Mesozoic Fishes 5 – Global Diversity and Evolution, G. Arratia, H.-P. Schultze & M. V. H. Wilson (eds.): pp. 385–418, 6 figs., 4 apps.
 – ISBN 978–3–89937–159–8

Limits and relationships of Paracanthopterygii: A molecular framework for evaluating past morphological hypotheses

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Abstract

Gadiforms and percopsiforms have historically been treated as prototypical or core paracanthopterygians. As such, they are the keys to unlocking the evolutionary history and limits of a revised Paracanthopterygii; therefore, we address the taxonomic compositions of gadiforms and percopsiforms and how they are related to each other and other putative basal acanthomorphs. We address these questions by first constructing a phylogenetic hypothesis based on multiple molecular loci. Both maximum likelihood and parsimony criteria strongly support a Paracanthopterygii comprised of Percopsiformes + [Zeiformes + (*Stylephorus* + Gadiformes)]. Polymixiids are sister to this clade. Polymixiids + paracanthopterygians are in turn sister to the acanthopterygians (batrachoidiforms, beryciforms, lophiiforms, ophidioids, percomorphs) in the parsimony analysis but sister to Acanthopterygii + Lampriformes (minus *Stylephorus*) in the likelihood analysis. Published morphological characters, putatively pertinent to paracanthopterygian systematics, were reviewed and evaluated by the direct examination of specimens. Results showed high congruence between the molecular tree and character-state distributions for many of the internal relationships. New interpretations of homologies of published characters are proposed based on topological and phylogenetic data.

Introduction

The superorder Paracanthopterygii (GREENWOOD et al. 1966: 387) was introduced as a diverse spiny-finned fish radiation "more or less comparable morphologically with that of the Acanthopterygii." Composed of their Batrachoidiformes, Gadiformes (including Ophidioidei and Zoarcoidei), Gobiesociformes, Lophiiformes, and Percopsiformes (Amblyopsidae, Aphredoderidae, Percopsidae), GREENWOOD et al. (1966: 352–353) used 27 "characteristic trends" as evidence of this group's common ancestry. They identified the batrachoidiforms, gadiforms, and percopsiforms as primitive members of the assemblage with the potential scenario that the batrachoidiforms and percopsiforms were derived from a "paraberycoid" stock (their quotes) that contributed to a gobiesociform-lophiiform lineage and a gadiform lineage (GREENWOOD et al. 1966: 388). Shortly thereafter, ROSEN & PATTERSON (1969) added polymixioids to the superorder. In the nearly fifty years since the Paracanthopterygii were conceived, various authors have implicitly or explicitly suggested including the Gobiiformes, Indostomidae, Myctophiformes, Stylephoridae, and Zeiformes (ROSEN & PATTERSON 1969; BANISTER 1970; FREIHOFER 1970; WILEY et al. 2000; CHEN et al. 2003; MIYA et al. 2003, 2005; HOLCROFT 2004; SMITH & WHEELER 2006). These proposals have been countered by numerous suggestions that removed all but the percopsiforms at some point or another (e. g., bythitoids to Percomorpha: GOSLINE 1971, MIYA et al. 2005, DETTAÏ & LECOINTRE 2005a,b, SMITH & WHEELER 2006; gobiesocoids, ophidioids, and zoarcoids to Percomorpha incertae sedis: GOSLINE 1971, CHEN et al. 2003, SMITH & WHEELER 2006; batrachoidiforms to Percomorpha: GOSLINE 1971, WILEY et al. 2000, DETTAÏ & LECOINTRE 2005a,b, MIYA et al. 2005, SMITH & WHEELER 2006; lophiiforms to Percomorpha: CHEN et al. 2003, MIYA et al. 2003, HOLCROFT 2004, SMITH & WHEELER 2006; gadiforms to Percomorpha: DETTAÏ & LECOINTRE 2004). PATTERSON & ROSEN (1989: 17) had a slightly different perspective when they stated that gadiforms "are almost exactly analogous to the Paracanthopterygii,"

implying that gadiforms, and their interrelationships and affinities, are the key to unlocking Paracanthopterygii. Concomitant with this extensive reshuffling of membership, the concept of Paracanthopteryii had also shifted from a phyletic assemblage (sensu GREENWOOD et al. 1966) to a nodal concept as the sister group of Acanthopterygii (e.g., ROSEN 1973: fig. 129, PATTERSON & ROSEN 1989: fig. 16).

In a reanalysis of Recent and putative fossil taxa within paracanthopterygians, MURRAY & WILSON (1999) recovered a monophyletic Paracanthopterygii (amblyopsids, aphredoderids, batrachoidiforms, bythitids, gadiforms, lophiiforms, ophidioids, percopsids, and several fossil representatives) but a polyphyletic Percopsiformes (aphredoderids were sister to percopsids, but amblyopsids were sister to the ophidioids plus lophiiforms-batrachoidiforms). A polyphyletic percopsiforms had been posited by ROSEN (1985), who supported an aphredoderid-amblyopsid relationship. Contrary to these results, the only molecular studies to include all percopsiform families (SMITH & WHEELER 2006, DILLMAN et al. 2011) recovered a monophyletic amblyopsid-aphredoderid-percopsid lineage, which was consistent with SPRINGER & JOHNSON (2004) and SPRINGER & ORRELL (2004), based on eight specializations of the dorsal gill arches and their musculature. None of these studies was designed to evaluate sister-group hypotheses of Paracanthopterygii.

Just as the membership of Paracanthopterygii has a storied history, the placement of this assemblage amongst basal acanthomorphs has been understandably as varied. JOHNSON & PATTERSON (1993), in a morphological analysis of Acanthomorpha and applying a nodal-based definition to Paracanthopterygii, noted several caudal-fin resemblances between zeiforms and percopsiforms (e.g., full spines on preural centra 1–2 and a free ural centrum 2 during development). In their study, zeiforms were removed from their traditional percomorph placement and resolved as the sister group of the Euacanthopterygii (i.e., Beryciformes sensu stricto + Percomorpha). Interestingly, GAYET (1980, and also publishing under the surname GAUDANT 1979), had earlier argued for a zeiform-paracanthopterygian alignment. However, a tetraodontiform-zeiform relationship became the popular consensus shortly thereafter (ROSEN 1984), and, thus, her work was largely dismissed (PATTERSON & ROSEN 1989). More recently, WILEY et al. (2000) recovered gadiforms and zeiforms as sister groups in a total-evidence analysis of 27 taxa, analyzing a matrix composed of 38 morphological characters drawn from JOHNSON & PATTERSON (1993) and 1674 base pairs from two ribosomal gene fragments (572 bp from mitochondrial 12S, and 1112 bp of nuclear 28S). Moveover, they recovered this novel clade sister to an "acanthopterygian-like" clade, both collectively the sister group of Percopsiformes. Interestingly, when their data set was partitioned, the analysis of morphology alone (WILEY et al. 2000: fig. 8a [mislabelled in their figure caption]) did not support or reject a gadiform-zeiform relationship; these two groups were in a polytomy that included nearly all their sampled acanthopterygians. Subsequent molecular studies, none of which have focused on addressing paracanthopterygian relationships, have typically supported gadiforms and zeiforms as sister groups (e.g., CHEN et al. 2003; MIYA et al. 2003, 2005; DETTAÏ & LECOINTRE 2005a,b; SPARKS et al. 2005; SMITH & WHEELER 2006; ROA-VARÓN & ORTÍ 2009; but see DETTAÏ & LECOINTRE 2004, MIYA et al. 2007: fig. 3b), but morphological support for this alignment has been elusive and poorly explored.

To complicate paracanthopterygian relationships further, MIYA et al. (2007), in a molecular study examining the results of separate analyses based on whole mitogenomes and a segment of the nuclear gene RAG1, recovered the supposed lampriform *Stylephorus* as sister to the Gadiformes. *Stylephorus* was subsequently placed in a new order, Stylephoriformes. Their Bayesian analysis of mitogenomic data identified a paracanthopterygian lineage consisting of [(Polymixiiformes + Percopsiformes) + ((Gadiformes + Stylephoriformes) + Zeiformes)]. Their Bayesian analysis of RAG1 sequences (MIYA et al. 2007: fig. 3b) recovered a clade composed of [(Stylephoriformes + Gadiformes) + Percopsiformes] that was in a polytomy with Aulopiformes, Myctophiformes, Polymixiiformes, Zeiformes, and (Lampriformes + Acanthopterygii). Morphological evidence of a stylephoriform-gadiform relationship was not explicitly evaluated by MIYA et al. (2007), but the distribution of lampriform synapomorphies in Stylephoriformes was discussed, noting, for example, that only one of four lampriform features (a mesethmoid posterior to the lateral ethmoids) was unambiguously shared with stylephoriforms. The authors noted that comprehensive morphological and molecular surveys of basal acanthomorphs are needed to explore this unique relationship further.

As highlighted above, molecular, morphological, and paleontological studies suggest that our understanding of the relationships among basal acanthomorphs, particularly the traditional paracanthopterygians, are in a tremendous state of flux. No fewer than twenty hypotheses exist for the higher-level relationships of basal acanthomorphs, and, perhaps not surprisingly, there is essentially no consensus of their relationships (partially summarized in LI et al. 2008). Our objectives, herein, are to use a focused molecular study to guide a morphological assessment of existing paracanthopterygian features among

basal acanthomorphs. In this study, we first construct robust phylogenetic hypotheses for the higher level relationships of basal acanthomorphs using a combination of mitochondrial and nuclear genes, and second, we evaluate, through the direct examination of specimens across basal acanthomorphs, previously published paracanthopterygian anatomical features, with emphasis on those suggested at the ordinal level, to assess the degree of morphological support for the molecular hypothesis. The morphological characters are plotted on the phylogeny to clarify their taxonomic distribution and possible evolution.

Materials and methods

Taxon sampling. Family-level sampling of the gadiforms, percopsiforms, and zeiforms was undertaken (Appendix 1) based on the results of ROSEN (1962), GOSLINE (1963), GREENWOOD et al. (1966), ROSEN & PATTERSON (1969), PATTERSON & ROSEN (1989), WILEY et al. (2000), MIYA et al. (2003, 2005, 2007), DETTAÏ & LECOINTRE (2004, 2005a,b, 2008), and ROA-VARÓN & ORTÍ (2009). Representatives of all basal acanthomorph groups (Beryciformes, Gadiformes, Lampriformes, Percopsiformes, Polymixiiformes, Stylephoriformes, and Zeiformes) were included. For more species-rich basal acanthomorph groups, exemplars were selected from the major phylogenetic lineages identified by TYLER et al. (2003, Zeiformes) and ROA-VARÓN & ORTÍ (2009, Gadiformes). Stomiiforms, ateleopodiforms, aulopiforms, myctophiforms, beryciforms, batrachoidiforms, lophiiforms, ophidiiforms, and percomorphs were also included to provide a more general context for interpreting basal acanthomorph and paracanthopterygian inter- and intrarelationships. The sternoptychid *Maurolicus* was designated as the root of the analysis.

Acquisition of nucleotide sequences. Fish tissues were preserved in 70–95 % ethanol prior to extraction of DNA. Nuclear and mitochondrial genes were chosen for their potential to discriminate higher level relationships. DNA was extracted from muscle or fin clips using a DNeasy Tissue Extraction Kit (Qiagen, Valencia, CA). The polymerase chain reaction was used to amplify all gene fragments. Double-stranded amplifications were performed in a 25 µL volume containing one Ready-To-Go PCR bead (GE Healthcare, Piscataway, NJ), 1.25 µL of each primer (10 pmol), and 2–5 µL of undiluted DNA extract. Primers and PCR conditions for novel sequences are listed in Appendix 2 and follow HOLCROFT (2004), SMITH & WHEELER (2004), and LI et al. (2007). For some RAG1 and ENC1 sequences, a nested PCR approach (LI et al. 2007) was used in a second PCR reaction. In these cases, the products of the first-round PCR were diluted 20 to 100 times and used as template for a second PCR with a set of primers nested within the product of the first PCR. The double-stranded amplification products were desalted and concentrated using AMPure (Agencourt Biosciences, Beverly, MA). Both strands of the purified PCR fragments were used as templates and amplified for sequencing using the amplification primers and a Prism Dye Terminator Reaction Kit Version 1.1 (Applied Biosystems, Foster City, CA) with minor modifications to the manufacturer's protocols. The sequencing reactions were cleaned and desalted using cleanSEQ (Agencourt Biosciences, Beverly, MA). The nucleotides were sequenced and the base pairs were called on a 3730 automated DNA sequencer (Applied Biosystems, Foster City, CA). Contigs were built in Sequencher (Gene Codes, Ann Arbor, MI) using DNA sequences from the complementary heavy and light strands. Sequences were edited in Sequencher and Bioedit (HALL 1999) and collated into fasta text files for alignment. The taxonomic terminals analyzed in the present study and GenBank accession numbers corresponding to the gene fragments sequenced (n=152) are listed in Appendix 3.

A total of 4,027 aligned base pairs were analyzed from seven fragments (six amplicons): mitochondrial 12S, tRNA-Val, and 16S and nuclear 28S, histone H3, ENC1, and RAG1. For the analyses, the 152 novel DNA sequences were combined with 187 previously published DNA sequences from the following sources: LÓPEZ et al. (2000, 2004), MIYA et al. (2001, 2003, 2007), CHEN et al. (2003, 2007), ISHIGURU et al. (2003), HOLCROFT (2004), SMITH & WHEELER (2004, 2006), SPARKS & SMITH (2004), SPARKS et al. (2005), LI et al. (2007, 2008), HOLCROFT & WILEY (2008), DeVANEY (2008), ROA-VARÓN & ORTÍ (2009), and DAVIS (2010). A total of 51 amplicons (13 %) could not be successfully sequenced (Appendix 3).

Phylogenetic analyses. Each of the six amplicons was aligned individually in MUSCLE (EDGAR 2004a,b) using default values, adjusted by eye, and then edited and concatenated in Mesquite 2.73 (MADDISON & MADDISON 2011). The molecular dataset is available on Dryad at http://dx.doi.org/10.5061/dryad.k4m8t. The maximum-likelihood dataset was broken into 12 partitions: mitochondrial ribosomal fragment (H1: 12S, tRNA-Val, and 16S), 28S nuclear fragment, RAG 1 insertion [see ROA-VARÓN & ORTÍ (2009)], and nine nuclear partitions corresponding to the first, second, and third position in each of the three protein-coding nuclear genes (histone H3, RAG1, and ENC1). The optimal nucleotide substitution model for each partition was determined empirically (Appendix 4) by comparing different models under an Akaike information criterion as executed in MrModeltest2 v.2.3 (NYLANDER 2004) and PAUP*. The maximum likelihood analysis was conducted in GARLI v2.0 (ZWICKL 2006), and the tree with the best likelihood score from 20 independent analyses was selected as the

prefered hypothesis. A nonparametric maximum-likelihood bootstrap analysis was conducted for 100 random pseudoreplicates to assess nodal support. The parsimony analysis was conducted in NONA (GOLOBOFF 1999) using gaps as a fifth state, and the topology with the fewest steps was used to evaluate evolutionary relationships and anatomical features. The analysis used 1000 replications with different random addition sequences of taxa. Each replication began with an initial Wagner tree followed by TBR (tree bisection and reconnection) branch swapping, keeping up to 10 trees per replication. All saved trees were then submitted to a final round of TBR branch swapping (command sequence: "h/10;rs0;mult*1000;max*;"). To assess nodal confidence, a nonparametric parsimony bootstrap analysis was conducted for 1000 random pseudoreplicates. We treat any resolved nodes in the optimal topologies as resolved (regardless of support), and recognize two levels of nodal support: ≥70 % represents moderate bootstrap support; ≥95 % represents a well-supported node or clade.

Osteological methods and terminology. Juvenile and adult specimens from museum collections were used in this study (Appendix 1); developmental series are not available for the studied taxa. Therefore, hypotheses of homology as presented herein are based on topological relationships among the osteological elements, similarities of their shapes, and intermediate conditions assessed in the framework of the phylogeny (RIEPPEL & KEARNEY 2002). Osteological specimens were cleared and double stained using the procedure of DINGERKUS & UHLER (1977) or using a modified version whereby a potassium hydroxide-alizarin red solution was substituted by an ethanol-alizarin red solution (SPRINGER & JOHNSON 2000). Prepared material was stored in 90 % glycerin. Specimens were examined, dissected, and drawn using a Wild MZ8 dissecting microscope and drawing attachment. Osteological character information published in the literature for gadiforms (ROSEN & PATTERSON 1969, PATTERSON & ROSEN 1989, COHEN 1984, ENDO 2002, WILEY & JOHNSON 2010), zeiforms (TYLER et al. 2003, WILEY & JOHNSON 2010), and percopsiforms (ROSEN 1962, ROSEN & PATTERSON 1969, MURRAY & WILSON 1999) was examined across basal acanthomorphs (Appendix 1).

We followed MONOD's (1968: 648) definition of the parhypural, which included the haemal arch of preural centrum 1 pierced at its base by the haemal canal and a lateral process at its proximal end. In other words, the parhypural of MONOD included both haemal arch and haemal spine. The 'lateral process' of MONOD had earlier been termed by NURSALL (1963) as the hypurapophysis. The hypurapophysis is a posteriorly to dorsoposteriorly directed process of varying shape on the lateral surface of the haemal arch of preural centrum 1. The parhypural may be fused with, articulate with, or detached from preural centrum 1, but, the parhypural is the posteriormost element through which the caudal vein and artery pass before bifurcating (NYBELIN 1963), except when its haemal arch is secondarily absent as discussed below.

