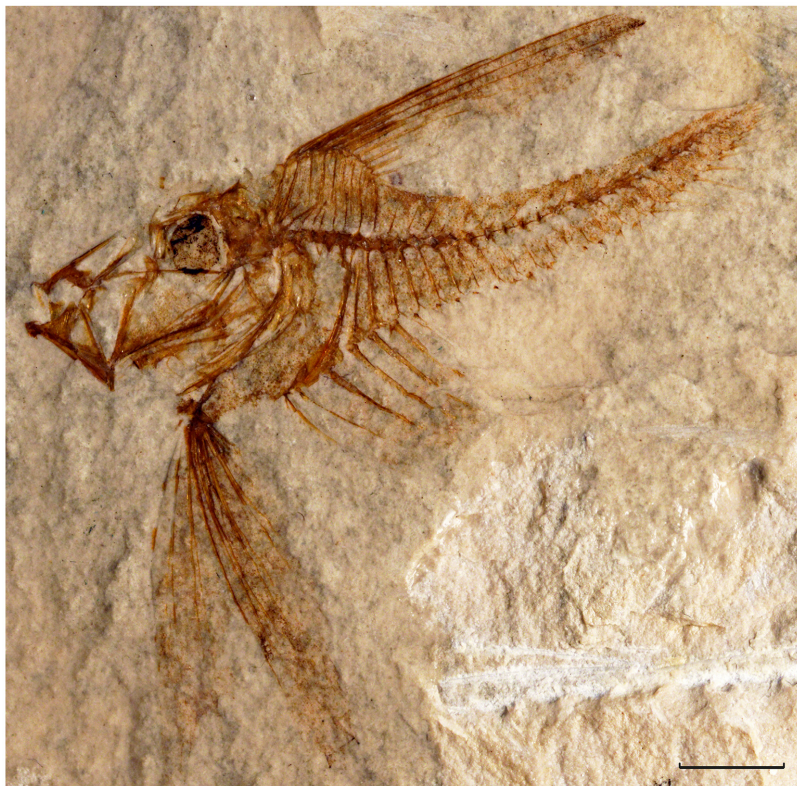
†*Bajaichthys* within zeiform phylogeny. In terms of overall shape, the very elongate †*Bajaichthys* contrasts with deep-bodied Zeiformes and probably had distinctive ecological habits. Our inferred placement of †*Bajaichthys* and other fossil taxa with extended caudal peduncles (e.g. †*Archaeozeus*) suggests that the elongate morphotype is ancestral for Zeiformes as a whole, and that the deep-bodied geometry typical of extant taxa probably appeared several times independently. However, these inferences must be considered preliminary due to low support for patterns of relationships within Zeiformes. The systematic reattribution of †*Bajaichthys* expands the taxonomic diversity of the Bolca fauna as well as the morphological and ecological diversity of the zeiform clade.

**Key words:** Eocene, Bolca, Teleostei, Lampridiformes, Zeiformes.

THE early Eocene (Ypresian) fauna of Bolca, Italy, is famous worldwide for its rich diversity of marine taxa, often preserved in stunning anatomical detail. The Bolca localities provide a key window into an early Cenozoic marine teleost assemblage, dominated by spiny-rayed teleost fishes (Acanthomorpha) as in modern marine environments (Blot 1980; Carnevale *et al.* 2014). It represents the oldest example of a modern tropical reef-associated fauna (Bellwood *et al.* 2016; Marramà *et al.* 2016) and includes some of the oldest representatives of many emblematic acanthomorph clades, such as the asymmetrical flatfishes (Friedman 2012) and the ultra-diverse gobioids (Bannikov & Carnevale 2016).

One of the most puzzling teleosts known from this fauna is †*Bajaichthys elegans*, represented by a single small specimen with an elongate body, very high dorsal fin,

elongate pelvic fins, and highly protrusible jaws (Figs 1–3). †*Bajaichthys* was initially described by Sorbini (1983) as a member of Zeiformes, a clade of acanthomorphs that includes well-known species such as the John Dory (*Zeus faber*) along with rarer, deep-sea taxa. He later changed his view (Sorbini & Bottura 1988) and attributed the taxon to Lampridiformes (opahs, oarfishes and allies). This interpretation, primarily based on the elongate body, extremely mobile jaws and apparent lack of dorsal- and anal-fin spines of †*Bajaichthys*, persists in the literature (Bannikov 2014a, b; Carnevale *et al.* 2014). However, some anatomical features apparent in available descriptions seem to contradict this attribution. Here, we redescribe the osteology of the holotype and only known specimen of †*Bajaichthys*, with the goal of deciphering its precise phylogenetic attribution.

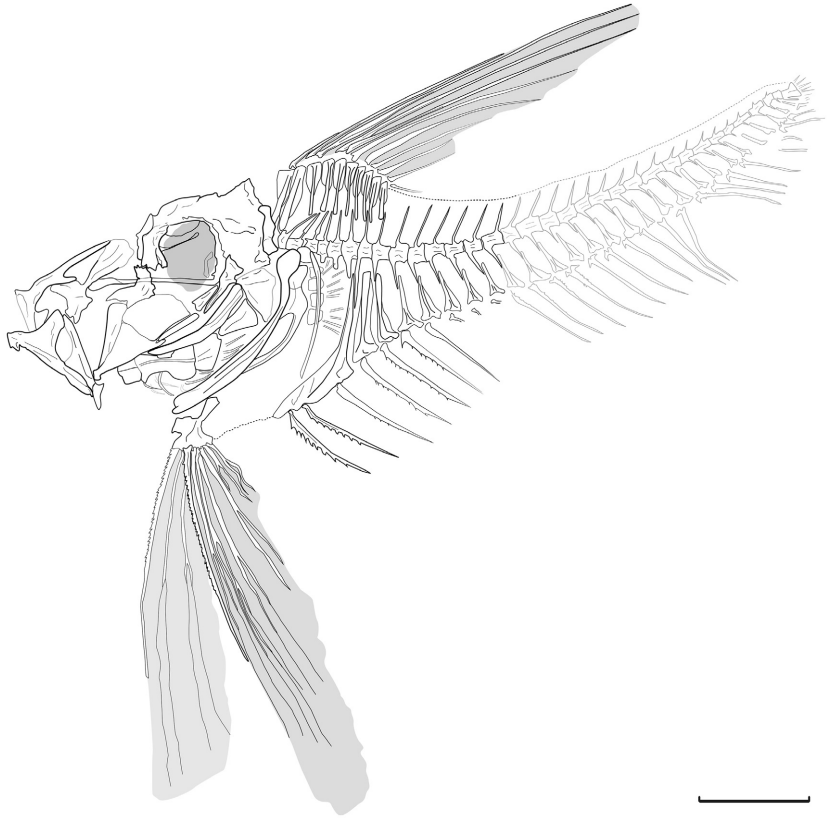


**FIG. 1.** †*Bajaichthys elegans*, photograph of the holotype MCSNV T.922. Scale bar represents 5 mm. Colour online.



**FIG. 2.** †*Bajaichthys elegans*, photograph of the holotype MCSNV T.923 (counterpart). Scale bar represents 5 mm. Colour online.

**FIG. 3.** †*Bajaichthys elegans*, interpretative drawing of the holotype MCSNV T.922/T.923. The grey areas are pigmented in the fossil. The grey lines are drawn from MCSNV T.923. Scale bar represents 5 mm.



## MATERIAL AND METHOD

The specimen studied here is part of the Baja collection, housed at the Museo Civico di Storia Naturale (MCSNV), Verona, Italy. It was examined using a Leica M80 stereomicroscope equipped with a camera lucida drawing arm; measurements were taken with a compass. To enhance details, the specimen was moistened with alcohol. All extinct taxa are indicated with a dagger (†).

## SYSTEMATIC PALAEOLOGY

TELEOSTEI Müller, 1845

ACANTHOMORPHA Rosen, 1973

Order ZEIFORMES Regan, 1910 *sensu* Johnson & Patterson, 1993

Family †BAJAICHTHYIDAE Bannikov & Sorbini *in* Bannikov, 2014a

Genus †BAJAICHTHYS Sorbini, 1983

†*Bajaichthys elegans* Sorbini, 1983

*Emended diagnosis.* Zeiform with an anteriorly deep body that tapers posteriorly. Skin covered with protuberances and small spines. Head large, with a low supraoccipital

crest. Vertebral column including 35 (8 + 27) vertebrae. Dorsal fin short-based but high, consisting of five spines and six unbranched soft rays. Ten dorsal-fin pterygiophores. Anal fin consisting of two serrated spines and 28 unbranched soft rays, converging with the caudal fin. 27 anal-fin pterygiophores, the first one enlarged and with three supernumerary elements. Caudal fin asymmetrical, with between five and seven rays. Pelvic fins long, jugular, with one serrated spine and six soft rays.

