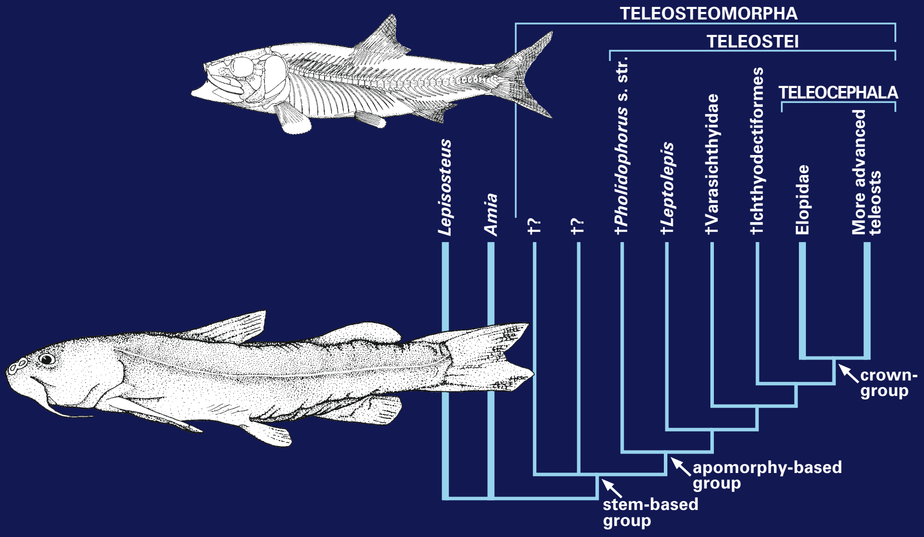
Origin and Phylogenetic Interrelationships of Teleosts

Honoring Gloria Arratia

Joseph S. Nelson, Hans-Peter Schultze &
Mark V. H. Wilson (editors)



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A teleost classification based on monophyletic groups

E. O. Wiley and G. David Johnson

Abstract

One hundred and eighteen major groups of teleost fishes are recognized as monophyletic on the basis of morphological synapomorphies. One hundred and twelve are formally classified. Only three of 54 orders and a single suborder are not supported as monophyletic groups. A Linnaean classification is proposed that incorporates new ranks and suffix endings that avoid ambiguity as to name ending and associated rank. The classification is considered an initial effort to consistently reorganize teleost classification using synapomorphies to circumscribe monophyletic groups.

Introduction

The classification of teleost fishes has undergone many revisions since Müller (1845) treated Teleostei as a vertebrate subclass. Much of this history was reviewed by Rosen (1985) and Stiassny et al. (2004), and our current views of fish classification in general are captured by Nelson (2006). Many of the taxonomic changes made since the seminal revision of Greenwood et al. (1966) have been directed toward making teleost classification more explicitly genealogical, following the Hennigian paradigm (Hennig 1966). Paraphyletic and even polyphyletic groups persist, primarily because of historical inertia. So, in the latest general revision of Nelson (2006) we encounter taxa that are unsupported by synapomorphic diagnoses and taxa, such as Perciformes, that no reasonable fish taxonomist can support as other than a convenient dumping ground. The resulting classification looks impressively detailed, but the emperor really has no clothes. It is time for a change.

The classification presented herein is an attempt to remedy or at least minimize the problem of groups that are of unknown or dubious status. With a few (notable) exceptions, each taxon among the teleost fishes is diagnosed by one or more synapomorphies. The original source of the synapomorphy and subgroups are noted, but this may or may not correspond to the first time the character was observed. The classification extends to the level of Order for more basal teleosts and suborder for euteleosts (Euteleosteomorpha). We have chosen to adopt a minimum number of hierarchical levels. Synapomorphies supporting nested clades are also listed, along with the inclusive names, but some of these names are not formally ranked. Although we differ in a few references, we cheerfully acknowledge that Nolf (1985) was an instrumental reference in associating clade names with authors.

One of the challenges of reforming euteleost classification is the challenge of name endings. The Zoological Code does not prescribe uniform name endings above the family level. However, ichthyologists were quick to accept a uniform ending for orders, adopted from Berg (1940, 1947). There is one significant benefit in adopting standard endings: groups with the same ending are exclusionary. If a species is a part of the Aulopiformes, it cannot be a part of the Myctophiformes. Unfortunately, many clade names have been formed with common endings such as “-morpha” and “ii” that do not perform this function. Thus, the Neopterygii includes the Paracanthopterygii and Acanthopterygii (Nelson 2006), and the Acanthopterygii includes the Euacanthopterygii (Johnson & Patterson 1993). We have chosen to adopt some uniform endings at certain levels of the hierarchy simply to see if the community finds them useful. The ICZN mandates neither priority nor specific endings for group names above the family level, and the community can accept or reject such endings as they wish. Little harm is done if the community does not find this useful; biological meaning is vested in the nature and constitution of the clade, not in its name ending. We have attempted to keep endings correlated with ranks at certain well-know hierarchical levels. The endings and the hierarchical rank associated with them is listed below, with their meanings. Many of the non-traditional name endings are taken from Stearn (1995).

Class	-ii (traditional usage)
Subclass	-variable (traditional)
Infraclass	-ei (traditional, following Teleostei)
Supercohort	-(o)cephala (following Teleocephala)
Cohort	-(o)morpha (following Osteoglossomorpha, etc.)
Subcohort	-i (traditional, following Ostariophysi)
Infracohort	-ia (Latin, “characteristic of”)
Section	-a (“of”)
Subsection	-ata (Latin, “likeness”)
Division	-acea (Latin, “resemblance”)
Series	-aria (Latin, “connection”)
Superorder	-ae (“of”)
Order	-(i)formes (traditional; Berg 1940, 1947)
Suborder	-oidei (traditional; Berg 1940, 1947)
Superfamily and below:	ICZN endings

From first principles of Phylogenetics, clades arise as single ancestral species. Thus, we should not expect that clades have more, or more distinctive, synapomorphies than the autapomorphies of single species, nor should we expect clades that happen to have the same rank to be equally distinct in terms of number of synapomorphies.

We have chosen to use rank as an indication of subordination. Ranked classifications are one of several methods to express a hierarchy by subordination of a list of names, ranking, rankless indentation and numerical prefixes (Wiley 1981). In Phylogenetics, ranks have no meaning relative to evolutionary biology; they are simply devices to express relative position of clades in the list hierarchy. Thus a family of percomorphs is not biologically comparable to a family of elopomorphs except to say that if there is evidence for their monophyly then both are examples of monophyletic groups. The only taxa that are directly comparable in a biological manner are sister taxa and species. Sister taxa are comparable because they have their origins in a common speciation event. Species are comparable because they are the results of speciation, a process. As there is no process of “generation” for genera or “familization” for families, it directly follows that simply because a clade is placed with the rank “family” does not mean that it is biologically comparable to any other taxon except its sistergroup. We note that the use of rankless classifications, ranking or indexing does not obviate the pre-evolutionary and largely platonic idea of the Scala Naturae that leads one to think that taxa with the same indentation, index or rank are somehow comparable. Only a full embrace of the evolutionary paradigm cures this problem.

With this in mind, we have taken the opportunity to conserve clades previously ranked as orders at their present levels. This required the use of some redundant names. There are two justifications for this, apart from the tangential names of this first classification using synapomorphies as diagnostic characters. First, it allows the use of a sequencing convention, saving certain favored and familiar ranks and their associated names for use at lower levels (e.g., the orders of percomorphid fishes). Second, it allows for the discovery of, and inclusion of, basal fossils or newly discovered living species that lie outside the diagnosis of the respective orders, and it permits known orders to be grouped into monophyletic groups without changes in rank.

We have compiled lists of characters held by ichthyologists to be synapomorphic and thus diagnostic for clades and, in a few cases, have added newly observed or considered ones. However, we have not checked characters nor conducted detailed studies on characters asserted by other authors to be diagnostic. Some of these asserted synapomorphies will certainly turn out to be homoplastic, ill-conceived, or diagnostic of more inclusive clades. Nevertheless, it is time to make an accounting of teleost synapomorphies, because those synapomorphies appear in the literature. This classification and account of synapomorphies that diagnose monophyletic groups is a beginning, not an end, to the larger effort of dealing with the phylogeny of Teleostei as a whole. We cannot make such a beginning without collating what we think the community knows about these groups and without disposing of groups for which there is no evidence of monophyly. Thus the reader should not misconstrue our intentions. They are specifically (1) to expose those groups that ichthyologists have asserted are confirmed by synapomorphies and thus are asserted to be clades and (2) to expose those groups for which no such evidence exists. Those who disagree with the assertion that Labriformes (for example) are not a clade have no argument from us; we only encourage such investigators to gather the conflicting evidence that demonstrates that Labriformes are not a clade in the form of a better corroborated phylogenetic hypothesis. Those who argue that the "Perciformes" we include should be dismembered have no argument from us; we encourage them to show us a hypothesis that allocates members of this non-group to monophyletic groups, new or existing that can be integrated with a logically consistent classification of teleosts.

We take note of certain homology problems that exist when actinopterygian fishes are compared to other groups. Specifically, it has been known at least since Jollie (1962) that actinopterygians do not have a sarcopterygian frontal and that more basal sarcopterygians (e. g., †*Eusthenopteron*) also lack a sarcopterygian frontal (see Wiley 2008 for short discussion). Thus the actinopterygian frontal is homologous with the sarcopterygian parietal and the actinopterygian parietal is homologous with the sarcopterygian post-parietal. For better or worse, actinopterygian systematists are not likely to adopt the terms parietal and post-parietal and drop the terms frontal and parietal, which would likely cause considerable confusion in interpreting literature about these bones within Actinopterygii. Thus, when we use the terms "frontal" and "parietal", they refer to the "actinopterygian frontal" and "actinopterygian parietal" and not to the "real" (by priority) frontal and parietals of apical sarcopterygians as seen in †*Panderichthys* and tetrapods.

Molecular data are of increasing importance in unraveling the evolutionary relationships of teleost fishes, and several of these studies are cited in the classification. However, molecular work is still in its infancy. Studies with different genes tend to yield different results that are difficult to compare, because the taxa are frequently different. To Smith & Wheeler (2004) and Li et al. (2009, "total evidence"), *Dactylopterus* is related to *Aulostomus*, whereas to Miya et al. (2005), *Dactylopterus* is related to gobies. Smith & Wheeler (2004) and Li et al. (2009) did not include a goby and Miya et al. did not include *Aulostomus*. Perhaps gobies, flying gurnards and some other groups are actually smegmamorphs; but Miya et al. (2005) placed flying gurnards and gobies near jacks in a relatively apical position, whereas Smith & Wheeler (2004) and Li et al. (2009) placed gurnards + *Aulostomus* in a basal or near basal position as sister to most of the remaining taxa included in their study (Smith & Wheeler 2004) or related to a polyphyletic Stromateiformes that includes *Kali*, bramids and scombrids, among others (Li et al. 2009). The effects of taxon sampling even using the same gene are also evident. *Emmelichthys* consistently groups with *Pterocaesio* in Yamanoue et al. (2007) and Miya et al. (2005). However, in Yamanoue et al. (2007), *Emmelichthys* + *Pterocaesio* (and *Lutjanus*) are sister to a group comprising a monodactylid and two haemulids and separated by chaetodontids and sparoids from the caproids, lophiiforms and tetraodontiforms, whereas in Miya et al. (2005), *Emmelichthys* + *Pterocaesio* are sister to a group composed of *Antigonia*, tetraodontiforms, and lophiiforms, but neither chaetodontids nor sparoids are included in the analysis. In Setiamarga et al. (2008) the sparids fall between the lophiiforms and tetraodontiforms but the analysis lacks monodactylids, chaetodontids and haemulids. In Thacker (2009), who used a subsample of mitochondrial genes, *Pterocaesio* is sister to *Satyrichthys* (an armored sea robin) and the pair is sister to *Cottus*, *Aptocyclus* (a cyclopterid) + *Arctoscopus* (a trichodontid). And, if we take the statistics seriously, many of the clade relationships shown would collapse into polytomies. We do not mean this as a criticism per se, recognizing that one must work with available specimens and data, and taxon selection is frequently a function of the aims of the study, be it molecular or morphological. Miya et al. (2005) were primarily attempting to place the notoriously difficult-to-sequence batrachoidiforms, Yamanoue et al. (2007) were attempting to place tetraodontiforms, Setiamarga et al. (2008) were focused on atherinomorphs, and Thacker (2009) was focused on gobies. None were particularly focused on percomorphs such as sparids or *Emmelichthys*. Nonetheless, these diverse results illustrate that the molecular evidence, even with the same gene, is not stable relative to taxon selection. One hopes that as the numbers of gene loci and taxa increase, the molecular evidence will converge on a solution that can be examined in light of morphological diversity. For example, Li et al. (2009) are using the criterion of clade repeatability (Chen et al. 2003) as a marker for phylogenetic accuracy. What all this signals now is that molecular analysis of teleost relationships is still in its infancy in terms of gene sampling and taxon sampling. We take note of molecular data and incorporate findings where we can do so.