An autogenous parhypural can be the result of multiple processes. First, the haemal spine and arch can both be present but simultaneously detached from preural centrum 1, resulting in a parhypural with a distinctly expanded and "blockish" proximal head. We argue that the "block" is due to the presence of the haemal arch. Consequently, a hypuraphysis may be present on a parhypural of this latter form. SCHLUETER & THOMERSON (1971: 333) illustrated this situation (fused spine and arch with a hypurapophysis all detached from preural centrum 1) in *Etheostoma caeruleum*. Alternatively, a very differently shaped parhypural is seen in many specimens examined for this paper, in which the proximal end of the parhypural is strongly tapered (e.g., *Forbesichthys*, *Phycis*, *Zenion*). Obviously, in such cases, a hypuraphophysis is not present and the traditional landmark of the last complete haemal arch through which the caudal artery runs cannot be used.

A variable number of hypural plates are found, all in association with (e.g., fused to, articulating with, or separated from and not connected by cartilage to) the ural centra. Traditional enumeration of autogenous ural centra is from anterior to posterior (diural terminology: ural centra 1 and 2 in the present study). We have retained the the diural terminology as much as possible for ease of comparison with previous work in the Paracanthopterygii (e.g., ROSEN & PATTERSON 1969, MARKLE 1989, FUJITA 1990, ENDO 2002 and TYLER et al. 2003). We acknowledge that the homology of numbered caudal elements may not be the same across all teleosts (SCHULTZE & ARRATIA 1989, ARRATIA & SCHULTZE 1992). However, pending developmental or fossil evidence to the contrary, we hypothesize in this paper that particular caudal elements seen within Paracanthopterygii are homologous throughout the group. For example, a second ural centrum is present in the outgroups including *Polymixia* and, within Paracanthopterygii, it is present (based on topology, similarity, and phylogeny) in percopsiforms, gadiforms, and the fossil †*Sphenocephalus*, and it appears to be present in *Stylephorus*. Therefore, it is more parsimonious to suggest that it is retained although fused with the terminal centrum of zeiforms rather than hypothesizing that it has been lost in these groups. In addition, in the gadiform *Gadella* (FUJITA 1990: fig 138 as *Physiculus*), hypurals 1 and 2 are partially fused to each other while hypurals 3–5 are partially fused to each other and these three are fused to ural centrum 2. Therefore, it is more parsimonious to suggest that these individual elements form two plates (i.e., hypural 1–2 and ural centrum 2 + hypural 3–5) found in other gadiforms.

Myological methods. Striated muscle nomenclature followed WINTERBOTTOM (1974a), in which muscles are identified using their attachment sites. This approach raises the possibility that identified muscles represent positional homologues that may not necessarily be evolutionary homologues.

Character selection. Ordinal level characters proposed by ROSEN & PATTERSON (1969) and PATTERSON & ROSEN (1989) for Paracanthopterygii, COHEN (1984) and ENDO (2002) for gadiforms, TYLER et al. (2003; see also TYLER & SANTINI 2005) for zeiforms, and ROSEN & PATTERSON (1969) and MURRAY & WILSON (1999) for percopsiforms were surveyed. It should be noted that there was considerable overlap and redundancy in characters used in the above studies. For example, MURRAY & WILSON (1999) restated and reanalyzed the characters proposed by PATTERSON & ROSEN (1989) as well as providing new characters. ENDO (2002) analyzed the characters of ROSEN & PATTERSON (1969) and PATTERSON & ROSEN (1989).

Morphological characters were mapped onto a topology based on our molecular likelihood phylogeny (Fig. 1A) using Mesquite V2.75 (MADDISON & MADDISON 2011) to help assess potential synapomorphies. Representative fossil taxa (†*Sphenocephalus*, †*Amphiplaga*, †*Mcconichthys* and †*Tricophanes*) were inserted in the tree according to our conservative assessment of their probable relationships. Relationships among zeiform families were taken from TYLER et al. (2003), while relationships among gadiform families were taken from the most recent comprehensive molecular (nuclear and mitochondrial) study of gadiform internal relationships by ROA-VARÓN & ORTÍ (2009).

Results

Molecular results. Maximum likelihood (Fig. 1A) and parsimony (Fig. 1B) analyses resulted in similar trees (79 % nodes shared) with most relationships outside of Gadiformes resolved and congruent. Of the 14 nodes that disagreed between the two methods, ten of these nodes specified gadiform intrarelationships, one node involved a placement of the Lampriformes at the base of the Acanthomorpha (parsimony) versus a sister-group relationship to [Beryciformes + Percomorpha] (likelihood), one node involved minor rearrangements between *Parazen* and *Zenion* (within Zeiformes), and the final two nodes were minor differences among percomorphs (*Arcos* and *Triacanthodes*). In total, 48 nodes (76 % of nodes) in the parsimony analysis and 41 nodes (65 %) in the likelihood analysis were recovered in more than 70 % of the sampled trees in the bootstrap analysis. Moreover, 34 nodes (54 %) in the parsimony analysis and 28 nodes (44 %) in the likelihood analysis were recovered in more than 95 % of the sampled trees in the bootstrap analyses. Therefore, the majority of deeper nodes in these topologies are well supported, particularly outside of the Gadiformes.

In agreement with MIYA et al. (2007), *Stylephorus* was recovered as the sister taxon to all Gadiformes. The combined clade was recovered as the sister to the Zeiformes, with Percopsiformes recovered as the sister group to [Zeiformes + (*Stylephorus* + Gadiformes)]. This node uniting Percopsiformes, Zeiformes, *Stylephorus*, and Gadiformes was also recovered in several recent studies (e. g., MIYA et al. 2001, 2003; SPARKS et al. 2005). Hereafter, unless specified, Paracanthopterygii are referenced as the lineage consisting of percopsiforms, gadiforms, *Stylephorus*, and zeiforms. Polymixiidae were recovered as the sister group to our paracanthopterygians. Given the instability of the position of polymixiids amongst basal acanthomorphs in this and other studies, we hesitate to include them in our paracanthopterygians.

Some of the recovered intraordinal relationships echoed those of previous studies, both molecular and morphological. Within Percopsiformes, Percopsidae are sister to Amblyopsidae + *Aphredoderus*, and two clades of cavefish [(*Amblyopsis* + *Forbesichthys*)] and [(*Chologaster* + *Speoplatyrhinus*) + *Typhlichthys*] are well supported. Our percopsiform intrarelationships are congruent with SMITH & WHEELER (2006) and DILLMAN et al. (2011). One notable incongruence with TYLER et al. (2003) is the polyphyly of Parazenidae *(Cyttopsis* and *Parazen)*. Our molecular study lacked *Cyttus*, which TYLER et al. (2003) concluded is the basal zeiform, but see HOLCROFT (2004) and MIYA et al. (2007) for a more nested placement of *Cyttus* within Zeiformes. Within Gadiformes, our topologies are not very well supported, consistent with each other, or in particular agreement with previous morphological (e. g., ENDO 2002) or molecular (e. g., ROA-VARÓN & ORTÍ 2009) hypotheses. We note, however, that the Lotidae *(Gaidropsarus* and *Lota)* are paraphyletic relative to *Gadus* in both analyses (also see ROA-VARÓN & ORTÍ 2009), *Bathygadus* and *Macuronus* were resolved as a clade, and *Euclichthys*, *Melanonus*, and *Merluccius* were resolved as a clade (also see ROA-VARÓN & ORTÍ 2009).

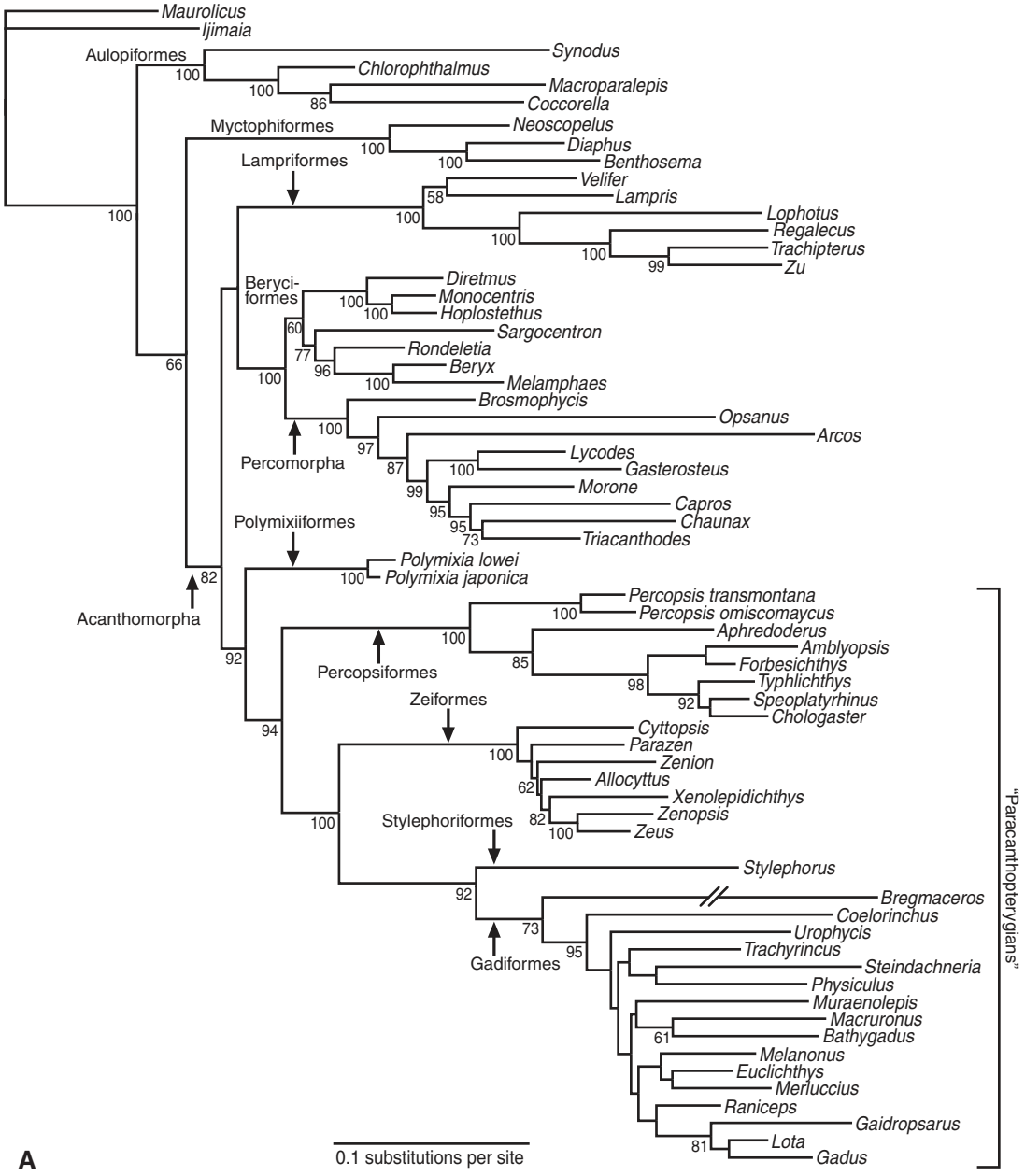
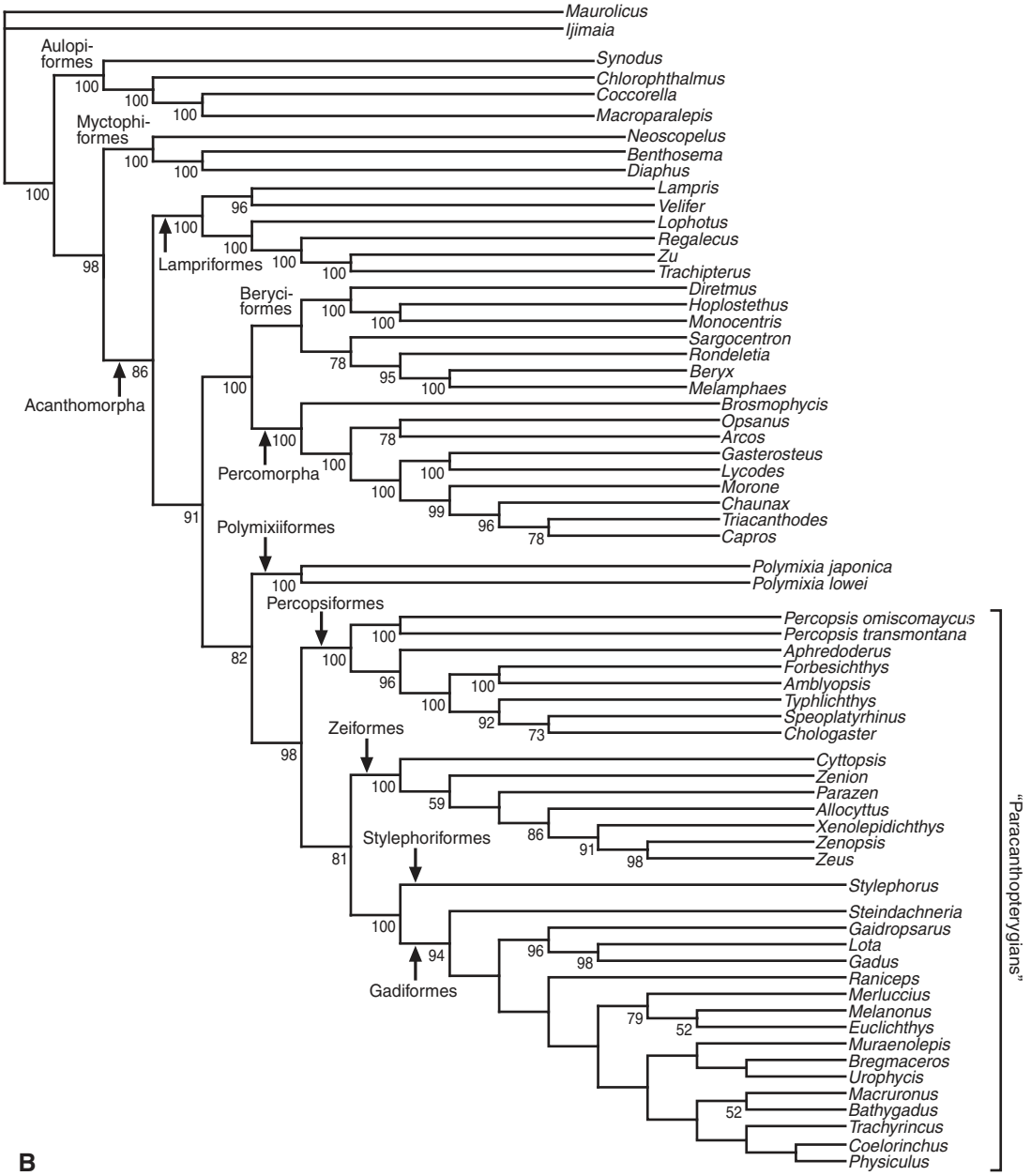


Fig. 1.
Phylogenetic hypotheses of basal euteleosts focusing on putative paracanthopterygian lineages based on nuclear and mitochondrial sequences using (**A**) maximum likelihood and (**B**) maximum parsimony. Sources of sequences are listed in Appendix 3, and parameters of tree construction are provided in Appendix 4 and the text. Trees were rooted using a sternoptychid *(Maurolicus)* and an ateleopodid *(Ijimaia)*. Numbers at nodes indicate bootstrap values greater than 50 %. We include the gadiforms, percopsiforms, stylephoriforms, and zeiforms as paracanthopterygians, but refrain from including polymixiiiforms at this time pending further support. The terminal branch of *Bregmaceros* was shortened for ease of tree presentation.



B

Fig. 1. (continued).

Morphological results. Twenty-six morphological characters proposed from the literature and evaluated by the direct examination of specimens (Appendix 1) were mapped onto a phylogenetic framework (Fig. 2) constructed from GRANDE et al. (this paper), TYLER et al. (2003) and ROA-VARÓN & ORTÍ (2009). Based on these characters, we find morphological support for a paracanthopterygian clade containing [Percopsiformes + ((Gadiformes + *Stylephorus*) + Zeiformes)] along with support for the clade (zeiforms + *Stylephorus* + gadiforms), moderate support for an alternative, percopsiform + gadiform relationship, and modest morphological support for the *Stylephorus* + gadiform clade.

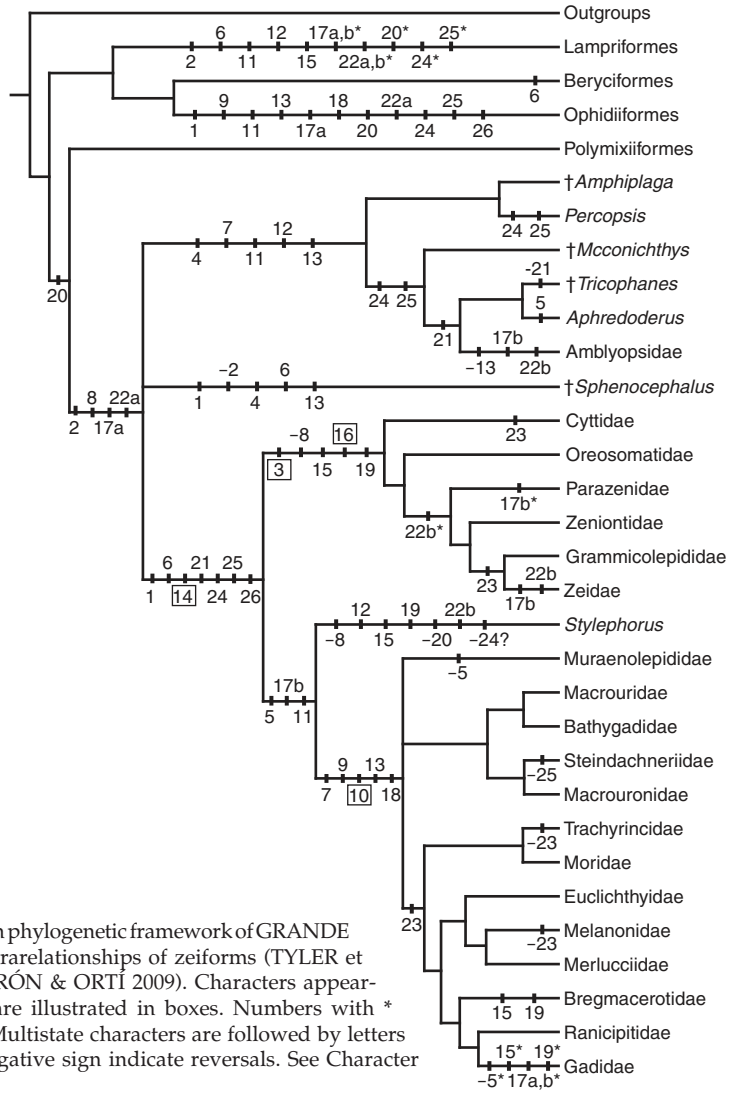


Fig. 2.
Morphological characters mapped on phylogenetic framework of GRANDE et al. (this paper) incorporating intrarelationships of zeiforms (TYLER et al. 2003) and gadiforms (ROA-VARÓN & ORTÍ 2009). Characters appearing only once on the cladogram are illustrated in boxes. Numbers with * indicate polymorphic conditions. Multistate characters are followed by letters a or b. Numbers preceded by a negative sign indicate reversals. See Character descriptions for details.

