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Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha)

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ABSTRACT

Lampridiformes is a peculiar clade of pelagic marine acanthomorph (spiny-rayed) teleosts. Its phylogenetic position remains ambiguous, and varies depending on the type of data (morphological or molecular) used to infer interrelationships. Because the extreme morphological specializations of lampridiforms may have overwritten the ancestral features of the group with a bearing on its relationships, the inclusion of fossils that exhibit primitive character state combinations for the group as a whole is vital in establishing its phylogenetic position. Therefore, we present an osteological dataset of extant (ten taxa) and fossil (14 taxa) acanthomorphs, including early Late Cretaceous taxa for which a close relationship with extant Lampridiformes has been suggested: †Aipichthyoidea, †Pharmacichthyidae and †Pycnosteroididae. We find that all three taxa plus Lampridiformes form a clade that we call Lampridomorpha. Under this hypothesis, †Aipichthyoidea is paraphyletic. The inclusion of fossils in the analysis changes the topology, highlighting their critical importance in phylogenetic studies of morphological characters. When fossils are included, Lampridomorpha is sister to Euacanthomorpha (all other extant acanthomorphs), concurring with most previous anatomical studies, but conflicting with most molecular results. Lampridomorpha as a whole was a major component of the earliest acanthomorph faunas, notably in the Cenomanian.

ADDITIONAL KEYWORDS: †Aipichthyoidea – Cretaceous – cladistics – Lampridomorpha – †Pharmacichthyidae – †Pycnosteroididae

INTRODUCTION

Lampridiformes is a peculiar clade of teleosts, strictly marine and pelagic, present in every ocean of the world. Extant lampridiform richness is relatively low, with about 20 species and 11 genera grouped in six families (Olney, 1984; Nelson, 2006; Roberts, 2012): Veliferidae (velifers), Lampridídae (opahs), Lophotidae (crestfishes), Radiicephalidae (tapertail), Trachipteridae (ribbonfishes) and Regalecidae (oarfishes). Stylephoridae (tube-eye) has been recently excluded from Lampridiformes by congruent molecular and morphological data (Miya *et al.*, 2007; Grande, Borden, & Smith, 2013). Contrasting with their low specific diversity, lampridiforms exhibit remarkable morphological disparity: from the small, deep-bodied velifers to the very large, ribbon-like oarfish. Deep-bodied forms (veliferids and lampridids) are referred to as "bathysomes", while ribbon-like taxa (lophotids, radiicephalids, trachipterids and regalecids) compose the taeniosomes (Regan, 1907; Olney, Johnson, & Baldwin, 1993; Wiley, Johnson, & Dimmick, 1998).

Lampridiformes have historically been difficult to classify amongst teleosts. Early works based on anatomy placed them in Acanthomorpha (spiny-rayed teleosts) and Acanthopterygii, close to or within the "perciforms" (e.g. Regan, 1907; Greenwood *et al.*, 1966). More recently, most morphological studies placed Lampridiformes as sister to Euacanthomorpha – that is, sister to all other acanthomorphs (Johnson & Patterson, 1993; Olney *et al.*, 1993; Wiley *et al.*, 1998; Wiley, Johnson, & Dimmick, 2000) – yet this view has been contested by some (Wu & Shen, 2004). Molecular studies are even more equivocal and suggested varying positions for Lampridiformes: sister to Euacanthomorpha (Wiley *et al.*, 1998, 2000; Smith & Wheeler, 2006; Grande *et al.*, 2013 with parsimony), to Polymixiiformes + Paracanthopterygii (Dettaï & Lecointre, 2005), to Polymixiiformes alone (Li *et al.*, 2009), to Percopsiformes (Dettaï & Lecointre, 2008; Li *et al.*, 2009), to Paracanthopterygii (Betancur-R. *et al.*, 2013a) and to Euacanthopterygii (Near *et al.*, 2012, 2013; Grande *et al.*, 2013 with maximum likelihood; Faircloth *et al.*, 2013). Molecular studies based on mitochondrial DNA suggested that Lampridiformes are sister to the non-acanthomorph Ateleopodiformes (Miya, Kawaguchi, & Nishida, 2001; Miya *et al.*, 2003) or Myctophiformes (Miya, Satoh, & Nishida, 2005; Miya *et al.*, 2007; Poulsen *et al.*, 2013), thus implying acanthomorph polyphyly.

Anatomically, Lampridiformes are very specialized, with their highly protractile jaws and peculiar fins with poorly developed spines (Oelschläger, 1976, 1983; Olney *et al.*, 1993). Due to their distinctive anatomy, Lampridiformes are difficult to relate to other acanthomorph

subgroups. This difficulty in formalizing hypotheses of homology between lampridiforms and other acanthomorphs explains, in part, the uncertainty arising from morphological studies, and difficulty in assessing the results of molecular analyses in the light of anatomical data. The discovery of fossil relatives of lampridiforms might therefore be especially helpful in identifying plesiomorphic conditions with a bearing on the phylogenetic affinities of the clade. Twelve entirely fossil genera of Lampridiformes have been described (for reviews, see Bannikov, 1999; Carnevale, 2004). They have been referred to crown-group Lampridiformes, as they present most of the anatomical specialisations of extant representatives (Bannikov, 1990, 1999; Sorbini & Sorbini, 1999). As such, these fossils do not bear very distinctive character state combinations that would inform us on the position of the group among Acanthomorpha.

Conversely, other fossil taxa might potentially be informative for the large scale relationships of Lampridiformes. These include several extinct acanthomorph groups that have been described from early Late Cretaceous outcrops in the Near East, England, Slovenia, Mexico, Morocco, and Italy. Most of them are coeval with the oldest known fossil Acanthomorpha, which are Cenomanian in age (93-100 Myr). In contrast, the oldest unequivocal lampridiform is the Campanian-Maastrichtian (70-83 Myr ago): †*Nardovelifer altipinnis* Sorbini & Sorbini, 1999, which has been interpreted as a close relative of modern veliferids. These extinct Cretaceous taxa are interesting in the context of lampridiform interrelationships for two reasons. First, they show mosaic character combinations that are not found in modern taxa, suggesting that they can add valuable information if included in a phylogenetic analysis of acanthomorphs. Second, they have been repeatedly nominated as potential sister-groups to Lampridiformes, although their phylogenetic position remains largely untested.

In this paper, we assess the phylogenetic position of Lampridiformes by including Acanthomorpha and closely related outgroup taxa – notably the Late Cretaceous fossil candidates as sister-groups of Lampridiformes – for the first time in the same phylogenetic analysis of morphological characters.

POTENTIAL CRETACEOUS RELATIVES OF LAMPRIDIFORMES

Five extinct taxa have been proposed as potential sister groups to lampridiforms: †Araripichthyidae, †Dinopterygidae, †Pycnosteroididae, †Pharmacichthyidae and †Aipichthyoidea.

†Araripichthyidae is a monogeneric family comprising four species (Alvarado-Ortega & Brito, 2011): †*Araripichthys castilhoi* Silva Santos, 1985 from the Albian of Brazil and Mexico; †*A. corythophorus* Cavin, 1997 from the Turonian of Morocco; †*A. axelrodi* Maisey & Moody, 2001 from the Aptian of Venezuela; and †*A. weberi* Alvarado-Ortega & Brito, 2011 from the Albian of Mexico. A close relationship between †*Araripichthys* and lampridiforms has been suggested by Maisey & Blum (1991: 215), because this genus shows a large ascending process on the premaxilla and absence of pelvic fins (a character present in only some taeniosomes); however, Maisey & Moody (2001) later argued that these features are probably convergent with lampridiforms, because †*Araripichthys* lacks most acanthomorph, ctenosquamate, and even euteleost synapomorphies. Cavin (2001) performed a phylogenetic analysis showing that †*Araripichthys* is closer to the non-acanthomorph euteleost *Esox* than to the acanthomorph †*Hoplopteryx*.

The four remaining taxa, †Dinopterygidae, †Pycnosteroididae, †Pharmacichthyidae and †Aipichthyoidea were grouped together by Patterson (1964) in the †Dinopterygoidei. In his review of Cretaceous acanthomorphs, he mentioned a possible relationship between lampridiforms and †dinopterygoids (1964: 473), an opinion strengthened by his subsequent work on the caudal skeleton (1968: 97). Oelschläger (1983: fig. 108) concurred with this opinion in his review of lampridiform anatomy. Patterson (1993: 36) later explained that his †Dinopterygoidei was most probably a non-monophyletic assemblage, lacking unique synapomorphies. We agree with Patterson's assessment, and will therefore treat the component groups of †Dinopterygoidei separately.

†Dinopterygidae consists of only one species, †*Dinopteryx spinosus* (Davis, 1887), from the Santonian of Sahel Alma, Lebanon. Little is known about this taxon, due to the poor preservation of the few specimens available, and Patterson (1993: 42) chose to consider it as an acanthomorph *incertae sedis*.

†Pycnosteroididae is represented by two species: †*Pycnosteroides levispinosus* (Hay, 1903) from the Cenomanian of Hajula, Lebanon and †*Magrebichthys nelsoni* Murray & Wilson, 2014 from the Cenomanian-Turonian of Agoult, Morocco. †*Pycnosteroides* has been well-described based on complete specimens, notably by Gayet (1980a), who considered this genus related to modern holocentrids (Gayet, 1982). Patterson (1993: 40) maintained the genus as Acanthomorpha *incertae sedis*. Murray & Wilson (2014) suggested that the whole family is part of the order Polymixiiformes, by finding †*Magrebichthys* in a polytomy with *Polymixia* and paracanthopterygians.

There are three species of †Pharmacichthyidae: †*Pharmacichthys venenifer* Smith Woodward, 1942, †*P. numismalis* Gayet, 1980a, both from the Cenomanian of Hakel, Lebanon, and †*P. judensis* Gayet, 1980b from the Cenomanian of Ein Yabrud, Palestine. Gayet (1980a,b,c) argued that †*Pharmacichthys* is not even an acanthomorph, whereas Rosen & Patterson (1969) and Patterson (1993) listed it amongst possible lampridiform relatives.

The super-family †Aipichthyoidea is a more diverse group, with 13 species included in eight genera and two families (Otero & Gayet, 1996; Alvarado-Ortega & Than-Marchese, 2012; Murray & Wilson, 2014). Family †Aipichthyidae includes †*Aipichthys* [five species: †*A. nuchalis* (Dixon, 1850), †*A. minor* (Pictet, 1850), †*A. pretiosus* Steindachner, 1860, †*A. velifer* Smith Woodward, 1901 and †*A. oblongus* Gayet, 1980a], †*Paraipichthys lusitanicus* Gaudant, 1978 and †*Freigichthys elleipsis* Otero, 1997. Family †Aipichthyoididae includes †*Aipichthyoides formosus* Gayet, 1980b, †*A. galeatus* Gayet, 1980b, †*Aspesaipichthys cavaensis* Taverne, 2004 and †*Zoqueichthys carolinae* Alvarado-Ortega & Than-Marchese, 2012. †*Errachidia pentaspinosa* Murray & Wilson, 2014 and †*Homalopagus multispinosus* Murray & Wilson, 2014 are two species with family *incertae sedis*. †Aipichthyoidea has a large geographical distribution: †*Aipichthyoides* and †*Freigichthys* are restricted to the East Mediterranean (Gayet, 1980b; Otero, 1997), but the five species of †*Aipichthys* are known from Lebanon, England and Slovenia (Patterson, 1964; Radovčić, 1975; Gayet, 1980a), †*Aspesaipichthys* is from Italy (Taverne, 2004), †*Paraipichthys* from Portugal (Gaudant, 1978), †*Zoqueichthys* from Mexico (Alvarado-Ortega & Than-Marchese, 2012) and finally †*Errachidia* and †*Homalopagus* are from Morocco (Murray & Wilson, 2014). All of these genera are Cenomanian (or Cenomanian-Turonian) of age, with the exception of †*Aspesaipichthys* which is younger (Campanian-Maastrichtian). Although Patterson (1964, 1993), Rosen & Patterson (1969) and Oelschläger (1983) suggested that †aipichthyids were related to lampridiforms, Gayet (1980a,b) proposed that they were closer to paracanthopterygians. Finally, Otero & Gayet (1995, 1996) placed †aipichthyoids as sister to Euacanthomorpha (see below), but not without mentioning a possible lampridiform affinity (1995: 223).

Few phylogenetic studies included these Cretaceous taxa. The first was presented by Otero & Gayet (1995, 1996), including only †aipichthyoids among our candidate taxa. They found that the superfamily is monophyletic and composed of two sister-groups: †Aipichthyidae (†*Aipichthys* and †*Paraipichthys*) and †Aipichthyoididae (†*Aipichthyoides*). Their analysis also retrieved †Aipichthyoidea as a sister-group to Euacanthomorpha, but lampridiforms were not included in the study. Alvarado-Ortega & Than-Marchese (2012),

then Murray & Wilson (2014) re-analysed Otero & Gayet's matrix, adding new taxa. They included †*Freigichthys* in †Aipichthyidae and †*Aspesaipichthys* and †*Zoqueichthys* in †Aipichthyoididae. Their results did not change the position of †aipichthyoids amongst Acanthomorpha, and lampridiforms were once again unrepresented in the data matrix. Thus, despite the fact that a relationship between Lampridiformes and – at least – †aipichthyoids had been repeatedly proposed in the literature before, all previous studies were unable to test this hypothesized relationship.

