Mesozoic Fishes 5 – Global Diversity and Evolution, G. Arratia, H.-P. Schultze & M. V. H. Wilson (eds.): pp. 419–455, 14 figs., 2 apps.
 – ISBN 978–3–89937–159–8

Comparative osteology and myology of the caudal fin in the Paracanthopterygii (Teleostei: Acanthomorpha)

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Abstract

There are no fewer than twenty phylogenetic hypotheses of basal acanthomorph relationships. Among basal acanthomorphs, the Paracanthopterygii have historically been one of the more difficult groups to characterize, leaving many systematists to question their composition and monophyly. Here we investigate the osteology and myology of the caudal fin of paracanthopterygians. We describe 26 characters (14 osteological, 12 myological) from Recent and fossil material and evaluated their congruence with a phylogenetic hypothesis [Polymixiiformes (Percopsiformes (Zeiformes (Gadiformes Stylephoriformes)))] derived from the analysis of DNA sequence data. Osteological characters support more basal nodes and nodes within zeiforms and percopsiforms. In contrast, myological characters reflected the unique caudal fin of gadiforms and stylephoriforms. Both types of characters revealed significant homoplasies when mapped onto the existing molecular hypothesis. Nonetheless, osteological homoplasy reflected the recurring trend among teleosts of simplification of the caudal skeleton. Myological homoplasy reflected in part the inclusion of fossil taxa and the unusual, but varied, states within gadiforms. Despite these issues and a general need for increased resolution of relationships within paracanthopterygian lineages, morphology of the caudal fin reasonably supported the revised relationships. Perhaps more importantly, it highlighted the significant work needed to place many fossil lineages accurately and to test hypotheses of homology.

Introduction

Paracanthopterygians are an enigmatic group of fishes with respect to membership and phylogeny. Originally conceived to characterize a more primitive group of bony fishes with near equal morphological diversity to acanthopterygians (GREENWOOD et al. 1966), paracanthopterygians have since been identified as the sister group of Acanthopterygii (e. g., ROSEN 1973, JOHNSON & PATTERSON 1993). The Gadiformes epitomize the group, but despite variable hypotheses identifying the sister group of gadiforms, monophyly of the Paracanthopterygii has proven difficult to demonstrate morphologically.

One contributing factor is that paracanthoptergyian membership has been misled by widespread convergence in morphology with other euteleosts, as recently suggested by molecule-based studies (e. g., WILEY et al. 2000, SMITH & WHEELER 2006, GRANDE et al. this volume). Whereas morphologists anticipated at least some of these novel relationships (e. g., zeiforms and gadiforms by GAYET 1980), it is doubtful morphologists would have forwarded other putative hypotheses (e. g., *Stylephorus* and gadiforms as sister groups by MIYA et al. 2007). In an earlier paper (GRANDE et al. this volume), we capitalized on a particular strength of molecular systematics, namely the ability to simultaneously analyze taxa traditionally aligned with paracanthopterygians (e. g., gadiforms, percopsiforms, lophiforms), novel putative members (e. g., *Stylephorus*, zeiforms), and basal acanthomorphs (e. g., lampriforms, polymixiiforms, beryciforms).

The teleostean caudal skeleton is a well-studied character complex with respect to function (e. g., LAUDER 1989), homology (e. g., POTTHOFF 1975, SCHULTZE & ARRATIA 1989, ARRATIA & SCHULTZE 1992), and phylogenetic signal (e. g., HOLLISTER 1936; GOSLINE 1961a; MONOD 1968; ARRATIA 1991, 1997; FUJITA 1990). More recently, developmental studies have led to re-interpretation of adult features

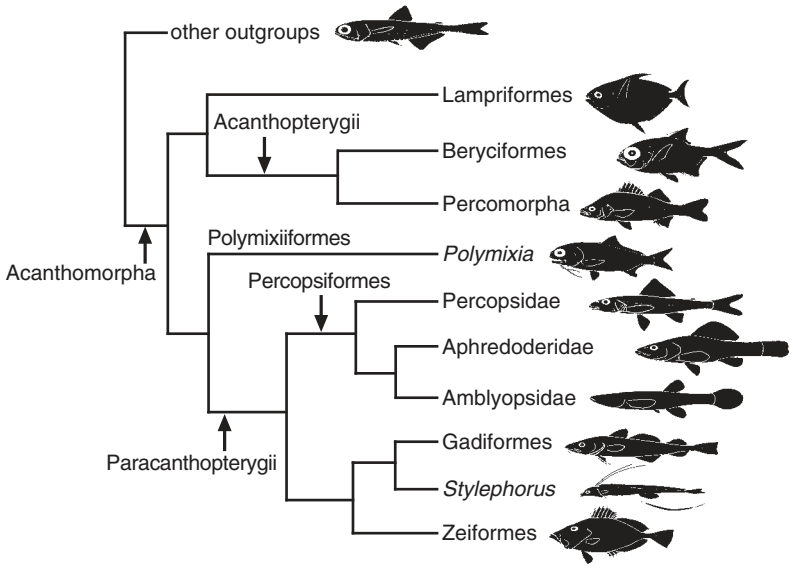

Fig. 1.
Simplified phylogenetic hypothesis of major paracanthopterygian clades based on nuclear and mitochondrial sequences and the maximum likelihood criterion (GRANDE et al. this volume). Fish silhouettes modified after NELSON (2006).

(KONSTANTINIDIS & JOHNSON 2012), revised assessments of homology (HILTON & JOHNSON 2007), and new evolutionary scenarios (GRÜNBAUM & CLOUTIER 2010) for some groups of teleosts. With respect to paracanthopterygians, caudal-fin anatomy has been applied to phylogenetic queries at the superordinal level (e.g., ROSEN & PATTERSON 1969, PATTERSON & ROSEN 1989, MURRAY & WILSON 1999) and within gadiforms (ENDO 2002) and zeiforms (TYLER et al. 2003). However, the interpretation of character state evolution and subsequent inferences of relationships relied on outgroup and ingroup constructions that differ from molecule-based hypotheses. Herein, we accept the revised membership and higher-level relationships of the Paracanthopterygii (Fig. 1) in order to interpret variation in the bones and muscles of the adult caudal fin.

Diversity of Paracanthopterygii

Readers should consult GRANDE et al. (this volume) for a review of earlier ideas about paracanthopterygian relationships, but the Paracanthopterygii as presently understood include four orders: Gadiformes, Percopsiformes, Stylephoriformes, and Zeiformes.

Percopsiformes contain three extant families, all of them restricted to freshwater habitats in North America. The Percopsidae (trout-perches), contain a single genus *Percopsis* with two species; the Aphredoderidae (pirate perches) contain the monotypic *Aphredoderus*; the Amblyopsidae (cavefishes) contain five genera *(Amblyopsis*, *Chologaster*, *Forbesichthys*, *Speoplatyrhinus*, and *Typhlichthys)* and six species. However, fossil percopsiforms are numerous, all from freshwater deposits in North America, and can be categorized as probable percopsids or probable aphredoderids. No fossil amblyopsids have been identified to date. Fossil percopsids include †*Amphiplaga* (Eocene, Wyoming), †*Erismatopterus* (Eocene, Wyoming), †*Lateopisciculus* (Paleocene, Alberta), and †*Massamorichthys* (Paleocene, Alberta). †*Libotonius* (Eocene), sometimes classified in the separate family †Libotoniidae, was recovered in a trichotomy with Aphredoderidae and Percopsidae by MURRAY & WILSON (1999) and is considered as a percopsid herein. †*Libotonius* has two species, †*Libotonius blakeburnensis* from British Columbia (WILSON 1977) and †*Libotonius pearsoni* from Washington State (WILSON 1979). The two species are similar anatomically but distinguishable by the number of precaudal and caudal vertebrae (WILSON 1977, 1979) and by the number of epurals (this study). †*Trichophanes* (late Eocene, Colorado) is recognized as an aphredoderid (ROSEN & PATTERSON 1969,

MURRAY & WILSON 1999), and we strongly suspect that †*Mcconichthys* GRANDE, 1988, the earliest (early Paleocene) paracanthopterygian from North America (Montana), is more closely related to aphredoderids than it is to percopsids. Known from only the holotype, this freshwater fish was originally placed in a trichotomy with lophiiforms-batrachoidiforms and gadiforms (GRANDE 1988).

The Gadiformes (cods, codlets, hakes, and grenadiers) are predominantly marine fishes and the most diverse taxonomically of the paracanthopterygian orders. The current classification recognizes three suborders and twelve families (ROA-VARÓN & ORTÍ 2009) of uncertain interrelationships. The fossil record of gadiforms, reviewed recently by KRIWET & HECHT (2008), is rich with otoliths, but few non-otolith fossils exist that retain an interpretable caudal fin. Of these, most are gadoids as might be expected, since macrouroids largely lack internal caudal skeletons as adults. The oldest known, but as yet, still undescribed, fossil gadoid is "†*Protocodus*" (cited by COHEN 1984) from the early Paleocene of Greenland (ROSEN & PATTERSON 1969). †*Palaeogadus* and †*Rhinocephalus*, both from the early Eocene, share numerous cranial features with merlucciids (FEDOTOV & BANNIKOV 1989). Later fossils (late Oligocene to Miocene) can be largely circumscribed within an extant lineage; for example, †*Pseudoraniceps*, †*Palaeomolva*, and †*Paratrisopterus* exhibit affinities to *Raniceps*, lotines, and gadines, respectively (FEDOTOV & BANNIKOV 1989 and references therein). Osteological states are gleaned from these references. We did examine †*Bregmaceros albyi* (Pliocene, Italy) and note that its caudal skeleton is consistent with that of extant codlets *(Bregmaceros)*.

The order Stylephoriformes includes only the single species *Stylephorus chordatus* (tube-eye or thread-tail). It is a marine, abyssal species with a ribbonlike body and highly modified skull and caudal fin. No fossil stylephorids are known.

The Zeiformes (dories) are deep-sea or mid-water marine fishes assigned to five or six families with about 25 genera and 50 species. Three fossil zeiforms are of particular note. †*Archaeozeus skamolensis* and †*Protozeus kuehnei* are putative basal zeiforms and sequential lineages to the extant zeiforms (TYLER & SANTINI 2005). Both species are from the late Paleocene-early Eocene of Denmark (TYLER et al. 2000), and all specimens are less than 11 mm in standard length. The oldest known zeiform, †*Cretazeus rinaldii* from the Upper Cretaceous of Italy, has been placed within Parazenidae as the sister to *Cyttopsis* + *Stethopristes* (TYLER & SANTINI 2005). Osteological character states of these taxa were taken from TYLER et al. (2000), BACIU et al. (2005), and the matrix of TYLER & SANTINI (2005: 164). In these publications, no detailed illustrations of the caudal fin were provided, so discrepancies between the matrix and text were settled using the text. A fourth putative zeiform fossil is †*Palaeocyttus*, described from a single specimen (9 mm SL, GAUDANT 1978) of poor preservation. The description of its caudal fin (PATTERSON 1993: 46) is similar to that of zeiforms, but PATTERSON felt its identification was unsubstantiated.

Polymixiiformes are the sister group to percopsiforms, gadiforms, stylephoriforms, and zeiforms (Fig. 1). While Recent species (n = 10) are confined to a single genus *(Polymixia)*, the fossil record is considerably more diverse as evidence by the marine fossils (e.g., †*Apricenaichthys*, †*Berycopsis*, †*Dalmatichthys*, †*Omosoma*, †*Omosomopsis*) assigned to Polymixiiformes (PATTERSON 1993, FOREY et al. 2003, NELSON 2006, TAVERNE 2011). Among those most relevant to our discussion are †*Apricenaichthys*, †*Omosoma*, †*Omosomopsis*, and †*Pycnosterinx*, all from the Late Cretaceous. Details of †*Apricenaichthys italicus* and †*Omosomopsis simum* are taken from the published literature (TAVERNE 2011, PATTERSON & ROSEN 1989, respectively), but we examined specimens of †*Omosoma* and †*Pycnosterinx*.

†Sphenocephaliformes are comprised entirely of fossil representatives. They have been recognized as percopsiforms (ROSEN & PATTERSON 1969) or as stem-paracanthopterygians (MURRAY & WILSON 1999), and we conservatively treat them in a polytomy with the two major clades of extant paracanthopterygians: percopsiforms and [gadiforms + stylephoriforms + zeiforms]. †Sphenocephaliformes are recovered from marine strata and comprised of two genera: †*Sphenocephalus* (Campanian of Germany, ROSEN & PATTERSON 1969) and †*Xenyllion* (early Cenomanian of Alberta and Utah, WILSON & MURRAY 1996, STEWART 1996, NEWBREY et al. this volume). Unfortunately, the caudal skeletons of †*Xenyllion* specimens are not preserved, so we rely on the well-preserved skeletal material of †*Sphenocephalus*.

Two other potential paracanthopterygians are worth mentioning. †*Trebiciania roseni* (early Paleocene, Italy, SORBINI & BANNIKOV 1996) shares a full spine on preural centrum 2, two epurals, and one supraneural with other paracanthopterygians, and the enigmatic fossil acanthomorph †*Asineops squamifrons* (Eocene, Wyoming) has a full neural spine on preural centrum 2, two epurals, but two supraneurals (ROSEN & PATTERSON 1969). Even though †*Trebiciania* and †*Asineops* were noted for their similarities to percopsiforms, a more precise determination of their relationships is wanting, and we recognize them herein as paracanthopterygian incertae sedis and acanthomorph incertae sedis, respectively.

Materials and methods

We describe the caudal-fin anatomy with respect to osteology and myology using juvenile and adult specimens of Recent and fossil material (Appendix 1). Developmental material is unavailable for most groups studied; therefore, homology was assessed by topology (i.e., spatial relationships to other structures) and linking or intermediate conditions in a phylogenetic context (RIEPPEL & KEARNEY 2002). In contrast to osteology, striated muscles are relatively undescribed within Euteleostei and required a broader taxonomic sampling to interpret variation.

Most figures are prepared from examined specimens. Where an earlier publication includes appropriate figures, we have based some of our illustrations on such figures, but always in light of our examinations and with necessary modifications to reflect these new interpretations.

Bones and muscles of the caudal fin are defined as they are introduced, and the polymixiiform condition is described first, followed by conditions in percopsiforms, gadiforms, stylephoriforms, and zeiforms. Representative lampriforms, beryciforms, aulopiforms, myctophiforms, and percomorphs are used to identify apomorphic character states within our ingroup. For bones, we also include fossil material to direct our inferences of polarity and homology. The uncertain placement of many fossil within existing phylogenies can yield equivocal optimizations of character changes; however, their inclusion can suggest new characters, identify novel character-states, and reveal character-state combinations that do not exist in extant taxa (WILSON 1992). Finally, evolutionary pathways of each character (Appendix 2) are mapped onto the revised phylogeny using Mesquite V2.75 (MADDISON & MADDISON 2011).

Osteological methods. Specimens were cleared and double stained for cartilage and bone using modified protocols of DINGERKUS & UHLER (1977), most notably the application of an ethanol-based, alizarin red solution (SPRINGER & JOHNSON 2000). Specimens were dissected, photographed, and illustrated using a combination of microscopes (Leica Wild M3Z and MZ8, Olympus SZX16) and attachments (camera lucida, digital camera). We retained the diural terminology when enumerating ural centra, in part for consistency with the published literature on these groups.

Myological methods. We identified muscles following WINTERBOTTOM (1974a) and described them as to their origins, insertions, attachments (muscular, tendinous), relative sizes, and orientations. Up to nine intrinsic muscles may be present in the teleostean caudal fin; we provide detailed descriptions for seven (interradialis, hypochordal longitudinalis, flexor dorsalis, flexor dorsalis superior, flexor ventralis externus, flexor ventralis, and flexor ventralis inferior) of these muscles. The proximalis, which spans the centra of the posteriormost vertebrae, is not well differentiated from the hypaxialis or epaxialis and therefore not considered further. The adductor dorsalis is a small, medial slip of muscle from the upper hypurals that typically inserts on the dorsalmost principal fin ray of the ventral series. It occurred sporadically in a few outgroups. Finally, the supracarinalis posterior and the infracarinalis posterior run from the dorsal and anal fin, respectively, to the caudal fin and are mentioned in passing.

Identification of caudal-fin rays. Description of muscles inserting on caudal-fin rays requires a consistent system for ennumerating the rays. We identified caudal rays as either 'principal' or 'procurrent' fin rays. By definition, principal caudal-fin rays are the branched rays of the caudal fin plus the first unbranched rays (both dorsally and ventrally) (HUBBS & LAGLER 1947). Rays in the dorsal series were denoted by a "d"; rays in the ventral series were denoted by a "v". Rays were then counted sequentially beginning from the midline (d1 and v1) and proceeding dorsally and ventrally. This counting method is in contrast to ARRATIA (2008: fig. 2). Using our notation, principal caudal-fin ray counts are provided as "d9v8", for example, which specifies nine dorsal principal rays and eight ventral principal rays. An insertion of "d2–4" denotes rays 2, 3, and 4 in the dorsal series are served by the muscle. Principal and procurrent rays are not differentiated using this notation (e.g., an insertion of d2–6 of the flexor dorsalis in *Parazen* includes four principal and one procurrent caudal-fin ray). However, we explicitly note when an insertion includes procurrent rays; otherwise, the reader can assume insertions are restricted to principal fin rays. All other rays in the caudal fin are procurrent rays and enumerated posteriorly to anteriorly, as in ARRATIA (2008: fig. 2). This system works well when both branched and unbranched rays are present, but in lampriforms, all caudal-fin rays are unbranched. Additionally, some gadiforms have structurally different rays or, as adults, lack an internal caudal fin but have ray-like elements. To highlight suspected analogues and unusual anatomies, terms such as 'caudal filaments' (e.g., *Stylephorus*, REGAN 1924) and 'pseudocaudal' rays (e.g., *Steindachneria*, FAHAY 1989) have been applied.

Distinguishing rays as members of the dorsal or ventral series is typically straightforward. In many fishes, a gap between fin rays at the lateral midline is an external landmark separating the dorsal and the ventral series. Internally, this gap (diastema) coincides with a bifurcation of arteries and veins serving the rays (SCHULTZE & ARRATIA 1989). Furthermore, the ventral series of rays is typically restricted to hypurals 1, 2, and the parhypurals, while the dorsal series of rays is restricted to the more dorsal hypurals. Alternatively, the interradialis

muscle can be a useful feature to discriminate rays as members of the dorsal or ventral series. Interradialis bundles, which connect adjacent caudal-fin rays, are triangular in outline and fibers in the dorsal series of rays run antero-ventrally from origin to insertion (from the base of a triangle to the apex); whereas, fibers of the ventral bundles run antero-dorsally. When a ray is absent on the lateral midline, a dorsally-directed and a ventrally-directed bundle of the interradialis co-occur and cross the lateral midline (the dorsal bundle is lateral to the ventral bundle, HOWES 1991: fig. 32b). When a ray is present on the lateral midline, dorsal and ventral bundles of the interradialis attach to this "central fin ray", and neither bundle crosses the lateral midline (HOWES 1991: fig. 31). Unfortunately, these different approaches may yield contradictory inferences.

Based soley on myology, a central fin ray is present in *Chologaster* and *Forbesichthys* (Amblyopsidae), the zeiform *Cyttus* (Cyttidae), and in *Centroberyx* (Berycidae). In each of these examples, the central fin ray abuts the ventral margin of the hypural plate dorsal of the lateral midline. In specimens examined specifically for this trait, caudal blood vessels run the length of the diastema, and thus ventral to the central fin ray. Our interpretation is that the central fin ray is abutting hypural 3, or the upper hypural plate includes hypural 3, and thus, the central fin ray is a member of the dorsal series (i.e., d1).