Characters of the jaws

1. "Gadoid notch": present in Gadiformes, Zeiformes, and †*Sphenocephalus*, convergent with ophidiiforms. A gadoid notch (Fig. 3A,B) is an indentation between the posterior margin of the postmaxillary process and the dorsal margin of the premaxilla. This is in contrast to the usual postmaxillary process (Fig. 3C) with its gently sloping border that typically creates a rounded or triangular outline. Gadiforms display substantial variation in the shape and extent of the notch among lineages and apparently within genera (compare *Merluccius* in MUJIB 1967, ROJO 1976, and INADA 1981 as pointed out by DUNN 1989: 221–222). As a further complication, the notch appears later in development so that juveniles may not possess the notch (e.g., DUNN 1989: figs. 6–7). In the descriptions below, we constrain our comments to non-larval specimens. This notch was observed by ROSEN & PATTERSON (1969) in gadoids (gadiforms minus muraenolepoids and their macrouroids), ophidioids, and †*Sphenocephalus*. It is also present in †*Xenyllion* and was used by MURRAY & WILSON (1999) as a synapomorphy of their Paracanthopterygii (†Sphenocephaliformes + Percopsiformes + Anacanthini), but its loss diagnosed their percopsiforms (i.e.,

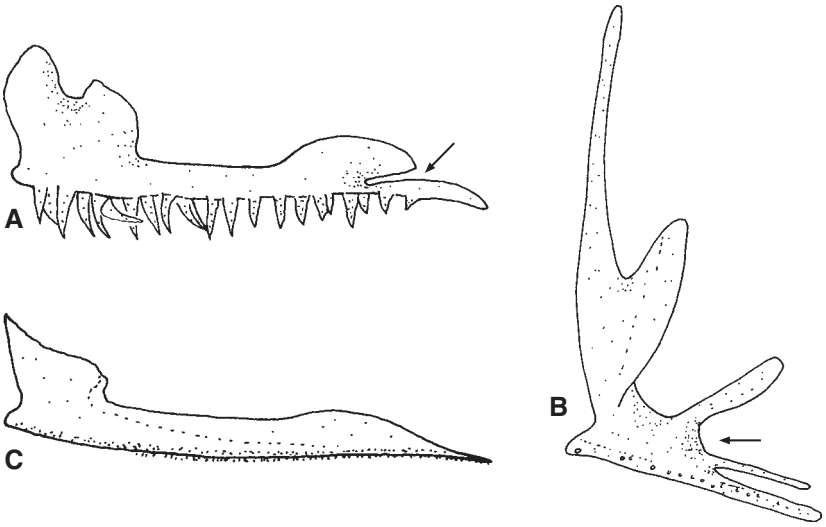


Fig. 3.
Gadoid notch in the postmaxillary process of the premaxilla, as represented by **A,** *Gadus macrocephalus* (KU 15063, 122.3 mm SL); **B,** *Zeus faber* (USNM 307842, dissected specimen); **C,** *Polymixia lowei* (UF 44346, 82.4 mm SL) without gadoid notch. Arrow points to gadoid notch. Anterior to the left.

Apherododeridae, †*Libotonius*, †*Mcconichthys*, and Percopsidae). A "gadoid notch" was observed in all gadiforms (Fig. 3A) (but see DUNN 1989: fig. 6 showing *Theragra* without a notch) and zeiforms (Fig. 2B) examined. We did not observe the notch in any percopsiforms (i. e., *Amblyopsis*, †*Amphiplaga*, *Apherododerus*, †*Erismatopterus*, *Forbesichthys*, †*Lateopisciculus*, †*Libotonius*, †*Massamorichthys*, *Percopsis*, or †*Trichophanes*). A postmaxillary process was present in *Polymixia*, but no gadoid notch was present (Fig. 3C). Beryciforms, lampriforms, and *Stylephorus* have neither a postmaxillary process nor a gadoid notch. A notch was observed in the ophidioids *Ophidion* sp. (USNM 345952) and *Otophidium omostigmum* (UNSM 345961), and thus considered a convergence with the notch in paracanthopterygians. The character is inapplicable in *Stylephorus* because it has lost the postmaxillary process. The uncertain relationship of †*Sphenocephalus* gives rise to two different optimizations. If †*Sphenocephalus* is more closeley related to percopsiforms, the gadoid notch could have appeared two times, once in †*Sphenocephalus* and again in the ancestor of Zeiformes, *Stylephorus* and Gadiformes, or it may have appeared once in Paracanthopterygii and then lost in Percopsiformes. If however, †*Sphenocephalus* is more closely related to Zeiformes, *Stylephorus* and Gadiformes, the notch likely appeared once. In Figure 3, the notch characterizes †*Sphenocephalus* and (zeiforms + *Stylephorus* + gadiforms). The presence of a gadoid notch in †*Sphenocephalus* may indicate a close relationship to zeiforms + *Stylephorus* + gadiforms.

2. Supramaxillae: lost in Paracanthopterygii, convergent with lampriforms. Paired supramaxillae are typically present among basal teleosts (PATTERSON 1964, ARRATIA 1997), although typically absent in osteoglossomorphs, for which a single supramaxilla is found on each side in just a few fossil genera (WILSON & MURRAY 2008). Two supramaxillae are retained in myctophiforms and aulopiforms, including the Cenomanian †*Ctenothrissa* (myctophiform; PATTERSON 1964) and †*Nematonotus* (aulopiform according to FOREY et al. 2003; described in detail by ROSEN & PATTERSON 1969). Among the †Sphenocephaliformes, which have been included within the Paracanthopterygii (ROSEN & PATTERSON 1969, WILSON & MURRAY 1996, MURRAY & WILSON 1999), a slender supramaxilla is found in the two species each of †*Sphenocephalus* and †*Xenyllion* (NEWBREY et al. this volume). *Polymixia* retains two pairs (ROSEN & PATTERSON 1969). A single supramaxilla is found on either side in typical ophidiiforms (ROSEN & PATTERSON 1969). Within our study group, they are absent in gadiforms, percopsiforms, *Stylephorus*, zeiforms, and lampriforms. Their loss is optimised parsimoniously in the ancestor of paracanthopterygians and a convergent loss occurs in lampriforms.

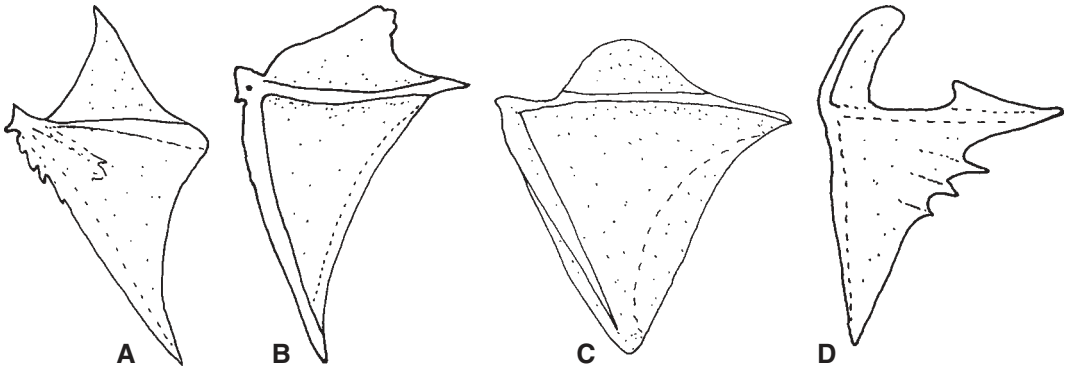


Fig. 4.
Opercular bones of percopsiforms and sphenocephaliforms. **A,** *Percopsis omiscomaycus* (FMNH 63444, 85.5 mm SL); **B,** *Aphredoderus sayanus* (KU 5032, 64.0 mm SL); **C,** †*Mcconichthys longipinnis* (redrawn from GRANDE 1988); **D,** †*Sphenocephalus fissicaudus* (redrawn from ROSEN & PATTERSON 1969). Anterior to the left.

Characters of the suspensorium

3. Size of the metapterygoid: reduced in Zeiformes. In zeiforms, the metapterygoid is reduced in size relative to the ectopterygoid and the entopterygoid. As a result of this reduction, the metapterygoid does not contact the quadrate (TYLER et al. 2003). The metapterygoid is low and broad in *Cyttus* (TYLER et al. 2003: fig. 7), but the metapterygoid is thin and approximately one-fourth the length of the symplectic in *Parazen* and *Zeus*. Of the zeiforms examined here, *Xenolepidichthys* has the largest metapterygoid; however, it is still relatively small, triangular in shape, and does not contact the quadrate. According to JOHNSON & PATTERSON (1993) and TYLER et al. (2003), the metapterygoid is lost in *Macrurocyttus*. In the other taxa examined (i.e., gadiforms, holocentrids, percopsiforms, and *Polymixia*), the metapterygoid is relatively robust and contacts the quadrate. In *Stylephorus,* the metapterygoid does not articulate with the quadrate but all of the pterygoid bones are reduced in size, and the metapterygoid is not any more reduced than the other pterygoid bones. Therefore, the reduction of the metapterygoid is considered diagnostic of zeiforms.

4. Shape of opercle: diamond-shaped in Percopsiformes and †Sphenocephaliformes. The diamond-shaped opercle of percopsiforms is distinctive and not observed in any other extant group examined in this study (Fig. 4). This distinctive opercle was observed in †*Sphenocephalus* (considered by ROSEN & PATTERSON 1969 to be a percopsiform) and †*Xenyllion* (WILSON & MURRAY 1996). In these fossil genera, the opercle has two distinctive regions: a triangular ventral portion positioned below a medial, horizontal ridge that extends posteriorly into a spine, and a large, dorsal extension above this horizontal ridge. It is this dorsal extension that produces the diamond shape characteristic of percopsiforms. In the percopsiforms examined and those illustrated in ROSEN & PATTERSON (1969), GRANDE (1988), MURRAY (1996), and MURRAY & WILSON (1996), the dorsal border is sharply pointed in *Aphredoderus* and *Percopsis* (Fig. 4A,B), but it is smoothly arced in †*Amphiplaga*, †*Erismatopterus*, †*Lateopisciculus*, †*Massamorichthys*, †*Mcconichthys* (Fig. 4C), and †*Trichophanes*. In †*Sphenocephalus* (Fig. 4D) and †*Xenyllion* (MURRAY & WILSON 1996: fig. 4g), the dorsal extension of the opercle is prominent but is interrupted by an oval excavation in its dorsal border. An opercle with a large dorsal extension was not observed in gadiforms, *Polymixia*, zeiforms, or any other fishes examined. This diamond shaped opercle consisting of a dorsal extension above the horizontal spine is considered here to be diagnostic of percopsiforms. Its occurrence also in †sphenocephalids might suggest a relationship between them and percopsiforms.

5. Spatial relationship of the levator arcus palatini to section A2 the adductor mandibulae: lateral position of the levator arcus palatini in Gadiformes (except gaidropsarines, *Muraenolepis*, and *Urophysis*) and *Stylephorus*. The levator arcus palatini, which originates on the skull and inserts on the supsensorium, lies lateral to the dorsal border of section A2 of the adductor mandibulae complex in *Aphredoderus*, *Stylephorus* (Fig. 5A; PIETSCH 1978: fig. 6) and gadiforms (Fig. 5B). In percopsids, amblyopsids, *Polymixia*,

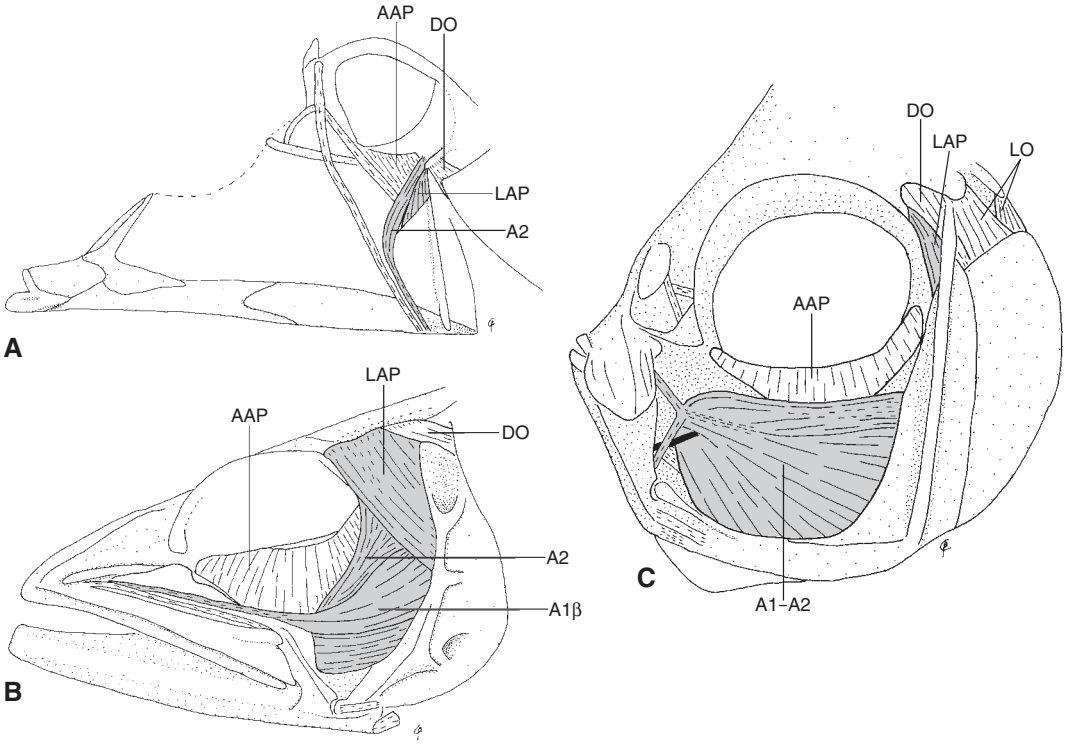


Fig. 5.
Myology of the *adductor mandibulae* in selected paracanthopterygians. **A,** *Stylephorus chordatus* (UF 166415, 189.5 mm SL); **B,** *Merluccius productus* (LACM 56764, 120.0 mm SL); **C,** *Xenolepidichthys dalgleishi* (USNM 377985, 67.2 mm SL). Abbreviations: **A1–A2**, section one of the adductor mandibulae – section two of the adductor mandibulae; **A1β**, beta sub-section of section A1 of the adductor mandibulae; **A2**, section two of the adductor mandibulae muscle; **AAP**, adductor arcus palatini; **DO**, dilatator operculi; **LAP**, levator arcus palatini. Anterior to the left.

and zeiforms (Fig. 5C), the ventral portion of the levator arcus palatini is medial, or does not contact, to the adductor mandibulae complex.

HOWES (1989, 1991, 1993) and ENDO (2002) hypothesized that the lateral position of the levator arcus palatini muscle relative to the adductor mandibulae was a synapomorphy of the gadiforms, rather, the condition appears to have arisen in *Aphredoderus* and the ancestor of gadiforms + *Stylephorus* amongst paracanthopterygians, with reversals in gaidropsarines, *Muraenolepis*, and *Urophysis*, as noted in ENDO (2002). In *Esox*, aulopiforms *(Cocorella*, *Parasudis*, and *Synodus)*, myctophiforms *(Diaphus* and *Neoscopelus)*, lampriforms *(Regalecus*, *Trachipterus*, *Velifer* as figured in WU & SHEN 2004: fig. 9, and *Zu)*, beryciforms, and percomorphs (*Gasterosteus*, *Morone*, and *Triacanthodes* as figured in WINTERBOTTOM 1974b: fig. 49 and WU & SHEN 2004: fig. 25), the ventral portion of the levator arcus palatini is medial to the adductor mandibulae complex. The levator arcus palatini is largely hidden in lateral view by the adductor mandibulae in ophidiiforms *(Lepophidium*, *Ogilbia*, and *Petrotyx)*, but it is only partially hidden in batrachoidiforms *(Porichthys)* and lophiiforms *(Histrio)*.

Known exceptions to the levator arcus palatini lying medial to section A2 are the syngnathids *Hippocampus reidi* and *H. zosterae* (LEYSEN et al. 2011: fig. 1) and *Syngnathus scovelli*. Yet other syngnathid genera (e.g., *Dunckerocampus dactyliophorus* [LEYSEN et al. 2011: fig. 5]) do not exhibit a lateral insertion of the levator arcus palatini, although in this case, it appears not to contact the adductor mandibulae because the levator arcus palatini is posteriorly displaced. Similarly, triacanthodids with elongated snouts (*Halimochirurgus* and *Macrorhamphosodes* as in WINTERBOTTOM 1974b: figs. 60 and 127, fig. 58 respectively) also have the levator arcus palatini and the adductor mandibulae separated by a hiatus.

We conclude that the lateral position of the levator arcus palatini characterizes *Stylephorus* + gadiformes with convergence in *Aphredoderus*.

