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***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 allies). Re-examination of the type and only specimen of †*Bajaichthys* contradicts this

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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) or the ultradiverse gobioids (Bannikov and Carnevale 2016).

One of the most puzzling teleosts known from this fauna is †*Bajaichthys elegans*, represented by a single small specimen with an elongated body, very high dorsal fin, elongated 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 shallow water species such as the John Dory (*Zeus faber*) along with rarer, deep-sea taxa. He

later changed his view (Sorbini and 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.

MATERIAL AND METHOD

[Figs 1-3 about here]

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 and measurements were taken with a compass. To enhance details, the specimen was moistened with alcohol. All extinct taxa are marked with daggers (†) preceding their names.

SYSTEMATIC PALAEOLOGY

ACANTHOMORPHA Rosen, 1973

Order ZEIFORMES Regan, 1910 *sensu* Johnson and Patterson, 1993 (see below)

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 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 and 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. Standard length (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).

[Fig. 4 about here]

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 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 as a nasal by Sorbini and 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 syndesmotically, 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 and 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 the earlier description of the material, Sorbini and 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. 3) 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 each other. 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. 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 articulated with the occipital region of the neurocranium, and its neural arches and spines are expanded antero-posteriorly. **It was not mentioned in earlier descriptions (Sorbini 1983; Sorbini and 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 fifteenth 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.

[Fig. 5 about here]

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 (apt; Fig. 5C). This first anal-fin pterygiophore is greatly expanded, with a strongly curved anterior profile.

Paired fins and girdles. The posttemporal and supracleithrum 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 and 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 specialisations of the palatine, premaxilla, maxilla and frontal bones (Oelschläger 1976, 1983). For this reason, several other elongated marine teleost taxa with very mobile jaws have been at some point aligned with Lampridiformes, including Ateleopodidae, Mirapinnidae and Stylephoridae (Rosen and 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 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). However, 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 Zeiformes 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*, *Allocyttus* and *Neocyttus*), Parazenidae (smooth dories: *Parazen*, *Cyttopsis* and *Stethopristes*), Zeniontidae (armoreye dories: *Zenion*, *Cyttomimus* and *Capromimus*), Grammicolepididae (tinsselfishes: *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 and 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 is 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 absent 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 and Bottura 1988); (4) the palatine does not bear teeth.

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

Previous phylogenetic studies of Zeiformes

[Fig.6 about here]

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 and Santini 2005). Based on a

survey of all major acanthomorph groups, Johnson and Patterson (1993) placed Zeiformes as the sister lineage of Beryciformes and Percomorpha (the latter including caproids and tetraodontiforms), and 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 and 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 and 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) includes a comprehensive coverage of every zeiform family and genus, and 20 out of about 30 extant species. However, it does not include any fossil taxa. A subsequent study (Tyler and Santini 2005) added the fossils †*Cretazeus*, †*Protozeus* and †*Archaeozeus* to the same morphological zeiform dataset. Both studies make 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 analyses of Tyler *et al.* (2003) support 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, are recovered in both cases. The analysis of Tyler and Santini (2005) yields 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 *Cyttopsis* 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 constrain the placement of the clade as a whole. The dataset of Miya *et al.* (2003), consisting of complete mitogenomes, recovers *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) includes seven zeiform terminal taxa for seven nuclear and mitochondrial loci. It recovers *Cyttopsis* as sister to all other Zeiformes, followed by *Parazen* and *Zenion*. The oreosomatid *Alloctytus* is sister to a clade formed by the grammicolepidid *Xenolepidichthys* and zeids (Fig. 6E). Both molecular studies then agree in the position of Parazenidae and Zeniontidae outside of a clade formed by Oreosomatidae, Zeidae and probably Grammicolepididae. In this regard, they contradict existing morphological studies (Fig. 6B, C), except when morphological characters are 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 freely available online on the Dryad Digital Repository (Davesne *et al.* 2016).

Analysis 1. In this analysis, we added †*Bajaichthys* to the morphological dataset of Tyler and Santini (2005). The original version of the dataset includes a range of outgroup taxa (tetraodontiforms, caproids) whose close relationship with zeiformes 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 and 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 and 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 Zeiformes 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 Dryad (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

[Figs 7-8 about here]

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 †*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 and 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 of 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.