The Classification

Below, we summarize our classification of Teleostei, grounded within Actinopterygii. We follow this overview with detailed diagnoses of each clade and call attention to groups that lack confirmation of their monophyletic nature. The classification follows the Annotated Linnaean system of Wiley (1979, 1981), which includes the listing convention of Nelson (1972) and the sedis mutabilis convention of Wiley (1979) to indicate polytomies in a list. We have taken the liberty of defaulting to two clades of neopterygians, Holostei and Teleostei, in anticipation of analyses by Lance Grande (Field Museum), but do not attempt to justify this decision herein.

- Class Actinopterygii
  - Subclass Cladistia
  - Subclass Chondrostei
  - Subclass Neopterygii
    - Infraclass Holostei
    - Infraclass Teleostei
    - Supercohort Teleocephala
      - Cohort Elopomorpha
        - Order Elopiformes
        - Order Albuliformes
        - Order Notacanthiformes
        - Order Anguilliformes
      - Cohort Osteoglossomorpha
        - Order Hiodontiformes
        - Order Osteoglossiformes
      - Cohort Otomorpha (= Otocephala, Ostarioclupeomorpha)
        - Subcohort Clupei
          - Order Clupeiformes
        - Subcohort Ostariophysi
          - Section Anotophysa
            - Order Gonorynchiformes
          - Section Otophysa
            - Superorder Cyprinae
              - Order Cypriniformes
            - Superorder Characiphysae
              - Order Characiformes
              - Order Siluriformes
              - Order Gymnotiformes
      - Cohort Euteleosteomorpha
        - Subcohort Protacanthopterygii
          - Order Argentiniformes
            - Suborder Argentinoidei
            - Suborder Alepocephaloidei
          - Order Salmoniformes
            - Suborder Esocoidei, sedis mutabilis
            - Suborder Osmeroidei, sedis mutabilis
            - Suborder Salmonoidei, sedis mutabilis
        - Subcohort Neoteleostei
          - Neoteleostei incertae sedis Order Ateleopodiformes
          - Infracohort Stomiatia
            - Order Stomiatiformes
          - Infracohort Eurypterygia
            - Section Aulopa
              - Order Aulopiformes
                - Suborder Synodontoidei
                - Suborder Chlorophthalmoidei

- Suborder Alepisauroidei
- Suborder Giganturoidei
- Section Ctenosquamata
  - Subsection Myctophata
    - Order Myctophiformes
  - Subsection Acanthomorphata
    - Division Lampridacea
      - Order Lampridiformes
    - Division Polymixiacea
      - Order Polymixiiformes
    - Division Percopsacea
      - Order Percopsiformes
    - Division Gadacea
      - Order Gadiformes
        - Suborder Melanonoidei
        - Suborder Macrouroidei
        - Suborder Gadoidei
    - Division Stephanoberycacea
      - Order Stephanoberyciformes
    - Division Zeacea
      - Order Zeiformes
    - Division Berycacea
      - Order Beryciformes
    - Division Percomorphacea
      - Series Smegmamorpharia
        - Incertae sedis in Smegmamorpharia:
          - Order Elassomatiformes
          - Order Mugiliformes
          - Order Synbranchiformes
            - Suborder Mastacembeloidei
            - Suborder Synbranchoidei
          - Order Gasterosteiformes
            - Suborder Gasterosteoidei
            - Suborder Syngnathoidei
        - Superorder Atherinomorphae
          - Order Atheriniformes
          - Order Beloniformes
            - Suborder Adrianichthyoidei
            - Suborder Exocoetoidei
          - Order Cyprinodontiformes
            - Suborder Aplocheiloidei
            - Suborder Cyprinodontoidei
  - Percomorphacea incertae sedis:
    - Order Acanthuriformes
    - Order Anabantiformes
      - Suborder Anabantoidei
      - Suborder Channoidei
    - Order Batrachoidiformes
    - Order Blenniiformes
    - Order “Caproiformes”
    - Order Carangiformes
    - Order Cottiformes
      - Suborder Cottoidei
      - Suborder Zoarcoidei
    - Order Dactylopteriformes

- Order Gobiesociformes
    - Suborder Gobiesocoidei
    - Suborder Callionymoidei
- Order Gobiiformes
- Order Icosteiformes
- Order Labriformes
- Order Lophiiformes
    - Suborder Lophioidei
    - Suborder Antennarioidei
    - Suborder Chaunacoidei
    - Suborder Ogcocephaloidei
    - Suborder Ceratioidei
- Order Nototheniiformes
- Order “Ophidiiformes”
    - Suborder “Ophidioidei”
    - Suborder Bythitoidei
- Order “Perciformes”
- Order Pholidichthyiformes
- Order Pleuronectiformes
    - Suborder Psettodoidei
    - Suborder Pleuronectoidei
- Order Scombriformes
- Order Scorpaeniformes new usage
    - Suborder Scorpaenoidei
    - Suborder Serranoidei
- Order Stromateiformes
- Order Tetraodontiformes
- Order “Trachiniformes”

Clades and Synapomorphies

The clades and “groups” recognized above are listed below, with synapomorphies and comments where noted in the literature. The synapomorphies diagnostic of the clades represent current hypotheses concerning those evolutionary innovations that are properties of the ancestral species of each clade. In many cases subclades may be diagnosed by modification of these synapomorphies (including the absence thereof). Thus, we do not expect the listed synapomorphies to be diagnostic, in the traditional sense, that is, to be present in all members of the clade. Furthermore, we cannot claim to have listed all morphological synapomorphies ever proposed for these clades, and cannot claim absolute objectivity in our recognition and listing of them.

Infraclass Teleostei Müller, 1845, sensu Arratia, 1999

Recent teleosts are unambiguously monophyletic, sharing many synapomorphies (de Pinna 1996). Different authors have been more or less inclusive in their circumscription of the group, with respect to fossils. For example, Patterson (1977) included †Pachycormiformes, †Aspidorhynchiformes and several other fossil groups as basal teleosts, whereas Arratia (2004) considered these fossil fishes to be neopterygians but their relationships to her Teleostei to be problematic, with more detailed studies of morphology and better preserved specimens needed. Inadequate preservation causes other problems. We circumscribe Teleostei as a clade that includes all fishes, fossil and living, that stem from the immediate ancestral species whose descendants include †*Pholidophorus bechei* and all more apical teleosts, but which do not include descendants of the ancestor of species of Holostei and thus adopt Teleostei sensu Arratia (1999) (this is a concession to the senior author, by the junior, who recognizes Teleostei as comprising only extant taxa). The exact constituents of this clade are yet to be determined, as the positions of certain fossil groups are subject to dispute. If groups such as †Pachycormiformes and †Aspidorhynchiformes are found to join the teleost branch of the neopterygian tree rather than having affinities with holostean fishes, then we would consider them to be parts of Teleostei, and thus expand the concept of Teleostei to one closer to that proposed by Patterson (1977), rather than adopt Teleosteomorpha sensu Arratia (2001). This preserves the neontological concept that there are two groups of living neopterygians, holosteans and teleosteans. de Pinna (1996) coined the name Teleocephala for the living teleost clades, making Teleocephala the same concept as Müller's original Teleostei. Obviously, the circumscription and diagnosis of Teleostei is controversial. We do not list the groups and synapomorphies up to Teleocephala but refer the reader to the latest available analysis (Arratia 1999).

Teleostei currently comprise, at minimum, †*Pholidophorus bechei*, †*Leptolepis coryphaenoides*, †*Tharsis*, †Varasichthyidae, †Ichthyodectiformes and Teleocephala. Arratia (1999) considers other members of †Pholidophoridae and †Leptolepidae not to be studied in sufficient detail for formal analysis. Teleostei are diagnosed by one unique and unreversed synapomorphy in the Arratia (1999) analysis and several synapomorphies that show some level of homoplasy. Synapomorphies are listed below.

1. Quadrate bearing elongate posteroventral process (Arratia & Schultze 1990).
2. Maxilla mobile (Patterson 1973; homoplastic, also found in †*Prohalecites*, a presumed holostean).
3. Coronoid bones absent (Nelson 1973; in some pholidophorids but condition in *P. bechei* unclear).
4. Articular fused with angular and retroarticular bones (Arratia 1999; variable among teleocephalans).
5. Neural spine of preural centrum 1 short or rudimentary (Arratia 1999; also present in †*Dapedium* and †*Prohalecites*, variable in teleocephalans).
6. Pectoral propterygium fused to first pectoral ray (Patterson 1977; also found in †*Prohalecites*).
7. Dorsal processes of bases of innermost principle caudal fin rays of upper lobe present (Arratia 1999; variable in teleocephalans).
8. Only ural neural arches modified as uroneurals (homoplastic, see note below).
9. Posterior myodome extending into basioccipital (Patterson 1973, 1975; variable in teleocephalans).
10. Frontal bones distinctly broader posteriorly than anteriorly (Arratia & Schultze 1987; reversed in osteoglosomorphs and in some ostariophysans).
11. Vomer single, median (Patterson 1977; homoplastic, found both below and above this node).

Müller (1845) included three characters for his Teleostei: 1) presence of long intermusculars (homologous to anterior epineurals formed in cartilage), 2) presence of two arterial valves in the conus arteriosis, and 3) lack of muscles at the base of the ventral aorta. Of these, †*Pholidophorus bechei* lacks long intermusculars but has short ones, whereas †*Leptolepis coryphaenoides* has long intermusculars as do most other basal teleosts known.

The presence or absence of uroneurals (synapomorphy 7) in aspidophynchids and pachychormids is controversial. Arratia (1999) acknowledges that one aspidorhynchid has true uroneurals (†*Vinctifer*) but considers them lacking in both pachychormids and other aspidorhynchids, contra Brito (1999).

Between the base of Teleostei, with the first branch leading to †*Pholidophorus bechei*, and the last common ancestor of Teleocephala, which comprises Recent teleosts and their fossil relatives, is a phylogenetic ladder comprising the following list: †*Leptolepis coryphaenoides*, †*Tharsis*, †Varasichthyidae, †Ichthyodectiformes and Teleocephala. Many of the familiar synapomorphies of Recent teleosts are actually synapomorphies of more or less inclusive clades within this ladder, as recognized by Patterson (1977, 1994), Patterson & Rosen (1977), Lauder & Liem (1983), Arratia & Schultze (1987), de Pinna (1996), and various phylogenetic analyses of Arratia, summarized in Arratia (1999). These clades remain unnamed and we refer the reader to the review by de Pinna (1996) and the formal analysis by Arratia (1999).

Supercohort Teleocephala de Pinna, 1996

Teleocephala comprise four cohorts of teleosts that include extant species: Elopomorpha, Osteoglossomorpha, Otomorpha, and Euteleosteomorpha, among which relationships are controversial. For example, Patterson & Rosen (1977) hypothesized that Osteoglossomorpha are basal relative to a monophyletic Elopomorpha + Clupeocephala (= Elopocephala) based on two synapomorphies (only two uroneurals extending anteriorly beyond U2 and epipleural intermuscular bones well developed). Arratia (1997) challenged both characters as ambiguous (i. e., homoplastic). Patterson (1998) countered by questioning Arratia's coding of certain characters, to which Arratia (1998) countered that Patterson had misinterpreted the coding, reiterating that she did not believe the monophyly of Elopocephala to be confirmed by synapomorphies. Arratia (1999) subsequently hypothesized a series of synapomorphies uniting

Osteoglossomorpha with Otomorpha + Euteleosteomorpha and recognized the clade Osteoglossocephala. Molecular results are mixed. Lê et al. (1991) found a sister group relationship between osteoglossomorphs and elopomorphs (28S rDNA), whereas mitogenomic analyses have found osteoglossomorphs basal to elopomorphs (Inoue et al. 2001, 2003) as hypothesized by Patterson & Rosen (1977). Nuclear data do not support either hypothesis (Li et al. 2008). We have chosen to recognize four cohorts and list them in phylogenetic order following Arratia (1999) but not to recognize any further groupings. The distribution of many of the synapomorphies diagnosing Teleocephala is not known because they have not been preserved in known fossils:

1. Three ossified and one cartilaginous pharyngobranchial with tooth plate (Arratia 1999, modified from Patterson 1973).
2. Craniotemporal muscle present (Stiassny 1986).
3. Uroneurals five or fewer (Arratia 1999).
4. "Upper" uroneurals three or fewer, oriented at angle to more anterior uroneurals (Arratia 1999, modified from Patterson & Rosen 1977).
5. Uroneural 1 reaching anterior to preural centrum 2.
6. Accessory nasal sacs present (Chen & Arratia 1994, de Pinna 1996).
7. Bases of dorsal fin rays aligned with hypurals (Arratia 1999).
8. Independent endoskeletal basihyal present.
9. Lateral forebrain bundle composed of myelinated fibers (de Pinna 1996).
10. Rostrolateral parts of lobus vestibulolateralis of cerebellum solid (de Pinna 1996).