Gadiforms, with the exception of morids and phycines, also have a central fin ray. Examination of a morid and phycine confirmed that the ray identified as d1 by its myology also sits at the ventral edge of the upper hypural plate. Examination of representative gadiforms with a central fin ray *(Gaidropsaurus*, *Lota*, *Macruronus*, *Merluccius*, *Microgadus)* indicated that this ray also sits along the ventral border of the upper hypural plate, leading us to conclude the ray is d1. *Bregmaceros* has a single hypural plate that lacks a diastema, but the central fin ray is below the lateral midline. In *Muraenolepis*, the interradialis is apparently absent between four fin rays at the midline, but these four rays lie against a hypural plate dorsal of the lateral midline (i.e., d1–4). In *Melanonus*, the caudal fin is extremely delicate and the muscles are poorly developed; conditions are our best hypotheses. Rays of *Melanonus* were assigned to the dorsal or ventral series using their location relative to the lateral midline in combination with the insertion of the flexor ventralis, which was assumed to insert on rays of only the ventral series–an assumption potentially false. Because of these varying conditions and confidences in assignment of this ray in gadiforms, the "central fin ray" notation was retained.

Results

Osteology

Preural centrum 1, the parhypural, and ural centra. Preural centra are positioned anterior to the ural centra and enumerated posterior to anterior (NYBELIN 1963: fig. 1). The parhypural is the haemal arch and spine of preural centrum 1 (MONOD 1968) and is pierced at its base by the haemal canal through which the caudal artery and vein pass. Posterior to the parhypural, both vein and artery are bifurcated and mark the location of ural centra. Since the parhypural represents the posteriormost element through which these vessels pass before bifurcating (NYBELIN 1963), the parhypural is readably identifiable, although in fossils only the existence of the arch can usually be verified. When correctly identified (SCHULTZE & ARRATIA 1989: 223 provide four criteria), preural centrum 1 is assumed homologous throughout actinopterygians (NYBELIN 1963, SCHULTZE & ARRATIA 1989) including teleosts (SCHULTZE & ARRATIA 1989). A postero-dorsally directed process on the lateral surface of the haemal arch of preural centrum 1, the hypurapophysis (NURSALL 1963), is variably present. While the hypurapophysis develops from the haemal arch (ARRATIA & SCHULTZE 1992), it can extend off the arch during growth, but we do not know of a case in which the hypurapophysis lies only on the haemal spine portion of the parhypural.

Preural centrum 1 is presumably fused to ural centrum 1 in all polymixiiforms and paracanthopterygians, extant and extinct forms. In these groups, an autogenous ural centrum (herein identified as ural centrum 2) articulates with the posterior border of preural centrum 1 + ural centrum 1 (Appendix 2). Only rarely has a third ural centrum been suspected in paracanthopterygians or polymixiiforms. ROSEN & PATTERSON (1969: 393) reported a specimen of †*Amphiplaga brachyptera* with three ural centra and illustrated it (1969: fig. 22b) as fused with uroneural 2 and supporting hypurals 5 and 6. ZEHREN (1979: 73) suspected the second ural centrum of his *Polymixia* specimen revealed its compound origin with a faint line on its surface. Among paracanthopterygians, only zeiforms, fossils and Recent species, have a single terminal centrum present (presumably preural centrum 1 + ural centrum 1 + ural centrum 2).

The parhypural contacts the compound preural centrum 1 + ural centrum 1 in polymixiiforms, fossil percopsids and aphredoderids, stem-paracanthopterygians, and †*Asineops*, but only in *Percopsis* (Fig. 4A) and several zeiforms (Figs. 10C,D) among extant paracanthopterygians. In *Bregmaceros* (Fig. 8D) and *Raniceps*, the parhypural may articulate with the proximal end of hypural 1+2. In those paracanthoterygians in

which the parhypural is detached from the vertebral column, the proximal end is typically tapered suggesting the absence of the haemal arch and consequently, the absence of the hypuraphophysis.

In the polymixiiform †*Apricenaichthys* and libotonid percopsids, even though the parhypural contacts a compound preural centrum 1 + ural centrum 1, the hypurapophysis appears to be absent. In contrast, the parhypural of the stem-paracanthopterygian †*Sphenocephalus* (Fig. 3), fossil percopsids †*Amphiplaga* (Fig. 4B) and †*Erismatopterus* (Fig. 4C), and fossil aphredoderid †*Trichophanes* (Fig. 5B) bears a small hypurapophysis.

The parhypural in most observed zeiforms is noticeably displaced from the terminal compound centrum (e. g., Fig. 9A,B), except in *Cyttus traversi*, *Parazen*, *Xenolepidichthys*, *Grammicolepis*, and *Cyttomimus* as in TYLER et al. (2003). Interestingly, these exceptions are the only zeiforms with a hypurapophysis (e. g., Fig. 10C) although the condition may be variable in *Xenolepidichthys* (Fig. 10D). In grammicolepidids (*Grammicolepis* and *Xenolepidichthys*, Fig. 10D), the proximal end of the parhypural forms a peg and socket articulation (TYLER et al. 2003) with the terminal compound centrum but this is not so in *Cyttomimus*, *Cyttus traversi*, and *Parazen*. In †*Cretazeus rinaldii*, the parhypural, which lacks a hypurapophysis, sits below the compound terminal centrum (TYLER et al. 2000). In the basal zeiforms †*Archaeozeus* and †*Protozeus*, the parhypurals closely contact the compound terminal centrum and probably do not have hypurapophyses (the matrix of TYLER & SANTINI 2005 indicates that †*Archaeozeus* has a hypurapophysis). These fossil taxa represent novel suites of character states in zeiforms.

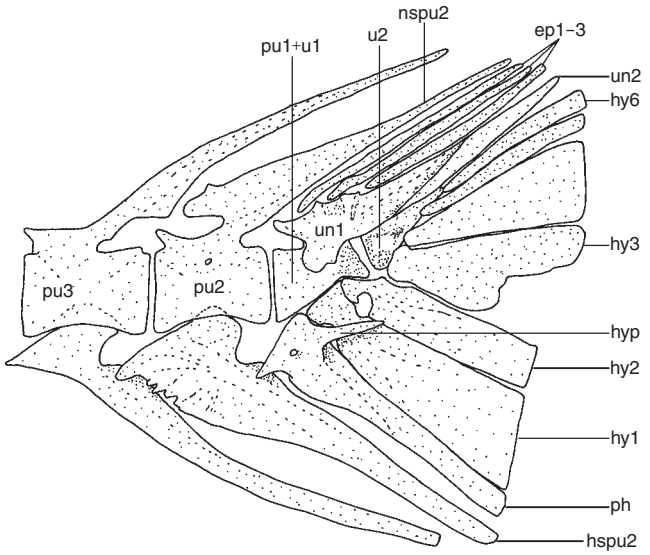

Fig. 2.
Caudal-fin osteology of the extant polymixiiform *Polymixia nobilis* (FMNH 64695, 104.0 mm SL). Abbreviations: **ep1–3,** epural 1,2,3; **hy1–6**, hypurals 1–6; **hyp**, hypurapophysis; **ph**, parhypural; **pu**, preural centrum; **u1,2**, ural centrum 1,2; **un1,2**, uroneural 1,2. Anterior is to the left.

In all zeiform taxa examined, arch-like structures extend dorsally from the terminal compound centrum (e. g., Fig. 10A), and to a lesser degree, from the compound elements of preural centrum 1 + ural centrum 1 and ural centrum 2 + hypurals 3–5 in some gadiforms (e. g., Figs. 7B, 8E). These extensions are paired and form a divot into which an epural can sit (Fig. 10C), although this latter relationship is rarely observed in gadiforms. GREENWOOD & ROSEN (1971: 14) identified these dorsal, laminar extensions as "rudimentary neural arches".

Amongst examined outgroups, the parhypural contacts the centrum, but a hypurapophysis is present only in *Lampris*, *Velifer*, *Ogilbia*, *Sirembo*, the beryciforms, *Fowlerichthys*, *Culaea*, and *Morone*. The point of contact is either a compound terminal centrum *(Opsanus*, *Morone*, *Culaea*, *Ogilbia*, ophidiids, *Melamphaes*, *Fowlerichthys)* or a fused preural centrum 1 + ural centrum 1. The parhypural can fuse with hypural 1 *(Melamphaes*, *Ogilbia*, *Opsanus)*. A compound preural centrum 1 + ural centrum 1 characterizes neoscopelids, whereas a compound terminal centrum characterizes myctophids (FUJITA 1990: table 2–5).

Hypurals. Hypurals are modified haemal spines (GOSLINE 1971) of ural centra that lack haemal arches. Hypurals display a remarkable array of fusion patterns in teleosts, but invariably, as the degree of fusion increases, confidence in identifying individual hypurals decreases. Ural centra are monospondylus (one neural and haemal arch per segment, SCHULTZE & ARRATIA 1989); consequently, the pattern of multiple hypurals associated with a single centrum has been used as evidence of (1) fusion of ural centra, (2) loss of ural centra, (3) or a combination of loss and fusion (SCHULTZE & ARRATIA 1989, ARRATIA & SCHULTZE 1992). In the majority of fishes herein, two hypurals are associated with ural centrum 1 and the remaining hypurals with ural centrum 2. We used hypural and parhypural locations, hypural sizes,

locations of diastema and caudal vessels to argue for individual hypural identification.

Among paracanthopterygian taxa, the number of hypural elements varies from one to six (Appendix 2), the extreme variation arising from the fusion or loss of hypural elements. *Polymixia* has six autogenous hypurals. Hypurals 1 and 2 and the parhypural articulate with a single element, and assumed preural centrum 1 + ural centrum 1, and hypurals 3–6 articulate with an autogenous ural centrum (Fig. 2). Hypural 3 bears a notch on its distal border, which forms an irregular outlined diastema. ZEHREN's (1979: 73) description of *Polymixia lowei* differs slightly from our observations in that hypurals 5 and 6 in our material have forked proximal ends, which in at least the case of hypural 5 lie on either side of the posteroventral edge of ural centrum 2. Hypural 6 may (Fig. 2) or may not (ZEHREN 1979: fig. 12) contact the second ural centrum. According to TAVERNE (2011), the polymixiiform fossil †*Apricenaichthys* has five hypural elements with two hypurals (1 and 2) contacting a compound preural centrum 1 + ural centrum 1. The remaining hypurals are associated with an autogenous ural centrum. A sixth hypural plate and diastema were not observed in either the holotype or paratype of †*Apricenaichthys*.

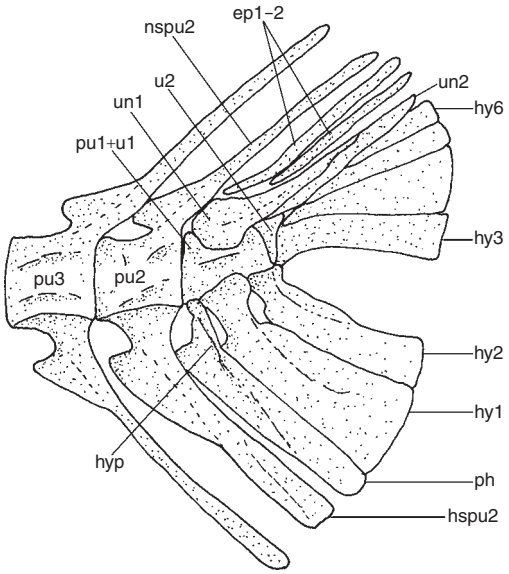

Fig. 3.
Caudal-fin osteology of the Cretaceous sphenocephaliform †*Sphenocephalus brachypterygius* (modified from ROSEN & PATTERSON 1969, fig. 35). Abbreviations: **ep1–2,** epural 1, 2; **hy1–6**, hypurals 1–6; **hyp**, hypurapophysis; **ph**, parhypural; **pu**, preural centrum; **u1**, **2**, ural centrum 1, 2; **un1**, **2**, uroneural 1, 2. Anterior is to the left.

Extant percopsids have four hypural elements; aphredoderids have three hypural elements, and amblyopsids have two hypural elements. In all percopsiforms, the lower hypural plate (presumed fusion of hypurals 1+2) lies below the diastema, and with the parhypural, either articulates with *(Percopsis)* or sits below a compound centrum interpreted as preural centrum 1 + ural centrum 1. Larval *Percopsis* (NYSM 58574) reveal a shared cartilage of the parhypural and the lower hypural plate that sits against this compound centrum. The upper hypural elements in *Percopsis* are interpreted as fused hypurals 3+4 that is itself fused with ural centrum 2 (Fig. 4A), along with two autogenous hypurals (hypurals 5 and 6). Some larval *Percopsis* (NYSM 58574, 60558) have a small gap or notch proximally between the elements of hypural 3+4 (and in one specimen, not yet fused to ural centrum 2); autogenous hypurals 5 and 6 are also present. In one larval specimen (NYSM 58574), hypurals 3 and 4 were only fused along their shared cartilaginous posterior borders. Otherwise the hypurals were comparable in size and position (contacting ural centrum 2) to the completely fused hypural 3+4. Intraspecific variation of fusion among hypurals in *Percopsis* is common. For example, ROSEN & PATTERSON (1969: fig. 16) illustrated three hypural elements and in their interpretation, the two upper plates were a fused element comprised of hypurals 3–5 and an autogenous hypural 6. Their hypothesis is consistent with our identification of autogenous hypurals 5 and 6 in *Percopsis* (Fig. 4A; FMNH 63457). Fossil percopsids (†*Amphiplaga*, †*Erismatopterus*, †*Lateopisciculus*, and †*Massamorichthys*) have six autogenous hypurals (Fig. 4B–E).

In the stem-percopsid †*Libotonius blakeburnensis*, remains of six hypural elements are seen. The parhypural and autogenous hypurals 1 and 2 articulate with the same bony compound element (preural centrum 1 + ural centrum 1) (WILSON 1977). Ural centrum 2 is in contact with hypurals 3–6, and a large diastema separates hypurals 2 and 3. At least in the holotype of †*Libotonius blakeburnensis*, hypurals 3–5 are partially fused retaining evidence of the original elements. The holotype (Fig. 4F) and two paratypes of †*L. pearsoni* revealed no hypural fusions, even though larger individuals may have a partial fusion of hypurals 4 and 5 (WILSON 1979).

In *Aphredoderus* and †*Trichophanes*, a large diastema is present, and the larger of the two upper hypural elements (fused hypurals 3–5) is fused to ural centrum 2. The third hypural element (hypural 6) is autogenous. A lower plate (fused hypurals 1+2) and parhypural articulate with a single bony centrum (preural centrum 1 + ural centrum 1). An 8.5 mm larval *Aphredoderus* (NYSM 67970) clearly shows three

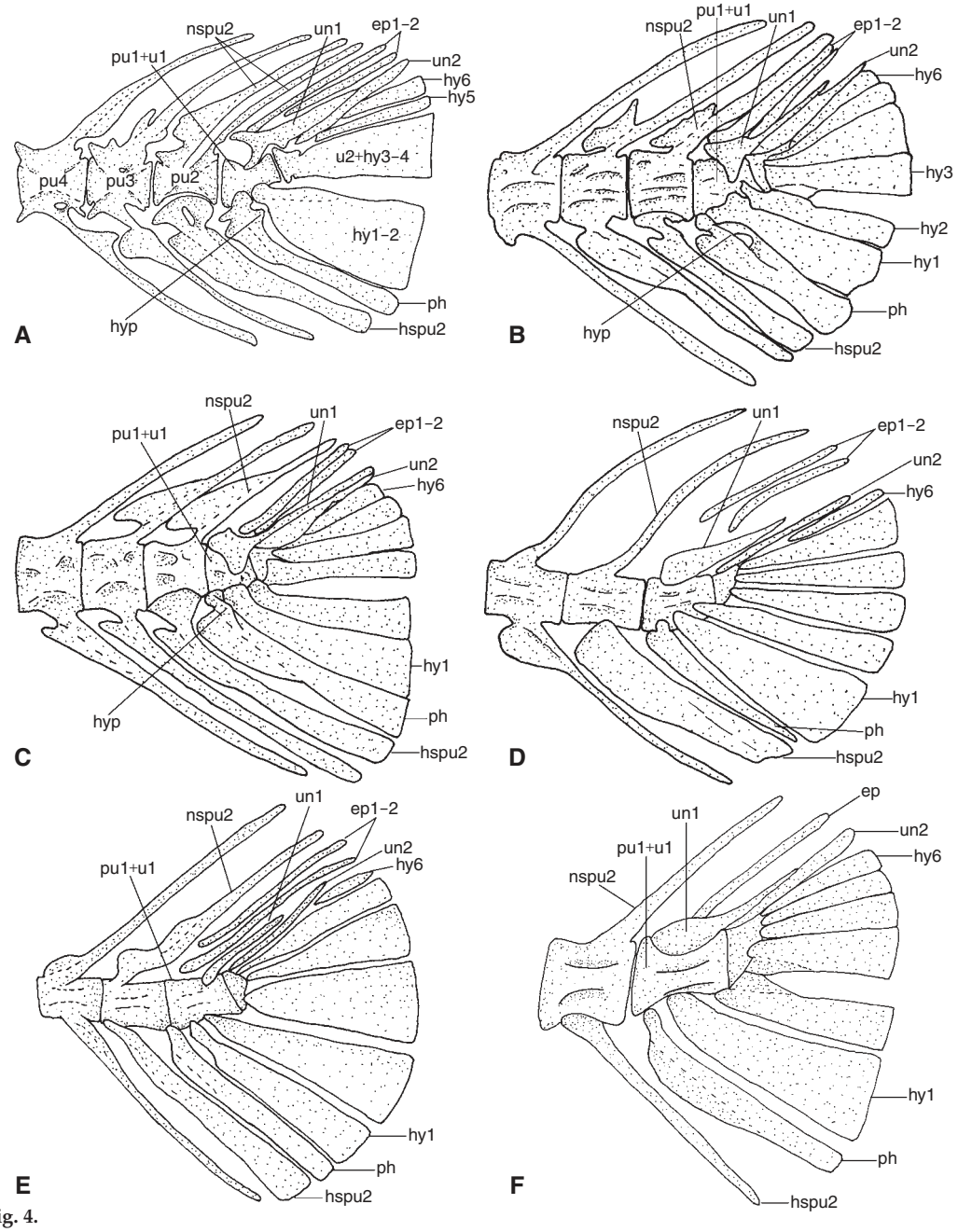

Fig. 4.

Caudal-fin osteology of extant and fossil percopsids and lobotoniids. **A,** *Percopsis omiscomaycus* (FMNH 63457, 66.0 mm SL); **B,** †*Amphiplaga brachyptera*, (after ROSEN & PATTERSON 1969: fig. 22 and examination of FMNH 19405, 73.0 mm SL); **C,** †*Erismatopterus levatus* (after ROSEN & PATTERSON 1960: fig. 26 and examination of specimens including AMNH 20367, 39.0 mm SL); **D,** †*Lateopisiciculus turrifumosis* (after MURRAY & WILSON 1996: fig. 5 and examination of UALVP 34771, tail only); **E,** †*Massamorichthys wilsoni* (after MURRAY 1996: fig. 7 and from examination of UALVP 25538, 134.0 mm SL); **F,** †*Libotonius pearsoni* (UALVP 13469, 20.0 mm SL). Abbreviations: **ep1–2,** epural 1, 2; **hy1–6**, hypurals 1–6; **hyp**, hypurapophysis; **ph**, parhypural; **pu**, preural centrum; **u1**,**2**, ural centrum 1, 2; **un1**,**2**, uroneural 1, 2. Anterior is to the left.

hypurals fusing to form a large plate, a free hypural 6, and distinct hypurals 1 and 2 prior to fusion. Moreover, these hypural plates share a proximal cartilage with the parhypural that articulates with an elongated centrum (fused preural centrum 1 + ural centrum 1 based on its length relative to preural centrum 2). In †*Mcconichthys*, two hypural plates are identifiable (likely hypurals 1 + 2 and hypurals 3–5) with the upper plate fused to ural centrum 2 (Fig. 5C, cf. GRANDE 1988). In amblyopsids (Figs. 6A–D), the upper hypural element (hypural 3-n) is fused to ural centrum 2.