*Holotype.* MCSNV T.922/T.923, a complete specimen in part and counterpart (Figs 1–3), 38.5 mm standard length (SL), from the Ypresian (late early Eocene) of the Pesciara site, Monte Bolca, Italy. The species is represented by the holotype only.

### *Systematic history*

A description of MCSNV T.922/T.923 first appeared in the catalogue of the Baja collection of Bolca fossils, presented at the Museo Civico di Storia Naturale, Verona (Sorbini 1983). In the first edition of this book, Sorbini proposed a new genus and species due to the peculiar appearance of the fossil, and suggested affinity with Zeiformes (and proximity with family Zeidae) due to ‘the

characters of the head skeleton, the number of vertebrae and the shape of the caudal fin' (Sorbini 1983, translated from the Italian). Consistent with a zeiform interpretation, Sorbini (1983) reported spiny rays in the dorsal, anal and pelvic fins. In a later edition of the same catalogue, published in 1985, the systematic attribution of †*Bajaichthys* is changed to Lampridiformes, with no reference to spiny rays in the description. In a subsequent, more complete description of the genus (Sorbini & Bottura 1988), its unusual mix of characters was used to justify the lampridiform interpretation (mobile jaws, absence of spiny rays, presence of an orbitosphenoid). Moreover, this study placed †*Bajaichthys* in a new suborder due to similarities to both existing 'Bathysomi' (low vertebral counts, vertical pectoral girdle, deep head; this group is now known to be paraphyletic: Olney *et al.* 1993; Wiley *et al.* 1998) and Taeniosomi (elongate body, reduced caudal fin and similar integument). Subsequent authors concurred with this interpretation (Olney *et al.* 1993; Bannikov 1999; Carnevale 2004), leading Bannikov (2014a) to erect the new family †Bajaichthyidae.

#### Description

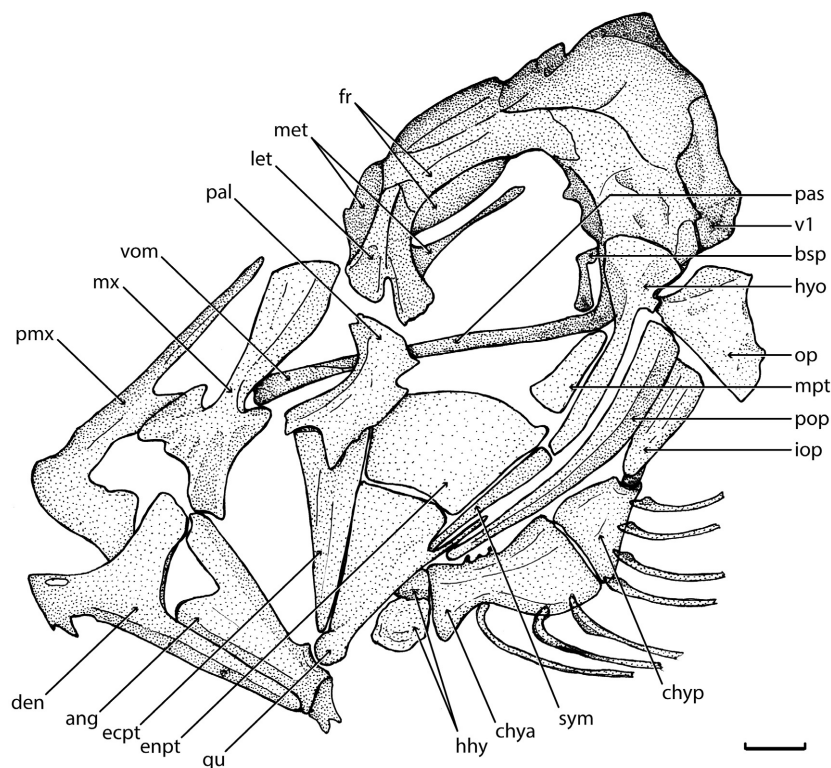
Body elongate and tapering posteriorly (Figs 1–3), its maximum depth is contained less than three times in standard length (SL). The head is large; its depth is

contained slightly more than three times in SL. The snout is well-developed and the orbit is moderately large. The dorsal profile of the body is characterized by a hump-like structure associated with the dorsal fin.

The short-based dorsal fin is extremely high (its height is contained less than two times in SL), similar to the pelvic fins (their length being contained slightly more than two times in SL). The anal-fin base shows remarkable posterior extension, and converges with the caudal fin. The mouth is terminal, with a relatively short gape. Because of the very anterior insertion of the anal fin, the abdominal cavity is much reduced.

*Measurements.* SL: 38.5 mm; maximum body depth: 14.2 mm (36.9% SL); head length: 14.0 mm (36.4% SL); head depth: 12.4 mm (32.2% SL); snout length: 7.8 mm (20.3% SL); orbit diameter: 3.1 mm (8.1% SL); pre-dorsal length: 15.5 mm (40.3% SL); pre-pectoral length: 14.3 mm (37.1% SL); pre-pelvic length: 11.8 mm (30.6% SL); pre-anal length: 14.3 mm (37.1% SL); pelvic fin length: 16.4 mm (42.6% SL); dorsal fin length: 21.2 mm (55.1% SL).

*Neurocranium.* The neurocranium is two times longer than deep. The ethmoid region was not fully ossified, as is clearly evident from the conspicuous gap between lateral ethmoids and vomer (vom; Fig. 4). This hiatus results in an apparent remarkable anterior extension of the parasphenoid and vomer beyond the anterior margin



**FIG. 4.** Reconstruction of the head of †*Bajaichthys elegans* in left lateral view, based on the holotype (MCSNV T.922/T.923). Scale bar represents 1 mm. *Abbreviations:* ang, anguloarticular; bsp, basisphenoid; chya, anterior ceratohyal; chyp, posterior ceratohyal; den, dentary; ecpt, ectopterygoid; enpt, endopterygoid; fr, frontal; hhy, hypohyals; hyo, hyomandibula; iop, interopercle; let, lateral ethmoid; met, mesethmoid; mpt, metapterygoid; mx, maxilla; op, opercle; pal, palatine; pas, parasphenoid; pmx, premaxilla; pop, preopercle; qu, quadrate; sym, symplectic; v1, first abdominal vertebra; vom, vomer.

of the lateral ethmoid. The morphology of the mesethmoid is difficult to interpret, possibly because it was largely cartilaginous. However, a median anterior bony lamina and a median bar (extending posteriorly and visible through the orbit) possibly represent the anterior and posterior processes of the mesethmoid, respectively. The median anterior bony lamina of the mesethmoid (met; Fig. 4) was erroneously considered to be a nasal by Sorbini & Bottura (1988). The lateral ethmoid is columnar, robust, with a notched ventral margin, and a lateral flange that forms the anterior wall of the orbit; it does not articulate with the parasphenoid and vomerine region syndesmatically, thereby suggesting that a relatively large cartilage was present in this region (let; Fig. 4). The frontals are the largest bones of the skull roof; each frontal articulates medially with its counterpart, forming a ventral groove which is expressed ventrally as a ridge, visible through the orbit (fr; Fig. 4). Such a modified anterior part of the skull roof probably accommodated the elongated ascending processes of the premaxillae and the associated rostral cartilage. The ventrally depressed medial part of the frontals was interpreted by Sorbini & Bottura (1988) as an orbitosphenoid, but we cannot observe any trace of this bone in the fossil. A short median crest is present on the posterior portion of the frontals, representing an anterior extension of the supraoccipital crest. The supraoccipital is dome-like, with irregular dorsal and posterior margins. The otic region of the neurocranium is difficult to interpret. The basisphenoid (bsp; Fig. 4) is relatively long and thick and almost contacts the parasphenoid ventrally. The basioccipital is robust. The parasphenoid is very elongate, nearly straight anteriorly and slightly curved in its posterior region (pas; Fig. 4). The vomer is very small, and poorly preserved. The presence or absence of teeth on this bone cannot be determined.