Cohort Elopomorpha Greenwood et al., 1966

Elopomorpha comprise the teleost orders Elopiformes, Albuliformes, Notacanthiformes, and Anguilliformes. There has been some controversy surrounding the monophyly of the clade and the relationships of various elopomorphs to other teleosts. Greenwood et al. (1966) recognized Elopomorpha with three subgroups; elopiformes + albuloids, notacanthoids, and anguilliforms + saccopharyngiforms. Gosline (1970) rejected monophyly, placing notacanthoids and anguilliforms + saccopharyngiforms as separate orders and elopiforms + albuloids as related to clupeoids and anotophysans in the order Clupeiformes. Nelson (1973), Patterson & Rosen (1977) and Robins (1989) recognized the group, but with different interrelationships. Forey et al. (1996) performed a combined molecular and morphological analysis that concluded elopomorph monophyly, but this view was challenged by Filleul & Lavoué (2001) and Obermiller & Pfeiler (2003) using ribosomal gene sequences. Li et al. (2008) found the clade unresolved using nuclear loci. Mitogenomic analysis by Inoue et al. (2003) is largely congruent with Forey et al. (1996), except for the placement of notacanthoids, and we accept the monophyly of Elopomorpha. Elopomorpha are diagnosed by the following synapomorphies:

1. Leptocephalus larval stage in development (Greenwood et al. 1966). This character was challenged by some authors, notably Nybelin (1971) and Hulet & Robins (1989), who argued that elongate and transparent larvae are found in other groups (e.g., clupeomorphs). Forey (1973a) and Forey et al. (1996) reviewed this controversy and defended the leptocephalus as a specialized larval form with its own unique properties that differ from superficially similar larvae in other groups.
2. Prenasal ossicles present (Forey 1973a, b). They are absent in ophichthids and saccopharyngids in the Forey et al. (1996) analysis, but present in more basal taxa.
3. Sternohyoideus originating mainly on the cleithrum (Greenwood 1977). This is reversed in eels.
4. Flagellum of spermatozoa with 9 + 0 axoneme arrangement and the proximal centriole divided into two elongate bundles of four- and five-triplet structure (Matthei & Matthei 1974, Jamieson 1991). This character is unique and unreversed in the Forey et al. (1996) analysis.
5. Compound neural arch forms in a mass of cartilage over first preural and first ural centrum (Arratia 1996, 1997).

Forey (1973a, b) and Forey et al. (1996) listed the presence of a pectoral splint as a synapomorphy diagnostic of the clade. Arratia (2008) challenged this conclusion, pointing out that "splints" that eventually fuse to the first lepidotrichium during growth in elopiforms studied by her are also found among more basal groups such as †ichthyodectids and †*Leptolepis coryphaenoides* and that the "splint" is missing in osteoglossomorphs and other more apical teleocephalans.

Nelson (1973) suggested one additional synapomorphy: fusion of the angular and retroarticular. This character was discussed by Forey et al. (1996), who noted that it also occurs in the osteoglossomorphs *Hiodon* and *Gymnarchus*. More study of its distribution is needed, but we note that large specimens of *Elops* and *Megalops* have the angular, retroarticular and articular bones fused (Arratia 1987, 1997), so study of fusion in large specimens is needed.

Order Elopiformes Gosline, 1960

Elopiformes comprise two families, Elopidae and Megalopidae. All authors who agree on the monophyly of Elopomorpha agree that Elopiformes are the basal clade. Forey et al. (1996) hypothesized one unique and unreversed morphological synapomorphy that can be used to diagnose the clade: posterior opening of the mandibular sensory canal medial in position (rather than lateral). However, this may depend on outgroup comparison and the character is not unique. Some basal fossils (e. g. †*Leptolepis coryphaenoides*; Arratia 1999) also have this state. If the state is plesiomorphic rather than apomorphic, then the lateral position of the opening is a synapomorphy of Osteoglossomorpha + Euteleosteomorpha (Arratia 1999). Johnson & Britz (this volume) proposed that the pattern of development of the basioccipital may also be unique to elopiforms.

Order Albuliformes sensu Forey et al., 1996

Albuliformes comprise two monotypic families, Albulidae and Pterothrissidae. Placement of notacanth fishes is controversial; Forey et al. (1996) followed Forey (1973a) in treating them as a separate order, but other authors (most recently Inoue et al. 2003, based on a mitogenomic analysis) included them within albuliforms. The relationship of Notacanthiformes to Anguilliformes based on morphological analysis (Forey et al. 1996) is supported by numerous synapomorphies, and we accept the placement of this order as the sister of Anguilliformes. Albuliformes are diagnosed by three unique, unreversed synapomorphies:
1. Subepiotic fossa present (Forey et al. 1996).
2. Ectopterygoid with dorsal process that rests on inner surface of adjacent infraorbital (Forey et al. 1996).
3. Presence of fenestra within hyomandibular and metapterygoid suture allowing deep portions of levator arcus palatine to pass through and insert on medial surface of palatine (Forey et al. 1996).

Two unique and unreversed synapomorphies unite Albuliformes with Notacanthiformes + Anguilliformes (Forey et al. 1996).
1. Infraorbital branch of buccal VII piercing premaxilla.
2. Premaxilla firmly attached or fused (missing?) to ethmoid.

Order Notacanthiformes Goodrich, 1909

Notacanthiformes comprise the families Halosauridae and Notacanthidae. Three unique and unreversed synapomorphies diagnose the order (Forey et al. 1996):
1. Large connective tissue nodule intercalated between pterygoid arch and maxilla (Greenwood 1977).
2. Maxilla with posteriorly directed spine (Forey et al. 1996).
3. Pelvic fin webs joined in ventral midline (Forey et al. 1996): eels lack pelvics.

Numerous synapomorphies unite Notacanthiformes and Anguilliformes. These may be grouped into characters that represent losses within the context of elopiform evolution (and frequently loss of states that are apomorphic at varying levels of teleost, actinopterygian, osteichthyan or even gnathostome phylogeny) and those that are apparent gains (acquisition of novelties). The following are from Forey et al. (1996) unless noted:
1. Orbitosphenoid absent.
2. Intercalar absent.
3. Uncinate process on epibranchial 3 absent.
4. Postcleithrum absent.
5. Mesocoracoid absent.
6. Distinct caudal fin absent, that is, a caudal fin distinct from the anal and/or dorsal fins.
7. Inner caudal rays not expanded.
8. Hypural 2 not fused to ural centrum.
9. Epaxial musculature inserting on rear wall of neurocranium entirely medial to posterior semicircular canal.

10. Pectoral girdle free from skull.
11. Parhypural fused with preural centrum 1.
12. Upper hypurals fused.
13. Upper hypurals fused to ural centrum.
14. Cartilage plate attached to neural arch of ural centrum 1 (Patterson & Rosen 1977).

Order Anguilliformes Goodrich, 1909

Anguilliformes as treated herein comprise four suborders: Anguilloidei (three families), Congroidei (nine families), Muraenoidei (three families) and Saccopharyngoidei (two to four families, depending on authority). This differs from the concept of Nelson (2006) and Robins (1989), who placed Saccopharyngoidei in their own order. Morphological and molecular analyses (Forey et al. 1996, Inoue et al. 2003) place saccopharyngoids within Anguilliformes, rendering Anguilliformes sensu Nelson (2006) and Robins (1989) paraphyletic. In the analysis of Forey et al. (1996), the following six characters were found to be synapomorphies of Anguilliformes that do not show homoplasy within Elopomorpha. We comment on and/or revise the description of some of these below:

1. "Canal-bearing extrascapular absent" is invalid. The extrascapular in eels is usually represented by several tubular ossicles surrounding the occipital commissural sensory and temporal canals, e.g., Allis (1903) (Colin Patterson, unpubl. MS).
2. Sympletic fused with quadrate (homology questionable in saccopharyngoids, see Forey et al. 1996: p. 188, character 18).
3. Gill arches displaced posteriorly free from neurocranium (first pharyngobranchial absent).
4. Gill rakers absent.
5. Pelvic girdle and fins absent.
6. Body scales absent or embedded and arranged in basket-weave fashion (Robins 1989).

Robins (1989) listed 43 characters of Anguilliformes, including the six listed above from Forey et al.'s analysis. These were not specifically said to be eel synapomorphies, and a number are primitive for teleosts or elopomorphs. However, many are apparently unique to eels, and below we list several of the osteological ones not listed by Forey et al. (1996):

1. Posttemporal absent (convergent in notacanthoids, McDowell, 1973).
2. Anterior end of ceratohyal elongated.
3. Anteriormost branchiostegals curve behind and above opercle.
4. Premaxillae fused to each other and to the ethmovomerine complex (absent in Ophichthidae?)

Robin's noted other reductive features of the suspensorium of eels, but admittedly did not understand the ontogeny and homology of the relevant elements sufficiently to accurately describe them. We leave this for an upcoming paper that will incorporate a critical evaluation of them from an unpublished manuscript by the late Colin Patterson. (Patterson, unpubl. MS).

Cohort Osteoglossomorpha Greenwood et al., 1966

Osteoglossomorpha comprise two orders, Hiodontiformes and Osteoglossiformes. Osteoglossomorpha have been the subject of three recent phylogenetic analyses (Hilton 2003, Zhang 2006, Wilson & Murray 2008). Our recognition of two living orders (Hiodontiformes and Osteoglossiformes) is consistent with all recent analyses, which are based on reinterpretation of several points of anatomy and a reconsideration of the characters and data matrix of Li & Wilson (1996). However, all three analyses differ considerably in the fossil taxa that are included as well as the number of characters and the interpretation of characters. As an example, Li & Wilson (1996) considered absence of a supraorbital as synapomorphic for Osteoglossomorpha; this was also included by Zhang (2006) in his list of characters for the cohort. Wilson & Murray (2008), however, accepted Hilton's (2003) conclusion that the state of the supraorbital was best coded as unknown in †*Lycoptera*, resulting in this character state dropping out of their 2008 list of synapomorphies. Zhang (2006) and Wilson & Murray (2008) both included a number of fossil taxa, including several recently described genera. Obviously, interpretations of missing data and the effect of missing data on interpretation of synapomorphy as well as the availability of fossil taxa (many basal) that were not available to each other or to Hilton (2003), has substantially affected studies of osteoglossomorph relationships. At this point we are simply considering various basal fossil bonytongues as incertae sedis in Cohort Osteoglossomorpha pending further analysis, following the call for on-going analysis by Wilson & Murray (2008). Each synapomorphy listed below reflects the inclusion of different fossil taxa in each analysis.

Hilton (2003) diagnosed Osteoglossomorpha with four synapomorphies:
1. Epipleural bones absent (Nelson 1969, Arratia 1999, Hilton 2003). Present in *Heterotis* (Patterson & Johnson 1995).
2. Sixteen principal branched caudal fin rays (Nelson 1969, Arratia 1999, Hilton 2003). Fewer than 16 in most Osteoglossiformes (all extant taxa except *Arapaima*; Nelson 1969).
3. One epural (Li & Wilson 1996). Epurals are absent in Osteoglossiformes (Nelson 1969).
4. Full neural spine on first preural centrum (Hilton 2003). Hilton (2003) discussed variation.

Zhang (2006) diagnosed Osteoglossomorpha with four unique and unreversed synapomorphies:
1. Supraorbital absent (Li & Wilson 1996).
2. Posterior opening of mandibular sensory canal placed lateral to angular portion of jaw.
3. "Shearing bite" between basihyal and lateral pterygoquadrate teeth (Greenwood et al. 1966).
4. Length of neural spine of preural centrum 2 less than length of same spine on preural centrum 3.

Wilson & Murray (2008) diagnosed Osteoglossomorpha with two synapomorphies:
1. One epural (Li & Wilson 1996).
2. Second infraorbital triangular or rectangular and smaller than third infraorbital (Li et al. 1997).

Order Hiodontiformes McAllister, 1968

Hiodontiformes comprise the family Hiodontidae. The number of synapomorphies diagnosing the order differs depending on author.

Hilton (2003) diagnosed Hiodontiformes with two synapomorphies:
1. Nasal bones tubular and strongly curved (Li & Wilson 1994).
2. Posterodorsal spine present on opercle (Li & Wilson 1994).

Wilson & Murray (2008) presented a more extensive list of synapomorphies. Note than many of these were discussed in earlier papers (Li et al. 1997, Li & Wilson 1999, Hilton 2003) and are the subject of various re-coding schemes, interpretations of morphology, or analyses of different taxa:
1. Frontal bone less than twice as long as parietal (Li et. al 1997).
2. Nasal bones tubular and strongly curved (Li & Wilson 1994).
3. Dermosphenotic triradiate (Li & Wilson 1996).
4. Two neurocranial heads on hyomandibular (Li & Wilson 1994).
5. Subopercular spine small and anterior to opercle (Li & Wilson 1994).
6. Opercle flattened, with posterior recurved process dorsal to hyomandibular articular facet (Li et al. 1997).
7. Anal fin sexually dimorphic (Li et al.1997).

Zhang (2006) also had only two unique synapomorphies for Hiodontiformes:
– Triradiate dermosphenotic and two neurocranial heads on hyomandibular.