The caudal skeleton of †*Sphenocephalus* (Fig. 3) is relatively unspecialized. There are six autogenous hypurals and a large diastema between hypurals 2 and 3. The parhypural, hypural 1, and hypural 2 contact a compound preural centrum 1 + ural centrum 1. It appears that only two of the four upper hypurals reach the rather small ural centrum 2 (Fig. 3). In both †*Asineops* and †*Trebiciania* the second ural centrum is fused to the upper hypural element; the lower hypurals are fused in †*Trebiciania* but not †*Asineops*. In †*Asineops*, hypurals 1 and 2, along with the parhypural, articulate with a single structure (presumably preural centrum 1 + ural centrum 1).

The morid and *Melanonus* caudal skeletons provide keys to the interpretation of the gadiform skeleton. All extant gadiforms we examined have two hypural elements with varying degrees of fusion among individual hypural plates. The lower hypural element lies below the lateral midline (*Steindachneria* may be an exception; see Fig. 7D). In *Steindachneria*, two cartilaginous plates (hypurals?) articulate with a half centrum (ural centrum 2?). Each plate supports two filamentous fin rays (pseudocaudal rays of FAHAY 1989). One ray is thick and rod-like, while the second, always positioned laterally, is extremely long, fragile and filament-like (Fig. 7D). In morids (Fig. 7A), *Euclichthys* (PAULIN 1983: fig. 5c), and *Raniceps* (DUNN & MATARESE 1984: fig. 148b), this lower plate is bifurcated distally, suggesting that it is comprised of hypurals 1 and 2. Along with the parhypural, this compound hypural plate sits below the assumed compound element, preural centrum 1 + ural centrum 1. Only in *Bregmaceros* is the lower hypural element fused to preural centrum 1 + ural centrum 1, and only in *Raniceps* (CAS 225749) did we observe the parhypural attached to the lower hypural plate, although not always (DUNN & MATARESE 1984: fig. 148b). The upper hypural plates in morids (Fig. 7A),

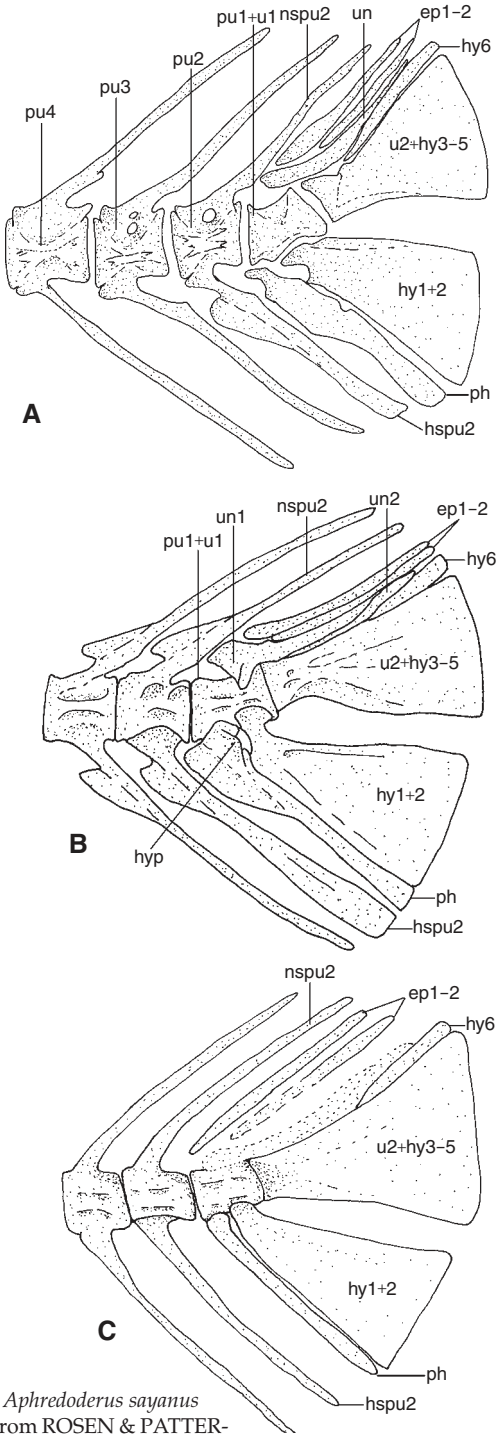

Fig. 5.
Caudal-fin osteology of extant and fossil aphredoderids. **A,** *Aphredoderus sayanus* (KU 5032, 63.0 mm SL); **B,** †*Trichophanes foliarum* (modified from ROSEN & PATTERSON 1969: fig. 19, FMNH PF14311, 105.9 mm SL); **C,** †*Mcconichthys longipinnis*, (FMNH PF12916, 264 mm SL). Abbreviations: **ep1–2,** epural 1, 2; **hy1–6**, hypurals 1–6; **hyp**, hypurapophysis; **ph**, parhypural; **pu**, preural centrum; **u1**, **2**, ural centrum 1, 2; **un1**, **2**, uroneural 1, 2. Anterior is to the left.

Euclichthys (PAULIN 1983: fig. 5c), *Melanonus* (PAULIN 1983: fig. 5a), and *Raniceps* are divided distally suggesting they are comprised of multiple hypurals, namely 3–5, and that hypural 6 is lost. Moreover, the upper plate is fused to ural centrum 2. We applied these interpretations to all gadiforms because the shapes of the corresponding elements are consistently similar. Examination of larval specimens (<38 mm SL) from three gadid subfamilies (gadines, gaidropsarines, phycines) did not resolve the fates of the hypural plates, because the upper and lower hypural plates were present as single entities. Even in specimens as small as 7.8 mm SL, the parhypural, lower, and upper hypural plates are each present as a single cartilaginous plate (*Microgadus proximus*, MATARESE et al. 1981).

The fossil "†*Protocodus*" (lower Paleocene) has five hypural plates (COHEN 1984), while †*Palaeogadus* and †*Bregmaceros albyi* have two hypural plates (FEDOTOV & BANNIKOV 1989), suggesting that hypural fusion is derived (COHEN 1984) and that gadoids had achieved their current patterns of hypural fusion by the early Eocene.

Stylephorus has three hypural elements, two of which lie below the lateral midline (Fig. 7E). The anteriormost hypural element is interpreted as the parhypural, as in PIETSCH (1978), and sits below a centrum hypothesized to be compound preural centrum 1 + ural centrum 1. Hypural 1 and 2 each support a single exceedingly long caudal filament, which may be greater than 2x the standard length (REGAN 1924, PIETSCH 1978). What is presumably a fused ural centrum 2 and upper hypurals (3-n) supports 5–6 short caudal rays that are deflected dorsally in adults (REGAN 1924).

Zeiforms have a single terminal centrum (presumed fusion of preural centrum 1 + ural centrum 1 + ural centrum 2) that is fused with most of the hypurals. The parhypural is autogenous but sits below this terminal centrum. Zeiforms have either one (*Zeus*, Fig. 10A, although this is not consistent within *Zeus*, see TYLER et al. 2003: fig. 88 lower) or two hypural elements. In zeiforms with two hypural plates, one is an elongated sliver that sits on the dorsal border of the larger plate. The lower hypural plate has a diastema that may be the extension of pre-fusion borders of hypurals 2 and 3, which now outline a proximal depression (e. g., *Zenion*; Fig. 9D). The plate below the diastema is assumed to contain hypurals 1 and 2 based on shallow, external grooves in cleared and stained specimens of *Zenion* (USNM 377986). The upper lobe of the plate probably contains hypural 3 since caudal vessels pass ventral to the lobe, but how many other plates are incorporated is difficult to determine. In some specimens, the posterior border of the dorsal lobe is emarginate (Fig. 10D; FUJITA 1990: figs. 188, 190; TYLER et al. 2003: fig. 88 lower) indicating a compound origin of at least two hypurals. In those species with an autogenous hypural (e. g., Fig. 9D), we hypothesize it is hypural 5 (as do MONOD 1968, FUJITA 1990, and TYLER et al. 2003) in contrast to ROSEN (1984: 32–33, fig. 31) who identified it as epural 3. Hypural 5 can be fused to (Fig. 10A), articulate with (Fig. 10B), or free from (Fig. 10D) the terminal centrum. Hypural 5 contacts the terminal centrum in a second specimen of *Xenolepidichthys* from the same lot (USNM 32016) as that illustrated in Figure 10D. When hypural 5 is not identifiable, we hypothesize that it has been incorporated into the compound plate with hypurals 3 and 4 (e. g., Fig. 9E).

Similar to Recent species, the fossil †*Cretazeus* has two hypural plates (potentially hypurals 1–4 and hypural 5), the larger of which is fused to a compound terminal centrum (TYLER et al. 2000). Hypural 5 lies along the dorsal border of the larger plate. The hypurals in †*Archaeozeus* and †*Protozeus* are described as "fused into a single plate that is fused to urostyle" (BACIU et al. 2005: 125).

Among outgroups, hypural fusion patterns vary greatly. Lampriforms can have three plates (hypural 1+2, hypural 3+4, hypural 5 in *Lampris*, OELSCHLÄGER (1974), or hypural 1, 2, and 3+n in *Zu*). Only the upper plate in *Zu* is fused to a centrum (ural centrum 2). *Radiicephalus* has four plates: two contact preural centrum 1 + ural centrum 1, and two contact ural centrum 2 (OLNEY et al. 1993). The ophidioids *(Otophidium*, *Sirembo)* have a single hypural plate that incorporates the parhypural, all of which fuse to the centrum. The bythitid *(Ogilbia)*, lophiiform *(Fowlerichthys)*, and batrachoids *(Opsanus*, *Porichthys)* have two plates (parhypural + hypurals 1+2, hypurals 3-n). In *Opsanus* and *Ogilbia*, the lower plate is fused to the terminal vertebrae, whereas in *Porichthys* and *Fowlerichthys*, the upper hypural plate is fused to the compound terminal centrum. The beryciforms and percomorphs vary from six *(Hoplostethus)*, and five *(Sargocentron*, *Morone)*, to one *(Culaea*, *Melamphaes)* hypural plate. Only the single plate is fused to a centrum, and in *Melamphaes*, the plate includes the parhypural. Each hypural (n=5) is clearly outlined in *Melamphaes* even though all appear fused. Conditions in the myctophiforms are as variable, with six hypurals in neoscopelids, four hypural plates in *Diaphus* (parhypural + hypurals 1+2, hypurals 3+4, hypural 5, hypural 6), or two plates in *Myctophum* (parhypural + hypurals 1+2, hypurals 3–6). None of these plates is fused to a centrum (FUJITA 1990: table 2–5).

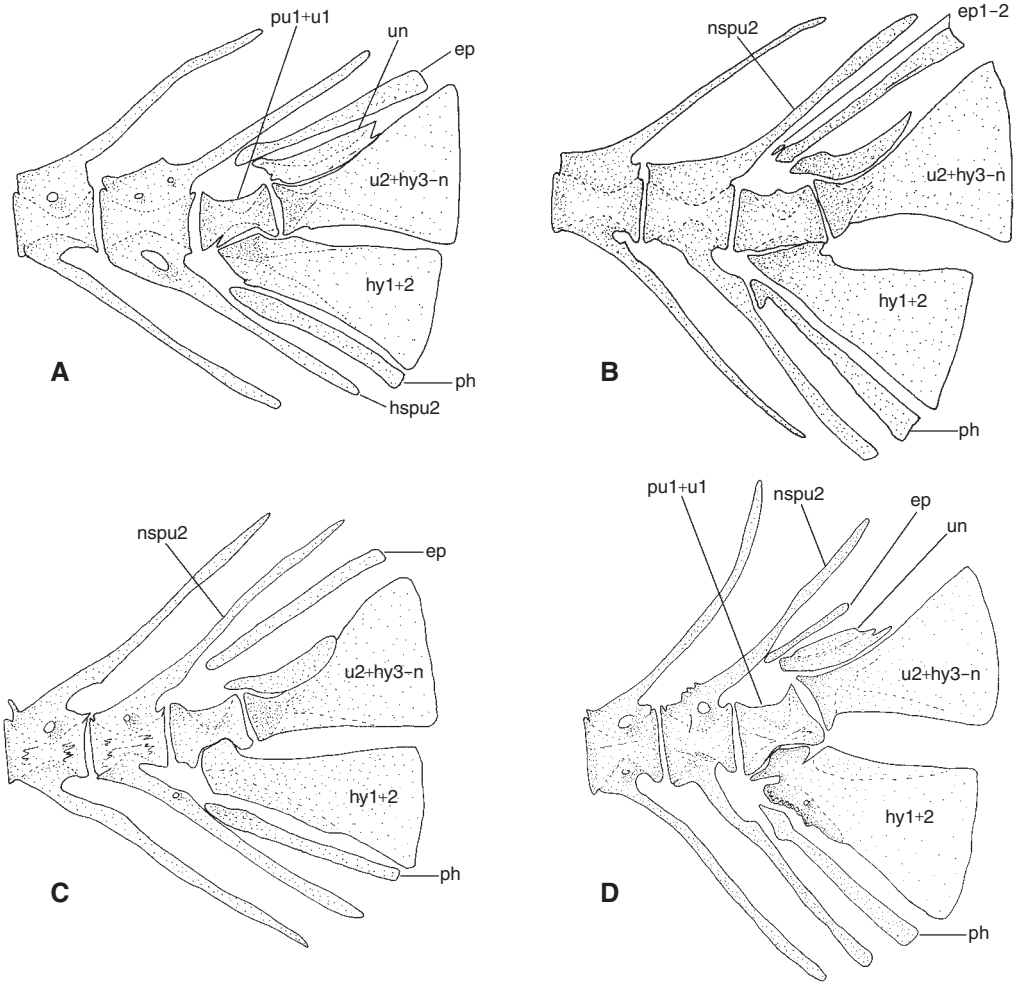

Fig. 6.
Caudal-fin osteology of extant amblyopsids. **A,** *Forbesichthys agassizii* (KU 17526, 50 mm SL); **B,** *Typhlichthys subterraneus* (after ROSEN & PATTERSON 1969: fig. 16d and examination of KU 12853, 35.0 mm SL); **C,** *Chologaster cornuta* (KU 8874, 41.0 mm SL); **D,** *Amblyopsis spelaea* (CAS 78143, disarticulated specimen). Abbreviations: **ep1–2,** epural 1, 2; **hy1+2**, fused hypurals 1–2; **hy3-n**, hypurals 3-n; **ph**, parhypural; **pu**, preural centrum; **u1**, **2**, ural centrum 1, 2; **un**, uroneural. Anterior is to the left.

Full neural spine on preural centrum 2. With the exception of *Steindachneria* (Fig. 7D), preural centrum 2 carried a full neural spine (i. e., spine length near equal to that on preural ural centrum 3) in all observed extant and fossil taxa of polymixiiforms, percopsiforms, gadiforms, and zeiforms, including †*Asineops* and †*Trebiciania*. In *Stylephorus*, the slender neural arches are paired and give rise to a delicate, but distinct, neural spine (REGAN 1924: 201, PIETSCH 1986: fig. 8) that is approximately one-third the length of the neural arch. The shape and structure of the arch and spine are comparable to that on preural centrum 3 (SIO 77-171); therefore, we consider the spine on preural centrum 2 as "full" length. The condition in *Trachyrincus* (Fig. 7C) appears to be a full spine, but we cannot explain the additional ornamentation. Amongst outgroups, a full spine on preural centrum 2 was present in batrachoids, *Ogilbia*, *Sirembo*, *Fowlerichthys*, and *Culaea*. In myctophoids and lampriforms, with the exceptions of *Trachipterus* (secondarily derived condition, ROSEN 1973) and *Zu*, the spine on preural centrum 2 is reduced (≤½ spine length of preural centrum 3) or forms an ornate crest. Given this distribution, a full neural spine on preural centrum 2 would appear

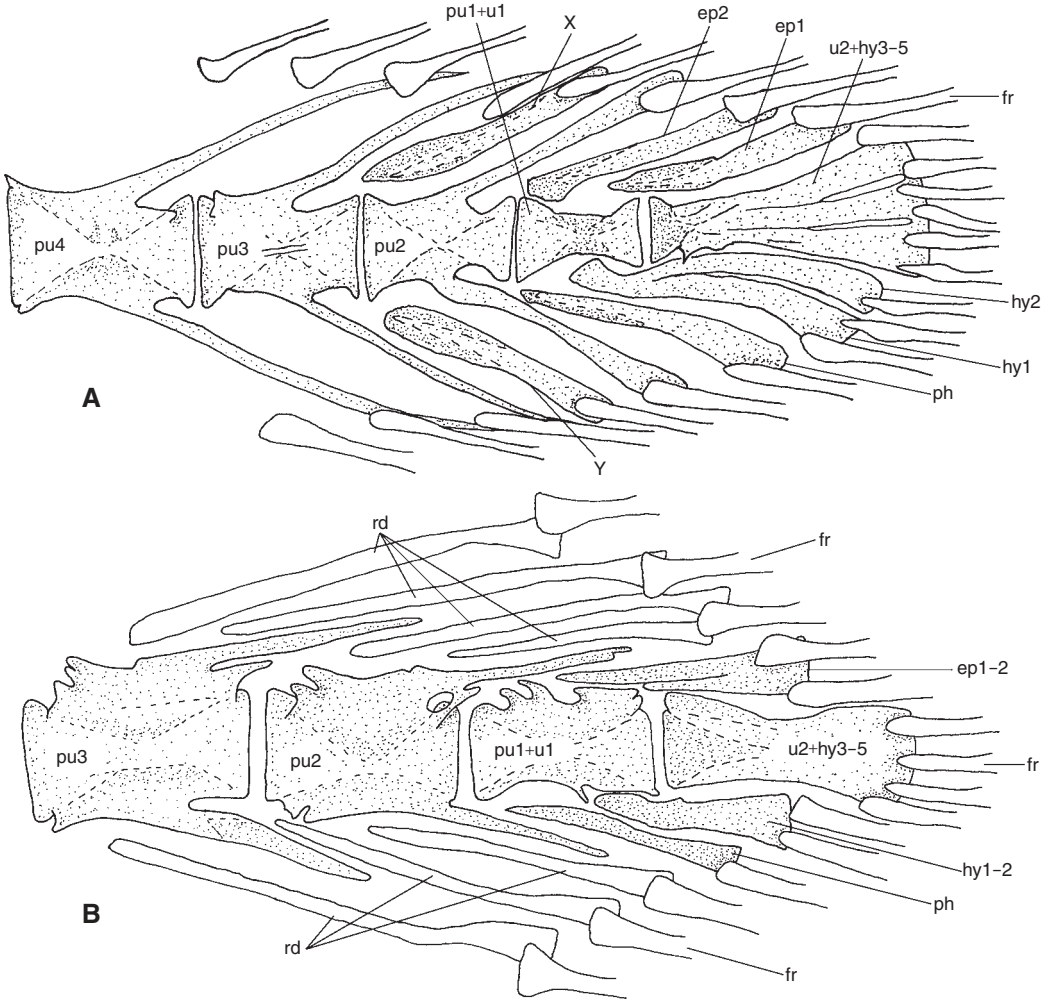

Fig. 7.
Caudal-fin osteology of extant gadiforms and stylephoriforms. **A,** *Gadella jordani* (modified from FUJITA 1990, fig. 138 as *Physiculus*); **B,** *Muraenolepsis orangiensis* (USNM 380031, 296.9 mm SL); **C,** *Trachyrincus scabrus* (modified from HOWES 1989: fig. 6 as *T. trachyrincus*); **D,** *Steindachneria argentea* (FMNH 67856, 143.1 mm SL); **E,** *Stylephorus chordatus* (SIO 60-130, tail only). Abbreviations: **ep,** epural; **fr**, fin ray; **hy1+2**, fused hypurals 1–2; **hy 3–5**, hypurals 3–5; **ph**, parhypural; **pu**, preural centrum; **rd**, radial; **u1**, **2**, ural centrum 1, 2; **X**, X bone; **Y**, Y bone. Anterior is to the left.

in the ancestor to polymixiiforms + paracanthopterygians and convergently in many distantly related percomorphs (Fig. 14). However, a full neural spine on preural centrum 2 is plesiomorphic for euteleosts (e. g., *Pimephales*, *Esox*). It is reduced in neoteleosts and becomes a crest in ctenosquamates (ROSEN 1984). Its presence in a number of unrelated acanthomorphs necessitates a mechanism, of which ROSEN (1973, 1984) proposed several including the fusion of preural centra 2 and 3 along with retention of the neural spine on preural centrum 3. ROSEN (1985) advised that "investigators would be foolhardy to base major taxonomic judgments upon it" [full neural spine on preural centrum 2] without ontogenetic evidence.