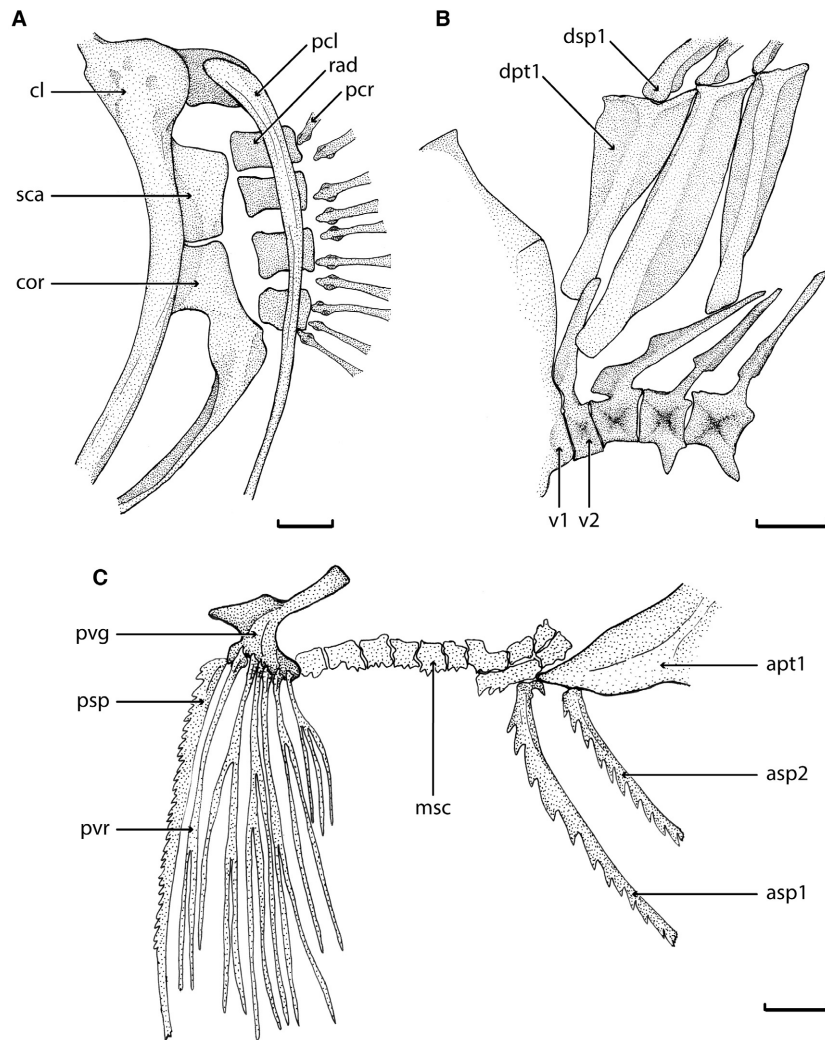
*Jaws.* The premaxilla (pmx; Fig. 4) has a very elongate ascending process, almost twice as long as the alveolar process. A spatulate articular process emerges along the posterior margin of the ascending process. A short postmaxillary process is present but does not seem to form a notch with the alveolar process. The maxilla (mx; Fig. 4) has an irregular morphology, with a distally expanded dorsal region. There is no supramaxilla. The dentary has a concave anterior profile, a well-developed coronoid process and a short, ventrally directed spine at the symphysis (den; Fig. 4). The anguloarticular (ang; Fig. 4) is approximately triangular with a concave anterior margin and an irregular serration posteriorly. There is a wide fenestra between the posterior margin of the dentary and the anterior margin of the anguloarticular. A small retroarticular can be observed at the posterior corner of the lower jaw. There is no evidence of oral teeth on either the premaxilla or dentary.

*Suspensorium.* The hyomandibula has a single articular head and a relatively short and nearly straight ventral shaft (hyo; Fig. 4). The opercular process is short and slightly ventrally oriented. The quadrate is large, fan-like, and bears a robust articular head (qu; Fig. 4). The symplectic is rod-like and relatively well-developed (sym; Fig. 4). The metapterygoid (mpt; Fig. 4) is remarkably reduced; its posterior margin is closely associated with the hyomandibula. In their earlier description of the material, Sorbini & Bottura (1988) erroneously identified the endopterygoid as the metapterygoid. The enlarged endopterygoid (enpt; Fig. 4) is quadrangular and separates the metapterygoid from the quadrate. The ectopterygoid (ecpt; Fig. 4) is oblong, with an expanded antero-dorsal end. The palatine (pal; Fig. 4) is oriented oblique to the parasphenoid, massive and irregular in outline; the maxillary process is short and does not contact the maxilla, suggesting that the palatine articulates only with the lateral ethmoid. There is no trace of palatine or pterygoid teeth.

*Opercular series.* Overall, the bones of the opercular series are much reduced. The preopercle (pop; Fig. 4) is narrow, elongate and slightly curved with a smooth posterior margin. The opercle (op; Fig. 4) is roughly triangular with a thickened antero-ventral margin. The interopercle (iop; Fig. 4) is oblong and laminar, and remarkably shorter than the overlying preopercle. The subopercle is not exposed in the fossil.

*Hyoid and gill arches.* The hyoid bar is elongate and shallow. The hypohyals (hhy; Fig. 4) cannot be distinguished from one another. The anterior ceratohyal (chya; Fig. 4) is constricted in its anterior half and strongly expanded posteriorly, forming a prominent ventral notch. Along its dorsal margin, a small concavity is bordered by two small symmetrical recurved processes that terminate in points. This peculiar embayment might represent a dorsally open 'beryciform' foramen. The posterior ceratohyal (chyp; Fig. 4) is approximately triangular, with a sigmoid postero-ventral margin; a cotyle in its postero-dorsal corner accommodates the interhyal. The articulation between the ceratohyals is not interdigitated. There are seven branchiostegal rays, of which the anterior three articulate with the anterior ceratohyal and the remaining four with the posterior ceratohyal. Two additional short disarticulated branchiostegal rays are visible at the level of the articulation between hypohyals and anterior ceratohyal, but their original position cannot be determined and they might belong to the right side of the body. Gill arches are not visible.

*Vertebral column.* The vertebral column consists of 35 (8 + 27) vertebrae (Figs 1–3), including the urostylar centrum. The first vertebra (v1; Figs 4, 5B) is closely



**FIG. 5.** Interpretative drawings of some postcranial elements of †*Bajaichthys elegans* in left lateral view, based on the holotype specimen (MCSNV T.922). A, detail of the pectoral girdle and pectoral-fin insertion. B, detail of the anterior vertebrae and dorsal-fin insertion. C, detail of the pelvic girdle and fin and anterior part of the anal fin. *Abbreviations:* apt, anal-fin pterygiophore; asp, anal-fin spine; cl, cleithrum; cor, coracoid; dpt, dorsal-fin pterygiophore; dsp, dorsal-fin spine; msc, modified ventral scales; pcl, postcleithrum; pcr, pectoral-fin rays; psp, pelvic-fin spine; pvg, pelvic girdle; pvr, pelvic-fin rays; rad, pectoral-fin radials; sca, scapula; v1, first abdominal vertebra. All scale bars represent 1 mm.

articulated with the occipital region of the neurocranium, and its neural arches and spines are expanded antero-posteriorly. This was not mentioned in earlier descriptions (Sorbini 1983; Sorbini & Bottura 1988). The second vertebral centrum is antero-posteriorly compressed (v2; Fig. 5B). The other abdominal centra are subrectangular, higher than long. The caudal centra height-to-length ratio decreases posteriorly and they become longer than high around the 15th centrum (Figs 1–3). The four posterior abdominal vertebrae bear robust parapophyses of gradually increasing size. The bases of the neural spines of the abdominal and anterior caudal vertebrae are weakly ossified. The neural spines of the second to sixth abdominal vertebrae are bent posteriorly, while the following ones are nearly vertical. Toward the posterior end of the body, the neural spines become gradually shorter and bent posteriorly. The haemal spines are stouter than their neural counterparts. They are short dorsal and ventral pre- and post-zygapophyses throughout the column. There is no

evidence of pleural ribs. However, a few fragmented epineurals can be recognized in the anterior part of the abdominal region, and these seem to articulate at the base of the neural arches.

*Median fins and supports.* The caudal skeleton and fin appear to be dorsoventrally asymmetric. The distal portions of at least two hypurals can be recognized in the counterpart T.923, but the caudal region is too poorly preserved to determine confidently the number of elements or their identities (Figs 1–3). Five to seven caudal-fin rays are feebly preserved. They do not overlap with the caudal skeleton.