6. Number of hyomandibular condyles: one in Zeiformes, *Stylephorus*, Gadiformes and †Sphenocephaliformes, two in Percopsiformes, two in *Polymixia*, variable among other outgroups. The hyomandibula forms the upper part of the jaw suspensorium and suspends the jaws to the cranium. Dorsally, the hyomandibula articulates with the otic capsule at the hyomandibular fossa, sphenotic, pterotic and prootic by means of one or two attachment points or condyles. A single hyomandibular condyle was presented by ENDO (2002) as a synapomorphy of Gadiformes, but a single hyomandibular condyle also characterizes all zeiforms examined. Our observations of *Stylephorus* are in agreement with the illustrations in PIETSCH (1978: figs. 3, 4) in that the hyomandibula has a single condyle. A single hyomandibular condyle was reported in †*Sphenocephalus* and †*Xenyllion* (WILSON & MURRAY 1996, NEWBREY et al. this volume). As reported by NEWBREY et al. (this volume), †*Xenyllion* exhibits both gadiform and percopsiform conditions. This condition of a single condyle differs from a hyomandibula with the distinct and often separated condyles seen in *Percopsis*, amblyopsids (e. g., *Amblyopsis*, *Chologaster*, *Forbesichthys*), and *Aphredoderus* (KU 33610, contra ROSEN & PATTERSON 1969: fig. 8). Based on our observations and those of OLNEY et al. (1993), lampriforms have a single hyomandibular condyle, whereas the hyomandibula in *Polymixia* has two condyles. Of the other outgroups, holocentrids have one hyomandibular condyle, but the ophidioids *(Ophidion*, *Otophidium)* have two. Once again the uncertain relationship of †*Sphenocephalus* gives rise to two different optimizations. If †*Sphenocephalus* is more closeley related to percopsiforms, the single condyle could have appeared two times, once in †*Sphenocephalus* and again in the ancestor of Zeiformes, *Stylephorus* and Gadiformes, or it may have appeared once in Paracanthopterygii and then lost in Percopsiformes. If however, †*Sphenocephalus* is more closely related to Zeiformes, *Stylephorus* and Gadiformes, the single condyle likely appeared once in the ancestor of the latter four taxa. In Figure 2, a single hyomandibular condyle characterizes †*Sphenocephalus* and (zeiforms + *Stylephorus* + gadiforms). As with the gadoid notch, the presence of a single hyomandibular condyle in †sphenocephaliforms might support a relationship with the latter clade.

Characters of the skull

7. Size of Intercalar: enlarged in Gadiformes and Percopsiformes. The intercalar (= opisthotic) is a paired membrane bone positioned between the exoccipital and the pterotic that attaches to the ventral arm of the posttemporal via a short ligament. It may overlie bones of the neurocranium or constitute part of the braincase. Its presence is variable, as is the presence of a foramen for the glossopharyngeal nerve (cranial nerve IX; see GILL 1996). In gadiforms, the intercalar is large. In extreme cases, as in *Gadus macrocephalus* (KU 15063), the intercalar extends anteriorly from the basioccipital to the anterior border of the prootic. Medially, the intercalar abuts the parasphenoid. Laterally it attaches to the posttemporal ligament via a robust lateral process. Essentially, the bone covers the ventral floor of the saccular chamber. A similarly large intercalar was observed in *Urophycis floridana* (FMNH 51025). Although most gadiforms examined exhibit the large intercalar (except *Melanonus* as noted in ENDO 2002: 91), the degree of enlargement varies. In *Bathygadus*, *Bregmaceros*, and *Muraenolepis*, the intercalar is approximately two-thirds that of *Gadus* or *Urophycis*. As illustrated in ROSEN & PATTERSON (1969: fig. 50), the fossil gadiform †*Rhinocephalus planiceps* (Eocene, London Clay) exhibits an intercalar comparable in size to that of *Gadus*. While the intercalar is large in most gadiforms, it does not always contain the glossopharyngeal foramen (*Lota* has a foramen at the junction of the intercalar, pterotic, and prootic as noted by MUJIB 1967 and GILL 1996). Percopsiforms also show enlargement of the intercalar; however, as seen in *Amblyopsis spelaea* (ROSEN & PATTERSON 1969: fig. 13; CAS 78143) and *Percopsis*, the intercalar is only about half the size of that in *Gadus*. However, GILL (1996) reported that the intercalar does not possess a glossopharnygeal foramen in some percopsiforms (*Aphredoderus* and *Typhlichthys*: foramen in exoccipital, *Percopsis*: foramen in intercalar or foramen in cartilaginous portion of otic bulla). The zeiforms observed and those reported in TYLER et al. (2003) have a reduced intercalar, approximately half the size as those found in percopsiforms. In *Zenopsis*, for example, the intercalar is a thin, circular, laminar bone positioned over the junction of the exoccipital, prootic, and pterotic; it is not part of the cranial wall. A similar intercalar was observed in *Xenolepidichthys* and *Zenion*. We could not positively identify an intercalar in the cleared and stained lampriforms examined (e. g., *Regalecus glesne* UF 101603, *Zu cristatus* UF 174636) although OLNEY et al. (1993) stated that the intercalar in lampriforms is small and does not contain the glossopharyngeal foramen. We do not

question their observation. It is possible that because the intercalar is so small and delicate in lampriforms, that it is more easily observable in larger specimens. An intercalar is absent in *Stylephorus*, as noted by STARKS (1908: 19) and REGAN (1924: 199). The intercalar present in *Polymixia lowei* is extremely small, and resembles, in this respect, what is observed in holocentrids (FMNH 86945), and what was reported by ROSEN & PATTERSON (1969) for *Aulopus* and *Neoscopelus*. The intercalar is absent in lophiiforms and batrachoidiforms, but GILL (1996 and citations therein) noted that the glossopharyngeal foramen is present in the intercalar in phylogenetically disparate groups such as beryciforms, gobioids, myctophids, and pleuronectiforms. Within our study therefore, the small intercalars in lampriforms, *Polymixia*, and zeiforms and the lack of an intercalar in *Stylephorus* mean that the enlarged intercalars of gadiforms and percopsiforms are optimized as independently derived.

8. Exoccipital facets: widely separated in Gadiformes, Percopsiformes, and †Sphenocephaliformes. ROSEN & PATTERSON (1969) found the exoccipital facets of the occipital condyle to be widely separated from each other and from the basioccipital facet in gadiforms, percopsiforms, and †*Sphenocephalus*. NEWBREY et al. (this volume) found a similar condition in the sphenocephalid †*Xenyllion*. MURRAY & WILSON (1999) used this character to diagnose their Paracanthopterygii (†Sphenocephaliformes + Percopsiformes + Anacanthini). Among the paracanthopterygians examined here, widely separated exoccipital condyles are not found in *Stylephorus* or in zeiforms, where the exoccipital facets are more narrowly spaced. *Polymixia* also exhibits narrowly spaced exoccipital facets. This character can thus be equally optimized in two ways: one origin in the ancestor of Paracanthopterygii with losses in zeiformes and *Stylephorus* as shown in Figure 2, or independently acquired by percopsiforms, gadiforms and †sphenocephalids.

9. Otolith shape: pince-nez-shaped in Gadiformes, convergent with ophidiiforms and batrachoidiforms. According to NOLF & STEURBAUT (1989a), the saccular otoliths of gadiforms are very large and characterized by a "pince-nez-shaped" sacculus. In addition, most gadiforms (with the exception of the phycines; NOLF & STEURBAUT 1989a) exhibit a collicular crest above the ostium-cauda junction of the crista inferior. According to NOLF & STEURBAUT (1989b), aphredoderids and percopsids exhibit a plesiomorphic morphology with respect to gadiforms (see NOLF 1985 for comparative illustrations among *Aphredoderus*, *Percopsis*, and *Raniceps*), but they also concluded that ophidiiform and batrachoidiform otoliths indicated a relationship with gadiforms. Based on our results, we agree with ENDO (2002), who considered "pince-nez-shaped" saccular otoliths to be diagnostic of Gadiformes, and we suggest that similarly shaped otoliths in ophidiiforms and batrachoidiforms are convergent.

Characters of the hyoid arch

10. Basihyal: lost in Gadiformes. The basihyal is absent in gadiforms (ENDO 2002). A basihyal is present and exceptionally enlarged in *Stylephorus* (Starks 1908: plate 4) and a basihyal is present in all other taxa examined in the present study. Although not referring to this character as a synapomorphy, ENDO (2002) used the absence of a basihyal in gadiforms as support for its monophyly. We consider the loss of the basihyal to be a likely synapomorphy of Gadiformes.

11. Beryciform foramen: absent in Gadiformes, *Stylephorus*, and Percopsiformes, convergent in ophidiiforms and lampriforms. A beryciform foramen is an oblong foramen in the dorsal half of the anterior ceratohyal (JOHNSON & PATTERSON 1993: fig. 15) that perforates the groove along which the hyoid artery runs (MCALLISTER 1968: 6). It is sometimes expanded to an excavation along the dorsal margin of the anterior ceratohyal by the partial loss of the dorsal margin. A beryciform foramen is found in a wide variety of teleosts, such as basal clupeomorphs, †ctenothrissiforms, and beryciforms (PATTERSON 1964, MCALLISTER 1968, ROSEN & PATTERSON 1969, GRANDE 1985, MURRAY & WILSON this volume), but the foramen is absent in gadiforms (including †*Rhinocephalus*) and percopsiforms (ROSEN & PATTERSON 1969). The foramen is, however, present in †Sphenocephaliformes (ROSEN & PATTERSON 1969, MURRAY & WILSON 1999, NEWBREY et al. this volume). We have observed a beryciform foramen also in *Polymixia* (see also ZEHREN 1979) and most zeiforms. In the zeiform *Parazen*, the beryciform foramen is represented only by a deep groove (TYLER et al. 2003: fig. 29). TYLER et al. (2003: fig. 46), however, note that an ontogenetic reduction of the beryciform foramen was observed in their specimens of *Zenion hololepis*, resulting in a deep groove along the surface of the ceratohyal. It is therefore possible that the size of the specimen being examined might influence the character state observed in some zeiforms. A beryciform foramen is absent in batrachoidiforms, myctophiforms (ROSEN & PATTERSON 1969), and in our specimens

of *Stylephorus*, the ophidiiform *Ophidion*, and the lampriform *Zu*. To summarize, a beryciform foramen is present in *Polymixia*, †sphenocephaliforms, zeiforms, and some but not all outgroups; the foramen is absent in gadiforms, lampriforms, percopsiforms, and *Stylephorus*. Assuming that the foramen was present in the ancestor of Paracanthopterygii, as indicated by *Polymixia*, the absence of the foramen has likely evolved more than once within our study group, separately in percopsiforms and in gadiforms + *Stylephorus*.

12. Number of branchiostegal rays: reduced in Percopsiformes, *Stylephorus*, convergent with lampriforms. Percopsiforms typically have six or fewer branchiostegals, although MCALLISTER (1968) reported seven in some specimens of *Percopsis*. MURRAY & WILSON (1999) used a reduction in the number of branchiostegal rays to six or fewer to distinguish their percopsiforms (Apheroderidae, †*Libotonius*, †*Mcconichthys*, Percopsidae) and amblyopsiforms from the rest of their Paracanthopterygii. However, *Stylephorus* has five or fewer branchiostegal rays (REGAN 1924: fig. 6). Typically, seven rays are found in gadiforms (MURRAY & WILSON 1996, although MCALLISTER noted rarely as few as five or as many as eight) and zeiforms (some *Macrurocyttus* with six; JOHNSON & PATTERSON 1993, TYLER et al. 2003), seven to nine rays in ophiidiforms (MCALLISTER 1968), usually four to seven rays in perciforms (MCALLISTER 1968), eight rays in most beryciforms/stephanoberyciforms (JOHNSON & PATTERSON 1993, TYLER et al. 2003), typically six rays or fewer (five in *Desmodema polystictum* SIO 76-167) in lampriforms (six or seven in *Lampris*; MCALLISTER 1968), seven or eight in *Polymixia* (eight includes a barbel splint: MCALLISTER 1968, ZEHREN 1979), at least seven rays, but probably eight, in †*Sphenocephalus* (MCALLISTER 1968), six to 11 rays in taxa now included within myctophiforms (MCALLISTER 1968), six rays in batrachoidiforms (MCALLISTER 1968), and typically five to six rays in lophiiforms (rarely four, MCALLISTER 1968). We conclude that, in general, the character is highly variable within basal acanthomorphs, but that the apparent reduction in number of branchiostegal rays to six or fewer in percopsiforms is convergent with the reduction to five or fewer in *Stylephorus*.

13. Percopsoid projection on fourth branchiostegal ray: present in Percopsiformes (with secondary loss in amblyopsids), †*Sphenocephalus*, and Gadiformes, convergent in ophiidiforms. A percopsoid projection, as defined by MCALLISTER (1968: 6), "is an angulation on the anterior base of the fourth branchiostegal." As per MCALLISTER (1968), percopsoid projections are found in percopsiforms (with the exception of amblyopsids), gadiforms, and ophidiiforms. Our observations support those of MCALLISTER (1968). Percopsoid projections were also observed on branchiostegal rays two through four, counting from posterior to anterior, in *Aphredoderus*. The projection on branchiostegal ray four in *Aphredoderus* is very small in comparison to those on rays two and three. In *Percopsis*, the projections were found on branchiostegal rays three though five. Percopsoid projections were absent in *Amblyopsis*, *Forbesichthys*, and *Typhlichthys*. Of the fossil percopsiforms, projections were reported by ROSEN & PATTERSON (1969) on the fourth and fifth branchiostegal rays of †*Trichophanes*, but not in †*Amphiplaga* or †*Erismatopterus*. WILSON (1979) reported that †*Libotonius* has percopsoid projections on some branchiostegal rays, and MURRAY (1996) reported projections on branchiostegal ray six in †*Massamorichthys*. Finally, ROSEN & PATTERSON (1969) reported projections on the posterior four branchiostegal rays in †*Sphenocephalus* and WILSON & MURRAY (1999) and NEWBREY (this volume) reported projections on multiple branchiostegals rays in †*Xenyllion*.

Percopsoid projections were observed on the fourth branchiostegal rays in all gadiforms examined in this study. In *Merluccius*, *Microgadus*, *Muraenolepis*, *Phycis*, and *Urophysis*, the projections are very pronounced and hook like. In *Bregmaceros* and *Gadus*, the projection is small and the condition on the fourth branchiostegal is visibly different from that on the more anterior rays. In *Melanonus*, projections were observed on branchiostegal rays two, three, and four. In *Urophysis*, projections were found on branchiostegal rays three and four. ROSEN & PATTERSON (1969) also reported projections in the fossil gadiform †*Rhinocephalus*. Of the ophidiiforms examined, projections were observed on branchiostegal rays two, three, and four.

Percopsoid projections were not observed in *Stylephorus*, zeiforms, *Polymixia*, myctophiforms, batrachoidiforms, or lophiiforms.

Although percopsoid projections were found on several branchiostegal rays among percopsiforms, gadiforms, and ophiidiforms, a projection was consistently found in those taxa on branchiostegal four. For now, we thus restrict this character to the presence of the percopsoid projection on ray four (sensu MCALLISTER) because of the difficulty in identifying homologous branchiostegal ray elements across all cyclosquamates. The origin of percopsoid projections is ambiguous. One possibility as shown in Figure 2 is that the presence of a percopsoid projection on the fourth branchiostegal ray was convergently acquired by percopsiforms (with secondary loss in amblyopsids) and gadiforms. The presence of the projections also in †*Sphenocephalus* may be explained more parsimoniously if †*Sphenocephalus* is a close relative of percopsi-

forms. A second possibility is that the percopsoid projections on the fourth branchiostegal evolved in the ancestor of paracanthopterygians and were lost by amblyopsids, zeiforms and *Stylephorus*. A convergence with ophidiiforms applies either way.

Characters of the anterior vertebrae

14. Association of first neural arch and spine with neurocranium: present in Gadiformes, *Stylephorus*, and Zeiformes.The first neural arch and spine are tightly bound to the supraoccipital crest in many gadiforms (e. g., *Melanonus, Muraenolepis, Phycis, and Urophycis*) as noted by COHEN (1984). However, the first neural arch and spine do not contact the back of the skull in all gadiforms (e. g., *Bregmaceros*, *Nezumia*, and *Theragra*). In zeiforms, TYLER et al. (2003: 19) used the close proximity of the first neural arch and spine to the exoccipitals as evidence of zeiform monophyly, noting convergent conditions in caproids *(Antigonia* and *Capros)* and at least one tetraodontiform *(Parahollardia)*. We found that the first neural arch and spine contacted the supraoccipital crest in addition to the exoccipital in *Parazen* (FMNH 67158) and *Xenolepidichthys* (USNM 320016). In grammicolepidids *(Macrurocyttus*, *Grammicolepis*, and *Xenolepidichthys)* and *Zenion*, the first neural spine extends dorsally, with the distal tip free of the skull (TYLER et al. 2003: 28). OLNEY et al. (1993: fig. 16) illustrated *Stylephorus* with the first neural spine contacting the neurocranium, although the specific bone was not identified. Our observation of a single specimen of *Stylephorus* (SIO 60-130) indicated that the neural spine could reach dorsally to a weakly developed supraoccipital crest, but the head of this specimen was hyperflexed posteriorly and the distal tip of the neural spine was not adhered to the skull. Lampriforms, except for *Lampris* and veliferids, display an anteriorly arcing first neural spine that, however, does not contact the skull (OLNEY et al. 1993: 158). In all other paracanthopteryians and non-paracanthopterygians examined, the first neural arch and spine do not contact the skull. In summary, the gadiforms, *Stylephorus*, and zeiforms share the potential synapomorphy of an association between the first neural arch and spine and the back of the skull. In most gadiforms and apparently *Stylephorus*, the first arch contacts the supraoccipital crest, while in zeiforms contact is normally with the exoccipitals and sometimes also with the supraoccipital crest.