Order Osteoglossiformes Greenwood et al., 1966

Osteoglossiformes comprise the Recent families Mormyridae, Notopteridae, and Osteoglossidae. In both Hilton (2003) and Wilson & Murray (2008), †*Ostariostoma* is the basal sistergroup and the name †Ostariostomatidae Schaeffer, 1949, is available if this position continues to hold up with further analysis.

Hilton (2003) diagnosed Osteoglossiformes with a restricted number of synapomorphies, reflecting imperfect preservation in the only known specimen of †*Ostariostoma* (three additional characters were interpreted as uniquely derived synapomorphies for Osteoglossiformes but could not be scored for †*Ostariostoma*):
1. One or two uroneurals (Li & Wilson 1996).
2. Six or fewer hypurals (Hilton 2003).

Wilson & Murray (2008) presented a more extensive list:
1. Angular and articular bones fused (noted by Nelson 1973 as a condition in some osteoglossomorphs).

2. Two or one uroneurals (Li & Wilson 1996).
3. Upper hypurals and second ural centrum fused (Li et al. 1997).
4. Ventral margin of opercle rounded or pointed and narrower than mid-point of opercle (Li et al. 1997).

Zhang (2006) had 8 characters at this node, but none is uniquely derived.

Clupeocephala sensu Arratia, 1997

Clupeocephala comprise the cohorts Otomorpha and Euteleosteomorpha and are not formally classified herein. This usage of the term was first proposed by Patterson & Rosen (1977), and its monophyly is not questioned. Synapomorphies are from Arratia (1997). The first two were originally described and suggested as clupeocephalan synapomorphies by Nelson (1973) and were discussed in detail and recognized formally as such by Patterson & Rosen (1977):

1. Retroarticular excluded from joint surface of quadrate.
2. Articular and angular bones fused.
3. No medial tooth plates on basibranchials 1-3 or on hypohyal cartilage.
4. No tooth plates associated with pharyngobranchials 1-3.
5. Neural arch of “first” ural centrum reduced or absent (first ural centrum is an ontogenetically fused U1 and U2 in polyural terminology).
6. Two anterior-most uroneurals present as long, separated bones.
7. Six or fewer hypurals.

Cohort Otomorpha new name
(= Otocephala Johnson et Patterson, 1996, Ostarioclupeomorpha Arratia, 1997)

Otomorpha comprise two clades ranked here as subcohorts, Clupei (herrings and kin) and Ostariophysi (minnows, etc.). Assertions that this group is monophyletic first came from molecular analyses (Lê et al. 1993, Lecointre 1995, Lecointre & Nelson 1996). Recent mitogenomic analyses (Ishguro et al. 2003, Lavoué et al. 2005) also found a relationship between otomorphs with alepocephaloids. In Ishiguro et al. (2003), alepocephalans are embedded in a paraphyletic Otomorpha as sister to gonorhynchiforms and clupeiforms, whereas in Lavoué et al. (2005), there is an unresolved trichotomy of clupeiforms, alepocephalans and a monophyletic Ostariophysi. Reconciliation of these results with previous hypotheses awaits corroboration with morphology and nuclear DNA analyses. Arratia (1999) diagnosed the clade (without alepocephalans) with three morphological synapomorphies; we note two additional character states:

1. Medial extrascapular fused (or ankylosed) to parietals or fused (or ankylosed) to both parietal and supraoccipital (Lecointre & Nelson 1996, as described by Arratia 1999).
2. Autopalatine ossifying early in ontogeny.
3. Bases of hypurals 1 and 2 not joined by cartilage at any growth stage.

Possible additional synapomorphies include:

4. Silvery area associated with gas bladder (Fink & Fink 1996: p. 232). The synapomorphy of having an anterior chamber of the gas bladder partly to completely covered by a silvery peritoneal tunic (Rosen & Greenwood 1970) was originally listed as an ostariophysan synapomorphy in Fink & Fink (1981).
5. Haemal spines anterior to that of second preural centrum fused to centra from a young juvenile stage. Lecointre & Nelson (1996) cited Fujita (1990) and stated that this fusion is more widespread than reported. Fink & Fink (1981: p. 341) also mentioned the widespread nature of the character but were assuming (following Patterson & Rosen 1977) that ostariophysans are basal euteleosts based on presence of breeding tubercles and lack of adipose fin (in basal members).

Subcohort Clupei new name
(= Clupeomorpha Greenwood et al., 1966)

Clupei comprise a number of basal fossil groups (Grande 1982, 1985) and the living order Clupeiformes. Herein we treat only Clupeiformes. Clupei (including fossil groups) are diagnosed by the following synapomorphies (from Grande 1985, unless noted):

1. Hypural 2 fused with first ural centrum at all stages of development.
2. Supratemporal commissural sensory canal passing through parietals and supraoccipital (Patterson & Rosen 1977, Grande 1982).
3. Otophysic connection involving diverticulum of gas bladder that penetrates exoccipital and extends into prootic within lateral wall of braincase (Rosen & Patterson 1977, Grande 1982).

Order Clupeiformes Goodrich, 1909

Clupeiformes comprise two extant suborders: Denticipitoidei (one family: Denticipitidae) and Clupeoidei (four families: Pristigastridae, Engraulididae, Chirocentridae, and Clupeidae). Synapomorphies diagnosing the order are from Grande (1985):

1. One or more abdominal scutes, each an unpaired element that crosses ventral midline of body (Whitehead 1963, Patterson 1970).
2. Otophysic connection wherein diverticulum of gas bladder penetrates exoccipital and expands to form ossified bulla in prootic and sometimes pterotic (Greenwood et al. 1966, see Grande 1985).

Subcohort Ostariophysi Sagemehl, 1885

Ostariophysi comprise five orders: Gonorynchiformes, Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes. Ostariophysans are diagnosed by a number of synapomorphies (Fink & Fink 1981). Fink et al. (1984) and Fink & Fink (1996) revisited many of these, eliminated some, and provided additional discussion, principally based on criticisms by other authors cited therein. We cite these criticisms and discussion sparingly here and refer the reader to Fink & Fink (1996) for literature and extended discussion. Synapomorphies are from Fink & Fink (1981) unless noted:

1. Basisphenoid absent.
2. Sacculi and lagenae positioned more posteriorly and nearer midline (Rosen & Greenwood 1970).
3. Dermal portion of palatine absent (see Fink & Fink 1981, 1996 for discussion).
4. Supramaxilla absent as separate ossification (presence of supramaxillae in some taxa considered neomorphic, not plesiomorphic; Fink & Fink 1996: p. 230).
5. Gas bladder divided into smaller anterior and larger posterior chambers, with ductus pneumaticus near constriction (Rosen & Greenwood 1970; for variation see Fink & Fink 1981); gas bladder reduced or lost in some lineages.
6. Peritoneal tunic of anterior chamber of gas bladder attached to anterior-most two ribs (Rosen & Greenwood 1970).
7. Dorsal mesentery suspending gas bladder heavily thickened anterodorsally near its attachment to vertebral column and with many transverse fibers.
8. Dorsomedial portions of anterior neural arches expanded and abutting each other and posterior margin of exoccipital, forming roof over neural canal.
9. Unattached neural arch anterior to arch of first centrum absent (see Fink & Fink 1996, for discussion). Note that the arch is absent in the two clupeiforms examined by Fink & Fink (1981).
10. Presence of unique alarm substance in epidermis (Fink & Fink 1981, Gayet 1986, Fink & Fink 1996); absent in gymnotiforms where signaling is electrical (Hopkins 1983).
11. Adductor mandibulae with superficial ventral division, not homologous to A1 division of higher teleosts. Fink & Fink (1981) discussed this character and cited George Lauder (Harvard University) for making the distinction. Considerable variation occurs, as discussed by Howes (1985) and Fink & Fink (1996). Apparently, siluriforms have the plesiomorphic condition of an undifferentiated adductor that inserts on the mandible and this is considered a reversal by Fink & Fink (1996).
12. Presence of nuptial tubercles with well-developed keratinous caps (Wiley & Collette 1970). Fink & Fink (1981) listed this character as a synapomorphy for Ostariophysi. Fink & Fink (1996: p. 211) noted that Roberts' (1982) character of unculi (keratinous unicellular projections of the epidermis) is more widespread among ostariophysans, but these (and keratinous tubercles) have not been observed in gymnotiforms (Arratia & Huaquín 1995).
13. Loss of supraneural 1 and its cartilaginous precursor (Hoffman & Britz 2006).

Section Anotophysa (= Anotophysi Rosen & Greenwood, 1970)

Anotophysa comprise a single order, Gonorhynchiformes, diagnosed below.

Order Gonorynchiformes Regan, 1909

Gonorynchiformes comprise three suborders, Chanoidei (Chanidae), Gonorynchoidei (Gonorynchidae), and Knerioidei (Kneriidae, Phractolaemidae). Synapomorphies diagnosing the clade are from Fink & Fink (1981) unless noted and those characters observable in both fossil and extant species are corroborated by Grande & Poyato-Ariza (1999):

1. Bone and cartilage of interorbital septum greatly reduced; orbitosphenoid absent; pterosphenoids small and widely separated.
2. Parietals greatly reduced. Grande & Poyato-Ariza (1999: p. 229) state: "parietals separated by supraoccipital".
3. Suspensorium elongate in parasagittal plane in region between articular condyle for quadrate and hyomandibular (see Arratia 1992, and Fink & Fink 1996: p. 225, for variation in other ostariophysans). Not listed in Grande & Poyato-Ariza (1999).
4. Epicentral bones present (Patterson & Johnson 1995). Listed in Grande & Poyato-Ariza (1999) as presence of three sets of intermuscular bones, including cephalic ribs.
5. Epibranchial organ present (Fink & Fink 1981), of distinctive morphology (Fink & Fink 1996: p. 231).
6. First neural arch especially enlarged, contacting occipital margin with extensive, tight joint. Characterized by Grande & Poyato-Ariza (1999) as first neural arch articulating with exoccipitals.
7. Teeth absent on fifth ceratobranchials.
8. Baudelot's ligament absent (Patterson & Johnson 1995, Fink & Fink 1996).
9. Anterior rib on third vertebrae distinctly larger than that on next few ribs (Fink & Fink 1996).
10. Oesophagus long and extending some distance into visceral cavity (Fink & Fink 1996).
11. Oesophagus with internal structure that includes spiral folds with secondary folds and posteriorly directed papillae; epithelium with large secretory cells (Fink & Fink 1996).
12. Second uroneural elongate anteroventrally (Fink & Fink 1996).

Comments: Exoccipitals or both exoccipitals and supraoccipital with prominent posterodorsal lateral margins, cited as a gonorynchiform synapomorphy in Fink & Fink (1981), was rejected by Fink & Fink (1996) based on new observations. Premaxilla a thin, flat bone cited as a gonorynchiform synapomorphy by Fink & Fink (1981) is considered by Fink & Fink (1996) to be of uncertain polarity based on variation. It is not listed in Grande & Poyato-Ariza (1999).

Section Otophysa (= Otophysi Rosen & Greenwood, 1970)

Otophysa comprise all non-gonorynchiform ostariophysans. Some of the original Fink & Fink (1981) characters have been removed or modified based on Fink et al. (1984), Fink & Fink (1996), and literature cited in these papers. Otophysa are diagnosed by the following synapomorphies taken from Fink & Fink (1981) unless noted:

1. Endochondral portion of metapterygoid an axe-shaped bone that is double-headed in basal order Cypriniformes and in Characiformes (see Siluriformes for single-headed state).
2. Anterior two (Cypriniformes) or one (Characiformes and Siluriformes) supraneurals expanded ventrally to form synchondral joint with neural arches of third and fourth vertebrae.
3. Elements of first neural arch modified to form scaphium and claustrum. Britz & Hoffman (2006) reviewed the history of homology concerning the claustrum and elegantly demonstrated that the claustrum in cypriniforms and siluriforms is homologous with the first supradorsals and that the claustrum of characiforms is a membrane bone.
4. Second neural arch modified to form intercalarium.
5. First four centra showing some foreshortening relative to more posterior centra (see Fink & Fink 1996, for discussion).
6. Anteriormost parapophyses, when present, fused to centra. This is possibly a synapomorphy of Ostariophysi (Fink & Fink 1996: p. 237).
7. Tripus present.
8. Os suspensorium present.

9. Pelvic girdle bifurcated anteriorly (there is homoplasy; see Fink & Fink 1996).
10. Compound caudal centrum present, composed of first preural centrum, "ural centra U1 and U2" (diural terminology) and anterior pair of uroneurals (there is considerable homoplasy; see Fink & Fink 1996).
11. Hypural 2 fused with compound caudal centrum (see Fink & Fink 1981, 1996, for discussion of homoplasy in this character).
12. Sinus impar present (see Fink & Fink 1981: p. 343, 1996: p. 243, for discussion).
13. Supradorsals 2 and all supradorsals posterior to vertebra 4 absent; neural complex formed by fusion of supradorsals 3 and 4 with supraneural 2 and 3 cartilages (Hoffman & Britz 2006).