MATERIAL AND METHODS

TAXONOMIC SAMPLING

Our data matrix includes 24 taxa. The 14 fossil taxa are early Late Cretaceous in age, and they include †*Ctenothrissa* sp. (outgroup), the three species of †*Pharmacichthys* (†*P. judensis*, †*P. numismalis*, †*P. venenifer*), †*Pycnosteroides levispinosus*, eight species from six different genera of †Aipichthyoidea (†*Aipichthys minor*, †*A. oblongus*, †*A. velifer*, †*Paraipichthys lusitanicus*, †*Freigichthys elleipsis*, †*Aipichthyoides galeatus*, †*Aspesaipichthys cavaensis*, †*Zoqueichthys carolinae*) and †*Sphenocephalus fissicaudus* Agassiz, 1838, one the oldest known paracanthopterygian, known by well-preserved specimens (Rosen & Patterson, 1969; but see Newbrey *et al.*, 2013). We chose not to include †*Araripichthys*, judging that Maisey & Moody (2001) and Cavin (2001) provided convincing evidence that this genus is not an acanthomorph. †*Dinopteryx* was also excluded, because the incompleteness of the available material made most relevant characters impossible to assess (Patterson, 1993).

The ten extant taxa were chosen from all major acanthomorph clades and closely related non-acanthomorphs. These include: the aulopiform *Synodus intermedius* (Spix & Agassiz, 1829) and the myctophiform *Gymnoscopelus* sp. as non-acanthomorph outgroups; the holocentrid *Myripristis* sp. for Euacanthopterygii; *Polymixia nobilis* Lowe, 1836 for Polymixiiformes; the percopsiform *Aphredoderus sayanus* (Gilliams, 1824) and the gadiform *Merluccius merluccius* (Linnaeus, 1758) for Paracanthopterygii; the veliferid *Metavelifer multiradiatus* (Regan, 1907), the lampridid *Lampris* spp. and the taeniosomes *Regalecus glesne* Ascanius, 1772 and *Trachipterus* spp. for Lampridiformes.

This sampling makes the present study the first to simultaneously include representatives from all extant acanthomorph subgroups (Lampridiformes and Euacanthopterygii were absent from Otero & Gayet, 1996) and Cretaceous fossils. This is also

the first time the placements of †*Pharmacichthys* and †*Pycnosteroides* have been assessed in a phylogenetic analysis.

The list of specimens examined is available in Table 1. Extant specimens are dry osteological preparations, unless otherwise stated. Taxa not included in Table 1 were coded exclusively from the literature.

PHYLOGENETIC ANALYSES

The character matrix was analysed using PAUP 4.0 (Swofford, 2001). All characters were unordered and assigned an equal weight of one, because we had no arguments on character ordering and polarity prior to the analyses.

We performed two consecutive phylogenetic analyses. Analysis 1 included the extant taxa only (ten taxa), with trees rooted with one of the outgroups (*Synodus*). We used the Exhaustive search algorithm for this analysis. Analysis 2 included all 24 taxa (fossil and extant), with trees still rooted with *Synodus*. Because 24 taxa exceed the capability of exhaustive algorithms, we used the Branch-and-Bound search algorithm in this analysis, with "furthest" addition sequence. Character polarity was determined a posteriori by the outgroup criterion.

Tree descriptions were computed in PAUP 3.1.1 (Swofford & Begle, 1993), for an accurate reconstruction of character states. We calculated the Bremer indexes automatically using a PAUP script generated with TreeRot v.2 (Sorenson, 1999).

RESULTS

CHARACTERS

The 39 skeletal characters used by Otero & Gayet (1995, 1996), and then by Alvarado-Ortega & Than-Marchese (2012) for aipichthyoid phylogeny were coded in our matrix. We also included 14 skeletal characters described by Olney *et al.* (1993) in their study of lampridiform intrarelationships, that are applicable in fossils. The characters that we used come from every region of the skeleton: cranial (Fig. 1), vertebral, dorsal (Fig. 2) and anal fins, caudal (Fig. 3) and appendicular skeleton (Fig. 4). In total, 67 characters have been coded; they are detailed in Table 2.

Characters 29, 43 and 64 are new, and they are described below. For description of the remaining characters, please refer to the appropriate references in Table 2.

Character 29:

Urohyal: 0 = not expanded ventrally; 1 = expanded by a large ventral lamina

The urohyal is a median unpaired membrane bone surrounded laterally by the gill arches and the branchiostegal rays (Fig. 1G-H). In lampridiforms, the ventral edge of the urohyal forms an extensive lamina (Fig. 1H, 4C), which is absent in most other acanthomorphs (Fig. 1G).

Character 43:

First soft ray of the dorsal fin elongated and unbranched: 0 = absent; 1 = present

The soft rays of the dorsal fin (posterior to the fin spines when they are present) are branched distally in most teleosts. In †aipichthyoids, †*Pharmacichthys* and lampridiforms, the first soft ray is unbranched and elongated when compared to the other dorsal soft rays.

Character 64:

Internal wings of the pelvic bone: 0 = separated; 1 = joined medially

Usually in acanthomorphs (Fig. 4D) and close relatives, both pelvic bones only contact each other at the level of their median processes (Stiassny & Moore, 1992: figs 2, 3). In †*Freigichthys*, †*Zoqueichthys* (Fig. 4E), lampridiforms (Fig. 4F) and most euacanthopterygians, the internal wings of the pelvic bones are expanded and make extensive contact with each other on a median line.

The complete data matrix (24 taxa, ten extant and 14 fossil; 67 characters) is available in Table 3. There is 11% missing data, noted as '?' in the matrix: this is mainly a result of incomplete fossils, but is also linked with extant Lampridiformes for characters 9, 14, and 15, because of the bad state of preservation of the collection material that we accessed. As a result of the chosen coding strategy, 2% of the character states are treated as inapplicable. They are noted '-' in the matrix. Only one character, character 18, is uninformative.

PHYLOGENETIC RESULTS

Analysis 1 (extant taxa only) yielded one parsimonious tree, with a tree length of 107 steps, a consistency index (CI) of 0.64, and a retention index (RI) of 0.71 (Fig. 5). Within the monophyletic Acanthomorpha, it places Lampridiformes sister to Paracanthopterygii (Gadiformes + Percopsiformes). This relationship is well-supported by seven unambiguous synapomorphies (see below).

Analysis 2 yielded 12 parsimonious trees of 155 steps in length, CI = 0.48 and RI = 0.72. These multiple most parsimonious trees largely reflect uncertain relationships within the genera †*Aipichthys* and †*Pharmacichthys*. The strict consensus is shown in Figure 6.

This analysis supports monophyly of Euacanthomorpha, with *Polymixia* sister to a clade formed by Euacanthopterygii (*Myripristis*) and Paracanthopterygii (including †*Sphenocephalus*). Sister to Euacanthomorpha is a clade including all †Aipichthyoidea, †Pharmacichthyidae and †*Pycnosteroides*, together with Lampridiformes (clade A). If fossils are not considered, Lampridiformes is therefore sister to Euacanthomorpha. Clade A is supported by eight unambiguous characters.

Within clade A, †*Paraipichthys*, †*Aipichthys*, †*Freigichthys*, †*Pycnosteroides* and †*Pharmacichthys* form clade B. †*Paraipichthys* is sister to all the other genera. †*Aipichthys* and †*Freigichthys* on one hand, †*Pycnosteroides* and †*Pharmacichthys* on the other form subclades.

A well-supported clade (clade C) groups together †Aipichthyoididae (*sensu* Alvarado-Ortega & Than-Marchese, 2012) and Lampridiformes, with †*Aipichthyoides* and †*Aspesaipichthys* closer to Lampridiformes (clade D) than to †*Zoqueichthys*.

In both analyses, Lampridiformes is monophyletic and supported by 12 (analysis 1) and ten (analysis 2) unambiguous synapomorphies, respectively. Our results are consistent with the previous morphological and molecular hypotheses of lampridiform intrarelationships (e.g. Olney et al., 1993; Wiley et al., 1998): veliferids (exemplified by *Metavelifer*) are sister to a clade composed by *Lampris* and taeniosomes (represented here by *Trachipterus* and *Regalecus*).

The complete list of character state changes is given in the Appendix. If inference for a character change on the parsimonious tree (or the strict consensus tree) provided several character distributions (resulting in an ambiguous state for some nodes), every possible optimization was considered before one was selected based on biological considerations.

DISCUSSION

TOPOLOGICAL IMPACT OF THE INCLUSION OF FOSSILS

The impact of fossils in phylogenetic reconstruction has been debated ever since the generalisation of cladistic methodology. Following claims that fossil taxa have little impact in topologies (e.g. Patterson, 1981), empirical studies have shown that all available taxa (extant and fossils) should be included in an analysis so that it can reflect most closely the

interrelationships of characters and taxa (Gauthier, Kluge, & Rowe, 1988; Donoghue *et al.*, 1989; Cobbett, Wilkinson, & Wills, 2007). Within acanthomorphs, studies have explored the importance of fossils for reconstructing the evolutionary acquisition of complex characters (e.g. Friedman, 2008; Friedman *et al.*, 2013), studying the sequence of character acquisition (e.g. Murray & Wilson, 1999) and influencing the topology, even when they are incomplete (e.g. Santini & Tyler, 2004).

The case of Lampridiformes is particularly interesting, because no enduring consensus has been reached on their phylogenetic position among acanthomorphs (see "Introduction"). This is especially true with datasets composed of nuclear genes that, in addition, consistently show low support values for the immediately more inclusive clade: for example 54% of bootstrap replicates in Betancur-R. *et al.* (2013a) and less than 70% in Near *et al.* (2013). Yet, under a certain threshold (for example, 95% according to Felsenstein, 1985), nodes should in principle be considered as statistically non-significant. New molecular studies, specifically sampling the base of the acanthomorph tree, are needed in order to better understand the source of these low nodal supports and conflicting topologies. In this context, assessing how taxonomic sampling impacts the reconstructions of topology and character evolution is particularly relevant, especially with fossils, which are absent from molecular datasets.

With the present study, we show another empirical case where fossils have a direct impact on a topology including numerous extant taxa. The phylogenetic position of Lampridiformes varies between our two analyses, which otherwise are based on identical datasets.

When only extant taxa are included (analysis 1), Lampridiformes is sister to Paracanthopterygii (Fig. 5), a position that has already been suggested by some molecular studies (e.g. Betancur-R. *et al.*, 2013a), but by no other morphological analyses to date. The Lampridiformes + Paracanthopterygii clade is then supported by at least seven synapomorphies: the loss of the antorbital (character 7, 0→1), the loss of postabdominal epineurals (character 36, 0→1), the presence of only one supraneural (character 38, 0→2), the fusion of the upper hypurals together (character 52, 0→1) and with the second ural centrum (character 53, 0→1), the fusion of the lower hypurals (character 54, 0→1) and the fusion of the postcleithra (character 61, 0→1).

The inclusion of fossils in analysis 2 (Fig. 6) changes the position of Lampridiformes relative to other extant taxa: their extant sister-group becomes Euacanthomorpha. Support for this hypothesis is also high, with at least five euacanthomorph synapomorphies (see "Taxonomy and character evolution" below).

Such incongruence between the results of both analyses means that at least one of the topologies is misleading and should be rejected, as well as the hypotheses of secondary homology it implies. All synapomorphies that support the Lampridiformes + Paracanthopterygii clade after analysis 1 are linked to reduction or fusion of bones (see above), characters for which primary homology hypotheses are difficult to formalize and which are known to have occurred independently in many different acanthomorph groups. In analysis 2, homology for these character states in Lampridiformes and Paracanthopterygii is rejected by the inclusion of additional data: new character state distributions from fossils. Thus, convergent appearance of the features in both clades is implied by analysis 2. Previously, the absence of the fossil taxa mistakenly supported a relationship between these two clades that show a high amount of character transformation (especially reduction), in a way similar to so-called long-branch attraction in molecular phylogenetics.

The result of analysis 2 (including fossils) shows congruence with previous morphological (Johnson & Patterson, 1993; Wiley *et al.*, 2000) as well as molecular analyses (Wiley *et al.*, 2000; Smith & Wheeler, 2006; Grande *et al.*, 2013 with parsimony).However, it contradicts other molecular results. For instance, the monophyly of Acanthomorpha (including Lampridiformes) is recovered unambiguously, in contrast with phylogenies based on the mitogenome (Miya *et al.*, 2001, 2003, 2005; Poulsen *et al.*, 2013). Other large-scale molecular studies using diverse markers and methods proposed a Lampridiformes-Euacanthopterygii clade (Near *et al.*, 2012, 2013; Faircloth *et al.*, 2013), which is not supported by our data. Should this alternative molecular hypothesis be confirmed by future studies, however, some lampridomorph characters are also found in euacanthopterygians and could be taken as potential evidence of a relationship between both clades. These include the anatomy of the pelvic skeleton (with the pelvic bones joined medially by their internal wings) and the presence of a pelvic spine in several taxa.

TAXONOMY AND CHARACTER EVOLUTION

Works such as Johnson & Patterson (1993), Olney *et al.* (1993) or Otero & Gayet (1996) established a framework for large-scale acanthomorph classification. Once we established that our second analysis (Fig. 6), including both extant Lampridiformes and Cretaceous fossils, efficiently sorted out homology and homoplasy in our character set, we were able to bring forth some new taxonomic hypotheses and confirm some others.

The classification of acanthomorphs we propose is as follows:

TELEOSTEI MÜLLER, 1846

NEOTELEOSTEI NELSON, 1969

EURYPTERYGII ROSEN, 1973

CTENOSQUAMATA ROSEN, 1973

ACANTHOMORPHA ROSEN, 1973

Included taxa: Euacanthomorpha (see below); Lampridomorpha (see below).

Eight unambiguous character states support Acanthomorpha.