Characters of the dorsal and anal fins and supraneurals

15. Dorsal and anal fin rays: unbranched in Zeiformes, *Stylephorus*, variable within Gadiformes, convergent with lampriforms. TYLER et al. (2003) used unbranched dorsal and anal fin rays to support zeiform monophyly. We agree with their observation with respect to zeiforms, but have also found unbranched dorsal and anal fin rays in the gadiforms *Bregmaceros, Phycis* and *Urophycis*. Unbranched dorsal and anal fin rays were observed in *Stylephorus* and in the lampriforms *Zu*, *Trachipterus*, and *Regalecus.* Branched dorsal and anal fin rays are present in beryciforms, gadiforms (noting three generic exceptions), percopsiforms, *Polymixia*, and †sphenocephaliforms. Thus, unbranched dorsal and anal fin rays may have evolved up to five times within the study group as illustrated in Figure 2.

16. Contact between first proximal radial of dorsal fin and first neural arch and spine: present in Zeiformes, absent in other taxa examined. In zeiforms (TYLER et al. 2003: fig 74) and lampriforms, the first dorsal fin is anteriorly displaced in comparison to that of the other taxa examined in this study. However, unlike in lampriforms, the first proximal radial of the dorsal fin is enlarged dorsoventrally in zeiforms, so that it contacts the posterior margin of the first neural arch. This condition was not observed in gadiforms, percopsiforms, *Polymixia*, *Stylephorus*, or the outgroups and remains as evidence of zeiform monophyly.

17. Number of supraneurals: reduced to one in Paracanthopterygii convergent with ophidiiforms and some lampriforms, further reduced to zero in amblyopsids, some zeiforms, *Stylephorus*, and some gadids. With the exception of phycines and their single supraneural, gadiforms lack supraneurals. In gadiforms, the first neural spine either abuts the back of the skull or is very close to it and consequently leaves no or little space for supraneurals. In most percopsiforms (e. g., *Percopsis*, †*Trichophanes*) and in †*Sphenocephalus*, one supraneural is present, but the amblyopsids *(Chologaster* and *Forbesichthys)* have none. Among zeiforms, one or zero supraneurals was observed. In some zeiforms *(Parazen*, *Zenopsis*, and *Zeus)*, the first pterygiophore of the dorsal fin is large and extends anteriorly to make contact with the back of the skull. In this configuration, supraneurals are absent. In *Allocyttus* (TYLER et al. 2003), *Cyttopsis*, *Cyttus*, *Stethopristes*, *Xenolepidichthys*, and *Zenion*, the dorsal fin is posteriorly displaced and the first pterygiphore

does not make contact with the back of the skull, allowing for one thin supraneural anterior to the first neural spine. Among lampriforms, *Zu* exhibits a similar condition to *Zenopsis* where no supraneural was observed. A single supraneural was present in *Lampris* (OLNEY et al. 1993: fig. 7). Three supraneurals are present in our material of *Polymixia*; they are wide and taper ventrally to extend between the first four neural spines (one in each interneural space). Three supraneurals were observed in most beryciforms, although two supraneurals were observed in *Holocentrus* (FMNH 86945) and *Hoplostethus* (TYLER et al. 2003). Supraneurals have not been identified in *Stylephorus*, in which the first neural spine is extremely elongated and is positioned close to, but not touching the neurocranium (OLNEY et al. 1993: fig. 16a). If the presence of three supraneurals was primitive for Polymixiiformes + Paracanthopterygii, a reduction to one supraneural is a possible synapomorphy for the Paracanthopterygii, and further reductions to zero occurred convergently in some Percopsiformes (i. e., amblyopsids), some Zeiformes (e. g., some Parazenidae and Zeidae), and the ancestor of *Stylephorus* + Gadiformes (with reversals in phycine gadids).

Characters of the pectoral girdle

18. Scapular foramen: not bounded solely by scapula in Gadiformes, convergent with some lophiiforms and ophidiiforms. A scapular foramen not solely surrounded by the scapula was used by MARKLE (1989: fig. 11) and ENDO (2002) to diagnose Gadiformes, even though it is shared by some lophiiforms. The foramen is completely surrounded by the scapula in batrachoidiforms, beryciforms, myctophiforms, some ophidiiforms according to MARKLE (1989), in most of our examined perciforms, in percopsiforms, *Polymixia*, and *Stylephorus* (STARKS 1908: pl. 5, REGAN 1924: fig. 8). ENDO (2002: 79) noted that variation within the gadiforms included a scapula-coracoid (MARKLE 1989: fig. 11b) and scapula-cartilage (MARKLE 1989: fig. 11c) foramen. The presence of a scapular foramen not bounded solely by the scapula is diagnostic of gadiforms, with convergence in some lophiiforms and ophidiiforms.

19. Pectoral fin rays: unbranched in Zeiformes, *Stylephorus*, and some gadiforms. TYLER et al. (2003) noted unbranched pectoral fin rays in zeiforms. Phycines and *Bregmaceros* are the only gadiforms with unbranched pectoral fin rays. Unbranched pectoral fin rays were also observed in *Stylephorus*. The presence of unbranched pectoral fin rays can be equally optimized in two ways: independent evolution in zeiforms, *Stylephorus*, and some derived gadiforms as illustrated in Figure 2, or evolving in the ancestor of gadiforms, *Stylephorus*, and zeiforms, with subsequent reversals in multiple gadiform lineages.

Characters of the caudal fin

20. Full neural spine on preural centrum 2: present in Paracanthopterygii and *Polymixia*, convergent in ophidiiforms and some lampriforms. PATTERSON & ROSEN (1989) considered the presence of a full spine on the second preural centrum to be diagnostic of their Paracanthopterygii. A brief history of the character is warranted. ROSEN (1973) concluded that a fully developed neural spine on preural centrum 2 was primitive for the euteleosts and possibly teleosts. As ROSEN (1973: 429) noted, the latter was in agreement with GOSLINE (1961), but it was in conflict with PATTERSON (1968). The spine was subsequently reduced in neoteleosts, resulting in a variety of process shapes. So, a full spine in acanthomorphs was interpreted as a reappearance by ROSEN (1973: 504). The ontogeny of how a full spine could have reappeared within acanthomorphs remains elusive, but it demands that subsequent studies critically scrutinize element homology of preural centrum 2 among acanthomorphs, as was done by HILTON & JOHNSON (2007) regarding the number of epurals in carangids. To highlight this point, ROSEN (1985: 44) warned, "investigators would be foolhardy to base major taxonomic judgements upon it [full spine on preural centrum 2] unless we could formulate an argument involving a unique ontogeny that documents the redevelopment of full NPU2".

A full spine on the second preural centrum is present in all paracanthopterygians and polymixiids (Fig. 6A–I; FUJITA 1990), with the exception of *Stylephorus*, which shows extreme caudal skeletal reduction (Fig. 6F; PIETSCH 1978), yet it displays either two (SIO 60-130) or one (UF 177452) small, neural spine on preural centrum 2. Fossil percopsiforms (†*Amphiplaga*: fig. 22, †*Erismatopterus*: fig. 26, †*Trichophanes*: fig. 19; ROSEN & PATTERSON 1969), as well as †*Mcconichthys*, †*Massamorichthys*, and †*Lateopisciculus* (GRANDE 1988: fig. 1; MURRAY 1996: fig. 7; MURRAY & WILSON 1996: fig. 5) and the sphenocephalid

†*Sphenocephalus* (ROSEN & PATTERSON 1969: fig. 35) also possess a full spine on preural centrum 2.

Among the lampriforms, the spine on preural centrum 2 in *Lampris* and *Velifer* is greatly reduced leaving only a "crest" (OLNEY et al. 1993: 144, ROSEN 1973). In *Zu* (UF 174636) and *Radiicephalus* (OLNEY et al. 1993), the spine is reduced to at most half the length of that on preural centrum 3, while in *Trachipterus* and *Desmodem* (FUJITA 1990) the spine appears to be complete. Beryciforms also exhibit an array of spine lengths on preural centrum 2. For example, in *Beryx* and *Holocentrus*, the spine on preural centrum 2 is reduced with only the neural crest remaining, while in *Eutaeniophorus* the spine on preural centrum 2 is elongate (FUJITA 1990). A full spine is absent in aulopiforms and myctophiforms (FUJITA 1990) but present in batrachoidiforms (FUJITA 1990), many perciforms, non-psettodid pleuronectiforms (GILL 1996), and tetraodontiforms (ROSEN 1984). As currently understood and identified across numerous studies, a full spine on preural centrum 2 is a synapomorphy of paracanthopterygians + *Polymixia* (Fig. 6A) (with a reduction of spine length in *Stylephorus*), and is convergently acquired by ophidiiforms, some lampriforms, some perciforms and pleuronectiforms (GILL 1996), and tetraodontiforms (ROSEN 1984).

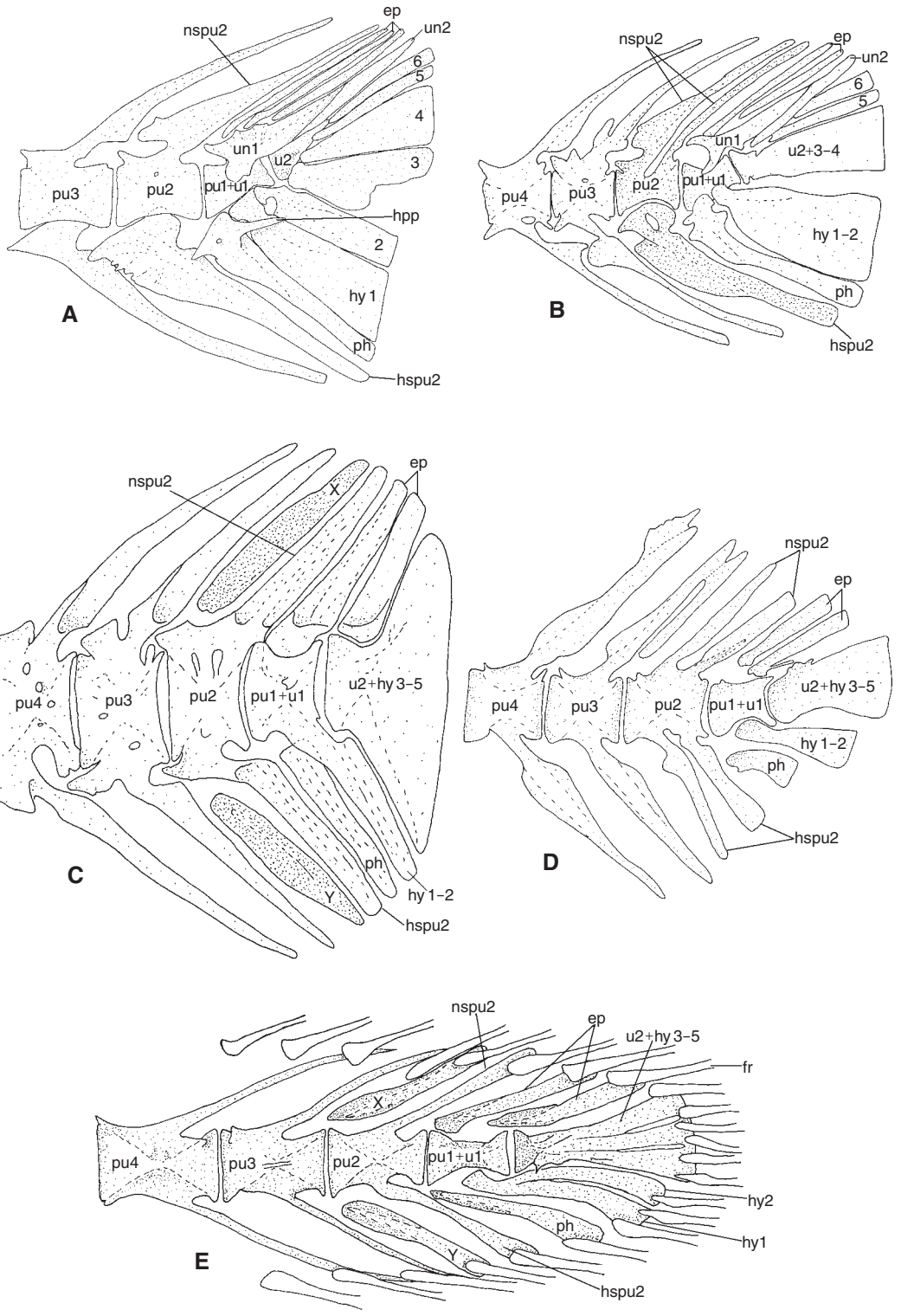
21. Haemal arch of preural centrum 1: lost in Gadiformes, *Stylephorus*, Zeiformes, and some extant Percopsiformes. In gadiforms, *Stylephorus,* some extant percopsiforms *(Amblyopsis*, *Chologaster*, *Forbesichthys*, *Typhlichthys)*, and zeiforms (Fig. 6C–I), the haemal arch of preural centrum 1 is absent. Its absence results in a hiatus between the haemal spine of preural centrum 1 and the centrum. In *Aphredoderus*, the arch is reduced, and both the arch and spine (i. e., parhypural) are separated from the centrum. In *Percopsis* (Fig. 6B) and the fossils †*Amphiplaga*, †*Erismatopterus*, †*Trichophanes* (ROSEN & PATTERSON 1969), †*Lateopisciculus* (MURRAY & WILSON 1996), †*Massamorichthys* (MURRAY 1996), and †*Sphenocephalus* (ROSEN & PATTERSON 1969), the haemal arch articulates with preural centrum 1 + ural centrum 1. In *Polymixia* (Fig. 6A), the haemal arch is present and articulates with preural centrum 1. In beryciforms and lampriforms, the haemal arch of preural centrum 1 makes contact with the centrum directly or through cartilage.

Given the basal position of *Percopsis* within the percopsiforms and the presence of the haemal arch in *Percopsis*, fossil percopsiforms (e. g., †*Amphiplaga*, †*Erismatopterus*, and †*Lateopisciculus,* as well as †*Trichophanes* and †*Massamorichthys*), and in †*Sphenocephalus*, we argue parsimonously that the loss of the arch is not a trait of the ancestor of paracanthopterygians. The loss likely occurred in the ancestor of the (zeiforms + *Stylephorus* + gadiforms) clade with a convergent reduction and subsequent loss in the ancestor of *Aphredoderus* and amblyopsids. The apparent reversal in †*Trichophanes* would be better explained as a primitive state if it were not an aphredoderid. Additional study of its relationships is warranted.

The absence of the hypurapophysis, a process of the haemal arch of the parhypural (NURSALL 1963), was hypothesized (TYLER et al. 2003) to characterize the zeiforms, with reversals in *Cyttominus*, *Cyttus traversi*, *Grammicolepis* (TYLER et al. 2003: 22), *Parazen*, and *Xenolepidichthys*. The hypurapophysis is also absent in gadiforms, percopsiforms (Fig. 6, with the exception of *Percopsis*, FMNH 63459), *Parahollardia* (tetraodontiform, TYLER et al. 2003), *Stylephorus,* and numerous perciforms (FUJITA 1990). It is present in *Polymixia*, many, but not all, myctophiforms (ROSEN & PATTERSON 1969), and lampriforms (e. g., *Lampris*; OLNEY et al. 1993). There is little phylogenetic information in the absence of the hypurapophysis that is not also contained in the absence of the haemal arch (character 21 herein).

22. Number of epurals: reduced in Paracanthopterygii, convergent in ophidiiforms. Paracanthopterygians share a reduction in the number of epurals from three in the outgroups to two. Within Paracanthopterygii, subsequent reduction in epural number occurs in amblyopsids and some zeiforms to one, and independently to none in *Stylephorus* (Fig. 6B–I). Two epurals are present in all gadiforms examined. *Aphredoderus*, *Percopsis* (Fig. 6B), and the fossil percopsiforms have two epurals, while one epural is present in amblyopsids *(Amblyopsis*, *Chologaster*, and *Typhlichthys).* One epural was observed in *Zeus* and *Zenopsis* (Fig. 6G,H) and was reported by TYLER et al. (2003: 17) to occur in *Capromimus*, *Cyttomimus*, *Macrurocyttus*, and *Stethopristes*. Two epurals were observed in *Xenolepidichthys* and *Zenion*, and additionally reported by TYLER et al. in *Allocyttus*, *Cyttopsis*, *Cyttus*, *Grammicolepis*, *Neocyttus*, *Oreosoma*, *Parazen,* and *Pseudocyttus.* TYLER et al. (2003) noted variation in the number of epurals within *Neocyttus,* but the most common condition they observed was one epural (contra TYLER et al. 2003: 17, matrix). Based on their preferred hypothesis, the condition of two epurals was deemed synapomorphic for zeiforms**,** with multiple transformations (TYLER et al. 2003: 22). Epurals are absent in *Stylephorus*. The paracanthopterygian sister group, *Polymixia,* has three epurals (Fig. 6A). One to three epurals have been reported in lampriforms (FUJITA 1990, OLNEY et al. 1993). Three epurals are found in many beryciforms (e. g., *Gibberichthys*, *Hoplostethus*, *Holocentrus*, and *Melamphaes*) and myctophiforms (FUJITA 1990).