Superorder Cyprinae new name

Cyprinae comprise the single order Cypriniformes, diagnosed below.

Order Cypriniformes Goodrich, 1909

Cypriniformes comprise six families of minnows: Cyprinidae, Psilorhynchidae, Gyrinocheilidae, Catostomidae, Cobitididae, and Balitoridae. Fink & Fink (1981) diagnosed the order with the following synapomorphies:

1. Kinethmoid bone present.
2. "Pre-ethmoid" tightly articulated between vomer and mesethmoid.
3. Presence of a dorsomedial process on anterior portion of autopalatine that abuts against mesethmoid.
4. Autopalatine articulating posteriorly in concave facet on endopterygoid.
5. Ectopterygoid failing to overlap autopalatine anteriorly.
6. Premaxilla extending farthest dorsally adjacent to midline rather than more laterally.
7. Fifth ceratobranchial enlarged, extending much farther dorsally than other ceratobranchials.
8. Teeth on fifth ceratobranchial ankylosed.
9 Lateral process of second centrum elongate, extending well into somatic musculature.

Superorder Characiphysae (= Characiphysi Fink et Fink, 1981)

Fink & Fink (1981) recognized an unranked Characiphysi comprising the orders Characiformes and Siluriformes, with siluriforms including both catfishes (siluroids) and knifefishes (gymnotoids). Fink & Fink (1996) recognized knifefishes as a separate order, Gymnotiformes. Synapomorphies diagnosing the monophyly of Characiphysae are from Fink & Fink (1981), unless noted:

1. Vomer articulating anteriorly with mesethmoid.
2. Mesethmoid with anteroventral process that articulates directly with premaxillae (see Fink & Fink 1981: p. 312, for variation).
3. Maxilla positioned posterolateral to lateral processes of mesethmoid, not articulating directly with mesethmoid (see Fink & Fink 1996, for discussion relative to gonorynchiforms).
4. Supraneural 2 and its cartilaginous precursor absent, neural complex formed by fusion of anteriorly shifted supraneural 3 cartilage with supradorsals 3 and 4 (Hoffman & Britz 2006, refinement of Fink & Fink 1996, based on ontogenetic study).
5. Anterior margin of third neural arch approaching posterior border of neurocranium closer than in cypriniform fishes (may be correlated with character state 10, below; Fink & Fink 1981).
6. Dorsal part of third neural arch with distinctly short, vertically oriented anterior margin (small or absent in characiforms); apparently restricted to basal taxa (see Fink & Fink 1996).
7. Presumed homologue of spine of third neural arch extending anterodorsally from arch, lateral to modified supraneural.
8. Fifth neural arch fused to centrum.
9. Anteriormost three vertebrae foreshortened, first most foreshortened (correlated with 6, above; Fink & Fink 1996).
10. Parapophysis absent on anterior centrum (occasionally lacking in non-basal cypriniforms; Fink & Fink 1996).
11. Baudelot's ligament attached to skull in region of cranial condyle or lagenar capsule (see Fink & Fink 1996, for discussion).

12. Haemal spine of preural centrum 2 fused to centrum, and parhypural and hypural 1 fused to compound terminal centrum (Fink & Fink 1996: pp. 240-241: see discussion of earlier characterizations appearing in Fink & Fink 1981, and Fink et al. 1984).
13. In addition to the above characters, Fink & Fink (1996) called attention to one neurological character presented by Striedter (1992): torus semicircularis with unique lateral line nucleus.

Two characters originally appearing in Fink & Fink (1981) are in need of further study (Fink & Fink 1996):

1. Scaphium extending well anterior to border of centrum 1.
2. Parapophysis portion of tripus attached to centrum by thick, flexible bony lamella that projects posterodorsally from centrum (Alexander 1964, Fink & Fink 1981); polarity is problematic.

Order Characiformes Goodrich, 1909

Characiformes comprise some 18 families currently recognized in Nelson (2006) and two suborders: Citharinoidei (two families: see Vari 1979 and Fink & Fink 1981, for analyses) and Characoidei (16 families). Synapomorphies diagnosing the order follow Fink & Fink (1981) unless otherwise noted:

1. Auditory foramen of prootic sensu Weitzman (1962) present.
2. Dorsomedial opening into posttemporal fossa present.
3. Lagenar capsule large, globular, and projecting well lateral to cranial condyle.
4. Replacement teeth for outer row of dentary and some premaxillary teeth forming in trenches or crypts.
5. Jaw teeth multicuspid (see Fink & Fink 1981, 1996, for variation and alternate hypotheses).
6. Third neural arch with elongate anterodorsal process that projects lateral to ascending process of intercalarium.
7. Hypural 1 separated from the compound centrum in adults (for variation see Fink & Fink 1981, 1996).

Siluriformes Hay, 1929 + Gymnotiformes Berg, 1940 (Siluriphysi Fink & Fink, 1996)

Fink & Fink (1996) restored the Neotropical knifefishes and electric eels to ordinal status. In order to show the sistergroup relationships between Siluriformes and Gymnotiformes, Fink & Fink (1996) coined the taxon Siluriphysi and placed it in an unranked classification as the sister of Characiformes within Characiphysi. This produces a situation of non-exclusion (a species can be both a characiphysan and a siluriphysan). We have chosen not to classify Siluriphysi. The community of ostariophysan researchers is better equipped than we to deal with the name. Synapomorphies diagnosing a clade composed of siluriform and gymnotiform fishes are listed below (from Fink & Fink 1981, 1996):

1. Dorsal portion of mesethmoid compressed, appearing slender in dorsal aspect (Fink & Fink 1996, discuss variation in catfishes, where state is found basally).
2. Intercalar absent.
3. Eye of adults reduced in size relative to circumorbital bones, lying farther from bony, inner border of circumorbital than in more basal orders or characiforms.
4. Sclerotic bones absent.
5. Infraorbital series largely (gymnotoids) or entirely (siluroids) composed of canal-bearing portions of each bone.
6. Supraorbital bone absent.
7. Ectopterygoid greatly reduced posteriorly (siluroids) or absent (gymnotoids).
8. Endochondral part of metapterygoid triangular and apparently equivalent to anterior half of metapterygoid of more basal otophysans and characiforms.
9. Opercle approximately triangular rather than rectangular.
10. Ligamentum primordium attached to dorsal tip of anguloarticular at coronoid process (rather than posteriorly near articular facet with quadrate). The fact that this ligament attaches to a cartilage (Arratia 1992) was noted by Fink & Fink (1996: p. 230), who suggested additional observations of gymnotiforms.
11. Single pharyngobranchial tooth plate.
12. Intercalarium lacking articular process and not articulating with centrum.
13. “Transverse process” of fourth centrum with ovoid anterolateral face that approaches suspensorium of pectoral girdle (see discussion in Fink & Fink 1981: p. 332).

14. Os suspensorium with elongate horizontal process closely applied to ventrolateral surface of vertebral centra 2-4 (gymnotoids) or complex centrum of siluroids.
15. All rib elements (particularly the fourth and tripus) projecting from centra at angle close to horizontal.
16. Baudelot's ligament robust and bifurcated distally.
17. More posterior pectoral fin rays offset posteriorly from anterior ray. This was inadvertently listed as a siluroid character in Fink & Fink 1996: p. 239).
18. Flanges on dorsal and ventral halves of pectoral-fin rays about equal in size.
19. Middle radial ossifications absent from all dorsal and anal fin pterygiophores.
20. Principal caudal fin-ray count 9/9 rather than 10/9 (also found in cypriniforms; all non-apteronotid gymnotiforms lack a caudal fin; see Fink & Fink 1996: p. 240).
21. Electroreception (character complex; Fink & Fink 1996).
22. Anterior lateral line with recurrent branch innervating electroreceptors of trunk (see Fink et al. 1984: p. 1041).
23. Development of cartilaginous bridges between supradorsals 3 and 4 of each side that fuse with supraneural 3 cartilage to form neural complex (Hoffman & Britz 2006).

In addition to the preceding characters, Fink & Fink (1996: pp. 219-220) detailed extensive lists of neurological characters collated by J. S. Albert and M. J. Lannoo (via personal communication) from the literature. The Albert and Lannoo characters were published subsequently (Albert et al. 1998, Albert 2001).

Order Siluriformes Hay, 1929

Siluriformes comprise some 35 extant families of catfishes (Nelson 2006), although the exact number and status of certain genera and higher taxa are uncertain (Lundberg & Friel 2003). Synapomorphies diagnosing the order are from Fink & Fink (1981, 1996):

1. Parietals ontogenetically fused to supraoccipital.
2. Autopalatine extending posterior to its articulation with lateral ethmoid and its posterior articular cartilage not continuous with cartilage of quadrate or metapterygoid.
3. Endopterygoid reduced to small plate of bone posteromedial to posterior tip of palatine; endopterygoid not in contact with posterior part of suspensorium (homology following Arratia 1992 and Fink & Fink 1996).
4. Metapterygoid placed anteroventral to quadrate, forming ventral border of suspensorium.
5. Symplectic and associated ventral process of quadrate absent.
6. Preopercle (no horizontal limb) and interopercle (small triangular bone) shortened on anteroposterior axis.
7. Subopercle absent.
8. Centra 2-4 fused into "complex centrum" (Fink & Fink 1981: p. 331).
9. Third and fourth neural arches fused to each other and to complex centrum. Fink & Fink (1981: pp. 330-331), list the neural arch and centrum fusion as separate characters.
10. Parapophysis (= lateral process) of second centrum absent.
11. Transformator processes of tripus separated posteriorly by width of complex centrum.
12. Ovoid anterior face of fourth centrum "transverse process" articulating directly with suspensorium of pectoral girdle. (See discussion in Fink & Fink 1981: p. 332 regarding composition of "transverse process".).
13. "Transverse process" of the fourth centrum fused to complex centrum.
14. Os suspensoria lacking posteromedial processes.
15. Suspensorium of pectoral girdle a single ossified element (see Fink & Fink 1981: pp. 333-334 for discussion).
16. Dorsal and pectoral fin spines present.
17. Scales absent.
18. Parurohyal (fusion of paired tendon bones and a basichondral element) present (Arratia & Schultze 1990).

Hoffman & Britz (2006) proposed an additional character: absence of supraneural 3 and its cartilaginous precursor, but they noted that *Diplomystes*, some ictalurids, pimelodids, and schilbiids retain supraneural 3, so resolution of this character will depend on intrarelationships among the catfishes.

Order Gymnotiformes Berg, 1940

Gymnotiformes comprise five families in two suborders, Gymnotoidei (Gymnotidae) and Sternopygoidei (Rhamphichthyidae, Hypopomidae, Sternopygidae, and Apteronotidae), and monophyly is well established (Fink & Fink 1981, 1996, Albert 2001). Synapomorphies diagnosing the clade are from Albert (2001) except those that conflict with siluriform + gymnotiform synapomorphies detailed by Fink & Fink (1981, 1996; e.g. triangular opercle):

1. Maxillary teeth absent.
2. Maxillary head articulating with autopalatine cartilage (also found in siluriforms, Arratia 1992).
3. Lateral ethmoid reduced, margins not contacting other bones of neurocranium (see Albert 2001, for variation).
4. Lateral margins of parasphenoid not extending to horizontal with trigeminal foramen.
5. Dorsal telencephalis region DCa large, Dm small. (Albert et al. 1998).
6. Eye subcutaneous (also found in some siluriforms; Arratia pers. comm.).
7. No accessory optic tract and nucleus (present in sternopygids).
8. No taste buds on extra-oral integument.
9. No alarm substances (Schreckstoff) or fright response.
10. Suite of characters associated with active, high frequency electroreception (Carr & Maler 1986).
11. Ampullary organs organized into rosettes.
12. Autopalatines unossified.
13. Metapterygoid triangular.
14. Ectopterygoid absent.
15. Endopterygoid teeth few or none.
16. Gill rakers reduced, not contacting gill bar (except *Electrophorus*, *Sternopygus*, *Rhabdolichops*, and *Sternarchella*).
17. Fifth epibranchial with elongate ascending process.
18. Pelvic fins and girdle absent (Fink & Fink 1981).
19. Claustrum absent (Fink & Fink 1981).
20. Capacity to regenerate postcoelomic axial structures.
21. Dorsal adipose fin absent (Fink & Fink 1981).
22. Anal fin long (Fink & Fink 1981), with more than 150 rays.
23. Anal-fin rays articulating with proximal anal-fin pterygiophores (Fink & Fink 1981).
24. Cartilaginous hypural-opisthural rod (except Apteronotidae), described by Fink & Fink (1981: p. 240) as “Caudal support skeleton consolidated into single element”.
25. Anus anterior to midlength of body (Fink & Fink 1981).
26. Hypaxial electric organs (see Albert 2001 for variation).
27. Jamming avoidance response (except *Sternopygus*).