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 elongated. 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 deep waters, while the Bolca fossil sites were deposited in a shallow water 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 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 and 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 sequence of 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; Baciú *et al.* 2005; Tyler and 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 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:

<http://dx.doi.org/10.5061/dryad.9k5p0>.

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FIGURE CAPTIONS

Fig. 1. †*Bajaichthys elegans*, photograph of the holotype MCSNV T.922. Scale bar represents 5 mm. [Intended for 2/3 page width]

Fig. 2. †*Bajaichthys elegans*, photograph of the holotype MCSNV T.923 (counterpart). Scale bar represents 5 mm. [Intended for 2/3 page width; if possible on the same page as Fig. 1]

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. [Intended for 2/3 page width; if possible on the same double page as Fig. 1 and aligned with it]

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, anterior-most vertebra; vom, vomer. [Intended for 2/3 page width]

Fig. 5. Interpretative drawings of some postcranial elements of †*Bajaichthys elegans* in left lateral view, based on the holotype specimen (MCSNV T.922). Scale bar represents 1 mm. 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; per, pectoral-fin rays; psp, pelvic-fin spine; pvg, pelvic girdle; pvr, pelvic-fin rays; rad, pectoral-fin radials; sca, scapula; v1, anterior-most vertebra. [Intended for 2/3 page width]

Fig. 6. Former phylogenetic hypotheses of Zeiformes intrarelationships. Only the zeiform part of the trees 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 and 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. [Intended for page width]

Fig. 7. Result of Analysis 1, with †*Bajaichthys* and *Merluccius* added to the morphological dataset of Tyler and Santini (2005). Strict consensus of the 16 parsimonious trees. Length = 386, CI = 0.584, RI = 0.604. [Intended for single column width]

Fig. 8. Result 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. **For the species names,**

see Fig. 5. [Intended for 2/3 page width]

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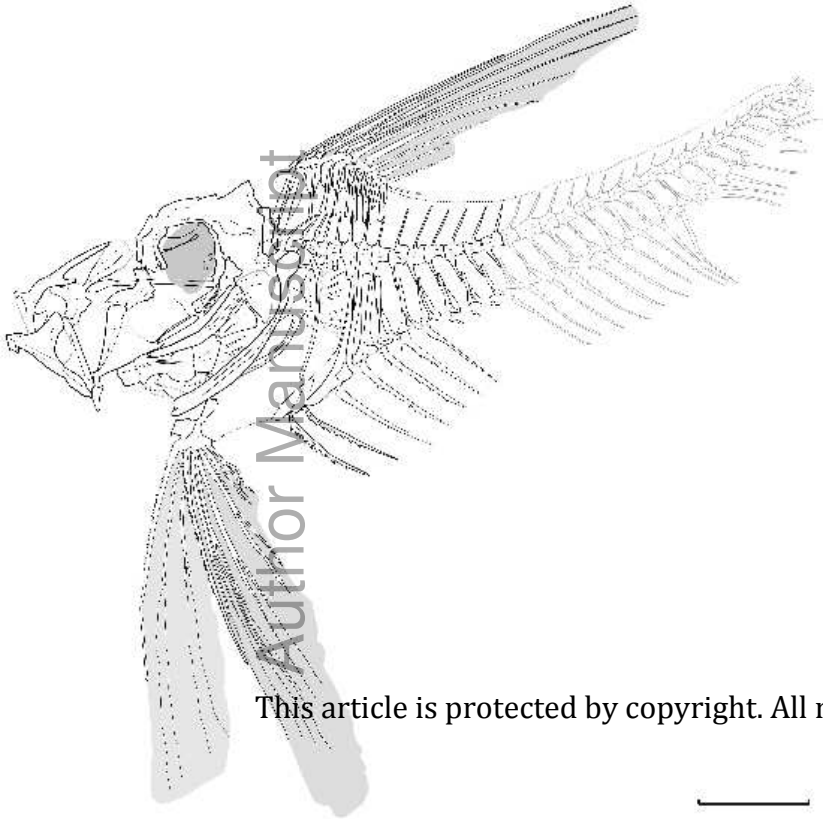