PATTERSON & ROSEN (1989), as restated by MURRAY & WILSON (1999), considered the reduction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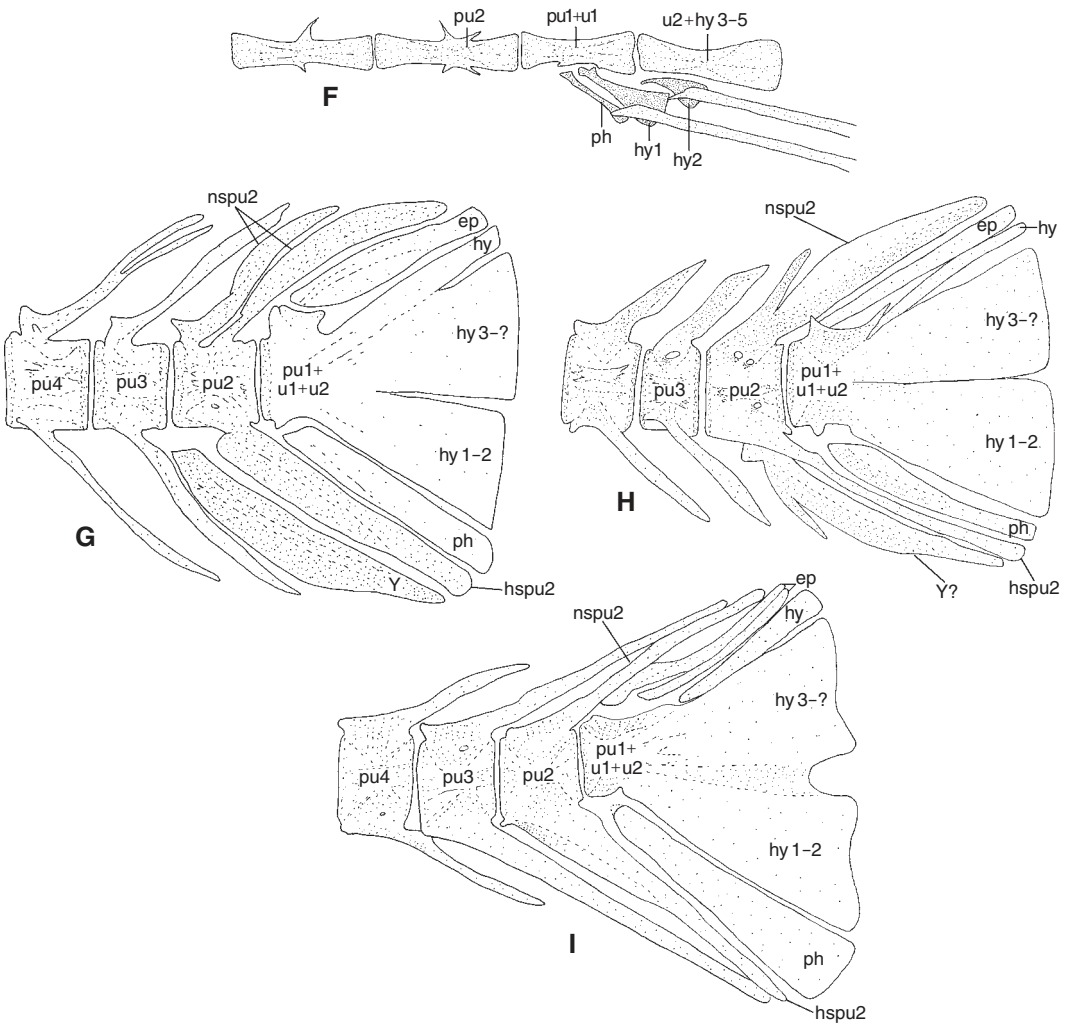

Fig. 6.
Caudal fin osteology of *Polymixia* (sister group to Paracanthopterygii) and selected paracanthopterygians. **A,** *Polymixia nobilis* (FMNH 64695, 104.0 mm SL); **B,** *Percopsis omiscomaycus* (FMNH 63457, 66.0 mm SL); **C,** *Bregmaceros cantori* (KU 30244, 51.0 mm SL); **D,** *Gadus macrocephalus* (KU 15063, 125.0 mm SL); **E,** *Gadella jordani*, modified from FUJITA 1990: fig 138 as *Physiculus*); **F,** *Stylephorus chordatus* (SIO 60-130, tail only); **G,** *Zeus faber* (USNM 307842, 55.0 mm SL); **H,** *Zenopsis conchifer* (USNM 392241, 80.0 mm SL); **I,** *Cyttopsis rosea* (USNM 377980, 97.6 mm SL). Abbreviations: **ep**, epural; **fr**, fin ray; **hpp**, hypurapophysis; **hspu2**, haemal spine on preural centrum 2; **hy**, hypural; **hy1–6**, hypurals 1–6; **hy 1–2**, hypurals 1+2; **nspu2**, neural spine on preural centrum 2; **ph**, parhypural; **pu1–4**, preural centrum 1–4; **pu1+u1**, preural centrum 1+ural centrum 1; **pu1+u1+u2+hy1–2+3–?**, preural centrum 1+ural centra 1+ural centrum 2+hypurals 1+2+3+?; **un1–2**, uroneural 1–2; **u2**, ural centrum 2; **u2+ hy 3–4**; ural centum 2+hypurals 3+4; **u2+hy 3–5**, ural centrum 2+hypurals 3+5; **X**, X bone; **Y**, Y bone. Anterior to the left.

in the number of epurals from three to two to be a synapomorphy of Paracanthopterygii, and we agree that this is the most likely interpretation. Subsequent reduction in epural number to one in amblyopsids is a synapomorphy of amblyopsids as suggested by MURRAY & WILSON (1999). The reduction to one in some zeiforms is convergent as noted by TYLER et al. (2003). The reduction to none in *Stylephorus* is suggested here to be an independent event.

23. Accessory caudal fin elements (X and Y bones): present in many Gadiformes and putatively in some Zeiformes. Elements called X (dorsal portion of caudal fin) and Y (ventral portion of caudal fin) bones are extra ossifications that lie between the neural and the haemal spines, respectively, of preural centra 2 and 3 (Fig. 6C,E). FAHAY & MARKLE (1984) proposed the Continuous Caudal Hypothesis in which X and Y bones, like spines of preural centrum 2, epurals, and the parhypural in fishes, are homologues of proximal pterygiophores of the dorsal and anal fins. Under this scenario, X and Y bones are median fin radials that have lost their fin rays. In contrast, ROSEN & PATTERSON (1969) argued in what MARKLE (1989) later called the Vertebral Subtraction Model, that X and Y bones represent remnants of neural and haemal spines resulting from centrum loss. The presence of X and Y bones has been proposed as a synapomorphy of gadiforms, with a reversal in adult lotines, gadines, and *Melanonus* (FAHAY & MARKLE 1984: table 76). X and Y bones are reported as both present (e.g., FAHAY & MARKLE 1984: 282, ENDO 2002: 93) and absent (e.g., PATTERSON & ROSEN 1989: 13, BALUSHKIN & PRIRODINA 2010) in *Muraenolepis*. We did not observe X and Y bones in our specimens of *Muraenolepis*. As illustrated in Figure 6G–H, autogenous accessory elements that might be Y bones were found in some zeiform taxa (e.g., *Xenolepidichthys*, *Zenopsis*, *Zeus*, and *Cyttus*). Double neural or haemal spines were also found frequently on preural centrum 2 in zeiforms (Fig. 6G). Additionally, some atherinomorphs (adrianichthyoids and *Pseudomugil*, JOHNSON & PATTERSON, 1993: 559) and channids (DAY 1914, MURRAY 2012) also have extra ossifications. In general, centra identified in this study as preural centrum 2 with double neural or haemal spines tend to be larger than preural centrum 3, which has single spines. If a one-to-one relationship between arches, spines, and centra is assumed, a possible explanation for the extra spines on larger centra is that preural centrum 2 is actually a fusion of two centra. We did not observe such accessory bones in any other extant taxa. Given the molecular tree and known taxonomic distribution of X or Y bones, the presence of accessory bones in the caudal fin between preural centra 2 and 3 is likely due to convergence in derived gadiforms and in two groups of zeiforms (in addition to other exceptions mentioned above) as illustrated in Figure 2.

24. Fusion of hypurals one and two: present in extant and some fossil percopsiforms, all gadiforms and zeiforms, but probably not *Stylephorus*, convergent in ophidiiforms and some lampriforms. Fusion of lower hypurals with each other is indicated by the shape of the combined element, its topological relationships, and cases of partial fusion (e.g., *Libotonius*, WILSON 1977: fig. 14e; *Melanonus* and *Mora*, ENDO 2002: fig. 26a,b; *Gadella*, FUJITA 1990). The two lower hypurals are fused with each other in *Percopsis* (Fig. 5B), aphredoderids and amblyopsids. In most gadiforms (Fig. 6C–D) hypurals one and two are completely fused to each other. That the lower hypural plate includes hypurals one and two is evidenced by the diagnostic feature of the gadiform family Moridae (Fig. 6E) where the two lower hypurals are fused proximally but remain separate distally (PAULIN 1983). In some gadiforms (Fig. 6C) the lower hypurals are also fused with the first preural and first ural centra, but in many others they remain separate (Fig. 6D,E).

In all zeiforms examined, the terminal element in the caudal skeleton apparently includes both of the lower hypurals plus the first preural centrum and ural centra one and two (Fig. 6G–I). Upper hypurals are nearly always included as well (see character 25 below). That the first preural centrum is included is indicated by the association with the parhypural, which lacks its haemal arch in this group (see character 21 above). Preural centrum one and ural centrum one are fused in basal acanthomorphs, suggesting that both are included in the zeiform compound element.

In *Stylephorus* (Fig. 6F), hypurals one and two appear to be separate (see discussion below for character 25). Unlike the condition in extant paracanthopterygians, the lower hypurals are unfused in many fossil percopsiforms and in †*Sphenocephalus* (e.g., ROSEN & PATTERSON 1969), in *Polymixia* (Fig. 6A), and in other outgroups such as the aulopiform †*Nematonotus* (ROSEN & PATTERSON 1969) and in myctophiforms (FUJITA 1990). The condition in lampriforms is variable with fusion in some (e.g., *Lampris* OLNEY et al. 1993), but no fusion in others (e.g., *Velifer* ROSEN 1973).

We conclude that fusion of the first two hypurals characterizes extant paracanthopterygians (except *Stylephorus*), but that the unfused condition in fossil percopsiforms and †*Sphenocephalus* raises the possibility as illustrated in Figure 2 that the fusion is convergent in percopsiforms and in the (zeiforms + *Stylephorus* + gadiforms) clade (reversed in *Stylephorus*). In either case, it is convergent in some lampriforms and in ophidiiforms.

25. Fusion of upper hypurals with each other and with ural centrum 2: present in *Percopsis*, aphredoderids, amblyopsids, gadiforms, zeiforms, possibly *Stylephorus*, convergent in ophidiiforms and some lampriforms. Fusion of upper hypurals with ural centrum 2 has been commonly suggested for paracanthopterygians (e.g., ROSEN & PATTERSON 1969, MARKLE 1989, ENDO 2002). Support for this fusion

comes from shape and size of the fused elements, their topological relationships, and cases of partial fusion (e.g., *Libotonius*, WILSON 1977: fig 14e; *Melanonus* and *Mora*, ENDO 2002: fig. 26a,b; *Gadella*, FUJITA 1990). In *Percopsis* (Fig. 6B, FMNH 63457) hypurals 3 and 4 are fused with ural centrum 2, but hypurals 5 and 6 are autogenous. In contrast, ROSEN & PATTERSON (1969) illustrated fused hypurals 3–5 with ural centrum 2 in *Percopsis*. In *Aphredoderus* and the fossil aphredoderid †*Tricophanes*, hypurals 3–5 are fused to each other and ural centrum 2, but hypural 6 remains distinct. In amblyopsids there are no autogenous upper hypurals but it is not clear whether three or four hypurals are fused to ural centrum 2. In all other fossil percopsiforms except possibly †*Mcconichthys*, all hypurals are separate and free from ural centrum 2, as they are in †S*phenocephalus* (ROSEN & PATTERSON 1969, GRANDE 1988).

In gadiforms with caudal fin skeletons, the terminal centrum consists of a fusion of ural centrum 2 + upper hypurals. Evidence that hypurals 3–5 form the upper hypural plate are the examples of partial fusion given above. In *Stylephorus* (Fig. 6F) the shape of the terminal element suggests a similar fusion but the lower hypurals remain unfused.

Zeiforms share a fusion of at least hypurals 1–4 with preural centrum 1 + ural centra 1 and 2 (TYLER et al. 2003). In all zeiforms examined, the fused upper and lower hypurals are either separated distally by a cleft (Fig. 6G,H) or, as seen in *Cyttopsis* (Fig. 6I), by a shallow groove that runs between the upper and lower units. In most zeiforms, the upper-most hypural, which might represent hypural 5 or hypural 6, is autogenous (e.g., *Cyttopsis*, *Zenion*, *Zenopsis*). Exceptions include *Macrurocyttus* (TYLER et al. 2003), *Xenolepidichthys* (e.g., USNM 320016), and *Zeus* (e.g., USNM 307842) where this hypural is completely or partially fused to preural centrum 1 + ural centra 1 and 2. In *Parazen* (TYLER et al. 2003; FMNH 67158), hypurals 3–4 (or 3–5) are fused to each other, but free from the terminal centrum, while hypural 5 (or 6) is autogenous.

In *Polymixia*, aulopiforms (e.g., *Synodus* FMNH 54389), beryciforms (e.g., *Holocentrus* FMNH 86945) and myctophiforms (FUJITA 1990) the upper hypurals remain autogenous. However, in ophidiiforms (FUJITA 1990) and some lampriforms (*Velifer*, ROSEN 1972), the upper hypurals are fused to each other and ural centrum 2. Therefore, fusion of upper hypurals with ural centrum 2 can be optimized in two ways: first, as evolving in the ancestor of all paracanthopterygians with losses in some fossil percopsiforms and †*Sphenocephalus*, and second, as evolving independently in extant clades of percopsiforms and in the ancestor of (zeiforms + *Stylephorus* + gadiforms) as illustrated in Figure 2. Either way, the fusion is convergent with ophidiiforms and some lampriforms.

26. Uroneural 1: not autogenous in gadiforms, *Stylephorus*, zeiforms, convergent in ophidiiforms. Autogenous uroneurals are present in all percopsiforms. Two autogenous uroneurals are present in percopsids (Fig. 6B) and aphredoderids, as well as in †*Sphenocephalus* (ROSEN & PATTERSON 1969). The number of autogenous uroneurals is reduced to one in amblyopsids, in which the uroneural is half the size of that in percopsids. Among gadiforms, and contrary to ROSEN & PATTERSON (1969), we did not observe autogenous uroneurals in any of our specimens, including *Urophycis*. Those authors, however, identified autogenous uroneurals in specimens of *Urophycis* and *Eretmophorus* (ROSEN & PATTERSON 1969: fig. 3c,d). Unfortunately, neither ages nor standard lengths were provided for those specimens. It is therefore possible that during development, autogenous uroneurals become lost or fused with the terminal complex of ural centrum 2 + hypurals 3–5. The examination of detailed developmental material should help to determine if uroneurals are lost or fused to other caudal elements in adult forms. Nevertheless, we argue that autogenous uroneurals are not present in adult gadiforms. In *Stylephorus* (Fig. 6F), autogenous uroneurals are not present. This is not surprising considering the extreme reduction of the caudal skeleton.

In Zeiformes, TYLER et al. (2003) used the absence of uroneurals and thus absence of a stegural as a synapomorphy of the order. We agree with TYLER et al. (2003) that zeiforms do not exhibit autogenus uroneurals. We also consider the condition in zeiforms (Fig. 6G–I) to be very interesting and different from that in gadiforms and *Stylephorus*. As seen in *Zeus* (Fig. 6G), paired dorsal extensions from the terminal centrum are positioned directly below the epural. In *Zenopsis* (Fig. 6H), each extension has a posteriorly projecting process/spine. In *Parazen* (TYLER et al.: fig. 34), the extensions are expanded both dorsoventrally and posteriorly. In *Xenolepidichthys* (TYLER et al.: fig. 69) the extension with dorsal and posterior processes appears to have a margin between it and the main body of the centrum, possibly suggesting a fusion of this element with the terminal centrum. In all zeiform taxa examined, these dorsal extensions, with or without processes, are paired and a space exists between the right and left sides. In some specimens, the proximal end of an epural fits into that space. We therefore hypothesize that, in zeiforms, the uroneural was not lost but incorporated into the terminal centrum. HILTON & JOHNSON (2007) similarly found

through developmental studies that uroneurals became fused to the terminal centrum in the carangids *Caranx* and *Selene*. The resulting structure closely resembles that seen here in zeiforms.

Of the outgroups, *Polymixia* exhibits two uroneurals. Autogenous uroneurals occur also in many other euteleosts, including myctophids (ROSEN & PATTERSON 1969), the lampriforms *Velifer* (ROSEN 1973), *Lampris*, and *Radiicephalus* (OLNEY et al. 1993), and holocentrids (ROSEN 1984). However, autogenous uroneurals are absent in other beryciforms (*Anoplogaster*, *Melamphaes*, TYLER et al. 2003).

In summary, we consider the absence of autogenous uroneurals, mechanism of absence yet to be determined, to be diagnostic of (zeiforms + *Stylephorus* + gadiforms), with a convergence in ophidiiforms.

A stegural process (e. g., ROSEN 1984) is an outgrowth of membrane bone extending anterodorsally from the margin of the first uroneural in many euteleosts. The uroneural with its stegural process is called the stegural by many authors (e. g., ROSEN 1984, ARRATIA & SCHULTZE 1992, LECOINTRE & NELSON 1996), while others restrict the term stegural to the process alone ("stegural process" of ROSEN 1984, TYLER et. al. 2003). We therefore retain the term 'stegural process' for the extension alone. Its presence was used by PATTERSON & ROSEN (1977) and by JOHNSON & PATTERSON (1996) as a synapomorphy of Euteleostei. In zeiforms and *Stylephorus*, autogenous uroneurals, and thus stegural processes, are absent (TYLER et al. 2003) and the same is true for gadiforms based on our material (e. g., *Gadus*, Fig. 6D). Stegural processes are, in contrast, present on the first uroneural of *Percopsis* (Fig. 6B), †*Amphiplaga*, and †*Tricophanes*, but not *Aphredoderus* or most amblyopsids (ROSEN & PATTERSON 1969). This survey of the loss of the stegural process suggests that it contains little information that is not also provided by reduction, loss, or fusion of the first uroneural.