1. Frontal branch of the sensory canal running through the frontal and pterotic in a groove (character 14, 0→1).

   In non-acanthomorph teleosts, this canal is enclosed within a bony tube. There is a reversal of this character state, at least in †*Pharmacichthys numismalis*.

2. Developed sagittal crest (character 16, 0→1).

   The sagittal crest primitively consists of the supraoccipital alone. It is secondarily reduced in taeniosome lampridiforms (exemplified by *Trachipterus* and *Regalecus*).

3. Dorsal limb of the posttemporal firmly bound to the epiotic (character 22, 0→1).

   This acanthomorph synapomorphy has been proposed first by Stiassny (1986).

4. Spines in the dorsal fin (character 42, 0→1).

   They are secondarily lost in *Merluccius* and all lampridiforms, except veliferids.

5. Hemaxanal complex (character 46, 0→1).

   This fusion of the anterior-most anal pterygiophores is secondarily lost in *Merluccius* and most lampridiforms.

6. Spines in the anal fin (character 47, 0→1).

   In several acanthomorph groups not included in the analysis (such as batrachoidiforms and nototheniids), spines are present in the dorsal fin only. This suggests that the presence of spines in the anal and dorsal fins is not phylogenetically linked and should be treated as two independent characters. This contradicts character 6 from Otero & Gayet (1996). Like the dorsal fin ones, anal fin spines are lost in *Merluccius* and lampridiforms excluding veliferids.

7. Loss of the urodermals (character 56, 0→1).

8. Loss of the dermal caudal scutes (character 57, 0→1).

Seven out of ten acanthomorph characters from Otero & Gayet (1996) are recovered here as acanthomorph synapomorphies. Their character 5 (neural spines fused to their centra)

– which is our character 33 (0→1) – is interpreted as a ctenosquamate synapomorphy instead. Their character 10 (reduction of the number of pelvic fin rays to seven, character 66, 0→1) is recovered as independently derived in euacanthomorphs (see below), †*Aipichthyoides* and Clade B (see below). Optimization of their character 3 (our character 15, 0→1) is ambiguous: it could also be a euacanthomorph synapomorphy.

EUACANTHOMORPHA JOHNSON & PATTERSON, 1993

Included taxa: Polymixiiformes (represented by *Polymixia*); Euacanthopterygii (represented by *Myripristis*); Paracanthopterygii (represented by †*Sphenocephalus*, *Aphredoderus* and *Merluccius*).

Five character states are unambiguously found to support a clade which includes *Polymixia*, *Myripristis*, †*Sphenocephalus*, *Aphredoderus* and *Merluccius*, to the exclusion of extant lampridiforms. This clade matches the one named Euacanthomorpha by Johnson & Patterson (1993).

1. Postmaxillary process of the premaxilla (character 1, 0→1).

   A posterior notch appears on this process in paracanthopterygians.

2. Spina occipitalis (character 23, 0→1).

   This character was interpreted as an acanthomorph synapomorphy by Stiassny (1986), who described it first.

3. Foramen in the distal ceratohyal (character 27, 1→0).

   A so-called "beryciform" foramen is also present in †*Ctenothrissa*, †*Pycnosteroides*, †*Pharmacichthys* and in veliferid lampridiforms. It is secondarily lost in extant paracanthopterygians.

4. Anterior epineurals originating on vertebral centra or transverse processes (character 35, 0→1).

   The state appears convergently in †*Pharmacichthys* and †*Pycnosteroides*.

5. Seven pelvic soft rays or less (character 66, 1→0).

   This character is interpreted as an acanthomorph synapomorphy by Otero & Gayet (1996, character 10).

Otero & Gayet (1996, character 11) proposed that a caudal fin with a maximum of 18 principal rays (our character 58, 0→1) was another synapomorphy of Euacanthomorpha. The optimization of this character state is ambiguous.

LAMPRIDOMORPHA

We propose to name Lampridomorpha the clade that unites Lampridiformes with †Pycnosteroididae, †Pharmacichthyidae and †Aipichthyoidea (Fig. 6, clade A). This name was already used in several studies (e.g McCune & Carlson, 2004; Dillman *et al.*, 2011) – sometimes as "Lampriomorpha" (Nelson, 2006) or "Lampridacea" (Wiley & Johnson, 2010), but always as a superorder with a taxonomic composition identical to the order Lampridiformes. Lampridomorpha is sister to Euacanthomorpha, therefore we suggest for subsequent workers to use this name for grouping Lampridiformes and all fossil taxa most closely related to them than to any other extant acanthomorph taxon (i.e. total-group Lampridiformes).

Included taxa: †*Pycnosteroides levispinosus* (Hay, 1903); †*Pharmacichthys venenifer* Smith Woodward, 1942; †*P. numismalis* Gayet, 1980a; †*P. judensis* Gayet, 1980b; †*Aipichthys minor* (Pictet, 1850); †*A. velifer* Smith Woodward, 1901; †*A. oblongus* Gayet, 1980a; †*Paraipichthys lusitanicus* Gaudant, 1978; †*Freigichthys elleipsis* Otero, 1997; †*Aipichthyoides galeatus* Gayet, 1980b; †*Aspesaipichthys cavaensis* Taverne, 2004; †*Zoqueichthys carolinae* Alvarado-Ortega & Than-Marchese, 2012; Lampridiformes.

Presumably included taxa (not present in our analysis): †*Aipichthys nuchalis* (Dixon, 1850); †*A. pretiosus* Steindachner, 1860; †*Aipichthyoides formosus* Gayet, 1980b; †*Errachidia pentaspinosa* Murray & Wilson, 2014; †*Homalopagus multispinosus* Murray & Wilson, 2014; †*Magrebichthys nelsoni* Murray & Wilson, 2014.

These taxa present most of the synapomorphies that characterise Lampridomorpha (see below). †*Errachidia* and †*Homalopagus* are retained as Lampridomorpha *incertae sedis*, as Murray & Wilson (2014: fig. 12) found in their analysis (although they considered them to be †Aipichthyoidea incertae sedis and included no living lampridomorphs in their analysis).

Within Lampridomorpha, our topology challenges the taxonomy established by previous studies. Indeed, Otero & Gayet's (1996) †Aipichthyoidea is not monophyletic: some of its representatives are most closely related to crown Lampridiformes, while others are grouped with the †Pycnosteroididae + †Pharmacichthyidae clade.

Furthermore, family †Aipichthyidae *sensu* Alvarado-Ortega & Than-Marchese (2012), is paraphyletic according to the position of †*Paraipichthys* as sister to all other members of clade B. The genus †*Aipichthys* is also paraphyletic, or should include †*Freigichthys*, a taxonomic revision already suggested by Alvarado-Ortega & Than-Marchese (2012: fig. 8).

Finally, family †Aipichthyoididae as proposed by these authors is also challenged by our results, †*Aipichthyoides* and †*Aspesaipichthys* being part of clade D, but not †*Zoqueichthys*.

Our results therefore imply that, instead of forming a clade, †Aipichthyoidea as a whole is a paraphyletic assemblage of Late Cretaceous acanthomorphs, more or less closely related to extant lampridiforms.

We found nine potential synapomorphies for Lampridomorpha, including eight whose optimisation is unambiguous.

1. Loss of the antorbital (character 7, 0→1).
   It also occurs convergently in extant paracanthopterygians.
2. Ascending process on the lachrymal (character 8, 0→1).
   It is present in †'aipichthyoids' and †*Pycnosteroides*, but appears independently in paracanthopterygians (Patterson & Rosen, 1989). It is optimised as lost in †pharmacichthyids and lampridiforms.
3. Single-headed cranial articular condyle on the hyomandibula (character 25, 0→1).
   Despite Oelschläger's (1983: 108) interpretation of the double-headed articular condyle as an "advanced" feature of percomorphs, the same state (Fig. 1D) occurs in myctophiforms (Paxton, 1972) and aulopiforms, suggesting that it is plesiomorphic for acanthomorphs. Therefore, we view the reduction to only one condyle as a derived character state of lampridomorphs (Fig. 1E, F), acquired convergently by some paracanthopterygians (Grande *et al.*, 2013) and by †*Ctenothrissa*.
4. All supraneurals anterior to the first neural spine (Fig. 2A, B; character 39, 0→1).
   The state is reversed in †*Pycnosteroides*.
5. First dorsal pterygiophore inserting anterior to the second neural spine (Fig. 2A, B; character 40, 0→1).
   This character is further derived in lampridiforms (Fig. 2B), †*Pycnosteroides* and two species of †*Pharmacichthys*, where the first dorsal pterygiophore inserts anterior to the first neural spine.
6. First soft ray of the dorsal fin elongated and unbranched (character 43, 0→1).
   In †*Aipichthys* (Fig. 2A), for example, the anterior-most dorsal fin ray that is branched is the second one. In taeniosome lampridiforms, all dorsal fin rays are unbranched. In all these cases, the first dorsal ray is also the longest (not visible in Fig. 2).
   We infer a reversal in †*Pycnosteroides*, where all dorsal fin rays are branched.
7. Pelvic girdle contacting the coracoids medially (character 63, 0→1).

Contact between the pelvic and pectoral girdles is common in acanthomorphs, as described by Stiassny & Moore (1992), but it can occur in different ways. In *Polymixia* and *Aphredoderus*, there is no contact. In *Merluccius* (Fig. 4A) and *Myripristis*, the pelvic girdle contacts the cleithra, but not the coracoids. In fossil lampridomorphs (Fig. 4B), it is unclear if it contacts both coracoids and cleithra, or just coracoids. In Lampridiformes (Fig. 4C) the pelvic girdle contacts an enlarged and ventrally expanded coracoid (Le Danois, 1955) – incorrectly referred to as an "hypocoracoid" by Gill (1903).

8. Pelvic bones joined medially by their internal wings (character 64, 0→1).

   This character also occurs in most euacanthopterygians, but not in polymixiiforms (Fig. 4D) or paracanthopterygians. While the character state is observable only in two of our fossil taxa (†*Freigichthys* and †*Zoqueichthys*; Fig. 4E), their respective positions in the final tree favours the interpretation that it appeared in the last common ancestor of lampridomorphs.

The following feature can also be optimised as a ctenosquamate synapomorphy:

9. Hypurostegy of the caudal fin rays (character 58, 0→1).

   The character is also present (amongst many others) in myctophids and in numerous euacanthopterygians (e.g. scombrids, carangids, luvarids, xiphioids). It is noteworthy that this ambiguous synapomorphy was the main argument that Patterson (1968, 1993) and later authors (e.g. Olney *et al.*, 1993) mentioned to justify a relationship between †aipichthyoids (Fig. 3D) and lampridiforms (Fig. 3E).

Otero & Gayet (1996) proposed four synapomorphies for their †Aipichthyoidea. Here we demonstrate that three of these (the loss of the antorbital, the anterior insertion of the supraneurals and the contact between pelvic and pectoral girdles) in fact characterize a more inclusive clade: they can be assigned without ambiguity to Lampridomorpha. Their last putative synapomorphy of †aipichthyoids (plate-like process on the hyomandibula: character 26, 0→1) is unambiguously optimised as a ctenosquamate synapomorphy. Therefore, our data do not support any synapomorphies for †Aipichthyoidea, which we regard as a non-monophyletic assemblage.

Some other character reconstructions of the present study are worth mentioning. For example, the true pelvic spine (character 67, 0→1) was thought to be a diagnostic character of acanthopterygians (Stiassny & Moore, 1992; Johnson & Patterson, 1993). There is a pelvic spine in at least two lampridomorphs, however: †*Pycnosteroides* (Fig. 4B) and

†*Magrebichthys* (Murray & Wilson, 2014). Murray & Wilson (2014) also described a spine in the pelvic fins of †*Errachidia* and †*Homalopagus*, but this interpretation is questionable because the structures are incomplete, and can also be interpreted as enlarged and unbranched soft rays (as in †*Aipichthys*). Therefore, when our data are considered, pelvic spines appeared at least twice independently: in Euacanthopterygii and in certain lampridomorphs.

UNNAMED CLADE B

Included taxa: †*Pycnosteroides levispinosus* (Hay 1903), †*Pharmacichthys venenifer* Smith Woodward 1942, †*P. numismalis* Gayet 1980a, †*P. judensis* Gayet 1980b, †*Aipichthys minor* (Pictet 1850), †*A. velifer* Smith Woodward 1901, †*A. oblongus* Gayet 1980a, †*Paraipichthys lusitanicus* Gaudant 1978, †*Freigichthys elleipsis* Otero 1997.
Presumably included taxa (not present in our analysis): †*Aipichthys nuchalis* (Dixon 1850), †*A. pretiosus* Steindachner 1860; †*Magrebichthys nelsoni* Murray & Wilson, 2014.

This clade (Fig. 6, clade B) is supported by only one synapomorphy:

1. Six or fewer soft rays in the pelvic fin (character 66, 0→2).
   The state is reversed in †*Freigichthys*, and also present in *Trachipterus* + *Regalecus*.
   The state of this character is unknown for †*Aipichthys oblongus*.

UNNAMED CLADE C

Included taxa: †*Aipichthyoides galeatus* Gayet 1980b, †*Aspesaipichthys cavaensis* Taverne 2004, †*Zoqueichthys carolinae* Alvarado-Ortega & Than-Marchese 2012, Lampridiformes.
Presumably included taxa (not present in our analysis): †*Aipichthyoides formosus* Gayet 1980b.

This clade (Fig. 6, clade C) is supported by two synapomorphies, both unique to it:

1. Frontal bone forming part of the sagittal crest (Fig. 1B, C), which usually (Fig. 1A) consists of the supraoccipital only (character 17, 0→1).
2. Long sagittal crest (Fig. 1B, C), extending from the nasal area to the occiput (character 20, 0→1).