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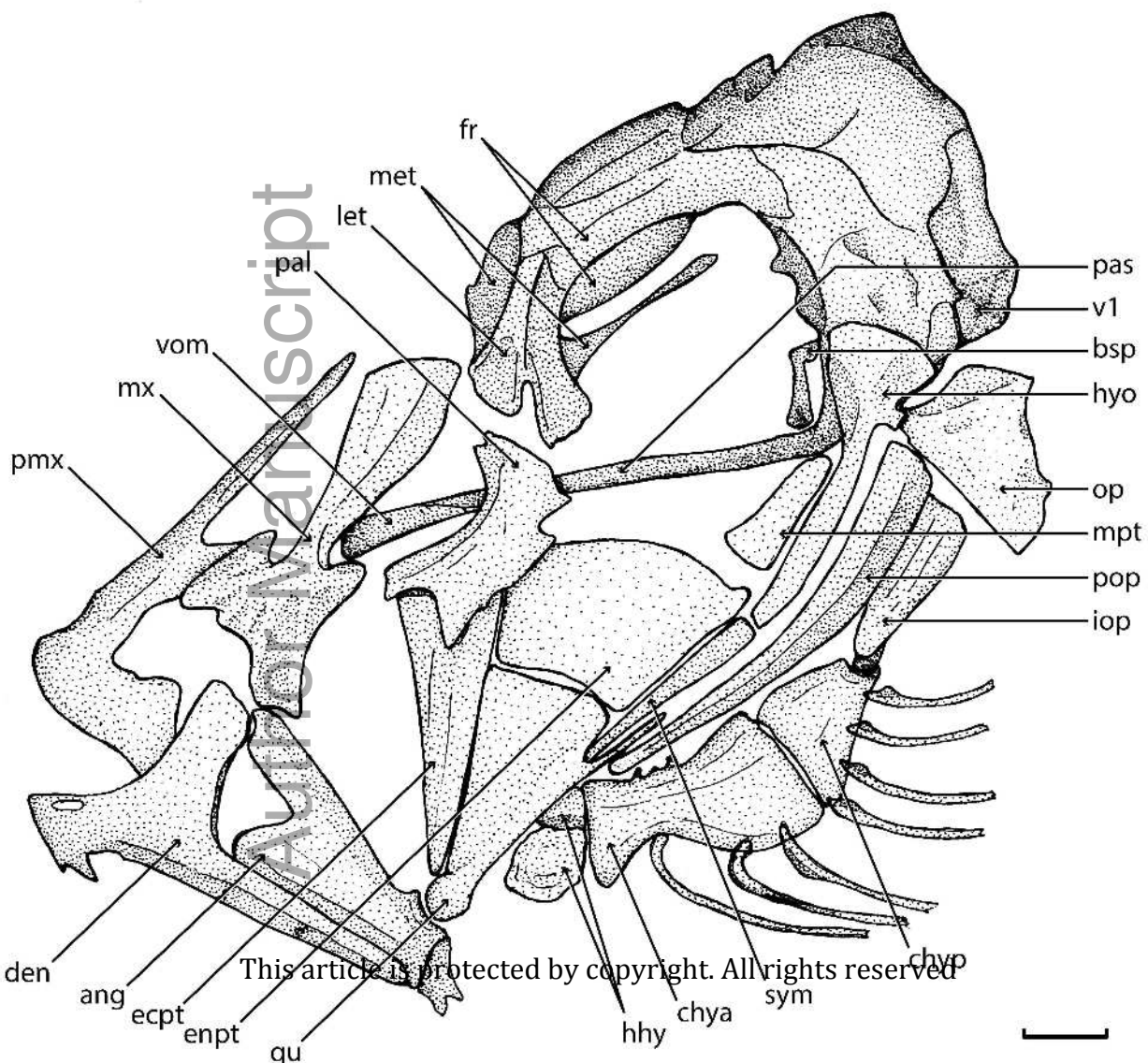
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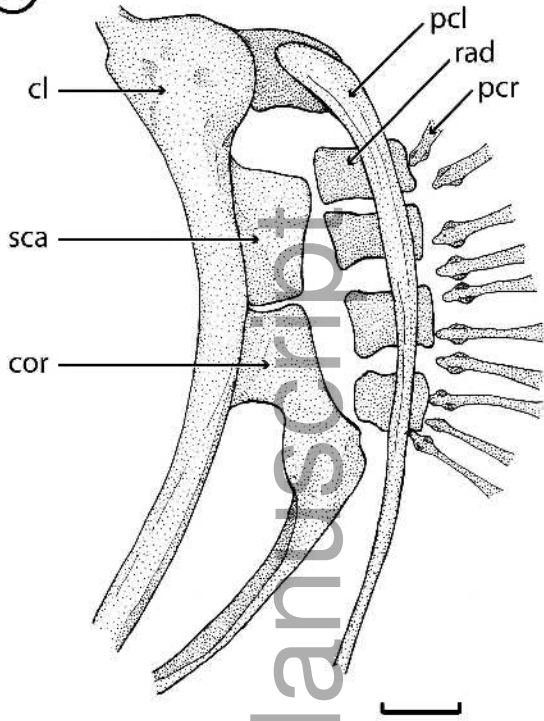