Discussion

The study of Paracanthopterygii has been controversial, and its taxonomic composition has been debated among ichthyologists for many years (see Introduction for history). The inclusion, based on molecular evidence, of *Stylephorus* within Paracanthopterygii as sister to gadiforms (MIYA et al. 2007) for example, had not been tested using morphological data and remained questionable. In addition, the inclusion of zeiforms within Paracanthopterygii based on molecular evidence (WILEY et al. 2000) still needed to be tested with morphology. This study is the first to examine paracanthopterygian limits and relationships within a phylogenetically robust and taxonomically equitable molecular dataset. Further, it provides the first morphological assessment of existing paracanthopterygian characters in light of our revised topology of basal acanthomorphs. Results from this study support a revised clade of paracanthopterygians by both molecular and morphological characters (Figs. 1, 2). Within paracanthopterygians, the monophyly of Percopsiformes, Zeiformes, *Stylephorus* and Gadiformes is supported (Figs. 1, 2) as are their interrelationships: Percopsiformes + [Zeiformes + (Gadiformes + *Stylephorus*)]. Interestingly, many of the morphological characters supporting various clades of Paracanthopterygii are reductive, including the loss of supramaxillary bones, and the reduction of supraneurals and epurals (Fig. 2). Although it is consistently recovered with molecular data (MIYA et al 2007; present study), only weak morphological evidence supports a [*Stylephorus* + Gadiformes] relationship (e. g., lateral position of the levator arcus palatini, absence of a beryciform foramen).

Subject to exceptions and alternate optimisations noted in the text above, the following morphological characters unite major clades in this study (Fig. 2). Paracanthopterygii are united by loss of supramaxillae, widely separated exoccipital facets, supraneurals reduced to one, and epurals reduced to two. The Percopsiformes are united by a diamond-shaped opercle, enlarged intercalar, loss of the beryciform foramen, six or fewer branchiostegal rays, and percopsoid projection on the 4th branchiostegal. The clade consiting of zeiforms + *Stylephorus* + gadiforms is united by a gadoid notch, single hyomandibular condyle, first neural arch and spine associated with neurocranium, loss of the haemal arch of preural centrum 1, fusion of hypurals 1 and 2, fusion of upper hypurals with each other and with ural centrum 2, and lack of an autogenous first uroneural. Zeiformes are united by a reduced metapterygoid, loss of wide separation of exoccipital facets, unbranched dorsal and anal rays, first proximal dorsal radial contacting first neural arch and spine, and unbranched pectoral rays. Gadiformes are united by an enlarged intercalar, a pince-nez-shaped saccular otolith, loss of the basihyal, presence of a percopsoid projection on the 4th branchiostegal, and scapular foramen not bordered only by the scapula.

The molecular phylogeny presented here provided a framework to examine longstanding characters in light of a new set of relationships where, for example, zeiforms are no longer sister to tetraodontiforms,

but to *Stylephorus* plus gadiforms within Paracanthopterygii. As a result, characters once thought exclusive to one particular group are now seen to be more inclusive, changing how we look at the evolution of these characters. One example is the association of the first neural arch and spine with the neurocranium (character 14), once used to diagnose zeiforms, but now reinterpreted as a synapomorphy of zeiforms + *Stylephorus* + gadiforms. Another is the presence of unbranched dorsal, anal and pectoral rays (characters 15 and 19), once thought to be synapomorphies of zeiforms (TYLER et al. 2003), but now seen to be shared with *Stylephorus* and some derived gadiforms. A third example is the complete neural spine on the second preural centrum (character 20), formerly explained by a special scenario (ROSEN & PATTERSON 1969) for the re-attachment of an epural to the second preural neural arch, but now seen to be primitive for Paracanthopterygii.

The study herein focused on the higher interrelationships of basal acanthomorphs to better understand the ordinal composition of Paracanthopterygii. Therefore, subsequent molecular work on paracanthopterygian and basal acanthomorph relationships should increase taxonomic and genetic sampling, particularly within the species-rich Gadiformes that presently have poorly-supported internal relationships. Further morphological work possibly focusing on the caudal skeleton and suspensorium, which have historically been excellent sources of phylogenetic information, should be explored in more detail. Historically important characters used in paracanthopterygian studies (e. g., evolution of accessory elements in the caudal fin skeleton, reduction of cranial elements in *Stylephorus*) would benefit from study of developmental series, which are not currently available. Such evidence would allow more robust tests of character-state homology.

Among the fossil paracanthopterygians examined, the phylogenetic position of †sphenocephalids (i. e., †*Sphenocephalus* and †*Xenyllion*) poses an interesting problem (Fig. 2). †Sphenocephalids share morphological characters with gadiforms (e. g., presence of a gadoid notch, one hyomandibular condyle), percopsiforms (e. g., diamond shaped opercle), and with both gadiforms and percopsiforms (e. g., presence of percopsoid projections on basibranchial 4, widely separated exoccipital facets). MURRAY & WILSON (1999) considered †sphenocephalids to be basal paracanthopterygians, whereas ROSEN & PATTERSON (1969) had considered †*Sphenocephalus* to be a percopsiform. The uncertain placement of †*Sphenocephalus* as either a gadiform, percopsiform or basal paracanthopterygian infuenced character optimization herein (see character descriptions). A better understanding of the morphology and evolutionary placement of †sphenocephalids will no doubt change and improve our understanding of the evolution of morphological characters within Paracanthopterygii in the future.

In summary, the study presented here provides a foundation for future studies of character evolution and of lower-level relationships within the Paracanthopterygii. The Paracanthopterygii are redefined and their limits (i. e., taxa included and taxa excluded) were tested using previously proposed morphological characters. These characters were vetted by means of detailed examinations of reference specimens, both fossil and extant. Additional molecular and morphological studies (e. g., intrarelationships of gadiforms and zeiforms, resolving the phylogenetic placementof †*Sphenocephalus*) will further increase our understand of this important fish group. Moreover, understanding the comparative morphology and phylogeny of the Paracanthopterygii is critical for a better understanding of the evolution of higher teleosts, including the early Late Cretaceous radiation of basal acanthomorphs and their origins within Euteleostei.

Acknowledgements

We thank the following people and their institutions for the loan of specimens or the gift of tissue or DNA extracts for our molecular analysis: A. ROA-VARÓN (Virginia Institure of Marine Sciences); G. ORTÍ (George Washington University, Washington, DC); J. BRUNER and M. V. H. WILSON (Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton); J. MAISEY (American Museum of Natural History, New York); D. CATANIA and T. IWAMOTO (California Academy of Sciences, San Francisco); J. FRIEL (Cornell University, Ithaca); L. PAGE and R. ROBINS (Florida Museum of Natural History, Gainesville); R. FEENEY and C. THACKER (Natural History Museum of Los Angeles County, Los Angeles); A. BENTLEY and E. WILEY (University of Kansas, Biodiversity Institute, Lawrence); K. HARTEL (Museum of Comparative Zoology, Boston); E. HOLM, H. LÓPEZ-FERNÁNDEZ, and R. WINTERBOTTOM (Royal Ontario Museum, Toronto); P. HASTINGS, C. KLEPADO, and H. WALKER (Scripps Institution of Oceanography, Marine Vertebrate Collection, La Jolla); R. MAYDEN (Saint Louis University Collection, Department of Biology, St. Louis); B. KUHAJDA (University of Alabama Ichthyology Collection, Tuscaloosa); J. WILLIAMS (National Museum of Natural History, Smithsonian Institution, Washington DC); K. MASLENIKOV and T. PIETSCH (The University of Washington Fish Collection, School of Aquatic and

Fishery Science, Seattle); and M. PEGG (University of Nebraska-Lincoln, School of Natural Resources). Much of the PCR and sequencing component of this research was conducted in the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution operated with support from the Pritzker Foundation. Many thanks go to S. REDDY (Loyola University Chicago) for allowing us to conduct molecular benchwork in her laboratory. We would like to thank the volume editors, reviewer G. ORTÍ, and an anonymous reviewer for their comments and suggestions. Special thanks go to A. BURDI (Loyola University Chicago) for her assistance with the figures in this manuscript, S. MOCHEL for her curatorial assistance, and L. GRANDE (Field Museum of Natural History, Chicago) for his critical and thoughtful comments on an earlier version of this manuscript. Many thanks go to M. V. H. WILSON (University of Alberta, Edmonton) for his careful editing, comments and help in formatting the text and figures within. The authors thank the National Science Foundation for their financial support, NSF DEB-0732589 to Grande, DEB-0716155, DEB-0732642 and DEB-1060869 to Smith, and DeepFin support (NSF DEB-0443470, PI: Ortí) to Borden.

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Appendix 1

For institutional appreviations we follow LEVITON et al. (1985) with two exceptions: "LUC" is the teaching and research collection in the Department of Biology at Loyola University Chicago, "SNR-UNL" is the teaching and research collection in the School of Natural Resources at the University of Nebraska-Lincoln. Total length (TL, snout to last vertebrae) applies to gadiforms that normally lack a caudal fin as adults. An asterisk denotes best "guess-estimate" standard lengths in damaged or distorted specimens.

Comparative material examined

Aulopiformes

Chlorophthalmidae: *Parasudis truculenta*, 2 spec. (SL: 120.8–137.4): USNM 398652 (alcohol); FMNH 67139 (c&s).
Evermanellidae: *Coccorella atlantica*, 2 spec. (SL: 75.45–146.56* mm): FMNH 79707 (c&s), USNM 398651 (alcohol).
Synodontidae: *Synodus poeyi*, 1 spec. (SL: 93.1 mm): FMNH 64823.

Batrachoidiformes

Batrachoididae: *Porichthys plectrodon*, 1 spec. (SL: 89.9 mm): KU 30140 (alcohol).

Beryciformes

Anoplogastridae: *Anoplogaster cornuta*, 2 spec. (SL: 84.7–84.7 mm): FMNH 66619 (c&s), USNM 206630 (alcohol).
Berycidae: *Centroberyx affinis*, 1 spec. (SL: 127.6 mm): USNM 176776 (alcohol).
Diretmidae: *Diretmus argenteus*, 1 spec. (SL: 82.4 mm): USNM 308026 (alcohol).
Gibberichthyidae: *Gibberichthys* sp. 1 spec. (SL: 43.9 mm): FMNH 65935 (c&s).
Holocentridae: *Holocentrus* sp., 3 spec. (SL: 29.8–41.9 mm): FMNH 86945 (c&s). – *Sargocentron bullisi*, 12 spec. (SL: 13.4–35.4 mm): FMNH 64347 (c&s). *Sargocentron coruscum*, 2 spec. (SL: 86.0–86.2 mm): FMNH 108287 (alcohol, c&s).
Melamphaidae: *Melamphaes lugubris*, 3 spec. (SL: 57.1–116.6 mm): USNM 288411 (alcohol), USNM 288414 (c&s). *Poromitra* sp., 1 spec. (SL: 91.3 mm); KU 28167 (c&s).
Rondeletiidae: *Rondeletia loricata*, 1 spec. (SL: 82.3 mm): USNM 206836 (alcohol).
Stephanoberycidae: *Stephanoberyx monae*, 1 spec. (SL: 57.1 mm) USNM 46124 (alcohol).
Trachichthyidae: *Hoplostethus mediterraneus*, 3 spec. (SL: 48.2–67.8 mm): FMNH 65559 (c&s), USNM 29052 (alcohol).

Esociformes

Esocidae: *Esox americanus*, 1 spec. (SL: 147.1 mm): FMNH 31768 (alcohol). *Esox americanus vermiculatus*, 1 spec. (SL: 113.0 mm): FMNH 7187 (c&s). *Esox lucius*, 1 spec. (SL: 213.9 mm): MCZ 6524 (alcohol).

Gadiformes

[Family names follow ROA-VARÓN & ORTÍ (2009). ENDO (2002) names follow in parentheses when different.]
Bathygadidae (Macrouridae): *Bathygadus cottoides*, 1 spec. (169.0 mm TL): CAS 218391 (alcohol).
Bregmacerotidae: *Bregmaceros cantori*, 1 spec. (SL: 49.5 mm): KU 30244 (c&s). *Bregmaceros* sp. 5 spec. (SL: 68.0–76.6 mm): USNM 398649 (alcohol), USNM 398649 (c&s), USNM 398650 (alcohol).
Gadidae – Gadinae: *Gadiculus argenteus*, 1 spec. (SL: 103.8 mm) LACM 56749 (c&s). *Gadus macrocephalus*, 2 spec. (SL: 120.5–122.3 mm): LACM 33868 (alcohol), KU 15063 (c&s). *Gadus morhua*, 2 spec. (SL: 12.1–103.8): ROM 62449 (c&s), ROM 48371 (alcohol). – *Melanogrammus* sp., 2 spec. (SL: 98.6–129.0 mm): LACM 56756 (c&s). – *Microgadus* sp. 1 spec. (SL: 21.5 mm): UW K72-P-P3/B3-0552-17 (c&s). *Microgadus proximus*, 3 spec. (SL: 56.9–99.4 mm): KU 6825 (alcohol), KU 6825 (c&s), USNM 59475 (c&s). *Microgadus tomcod*, 1 spec. (SL: 115.6 mm): USNM 73480 (alcohol). – *Theragra chalcogramma*, 4 spec. (SL: 74.5–87.8 mm): KU 6829 (alcohol), KU 6829 (c&s), USNM 53893 (alcohol).
Gaidropsarinae: *Gaidropsarus mediterraneus*, 2 spec. (SL: 126.7–180.4 mm): FMNH 71280 (alcohol), FMNH 71280 (c&s).
Lotinae: *Enchelyopus cimbrius*, 1 spec. (SL: 25.5 mm): UW ALB81-14 (c&s). – *Lota lota lacustris*, 3 spec. (SL: 44.8–176.4): FMNH 63458 (alcohol, c&s), LACM 39590 (alcohol).
Phycinae: *Phycis blennoides*, 3 spec. (SL: 120.2–128.1 mm): USNM 232482 (alcohol), USNM 232482 (c&s). *Phycis chesteri*, 2 spec. (SL: 130.5–190.5 mm): LACM 56741 (c&s). *Phycis phycis*, 1 spec. (SL: 80.0 mm): FMNH 69332 (c&s). – *Urophycis cirrata*, 1 spec. (SL: 158.5 mm): LACM 56745 (c&s). *Urophycis earllii*, 1 spec. (SL: 163.4 mm): LACM 56750 (c&s). *Urophycis floridana*, 3 spec. (SL: 109.5–117.4 mm): FMNH 51025 (alcohol, c&s).
Macrouridae: *Coelorinchus carminatus*, 1 spec. (SL: 191.9 mm): FMNH 66027 (alcohol). – *Coryphaenoides striaturus*, 2 spec. (SL: 153.4–183.0 mm): KU 33410 (alcohol), KU 33410 (c&s). – *Hymenocephalus italicus*, 1 spec. (SL: 121.1 mm): FMNH 67837 (c&s). – *Nezumia aequalis*, 4 spec. (SL: 158.7–194.2 mm): FMNH 67788 (alcohol, c&s), KU 27241 (c&s).

Macruronidae: *Macruronus novaezelandiae*, 1 spec. (SL: 437.8 mm): CAS 213332 (alcohol). *Macruronus* sp., 1 spec, (SL: 135.0 mm): LACM 56759 (c&s).
Melanonidae: *Melanonus zugmayeri*, 5 spec. (SL: 64.4–103.2 mm): FMNH 65807 (alcohol, c&s).
Merlucciidae: *Merluccius albidus*, 4 spec. (SL: 120.5–151.8 mm): FMNH 69318 (alcohol, c&s). *Merluccius gayi*, 1 spec. (SL: 173.1 mm): KU 14653 (alcohol). *Merluccius productus*, 1 spec. (SL: 120.0 mm): LACM 56764 (alcohol).
Moridae: *Lotella fernandeziana*, 4 spec. (SL: 108.8–153.2 mm): FMNH 107269 (alcohol, c&s). – *Tripterophycis gilchristi*, 2 spec. (SL: 136.6–166.7 mm): KU 33411 (alcohol), USNM 280753 (c&s).
Muraenolepididae: *Muraenolepis microps*, 2 spec. (SL: 201.4–225.7 mm): USNM 320552 (alcohol, c&s), USNM 371695 (c&s). *Muraenolepis orangiensis*, 1 spec. (SL: 296.9 mm): USNM 380031 (alcohol, c&s). *Muraenolepis* sp., 1 spec. (SL: 136.3 mm): USNM 372261 (alcohol). – *Notomuraenobathys microcephalus*, 1 spec. (SL: 89.2 mm): USNM 371678 (c&s).
Ranicipitidae: *Raniceps raninus*, 1 spec. (SL: 190.0 mm): CAS 22574 (C&S).
Steindachneridae: *Steindachneria argentea*, 5 spec. (TL: 143.1–205.6 mm): FMNH 46476 (alcohol, c&s), FMNH 67856 (c&s).
Trachyrincidae – Macrouroidinae (Macrouridae): *Squalogadus modificatus*, 1 spec. (TL: 321.1* mm): CAS 90618 (alcohol).

Gasterosteiformes
Gasterosteidae: *Gasterosteus aculeatus*, 2 spec. (SL: 53.4–54.9 mm): LUC (alcohol); – *Hippocampus zosterae*, 1 spec. (SL: 36.9* mm): FMNH 80509 (alcohol).
Syngnathidae: *Syngnathus scovelli*, 1 spec. (SL: 121.3 mm): FMNH 83883 (alcohol).

Lampriformes
Regalecidae: *Regalecus glesne*, 2 spec. (TL: 200.0–256.6* mm): UF 101603 (c&s), UF 101603 (alcohol).
Trachipteridae: *Desmodema polystictum*, 1 spec. (SL: 111.5 mm) SIO 76-167 (c&s). – *Trachipterus altivelis*, 2 spec. (SL: 237.6 mm, TL: 184.35* mm): LACM 6937-1 (alcohol), LACM 9887-2 (alcohol). – *Zu cristatus*, 2 spec. (SL: 160.0–213.7 mm): UF 174636 (c&s), UF 112235 (alcohol).

Lophiiformes
Antennariidae: *Histrio histrio*, 1 spec. (SL: 44.8 mm): FMNH 46140 (alcohol).