Both synapomorphies are unknown in †*Aspesaipichthys*, due to its incomplete preservation. They are reversed in taeniosome lampridiforms (*Trachipterus* + *Regalecus*), which are characterised by reduced crests.

UNNAMED CLADE D

Included taxa: †*Aipichthyoides galeatus* Gayet 1980b, †*Aspesaipichthys cavaensis* Taverne 2004, Lampridiformes.

Presumably included taxa (not present in our analysis): †*Aipichthyoides formosus* Gayet 1980b.

This clade (Fig. 6, clade D) is supported by three synapomorphies:

1. Mesethmoid median or posterior to the lateral ethmoids (character 6, 0→1).

   In acanthomorphs, the mesethmoid is generally located anterior to the lateral ethmoids (Fig. 1A). In †*Aipichthyoides*, the mesethmoid composes the sagittal crest; dorsally it is median to the lateral ethmoids (Fig. 1B). In lampridiforms (Olney *et al.*, 1993: 148), the mesethmoid is partly median, partly posterior (Fig. 1C), or completely posterior (in taeniosomes) to the lateral ethmoids.

2. Five hypurals or fewer (character 51, 0→1).

   There is a reversal in veliferids (Fig. 3C), a convergence in euacanthopterygians and some paracanthopterygians.

3. Lower hypurals fused together (character 54, 0→1).

   In †*Aipichthyoides*, †*Aspesaipichthys* (Fig. 3B) and veliferids (Fig. 3C), hypurals one and two are joined together at the base, thus partially fused together. The fusion is complete in *Lampris*. This state is convergent in *Aphredoderus* and *Merluccius*.

LAMPRIDIFORMES GOODRICH, 1909

Synonyms: Allotriognathi Regan, 1907; Lampriformes Goodrich, 1909.

Remark: A debate exists on whether the order should be named "Lampriformes" or "Lampridiformes". "Lampriformes" has been used several times following the recommendations of Steyskal (1980), for example in Olney (1984), Grande *et al.* (2013) and most notably, in Nelson's widely used handbook *Fishes of the World* (Nelson, 2006) as well as in the online database *FishBase* (Froese & Pauly, 2014; http://www.fishbase.org). However, Patterson, in an appendix to Olney *et al.* (1993), advocated the use of "Lampridiformes". This orthography has been followed by the vast majority of recent phylogenetic papers, including the review of teleost classification by Wiley & Johnson (2010) and the *DeepFin-EToL* classification (Betancur-R. *et al.*, 2013b).Therefore, we chose to maintain current usage and use the name "Lampridiformes".

Included taxa: see reviews in Olney *et al.*, 1993; Roberts, 2012.

Olney *et al.* (1993) proposed four osteological synapomorphies for Lampridiformes. All of these were retrieved here (one has an ambiguous optimisation and another is not a discrete character state in our matrix) and we propose additional ones, for a total of 14 synapomorphies (four cannot be unambiguously assigned to the clade because of missing data in the fossil sister groups).

1. Ascending process of the premaxilla equal or longer than the alveolar process (character 2, 0→1).

   An elongate ascending process is a lampridiform synapomorphy according to Olney *et al.* (1993: 148).

2. Loss of the supramaxillae (character 3, 0→2).

   It is also the case in modern paracanthopterygians and in myctophids, by convergence.

3. Loss of the anterior palatine process (character 4, 0→1).

   This lampridiform synapomorphy according to Olney *et al.* (1993: 147) is here optimised as ambiguous, because the character state data are missing for the immediate fossil outgroups in our matrix.

4. Loss of the ascending process on the lachrymal (character 8, 1→0).

   This is a reversal of Lampridomorpha character number one.

5. "Vault" or "cradle" on the frontal, accommodating the premaxilla and the rostral cartilage (character 12, 0→1).

   This state is part of Olney *et al.*'s (1993: 148) synapomorphy number three.

6. Seven or fewer branchiostegal rays (character 28, 1→2).

   This state is convergent with paracanthopterygians and *Polymixia*.

7. Urohyal expanded by a large ventral lamina (Fig. 1H; character 29, 0→1).

   The optimisation is ambiguous for this state because of missing data in fossils. A large ventral lamina on the urohyal is also present in many deep-bodied euacanthopterygians not included in the analysis like menids and some carangids.

8. Epineurals lost on the postabdominal vertebrae (character 36, 0→1).

   This state is convergent with extant paracanthopterygians.

9. Loss of the epipleurals (character 37, 0→1).

   An independent loss occurred in Euacanthopterygii+Paracanthopterygii and in †*Pycnosteroides*

10. Only two supraneurals (character 38, 0→2).

All Lampridiformes included in our analysis have one supraneural at most (hence the character state presented here). However, *Velifer hypselopterus* (not included) is the only extant species with two supraneurals (Fig. 2B), suggesting that the reduction to two supraneurals is the lampridiform synapomorphy. Such a reduction is convergent with paracanthopterygians and *Myripristis*.

11. First dorsal pterygiophore inserting anterior to the first neural spine (Fig. 2B; character 40, 1→2).
    This character state is also observed (by convergence) in the †*Pharmacichthys* + †*Pycnosteroides* clade (with a reversion in †*Pharmacichthys venenifer*) and in euacanthopterygians not included in the analysis such as echeneids, pleuronectoids, pataecids and coryphaenids.
12. Upper hypurals fused together (Fig. 3B, C; character 52, 0→1).
    The character can also be considered a synapomorphy of a potential †*Aspesaipichthys*+Lampridiformes clade (recovered in several parsimonious trees), convergent with modern paracanthopterygians.
13. Upper hypurals fused to the second ural centrum (Fig. 3C; character 53, 0→1).
    While it could also be interpreted as convergent in lampridids and veliferids, we follow Wiley & Johnson (2010), who favoured this character state as a lampridiform synapomorphy – as already noted by Patterson (1968). There is a reversal in taeniosomes, which have greatly modified caudal skeletons presumably associated with reduction of the caudal fin. The state is also convergent with extant paracanthopterygians.
14. Postcleithra fused together (character 61, 0→1).
    This state is convergent with extant paracanthopterygians.

Our results are consistent with the previous ones regarding relationships within Lampridiformes (e.g. Olney et al., 1993; Wiley et al., 1998): veliferids are sister to a clade composed by lampridids and taeniosomes.

CONCLUSIONS

For the first time, Late Cretaceous acanthomorphs of uncertain affinities are included in a phylogenetic analysis along with representatives of all the major acanthomorph subgroups. Thanks to this taxonomic sampling allowing a better comprehension of character state

distribution among acanthomorphs, we are able to propose here new arguments concerning the phylogenetic position of Lampridiformes. Our results support a topology that is congruent with some previous works, both anatomical (Johnson & Patterson, 1993; Olney *et al.*, 1993) and molecular (Wiley *et al.*, 1998, 2000; Smith & Wheeler, 2006; Grande *et al.*, 2013). The present study is thus a new example of the interest of including fossils in phylogenetic studies where the extant taxa have very modified anatomies leading to ambiguities in assessment of potential homologies (e.g. Santini & Tyler, 2004; Friedman, 2012).

In addition to the position of Lampridiformes, we were able to clarify the relationships and taxonomy of the Cretaceous fossils we used, suggesting that †"aipichthyoids", †pharmacichthyids and †pycnosteroidids are indeed closely related to modern lampridiforms and demonstrating the paraphyly of †Aipichthyoidea.

The clade Lampridomorpha has been expanded in its composition, as it now includes extinct lineages along with the extant Lampridiformes. Our results show (Fig. 7) that lampridomorphs were already present in the Cenomanian, which is about 20 Myr earlier than the previously accepted oldest occurrence of the group (with †*Nardovelifer* in the Campanian-Maastrichtian). Thus, the oldest lampridomorphs are the same age as the oldest representatives of the other main acanthomorph subclades: Polymixiiformes (†*Homonotichthys* and †*Omosoma* from England, Lebanon and Morocco), Paracanthopterygii (†*Xenyllion* from North America) and Euacanthopterygii (diverse "beryciform" genera from Lebanon, Palestine, England, Portugal, Morocco, Slovenia and Mexico), which are all from the Cenomanian or Turonian (Patterson, 1993; Wilson & Murray, 1996; Newbrey *et al.*, 2013).

The present study offers a new glimpse of the early evolution of lampridiforms, and of acanthomorphs as a whole. We show that lampridomorphs were a diverse group in the Cretaceous, represented by at least 14 species in the Cenomanian, which is an important part of the total acanthomorph diversity known at the time. Consistent with other acanthomorph groups (Friedman, 2010; Near *et al.*, 2013), it was later, in the Paleogene, that the clade diversified while developing numerous morphological innovations (Bannikov, 1999; Carnevale, 2004). These are the profound modification of the jaws articulations, reduction of spinous component of fins and adaptation to a pelagic environment that are characteristic of the extant Lampridiformes.

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TABLES

Table 1: List of the specimens used to code the characters in the study.
Column 1 = taxon name; column 2 = specimen number; column 3 = technique(s) used.
Institutional abbreviations: AMNH = American Museum of Natural History, New York City, USA; AMS = Australian Museum, Sydney, Australia; MNHN = Muséum national d'Histoire naturelle, Paris, France; NHMUK = Natural History Museum, London, UK; ZMUC = Zoological Museum – University of Copenhagen, Denmark

Outgroups		
Synodus intermedius	ZMUC P2394016	direct observation and photos
Gymnoscopelus sp.	MNHN research collection	dissection, X-ray computed tomography
†*Ctenothrissa protodorsalis*	MNHN.F.HAK22	binocular microscope
†*Ctenothrissa signifer*	NHMUK PV P47524	binocular microscope and photos
†*Ctenothrissa vexillifer*	MNHN.F.HAK39	binocular microscope
†*Ctenothrissa vexillifer*	MNHN.F.HAK104	binocular microscope
Potential Cretaceous sister-groups of Lampridiformes		
†*Pharmacichthys numismalis*	MNHN.F.HAK3	binocular microscope
†*Pharmacichthys venenifer*	MNHN.F.HAK7	binocular microscope
†*Aipichthys minor*	MNHN.F.HAK1938	binocular microscope
†*Aipichthys minor*	MNHN.F.HAK94	binocular microscope
†*Aipichthys velifer*	MNHN.F.HAK57	binocular microscope
†*Aipichthys velifer*	NHMUK PV P4743	binocular microscope and photos
†*Aipichthys velifer*	NHMUK PV P4744	binocular microscope and photos
†*Pycnosteroides levispinosus*	MNHN.F.HDJ105	binocular microscope
†*Pycnosteroides levispinosus*	NHMUK PV P13901	binocular microscope and photos
Polymixiiformes		
Polymixia cf.*nobilis*	MNHN.IC.2006-1740	X-ray radiographs of alcohol specimen, X-ray computed tomography
Polymixia nobilis	NHMUK 95.5.28.1	direct observation and photos
Paracanthopterygii		
Aphredoderus sayanus	MNHN.IC.1987-0864	X-ray radiographs of alcohol specimen
†*Sphenocephalus fissicaudus*	NHMUK PV P8772	binocular microscope and photos
†*Sphenocephalus fissicaudus*	NHMUK PV P8774	binocular microscope and photos
Merluccius merluccius	Research collection	dissection
Merluccius merluccius	ZMUC 215	direct observation and photos
Euacanthopterygii		
Myripristis sp.	Research collection	dissection
Lampridiformes		
Velifer hypselopterus	MNHN.IC.1982-0025	X-ray radiographs of alcohol specimens, X-ray computed tomography
Velifer hypselopterus	AMS 21840020	cleared and stained, photos
Metavelifer multiradiatus	AMNH 214663 SD	direct observation and photos
Metavelifer multiradiatus	AMNH 219280 SD	direct observation and photos

Metavelifer multiradiatus	AMNH 91808 SD	direct observation and photos
Metavelifer multiradiatus	AMNH 91800 SD	direct observation and photos
Metavelifer multiradiatus	AMNH 91798 SD	direct observation and photos
Lampris guttatus	ZMUC 74	direct observation and photos
Lampris guttatus	AMNH 79669 SD	direct observation and photos
Lampris guttatus	AMNH 21720 SD	direct observation and photos
Lampris guttatus	MNHN.ZA.1883-1795	direct observation
Lampris immaculatus	MNHN research collection	dissection
Lampris sp.	AMNH 21766 SD	direct observation and photos
Trachipterus arcticus	ZMUC 1890 31	direct observation and photos
Trachipterus arcticus	AMNH 79627 SD	direct observation and photos
Trachipterus jacksonensis	AMNH 098555 SD	direct observation and photos
Trachipterus jacksonensis	AMNH 093409 SD	direct observation and photos
Regalecus glesne	AMNH 093518 SD	direct observation and photos

Table 2: List of the characters used in the study. Column 1 = character number; column 2 = character description; column 3 = references.