No supraneural is preserved (Fig. 5B), but the presence of a cartilaginous one cannot be excluded. The dorsal fin originates at the level of the third abdominal vertebra and contains eleven elements supported by ten pterygiophores (Figs 1–3). All of these are non-bifurcated and non-segmented and the first five are tentatively regarded as spines

because of their robustness and pointed distal tips. The first spine is in supernumerary association with the first dorsal pterygiophore (Fig. 5B). It is much shorter than the posterior ones. Stout spinules diverge dorsolaterally from the base of the rays. The first dorsal-fin pterygiophore (dpt1; Fig. 5B) inserts in the first interneural space. The third and fifth interneural spaces are vacant. The main shaft of the pterygiophores is robust and supports anterior and posterior bony laminae. The anal fin inserts at the level of the fourth abdominal vertebra. It consists of two spines plus 28 rays, supported by 27 pterygiophores (Figs 1–3). All the rays are non-bifurcated, and all but the posteriormost are non-segmented. All the rays have ventro-laterally protruding spines at their base, and serrated lateral margins. The anal-fin spines are also serrated anteriorly (asp1-2; Fig. 5C). The spines and the anteriormost ray are in supernumerary association on the first anal-fin pterygiophore (apt1; Fig. 5C). This first anal-fin pterygiophore is greatly expanded, with a strongly curved anterior profile.

*Paired fins and girdles.* The posttemporal and supraclithrum are not clearly recognizable. The cleithrum is crescent-shaped, with a spatulate ventral end (cl; Fig. 5A). The scapula and coracoid are well-developed. The scapular foramen is not recognizable. There is an elongate, sabre-shaped postcleithrum (pcl; Fig. 5A). It appears to have an expanded proximal portion that articulates with the cleithrum. We cannot determine if this expansion represents a separate postcleithral element. There are four, weakly ossified pectoral-fin radials (rad; Fig. 5A). At least ten apparently unbranched rays (pcr; Fig. 5A) are supported by the pectoral-fin radials. The pectoral fin inserts at mid-height along the flanks. The pelvic fins are jugular and contain a single spine with an anterior serrated margin, plus six multifurcated rays (Fig. 5C). The two anterior rays are the longest. The main shaft of the basipterygium (pvg; Fig. 5C) is nearly vertical and reaches the ventral margin of the cleithrum. There is an anterior process with an irregular profile corresponding to the external ventral wing of Stiassny & Moore (1992). The post-pelvic process is short and stout.

*Integument.* The entire body, including the nape and cheek, is covered with modified scales. Each of these scales consists of a rounded base from which a single pointed posteriorly recurved spinule protrudes. Posterior to the dorsal fin, the dorsal margin of the body is characterized by a dense accumulation of larger scale spinules with dorsally oriented tips. A series of modified spiny scales occurs on the ventral margin of the body between the pelvic and anal fins (msc; Fig. 5C). A large, subrectangular scale with a serrated anteroventral margin partially overlaps the anteroventral tip of the first anal-fin

pterygiophore. On both dorsal and pelvic fins, the membrane that originally connected the rays is preserved as a thin pigmented film (Figs 1–3).

## SYSTEMATIC POSITION OF †*BAJAICHTHYS*

### †*Bajaichthys* as a lampridiform

Most modern representatives of Lampridiformes (= Lampriformes in Nelson *et al.* 2016) have a very peculiar morphology, exemplified by the large, elongate, and laterally flattened Taeniosomi (oarfishes, crestfishes, ribbonfishes). Lampridiformes are also characterized by highly mobile upper jaws, owing to specializations of the palatine, premaxilla, maxilla and frontal bones (Oelschläger 1976, 1983). For this reason, several other elongate marine teleost taxa with very mobile jaws have been at some point aligned with Lampridiformes, including Ateleopodidae, Mirapinnidae and Stylephoridae (Rosen & Patterson 1969). These three taxa are now excluded from Lampridiformes and recognized respectively as a separate non-acanthomorph order Ateleopodiformes, as larval Cetomimidae ('Beryciformes') and as an isolated lineage close to Gadiformes and Zeiformes (Olney *et al.* 1993; Miya *et al.* 2007; Johnson *et al.* 2009; Near *et al.* 2012; Betancur-R. *et al.* 2013; Grande *et al.* 2013a; Chen *et al.* 2014).

Similarly, our close re-examination of †*Bajaichthys* suggests that it does not belong to Lampridiformes. It does not show some of the synapomorphies of the larger clade Lampridomorpha (Davesne *et al.* 2014; Delbarre *et al.* 2016), such as the overlap of the caudal-fin rays with the caudal skeleton (hypurostegy). Moreover, numerous synapomorphies of Lampridiformes are either missing or show non-equivalent states (Olney *et al.* 1993; Davesne *et al.* 2014, 2016): (1) there is no frontal 'vault'; (2) the mesethmoid expands anteriorly and posteriorly to the lateral ethmoids, while in modern lampridiforms it only expands posteriorly; (3) the articulation between the anterior ceratohyal and the ventral hypohyal is not condylar; (4) the anteriormost dorsal-fin pterygiophore inserts posterior to the first neural spine. Additional features, found in all Lampridiformes except for Veliferidae (Olney *et al.* 1993) are also missing in †*Bajaichthys*: (1) there are four autogenous pectoral-fin radials (instead of three); (2) there are 35 vertebrae in total (instead of more than 40); (3) the base of the pectoral fin is vertically oriented (instead of horizontal). Finally, the dorsal-fin base is always longer than the anal-fin base in lampridiforms, especially in taeniosomes that have a reduced or absent anal fin (Olney *et al.* 1993; Bannikov 1999). By contrast, †*Bajaichthys* has an anal-fin base that greatly exceeds the length of the

dorsal-fin base. In the light of these observations, we reject its attribution to Lampridiformes.

#### †*Bajaichthys* as a zeiform

Modern diversity within the exclusively marine order Zeiformes (without Caproidae, *sensu* Johnson & Patterson 1993) consists of approximately 30 species divided between six recognized families (Tyler *et al.* 2003; Nelson *et al.* 2016): Cyttidae (lookdown dories: genus *Cyttus*), Oreosomatidae (oreos: *Oreosoma*, *Pseudocyttus*, *Alloctytus* and *Neocyttus*), Parazenidae (smooth dories: *Parazen*, *Cyttopsis* and *Stethopristes*), Zeniontidae (armoreye dories: *Zenion*, *Cyttomimus* and *Capromimus*), Grammicolepididae (tinselfishes: *Grammicolepis*, *Macrurocyttus* and *Xenolepidichthys*) and Zeidae (dories: *Zeus* and *Zenopsis*).

The fossil record of Zeiformes extends to the Late Cretaceous, with †*Cretazeus rinaldii* from the outcrops of Cava, near Nardò, Italy (Tyler *et al.* 2000), tentatively considered to be Campanian in age (Schlüter *et al.* 2008; Chen *et al.* 2014). Another putative Cretaceous genus, †*Palaeocyttus princeps* from the Cenomanian of Portugal (Gaudant 1978), is even older. However, the holotype and only specimen is poorly preserved and provides few convincing characters, casting doubt over its attribution to Zeiformes (Patterson 1993; Tyler *et al.* 2003). Two additional fossil genera are known from the early Palaeogene: †*Archaeozeus skamolensis* and †*Protozeus kuehnei*, from the earliest Eocene (Ypresian) Fur Formation of Denmark (Tyler *et al.* 2000; Baciu *et al.* 2005). Another undescribed zeiform taxon is also found in this formation (Bonde *et al.* 2008). Most post-Eocene fossil zeiforms are attributable to the extant genera *Zeus* and *Zenopsis* (Baciu *et al.* 2005; Santini *et al.* 2006).

†*Bajaichthys* shows numerous characters regarded as synapomorphies of Zeiformes (Tyler *et al.* 2003; Tyler & Santini 2005): (1) the metapterygoid is reduced in size and does not contact the quadrate; (2) the anterior ceratohyal has a prominent ventral notch; (3) there are seven branchiostegal rays; (4) the dorsal fin inserts in the first interneural space; (5) there are two anal-fin spines; (6) pectoral-fin rays are unbranched; (7) there is a single pelvic-fin spine. Moreover, †*Bajaichthys* shows several of the synapomorphies supporting a larger Gadiformes + Zeiformes clade, many of which are not observed in Lampridiformes (Grande *et al.* 2013a; Davesne *et al.* 2016): (1) the neural spine of the first abdominal vertebra is closely associated with the neurocranium; (2) the second abdominal vertebra is shortened; (3) the orbitosphenoid is absent (although described present by Sorbini & Bottura 1988); (4) the palatine does not bear teeth.