Fusion of arches to preural centra 2 and 3. In *Polymixia* and the fossil †*Apricenaichthys*, the haemal arches of preural centra 2 and 3 are not fused to their corresponding centra, but the respective neural arches are fused to their centra. In *Percopsis* and *Urophycis*, only the haemal arch of preural centrum 2 is not fused

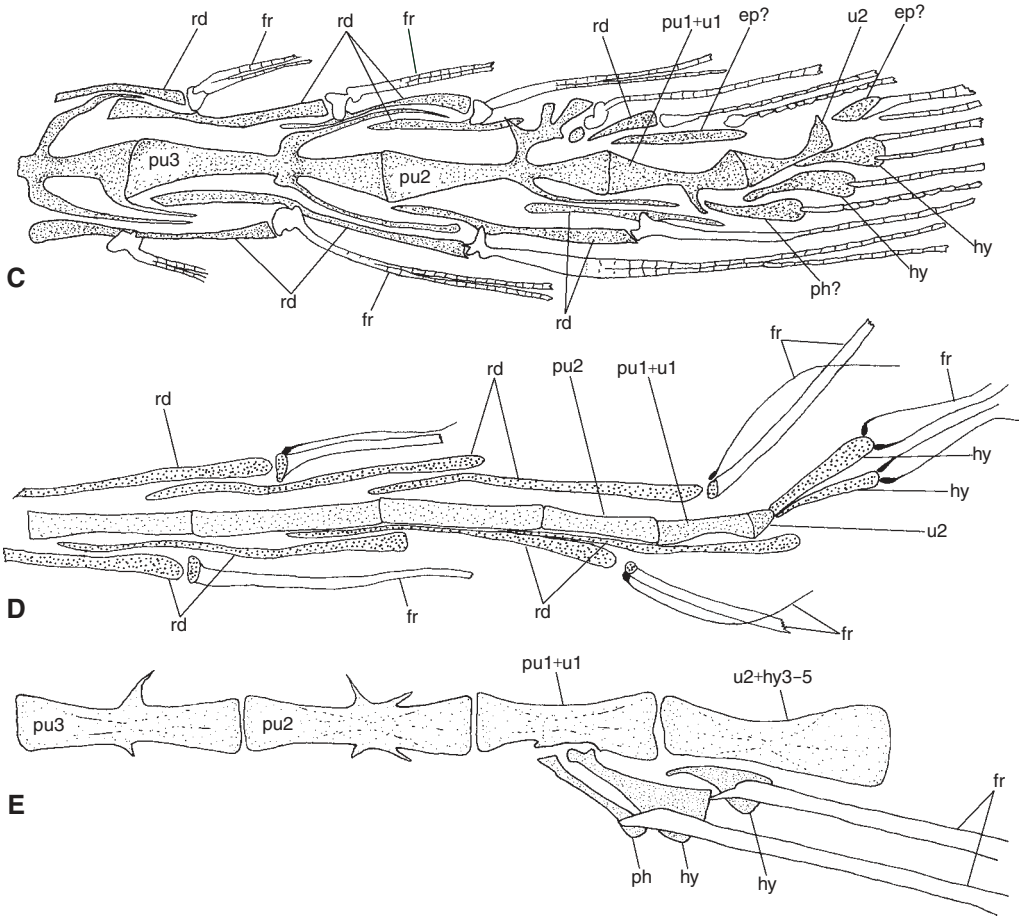

Fig. 7. (continued).

to its centrum, but in the remaining percopsiforms and gadiforms examined, the arches of preural centra 2 and 3 appear fused to their respective centra. Our examinations of the fossil percopsids †*Lateopisciculus* and †*Massamorichthys* (Figs. 4D–E) suggest that the neural arch and preural centrum 2 are fused (contra MURRAY 1996). The haemal arch of preural centrum 2 is not fused to its centrum in †*Libotonius pearsoni* or †*Trichophanes*. In †*Cretazeus rinaldii*, the full neural spine of preural centrum 2 is continuous with (fused to?) the arch and centrum, but the haemal spines of preural centra 2, and probably 3, in †*Archaeozeus* are autogenous (BACIU et al. 2005). In extant zeiforms, the neural and haemal arches appear fused to their respective centra. The outgroups displayed a number of conditions from four fusions (i.e., haemal and neural arches fused to preural centra 2 and 3) in the batrachoids, *Fowlerichthys*, *Otophidium*, *Melamphaes*, *Culaea*, to only the neural arches fused in *Morone* and *Sargocentron*, and only the neural arch of preural centrum 3 fused in *Hoplostethus*.

Multiple spines on preural centra 2 and 3. We encountered double neural or haemal arches and spines on preural centra, particularly preural centrum 2. Multiple arches and spines on a single centrum (e.g., BIRD & MABEE 2003) can in theory result from the displacement of arches (e.g., *Elops*: SCHULTZE & ARRATIA 1988, *Oncorhynchus*: ARRATIA & SCHULTZE 1992) or from fusions of centra. TYLER et al. (2003) posited fusion of preural centra. Their inference was based on an enlarged second preural centrum bearing deep lateral grooves along the neural and haemal spines in *Neocyttus* (fig. 23b). Similarly, ROSEN & PATTERSON (1969: fig. 3e: *Eretmophorus*) identified a fused preural centrum bearing two neural and haemal spines.

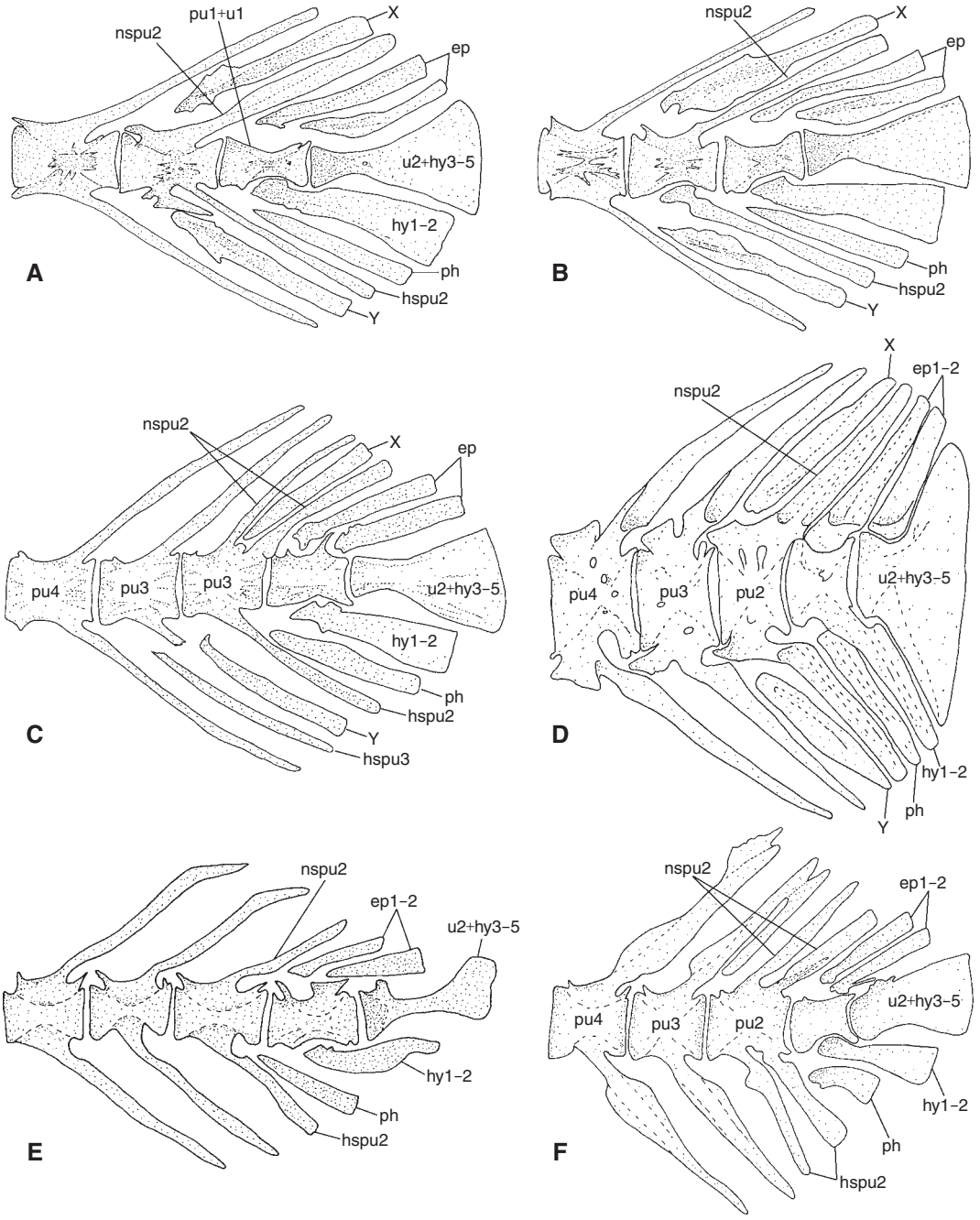

Fig. 8.
Caudal–fin osteology of extant gadiforms. **A,** *Phycis blennoides* (USNM 232482, 122 mm SL); **B,** *Urophycis cirrata*, (LACM 56745m SL: 158.5 mm); **C,** *Merluccius albidus* (FMNH 69318; 160.0 mm SL); **D,** *Bregmaceros cantori* (KU 30244, 51.0 mm SL); **E,** *Lota lota lacustris* (FMNH 63458, 142 mm SL); **F,** *Gadus macrocephalus* (KU 15063, 125.0 mm SL). Abbreviations: **ep1–2,** epural 1, 2; **hy1–2**, hypurals 1–2; **hy3–5**, hypurals 3–5; **ph**, parhypural; **pu**, preural centrum; **u1**, **2**, ural centrum 1, 2; **X**, X bone; **Y**, Y bone. Anterior is to the left.

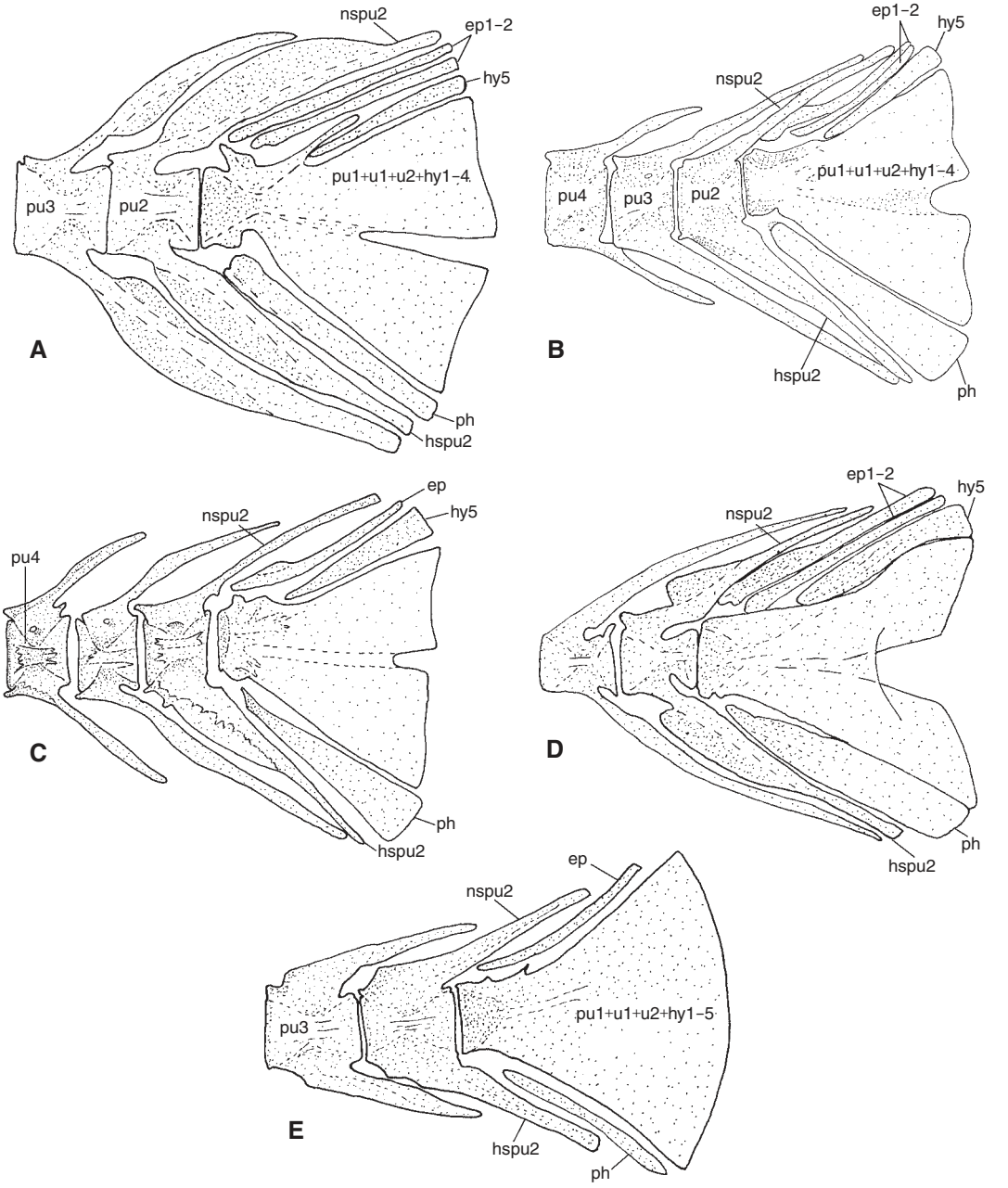

Fig. 9.
Caudal-fin osteology of more basal extant zeiforms. **A,** *Cyttus australis* (after TYLER et al. 2003: fig 15, and from examination of LACM 42620, 100.2 mm SL); **B,** *Cyttopsis rosea* (USNM 377980, 97.6 mm SL); **C,** *Stethopristes eos* (USNM, 226570, about 80 mm SL, post-cranial only); **D,** *Zenion hololepis* (after TYLER et al. 2003: fig. 53 and our examination of USNM 377986, 86 mm SL); **E,** *Macrurocyttus acanthopodus* (modified from TYLER et al. 2003: fig. 72). Abbreviations: **ep1–2,** epural 1, 2; **hy1–5**, hypurals 1–5; **ph**, parhypural; **pu**, preural centrum; **u1**, **2**, ural centrum 1, 2. Anterior is to the left.

In examined specimens of *Polymixia (P. lowei*, *P. berndti*, and *P. nobilis)* and in those included by ROSEN & PATTERSON (1969) and FUJITA (1990, *P. japonica*), double neural or haemal spines were not present on any preural centrum. Similarly, the only fossil polymixiid in which double spines on preural centrum 2 has been seen is †*Omosomopsis* (PATTERSON & ROSEN 1989: 12, fig. 4d). Double neural or haemal spines on a preural centrum, particularly preural centrum 2, was observed in *Percopsis* and *Forbesichthys*, and illustrated in *Aphredoderus*, *Chologaster*, and *Typhlichthys* by ROSEN & PATTERSON (1969: fig. 16). In †*Trichophanes foliarum* and †*Libotonius blakeburnensis*, doubling of either neural or haemal spines was absent. Most gadiforms carried double-spined preural centra, a doubling that TREMBLAY et al. (1984) considered common, at least in haddock. As an extreme example of the variation and the number of centra involved, FAHAY (1989: 150) posited fusions to explain "double neural and haemal arches and spines on the last centrum and triple neurals and haemals on the fourth centrum from the rear" in *Steindachneria*. In *Stylephorus*, we can identify a single neural and haemal spine and paired, but open, laminar extensions of the arches posteriorly (Fig. 7E). Double neural or haemal spines are frequently seen on preural centrum 2 of some zeiforms (e.g., Figs. 10A,B), and some of these centra tend to be larger than those with a single spine (e.g., TYLER et al. 2003: fig. 23b).

In †*Asineops squamifrons*, the haemal spine of preural centrum 2 is doubled, and ROSEN & PATTERSON (1969: 415) found specimens with triple haemal spines and double or single neural spines on preural centrum 2, which they hypothesized, were due to fusion.

Among lampriforms, *Trachipterus* has two neural spines on preural centrum 2 (ROSEN 1973: 486, fig. 112) or a compound ossification of preural centrum 3+4 (FUJITA 1990: 351, fig. 170), and *Zu* has two haemal spines on preural centrum 3. Amongst other outgroups, specimens of *Coccorella* and *Ogilbia* had two neural spines on preural centrum 3, a specimen of *Esox* had two neural spines on preural centrum 2, and one of *Culaea* had two neural and haemal spines on preural centrum 2. Overall, preural centrum 2 had multiple spines most frequently, and the doubling was predominantly that of neural spines.

Epurals. Epurals are neural spines that have lost their connection to a neural arch of the ural or preural centra and are anterior to the uroneurals (MONOD 1968, SCHULTZE & ARRATIA 1989). They are unpaired, typically rod-like in shape and variable in number (Appendix 2).

Recent and fossil polymixiiforms have three epurals that contact uroneural 1.

Extant percopsiforms share a reduction in the number of epurals (2 in percopsids, Fig. 4A, and aphredoderids, Fig. 5A; 1 or 2 in amblyopsids, Figs. 6A–D). Conditions are polymorphic in *Amblyopsis* (Fig. 6D versus ROSEN & PATTERSON 1969: fig. 16e) and *Typhlichthys* (KU17526 versus Fig. 6B). Fossil percopsids (†*Amphiplaga*, †*Erismatopterus*, †*Lateopisciculus*, and †*Massamorichthys*) and aphredoderids (†*Trichophanes*) all have two epurals, as do †*Asineops*, †*Trebiciania* and the stem-paracathopterygian †*Sphenocephalus*. The aphredoderid †*Mcconichthys longipinnis* has at least one epural and †*Libotonius* species are polymorphic (two epurals in †*L. blakeburnensis*, one epural in †*L. pearsoni*, Fig. 4F).

Most gadiforms have two epurals assuming a correct interpretation of *Trachyrincus* elements (Fig. 7C). *Steindachneria* has either zero (our observation, Fig. 7D) or one (FAHAY 1989) epural. We found two instances of what we identified as three epurals in *Gaidropsarus mediterraneus* (FMNH 71280) and *Melanonus zugmayeri* (FMNH 65807). In the former specimen, the anteriormost epural was greatly shortened (there is also a deformity in the dorsal portion of the caudal fin that includes this epural) but as wide as the other two epurals. In the latter specimen, epurals were of equal size but fused to each other along a significant portion of their lengths. We consider these apparent occurrences of three epurals as anomalies pending more specimens. *Stylephorus* lacks epurals.

When two epurals are present in zeiforms, the anteriormost is thicker and longer and can extend to the terminal compound centrum. One epural is present in zeids (*Zeus* and *Zenopsis*, Fig. 10A,B), *Stethopristes* (Fig. 9C), *Capromimus*, *Cyttomimus*, *Macrurocyttus* (Fig. 9E), and some specimens of *Neocyttus* (TYLER et al. 2003: figs. 23, 59, 72). The Cretaceous zeiform †*Cretazeus rinaldii* has two epurals, but conditions in †*Archaeozeus* and †*Protozeus* are indeterminate (TYLER & SANTINI 2005).