1	*Postmaxillary process of the premaxilla*: 0 = absent; 1 = present; 2 = present with a "gadoid" notch	Patterson & Rosen, 1989
2	*Ascending process of the premaxilla*: 0 = shorter than the alveolar process; 1 = equal to or longer than the alveolar process	Olney *et al*., 1993: character 3, in part
3	*Number of supramaxillae*: 0 = two ; 1 = one ; 2 = none	Otero & Gayet, 1996: characters 24, 31 & 46; Alvarado-Ortega & Than-Marchese, 2012: character 28
4	*Anterior palatine process*: 0 = present; 1 = absent	Olney *et al*.,1993: character 1
5	*Lateral ethmoid*: 0 = not linked to the palate-quadrate region; 1 = linked to the palate-quadrate region by a narrow process	Gayet, 1979
6	*Mesethmoid*: 0 = anterior to the lateral ethmoid (Fig. 1A); 1 = median or posterior to the lateral ethmoid (Fig. 1B, C)	Olney *et al*., 1993: character 2
7	*Antorbital*: 0 = present; 1 = absent	Otero & Gayet, 1996: character 14
8	*Ascending process of the lachrymal*: 0 = absent; 1 = present	Otero & Gayet, 1996: character 39
9	*Supraorbital sensory canal*: 0 = fully ossified; 1 = middle and anterior part of the canal are not ossified	Otero & Gayet, 1996: characters 29 & 37; Alvarado-Ortega & Than-Marchese, 2012: character 32
10	*Orbitosphenoid*: 0 = present ; 1 = absent	Otero & Gayet, 1996: character 38
11	*Basisphenoid*: 0 = present; 1 = absent	Otero & Gayet, 1996: character 30
12	*Frontal vault or cradle*: 0 = absent; 1 = present	Olney *et al*.,1993: character 3, in part
13	*Interfrontal flat*: 0 = absent; 1 = present	Otero & Gayet, 1996: character 23
14	*Frontal branch of the sensory canal*: 0 = runs through the frontal and pterotic in a closed tube; 1= runs through the frontal and pterotic in a groove	Otero & Gayet, 1996: character 2
15	*Preopercular branch of the sensory canal*: 0 = opens throughout pores; 1 = opens throughout an indentation	Otero & Gayet, 1996: characters 3 & 25; Alvarado-Ortega & Than-Marchese, 2012: character 3
16	*Size of the sagittal crest (composed at least by the supraoccipital*): 0 = absent or small crest; 1 = developed sagittal crest	Olney *et al*., 1993: character 14; Otero & Gayet, 1996: character 1
17	*Frontal bone forming part of the sagittal crest*: 0 = absent (Fig. 1A); 1 = present (Fig. 1B, C)	Otero & Gayet, 1996: character 18, in part; Alvarado-Ortega & Than-Marchese, 2012: character 18

18	*Mesethmoid bone forming part of the sagittal crest*: 0 = absent (Fig. 1A, C); 1 = present (Fig. 1B)	Otero & Gayet, 1996: character 18, in part; Alvarado-Ortega & Than-Marchese, 2012: character 19
19	*Posterior edge of the sagittal crest*: 0 = convex (rounded crest, Fig. 1B, C); 1 = concave (half-boomerang shaped crest, Fig. 1A)	Alvarado-Ortega & Than-Marchese, 2012: character 20
20	*Length of the sagittal crest*: 0 = short, entirely behind the orbit (Fig. 1A); 1 = long, from the nasal area to the occiput (Fig. 1B, C)	Alvarado-Ortega & Than-Marchese, 2012: character 21
21	*Thickened anterior edge of the sagittal crest*: 0 = absent; 1 = present	Alvarado-Ortega & Than-Marchese, 2012: character 22
22	*Dorsal limb of the posttemporal*: 0 = not firmly bound to the epiotic; 1 = firmly bound to the epiotic	Stiassny, 1986; Johnson & Patterson, 1993: character 5
23	*Spina occipitalis*: 0 = absent; 1 = present	Otero & Gayet, 1996: character 12
24	*Foramen magnum*: 0 = dorsal to the tripartite occipital condyle; 1 = bounded laterally by the exoccipital condyles	Olney *et al*., 1993: character 12
25	*Cranio-hyomandibular condyle*: 0 = two-headed (Fig. 1D); 1 = single-headed (Fig. 1E, F)	Oelschläger, 1983; Grande *et al.*, 2013: character 6
26	*Plate-like anterior process of the hyomandibula*: 0 = absent; 1 = present	Otero & Gayet, 1996: character 15
27	*"Beryciform" foramen in the distal ceratohyal*: 0 = present; 1 = absent	Oelschläger, 1983
28	*Number of branchiostegal rays*: 0 = nine or more; 1 = eight; 2 = seven or less	Otero & Gayet, 1996: characters 4, 27 & 41; Alvarado-Ortega & Than-Marchese, 2012: character 4
29	*Urohyal*: 0 = not expanded ventrally (Fig. 1G); 1 = expanded by a large ventral lamina (Fig. 1H)	New
30	*Posterior border of the preopercular*: 0 = smooth; 1 = spiny	Otero & Gayet, 1996: character 33
31	*Posterior border of the opercular*: 0 = smooth ; 1 = spiny	Otero & Gayet, 1996: character 40
32	*Total number of vertebrae*: 0 = less than 40; 1 = 40-60; 2 = 60 or more	Olney *et al*., 1993: characters 10 & 25
33	*Neural spines of vertebral centra (unknown for the first neural spine of most fossils)*: 0 = autogenous; 1 = fused with the centrum	Otero & Gayet, 1996: character 5
34	*Orientation of the first neural spine*: 0 = inclined posteriorly; 1 = inclined anteriorly and in close association with the cranium	Olney *et al*., 1993: character 16
35	*Point of origin of anterior epineurals*: 0 = neural arches or	Otero & Gayet, 1996: character 13

	spines; 1 = centra or transverse processes	
36	*Epineurals on the postabdominal vertebrae*: 0 = present; 1 = absent	Otero & Gayet, 1996: character 44
37	*Epipleurals*: 0 = present; 1 = absent	Otero & Gayet, 1996: character 43
38	*Number of supraneurals (predorsals in Otero and Gayet 1996)*: 0 = three (Fig. 2A); 1 = two (Fig. 2B); 2 = one; 3 = none	Olney *et al.*, 1993: character 13; Otero & Gayet, 1996: character 16, in part; Alvarado-Ortega & Than-Marchese, 2012: character 16
39	*Position of supraneurals*: 0 = at least one posterior to the first neural spine; 1 = all anterior to the first neural spine (Fig. 2A, B)	Otero & Gayet, 1996: character 16, in part; Alvarado-Ortega & Than-Marchese, 2012: character 17, in part
40	*Position of the first dorsal pterygiophore*: 0 = posterior to the second neural spine; 1 = anterior to the second neural spine (Fig. 2A); 2 = anterior to the first neural spine (Fig. 2B)	Olney *et al*., 1993: character 4, in part
41	*Orientation of the first two dorsal pterygiophores*: 0 = vertical (Fig. 2A, B); 1 = inclined forward over neurocranium	Olney *et al.*, 1993: character 15
42	*Spines on the dorsal fin*: 0 = absent; 1 = present (Fig. 2A, B)	Otero & Gayet, 1996: character 6, in part
43	*Elongated and unbranched first soft ray of the dorsal fin*: 0 = absent; 1 = present (Fig. 2A, B)	New
44	*Soft rays of the dorsal fin*: 0 = at least some branched rays; 1 = all rays unbranched	Grande *et al.*, 2013: character 15
45	*Anal fin*: 0 = present; 1 = absent	Olney *et al.*, 1993: character 30
46	*Hemaxanal complex*: 0 = absent; 1 = present	Otero & Gayet, 1996: character 7
47	*Spines on the anal fin*: 0 = absent; 1 = present	Otero & Gayet, 1996: character 6, in part
48	*Neural spine of the second preural vertebra*: 0 = short and leaf-shaped; 1 = long and spine-like	Otero & Gayet, 1996: character 28
49	*Stegural*: 0 = autogenous; 1 = fused to the first ural centrum	Grande *et al.*, 2013: character 26
50	*Number of epurals*: 0 = three; 1 = two	Otero & Gayet, 1996: characters 19 & 35; Alvarado-Ortega & Than-Marchese, 2012: character 23
51	*Number of hypurals*: 0 = six (Fig. 3A, C); 1 = five or less (Fig. 3B)	Otero & Gayet, 1996: character 20
52	*Upper hypurals*: 0 = independent bones (Fig. 3A); 1 = fused together (Fig. 3B, C)	Otero & Gayet, 1996: character 48

53	*Upper hypurals*: 0 = autogenous to the ural centra (Fig. 3A, B); 1 = fused to the second ural centrum (Fig. 3C)	Wiley & Johnson, 2010: character 5
54	*Lower hypurals*: 0 = independent bones (Fig. 3A); 1 = fused together (Fig. 3B, C)	Grande *et al*., 2013: character 24
55	*Lower hypurals*: 0 = autogenous (Fig. 3A, C); 1 = fused to the pseudurostylar centrum (PU1+U1) (Fig. 3B)	Otero & Gayet, 1996: character 21
56	*Urodermals*: 0 = present; 1 = absent	Otero & Gayet, 1996: character 8
57	*Dermal caudal scutes*: 0 = present; 1 = absent	Otero & Gayet, 1996: character 9
58	*Overlap of the caudal skeleton by the caudal fin rays*: 0 = little overlap; 1 = extensive overlap (hypurostegy) (Fig. 3D, E)	Le Danois & Le Danois, 1964; Patterson, 1968; Oelschläger, 1974
59	*Number of principal rays in the caudal fin*: 0 = nineteen or more; 1 = eighteen or less	Otero & Gayet, 1996: character 11
60	*Supracleithrum*: 0 = smooth; 1 = spiny	Otero & Gayet, 1996: character 34
61	*Postcleithra*: 0 = separate bones; 1 = two bones fused together	Otero & Gayet, 1996: character 47
62	*Number of autogenous pectoral fin radials*: 0 = four; 1 = three	Olney *et al*.,1993: character 7
63	*Contact between the pelvic girdle and the coracoid*: 0 = absent (Fig. 4A); 1 = present (Fig. 4B, C)	Gill, 1903; Le Danois, 1955; Stiassny & Moore, 1992: character 5, in part; Otero & Gayet, 1996: character 17, in part
64	*Internal wings of the pelvic bone*: 0 = separated (Fig. 4D); 1 = joined medially (Fig. 4E, F)	New
65	*Median processes of the pelvic bones:* 0 = non-overlapping (Fig. 4E, F); 1 = overlapping medially (Fig. 4D)	Stiassny & Moore, 1992: character 1, in part
66	*Number of pelvic soft rays*: 0 = eight or more ; 1 = seven; 2 = six or less	Otero & Gayet, 1996: characters 10 and 22; Alvarado-Ortega & Than-Marchese, 2012: character 10
67	*Pelvic spine*: 0 = absent; 1 = present (Fig. 4B)	Stiassny & Moore, 1992: character 3; Johnson & Patterson, 1993: character 13

Table 3: Character matrix used in the study.

'†' denotes an extinct taxon; '?' denotes an unknown character state; '-' denotes an unapplicable character state.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Synodus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnoscopelus	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	-	-	-	-	-	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
†*Ctenothrissa*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0
†*Pharmacichthys venenifer*	0	0	0	0	1	0	1	0	0	0	0	0	0	?	?	1	0	0	1	0	0	1	?	?	1	1	0	1	?	0	0	0	1	0	1	0	0	1	1	1	0	1	1	0	0	1	1
†*P. numismalis*	0	0	0	?	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	?	?	1	1	?	?	?	0	0	0	1	0	1	0	0	1	1	2	0	1	1	0	0	1	1
†*P. judensis*	0	0	0	0	1	0	1	?	?	0	0	0	0	?	?	1	0	0	1	0	0	1	?	?	1	1	?	?	?	0	0	0	?	0	1	0	0	1	1	2	0	1	?	0	0	1	1
†*Aipichthyoides*	?	0	0	?	0	1	1	1	0	0	0	0	0	1	1	1	1	1	0	1	0	1	?	?	1	1	1	1	?	0	0	0	1	0	?	0	0	0	1	1	0	1	1	0	0	1	1
†*Paraipichthys*	0	?	?	?	0	0	?	?	0	?	?	?	0	?	0	1	0	0	0	0	0	?	?	?	1	?	?	?	?	0	0	0	?	0	?	?	?	0	1	?	?	1	1	0	0	1	1
†*Aipichthys velifer*	0	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	1	0	1	1	?	?	1	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1
†*A. oblongus*	0	?	?	?	0	0	1	?	0	0	0	0	1	1	0	1	0	0	1	0	1	?	?	?	1	1	?	?	?	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1
†*A. minor*	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	1	1	?	?	1	1	1	1	?	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1
†*Freigichthys*	0	0	?	0	0	0	1	1	0	0	?	0	1	1	1	1	0	0	1	0	1	1	?	?	1	1	?	?	?	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1
†*Aspesaipichthys*	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	?	?	0	0	0	0	?	?	?	?	0	1	1	0	1	?	0	0	?	?
†*Zoqueichthys*	0	0	0	?	0	0	1	1	?	0	0	0	0	?	?	1	1	0	0	1	0	1	?	?	1	1	?	1	?	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1
†*Pycnosteroides*	?	0	0	0	0	0	1	1	?	0	0	0	0	1	0	1	0	0	1	0	0	1	?	?	1	1	0	1	0	0	0	0	1	0	1	0	1	1	0	2	0	1	0	0	0	1	1
Polymixia	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	1	0	2	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	1
†*Sphenocephalus*	2	0	1	0	0	0	0	1	?	1	1	0	0	1	1	1	0	0	1	0	0	1	?	?	1	0	0	2	0	1	1	0	1	1	?	?	?	2	0	0	0	1	0	0	0	1	1
Aphredoderus	0	0	2	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	0	0	1	1	0	0	0	1	2	0	1	1	0	1	1	1	1	1	2	0	0	0	1	0	0	0	1	1
Merluccius	2	0	2	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	1	2	0	1	1	1	1	1	1	1	1	3	-	0	0	0	0	0	0	0	0
Myripristis	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1	1
Metavelifer	0	1	2	1	0	1	1	0	0	0	0	1	0	?	?	1	1	0	0	1	0	1	0	0	1	1	0	2	1	0	0	0	1	0	0	1	1	2	1	2	0	1	1	0	0	1	1
Lampris	0	1	2	1	0	1	1	0	0	0	0	1	0	?	?	1	1	0	0	1	0	1	0	1	1	0	1	2	1	0	0	1	1	0	-	1	1	2	1	2	0	0	1	0	0	0	0
Trachipterus	0	1	2	1	0	1	1	0	?	0	0	1	0	?	?	0	-	-	-	-	-	1	0	0	1	0	1	2	1	0	0	2	1	1	-	1	1	3	-	2	1	0	1	1	1	-	-
Regalecus	0	1	2	1	0	1	1	0	?	0	0	1	0	?	?	0	-	-	-	-	-	1	0	0	1	0	1	2	1	0	0	2	1	1	-	1	1	3	-	2	1	0	1	1	1	-	-