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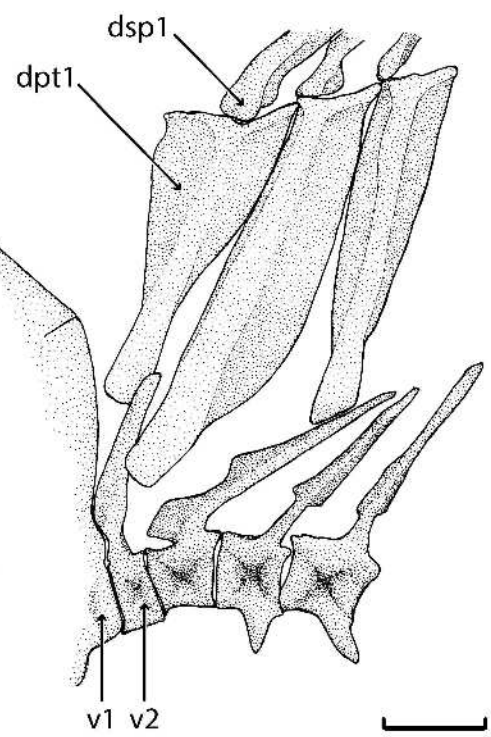
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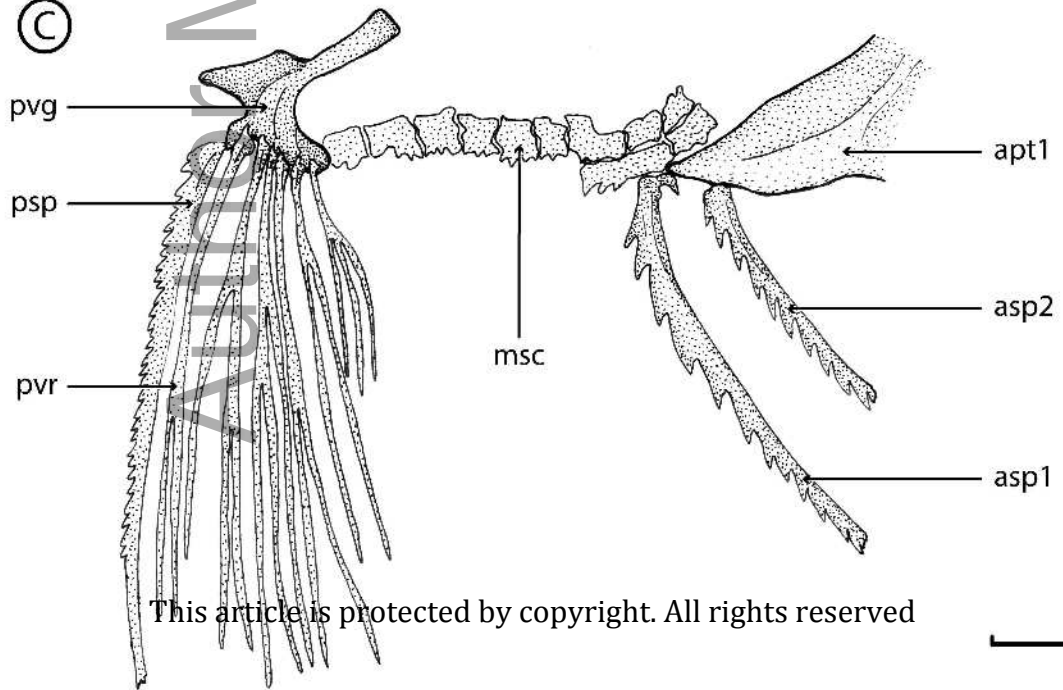
(A)