Among lampriforms, the number of epurals varies from three in *Velifer* (OELSCHLÄGER 1974), to two in *Lampris* and *Trachipterus* (OELSCHLÄGER 1983, OLNEY et al. 1993), to none in *Radiicephalus* (OLNEY et al. 1993) or *Zu*. Neoscopelids, beryciforms, and *Morone* have three epurals in our material; the batrachoidiform and the myctophid *Diaphus* have two epurals (perhaps *Ogilbia* also), while all the other examined outgroups have one epural.

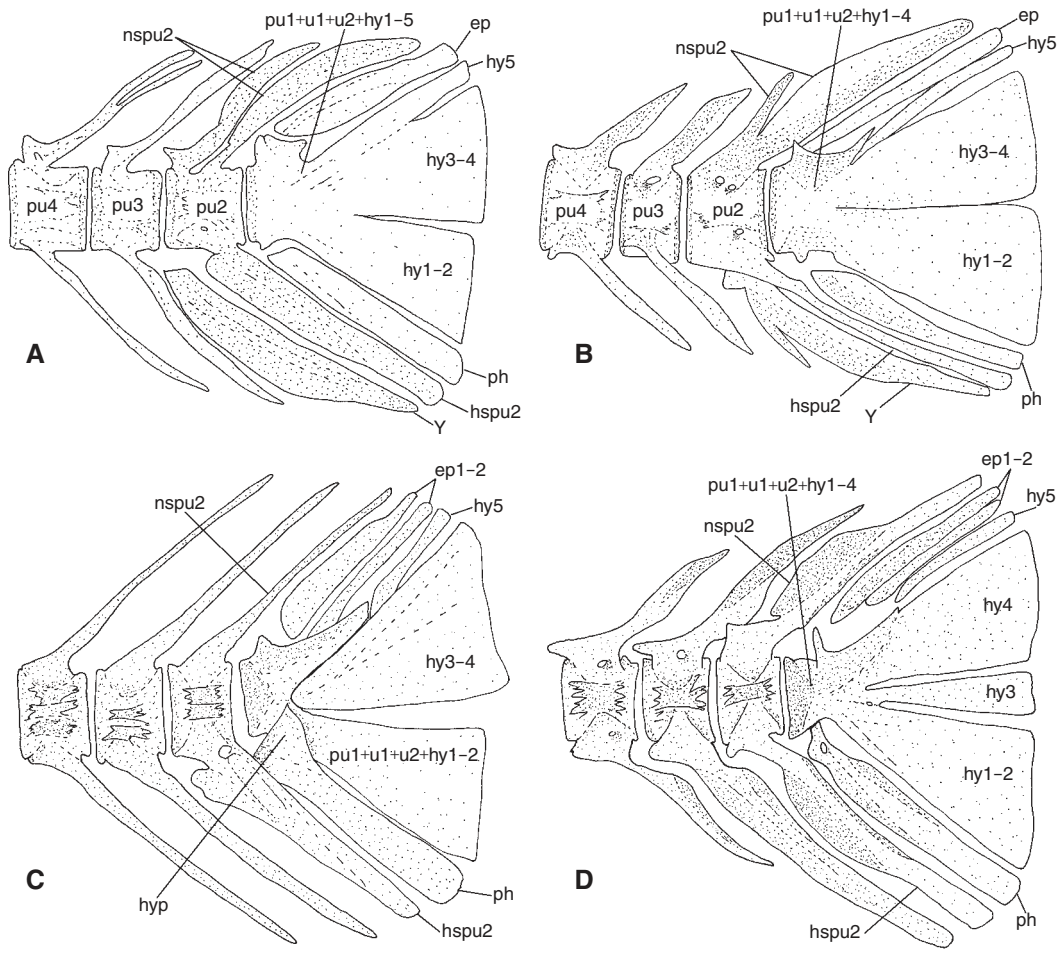

Fig. 10.
Caudal-fin osteology of more derived extant zeiforms. **A,** *Zeus faber* (USNM 307842, 55.0 mm SL); **B,** *Zenopsis conchifer* (USNM 392241, 80.0 mm SL); **C,** *Parazen pacificus* (FMNH 672158, 125.0 mm SL); **D,** *Xenolepidichthys dalgleishi* (USNM 320016, post-cranial only). Abbreviations: **ep1–2,** epural 1, 2; **hy1–5**, hypurals 1–5; **hyp**, hypurapophysis; **ph**, parhypural; **pu**, preural centrum; **u1**,**2**, ural centrum 1, 2; **u2**, ural centrum 2; **Y**, Y bone. Anterior is to the left.

Uroneurals and stegural process. Uroneurals are neural arch derivatives of ural centra and take on a variety of shapes. The paired anteriormost uroneural (usually termed uroneural 1) may bear, especially in euteleosts, an outgrowth of membranous bone (ARRATIA & SCHULTZE 1992: 216). This outgrowth is the stegural process of GRANDE et al. (this volume).

In the polymixiiforms *Polymixia* and †*Apricenaichthys*, two uroneurals are present, and the first uroneural bears a stegural process. At least in *Polymixia*, the first uroneural contacts the three epurals.

Percopsis has two uroneurals, but unlike *Polymixia*, uroneural 1 has a much smaller stegural process. Uroneural 1 extends anteriorly over preural centrum 1 + ural centrum 1 and terminates in a half-moon or sickle shape anteriorly and usually contacts the anteriormost epural (Fig. 4A). The number of uroneurals is reduced to one in *Aphredoderus* and amblyopsids but all extant species lack a stegural process. The uroneural in *Aphredoderus* is long and extends nearly to the distal tip of the epurals (Fig. 5A). The sole uroneural in amblyopsids is small, crescent shaped, and scarcely if at all overlaps the posterior margin of preural centrum 1 + ural centrum 1 (e. g., Figs. 6A,C). Fossil percopsids (Figs. 4B–F) and aphredoderids

(Figs. 5B,C) have two uroneurals, the anteriormost of which may bear a small stegural process (ROSEN & PATTERSON 1969, GRANDE 1988, MURRAY 1996, MURRAY & WILSON 1996). †*Sphenocephalus* similarly has two uroneurals (Fig. 3), in which the stegural process is better developed than that of *Percopsis* but not as developed as that of *Polymixia*. †*Asineops* has at least one uroneural (ROSEN & PATTERSON 1969: 415).

Uroneurals are typically absent in gadiforms, and the mechanism for absence is unknown even when developmental series have been surveyed (*Microgadus proximus*, MATARESE et al. 1981). MARKLE (1982: fig. 7b) reported one uroneural in *Bregmaceros* (contra our observations, FUJITA 1990: fig. 139, and those of ENDO 2002: fig. 26e, neither of whom labeled an uroneural). ROSEN & PATTERSON (1969) illustrated one uroneural in *Eretmophorus* (fig. 3d, Moridae) and something uroneural-like in *Urophycis* (fig. 3c), but did not label it. No uroneurals have been reported, and we did not observe any such elements in *Stylephorus* or any of the examined zeiforms. As in extant zeiforms, uroneurals and a stegural process are absent in †*Cretazeus*. In the basal zeiforms, †*Archaeozeus* and †*Protozeus* have one uroneural that lacks a stegural process but bears an unusual knob at its distal end (BACIU et al. 2005).

Lampriforms have zero (*Zu*, *Desmodema*: FUJITA 1990: fig. 171), one (*Lampris*: OELSCHLÄGER 1974, *Trachipterus*: OELSCHLÄGER 1983), or two uroneurals (*Velifer*: OELSCHLÄGER 1974). When an uroneural is present, a stegural process is also present. *Neoscopelus* (FUJITA 1990: figs. 115-6), *Morone*, and the beryciform *Sargocentron* have two uroneurals; only *Sargocentron* lacks a stegural process. *Diaphus* and the beryciforms *Hoplostethus* and *Melamphaes* have one uroneural, but again, the beryciforms lacked a stegural process. *Ogilbia* appears to possess one uroneural (assuming two epurals) that lack a stegural process. We did not observe uroneurals in other outgroups.

Autogenous accessory ossifications. Termed "X" and "Y" bones in gadiforms, these bones lie in the mid-sagittal plane, are unpaired, and lie anterior to the neural (X bones) or the haemal (Y bones) spines of preural centrum 2. Differing interpretations identify them as dorsal and anal-fin pterygiophores that have lost their rays (MARKLE 1982, FAHAY & MARKLE 1984) or as neural and haemal spines of centra that have been either lost or fused (ROSEN & PATTERSON 1969). We subscribe to the latter hypothesis supported in part by one morid gadiform (*Gadella*, FMNH 65712) in which the X bone was attached to preural centrum 2 via a narrow bridge of bone.

Accessory bones are common in gadiforms and rare in zeiforms. We observed X and Y bones in our targeted gadiforms with the exception of adult lotines, gadines, *Macruronus*, *Melanonus*, *Muraenolepis*, *Steindachneria*, and *Trachyrincus* (for a listing by gadiform genera and species, see MARKLE 1982: table 5 and FAHAY & MARKLE 1984: table 76). However, larval gadines and lotines usually lose X and Y bones during ontogeny (e. g., MARKLE 1982: fig. 9 of *Lota* development), but adults can retain them (e. g., Fig. 8F, putative X bone partially fused to the neural spine of preural centrum 3 in *Gadus*). We did not observe X and Y bones in *Muraenolepis* (Fig. 7B, contra FAHAY & MARKLE 1984: 282; ENDO 2002: fig. 26f). Of the few non-otolith gadiform fossils, "†*Protocodus*", †*Palaeogadus*, †*Palaeomolva*, †*Paratrisopterus*, and †*Bregmaceros albyi* have X and Y bones (COHEN 1984, FEDOTOV & BANNIKOV 1989). †*Pseudoraniceps* has at least Y bones but probably not X bones (FEDOTOV & BANNIKOV 1989 and references therein). In zeiforms, autogenous accessory bones were present in *Zenopsis* (FUJITA, 1990, TYLER et al. 2003), *Zeus* (TYLER et al. 2003), *Cyttus traversi* (USNM 308020 alcohol specimen, Y-like bone between preural centra 3 and 4), †*Zeus primaevus* (BACIU et al. 2005, Y bone), and the polymixiid †*Omosomopsis* (PATTERSON & ROSEN 1989: 12, fig. 4d, Y bone).

In gadiforms, X and Y bones tend to co-occur (Figs. 7A, 8A–D), although sometimes only one is present (e. g., *Euclichthys*, PAULIN 1983: fig. 5c and *Raniceps*, DUNN & MATARESE 1989: fig. 148b but see PATTERSON & ROSEN 1989: fig. 6, MARKLE 1989: fig. 17a, and ENDO 2002: fig. 26d, which illustrate intraspecific variation as both X and Y are present). This co-occurrence of bones is not the case in zeiforms, in which only Y bones are present.

Amongst other fishes, accessory bones have been identified in *Oryzias latipes* (beloniform, FUJITA 1990: fig. 162), *Pseudomugil* (atheriniform, JOHNSON & PATTERSON 1993: 559) and channids (DAY 1914, FUJITA 1990, MURRAY 2012). DUNN (1983: 9) listed cynoglossids as also having these ossifications but provided no further reference. In a single specimen of *Symphurus atramentatus*, we observed a bone between the neural spines of preural centra 2 and 3 and one between the haemal spines of preural centra 3 and 4. Both bones retained a pterygiophore-like shape (cartilaginous tips, expanded distally) and assisted in supporting the last dorsal and anal fin ray (CHAPLEAU 1988). The location of these accessory bones is apparently highly variable in cynoglossids as CHAPLEAU (1988) illustrated conditions where

(1) these two bones lie between their respective spines of preural centra 2 and 3 and articulate with a ray (figs. 14a and d, *Cynoglossus cynoglossus* and *Parapaglusia bilineata*), (2) they are absent (fig. 14b, *Symphurus plagusia*), or (3) the dorsal bone is absent but a greatly shortened ventral bone (~ ½ length of the preceding pterygiophore) does not articulate with a ray (fig. 14c, *Symphurus australis*).

Relationship between accessory bones, double-spined preural centra, and pterygiophore length in the gadiform caudal fin. The isocercal tail in gadiforms supports very few principal caudal-fin rays using the conventional means of correspondence with hypural plates (MARKLE 1982: table 5, DUNN 1983). In addition, the gadiform caudal fin has a variable relationship with the other median fins and as such, can be grouped into one of three categories: (1) separated from the dorsal and anal fins, (2) continuous with at least one of the dorsal or anal fins, or (3) absent in adults. All gadiforms with a caudal fin separated externally from the dorsal and the anal fins (*Bregmaceros*, *Euclichthys*, gadines, gaidropsarines, lotines, merlucciids, morids, phycines, and *Raniceps*) have accessory bones. Moreover, these lineages are the only gadiforms to have accessory bones (Figs. 7A, 8A–D), which can range in length from long (comparable in length to vertebral spines, Fig. 8A) to short (cartilaginous nubbins, MARKLE 1989: fig. 17a). Accessory bones can appear between preural centra 3 and 4 (e. g., PATTERSON & ROSEN: 1989: fig. 5b *Lotella callarias*) or between the doubled neural spines of preural centrum 2 (*Gaidropsarus*, FMNH 71280). Additionally, these lineages often exhibit a doubling of neural and haemal spines on preural vertebra, usually preural centrum 2 (e. g., MARKLE 1982: figs. 8b [*Gaidropsarus*], 8e [*Melanogrammus*], 8f [*Gadus*], 9b [*Lota*]; PATTERSON & ROSEN 1989: fig. 6 [*Euclichthys*]; ENDO 2002: fig. 26h [*Brosme*]). Finally, short proximal radials of the dorsal and anal fins articulate with neural and haemal spines distally in these fishes.

Only a few gadiform lineages have a caudal fin continuous with at least one of the dorsal or anal fins *(Macruronus*, *Melanonus*, *Muraenolepis*, and *Trachyrincus)*, but none have accessory bones (Figs. 7B,C). In these fishes, fewer instances of double spines on preural centra were observed or have been recorded in the literature (e. g., MARSHALL 1966: 277, *Macruronus* with two neural arches; MARKLE 1989: fig. 17b, *Muraenolepis*), although this could reflect a smaller sample size. The proximal radials are elongated and extend to close proximity of vertebral centra (Fig. 7B).

Finally, an internal caudal skeleton is lacking in more than 50 % of adult gadiforms (COHEN 1984: 260). In lieu of an internal support system, the dorsal and anal fins converge at the tip of the 'tail', but a label such as 'tailless' may be an over simplification for some. For example, in larger specimens of *Steindachneria*, an internal caudal skeleton can be absent, presumably the result of breakage during life. In smaller specimens (Fig. 7D, 143.1 mm SL, FMNH 67856; FAHAY 1989, 1.9–87.8 mm SL specimens) skeletal elements are present, but hypotheses of homology among caudal elements in *Steindachneria* are tenuous at best (FAHAY 1989: 156). Elongated pterygiophores extend to the margins of the vertebral centra (Fig. 7D) and appear to provide internal support to the "caudal fin". Overall, the co-occurrences of accessory bones, doubled-spined preural centra, and shorter pterygiophores are broadly diagnostic of gadoids.

Myology

Interradialis. The interradialis extends between adjacent caudal-fin rays, can span multiple rays, and controls the adduction of rays. It is exceptionally well developed in *Polymixia* (Fig. 11A), spanning d6-v7/8, and hides the proximal halves of the caudal rays in lateral view. A medial and separate division spans d6–10 proximally.

The percopsiforms show great variation in the size and insertion of the interradialis. In *Percopsis* (Fig. 11B), fibers overlap rays d7/8–v8/9, with a section across d9–10. Similarly, in *Aphredoderus*, the interradialis spans some combination of d8/9–v8/9, with a medial and dorsal section serving d7–9, d8–10, or d7–10. Notable variation occurs within Amblyopsidae, as the interradialis spans d4–v4, d6–v10, d8–v8, and d9–v9 in *Chologaster*, *Forbesichthys*, *Amblyopsis spelaea*, and *Typhlichthys*, respectively.

In gadiforms, the interradialis is present only between the rays and does not overlap them laterally (Fig. 12A–B; HOWES 1991: figs. 27, 31). In gadiforms with a distinct caudal fin (i. e., separated from the dorsal and anal fins), bundles are present between all, or virtually all, caudal rays (principal and procurrent). In several instances (e. g., *Euclichthys*), its presence between the anteriormost and succeeding procurrent rays is equivocal. In examined gadiforms with continuous median fins, the interradialis may occur between the 11 central-most rays in *Trachyrincus* (3 dorsal-fin rays, 4 rays on the upper hypural plate, 2 rays on the lower plate, 1 on the parhypural, 1 anal-fin ray), 12 in *Macruronus*, or 44–48 rays (yet not the four rays sitting on hypural plate 3–5) in *Muraenolepis*. In all cases, insertion includes rays of the dorsal and the anal fins.

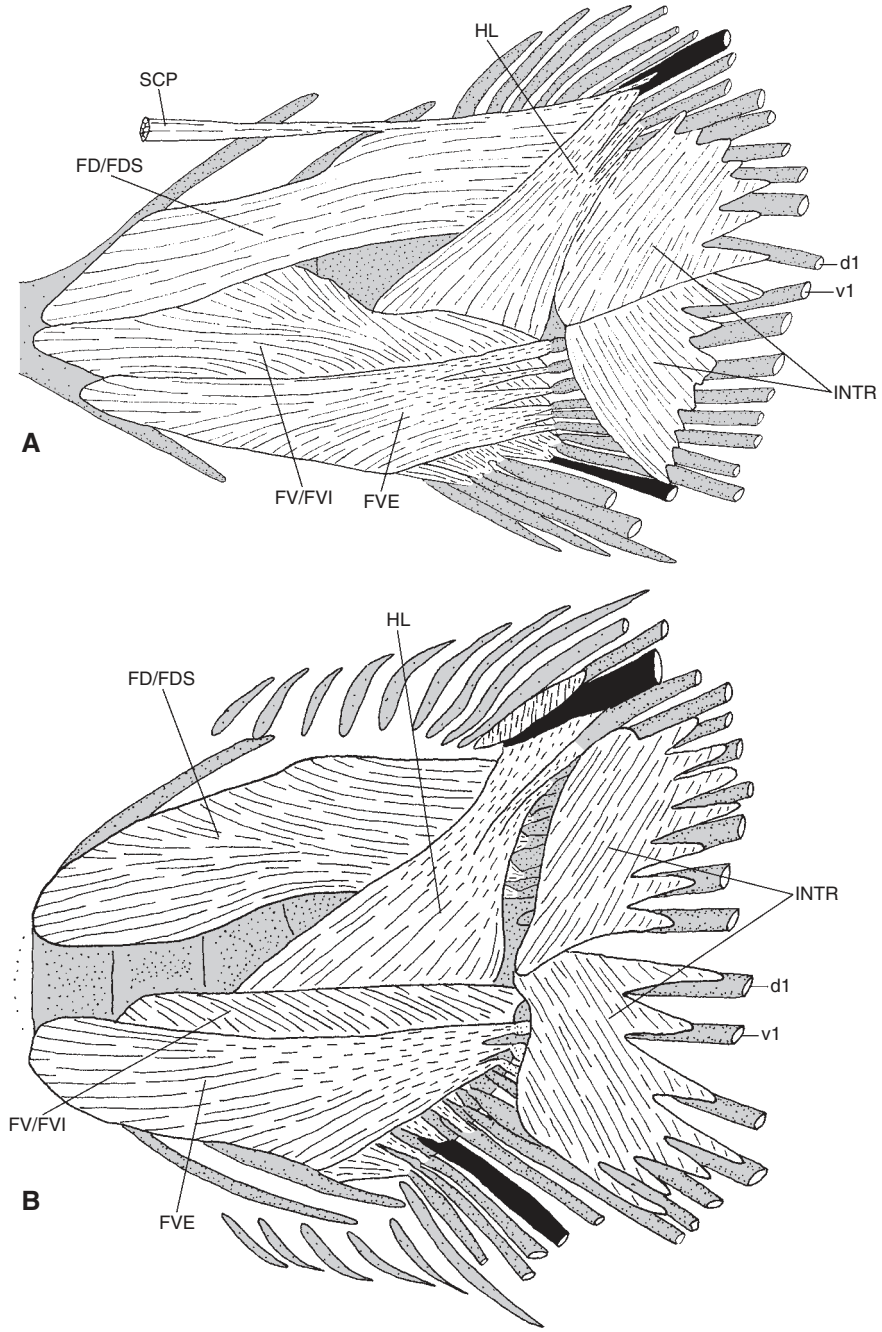

Fig. 11.
Myology of the caudal fin in selected polymixiiforms and percopsiforms. **A,** *Polymixia lowei* (USNM 185284; 82.4 mm SL); **B,** *Percopsis omiscomaycus* (FMNH 63459; 57.8 mm SL). Black rays indicate extent of the principal fin rays. Hypural plates medial to the fin rays have not been stippled in order to highlight insertions on the rays. Abbreviations: **d1**, first principal caudal-fin ray in the dorsal series; **FD**, flexor dorsalis; **FDS**, flexor dorsalis superior; **FV**, flexor ventralis; **FVE**, flexor ventralis externus; **FVI**, flexor ventralis inferior; **HL**, hypochordal longitudinalis; **INTR**, interradialis; **SCP**, supracarinalis posterior; **v1**, first principal caudal-fin ray in the ventral series. Anterior is to the left.