Table 3 (continued):

	48	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**
Synodus	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
Gymnoscopelus	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
†*Ctenothrissa*	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	?	?	0	0
†*Pharmacichthys venenifer*	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	?	?	2	0
†*P. numismalis*	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	?	?	2	0
†*P. judensis*	0	1	0	0	0	0	0	0	?	1	1	0	0	0	?	1	?	?	2	0
†*Aipichthyoides*	0	0	1	1	0	0	1	1	1	1	1	0	0	0	0	1	?	?	1	0
†*Paraipichthys*	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	1	?	?	2	0
†*Aipichthys velifer*	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	?	?	2	0
†*A. oblongus*	0	0	0	0	0	0	0	0	1	1	1	?	0	0	0	1	?	?	?	0
†*A. minor*	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	?	?	2	0
†*Freigichthys*	0	0	0	?	?	0	?	0	1	1	1	?	0	0	0	1	1	0	1	0
†*Aspesaipichthys*	0	0	0	1	1	0	1	1	1	1	1	0	?	?	?	?	?	?	?	?
†*Zoqueichthys*	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0
†*Pycnosteroides*	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	?	?	2	1
Polymixia	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0
†*Sphenocephalus*	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	?
Aphredoderus	1	0	1	0	1	1	1	0	1	1	0	1	1	1	0	0	0	1	1	0
Merluccius	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	0	0	1	0
Myripristis	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	1	1	0	1	1
Metavelifer	0	0	0	0	1	1	1	0	1	1	1	0	0	1	0	1	1	0	0	0
Lampris	0	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	1	0	0	0
Trachipterus	1	0	1	1	1	0	1	0	1	1	0	1	0	1	1	1	1	0	2	0
Regalecus	-	-	-	1	-	-	-	0	1	1	0	1	0	1	1	1	1	0	2	0

FIGURES

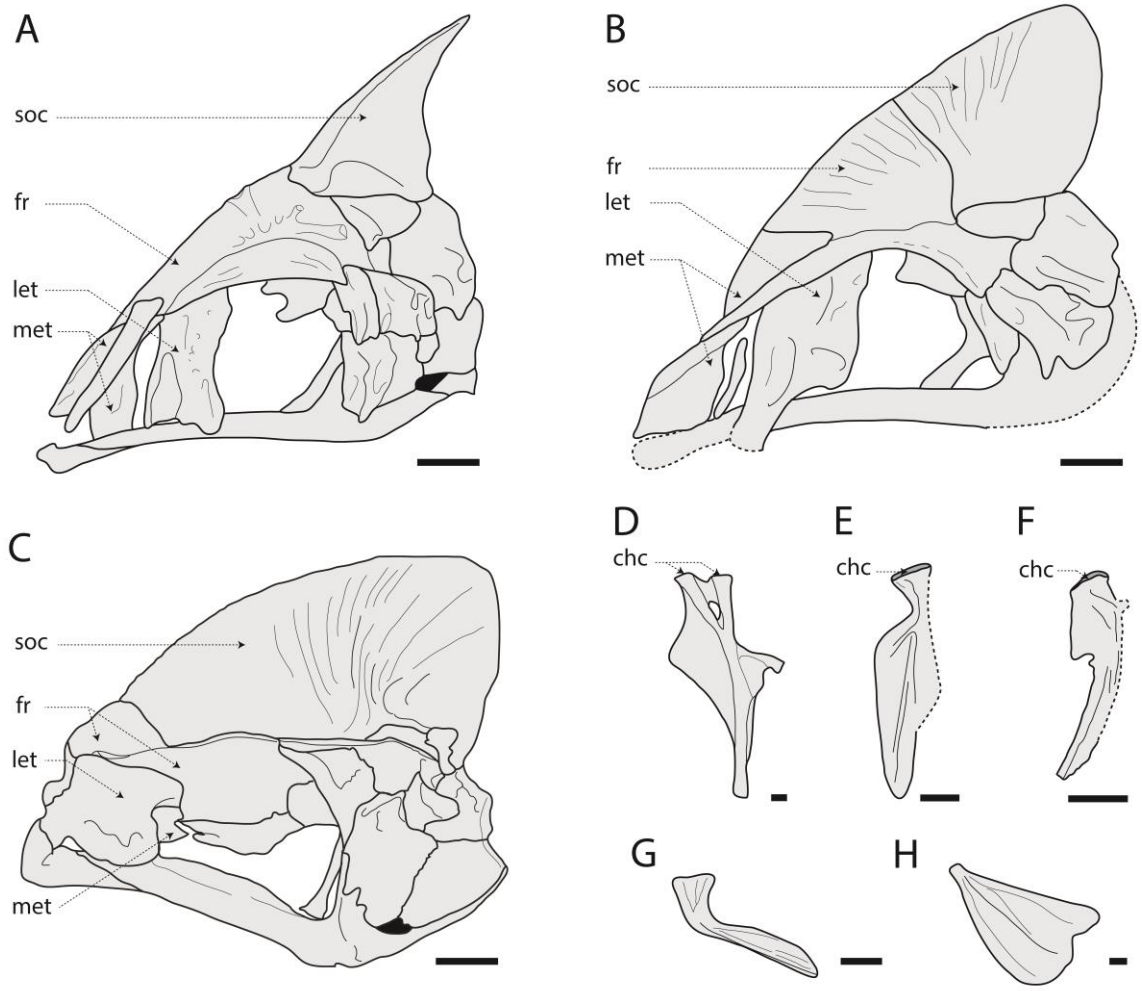

Figure 1. Cranial skeleton of several taxa studied. A, neurocranium of †*Aipichthys velifer* (reconstruction), after Gayet (1980a: fig. 25). Scale bar: 2 mm. B, neurocranium of †*Aipichthyoides galeatus* (reconstruction), after Gayet (1980b: fig. 8). Scale bar: 3 mm. C, neurocranium of *Lampris guttatus*, after Oelschläger (1983: Fig. 12). Scale bar: 2 cm. D, left hyomandibula of the myctophiform *Lampanyctus* sp., after Paxton (1972: fig. 7B). Scale bar: 1 mm. E, left hyomandibula of †*Aipichthys minor*, after Otero & Gayet (1996: fig. 8A). Scale bar: 1 mm. F, left hyomandibula of *Metavelifer multiradiatus*, AMNH 91808SD. Scale bar: 1 cm. G, urohyal of *Merluccius*, MNHN research collection. Scale bar: 1 cm. H, urohyal of *Lampris guttatus*, AMNH 79669SD. Scale bar: 1 cm. Abbreviations: chc, cranio-hyomandibular condyle; fr, frontal; let, lateral ethmoid; met, mesethmoid; soc, supraoccipital.

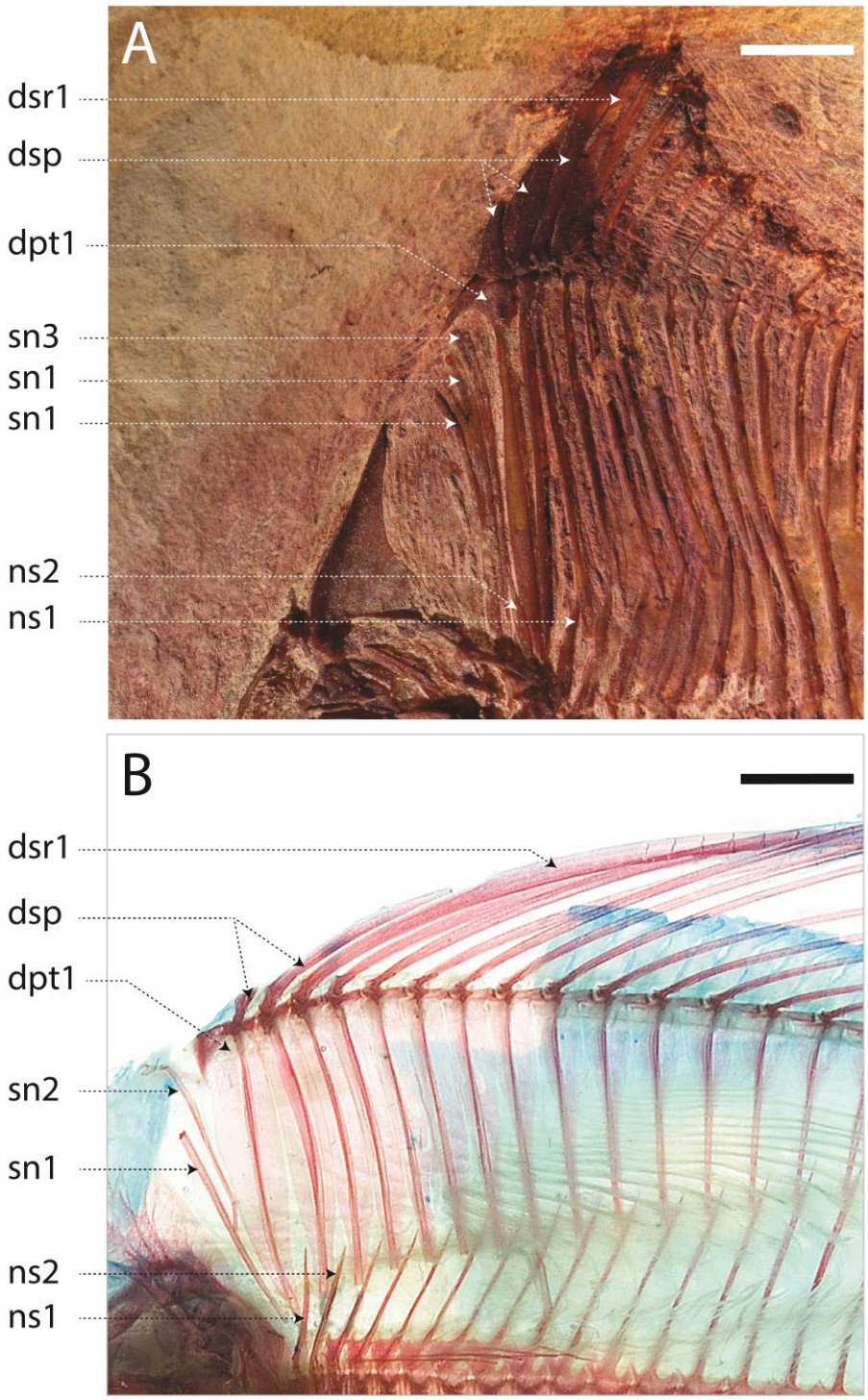

Figure 2. Dorsal fin skeleton of two studied taxa. A, †*Aipichthys velifer*, MNHN.F.HAK57. Scale bar: 1 cm. Photo D. Davesne. B, *Velifer hypselopterus* (Veliferidae), AMS 21840020. Scale bar: 5 mm. Photo courtesy D. Johnson. Abbreviations: dpt, dorsal pterygiophore; dsp, dorsal spine; dsr, dorsal soft ray; ns, neural spine; sn, supraneural.