Finally, some characters are shared by †*Bajaichthys*, lampridiforms and zeiforms (Olney *et al.* 1993; Tyler &

Santini 2005). These include the absence of supramaxillae, the elongate ascending processes of premaxillae (but the articular and postmaxillary processes are well-developed in †*Bajaichthys* and Zeiformes, while it is not the case in lampridiforms), the reduction in number of caudal-fin rays and the unbranched dorsal- and anal-fin rays (only in taeniosome lampridiforms); we interpret these as convergent losses.

This combination of characters confirms Sorbini's (1983) initial intuition that †*Bajaichthys* is a zeiform rather than a lampridiform. In order to establish its precise phylogenetic position within the group, we performed a series of phylogenetic analyses using a combination of morphological and molecular datasets.

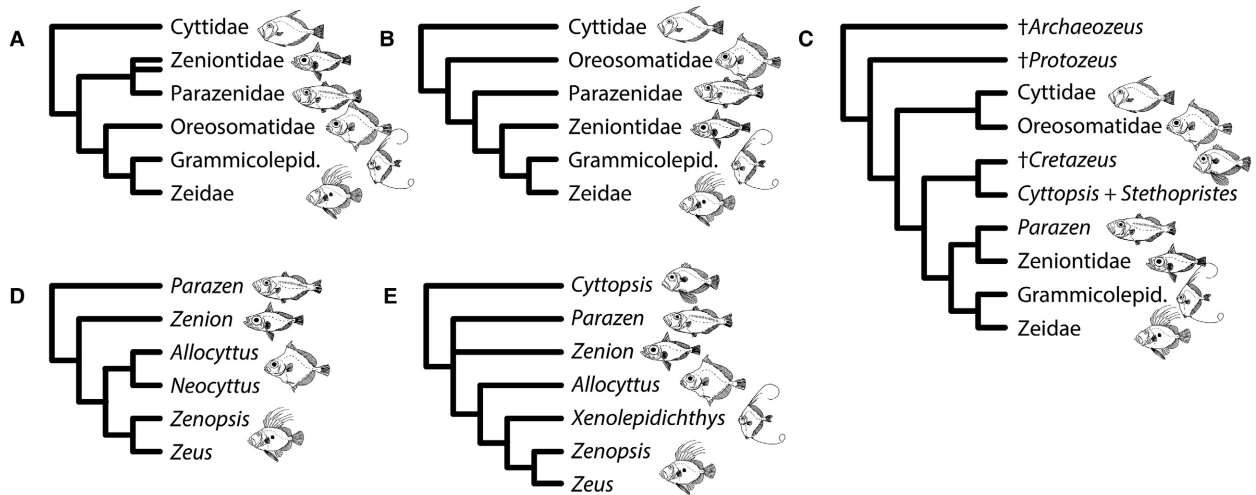
## PHYLOGENETIC ANALYSIS

### *Previous phylogenetic studies of Zeiformes*

The phylogenetic position of Zeiformes amongst Acanthomorpha has been the subject of considerable debate. A clade uniting them with Tetraodontiformes (pufferfishes and allies) and Caproidae (boarfishes) was proposed on the basis of osteological arguments (Rosen 1984) and formal phylogenetic analyses (Tyler *et al.* 2003; Tyler & Santini 2005). Based on a survey of all major acanthomorph groups, Johnson & Patterson (1993) placed Zeiformes as the sister lineage of Beryciformes and Percomorpha (the latter including caproids and tetraodontiforms), within Acanthopterygii. On the other hand, phylogenetic studies based on molecular data consistently find that Zeiformes are close relatives to Gadiformes (cods and allies) and the tube-eye *Stylephorus* (Wiley *et al.* 2000; Miya *et al.* 2001, 2003, 2007; Dettai & Lecointre 2005; Betancur-R. *et al.* 2013; Grande *et al.* 2013a; Near *et al.* 2013; Chen *et al.* 2014), excluding them from both Percomorpha and Acanthopterygii. This most recent placement has found additional support in the reinvestigation of morphological data (Borden *et al.* 2013; Grande *et al.* 2013a; Davesne *et al.* 2016).

In contrast to the wide body of literature targeting the placement of zeiforms within acanthomorphs, few studies have explored relationships within Zeiformes (Fig. 6). Based on a survey of morphological characters within a wide acanthomorph sampling, Johnson & Patterson (1993) proposed that Parazenidae and Zeniontidae are probably sister to all remaining Zeiformes, as they retain plesiomorphic conditions for several characters, including a first neural spine not entirely applied to the neurocranium, and a single vacant interneural space below the dorsal fin. The morphological matrix of Tyler *et al.* (2003) comprehensively included every zeiform family and genus, and 20 out of about 30 extant species. However, it did not include any





**FIG. 6.** Published phylogenetic hypotheses of Zeiformes intrarelationships. Only the zeiform part of each tree is shown. A, topology of Tyler *et al.* (2003), based on morphological data, with characters treated as ordered. B, topology of Tyler *et al.* (2003), based on morphological data, with characters treated as unordered. C, topology of Tyler & Santini (2005), based on morphological data, using only *Sargocentron* and *Melamphaes* as outgroup taxa. D, topology of Miya *et al.* (2003), based on mitogenomic data. E, topology of Grande *et al.* (2013a), based on molecular data (three mitochondrial and four nuclear markers); the irresolution reflects differences in tree topology when data are analysed using parsimony or maximum likelihood.

fossil taxa. A subsequent study by Tyler & Santini (2005) added the fossils †*Cretazeus*, †*Protozeus* and †*Archaeozeus* to the same morphological zeiform dataset. Both studies made use of an extensive outgroup including representatives of ‘Beryciformes’, ‘Percoidei’, Tetraodontiformes and Caproidae, following the hypothesis that the latter two and Zeiformes form a clade (Rosen 1984).

The analysis of Tyler *et al.* (2003) supported different patterns of zeiform intrarelationships depending on whether particular characters are assigned ordered or unordered states (Fig. 6A, B). However, the position of Cyttidae as sister to all other Zeiformes, and the sister group relationship of Grammicolepididae and Zeidae, was recovered in both cases. The analysis of Tyler & Santini (2005) yielded yet another topology (Fig. 6C) when a ‘reduced’ outgroup consisting only of ‘Beryciformes’ is used: Grammicolepididae + Zeidae is sister to a clade formed by *Parazen* and Zeniontidae, while Cyttidae and Oreosomatidae are sister-groups. †*Archaeozeus* and †*Protozeus* are recovered as successive outgroups to the zeiform crown, while †*Cretazeus* is nested within the crown-group, as sister to the parazenids *Cyttopsidae* and *Stethopristes*.

No molecular phylogenetic study to date has been designed specifically to resolve zeiform intrarelationships. Instead, most molecular datasets include only a few representative zeiform taxa in order to resolve the placement of the clade as a whole. The dataset of Miya *et al.* (2003), consisting of complete mitogenomes, recovered *Parazen* and *Zenion* as outgroups to a clade formed by Oreosomatidae and Zeidae (Fig. 6D). The most comprehensive molecular study performed to date (Grande *et al.* 2013a,

*b*) included seven zeiform terminal taxa (from all families except Cyttidae) for seven nuclear and mitochondrial loci. It recovered *Cyttopsidae* as sister to all other Zeiformes, followed by *Parazen* and *Zenion*. The oreosomatid *Allocyttus* is sister to a clade formed by the grammicolepidid *Xenolepidichthys* and zeids (Fig. 6E). Both molecular studies then agreed on the position of Parazenidae and Zeniontidae outside a clade formed by Oreosomatidae, Zeidae and probably Grammicolepididae. In this regard, they contradicted existing morphological studies (Fig. 6B, C), except when morphological characters were ordered (Fig. 6A).

#### Analyses performed

In order to infer the phylogenetic position of †*Bajaichthys* within Zeiformes, we performed two phylogenetic analyses. The associated taxon-by-character matrices are available online in the Dryad Digital Repository (Davesne *et al.* 2017).