Additional diagnostic synapomorphies in Fink & Fink (1981, 1996):

1. Anterior and posterior parts of bifurcate Baudelot’s ligament attach to cleithrum (see variation in Fink & Fink 1981).
2. Anteroventral process on third neural arch, articulating with dorsal prominence on second centrum in gymnotoids. Originally thought to diagnose Siluriformes + Gymnotiformes, now diagnosing only Gymnotiformes (Fink & Fink (1996: p. 236).

Cohort Euteleosteomorpha (= Euteleostei Greenwood et al., 1966)

Euteleosteomorpha comprise teleost clades that, together, form the sister to Otomorpha. Johnson & Patterson (1996) hypothesized three synapomorphies:

1. Pattern 2 supraneurals. First supraneural develops independently of and is usually larger than and separated by two or more neural spines from succeeding supraneurals, which develop in rostral and caudal gradients from a focus midway between occiput and dorsal fin origin.
2. Stegural with anterodorsal membranous growth. Absence in Argentinoidei is secondary by parsimony optimization.
3. Caudal median cartilages present. Absence in Esocoidei and Acanthomorphata is secondary by parsimony optimization.

Subcohort Protacanthopterygii Greenwood et al., 1966

Protacanthopterygii comprise three orders that form the basal clade of Euteleosteomorpha. The monophyly of the clade when pikes and relatives (Esocoidei) are included is contentious. Johnson & Patterson (1996) presented morphological evidence that pikes and relatives (Esocoidei) are the sistergroup of Neoteleostei. This is challenged by a variety of DNA evidence that strongly corroborates monophyly of Salmoniformes including Esocoidei (López et al. 2004, and citations therein). Johnson & Patterson (1996) proposed two synapomorphies diagnosing their Protacanthopterygii, both of which must be considered reversals in esocoids when they are included as they are here:

1. Epicentrals cartilaginous.
2. Absence of forking in epineurals and epipleurals.

Order Argentiniformes Johnson & Patterson, 1996

Argentiniformes comprise two suborders, Argentinoidei and Alepocephaloidei. Synapomorphies diagnosing the suborder are as follows:

1. Crumenal organ present (Johnson & Patterson 1996).
2. Distal parts of first two to four epineurals descended (Johnson & Patterson 1996).
3. Caudal median cartilages together supporting lowermost ray of upper caudal lobe (Johnson & Patterson 1996).

Suborder Argentinoidei: Argentinoidei comprise three families: Argentinidae, Opisthoproctidae, and Microstomatidae. Synapomorphies diagnosing the suborder are from Johnson & Patterson (1996):

1. Medial part of occipital commissural sensory canal carried by parietals.
2. Endopterygoid teeth absent.
3. Metapterygoid reduced.
4. Premaxillae and maxillae toothless.
5. Supramaxillae absent.
6. Basibranchials 1-3 toothless.
7. Pharyngobranchials 2 and 3 toothless.
8. Accessory neural arch absent.
9. Uroneural 1 without membranous anterodorsal outgrowth.

Suborder Alepocephaloidei: Alepocephaloidei comprise three families: Platytroctidae, Bathylaconidae, and Alepocephalidae. Synapomorphies diagnosing the suborder are from Johnson & Patterson (1996):

1. Parietals separated by supraoccipital.
2. Posttemporal fossa absent.
3. Branchiostegal cartilages present.
4. Dorsal part of opercle reduced.
5. Epipleural bones extending forward to about vertebra 3.
6. Urodermal absent.
7. No more than one postcleithrum.
8. Adipose fin absent.
9. Gas bladder absent.

Order Salmoniformes Greenwood et al., 1966

Salmoniformes comprise three suborders: Osmeroidei, Salmonoidei, and Esocoidei. The only candidate for a morphological synapomorphy is the presence of a single supramaxilla, which is convergent with that of ostariophysans. Thus, the monophyly of this group must rest on the molecular evidence presented by López et al. (2004) who found a sistergroup relationship between salmonoids and esocoids, but Johnson & Patterson (1996) found considerable evidence for an osmeroid + salmonoid relationship. We have not included the synapomorphies listed at various levels by Sanford (2000) in his treatise on salmonoid osteology and phylogeny, because his parsimony analysis did not include the characters described and analyzed four years earlier by Johnson & Patterson (1996). We are not suggesting that these characters are not informative, but we believe that their validity cannot be evaluated in the current context without a formal analysis that includes the latter characters. We list the three salmoniform suborders sedis mutabilis, awaiting a resolution of the conflict between the morphological and molecular evidence.

Suborder Esocoidei, sedis mutabilis: Esocoidei comprise the single family Esocidae, diagnosed by the following synapomorphies from Johnson & Patterson (1996) except where noted:

1. Paired, elongate, proethmoids (Rosen 1974).
2. Basibranchial tooth plate in two parts.
3. First pharyngobranchial conical with tip enclosed in bone.
4. Single upper pharyngeal tooth plate is fourth rather than fifth upper pharyngeal tooth plate.
5. Single postcleithrum present, homologous with postcleithrum 3 of other teleosts (also found in some galaxioids, one aulopiform genus, *Bathypterois*, and some apical acanthomorphs; Johnson & Patterson 1996).
6. Ossified middle radials of dorsal and anal fins developing only on central pterygiophores *(Esox, Umbra)* or not ossifying at all *(Dallia, Novumbra)*.
7. Cheek and operculum scaled (also found in aulopiforms, ctenosquamates, some apical elopomorphs and one alepocephalid: Johnson & Patterson 1996).

Osmeroids and esocoids share two reductive apomorphies interpreted as convergent by Johnson & Patterson (1996):

1. Orbitosphenoid absent.
2. Articular reduced.

Osmeroids and salmonoids share a number of synapomorphies lacking in esocoids. There is thus conflict between the morphology-based hypothesis and the molecular results of López et al. (2004) that place esocoids and salmonoids as sisters. The synapomorphies shared by osmeroids and salmonoids are listed below (from Johnson & Patterson 1996 unless noted):

1. Dermethmoid and supraethmoid as separate ossifications.
2. Posttemporal fossa open.
3. Fourth upper pharyngeal tooth plate absent (but see discussion in Johnson & Patterson 1996: p. 277).
4. Epineurals fused to neural arches on no more than first vertebra.
5. Last few neural and haemal spines keel-like distally.
6. Uroneural 2 anterodorsal to uroneural 1.
7. Scales without radii (considered independently derived in salmonoids and osmerids by Sanford 2000).
8. Nuptial tubercles present (convergent with ostariophysans).
9. Diadromy.

Suborder Osmeroidei, sedis mutabilis: Osmeroidei sensu Johnson & Patterson (1996) comprise two superfamilies and three families: Osmeroidea (Osmeridae, including former members of Salangidae) and Galaxioidea (Retropinnidae and Galaxiidae). Synapomorphies diagnosing the suborder are from Johnson & Patterson (1996):

1. Ventral condyle on pelvic girdle.
2. Basisphenoid absent (reversed in *Lepidogalaxias*).
3. Columnar coronoid process present on cleithrum (lost in Galaxiidae).
4. Preural centrum 1 and ural centrum 1 fused (diural terminology; reversed in *Lepidogalaxias*).

Johnson & Patterson (1996) listed additional characters interpreted as synapomorphic, but which show additional variation among members of the suborder:

1. First pectoral radial enlarged and modified (reversed in *Mallotus*, salangids, and Galaxiidae).
2. Postcleithra absent (reappears in *Lovettia* and some galaxiids).
3. Gill rakers toothless (reversed in *Retropinna*).

Suborder Salmonoidei, sedis mutabilis: Salmonoidei comprise two families, Salmonidae and Coregonidae (Sanford 1990, 2000, Johnson & Patterson 1996), recognized by Stearley & Smith (1993) as subfamilies. Synapomorphies diagnosing the suborder are:

1. Tetraploid genome (Sanford 1990, 2000; Stearley & Smith 1993).
2. Deep posterior myodome, with eye muscles passing through myodome and attaching to trunk muscles (Sanford 1990, 2000).
3. Peg-and-socket arrangement of posterior haemal arches in caudal region (Rosen 1974, Sanford 1990, 2000; Stearley & Smith 1993).

4. Anterodorsal process on medial pelvic radial (Sanford 1990, 2000).
5. Basihyal teeth present and randomly scattered (Sanford 2000).
6. Vertebral centra pitted (Sanford 2000).

Subcohort Neoteleostei Nelson, 1969

Neoteleostei comprise all clades apical to Protacanthopterygii, and are diagnosed by the following synapomorphies.

1. Retractor dorsalis present (Rosen 1973, Johnson 1992).
2. Third internal levator inserting on fifth upper pharyngeal tooth plate (Johnson 1992), but note that homology of this element in stomiatiforms has not been evaluated from an ontogenetic perspective).
3. Type 4 tooth attachment (Fink 1981, Fink & Weitzman 1982).
4. Transversus dorsalis attaching to second epibranchial (Springer & Johnson 2004).
5. Transversus epibranchialis 2 present (Springer & Johnson 2004).

Order Ateleopodiformes (= Ateleopiformes Berg, 1937), Neoteleostei incertae sedis

Ateleopodiformes comprise the single family Ateleopodidae. The placement of ateleopodids has a checkered history. Rosen & Patterson (1969) proposed a close relationship between eutaeniophorids, mirapinnids, ateleopodids and lampridiforms based on perceived similarities in jaw structure and caudal skeleton. Subsequently, Rosen (1973) and Bertelsen & Marshall (1984) showed convincingly that the former two families are most closely related to stephanoberyciform cetomimids. Rosen (1973) also rejected the hypothesis that ateleopodids are closely related to lampridiforms, but subsequent classifications (Nelson 1984, Smith & Heemstra 1986, Eschmeyer 1990) continued to accept it. Olney et al. (1993) noted that ateleopodids lack all four diagnostic apomorphies of lampridiforms, the four acanthomorph synapomorphies proposed by Stiassny (1986), the single unequivocal synapomorphy of the Ctenosquamata proposed by Johnson (1992), the three eurypterygian synapomorphies considered valid by Johnson (1992), the most convincing, unique synapomorphy of aulopiforms (Johnson 1992) and the eight stomiatiform synapomorphies identified by Fink & Weitzman (1982). They concluded that ateleopodids are neoteleosts because they have a retractor dorsalis and have the third internal levator inserting on the fifth upper pharyngeal tooth plate (a character that needs further investigation from an ontogenetic perspective), a tripartite occipital condyle and Type 1 tooth attachment, and, accordingly, placed them in an unresolved trichotomy with stomiatiforms and eurypterygians. In their phylogenetic analysis of 100 complete mitochondrial genome sequences, Miya et al. (2003) placed ateleopodids as the sistergroup of lampridiforms, and Sasaki et al. (2006) argued, unconvincingly we believe, that there is morphological evidence to support that hypothesis. Miya et al.'s (2005) analysis of 102 complete mitochondrial genome sequences rejects the lampridiform connection hypothesized by Miya et al. (2003) and places ateleopodids between aulopiforms and ctenosquamates. Springer & Johnson (2004: p. 73) noted that a distinctive configuration of the retractor dorsalis and absence of a sphincter esophagi division are possible synapomorphies of ateleopodids and aulopiforms. Additional evidence in the configuration of the pelvic girdle corroborates this hypothesis (Johnson et al. in prep.). Ateleopodiforms are diagnosed by numerous apomorphies, including the following (only the first two of which have been confirmed in all species):

1. Head relatively large and bulbous, body elongate, tapering, with short (13 or fewer rays) dorsal fin placed just behind head, and very long (70-120 rays) anal fin, confluent with the caudal fin, except in *Guntherus*.
2. Snout gelatinous.
3. Cephalic lateral-line canals represented by numerous broad, bony ossicles (illustrated for *Ateleopus* by Sasaki et al. 2006: fig. 1).
4. Propercle greatly reduced, preoperculomandibular canal with direct connection to infraorbital canal (Sasaki et al. 2006: fig. 1, for *Ateleopus*).
5. Single broad supraneural inserting between open bases of first two neural arches (Olney et al. 1993: fig. 13, for *Ateleopus*).
6. Upper pharyngeal tooth plates fragmented into many small groups and not fused to largely cartilaginous second and third pharyngobranchials (Rosen 1973, Olney et al. 1993).
7. Fourth pharyngobranchial and fourth upper pharyngeal tooth plates absent (Olney et al. 1993).

Infracohort Stomiatia new

Stomiatia comprise the single order Stomiatiformes. Diagnosis is identical to the order.