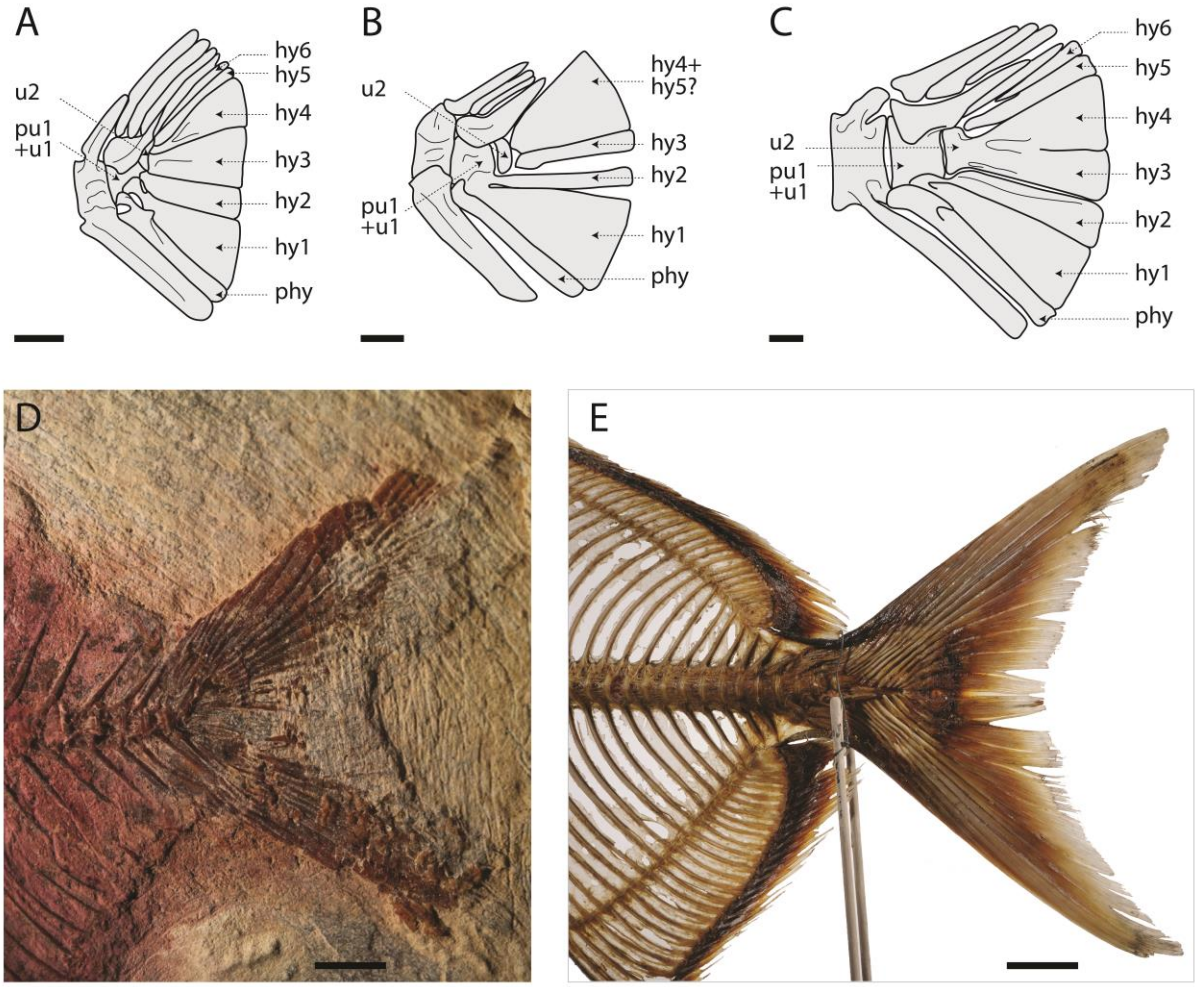

Figure 3. Caudal skeleton of several studied taxa. A, †*Aipichthys minor* (reconstruction), after Patterson (1968: fig. 11A). Scale bar: 1 mm. B, †*Aspesaipichthys cavaensis* (reconstruction), after Taverne (2004: fig. 7). Scale bar: 1 mm. C, *Velifer hypselopterus* (=*V. africanus*) (Veliferidae), after Oelschläger (1983: Fig. 82). Scale bar: 1 mm. D, †*Aipichthys velifer*, MNHN.F.HAK57, showing hypurostegy of the caudal fin rays. Scale bar: 5 mm. Photo D. Davesne. E, *Lampris guttatus*, ZMUC 74, showing hypurostegy of the caudal fin rays. Scale bar: 5 cm. Photo M.A. Krag. Abbreviations: hy, hypural; phy, parhypural; pu, preural vertebral centrum; u, ural vertebral centrum.

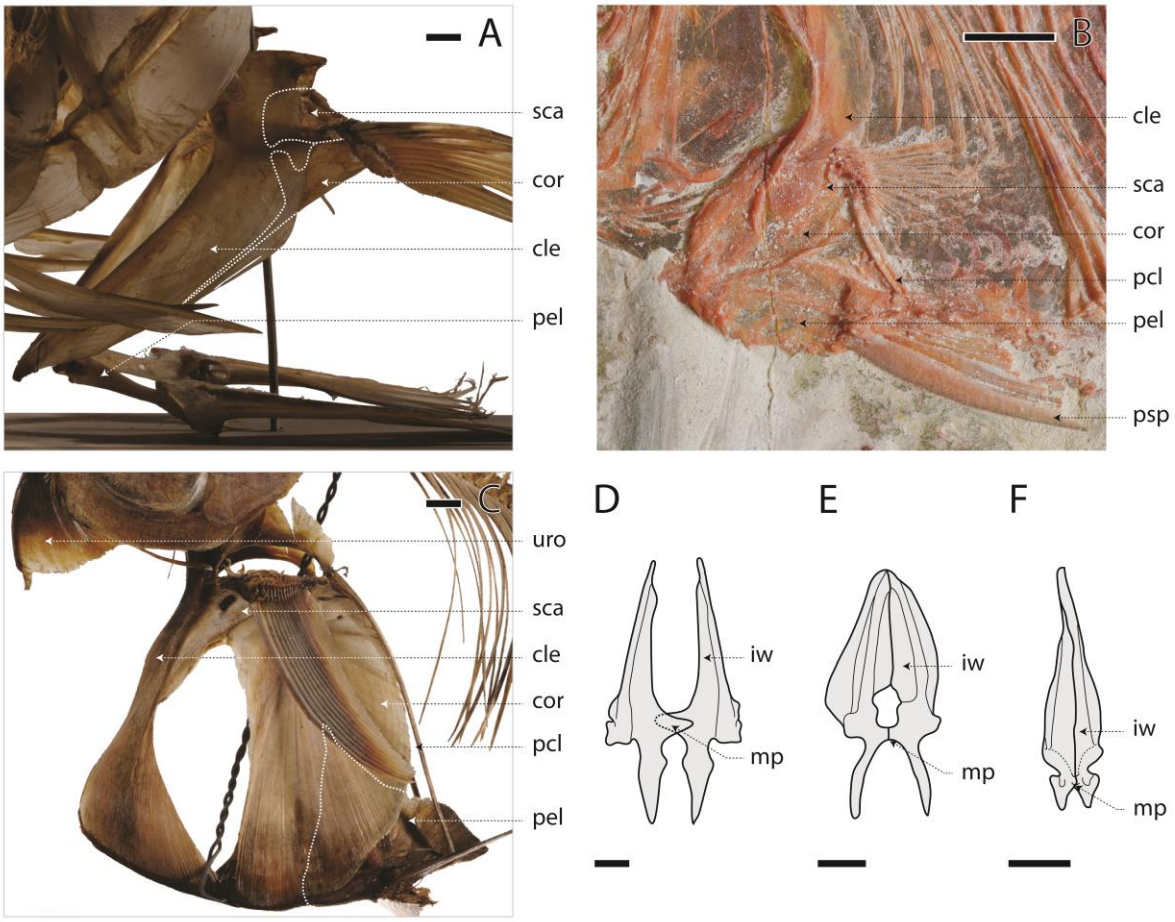

Figure 4. Appendicular skeleton of several studied taxa. A, pectoral and pelvic girdles of *Merluccius merluccius*, ZMUC 215x, with shapes of scapula and coracoid outlined. Scale bar: 2 cm. Photo M.A. Krag. B, pectoral and pelvic girdles of †*Pycnosteroides levispinosus*, MNHN.F.HDJ105. Scale bar: 5 mm. Photo D. Davesne. C, pectoral and pelvic girdles of *Lampris guttatus*, ZMUC 74, with shape of the pelvic girdle outlined. Scale bar: 5 cm. Photo M.A. Krag. D, pelvic girdle of *Polymixia* sp. in ventral view, after Stiassny & Moore (1992: fig. 3). Scale bar: 2 mm. E, pelvic girdle of †*Zoqueichthys carolinae* in ventral view, after Alvarado-Ortega & Than-Marchese (2012: fig. 5). Scale bar: 1 mm. F, pelvic girdle of *Metavelifer multiradiatus*, AMNH 91800SD, in ventral view. Scale bar: 2 mm. Abbreviations: cle, cleithrum; cor, coracoid; iw, internal wing of the pelvic girdle; mp, median process of the pelvic girdle; pcl, postcleithrum; pel, pelvic girdle; psp, pelvic spine; sca, scapula; uro, urohyal.

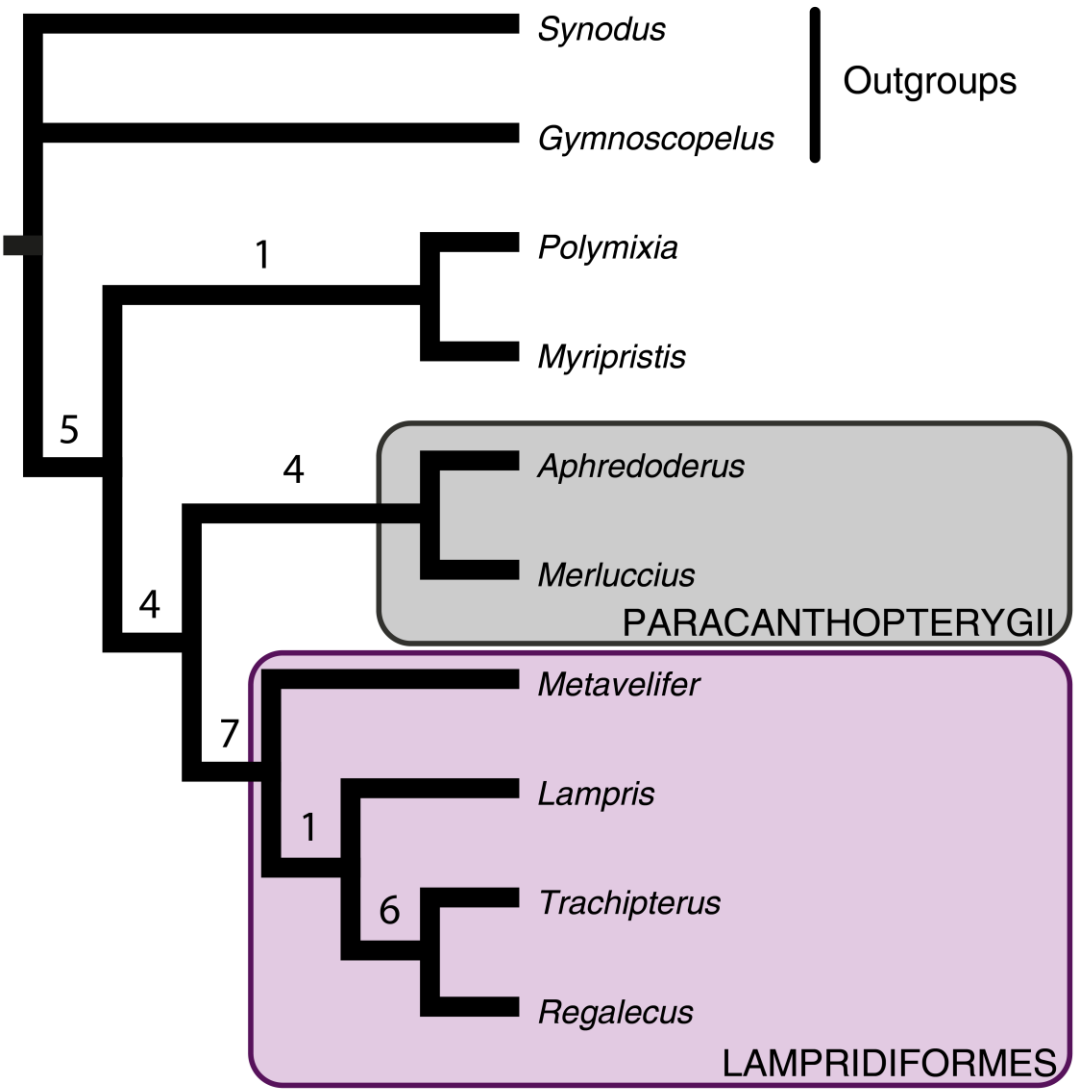

Figure 5. Most parsimonious tree obtained after analysis 1 (only the ten extant taxa included). Numbers above branches are Bremer indexes. Length = 107, CI = 0.64, RI = 0.71.

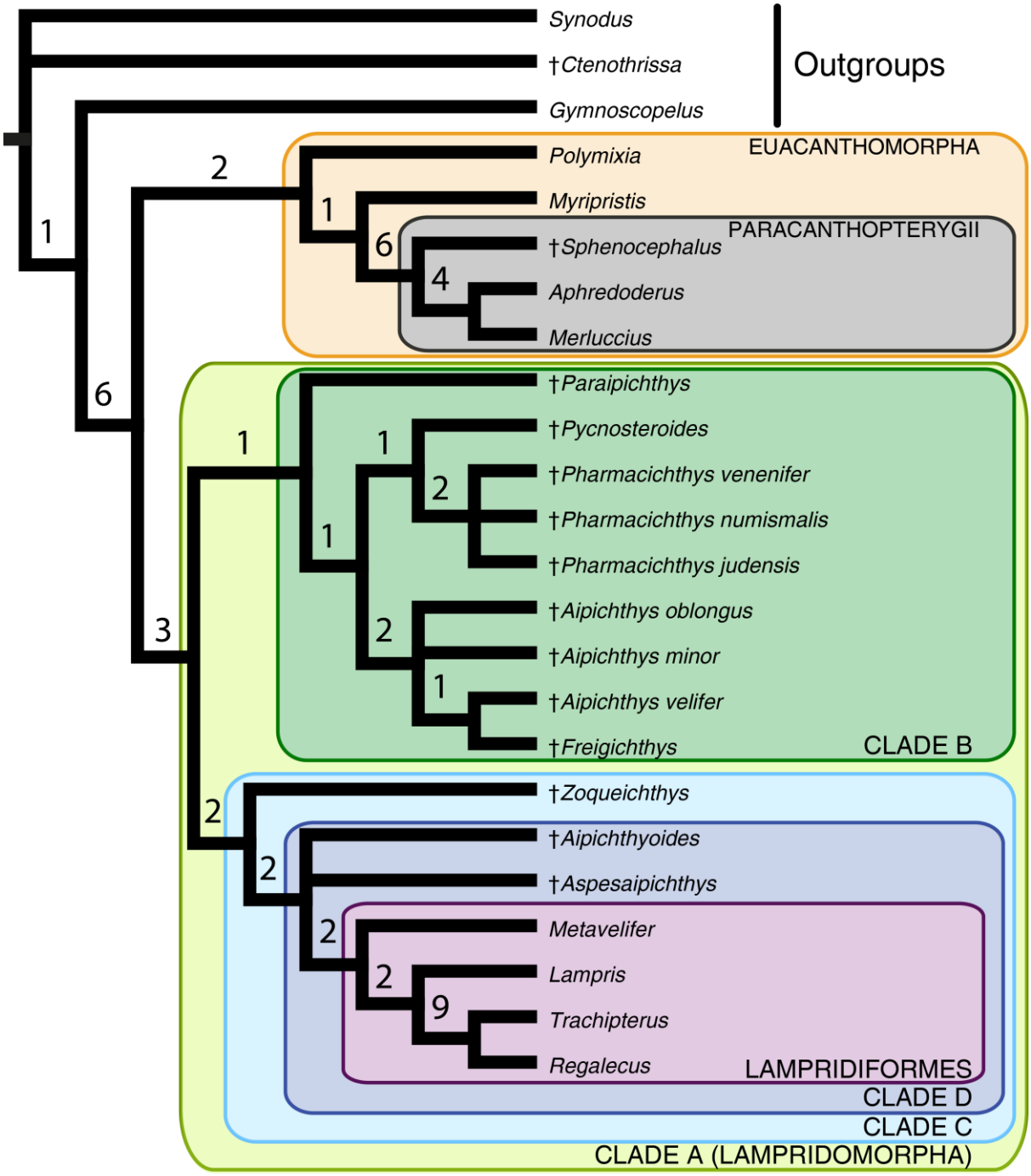

Figure 6. Strict consensus of the 12 most parsimonious trees obtained after analysis 2 (all 24 taxa, fossil and extant, included). Fossil taxa are indicated by daggers (†). Numbers above branches are Bremer indexes. Length = 155, CI = 0.48, RI = 0.72.