**Analysis 1.** In this analysis, we added †*Bajaichthys* to the morphological dataset of Tyler & Santini (2005). The original version of the dataset included a range of outgroup taxa (tetraodontiforms, caproids) whose close relationship with zeiforms is overwhelmingly contradicted by molecular (Miya *et al.* 2003; Holcroft 2004; Betancur-R. *et al.* 2013; Grande *et al.* 2013a; Near *et al.* 2013) and morphological evidence (Johnson & Patterson 1993; Chanet *et al.* 2013). Hence, we excluded these taxa from the

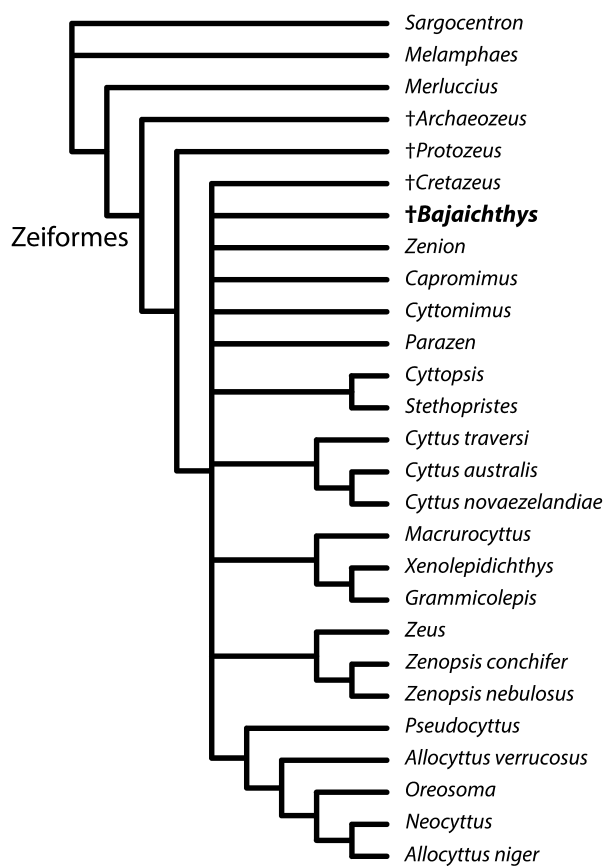
analysis, retaining the ‘beryciforms’ *Sargocentron* and *Melamphaes* (as in the ‘reduced’ dataset of Tyler & Santini). In addition, we included *Merluccius* as a representative of Gadiformes, the probable closest zeiform outgroup. We used TNT version 1.1 (Goloboff *et al.* 2008) to perform a new technology parsimony search with the default parameters for sectorial search, ratchet, drift (10 iterations each) and tree fusing, and hitting minimal tree length ten times. All the characters were unordered and assigned an equal weight of 1, with taxa showing multiple states of the same character treated as polymorphic. All networks were rooted on *Sargocentron*.

**Analysis 2.** The results of the morphological and molecular analyses of zeiform intrarelations differ markedly (Fig. 6), making a consensus difficult to reach. Moreover, our analysis of morphological data alone provided insufficient resolution to make well-supported claims about either zeiform phylogeny or the position of †*Bajaichthys* (see Results below). We therefore combined the morphological data of Analysis 1 to the molecular dataset of Grande *et al.* (2013b), currently the most comprehensive molecular sampling of zeiform taxa. The original molecular dataset includes 65 species of acanthomorphs and closely related taxa, ten of them (including all seven Zeiformes) being also present in Analysis 1. It uses sequences from seven markers: the mitochondrial tRNA-Val, 12S and 16S rDNA and four nuclear loci (28S rDNA, ENC1, histone H3 and RAG1). We downloaded the original dataset from the Dryad Digital Repository (Grande *et al.* 2013b), retaining the original alignment.

The dataset of combined aligned molecular and morphological data includes a total of 82 taxa and 4134 characters. We analysed this dataset with TNT, using the same parameters as for Analysis 1. We also used TNT to run 100 replicates of a bootstrap analysis, retaining all clades found with a frequency  $\geq 50\%$ . Trees were rooted with *Maurolicus* (Stomiiformes).

## Results

**Analysis 1.** This analysis yielded 16 parsimonious trees, with a length of 386 steps, a consistency index (CI) of 0.584 and a retention index (RI) of 0.604. The strict consensus tree (Fig. 7) recovers †*Bajaichthys* within a monophyletic Zeiformes, confirming our new systematic attribution. †*Archaeozeus* and †*Protozeus* are successive sister groups to a clade consisting of all other zeiforms. Extant families Cyttidae, Grammicolepididae, Zeidae and Oreosomatidae are recovered as monophyletic, but their interrelationships are unresolved. Families Parazenidae and Zeniontidae are not recovered in the strict consensus tree. The precise phylogenetic position of †*Cretazeus* and

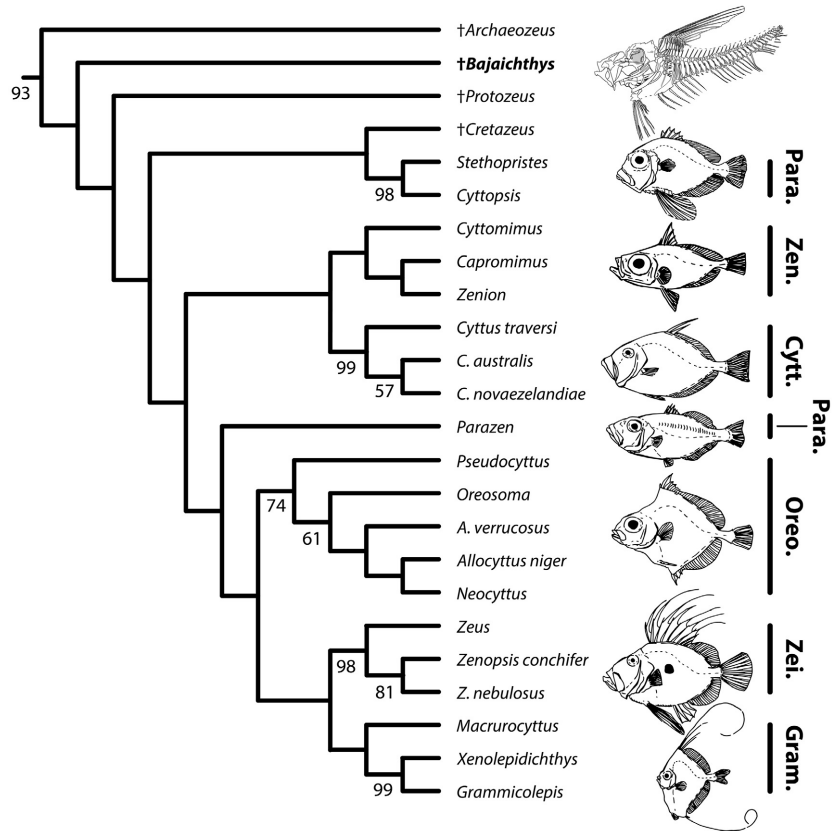


**FIG. 7.** Results of Analysis 1, with †*Bajaichthys* and *Merluccius* added to the morphological dataset of Tyler & Santini (2005). Strict consensus of the 16 parsimonious trees. Length = 386, CI = 0.584, RI = 0.604.

†*Bajaichthys* within Zeiformes is unclear. Given that the dataset used for this analysis yields an almost entirely resolved zeiform phylogeny when †*Bajaichthys* is not included (Tyler & Santini 2005), it is likely that the unusual combination of anatomical features observed in †*Bajaichthys* explains this decrease in resolution.

**Analysis 2.** This analysis yielded one parsimonious tree, with a length of 13 220 steps, a CI of 0.332 and a RI of 0.560. Outside Zeiformes, the topology is identical to the one of the original study (Grande *et al.* 2013a). Within Zeiformes, the tree (Fig. 8) shows †*Archaeozeus*, †*Bajaichthys* and †*Protozeus* as successive sister groups to the zeiform crown. †*Cretazeus* is sister to the extant parazenids *Stethopristes* and *Cyttopsis*, while *Parazen* is separated from the other members of the family. Zeniontidae and Cyttidae form a clade, as do Oreosomatidae, Grammicolepididae and Zeidae. The support for this topology is low: bootstrap values exceeding 50% are only associated with the established extant families and Zeiformes as a whole.

**FIG. 8.** Results of Analysis 2, with the morphological data of Analysis 1 combined with the molecular dataset of Grande *et al.* (2013a). Only the zeiform part of the tree is shown. Parsimonious tree, length = 13 220, CI = 0.332, RI = 0.560. Bootstrap values are shown at the nodes when  $\geq 50\%$ . Abbreviations: Cytt., Cyttidae; Gram., Grammicolepididae; Oreo., Oreosomatidae; Para., Parazenidae; Zei., Zeidae; Zen., Zeniontidae.