Order Stomiatiformes Rosen, 1973 (= Stomiiformes Fink et Weitzmann, 1982)

Stomiatiformes comprise the following families: Diplophidae (sensu Nelson 2006), Gonostomatidae, Sternoptychidae, "Photichthyidae", and Stomiatidae. "Photichthyidae" are paraphyletic, with genera more *(Ichthyococcus)* or less *(Yarrella)* closely related to Stomiatidae (see Harold & Weitzman 1996). The order is diagnosed by the following synapomorphies, most of which were accepted by Harold & Weitzman (1996) and Harold (1998):

1. Single, broad termination of second epibranchial articulating with second and third pharyngobranchials (Rosen 1973).
2. Unique photophore structure (Fink & Weitzman 1982).
3. Type 3 tooth attachment (Fink & Weitzman 1982).
4. Medial section of adductor mandibulae divided into two sections, one inserting dorsally directly on maxilla, the other on primordial ligament. The medial division is hypothesized not to be homologous with the A1β of neoteleosts (Fink & Weitzman 1982: p. 72).
5. Unique ethmoid-contralateral premaxillary ligament crossing pattern (Fink & Weitzman 1982).
6. Posterior branchiostegal rays greatly enlarged (Fink & Weitzman 1982).
7. Some branchiostegals rays articulating with ventral hypohyals (Fink & Weitzman 1982).
8. Rete mirabile located at posterior end of gas bladder (Fink & Weitzman 1982).
9. Component of obliquus dorsalis 4 attached to pharyngobranchial 4 (Springer & Johnson 2004).
10. Adductor 5 attached to epibranchial 4 (Springer & Johnson 2004).

Infracohort Eurypterygia (= Eurypterygii Rosen, 1973)

Eurypterygia comprise Aulopa plus Ctenosquamata and are diagnosed by the following synapomorphies:

1. Tooth plate fused to third epibranchial (Johnson 1992).
2. Presence of discrete interoperculohyoid ligament. Stiassny (1996) argued that this is a ctenosquamate synapomorphy, but Johnson's (1992) observations agree with those of Lauder (1982, 1983) that a shift in insertion of the mandibulohyoid ligament (i.e., the advent of an interoperculohyoid ligament) diagnoses the Eurypterygia.
3. Fusion of ventral half of medial pelvic ray to medial half of medial pelvic radial (Johnson 1992).
4. Transversus epibranchialis 4 present (Springer & Johnson 2004).
5. Attachment of transversus dorsalis includes second pharyngobranchial (Springer & Johnson 2004).

Section Aulopa new

Aulopa comprise the single order Aulopiformes. Diagnosis is identical to the order.

Order Aulopiformes Rosen, 1973

Aulopiformes comprise four suborders in the following phylogenetic sequence: Synodontoidei, Chlorophthalmoidei, Alepisauroidei, and Giganturoidei. The order is diagnosed by the following characters, recently reviewed and augmented by Johnson et al. (1996), Baldwin & Johnson (1996), and Sato & Nakabo (2002):

1. Uncinate process on second epibranchial elongate (Rosen 1973).
2. Cartilaginous condyle on pharyngobranchial 3 for articulation of epibranchial 2 absent (Johnson 1992).
3. Epipleural series extending anteriorly to at least vertebra 2 (Patterson & Johnson 1995).
4. Larvae with peritoneal pigment (R. K. Johnson 1982).
5. One or more anterior epipleurals displaced dorsally into horizontal septum (noted by Patterson & Johnson 1995, recognized as synapomorphic by Baldwin & Johnson 1996).
6. Absence of gas bladder (noted by previous authors such as Marshall 1954 and R. K. Johnson 1982; recognized as synapomorphic by Baldwin & Johnson 1996).
7. Medial processes of pelvic girdle joined by cartilage (Baldwin & Johnson 1996).

Other possible synapomorphies:

1. Benthic habitus (Baldwin & Johnson 1996).
2. Retractor dorsalis with distinctive configuration (Springer & Johnson 2004).
3. Sphincter esophagi simple, undivided (Springer & Johnson 2004).

Suborder Synodontoidei sensu Baldwin & Johnson, 1996: Synodontoidei comprise three families, in phylogenetic order following Baldwin & Johnson (1996): Aulopidae, Pseudotrichonotidae, and Synodontidae. The suborder is diagnosed by the following synapomorphies, summarized from Johnson et al. (1996) and Baldwin & Johnson (1996) (however, see Sato & Nakabo (2002), for a shorter and somewhat different list with the inclusion of their Paraulopidae):

1. Fifth ceratobranchials separated from main body of fourth basibranchial cartilage by tail of cartilage or trail of small nubbins of cartilage extending posteriorly.
2. Anterior ceratohyal with autogenous cartilage along ventral margin.
3. Six or more branchiostegals on proximal ceratohyal (noted by McAllister 1968, analyzed by Johnson et al. 1996).
4. Distal end of first one to three epineurals displaced ventrally (reversed in *Saurida* and *Harpadon*).
5. Accessory neural arch present.
6. All ribs ossified in membrane bone.
7. Proximal portion of most principal caudal fin rays with modified segment.
8. Caudal median cartilages absent (homoplastic loss also found in three genera of Ipnopidae and all Acanthomorphata).
9. Neural and haemal spines of preural centrum 2 and 3 expanded (*Harpadon* excepted).
10. Posterior pelvic processes elongate, widely separated.

Suborder Chlorophthalmoidei sensu Baldwin & Johnson, 1996: Chlorophthalmoidei comprise three families, in phylogenetic order following Baldwin & Johnson (1996): Chlorophthalmidae, Notosudidae, Ipnopidae. They diagnosed the suborder by the following synapomorphies (however, see Sato & Nakabo 2002, for a shorter and somewhat different list with their inclusion of *Bathysauroides*):

1. Pharyngobranchial 2 with no extra uncinate process posteriorly, but with expanded posterior base.
2. Premaxilla with dorsomedially directed process on medial edge.
3. Single supraneural (homoplastic).
4. Large lateral pelvic process retained during development, sometimes ossified in adults (also found in *Scopelarchus analis*, an alepisauroid).
5. Pupil with aphakic space, keyhole or elliptical in shape (absent in ipnopids due to eye reduction).

Suborder Alepisauroidei sensu Baldwin & Johnson, 1996: Alepisauroidei comprise four families, in phylogenetic order following Baldwin & Johnson (1996): Alepisauridae, Paralepididae, Evermannellidae, and Scopelarchidae. They diagnosed the suborder by the following synapomorphies from Baldwin & Johnson 1996 (however, see Sato & Nakabo 2002, for a shorter and somewhat different list for the same group):

1. Second pharyngobranchial tooth plate absent (an exception is the scopelarchid *Benthalbella*). This character shows considerable homoplasy.
2. Tooth plate of third pharyngobranchial reduced, teeth restricted to lateral edge of ventral surface (homoplastic with similar condition in synodontoids *Harpadon* and *Saurida*).
3. Teeth on ceratobranchial 5 restricted to medial edge of anterodorsal surface ("tentative" polarization by Baldwin & Johnson 1996: p. 372; exceptions noted in that paper).
4. Gill rakers not extending onto third hypobranchials (homoplastic, with three losses among aulopiforms and reacquisition in some paralepidids).
5. Eight infraorbitals (ambiguous).
6. Two supraneurals (homoplastic).
7. Autogenous lateral pelvic cartilages present (homoplastic with Myctophiformes).
8. Pectoral fins set low on body, pelvic fins abdominal in position (convergent with plesiomorphic gnathostome body plan but reacquired by this clade within Aulopiformes).
9. Pectoral fin base oriented more horizontally than vertically.
10. Margin of anal fin deeply indented near anterior end.

Suborder Giganturoidei sensu Baldwin & Johnson, 1996: Baldwin & Johnson (1996) included two families, Bathysauridae and Giganturidae and the monotypic *Bathysauroides gigas* in their Giganturoidei. They diagnosed the suborder by the following synapomorphies (however see Sato & Nakabo 2002), for a shorter and somewhat different list with their exclusion of *Bathysauroides*):

1. First pharyngobranchial very long, about 33 % length of first epibranchial.
2. Caudal vertebrae comprising less than 25 % of total number of vertebrae (convergent with a similar low number in synodontid-harpadontid clade within Synodontoidei).
3. Three postcleithra (absent in *Gigantura*).
4. Eyes elliptical (except in giganturids, which have anteriorly directed telescopic eyes). This is part of a complex multicharacter transformation series discussed by Baldwin & Johnson (1996: pp. 392-393).

Section Ctenosquamata Rosen, 1973

Ctenosquamata form a clade comprising Myctophata and Acanthomorphata. They are diagnosed by the following synapomorphies based on Johnson (1992) and Stiassny (1996):

1. Fifth upper pharyngeal tooth plate and associated third internal levator muscle absent (Johnson 1992).
2. Two posterior ceratohyal branchiostegal rays present (Stiassny 1996).
3. Craniotemporalis absent (Stiassny 1996).
4. Supraorbital bones absent (Stiassny 1996).
5. Neural arches of first vertebra fused distally (Stiassny 1996)

Comment: Presence of a discrete interoperculohyoid ligament was cited by Stiassny as a ctenosquamate synapomorphy, but Johnson's (1992) observations agree with those of Lauder (1982, 1983) that a shift in insertion of the mandibulohyoid ligament (i. e., the advent of an interoperculohyoid ligament) diagnoses the Eurypterygia.

Subsection Myctophata new

Myctophata comprise a single order, Myctophiformes. The diagnosis is identical to that of the order.

Order Myctophiformes Regan, 1911a

Myctophiformes comprise two monophyletic families, Neoscopelidae and Myctophidae (Stiassny 1996) and are diagnosed by the following synapomorphies recently reviewed and augmented by Stiassny (1996) and Springer & Johnson (2004):

1. Median dorsal keel on presence on mesethmoid (Stiassny 1986).
2. Median maxillo-premaxillary buccal ligaments (VIII) insert on contralateral buccal elements (Stiassny 1986).
3. Large tooth plate fused to proximal face of fourth ceratobranchial (Stiassny 1996).
4. First external levator reduced or absent (Stiassny 1996).
5. First centrum with enlarged, cone-like parapophyses (Stiassny 1986).
6. Adipose fin support ventrally inserted into supracarinalis posterior muscle mass (Stiassny 1996).
7. Tranversus pharyngobranchiales 2a and 2b present (Springer & Johnson 2004).

Subsection Acanthomorphata (= Acanthomorpha Rosen, 1973)

Acanthomorphata comprise Lampridacea and all more apical teleosts, classified here at the level of division and in phylogenetic sequence. They are diagnosed by the following synapomorphies:

1. Median palato-maxillary ligament absent (Stiassny 1986).
2. Palato-vomerine ligament divided (Stiassny 1986).
3. Median rostral cartilage strongly bound to premaxillary ascending processes by well-developed rostro-premaxillary ligaments (Hartel & Stiassny 1986, Stiassny 1986, Johnson & Patterson 1993).
4. Dorsal limb of posttemporal firmly bound to epioccipital (Stiassny 1986, Johnson & Patterson 1993).
5. Medial pelvic process ossified distally (Johnson & Patterson 1993).
6. Anterior and medial infracarinales separate (Stiassny 1993, Johnson & Patterson 1993).
7. True (azygous, unsegmented, bilaterally fused) dorsal and anal fin spines present (Johnson & Patterson 1993: there are notable exceptions, e. g., many gadiforms and most lampridiforms and a number of "Perciformes" sensu lato).

8. First centrum with anterior surface bearing distinct facets that articulate with exoccipital condyles (Rosen 1985, Johnson & Patterson 1993).
9. Median caudal cartilages absent (Fujita 1990, Johnson & Patterson 1993).

Division Lampridacea new

Lampridacea comprise a single order, Lampridiformes. The diagnosis is identical to that of the order.

Order Lampridiformes Goodrich, 1909

Lampridiformes comprise seven monophyletic families, Veliferidae, Lamprididae, Stylephoridae, Lophotidae, Radiicephalidae, Trachipteridae, and Regalecidae. Phylogenetic analysis by Olney et al. (1993) on the basis of morphology was largely corroborated by molecular analysis by Wiley et al. (1998). Placement of Stylephoridae within Lampridiformes (not analyzed by Wiley et al. 1998) was challenged by Miya et al. (2007), who placed the family more apically, near Gadiformes, based on molecular evidence. Additional morphological evidence challenges this hypothesis (Johnson, et al, in prep). The order is diagnosed by the following synapomorphies:
1. Anterior palatine process (palatine prong) and anterior palatomaxillary ligament absent (Olney et al. 1993).
2. Mesethmoid posterior to lateral ethmoids (Regan 1907, Oelschlager 1983, Olney et al. 1993).
3. Elongate ascending processes of premaxillae and large rostral cartilage inserting into frontal vault or cradle (Olney et al. 1993).
4. First dorsal pterygiophore inserting anterior to first neural spine (Olney et al. 1993).
5. Second ural centrum free from fused first ural and preural centra and fused posteriorly to upper hypural plate (noted by Patterson 1968; recognized here as synapomorphic).

Euacanthomorpha (Johnson & Patterson 1993): Polymixiacea, Percopsacea and more apical acanthomorph fishes form a clade (not classified herein) diagnosed by the following synapomorphies from Johnson & Patterson (1993), unless noted:
1. First epineural displaced ventrally into horizontal septum.
2. Posterior pelvic process ossified distally.
3. Spina occipitalis of supraoccipital present, extending ventrally between exoccipitals to dorsal margin of foramen magnum (first proposed by Stiassny 1986 as a synapomorphy for Acanthomorpha).
4. Point of origin of anterior epineurals displaced ventrally onto centra or parapophyses.

Division Polymixiacea new

Polymixiacea comprise the single order Polymixiiformes. The diagnosis is identical to that of the order.