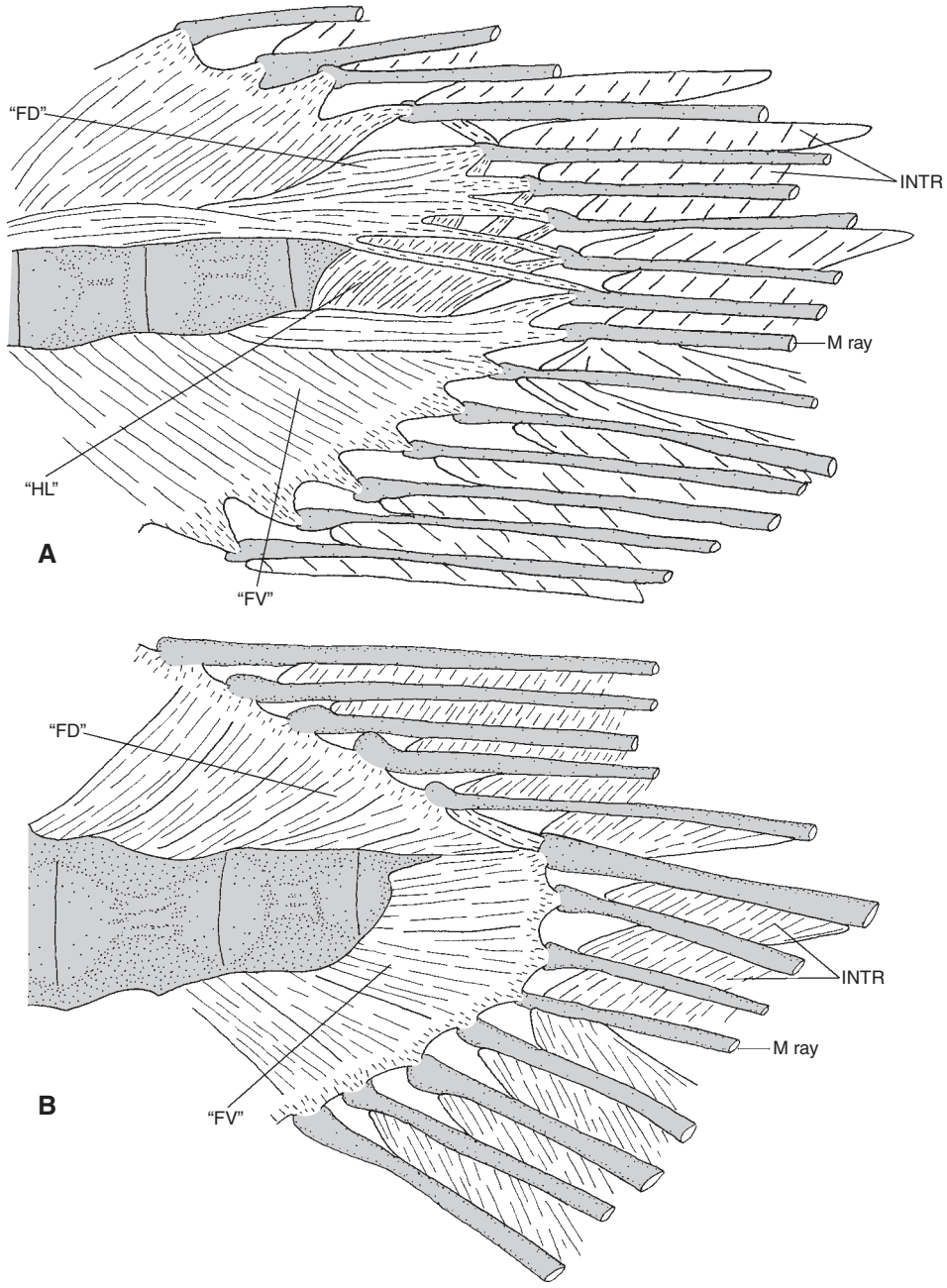

Fig. 12.
Myology of the caudal fin in gadiforms. **A,** *Merluccius productus* (LACM 56764; 120.0 mm SL); **B,** *Gadus macrocephalus* (LACM 33868; 122.3 mm SL). Abbreviations: **FD**, flexor dorsalis; **FV**, flexor ventralis; **HL**, hypochordal longitudinalis; **INTR**, interradialis; **M ray**, "central fin ray" of HOWES 1991. Anterior is to the left. Quotation marks indicated potential homoplasy with non-gadiform teleosts (see HOWES 1991).

HOWES (1991) considered the interradialis in gadiforms to be analogues to the interradialis in other teleosts. In fact, HOWES (1991) asserted that none of the caudal-fin muscles in gadoids had homologues in teleosts. In order to explain how interradialis bundles appeared unexpectedly between procurrent rays, he posited that interradialis bundles were modified depressors of the dorsal and anal fin (HOWES 1991: 106). If the gadiform interradialis was derived from depressors of the dorsal and anal fins, we might anticipate that similar bundles could be present between rays of the dorsal and anal fins in any fish with a separated caudal fin. However, we did not observe interradialis bundles between fin rays of the dorsal and anal fins in gadiforms with a separated caudal fin, and WINTERBOTTOM (1974a: 282) did not report any instances of the interradialis serving dorsal or anal fins in the teleosts he surveyed. The interradialis is also absent in gadiforms that have a greatly reduced or absent internal caudal skeleton (e.g., *Bathygadus*, *Coelorinchus*, *Nezumia*). A more parsimonious explanation at this time is the anterior migration of the interradialis onto the dorsal and anal fin rays in gadiforms with continuous median fins. The interradialis appears to be absent in *Stylephorus* although connective tissue attaches v1 and v2 and the dorso-anterior corner of v1 to the postero-lateral surface of ural centrum 2+hy3-n.

In zeiforms, a large interradialis lies between rays but also across them laterally (Fig. 13). Coverage of the fin rays ranges from d5–v7 *(Cyttus australis*, *Oreosoma*, and *Zenion)*, d6–v6 *(Zeus)*, and d6–v7 *(Cyttopsis*, *Cyttus traversi*, *Parazen*, *Xenolepidichthys*, and *Zenopsis)*. Only *Oreosoma* has an additional dorsal and medial section that serves d5–6.

The interradialis is well developed in most beryciforms and hides the proximal ends of the rays in lateral view. The basic muscle coverage is d9–v9 *(Anoplogaster*, *Diretmus*, and *Rondeletia)* with additional dorsal sections serving d7–11 *(Centroberyx)*, d8–11 *(Hoplostethus)*, or d9–10 *(Melamphaes)*. The interradialis is well developed in lampriforms *(Regalecus*; OELSCHLÄGER 1983: fig. 78c, *Trachipterus*, *Zu)* and spans all fin rays (d8v6 in *Trachipterus*, d8v5 in *Zu*) laterally but apparently not between adjacent fin rays.

In *Esox*, *Synodus*, myctophids *(Neoscopelus*, *Diaphus)*, ophidiids *(Lepophidium*, *Petrotyx)*, bythitids *(Ogilbia)*, and probably most percomorphs (*Morone*, *Gasterosteus*, and *Triacanthodes* as in WINTERBOTTOM 1974b: 126, fig. 56), the interradialis crosses multiple fin rays laterally. In the lophiiform *Histrio* and the gasterosteiform *Culaea*, only a few fibers proximally located pass lateral to the rays.

Hypochordal longitudinalis. The hypochordal longitudinalis originates from hypurals 1 and 2, occassionally hypural 3, a combination of ural centra, preural centrum 1 or the products of their fusions, and the hypurapophysis when present. The muscle is obliquely oriented, with the origin anterior and ventral to the insertion. Insertion is by distinct, often long, tendons to the ventral surface of a variable number of principal fin rays in the dorsal half of the caudal fin. Insertion sites migrate distally as the distance from the lateral midline increases. The hypochordal longitudinalis has a noteworthy spatial relationship with the flexor dorsalis and flexor ventralis muscles. The hypochordal longitudinalis is lateral to the flexor dorsalis and medial to the dorsal border of the flexor ventralis. In polymixiids, the muscle has an insertion of d6–9 (Fig. 11A).

Percopsiforms display a significant amount of variation in its insertion. Bilateral dissections of *Percopsis* reveal both intra-specific variation and intra-individual variation (i.e., asymmetry), suggesting that the phenomenon is not solely due to dissection or observation error. The most frequent percopsid insertion is d6–9 (Fig. 11B), but we also observed insertions of d7–9, d5–9 (one side of one individual), and d8–9 (one side of one individual) in *Percopsis omiscomaycus*. The most frequent asymmetrical combination is d6–9 and d7–9. All aphredoderid specimens that we examined share a d6–9 insertion. Amblyopsids are highly variable: d2/3/4–6 (*Forbesichthys*, d4–6 being the most common), d1–3 *(Chologaster)*, and d1–5 *(Amblyopsis* and *Typhlichthys)*. Fewer amblyopsid specimens were available for dissection, so comments on intraspecific variation and asymmetry in this group are premature.

When the muscle is present in gadiforms, fibers are obliquely oriented, as one would expect. Fibers originate primarily on the lower hypural plate(s), medial to the flexor ventralis, and insert on principal fin rays dorsal to the lateral midline. However the muscle is medial to the flexor dorsalis (Appendix 2), and the bundle as a whole is rectangular with very short tendons (not triangular with tapering, long tendons as in other teleosts). If this bundle is the hypochordal longitudinalis (contra HOWES 1991), it is present in all but *Muraenolepis* (HOWES 1991), *Trachyrincus*, gadines (Fig. 12B; SYMMONS 1979), lotines, and *Gaidropsarus*. When it is present, it inserts on d3–6 *(Lotella*, *Melanonus*, and *Phycis)*, d2–5 (*Merluccius*, Fig. 12A), d2–6 *(Tripterophycis*, *Urophycis)*, d3 *(Euclichthys)*, d4 *(Bregmaceros)*, and central fin ray-d2 *(Macruronus)*. We failed to observe the hypochordal longitudinalis in *Stylephorus*.

HOWES (1991) identified this muscle as the "hypural segment of hypaxial muscle" (HOWES 1991: 100,

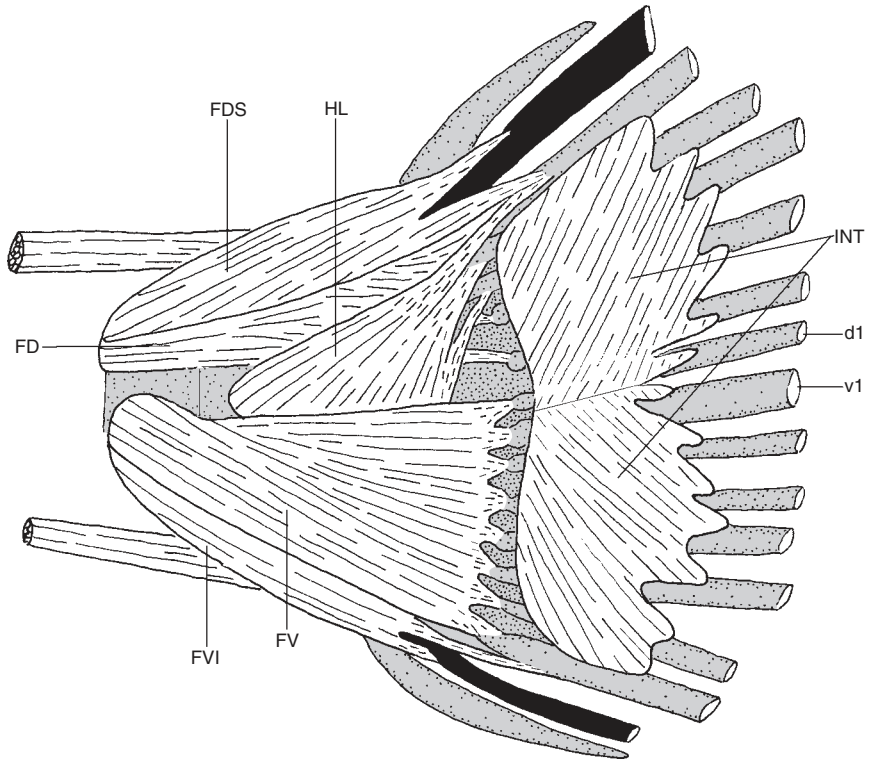

Fig. 13.
Myology of the caudal fin in zeiforms. *Xenolepidichthys dalgleishi* (USNM 377985; 67.2 mm SL). Black rays indicate extent of the principal fin rays. Abbreviations: **d1**, first principal caudal-fin ray in the dorsal series; **FD**, flexor dorsalis; **FDS**, flexor dorsalis superior; **FV**, flexor ventralis; **FVI**, flexor ventralis inferior; **HL**, hypochordal longitudinalis; **INTR**, interradialis; **v1**, first principal caudal-fin ray in the ventral series. Anterior is to the left.

"hsh" in fig. 27). His name emphasizes its origin on the lower hypural plate and its presumed analogous relationship to the hypochordal longitudinalis in non-gadiform teleosts. HOWES (1991: 106) rejected its homology with the hypochordal longitudinalis because (1) the origin of the "hypural segment of hypaxial muscle" does not include the hypurapophysis, (2) it does not narrow at its insertion, and (3) it is not separated from the interradialis by a thick, connective tissue over the anterior ends of the caudal rays (at least in acanthopterygians, HOWES' note). We address his criteria and observe that the presence of the hypochordal longitudinalis is independent of that of the hypurapophysis. For example, the hypurapophysis may be absent (e.g., *Zenion*) or present (e.g., *Xenolepidichthys*) and yet both species have a hypochordal longitudinalis. The hypochordal longitudinalis in gadiforms has very short insertional tendons. These short tendons necessitate that the bulkiness of the muscle fibers is retained throughout the muscle's length (Fig. 12A) giving it a rectangular outline. In contrast, when the hypochordal longitudinalis tapers noticeably, muscle fibers grade into long tendons, and the muscle loses much of the its bulkiness distally (Fig. 11A). The posterior border of the gadiform hypochordal longitudinalis is not attached to bone or connective tissue and a small space exists between it and the anterior tips of the caudal rays. More disconcerting than HOWES' points is the medial location of the muscle relative to the flexor dorsalis, or a muscle we identify as the flexor dorsalis. If the "hsh" is not the homologue to the hypochordal longitudinalis, can the latter be lost and subsequently replaced?

In fact, the hypochordal longitudinalis is absent in *Fundulus* (GRENHOLM 1923: fig. 42, pers. obs.), but there is no analogue. Conceivably then, the hypochordal longitudinalis could have been lost and replaced functionally and topologically in some gadiforms. However, in the absence of convincing evidence to the contrary, we assume that the muscles of the caudal fin in gadiforms are teleosts homologues, but readily concede that their myology is as perplexing as their osteology.

In zeiforms, the hypochordal longitudinalis serves relatively few rays; an insertion of d3–5 occurs in all but Zeidae (*Zenopsis* d2–5 and *Zeus* d4–5) and Grammicolepididae (d4–6, Fig. 13).

Beryciforms have an insertion of d6–10 *(Anoplogaster*, *Diretmus*, *Hoplostethus*, and *Stephanoberyx)* or d7–10 *(Centroberyx*, *Melamphaes*, and *Rondeletia)*. In the lampriforms *Trachipterus* and *Zu*, the hypochordal longitudinalis inserts on the dorsalmost caudal filament (d8) and lies lateral to the flexor dorsalis, as expected. In other outgroups, the hypochordal longitudinalis serves rays d5 and those more dorsal in *Esox*, the aulopiform *Synodus*, myctophids *(Diaphus* and *Neoscopelus)*, and the percomorphs *Culaea*, *Gasterosteus*, and *Morone* but not in *Triacanthodes* (d2–4, WINTERBOTTOM 1974b: 10).

Flexor dorsalis and flexor dorsalis superior. The flexor dorsalis originates from a variable number of centra, neural arches, and neural spines to insert tendinously on a variable number of dorsal principal caudal-fin rays. The insertion site shifts from the anterior end of a ray for those close to the lateral midline to a more distal and ventral site on a ray removed from the lateral midline. The flexor dorsalis superior lies dorsal to the flexor dorsalis and originates from neural spines, epurals, and occasionally procurrent rays. Insertion of the flexor dorsalis superior is tendinous on the more dorsal principal caudal-fin rays and/or the posteriormost procurrent rays. The flexor dorsalis is not always differentiable from the flexor dorsalis superior.

In *Polymixia*, the flexor dorsalis inserts on rays d1/2–8, and a separate bundle identified as the flexor dorsalis superior inserts on d9 only (Fig. 11A). Ray d9 is a principal caudal-fin ray by definition (*P. berndti*: d10v10. *P. lowei*: d9v9) but it is branched in *P. berndti* and unbranched in *P. lowei*.

In percopsiforms, a single mass serves the dorsal principal caudal-fin rays. The most frequent insertion in *Percopsis* is d2–8 (but may include d1 and/or d9; Fig. 11B) with a typical ray count of d9v9. *Aphredoderus sayanus* has an insertion of d1–7 and ray counts of d8v8, d8v9, and d9v9. Amblyopsids have insertions of d1–9 in *Amblyopsis* (d7v7) and *Chologaster* (d6v6 and d6v5), d1–10 in *Typhlichthys* (d7v5*, minimally five rays in the ventral series), and d1/2–11/12 in *Forbesichthys* (d9v7 and d8v7). The flexor dorsalis inserts only on branched rays in percopsids and aphredoderids, but on both branched and unbranched rays, including procurrent rays, in amblyopsids (Fig. 14).

In gadiforms, muscles serving the dorsal series of rays have a unique structure (HOWES 1991: fig. 27). Fibers nearest the lateral midline are horizontally oriented, serve rays (via long tendons) supported by the upper hypural plate(s), and often form a discrete section (e.g., *Merluccius*, Fig. 12A). This section is lateral to the hypochordal longitudinalis, when the latter is present. The obliquely oriented bundles serve the remainder of the rays. These bundles are structurally reminiscent of the compound erectors and depressors that serve rays of the dorsal or anal fin (HOWES 1991). The insertion from these gadiform bundles varies from two adjacent tendons to a single, broad insertion, the latter just as the erectors and depressors that serve the last ray(s) of the dorsal or anal fin (WINTERBOTTOM 1974a: 283).

Variation is present in the number of rays served by the horizontal section: d1–5/6 (*Merluccius*, morids), v1-central fin ray-d3 *(Microgadus)*, central fin ray-d3 *(Theragra)*, d1–4 *(Muraenolepis*, *Trachyrincus)*, d1–2 *(Macruronus)*, and d1–3 *(Euclichthys)*. In other gadiforms, this horizontal section is not readily differentiable from the other bundles, but the insertion of the single mass varies and includes d1 *(Lota*, *Melanonus)*, d3 *(Phycis)*, d4 *(Bregmaceros)*, and d5 *(Urophycis)*.