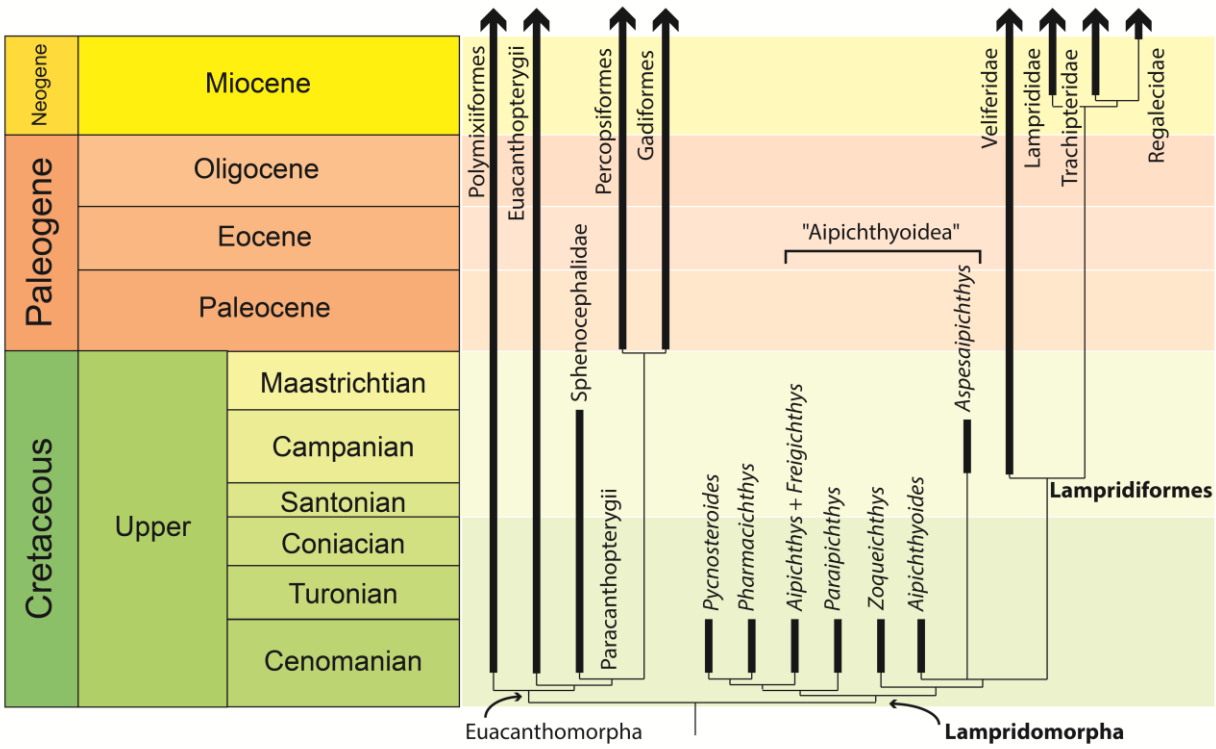

Figure 7. Hypothesis of acanthomorph interrelationships suggested by our results, with ages of taxa highlighted (thick lines). Position of internal nodes does not reflect divergence times.

APPENDIX

COMPLETE LIST OF CHARACTER STATE CHANGES

Character state changes in italics are ambiguous optimizations that we chose based on biological considerations. Character state changes in bold are unique to the clade (with no homoplasy outside the clade).

Analysis 1 (ten taxa, all extant):
Synodus autapomorphy: **33 (1→0)**
Gymnoscopelus autapomorphies: *3 (0→2)*; 10 (0→1); 26 (0→1); *31 (0→1)*; 49 (0→1); 58 (0→1)
Acanthomorpha: **14 (0→1); 15 (0→1); 16 (0→1); 22 (0→1)**; **28 (0→2)**; *42 (0→1)*; *46 (0→1)*; *47 (0→1)*; *56 (0→1)*; **57 (0→1)**
Polymixia + *Myripristis*: **1 (0→1)**; *23 (0→1)*; 27 (1→0); *35 (0→1)*; *66 (0→1)*
Polymixia autapomorphies: 26 (0→1); 48 (0→1); 59 (0→1); 65 (0→1)
Myripristis autapomorphies: **28 (2→1)**; 30 (0→1); *31 (0→1)*; *37 (0→1)*; **38 (0→1)**; 51 (0→1); 60 (0→1); 63 (0→1); 64 (0→1); **67 (0→1)**
Paracanthopterygii + Lampridiformes: *3 (0→2)*; **7 (0→1)**; **36 (0→1)**; *37 (0→1)*; **38 (0→2)**; **52 (0→1); 53 (0→1); 54 (0→1); 61 (0→1)**
Aphredoderus + *Merluccius* (= extant Paracanthopterygii): **8 (0→1)**; **9 (0→1)**; 10 (0→1); **11 (0→1)**; *23 (0→1)*; 30 (0→1); *31 (0→1)*; 34 (0→1); *35 (0→1)*; 48 (0→1); *50 (0→1)*; 59 (0→1); 60 (0→1); *66 (0→1)*
Aphredoderus autapomorphies: **19 (0→1)**; 65 (0→1)
Merluccius autapomorphies: **1 (0→2)**; 24 (0→1); *25 (0→1)*; 32 (0→1); 38 (2→3); *42 (1→0)*; *46 (1→0)*; *47 (1→0)*; 49 (0→1); 51 (0→1)
Lampridiformes: **2 (0→1); 4 (0→1); 6 (0→1); 12 (0→1); 17 (0→1); 20 (0→1)**; *25 (0→1)*; **29 (0→1)**; **39 (0→1) 40 (0→2); 43 (0→1)**; *58 (0→1)*; 63 (0→1); 64 (0→1)
Metavelifer autapomorphies: 26 (0→1); 27 (1→0)
Lampris + *Trachipterus* + *Regalecus*: *32 (0→1)*; *42 (1→0)*; *46 (1→0)*; *47 (1→0)*; *50 (0→1)*; 51 (0→1); **62 (0→1)**
Lampris autapomorphy: 24 (0→1)
Trachipterus + *Regalecus* (= Taeniosomi): 16 (1→0); *32 (1→2)*; 34 (0→1); 38 (2→3); **41 (0→1); 44 (0→1); 45 (0→1)**; **58 (1→0)**; 59 (0→1); **66 (0→2)**
Trachipterus autapomorphies: *48 (0→1)*; *53 (1→0)*
Regalecus autapomorphies: none

Analysis 2 (24 taxa, extant and fossils):
Remark: The topology presented here is a strict consensus of 12 parsimonious trees, resulting in polytomies. We chose to present "hard" polytomies, where character states are assumed to have appeared independently from other branches in the polytomy. One should remember, however, that this topology does not always reflect the most parsimonious interpretation possible.
Synodus autapomorphies: none

†*Ctenothrissa* autapomorphies: 25 (0→1); 27 (1→0); 63 (0→1)
Gymnoscopelus + Acanthomorpha (= Ctenosquamata): **26 (0→1)**; **33 (0→1)**
Gymnoscopelus autapomorphies: 3 (0→2); 10 (0→1); 31 (0→1); 49 (0→1); *58 (0→1)*
Acanthomorpha: **14 (0→1); 16 (0→1); 22 (0→1);** ***28 (0→1)*****; 42 (0→1); 46 (0→1); 47 (0→1); 56 (0→1); 57 (0→1)**
Euacanthomorpha: **1 (0→1)**; *15 (0→1)*; **23 (0→1);** 27 (1→0); 35 (0→1); 66 (0→1)
Polymixia autapomorphies: *28 (1→2)*; *48 (0→1)*; *59 (0→1)*; *65 (0→1)*;
Myripristis + Paracanthopterygii: 26 (1→0); **30 (0→1)**; 31 (0→1); 37 (0→1); **60 (0→1)**
Myripristis autapomorphies: *38 (0→1)*; 51 (0→1); 63 (0→1); 64 (0→1); *65 (1→0)*; 67 (0→1)
Paracanthopterygii: **1 (1→2)**; *3 (0→1)*; 8 (0→1); 10 (0→1); **11 (0→1)**; *28 (1→2)*; 34 (0→1); *38 (0→2)*; *48 (0→1)*; 50 (0→1); *59 (0→1)*
†*Sphenocephalus* autapomorphies: *19 (0→1)*; *25 (0→1)*; *65 (0→1)*
Aphredoderus + *Merluccius*: *3 (1→2)*; 7 (0→1); ***9 (0→1)***; 27 (0→1); *36 (0→1)*; 52 (0→1); 53 (0→1); 54 (0→1); 61 (0→1)
Aphredoderus autapomorphies: 1 (2→0); *19 (0→1)*; *65 (0→1)*
Merluccius autapomorphies: 24 (0→1); *25 (0→1)*; 32 (0→1); 38 (2→3); 42 (1→0); 46 (1→0); 47 (1→0); 49 (0→1); 51 (0→1)
Clade A (=Lampridomorpha): 7 (0→1); 8 (0→1); 25 (0→1); **39 (0→1); 40 (0→1); 43 (0→1)**; *58 (0→1)*; 63 (0→1); 64 (0→1)
Clade B: 66 (0→2)
†*Paraipichthys* autapomorphies: none
†*Pycnosteroides* + †*Pharmacichthys* + †"*Aipichthys*" + †*Freigichthys*: 19 (0→1)
†*Pycnosteroides* + †*Pharmacichthys*: 27 (1→0); 35 (0→1); 38 (0→1); 40 (1→2)
†*Pycnosteroides* autapomorphies: 37 (0→1); 39 (1→0); 43 (1→0); 48 (0→1); 59 (0→1); 67 (0→1)
†*Pharmacichthys*: **5 (0→1)**; 8 (1→0); 49 (0→1); 56 (1→0)
†*P. venenifer* autapomorphy: 40 (2→1)
†*P. numismalis* autapomorphy: *14 (1→0)*
†*P. judensis* autapomorphies: none
†"*Aipichthys*" + †*Freigichthys*: 3 (0→1); **13 (0→1); 21 (0→1)**
†*A. oblongus* autapomorphies: none
†*A. minor* autapomorphies: none
†*A. velifer* + †*Freigichthys*: *15 (0→1)*
†*A. velifer* autapomorphies: none
†*Freigichthys* autapomorphy: 66 (2→1)
Clade C: **17 (0→1); 20 (0→1)**
†*Zoqueichthys* autapomorphies: none
Clade D: **6 (0→1)**; 51 (0→1); 54 (0→1)
†*Aipichthyoides* autapomorphies: *15 (0→1)*; **18 (0→1)**; 50 (0→1); *55 (0→1)*; 66 (0→1)
†*Aspesaipichthys* autapomorphies: 26 (1→0); 33 (1→0); *52 (0→1)*; *55 (0→1)*
Lampridiformes: **2 (0→1)**; 3 (0→2); ***4 (0→1)***; 8 (1→0); **12 (0→1)**; 28 (1→2); ***29 (0→1)***; 36 (0→1); 37 (0→1); 38 (0→2); 40 (1→2); *52 (0→1)*; *53 (0→1)*; 61 (0→1)
Metavelifer autapomorphies: 27 (1→0); 51 (1→0)

Lampris + *Trachipterus* + *Regalecus*: 26 (1→0); *32 (0→1)*; 42 (1→0); *46 (1→0)*; *47 (1→0)*; 50 (0→1); **62 (0→1)**
Lampris autapomorphy: 24 (0→1)
Trachipterus + *Regalecus* (= Taeniosomi): **16 (1→0)**; **32 (1→2)**; 34 (0→1); 38 (2→3); **41 (0→1); 44 (0→1); 45 (0→1)**; **58 (1→0)**; 59 (0→1); 66 (0→2)
Trachipterus autapomorphies: *48 (0→1)*; *53 (1→0)*
Regalecus autapomorphies: none