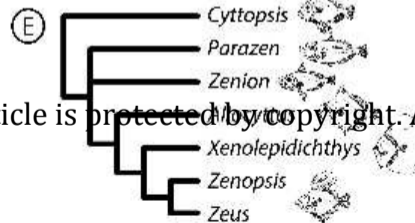
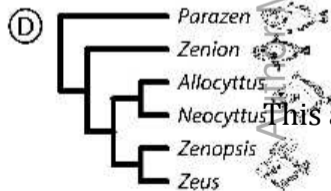
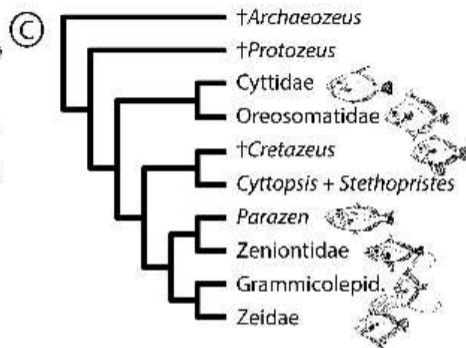
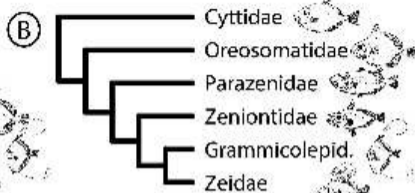


(B)



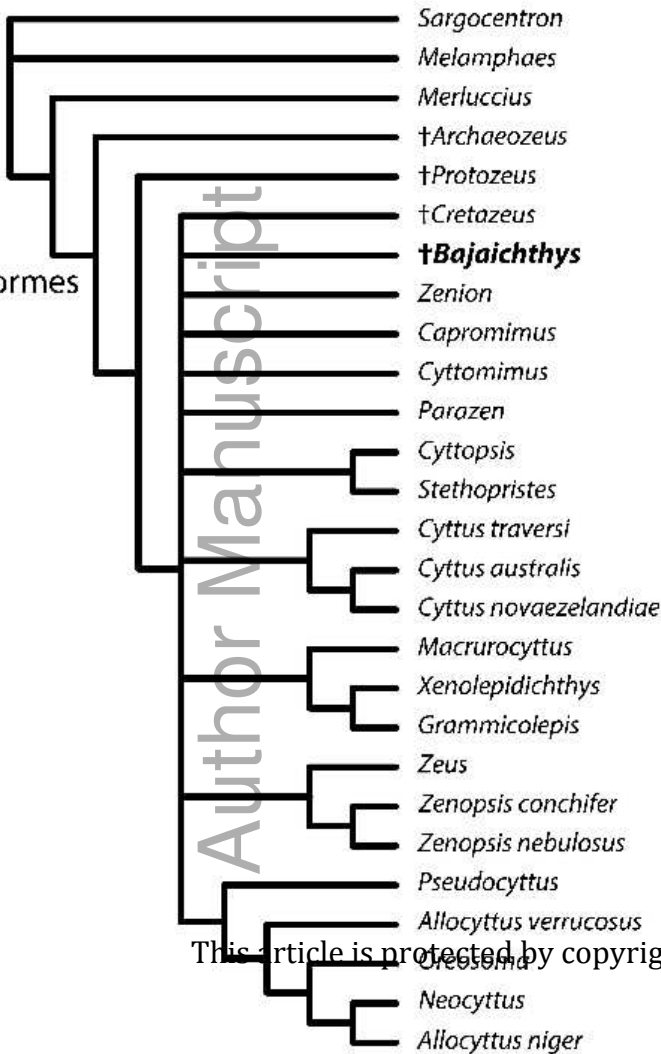
(C)





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