In *Stylephorus* a bundle that originates from a myocommatum shared with epaxialis fibers inserts on the dorsalmost ray (d4). This bundle is well developed, the fibers are obliquely oriented, and it lies has a similar spatial relationship of a bundle in lampriforms we identified as the flexor dorsalis superior. An extremely small tendon connects the dorsal fin to d4, and we identify this bundle as the supracarinalis superior. The flexor dorsalis is problematic. If it exists, it is heavily graded with the overlying epaxialis and becomes entirely aponeurotic lateral to ural centrum 2+hy3-n. Anteriorly fibers grade with the body musculature and preural centra. This aponeurosis appears to attach to all the dorsal rays. OELSCHLÄGER (1983: fig. 78e) illustrated an aponeurosis (flexor dorsalis?) that serves four of the five dorsal rays. We will tentatively identify this bundle as the flexor dorsalis.

A partially separable flexor dorsalis and flexor dorsalis superior characterize zeiforms with the exception of *Zeus faber*, which has a single mass inserting on d3–6 (d6v7). In *Xenolepidichthys* (d7v8, Fig. 13), although partially separable, both muscles are heavily graded as to be functionally one mass inserting on rays d2–6/7. In the majority of zeiforms (*Cyttopsis rosea*, *Cyttus*, *Oreosoma atlanticum*, *Zenion hololepis*, and *Zenopsis conchifer*, all d6v7), the flexor dorsalis and the flexor dorsalis superior are separable and collectively insert on d2–6. *Parazen* is unique among zeiforms; the flexor dorsalis inserts on d2–6 and includes a procurrent ray (d5v6). *Parazen pacificus* has two long, unbranched rays above and below the branched

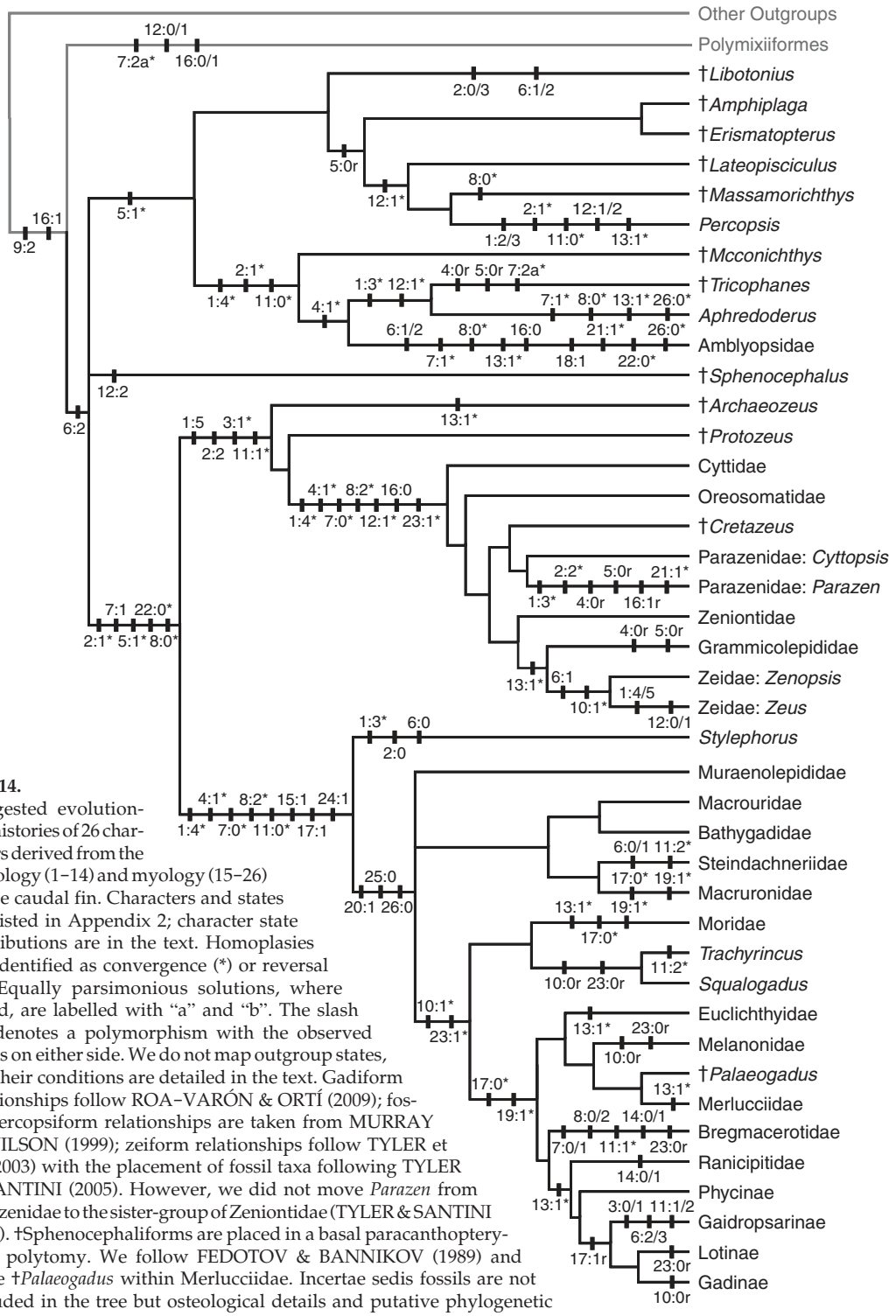

Fig. 14.
Suggested evolutionary histories of 26 characters derived from the osteology (1–14) and myology (15–26) of the caudal fin. Characters and states are listed in Appendix 2; character state distributions are in the text. Homoplasies are identified as convergence (*) or reversal (r). Equally parsimonious solutions, where noted, are labelled with "a" and "b". The slash (/) denotes a polymorphism with the observed states on either side. We do not map outgroup states, but their conditions are detailed in the text. Gadiform relationships follow ROA-VARÓN & ORTÍ (2009); fossil percopsiform relationships are taken from MURRAY & WILSON (1999); zeiform relationships follow TYLER et al. (2003) with the placement of fossil taxa following TYLER & SANTINI (2005). However, we did not move *Parazen* from Parazenidae to the sister-group of Zeniontidae (TYLER & SANTINI 2005). †Sphenocephaliforms are placed in a basal paracanthopterygian polytomy. We follow FEDOTOV & BANNIKOV (1989) and place †*Palaeogadus* within Merlucciidae. Incertae sedis fossils are not included in the tree but osteological details and putative phylogenetic affinities are discussed in the text.

fin rays (KOTLYAR 2001: fig. 4, TYLER et al. 2003: fig. 34); intrinsic caudal-fin muscles serve all four of these rays.

Beryciforms display a range of insertions of the flexor dorsalis-flexor dorsalis superior including d1–10 *(Diretmus*, *Melamphaes*, and *Hoplostethus)*, d1–9 *(Rondeletia)*, d2–9 *(Centroberyx* and *Stephanoberyx)*, and d2–10 *(Anoplogaster)*. Only *Melamphaes* has a distinct flexor dorsalis superior, and it serves d10. The flexor dorsalis is restricted to the branched principal fin rays in *Centroberyx* and *Rondeletia* but includes the dorsalmost, and therefore unbranched, principal fin ray in other beryciforms (indeterminate in *Stephanoberyx*). In *Centroberyx*, a ligament connects d1 and d2, and d1 is served by only the interradialis.

In the lampriforms *Trachipterus* and *Zu*, a single muscle mass passes medial to the hypochordal longitudinalis and inserts on what appears to be all of the rays in the dorsal series. Dorsal to this muscle is a well-developed bundle identified as the flexor dorsalis superior. It shares a myocommatum with the epaxialis anterior to the origin of the flexor dorsalis and inserts on the d8, the dorsalmost ray. In addition, a supracarinalis posterior serves d8.

Esox, *Synodus*, myctophids *(Neoscopelus* and *Diaphus)*, beryciforms, *Histrio*, *Ogilbia*, *Porichthys*, ophidiids, and probably most percomorphs (*Morone*, *Gasterosteus*, *Triacanthodes* in WINTERBOTTOM 1974b: fig. 56) lack compound bundles (character 20, state 0) of the flexor dorsalis. The flexor dorsalis and flexor dorsalis superior are separable in myctophiforms, *Polymixia*, zeiforms, *Porichthys*, *Histrio*, *Ogilbia*, and *Culaea*, but appear as a single mass in percopsiforms, beryciforms, ophidiids, and *Morone*.

Flexor ventralis externus. The flexor ventralis externus is the most lateral of the caudal-fin muscles below the lateral midline and originates from a variable number of centra and haemal spines. The muscle is horizontally oriented, and grades into an aponeurosis posteriorly, from which long tendons arise and insert on ventral caudal-fin rays.

The flexor ventralis externus is present in polymixiids (Fig. 11A, v1/2–6), percopsids (Fig. 11B, variation and asymmetry include: v1–4, v2–4, v2–3, v1–5, and even v2–8, with v2–4 the most frequent observation), and *Aphredoderus* (v1–2, v1–3, v2–3, v2–4, and one case of v1–2, 5–6). In beryciforms, with the exception of *Diretmus*, the flexor ventralis externus is present (*Rondeletia*, *Hoplostethus*: v1–6, *Anoplogaster*: v1–5, *Stephanoberyx*: v1–7, *Melamphaes*: v1–7–d1, and *Centroberyx*: v2–6/7). Among other taxa examined, the flexor ventralis externus is present in *Esox* (v1–3, v1–2), *Parasudis* (v1–7), *Diaphus* (v1–8), *Histrio* (v1–5), *Ogilbia* (v1–2, minimally), *Gasterosteus* (v2–4), *Culaea* (v1–4), *Morone* (v1–2), and *Triacanthodes* (v1–2, WINTERBOTTOM 1974b: 10). The flexor ventralis externus is not identified in amblyopsids, gadiforms (Figs. 11A–B), zeiforms (Fig. 13), *Stylephorus*, *Porichthys*, *Neoscopelus*, *Coccorella*, and ophidiids (Appendix 2). In lampriforms *(Trachipterus*, *Zu)*, we did not observe the flexor ventralis externus, although there is an aponeurosis (no muscle fiber observed) that is partially consistent with the location and orientation of the flexor ventralis externus.

Flexor ventralis and flexor ventralis inferior. The flexor ventralis is medial to the flexor ventralis externus and is the largest muscle serving the rays of the ventral series. Its origin may include preural centra and haemal spines, hypural plates, the parhypural, the hypurapophysis, and ural centra. Fibers are horizontally oriented at the lateral midline but run more obliquely as distance from the midline increases. Insertion is by short tendons to the anterior and anterodorsal surfaces of the fin rays. The flexor ventralis inferior serves fewer and more ventral rays than the flexor ventralis and is the ventral counterpart of the flexor dorsalis superior. The flexor ventralis and flexor ventralis inferior are often fused into a single muscle mass or grade into each other, especially near their origins. In polymixiids, the flexor ventralis inserts on v1–9 and a distinct flexor ventralis inferior inserts on v10–12 (Fig. 11A).

In percopsids, the flexor ventralis inserts on v1–8 with little variation, and the flexor ventralis inferior inserts most commonly on v9–11 but occasionally includes v12 (Fig. 11B) or v13 (asymmetric variation). The flexor ventralis and flexor ventralis inferior are graded anteriorly. Aphredoderids have a single muscle mass that inserts on v1–9. Amblyopsids also have a single muscle mass with varying degrees of separation, again mostly laterally. In *Chologaster*, a single mass with only partial, lateral separation inserts on v1–7. What is unusual in this case is that this partial separation occurs between v2–3 or v3–4. *Forbesichthys* and *Typhlichthys* have insertions of v1–9, and *Amblyopsis* has one of v1–8/9.

In gadiforms, the flexor ventralis, like the flexor dorsalis, can have compound bundles with either two adjacent tendons or a single, broad tendon inserting on a given ray (e.g., HOWES 1991: fig. 27a). The muscle can appear either as distinct bundles, based largely on fiber direction with small gaps between groups of fibers, or as a single mass, particularly along the lateral midline. The insertion appears to invariably include the first ventral procurrent ray (in gadiforms with an isolated caudal fin) but variably

extends dorsally to v4 *(Bregmaceros)*, v1 *(Lota*, *Macruronus*, *Microgadus*, and *Melanonus)*, central fin ray *(Theragra)*, d1 (Fig. 12A, *Merluccius*, *Euclichthys*, *Urophycis*, and morids), d2 *(Phycis)*, d3 (Fig. 12B, *Gadus*), or d5 *(Gaidropsaurus)*. In *Muraenolepis* and *Trachyrincus* (continuous caudal fin with dorsal and anal fins), fibers consistent with the flexor ventralis serve rays on the lower hypural plate and paryhypural but do not include rays in the dorsal series.

The flexor ventralis is the most readily identifiable muscle in *Stylephorus*. It originates from preural centrum 1 + ural centrum 1 and runs obliquely to insert on the lateral, proximal surface of ray v2. The infracarinalis posterior inserts on the ventral, proximal face of ray v2. In one dissection, we observed a bundle that originates from preural centrum 2 and runs obliquely as it passes ventral of the flexor ventralis to insert on one of the two small splints of bone anterior to v2. We cautiously identify this bundle as the flexor ventralis inferior.

Zeiforms have remarkable consistency in the pattern of the flexor ventralis and flexor ventralis inferior. With the exception of *Cyttopsis* and *Zeus*, the flexor ventralis inserts on d1–v7 and is partially separable into two or three sections, of which one serves d1. The flexor ventralis in *Cyttopsis* inserts on v1–7. In *Zeus*, the flexor ventralis inserts on d2–v7. One individual of *Zenopsis* exhibits a flexor ventralis that serves d2–v7 on one side and d1–v7 on the other side. The flexor ventralis inferior is differentiable from the flexor ventralis and inserts on v7 with the exception of *Cyttus australis* and *Xenolepidichthys* (v7–8, Fig. 13), *Zenopsis* (v6–7), and *Zeus* (v5/6–7). Similar to their dorsal antagonists, the flexor ventralis-flexor ventralis inferior mass is restricted primarily to the principal fin rays with the exception of *Parazen* (noted above) and *Cyttus australis*.

It is not uncommon to find an aponeurosis connecting d1 and the flexor ventralis (WINTERBOTTOM 1974a: 292). What is interesting is that the flexor ventralis may serve not only d1 but also d2, and this trend is common in gadiforms and zeiforms, and in a twist, ray v1 in *Microgadus* is served by both the flexor dorsalis and ventralis. By far the most confusing situation to understand functionally is *Urophycis* in which d2–4 are not served by either flexor although rays dorsal and ventral to these are served by the flexors.

The beryciform flexor ventralis and flexor ventralis inferior are easily differentiable, with the flexor ventralis serving v1–9 in all but *Melamphaes* (d1–v8) and *Stephanoberyx* (d1–v9). The flexor ventralis inferior inserts on v10–11 in all but *Melamphaes* (v9–10) and *Stephanoberyx* (v10).

In lampriforms, we found a single bundle (flexor ventralis + flexor ventralis inferior?) in trachipterids *(Trachipterus* and *Zu)* that originates from a shared myocommatum with the hypaxialis and preural centra to insert on v4 in *Zu* and probably v5 in *Trachipterus* (the last ray is a small nub of bone in both species). A much smaller and bilaterally paired tendon runs along the ventral surface of the flexor ventralis to a caudal ray; this is the infracarinalis posterior.

Esox, *Synodus*, myctophids *(Neoscopelus* and *Diaphus)*, beryciforms, *Porichthys*, ophidids, *Ogilbia*, *Histrio*, and probably most percomorphs (*Morone*, *Gasterosteus*, and *Triacanthodes* in WINTERBOTTOM 1974b: fig. 56) do not have compound flexor ventrales (Appendix 2). Ophidiids and *Porichthys* have a single, largely undifferentiable muscle mass (albeit subjectively separable) serving the fin rays of the ventral lobe (Appendix 2).

Extent of the origin of intrinsic caudal-fin muscles. The centra and a portion of ural centrum 2 are largely exposed following removal of the epaxialis and hypaxialis in gadiforms (Fig. 12A, HOWES 1991: fig. 27a), *Stylephorus*, and lampriforms. In all other paracanthopterygians examined, caudal muscles originate on the ural centra and posterior preural centra thereby hiding them in lateral view (Fig. 11B). This latter pattern also characterizes *Esox*, *Synodus*, myctophids *(Neoscopelus* and *Diaphus)*, beryciforms, *Histrio*, *Porichthys*, *Ogilbia*, ophidiids, and probably most percomorphs but at least *Gasterosteus*, *Morone*, and *Triacanthodes* (as in WINTERBOTTOM 1974b: fig. 56).

Discussion

According to ROSEN & PATTERSON (1969: 462) "no single character or combination of characters can be found that occurs in all paracanthopterygians". Given the taxonomic composition considered by ROSEN & PATTERSON (1969), they may have been correct. Yet, a revised Paracanthopterygii consisting of percopsiforms, gadiforms, *Stylephorus*, and zeiforms is diagnosable based on both molecules (e.g., mitochondrial and nuclear genes) and morphology (e.g., loss of supramaxillae, widely separated exoccipital facets, supraneurals reduced to one; GRANDE et al. this volume).

We recovered characters of the caudal fin (Appendix 2) that provide additional morphological support for the monophyly of paracanthopterygians and their intrarelationships, albeit with non-trivial amounts of homoplasy (Fig. 14). The simplification (fusion and loss) of the caudal skeleton is a significant contributor to nodal support and is evidenced by nearly every aspect of the caudal skeleton as the number of epurals, uroneurals, and hypurals are reduced from the relatively plesiomorphic conditions seen, for example, in the outgroup Polymixiiformes. Further, the bony elements that remain exhibit increased fusion as exemplified in the zeiform caudal skeleton. Myological evidence highlights the uniqueness of the gadiform caudal fin. In these fishes, loss of intrinsic muscles and the re-shuffling of those that remain contribute to this uniqueness (HOWES 1991).

Osteological and myological characters are not randomly distributed among paracanthopterygians (Fig. 14). Very few derived character states are seen in fossil percopsids and sphenocephaliforms. Derived osteological characters are clustered among Recent percopsiforms and the stem lineages of gadiforms, stylephoriforms, and zeiforms. In contrast, myological states are clustered at the stylephoriform + gadiform, gadiform, and gadoid nodes. In fact, nearly two-thirds of the myological state changes occurred in these lineages. If the pattern of shared homoplasies among the myological characters is suggestive of potential errors in the phylogeny of gadiforms, then *Macruronus*, morids, *Squalogadus*, and *Trachyrincus* are prime targets for additional study. For example, the relationships of these four taxa posited by ENDO (2002: fig. 28, *Squalogadus* and *Trachyrincus* as macrouroids, and *Macruronus* as a gadoid) are more congruent with some characters (e.g., character 17, presence/absence of the hypochordal longitudinalis) than the relationships inferred from molecular sequences. Similarly, homoplasy patterns within percopsiforms suggest that further refinement of fossil placement is possible. Perhaps the abundance of homoplasy in the caudal fin is to be expected (e.g., JOHNSON & PATTERSON 1993, GILL 1996) given the morphological disparity, ecological diversity, and antiquity of these lineages (e.g., major clades originating in the Cretaceous; NEAR et al. 2012: fig. 1).

Overall, the caudal skeleton of paracanthoptherygians ranges from generalized forms with many autogenous bones (e.g., fossil percopsiforms) to more derived skeletons characterized by fusions (e.g., zeiforms) and putative losses (e.g., *Stylephorus*) of bony elements. This macroevolutionary trend toward the 'simplification' of the caudal skeleton characterizes teleosts as a whole (GOSLINE 1971), and its presence should not be surprising among paracanthopterygians. The simplification of the caudal skeleton is well illustrated by Percopsiformes, in which fossil percopsids exhibit a relatively unconsolidated caudal skeleton (six autogenous hypurals, two epurals, and two uroneurals) in contrast to Recent amblyopsids that have only two hypural plates, one of which is fused to ural centrum 2, one or two epurals, and one uroneural.