Myctophiformes
Myctophidae: *Diaphus splendidus*, 1 spec. (SL: 127.6 mm): FMNH 120701 (alcohol).
Neoscopelidae: *Neoscopelus microchir*, 1 spec. (SL: 107.4 mm): FMNH 119741 (alcohol).

Ophidiiformes
Bythitoidei
Bythitidae: *Ogilbia* sp., 1 spec. (SL: 58.7 mm): KU 21552 (alcohol).

Ophidioidei
Ophidiidae: *Lepophidium kallion*, 1 spec. (117.4 mm): UF 211637 (alcohol). – *Petrotyx* sp., 1 spec (160.4 mm): USNM 367977 (alcohol).

Percomorpha
Moronidae: *Morone americana*, 1 spec. (SL: 107.0 mm): SNR-UNL (alcohol); *Morone chrysops*, 1 spec. (SL: 112.7 mm): LUC (alcohol).

Percopsiformes
Amblyopsidae: *Amblyopsis spelaea*, 4 spec. (SL: 60.0–74.2 mm): CAS 78143 (alcohol, dissected c&s), USNM 44435 (alcohol). – *Chologaster cornuta*, 4 spec. (SL: 28.9–39.1 mm): KU 8874 (c&s), USNM 237005 (alcohol). – *Forbesichthys agassizii*, 5 spec. (SL: 31.3–47.6 mm): CU 22608 (alcohol), CU 30975 (alcohol), KU 17526 (alcohol, c&s), KU 17527 (alcohol). – *Typhlichthys subterraneus*, 1 spec. (SL: 40.2 mm): USNM 36806 (alcohol).
Aphredoderidae: *Aphredoderus sayanus*, 9 spec. (SL: 34.5–85.1 mm): KU 2412 (c&s), KU 5032 (alcohol, c&s), KU 33610 (alcohol, c&s), FMNH 78533 (c&s), USNM 84051 (alcohol), USNM 396352 (alcohol). – †*Trichophanes foliarum*, 2 spec. (SL: 70.0–105.9 mm): AMNH 18924, FMNH PF 14311.
Libotoniidae: †*Libotonius pearsoni*, (SL: 15.1–22.2 mm): UALVP 14765a (paratype), UALVP 13466 (holotype).
Percopsidae: *Percopsis omiscomaycus*, 25 spec. (SL: 35.6–115.3 mm): FMNH 63444 (c&s), FMNH 63459 (alcohol, c&s), FMNH 86990 (alcohol, c&s), KU 7949 (alcohol), KU 10476 (alcohol). *Percopsis transmontana*, 2 spec. (SL: 49.10–63.0 mm): USNM 366393 (alcohol). – †*Amphiplaga brachyptera*, 2 spec. (SL: 50.0–73.0 mm) AMNH 19405, FMNH PF 15376. – †*Erismatopterus* sp. 4 spec. (SL: 44.0–73.0 mm): AMNH 110, AMNH 1353, AMNH 3999, AMNH 20367. – †*Massamorichthys wilsoni* (SL: 80.7–140.8 mm): UALVP 30842a&b, 39094 (no caudal fin), 38520a&b. – †*Lateopisciculus turrifumosus* (SL: 24.9–58.5 mm): UALVP 21541, UALVP 34771 (holotype).

Polymixiiformes

Polymixiidae: *Polymixia berndti*, 1 spec. (SL: 81.6 mm): USNM 389346 (c&s). *Polymixia lowei*, 2 spec. (SL: 82.4–107.5 mm): USNM 398653 (alcohol, c&s). *Polymixia nobilis*, 1 spec. (SL: 100.0 mm): FMNH 64695 (c&s).

Stylephoriformes

Stylephoridae: *Stylephorus chordatus*, 6 spec. (SL: 113.4–203.0 mm): UF 165295 (alcohol), UF 166415 (alcohol), UF 177452 (c&s tail only), UF 222883 (c&s, dissected), SIO 60-130 (c&s tail only), SIO 77-171 (c&s).

Zeiformes

[Zeiform classification follows TYLER et al. (2003)].

Cyttidae: *Cyttus australis*, 1 spec. (SL: 99.6 mm): LACM 42620 (alcohol). *Cyttus traversi*, 1 spec. (SL: 100.4 mm): USNM 308020 (alcohol).

Grammicolepididae: *Xenolepidichthys dalgleishi*, 8 spec. (SL: 65.2–83.3 mm): USNM 320016 (c&s), USNM 377985 (alcohol, c&s), USNM 398654 (alcohol).

Oreosomatidae: *Oreosoma atlanticum*, 1 spec. (SL: 112.85 mm): KU 33415 (alcohol).

Parazenidae: *Cyttopsis rosea*, 5 spec. (SL: 73.40*–97.6 mm): FMNH 67091 (c&s), USNM 377980 (alcohol, c&s). – *Parazen pacificus*, 3 spec. (SL: 71.30*–110.7 mm): FMNH 67158 (c&s), USNM 364277 (alcohol). – *Stethopristes eos*, 2 spec. (SL: 105.2, dissected): USNM 226570 (c&s).

Zeidae: *Zenopsis conchifer*, 7 spec. (SL: 70.3–84.7 mm); FMNH 67179 (c&s), USNM 159819 (c&s), USNM 372241 (alcohol, c&s). – *Zeus faber*, 7 spec. (SL: 49.8–79.6 mm): USNM 307842 (c&s), USNM 325986 (alcohol, c&s).

Zeniontidae: *Capromimus abbreviatus*, 1 spec. (SL: 60.4 mm): LACM 11490 (c&s). – *Zenion hololepis*, 7 spec. (SL: 48.3*–86.8 mm): USNM 377986 (alcohol), USNM 377986 (c&s).

Incertae sedis

Asineopidae: †*Asineops squamifrons*, 5 spec. (SL: 51.0–164.1 mm): AMNH 2531 (caudal fin only), AMNH 3992, FMNH PF 9900a&b, FMNH PF 10546a&b, UALVP 17829.

Appendix 2

List of primers, sources and annealing temperatures for the newly obtained sequences used in this study.

Primary annealing

Primer name	Primer sequence	temperature (°C)
tRNA-Val-16S (TITUS 1992, FELLER & HEDGES 1998)		
12SL13-L	5'-TTAGAAGAGGCAAGTCGTAACATGGTA-3'	48°
TitusI-H	5'-GGTGGCTGCTTTTAGGCC-3'	48°
16Sar-br (KOCHER et al. 1989, PALUMBI 1996)		
16Sar-L	5'-CGCCTGTTTATCAAAAACAT-3'	48°
16Sbr-H	5'-CCGGTCTGAACTCAGATCACGT-3'	48°
Histone H3 (COLGAN et al. 1998)		
H3a-L	5'-ATGGCTCGTACCAAGCAGACVGC-3'	48°
H3b-H	5'-ATATCCTTRGGCATRATRGTGAC-3'	48°
28S (HILLIS & DIXON 1991)		
28SV	5'-AAGGTAGCCAAATGCCTCGTCATC-3'	48°
28SJJ	5'-AGGTTAGTTTTACCCTACT-3'	48°
ENC1 (LI et al 2007)		
ENC1_F85	5'-GACATGCTGGAGTTTCAGGA-3'	53°
ENC1_R982	5'-ACTTGTTRGCMACTGGGTCAAA-3'	53°
ENC1_F88	5'-ATGCTGGAGTTTCAGGACAT-3'	62°
ENC1_R975	5'-AGCMACTGGGTCAAACTGCTC-3'	62°
RAG1 (LÓPEZ et al 2004)		
RAG1F1	5'-CTGAGCTGCAGTCAGTACCATAAGATGT-3'	53°
RAG1R1	5'-CTGAGTCCTTGTGAGCTTCCATRAAYTT-3'	53°
RAG1R2	5'-TGAGCCTCCATGAACTTCTGAAGRTAYTT-3'	51°
RAG1R3	5'-GTCTTGTGSAGGTAGTTGGT-3'	51°

Appendix 3

Catalogue numbers for tissue samples and GenBank accession numbers for sequences of six loci used in phylogenetic analyses. Bolded accession numbers indicate sequences newly generated for this study. GenBank accession numbers denoted by * were obtained from congeneric species. The notation N/A refers to amplicons that could not be successfully amplified and/or sequenced.

Terminal taxon	Source	tRNA-Val,12S	16S	28S	H3	RAG1	ENC1	*congener used
Maurolicus muelleri	AMNH Uncat.	**JX121820**	**JX121793**	**JX121769**	**JX121708**	N/A	**JX121736**	
Ijimaia antillarum	KU 5411	**JX121821**	**JX121794**	**JX121770**	**JX121709**	EU366725	**JX121737**	
Synodus variegatus	AMNH Uncat.	DQ533309	DQ532969	DQ533129	DQ533466	EU366720	EU366626	
Chlorophthalmus agassizi	AMNH Uncat	DQ533178	DQ027906	DQ028166	DQ028078	EU366695	EU366600	
Macroparalepis johnfitchi	SIO 94-266	N/A	**JX121795**	**JX121771**	N/A	EU366722	EU366628	
Coccorella atlantica	SIO 02-47	DQ533180	DQ027905	DQ028165	DQ028077	EU366696	EU366601	
Neoscopelus macrolepidotus	KU 3291	DQ533251	DQ532916	DQ533075	DQ533413	EU366727	EU366632	
Benthosema glaciale	AMNH Uncat.	DQ533160	DQ532843	DQ532998	DQ533340	EU366728	N/A	
Diaphus theta	SIO 93-298	**JX121822**	**JX121796**	**JX121772**	N/A	EU477496*	N/A	*D. effulgens
*Polymixia japonic*a	KU 439	DQ533274	DQ532939	DQ533098	DQ533436	AY308765	EU366636	
Polymixia lowei	AMNH Uncat.	AY538862, AY539479	AY538966	AY539071	AY539175	FJ896463	**JX121738**	
Percopsis omiscomaycus	UAIC 11239.05	AY655518	AY655503	AY655695	AY655595	**JX121696**	**JX121739**	
Percopsis transmontana	KU 1893	NC_003168	NC_003168	**JX121773**	**JX121710**	AY308766	**JX121740**	
Aphredoderus sayanus	KU 8756	DQ533156	DQ027910	DQ028169	DQ028082	FJ215201	EU002019	
Amblyopsis spelaea	WC1	**JX121823**	**JX121797**	**JX121774**	**JX121711**	**JX121697**	**JX121741**	
Forbesichthys agassizii	SLUC 261.01	**JX121824**	**JX121798**	**JX121775**	**JX121712**	N/A	N/A	
Typhlichthys subterraneus	KU 8754	**JX121825**	**JX121799**	N/A	**JX121713**	N/A	**JX121742**	
Chologaster cornuta	AMNH Uncat.	DQ533179	DQ532857	DQ533012	DQ533354	**JX121698**	**JX121743**	
Speoplatyrhinus poulsoni	UAIC 11125.01	**JX121826**	**JX121800**	**JX121776**	N/A	N/A	N/A	
Cyttopsis rosea	KU 8315	**JX121827**	**JX121801**	N/A	**JX121714**	N/A	**JX121744**	
Parazen pacificus	FMNH 120892	**JX121828**	NC_004396	N/A	**JX121715**	N/A	**JX121745**	
Zenion sp.	R. Hanel	**JX121829**	NC_004397*	**JX121777**	**JX121716**	N/A	N/A	*Z. japonicum
Allocyttus folletti	SIO 97-120	**JX121830**	**JX121802**	N/A	**JX121717**	AY308781*	N/A	*A. verrucosus
Xenolepidichthys dalgleishi	R. Hanel	DQ533323	DQ532982	DQ533142	DQ533479	N/A	**JX121746**	
Zeus faber	FMNH 119737	DQ533327	DQ027916	DQ028175	DQ028086	FJ215202	EU002038	
Zenopsis conchifer	AMNH Uncat.	**JX121831**	**JX121803**	**JX121778**	**JX121718**	AY308778	**JX121747**	
Stylephorus chordatus	KU 5228	NC_009948	**JX121804**	N/A	N/A	EF094952	**JX121748**	
Bregmaceros pescadorus	FMNH 120873	NC_008124*	**JX121805**	**JX121779**	**JX121719**	N/A	N/A	*B. nectabanus
Coelorinchus scaphopsis	SIO 97-184	**JX121832**	**JX121806**	**JX121780**	**JX121720**	FJ215219*	**JX121749**	*C. kermadecus
Physiculus fulvus	AMNH Uncat.	**JX121833**	**JX121807**	**JX121781**	N/A	FJ215253	N/A	

Trachyrincus murrayi	GO 292	NC_008224	FJ215194	N/A	**JX121721**	FJ215297	**JX121750**	
Steindachneria argentea	KU 4002	**JX121834**	**JX121808**	N/A	N/A	FJ215292	N/A	
Macruronus magellanicus	G. Carvalho	**JX121835**	**JX121809**	**JX121782**	**JX121722**	FJ215259*	N/A	*M. novaezelandiae*
Bathygadus melanobranchus	CAS 224389	**JX121836**	**JX121810**	N/A	**JX121723**	FJ215208	**JX121751**	
Melanonus zugmayeri	R. Hanel	**JX121837**	**JX121811**	**JX121783**	**JX121724**	FJ215264	**JX121752**	
Euclichthys polynemus	GO 34	FJ215135	FJ215136	N/A	N/A	N/A	**JX121753**	
Merluccius productus	SIO Uncat.	DQ533243	DQ532909	DQ533068	DQ533406	FJ215272	N/A	
Muraenolepis microps	R. Hanel	**JX121838**	**JX121812**	**JX121784**	**JX121725**	FJ215277	N/A	
Raniceps raninus	R. Hanel	**JX121839**	**JX121813**	**JX121785**	**JX121726**	FJ215290	**JX121754**	
Urophycis regia	AMNH Uncat.	**JX121840**	**JX121814**	**JX121786**	**JX121727**	FJ215301	N/A	
Gaidropsarus argenteus	GO 167	**JX121841**	**JX121815**	**JX121787**	**JX121728**	FJ215243	N/A	
Lota lota	KU 3772	DQ533233	**JX121816**	DQ028170	DQ028083	FJ215254	**JX121755**	
Gadus morhua	KU 2937	NC_002081	**JX121817**	**JX121788**	**JX121729**	FJ215242	EU002017	
Velifer hypselopterus	R. Hanel	**JX121842**	DQ027907	N/A	DQ028079	EF094949*	EU366633*	*V. multiradiatus*
Lampris guttatus	SIO 01-123	DQ533220	DQ027908	DQ028167	DQ028080	AY308764	N/A	
Lophotus lacepede	KU 6557	**JX121843**	**JX121818**	**JX121789**	**JX121730**	EF094950*	N/A	*L. capellei*
Regalecus glesne	SIO 96-82	DQ533287	DQ532951	DQ533111	DQ533448	EF107625	N/A	
Zu cristatus	KU 5282	NC_003167	NC_003167	**JX121790**	**JX121731**	FJ896462	N/A	
Trachipterus trachypterus	FMNH 121027	**JX121844**	DQ027909	DQ028168	DQ028081	EF094951*	N/A	*T. arcticus*
Diretmus argenteus	KU 8131	**JX121845**	**JX121819**	N/A	**JX121732**	**JX121699**	**JX121756**	
Monocentris japonica	R. Hanel	**JX121846**	NC_004392	**JX121791**	**JX121733**	**JX121700**	**JX121757**	
Hoplostethus mediterraneus	G. Lecointre	AY538864, AY539481	AY538968	AY539073	AY539177	EF095635	**JX121758**	
Sargocentron sp.	AMNH Uncat.	DQ533290	DQ532953	DQ533113	DQ533450	AY308770*	**JX121759**	*S. vexillarium*
Rondeletia loricata	AMS NI198	DQ533288	DQ027917	DQ028176	DQ028087	**JX121701**	**JX121760**	
Beryx splendens	R. Hanel	DQ533161	DQ027918	DQ028177	DQ028088	EF095636	**JX121761**	
Melamphaes lugubris	SIO 93-298	DQ533241	DQ532908	DQ533067	DQ533405	FJ896467*	N/A	*M. suborbitalis*
Brosmophycis marginata	AMNH Uncat.	DQ533164	DQ027914	DQ028173	N/A	**JX121702**	**JX121762**	
Opsanus beta	AMNH Uncat.	DQ533260	DQ532925	DQ533084	DQ533422	**JX121703**	**JX121763**	
Arcos sp.	KU 149	AP004452	AP004452	**JX121792**	**JX121734**	**JX121704**	**JX121764**	
Gasterosteus aculeatus	M. Bell	**JX121847**	DQ027919	DQ028178	**JX121735**	EF033039	N/A	
Lycodes diapterus	SIO 95-02	AY538957, AY539574	AY539062	AY539166	AY539271	**JX121705**	**JX121765**	
Morone saxatilis	AMNH Uncat.	AY538941, AY539558	AY539046	AY539150	AY539255	**JX121706**	**JX121766**	
Capros asper	AMNH Uncat.	DQ533166	DQ532846	DQ533001	DQ533343	EF095638	**JX121767**	
Triacanthodes anomalus	KU 3021	DQ533314	DQ532973	DQ533133	DQ533470	AY308788	EF539259	
Chaunax suttkusi	R. Hanel	DQ533174	DQ532853	DQ533008	DQ533350	**JX121707**	**JX121768**	

Appendix 4

Nucleotide substitution parameters for the sequenced partitions as determined by MrModeltest2 v.2.3 for the maximum likelihood analysis.

Partition		Genome	Substitution model	No. of aligned base pairs
ribosomal 12S/16S		mitochondrial	GTR+I+G	1263
ribosomal 28S		nuclear	GTR+I+G	691
H3	position 1	nuclear	JC+G	333
	position 2		GTR	
	position 3		GTR+G	
ENC1	position 1	nuclear	GTR+G	790
	position 2		GTR+I	
	position 3		GTR+G	
RAG1	position 1	nuclear	GTR+I+G	722
	position 2		GTR+I+G	
	position 3		GTR+G	

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