**DISCUSSION**

The reinterpretation of †*Bajaichthys* as a zeiform considerably expands the morphological diversity found within the order. Unique for zeiforms is the very long anal fin that converges with the caudal fin, while the dorsal fin is much shorter and very high. These features occur convergently in other teleosts such as Macrouridae (Gadiformes), Ateleopodidae (Ateleopodiformes) and Halosauridae (Notacanthiformes). These taxa are principally demersal, using undulations of the postabdominal region of the body to propel themselves at a short distance from the sea bottom while feeding (Marshall 1979; Cohen *et al.* 1990). Given their remarkable overall resemblance, it is possible that †*Bajaichthys* had a similar ecology (Bannikov 2014a). However, these modern taxa are mostly found in the deep ocean, while the Bolca fossil sites were deposited in a shallow marine context (Marramà *et al.* 2016). Most modern zeiforms are found in greater depths as well, which could explain why †*Bajaichthys* is so far the only representative of the order known in the Bolca fauna (Bannikov 2014b; Carnevale *et al.* 2014). Its redescription as a member of Zeiformes therefore expands the taxonomic and ecological diversity of the Bolca fauna.

The notable elongation of the body observed in †*Bajaichthys* contrasts with the typical deep-bodied appearance of most zeiforms. However, somewhat elongate bodies with a notably slender caudal peduncle are also observed in the fossil taxa †*Cretazeus*, †*Archaeozeus* and the undescribed taxon from the early Eocene of Denmark (Tyler *et al.* 2000; Bonde *et al.* 2008). The phylogenetic positions of †*Archaeozeus* and †*Bajaichthys* as stem Zeiformes according to our combined phylogenetic analysis (Fig. 8) suggests that this elongate morphotype might represent the ancestral condition for the clade as a whole. Given that the closest extant relatives of Zeiformes are probably the elongate Gadiformes and *Stylephorus*, our phylogenetic results then support the hypothesis that the deep-bodied morphotype of most zeiforms is a derived condition. However, inferred relationships within crown Zeiformes suggest a more complex morphological evolution. It has been proposed that Zeniontidae and Parazenidae retain most of the ancestral characters of modern zeiforms (Johnson & Patterson 1993) and representatives of these families are more elongate than the others, especially the genera *Parazen* and *Zenion*. However, our combined analysis (Fig. 8) recovers the moderately deep-bodied *Stethopristes* and *Cyttopsis* as the earliest diverging modern taxa, while zeniontids and *Parazen* are

placed as sister lineages of two different deep-bodied clades. It is therefore possible that the deep-bodied morphotype evolved several times independently in Zeiformes, being particularly pronounced in the clade including Oreosomatidae, Zeidae and Grammicolepididae.

These inferences must be tempered by the fact that the phylogenetic relationships recovered by our results are weakly supported, and that the morphological dataset appears highly sensitive to the addition of new taxa (in this case, †*Bajaichthys* and *Merluccius*). Moreover, the combined topology is largely congruent with the ones recovered by molecular data alone (Fig. 6D, E), suggesting that it is largely structured or at least strongly influenced by the latter. The instability of results supported by morphological data alone (Fig. 7), along with the lack of a molecular dataset with a dense sampling within Zeiformes, raises the possibility that our reconstructed relationships might not reflect zeiform evolution accurately.

Obtaining a well-resolved and well-supported phylogeny of Zeiformes is crucial for answering key questions related to the pattern and the timing of major divergences and character evolution within this unusual group. For instance, the current position of †*Cretazeus*, nested within the crown-group, implies that at least five different zeiform lineages were present in the Campanian, but no other Late Cretaceous zeiform fossils are yet known that might substantiate this prediction. In many ways, Zeiformes represents an ideal teleost group for integrated phylogenetic study. Despite numbering only a few dozen species, modern zeiformes display ample morphological and ecological variety, and their modest numbers render near-exhaustive sampling of lineages tractable. This modern diversity is complemented by a suite of well-described fossils (Tyler *et al.* 2000; Baciu *et al.* 2005; Tyler & Santini 2005), opening a window on phenotypic diversity in the earlier history of the clade. If the most conspicuous shortcomings are overcome, by obtaining extensive molecular data for several poorly-known deep-sea lineages and by investigating overlooked morphological complexes (e.g. muscles, soft tissues), integrative phylogenetic studies (a new one being in preparation, T. Grande pers. comm.) could increase substantially our understanding of this peculiar teleost group.

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## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9k5p0>

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## REFERENCES

- BACIU, D.-S., BANNIKOV, A. F. and TYLER, J. C. 2005. Revision of the fossil fishes of the family Zeidae (Zeiformes). *Bollettino del Museo Civico di Storia Naturale di Verona*, **29**, 95–128.
- BANNIKOV, A. F. 1999. A review of fossil Lampridiformes (Teleostei) finds with a description of a new Lophotidae genus and species from the Oligocene of the Northern Caucasus. *Paleontological Journal*, **33**, 68–76.
- 2014a. A new genus of the family Palaeocentrotidae (Teleostei, Lampridiformes) from the Oligocene of the Northern Caucasus and comments on other fossil Veliferoidei. *Paleontological Journal*, **48**, 624–632.
- 2014b. The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, **12**, 23–34.
- and CARNEVALE, G. 2016. †*Carlomonnius quasigobius* gen. et sp. nov.: the first gobioid fish from the Eocene of Monte Bolca, Italy. *Bulletin of Geosciences*, **91**, 13–22.
- BELLWOOD, D. R., GOATLEY, C. H. R. and BELLWOOD, O. 2016. The evolution of fishes and corals on reefs: form, function and interdependence. *Biological Reviews*, published online 11 March. doi: 10.1111/brv.12259
- BETANCUR-R., R., BROUGHTON, R. E., WILEY, E. O., CARPENTER, K., LÓPEZ, J. A., LI, C., HOLCROFT, N. I., ARCILA, D., SANCIANGCO, M., CURETON, J. C., ZHANG, F., BUSER, T., CAMPBELL, M. A., BALLESTEROS, J. A., ROA-VARÓN, A., WILLIS, S., BORDEN, W. C., ROWLEY, T., RENEAU, P. C., HOUGH, D. J., LU, G., GRANDE, T., ARRATIA, G. and ORTÍ, G. 2013. The tree of life and a new classification of bony fishes. *PLoS Currents Tree of Life*, published online 18 April. doi: 10.1371/currents.tol.53ba26640df0cace755bb165c8c26288
- BLOT, J. 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). *Bulletin du Muséum national d'Histoire naturelle, Paris*, **2C**, 339–396.
- BONDE, N., ANDERSEN, S., HALD, N. and JAKOBSEN, S. L. 2008. *Danekræ – Danmarks bedste fossiler*. Gyldendal, Copenhagen.
- BORDEN, W. C., GRANDE, T. and SMITH, W. L. 2013. Comparative osteology and myology of the caudal fin in the Paracanthopterygii (Teleostei: Acanthomorpha). 419–455. *In*

- ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 5. Global diversity and evolution*. Friedrich Pfeil.
- CARNEVALE, G. 2004. The first fossil ribbonfish (Teleostei, Lampridiformes, Trachipteridae). *Geological Magazine*, **141**, 573–582.
- BANNIKOV, A. F., MARRAMÀ, G., TYLER, J. C. and ZORZIN, R. 2014. The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates. *Rendiconti della Società Paleontologica Italiana*, **4**, 37–63.
- CHANET, B., GUINTARD, C., BETTI, E., GALLUT, C., DETTAI, A. and LECOINTRE, G. 2013. Evidence for a close phylogenetic relationship between the teleost orders Tetraodontiformes and Lophiiformes based on an analysis of soft anatomy. *Cybium*, **37**, 179–198.
- CHEN, W.-J., SANTINI, F., CARNEVALE, G., CHEN, J.-N., LIU, S.-H., LAVOUÉ, S. and MAYDEN, R. L. 2014. New insights on early evolution of spiny-rayed fishes (Teleostei: Acanthomorpha). *Frontiers in Marine Science*, **1**, 53.
- COHEN, D. M., INADA, T., IWAMOTO, T. and SCIALABBA, N. 1990. *FAO species catalogue vol. 10. Gadiform fishes of the world*. Food & Agriculture Organization of the United Nations.
- DAVESNE, D., FRIEDMAN, M., BARRIEL, V., LECOINTRE, G., JANVIER, P., GALLUT, C. and OTERO, O. 2014. Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha). *Zoological Journal of the Linnean Society*, **172**, 475–498.
- GALLUT, C., BARRIEL, V., JANVIER, P., LECOINTRE, G. and OTERO, O. 2016. The phylogenetic intrarelations of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): fossil taxa increase the congruence of morphology with molecular data. *Frontiers in Ecology & Evolution*, **4**, 129.
- CARNEVALE, G. and FRIEDMAN, M. 2017. Data from: *Bajaichthys elegans* from the Eocene of Bolca (Italy) and the overlooked morphological diversity of Zeiformes (Teleostei, Acanthomorpha). *Dryad Digital Repository*. doi: 10.5061/dryad.9k5p0
- DELBARRE, D. J., DAVESNE, D. and FRIEDMAN, M. 2016. Anatomy and relationships of †*Aipichthys pretiosus* and †*Aipichthys nuchalis* (Acanthomorpha: Lampridomorpha), with a review of Late Cretaceous relatives of oarfishes and their allies. *Journal of Systematic Palaeontology*, **14**, 545–567.
- DETTAI, A. and LECOINTRE, G. 2005. Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. *Comptes Rendus Biologies*, **328**, 674–689.
- FRIEDMAN, M. 2012. Osteology of †*Heteronectes chaneti* (Acanthomorpha, Pleuronectiformes), an Eocene stem flatfish, with a discussion of flatfish sister-group relationships. *Journal of Vertebrate Paleontology*, **32**, 735–756.
- GAUDANT, M. 1978. Contribution à l'étude anatomique et systématique de l'ichthyofaune cénomaniennne du Portugal. Première partie: les 'acanthoptérygiens'. *Comunicações dos Serviços Geológicos de Portugal*, **63**, 105–149.
- GOLOBOFF, P. A., FARRIS, J. S. and NIXON, K. C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.
- GRANDE, T., BORDEN, W. C. and SMITH, W. L. 2013a. Limits and relationships of Paracanthopterygii: a molecular framework for evaluating past morphological hypotheses. 385–418. In ARRATIA, G., SCHULTZE, H.-P. and WILSON, M. V. H. (eds). *Mesozoic fishes 5. Global diversity and evolution*. Friedrich Pfeil.
- — — 2013b. Data from: Limits and relationships of Paracanthopterygii: a molecular framework for evaluating past morphological hypotheses. *Dryad Digital Repository*. doi: 10.5061/dryad.k4m8t
- HOLCROFT, N. I. 2004. A molecular test of alternative hypotheses of tetraodontiform (Acanthomorpha: Tetraodontiformes) sister group relationships using data from the RAG1 gene. *Molecular Phylogenetics & Evolution*, **32**, 749–760.
- JOHNSON, G. D. and PATTERSON, C. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science*, **52**, 554–626.
- PAXTON, J. R., SUTTON, T. T., SATOH, T. P., SADO, T., NISHIDA, M. and MIYA, M. 2009. Deep-sea mystery solved: astonishing larval transformations and extreme sexual dimorphism unite three fish families. *Biology Letters*, **5**, 235–239.
- MARRAMÀ, G., BANNIKOV, A. F., TYLER, J. C., ZORZIN, R. and CARNEVALE, G. 2016. Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **454**, 228–245.
- MARSHALL, N. B. 1979. *Developments in deep-sea biology*. Blandford Press, Poole, Dorset.
- MIYA, M., KAWAGUCHI, A. and NISHIDA, M. 2001. Mitogenomic exploration of higher teleostean phylogenies: a case study for moderate-scale evolutionary genomics with 38 newly determined complete mitochondrial DNA sequences. *Molecular Biology & Evolution*, **18**, 1993–2009.
- TAKESHIMA, H., ENDO, H., ISHIGURO, N. B., INOUE, J. G., MUKAI, T., SATOH, T. P., YAMAGUCHI, M., KAWAGUCHI, A., MABUCHI, K., SHIRAI, S. M. and NISHIDA, M. 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics & Evolution*, **26**, 121–138.
- HOLCROFT, N. I., SATOH, T. P., YAMAGUCHI, M., NISHIDA, M. and WILEY, E. O. 2007. Mitochondrial genome and a nuclear gene indicate a novel phylogenetic position of deep-sea tube-eye fish (Stylephoridae). *Ichthyological Research*, **54**, 323–332.
- MÜLLER, J. 1845. Über den Bau und die Grenzen der Ganoïden, und über das natürliche System der Fische. *Abhandlungen der Königlischen Akademie der Wissenschaften zu Berlin*, **1844**, 117–216.
- NEAR, T. J., EYTAN, R. I., DORNBURG, A., KUHN, K. L., MOORE, J. A., DAVIS, M. P., WAINWRIGHT, P. C., FRIEDMAN, M. and SMITH, W. L. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences*, **109**, 13698–13703.
- DORNBURG, A., EYTAN, R. I., KECK, B. P., SMITH, W. L., KUHN, K. L., MOORE, J. A., PRICE, S.

- A., BURBRINK, F. T., FRIEDMAN, M. and WAINWRIGHT, P. C. 2013. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of the National Academy of Sciences*, **110**, 12738–12743.
- NELSON, J. S., GRANDE, T. C. and WILSON, M. V. H. 2016. *Fishes of the world*, 5th edn. John Wiley & Sons.
- OELSCHLÄGER, H. A. 1976. On the evolution and ecological adaptations of the Allotriognathi. *Revue des Travaux de l'Institut des Pêches Maritimes*, **40**, 691–694.
- 1983. Vergleichende und funktionelle Anatomie der Allotriognathi (= Lampridiformes), ein Beitrag zur Evolutionsmorphologie der Knochenfische. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **541**, 1–127.
- OLNEY, J. E., JOHNSON, G. D. and BALDWIN, C. C. 1993. Phylogeny of lampridiform fishes. *Bulletin of Marine Science*, **52**, 137–169.
- PATTERSON, C. 1993. An overview of the early fossil record of acanthomorphs. *Bulletin of Marine Science*, **52**, 29–59.
- REGAN, C. T. 1910. The anatomy and classification of the teleostean fishes of the order Zeomorphi. *Annals & Magazine of Natural History*, **8**, 481–484.
- ROSEN, D. E. 1973. Interrelationships of higher euteleostean fishes. 397–513. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). *Interrelationships of fishes*. Academic Press.
- 1984. Zeiforms as primitive plectognath fishes. *American Museum Novitates*, **2782**, 1–45.
- and PATTERSON, C. 1969. The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History*, **141**, 357–474.
- SANTINI, F., TYLER, J. C., BANNIKOV, A. F. and BACIU, D.-S. 2006. A phylogeny of extant and fossil buckler dory fishes, family Zeidae (Zeiformes, Acanthomorpha). *Cybium*, **30**, 99–107.
- SCHLÜTER, M., STEUBER, T. and PARENTE, M. 2008. Chronostratigraphy of Campanian–Maastrichtian platform carbonates and rudist associations of Salento (Apulia, Italy). *Cretaceous Research*, **29**, 100–114.
- SORBINI, L. 1983. *La collezione Baja di pesci e piante fossili di Bolca*. Museo Civico di Storia Naturale, Verona.
- and BOTTURA, C. 1988. *Bajaichthys elegans*, an Eocene lampridiform from Bolca (Italy). *Bollettino del Museo Civico di Storia Naturale di Verona*, **14**, 369–380.
- STIASSNY, M. L. J. and MOORE, J. A. 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph intrarelations. *Zoological Journal of the Linnean Society*, **104**, 209–242.
- TYLER, J. C. and SANTINI, F. 2005. A phylogeny of the fossil and extant zeiform-like fishes, Upper Cretaceous to Recent, with comments on the putative zeomorph clade (Acanthomorpha). *Zoologica Scripta*, **34**, 157–175.
- BRONZI, P. and GHIANDONI, A. 2000. The Cretaceous fishes of Nardò 11°. A new genus and species of Zeiformes, *Cretazeus rinaldii*, the earliest record for the order. *Bollettino del Museo Civico di Storia Naturale di Verona*, **24**, 11–28.
- O'TOOLE, B. and WINTERBOTTOM, R. 2003. Phylogeny of the genera and families of Zeiform fishes, with comments on their relationships with tetraodontiforms and caproids. *Smithsonian Contributions to Zoology*, **618**, 1–110.
- WILEY, E. O., JOHNSON, G. D. and DIMMICK, W. W. 1998. The phylogenetic relationships of lampridiform fishes (Teleostei: Acanthomorpha), based on a total-evidence analysis of morphological and molecular data. *Molecular Phylogenetics & Evolution*, **10**, 417–425.
- ——— 2000. The interrelationships of acanthomorph fishes: a total evidence approach using molecular and morphological data. *Biochemical Systematics & Ecology*, **28**, 319–350.