Inclusion of fossils influenced our conclusions about character evolution. For example, a fusion of the upper hypurals with ural centrum 2 could support Paracanthopterygii, but inclusion of stem-percopsiforms and fossil percopsids, in which hypurals are not fused to ural centra, demonstrates that the fusion occurred in more derived percopsiforms. In addition, fossils have revealed new suites of character states (e.g., †*Archaeozeus* and †*Protozeus* are the only zeiforms with epurals, †*Amphiplaga* and other fossil percopsids lack fusion of any hypurals). Their placement as basal zeiforms and derived percopsids, respectively, has important implications for understanding the finer details of macroevolutionary trends with Paracanthopterygii. As another example, fossil aphredoderids have a parhypural that contacts the vertebral column, yet *Aphredoderus* and amblyopsids have a detached parhypural. These examples demonstrate how the omission of fossils would yield a different polarization and resolution of character transformation series and interpretation of macroevolutionary patterns.

Inferring myological states from skeletons, including fossils, is extremely difficult. This is particularly evident when comparing gadiforms and percopsiforms, which have similar osteologies but starkly different myologies. In general, myological patterns of origin and insertion do not echo the patterns of bony fusions, losses, and complexity. In the most general of terms, muscles appear to be more evolutionarily conservative than bones (BORDEN 1999, DIOGO 2004) even within diverse lineages and at various taxonomic ranks. Consequently, the number of osteological characters usually outnumbers myological characters, but a tradeoff has been suggested whereby myology might contain less homoplasy. In this study, we recognized 14 osteological and 12 myological characters, yet the osteological characters are diagnostic of deeper nodes, and both character sets display ample homoplasy. Unknown and inapplicable character states (fossil taxa, loss of muscles, loss of caudal fins) contribute to equivocal optimizations and to ambiguous evolutionary histories.

In conclusion, suites of character states derived from the osteology and myology of the caudal fin support many of the clades of the revised Paracanthopterygii (percopsiforms, gadiforms, stylephoriforms, zeiforms). Significant work remains to place the many lineages of paracanthopterygians and related acanthomorphs, work that could greatly alter and improve our understanding of the macroevolutionary history of the group. Despite an anticipated increase in available data from fossils, extant morphologies, and molecules, systematists will still have the large task of reconciling disparity in their phylogenetic signals.

Acknowledgements

We thank R. WINTERBOTTOM, E. O. WILEY, two anonymous reviewers, and editor G. ARRATIA, all of whom provided comments and suggestions that contributed to an improved manuscript. We are grateful to M. WILSON for constructive critiques of text, insight on fossil paracanthopterygians, and figure formatting. M. MALONE assisted with figure preparation. This study was not possible without the specimens generously loaned by J. BRUNER and A. MURRAY (University of Alberta Laboratory for Vertebrate Paleontology, 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 Museum of Vertebrates, Ithaca); L. GRANDE, S. MOCHEL and K. SWAGEL (Field Museum Natural History, Geology and Zoology Departments, Chicago); L. ROBINS and L. PAGE (Florida Museum of Natural History, Gainesville); C. THACKER and R. FEENEY (Natural History Museum of Los Angeles County, Los Angeles); A. BENTLEY and E. WILEY (University of Kansas Biodiversity Institute); K. HARTEL (Museum of Comparative Zoology, Boston); E. HOLM, H. LOPEZ-FERNANDEZ, and R. WINTERBOTTOM (Royal Ontario Museum, Department of Natural History, Toronto); M. NEWBERY (Royal Tyrrell Museum of Paleontology, Drumheller), P. HASTINGS, C. KLEPADO, and H. WALKER (Scripps Institution of Oceanography, Marine Vertebrate Collection, La Jolla); J. WILLIAMS (National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Zoology, Washington D. C.); K. MASLENIKOV and T. PIETSCH (University of Washington, College of Ocean and Fishery Sciences, Seattle); D. BRAY (Museum Victoria, Melbourne), R. MORSE and B. WEATHERWAX (New York State Museum, Albany), and M. PEGG (University of Nebraska-Lincoln, School of Natural Resources, Lincoln). The National Science Foundation generously supported T. GRANDE (NSF DEB-0732589) and W. SMITH (DEB-0716155, DEB-0732642, DEB-1060869). C. BORDEN was supported by DeepFin, an NSF Research Coordination Network grant (DEB- 0443470) awarded to G. ORTÍ and a research assistanceship through T. GRANDE.

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Appendix 1

Material examined

Institutional abbreviations follow SABAJ PÉREZ (2012), with two additions: "LUC" is the teaching and research collection in the Department of Biology at Loyola University Chicago, and "SNR-UNL" is the teaching and research collection in the School of Natural Resources at the University of Nebraska-Lincoln. An asterisk denotes best "guess-estimate" of standard lengths (SL) in damaged or distorted specimens. Total length (TL, snout to last vertebrae) typifies adult gadiforms that normally lack an internal caudal-fin and those lampriforms in which the caudal-fin is normally present but missing. We recognize Stylephoriformes sensu MIYA et al. (2007). Gadiform classification follows ROA-VARÓN & ORTÍ (2009), but ENDO's (2002) family names are noted in parentheses when different. Zeiform classification follows TYLER et al. (2003). "Percomorpha" is used to capture all non-beryciform acanthopterygians. A dagger ("†") identifies fossil forms, which are integrated within Recent material when appropriate.

Salmoniformes
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).

Aulopiformes
Incertae sedis: †*Nematonotus longispinus*, 2 spec. (SL: ~68.0–79.0 mm), AMNH 3679, AMNH 3682 (no head).
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 (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).

Polymixiiformes
Polymixiidae: *Polymixia berndti*, 1 spec. (SL: 81.6 mm): USNM 389346 (c&s). *Polymixia lowei*, 2 spec. (SL: 82.40–107.50 mm): USNM 398653 (alcohol, c&s). *Polymixia nobilis*, 1 spec. (SL: 100.0 mm): FMNH 64695 (c&s).
Incertae sedis: †*Omosoma pulchellum*, 2 spec. (SL: 40–41 mm): AMNH 6100, AMNH 6101. †*Omosoma intermedium*, 1 spec. (SL: incomplete skeleton): AMNH 6102. – †*Pycnosterinx discoideus*, 1 spec. (SL: 52 mm): AMNH 3880. †*Pycnosterinx russeggeri*, 1 spec. (SL: 61 mm): AMNH 3876.

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*, 10 spec. (SL: 8.5–85.1 mm): KU 2412 (c&s), KU 5032 (alcohol, c&s), KU 33610 (alcohol, c&s), FMNH 78533 (c&s), NYSM 67970 (c&s), USNM 84051 (alcohol), USNM 396352 (alcohol). – †*Trichophanes foliarum*, 3 spec. (SL: 70.0–105.9 mm): AMNH 18924, FMNH PF 14311, UALVP 27059.
Libotoniidae: †*Libotonius pearsoni*, 3 spec. (SL: 15.1–22.2 mm): UALVP 14765 a (paratype), UALVP 13466 (holotype), UALVP 13469.
Mcconichthyidae: †*Mcconichthys longipinnis*, 1 spec. (SL: 264.0 mm): FMNH PF12916 (holotype).
Percopsidae: †*Amphiplaga brachyptera*, 2 spec. (SL: 50.0–73.0 mm) AMNH 19405, FMNH PF 15376. – †*Erismatopterus* sp. 6 spec. (SL: 44.0–73.0 mm): AMNH 110, AMNH 1353, AMNH 3999, AMNH 20367, RTMP PC 1983.155.13,

RTMP PC 1983.155.14. – †*Lateopisciculus turrifumosus*, 3 spec. (SL: 25.0–58.5 mm): UALVP 21541.1 (paratype, caudal-fin only), UALVP 22870, UALVP 34771 (holotype), UALVP 34772 (paratype). – †*Massamorichthys wilsoni*, 7 spec. (SL: 60.0–40.8 mm): UALVP 23732 (partial), UALVP 25446, UALVP 25525, UALVP 25538, UALVP 25557, UALVP 30842 a & b, UALVP 38520 a & b. – *Percopsis omiscomaycus*, 28 spec. (SL: 16.4–115.3 mm): FMNH 63444 (c&s), FMNH 63459 (alcohol, c&s), FMNH 86990 (alcohol, c&s), KU 7949 (alcohol), KU 10476 (alcohol), NYSM 58574 (c&s), NYSM 60558 (c&s). *Percopsis transmontana*, 2 spec. (SL: 49.10–63.0 mm): USNM 366393 (alcohol).

Gadiformes

Bathygadidae (Macrouridae): *Bathygadus cottoides*, 1 spec. (TL: 169.0 mm): CAS 218391 (alcohol).

Bregmacerotidae: †*Bregmaceros albyi*, 1 spec. (SL: 50.0 mm SL): AMNH 796. *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*, 3 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*, 4 spec. (SL: 44.8–176.4): FMNH 63458 (alcohol), FMNH 63458 (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), FMNH 51025 (c&s).

Euclichthyidae: *Euclichthys polynemus*, 1 spec. (SL: 164.2 mm): NMV A6212 (alcohol).

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), FMNH 67788 (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) FMNH 65807 (c&s).

Merlucciidae: *Merluccius albidus*, 4 spec. (SL: 120.5–151.8 mm): FMNH 69318 (alcohol), FMNH 69318 (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: *Gadella maraldi*, 1 spec. (SL: 111.7 mm): FMNH 65712 (c&s). – *Lotella fernandeziana*, 4 spec. (SL: 108.8–153.2 mm): FMNH 107269 (alcohol), FMNH 107269 (c&s). – *Tripterophycis gilchristi*, 2 spec. (SL: 136.6–166.7 mm): KU 33411 (alcohol), USNM 280753 (c&s).

Muraenolepididae: *Muraenolepis marmorata*, 1 spec. (SL: 297.0 mm): LACM 10447-4 (alcohol). *Muraenolepis microps*, 1 spec. (SL: 225.7 mm): USNM 371695 (c&s). *Muraenolepis orangiensis*, 1 spec. (SL: 296.9 mm): USNM 380031 (alcohol, c&s). *Muraenolepis orangiensis*?, 1 spec. (SL: 201.4 mm): USNM 320552 (c&s and alcohol). *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 225749 (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).

Trachyrincinae (Macrouridae): *Trachyrincus longirostris*, 1 spec. (SL: 402.8 mm): NMV A10677 (alcohol).

Stylephoriformes

Stylephoridae: *Stylephorus chordatus*, 7 spec. (SL: 113.4–203.0 mm): UF 165295 (alcohol), UF 166415 (alcohol), UF 177452 (c&s), UF 222883 (c&s and dissected), SIO 60-130 (alcohol), SIO 77-167, SIO 77-171 (c&s tail only).

Zeiformes

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*, 4 spec. (SL: 71.30*–110.7 mm): FMNH 67158 (alcohol), 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). *Zenopsis ocellatus*, 1 spec. (SL: 68.9): FMNH 67179 (alcohol). – *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, c&s).

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).

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).

Batrachoidiformes

Batrachoididae: *Opsanus beta*, 1 spec. (SL: 91.8 mm): KU 18048 (c&s). – *Porichthys plectrodon*, 2 spec. (SL: 41.8–89.9 mm): KU 27037 (c&s), KU 30140 (alcohol).

Gasterosteiformes

Gasterosteidae: *Culaea inconstans*, 9 spec. (SL: 22.6–45.2 mm): FMNH 73359 (alcohol), FMNH 73359 (c&s). – *Gasterosteus aculeatus*, 2 spec. (SL: 53.4–54.9 mm): LUC (alcohol).

Lophiiformes

Antennariidae: *Fowlerichthys radiosus*, 3 spec. (SL: 22.9–41.4 mm): FMNH 46753 (c&s). – *Histrio histrio*, 3 spec. (SL: 42.9–51.1 mm): FMNH 46140 (alcohol), KU 10029 (c&s).

Percomorpha

Bythitidae: *Ogilbia cayorum*, 1 spec. (SL: 43.6 mm): FMNH 48130 (c&s). *Ogilbia* sp., 1 spec. (SL: 58.7 mm): KU 21552 (alcohol).

Moronidae: *Morone americana*, 1 spec. (SL: 107.0 mm): SNR-UNL (alcohol). *Morone chrysops*, 1 spec. (SL: 112.7 mm): LUC (alcohol). *Morone mississippiensis*, 1 spec. (SL: 71.2 mm): LUC (c&s).

Ophidiidae: *Lepophidium kallion*, 1 spec. (117.4 mm): UF 211637 (alcohol). – *Otophidium omostigma*, 1 spec. (SL: 112.3 mm): USNM 34596 (c&s). – *Petrotyx hopkinsi*, 1 spec (160.4 mm): USNM 367977 (alcohol). – *Sirembo imberbis*, 1 spec. (SL: 115.4 mm): KU 30050 (c&s).

Pleuronectiformes

Cynoglossidae: *Symphurus atramentatus*, 1 spec. (SL: 76.0 mm): SIO uncat. (c&s).

Incertae sedis

Asineopidae: †*Asineops squamifrons*, 6 spec. (SL: 51.0–164.1 mm): AMNH 2531 (caudal fin only), AMNH 3992, FMNH PF 9900a&b, AMNH FF 2546 (caudal skeleton incomplete), FMNH PF 10546a&b, UALVP 17829.

Appendix 2

Description of characters

Twenty-six characters and their states in polymixiiforms and paracanthoptyergians are summarized from the osteology (1–14) and myology (15–26) of the caudal skeleton. Seven osteological characters from the previous literature and discussed by GRANDE et al. (this volume) are included here. Four of these seven characters are applied directly, two are re-defined, and one is split into two characters (number of uroneurals, presence of stegural process on uroneural 1). Osteological characters are inapplicable to adult bathygadid, macrourid, and *Squalogadus* gadiforms, all of which lack a recognizable caudal skeleton. Myological characters are inapplicable to these same gadiforms, fossil taxa, and *Steindachernia* because of extreme caudal reduction. These inapplicable and unavailable states (characters 15, 16, 18, 19) are neither mentioned further in the character descriptions below nor plotted on the revised phylogeny of GRANDE et al. (this volume: fig. 2; Fig. 14). Multi-state characters are unordered.

Character 1 – Number of autogenous hypural plates: [state 0]: 6 plates; [1]: 5; [2]: 4; [3]: 3; [4]: 2; [5]: 1 plate.

Character 2 – Fusion pattern among hypurals: [0]: upper hypurals only variously fused; [1]: upper and lower hypurals fused but not across lateral midline; [2]: upper and lower hypurals fused across lateral midline; [3]: hypurals not fused.

Character 3 – Fusion of preural centrum 1 with ural centra: [0]: preural centrum 1 + ural centrum 1; [1]: preural centrum 1 + ural centra 1–2.

Character 4 – Spatial relationship of parhypural (including haemal spine and haemal arch where present) with preural centrum 1 or compound centrum: [0]: contact; [1]: no contact.

Character 5 – Hypurapophysis: [0]: present; [1]: absent.

Character 6 – Number of epurals: [0]: 0; [1]: 1; [2]: 2; [3]: 3.

Character 7 – Number of uroneurals: [0]: 0; [1]: 1; [2]: 2.

Character 8 – Stegural process: [0]: absent; [1]: present; [2]: not applicable.

Character 9 – Dorsal surface of preural centrum 2: [0]: small crest only; [1]: short, broad spine; [2]: full-length spine; [3]: absent. "Crest" is a small extension of bone, probably neural arch. "Short" is one-half the length of that on preural centrum 3.

Character 10 – Accessory bones (X and/or Y bones of gadiforms): [0]: absent; [1]: present. This character essentially identifies a polymorphism; not all specimens of a given species had accessory bones. *Cyttus traversi* (USNM 308020) had an accessory bone between haemal spines of preural centra 3 and 4, but we did not include it on Figure 14.

Character 11 – Fusion pattern of hypurals with ural centra: [0]: some hypurals fused to ural centrum 2 only; [1]: some hypurals fused to both ural centrum 1 and ural centrum 2; [2]: no fusion of hypurals to either ural centrum 1 or 2.

Character 12 – Number of hypural plates not contacting any ural centrum: [0]: 0; [1]: 1; [2]: 2.

Character 13 – Presence of multiple spines on preural centrum 2 or 3: [0]: not observed; [1]: observed. This character essentially identifies a polymorphism; not all specimens of a given species had multiple spines on these preural centra.

Character 14 – Parhypural fused to at least hypural 1: [0]: no; [1]: yes.

Character 15 – Location of interradialis: [0]: across and between fin rays; [1]: between fin rays only; [2]: not applicable. Lampriforms are diagnosed by an interradialis that occurs only across rays, not between them, but that state is not considered further. Among paracanthopterygians dissected for myology, *Stylephorus* is the only one in which the interradialis was not confidently observed.

Character 16 – Insertion site of interradialis: [0]: principal caudal rays only; [1]: principal caudal and other rays (procurrent and/or anal-fin/dorsal-fin rays); [2]: not applicable. *Stylephorus* is the only paracanthopterygian with the "not applicable" state.

Character 17 – Hypochordal longitudinalis: [0]: present; [1]: absent.

Character 18 – Insertion site of hypochordal longitudinalis: [0]: insertion includes dorsalmost principal caudal ray; [1]: insertion does not include at least dorsalmost two principal caudal ray 2; [2]: not applicable. "Not applicable" describes *Stylephorus*, *Muraenolepis*, *Trachyrincus*, gaidropsarines, lotines, and gadines, because they lack a hypochordal longitudinalis muscle.

Character 19 – Spatial relationship of hypochordal longitudinalis and flexor dorsalis: [0]: hypochordal longitudinalis lateral to flexor dorsalis; [1]: hypochordal longitudinalis medial to flexor dorsalis; [2] not applicable. "Not applicable" describes *Stylephorus*, *Muraenolepis*, *Trachyrincus*, gaidropsarines, lotines, and gadines, because they lack a hypochordal longitudinalis muscle.

Character 20 – Structure of the flexor dorsalis and flexor ventralis: [0]: single bundle serves each ray; [1]: at least some bundles serving a single ray are compound. The flexor dorsalis and flexor ventralis are separate muscles

and may arguably represent two characters. However, given that compound bundles only occur in gadiforms, and when they occur, they are seen in both muscles, we treat the overall condition as a single character.

Character 21 – Insertion site of flexor dorsalis and flexor ventralis: [0]: principal caudal rays only; [1] principal caudal and procurrent rays. Although the conditions in the two muscles may arguably represent separate characters, given that they co-occur in amblyopsids and *Parazen*, we treat the overall condition as a single character.

Character 22 – Flexor ventralis externus: [0]: absent; [1]: present.

Character 23 – Flexor ventralis serves at least one principal caudal ray in dorsal series: [0]: no; [1]: yes.

Character 24 – Majority of ural centra and preural centra 2–4 exposed after removal of body musculature: [0]: no; [1]: yes. See text for further explanation.

Character 25 – Presence of distinct and largely separable flexor dorsalis from flexor dorsalis superior: [0]: single, largely undifferentiable, muscle mass; [1]: two, largely separable muscles. Separation of bundles was evaluated adjacent to the insertional site and laterally in the main muscle mass near the origin. Occasionally, insertions of the two muscles overlapped on a single ray and the boundaries of the muscles were easier to identify. The presence of a single, undifferentiated muscle mass does not address if the flexor dorsalis superior is graded or lost. We suggest that, since the flexor dorsalis superior inserts on the more dorsal fin rays (typically non-principal fin rays) and the insertion of the single mass includes those rays, the two muscles are present but largely undifferentiable. WINTERBOTTOM (1974: 292) stated that the flexor dorsalis superior and the flexor ventralis inferior (see below) co-occur. Since every examined paracanthopterygian had either a differentiable flexor dorsalis superior or a flexor ventralis inferior, we assumed that its counterpart was also present, albeit undifferentiable (i.e., graded).

Character 26 – Presence of distinct flexor ventralis, largely separable from flexor ventralis inferior: [0]: single, largely undifferentiable muscle mass; [1]: distinct, largely separable muscles. Comments are similar to those of character 25.

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