Order Polymixiiformes Lowe, 1838

Polymixiiformes comprise the single family Polymixiidae, which includes the recent *Polymixia* and associated fossil genera (see Patterson 1993). Synapomorphies diagnosing the order (family, genus) are:
1. Palato-premaxillary ligament passing between maxillary lateral processes (Stiassny 1986).
2. Chin barbel supported by anterior branchiostegal rays present.

Holacanthopterygii Johnson & Patterson, 1993

Holacanthopterygii, not classified herein, comprise Percopsacea and more apical acanthomorph fishes diagnosed by the following synapomorphies from Johnson & Patterson (1993):
1. Epipleurals absent.
2. Epicentral ligaments absent anteriorly.
3. Distal parts of anterior epineurals displaced ventrally into horizontal septum.

Division Percopsacea new

Percopsacea comprise the single order Percopsiformes with three families. Diagnosis is identical to that of the order.

Order Percopsiformes Berg, 1937

Percopsiformes comprise three families; Percopsidae, Aphredoderidae, and Amblyopsidae. Rosen (1985) and Patterson & Rosen (1989) found no convincing synapomorphies for this clade but supported the monophyly of aphredoderids + amblyopsids based on the shared specializations of a thoracic anus and segmented premaxilla. Murray & Wilson (1999) claimed that their inclusion of fossil taxa in a phylogenetic analysis resolved the percopsiform monophyly problem by restricting the group to percopsids + aphredoderids and embedding the amblyopsids within the more derived Anacanthini. This hypothesis requires the unlikely proposition that the thoracic anus and segmented premaxilla were acquired independently in aphredoderids and amblyopsids. Springer & Johnson (2004) rejected Murray & Wilson's (1999) analysis and listed eight specializations of the gill arches that, in combination, provide strong evidence for percopsiform monophyly, the following two of which appear to be unique among fishes:

1. Transverses dorsales and obliquii dorsales, combined, with a trapezoidal appearance in dorsal view.
2. Obliquus dorsalis 4 (a branch of OD3-4) extending posteriorly, passing dorsal to articulation between uncinate processes of third and fourth epibranchials to insert on levator process of fourth epibranchial.

Division Gadacea new

Gadacea comprise the single order Gadiformes. Diagnosis is identical to that of the order.

Order Gadiformes Goodrich, 1909

Gadiform intrarelationships and the taxonomy of subclades have been the subject of considerable controversy. Markle (1989) and Howes (1989) presented starkly contrasting phylogenetic hypotheses based on different sets of synapomorphies. Markle recognized four suborders, whereas Howes recognized two. Cohen et al. (1990), with no phylogenetic analysis, recognized no suborders. Endo (2002) revisited gadiforms in a comprehensive phylogenetic analysis that forms the basis for the classification within the order presented below. We note that Endo (2002) restricted his outgroup comparisons to other "paracanthopterygians", including some groups now displaced to the percomorphs (batrachoidiforms, lophiiforms), as well as others still in phylogenetic proximity to gadiforms (i. e., the relatively basal Percopsiformes) and the effects of including taxa such as the Zeiformes (as suggested by DNA sequence data; Wiley et al. 2000, Miya et al. 2003) is not known. Endo (2002) discussed several characters proposed by previous authors (e. g., Rosen & Patterson 1969, Patterson & Rosen 1989) as synapomorphic for the group which he found to be problematic or in need of further investigation. The order is diagnosed by the following synapomorphies from Endo (2002):

1. Scapular foramen between scapula and coracoid (Markle 1989, Endo 2002). Endo (2002) noted that a similar state is found in some lophiiforms.
2. Pince-nez shaped sulcus and lateral collicular on otolith (Nolf & Steubaut 1989).
3. Levator arcus palatini lying laterally on adductor mandibulae A2 (Howes 1989). Endo (2002) noted that this character state is reversed in two genera, *Urophycis* and *Muraenolepis*.
4. Single hyomandibular condyle (Endo 2002). As noted by Endo (2002), this state is also found in *Aphredoderus* (Rosen 1962) and the ceratioid *Bertella* (Pietsch 1974).
5. Basihyal absent (Endo 2002).

One seemingly unique character did not appear in Endo's (2002) synapomorphy list: Yolk-sac and first feeding larvae with a lateral anus through the fin fold (Fahay & Markle 1984). Endo (2002) probably did not list this character as synapomorphic for the order because the state is unknown in some species.

Suborder Melanonoidei: Melanonoidei comprise a single family (Melanonidae) with two species of *Melanonus*. Endo (1993) accepted all four synapomorphies proposed by Howes (1993):

1. Supraoccipital excluded from margin of foramen magnum (Howes 1993).
2. Cranial neuromast pattern and innervation consisting of numerous flange-like structures on skin covering infraorbitals, snout, cheek muscles, preopercle and top of head, innervated by ramus canalis lateralis via complex nerve network; and button-like structures on lower cheek, snout and frontal (Howes 1993).

3. Brain positioned well forward with telencephalon and anterior part of mesencephalon being anteriorly displaced beyond cranial cavity so as to lie in orbital cavity formed by enlarged pterosphenoids (Howes 1993).
4. Enlarged pterosphenoids contacting lateral ethmoids (Howes 1993).

Synapomorphies uniting Macrouroidei + Gadoidei:
1. Anterior part of rectus communis attaching to urohyal ligamentous (Endo 2002).
2. Intercalar enlarged and forming part of posterior wall of cranium (Endo 2002) (reversed and not enlarged in *Squalogadus*).
3. Two non-segmented rays (pseudospines) articulating with first dorsal radial (Endo 2002).

Suborder Macrouroidei sensu Endo, 2002: Macrouroidei comprise two families, Macrouridae and Steindachneriidae. Synapomorphies diagnosing the suborder are from Endo (2002):
1. Transverse median process of pelvic girdle extended almost transversely, facing its contralateral member in midline.
2. Caudal skeleton absent.

Suborder Gadoidei sensu Endo, 2002: Gadoidei comprise eight families: Euclichthyidae, Moridae, Macruronidae, Merluciidae, Ranicipitidae, Bregmacerotidae, and Gadidae. Only Moridae and Gadidae have more than two genera. Endo (2002) hypothesized a single synapomorphy uniting the clade: presence of X and Y bones in caudal skeleton (Markle 1989).

Acanthopterygii sensu stricto (Johnson & Patterson 1993), not classified here: Stephanoberyciformes, Zeiformes, Beryciformes s. s., and Percomorpha, form a monophyletic clade diagnosed by the following synapomorphies:
1. Pelvic fin spine present. This is a variable character lost in some members of each major group (see discussion in Johnson & Patterson 1993).
2. Free pelvic radials reduced in size and/or number (Johnson & Patterson 1993).
3. Pelvic bones with anteromedial (styliform) processes (Stiassny & Moore 1992). This is lacking in non-melamphaid stephanoberyciforms, zeiforms, some atherinomorphs, and all gasterosteiforms (Johnson & Patterson 1993).

Division Stephanoberycacea new

Stephanoberycacea comprise the single order Stephanoberyciformes. Diagnosis is identical to the order.

Order Stephanoberyciformes Berg, 1937

Stephanoberyciformes comprise seven families: Melamphaidae, Stephanoberycidae, Gibberichthyidae, Rondeletiidae, Hispidoberycidae, Barbourisiidae, and Cetomimidae (Megalomycteridae and Mirapinnidae were recently synonymized with Cetomimidae by Johnson et al. 2009). They are diagnosed as follows:
1. Extrascapular, when present, greatly enlarged, partially or entirely covering parietal (Johnson & Patterson 1993).

Moore's (1993) analysis identified several reductive synapomorphies of stephanoberyciforms, all of which are homoplasious at various levels within acanthomorphs. These include absence of a subocular shelf, orbitosphenoid, and basi- and hypobranchial tooth plates.

Comment: The subject of beryciform (s.l.) relationships remains contentious. Based on two characters of pelvic fin anatomy, Stiassny & Moore (1992) proposed that holocentrids are more closely related to percomorphs than to other beryciforms (they also found no evidence to unite berycids with the latter). Johnson & Patterson (1993) discussed and rejected those two characters. Moore (1993) hypothesized that the remaining berycoids (his Trachythioidei) are related to the stephanoberyciforms (his Stephanoberycoidei) based on three reductive characters, also discussed and rejected by Johnson & Patterson (1993), who proposed that Stephanoberyciformes and Beryciformes are each monophyletic and are successive sistergroups of the Percomorpha. Molecular studies to date do not support separation of Stephanoberyciformes and Beryciformes, but consistently include both holocentrids and berycids within a monophyletic stephanoberyciform-beryciform clade.

Zeacea, Berycacea, and Percomorphacea comprise a clade diagnosed by the following synapomorphies, none of which is unique to this clade:

1. Baudelot's ligament originates on occiput. (Johnson & Patterson 1993). The only taxa with Baudelot's ligament originating exclusively on the occiput below this node in the Johnson & Patterson (1993) scheme are ophidiiforms and batrachoidiforms. That character conflict is resolved with the new placement of those groups here within the Percomorphacea, wherein only a few taxa, (e. g., agonids, champsodontids, some zoarcoids) show a reversal to origin on V1.
2. Dorsal fin advanced, with first dorsal pterygiophore inserting anterior to fourth (berycids) or third (others) neural spine (Johnson & Patterson 1993). Character conflict in ophidiiforms, lophiiforms and gadiforms is resolved by their treatment herein as percomorphs. The dorsal fin is apparently independently advanced in lampridiforms and secondarily posteriorly displaced in some percomorphs.
3. Anterior epineurals displaced ventrally onto ribs (Johnson & Patterson 1993). This is homoplasious in Percopsiformes.

Division Zeacea new

Zeacea comprise the single order Zeiformes. Diagnosis is identical to that of the order.

Order Zeiformes Regan, 1909

Zeiformes comprise five families: Parazenidae, Macrurocyttidae, Zeidae, Oreosomatidae, and Grammicolepididae. They are diagnosed by the following synapomorphies from Johnson & Patterson (1993) unless noted (most also recognized by Tyler et al. 2003):

1. Distal parts of proximal-middle dorsal fin radials laterally expanded.
2. Distal radials of spinous portion of dorsal fin absent or reduced to tiny cartilaginous or partly ossified elements.
3. Palatine with mobile articulation with dorsally truncated ectopterygoid.
4. Metapterygoid extremely reduced (probably correlated with 3).
5. Anterior vertebral centra with unusually flexible articulations; ribs, when present, never anterior to fourth vertebra.
6. Upright columnar processes on second and third pharyngobranchials (Rosen 1973).
7. Fourth pharyngobranchial and upper pharyngeal tooth plate absent.
8. Continuous medial cartilage below frontals running from ethmoid cartilage to parasphenoid.
9. Full neural spine on second preural centrum.
10. Parhypural truncated proximally (also found in gobiesocids and gobioids, Winterbottom 1993a, among others).
11. Hypurals 1 + 2 + 3 + 4 fused and fused to centrum (Tyler et al. 2003).
12. Dorsal-, anal-, and pectoral-fin rays unbranched (Tyler et al. 2003).

Euacanthopterygii (Johnson & Patterson 1993) are not classified here. Berycacea and Percomorphacea form a clade diagnosed by the following synapomorphies:

1. Pelvic spine asymmetrical, with medial process that grasps bony shelf or ring at posterior corner of pelvic girdle (Gosline 1961, Rosen & Patterson 1969, Mok & Chang 1986, Johnson & Patterson 1993).
2. "Chain-link" articulation of dorsal fin spines (Johnson & Patterson 1993).
3. Supraneurals ossified distally (Johnson & Patterson 1993).
4. Second ventral procurrent caudal fin ray shortened proximally such that its base is set back from bases of adjacent fins (Johnson 1975, Johnson & Patterson 1993).
5. "Myoseptal ligament" present from postcleithrum to posterolateral corner of pelvic girdle (Johnson & Patterson 1993). This was riginally proposed by Stiassny & Moore (1992) as an acanthomorph character; see Johnson & Patterson (1993) for discussion.

Division Berycacea new

Berycacea comprise a single order. The diagnosis is that of the order.

Order Beryciformes Günther, 1880 (sensu Johnson & Patterson, 1993)

Beryciformes sensu Johnson & Patterson (1993) comprise seven families: Holocentridae, Berycidae, Anoplogastridae, Diretmidae, Trachichthyidae, Anomalopidae, and Monocentrididae. The order is diagnosed by the following synapomorphies:

1. Jakubowski's organ: buccal-innervated terminal supraorbital neuromast(s) with associated modification of nasal bone and contact between tips of supraorbital and infraorbital canals (Jakubowski 1974, Freihofer 1978, Johnson & Patterson 1993).
2. Pharyngobranchial 4 absent (Johnson & Patterson 1993).

Division Percomorphacea new (= Percomorphi Cope, 1871)

Percomorphacea, formerly Percomorpha, as circumscribed by Johnson & Patterson (1993), comprise one putatively monophyletic series, Smegmamorpharia (= Smegmamorpha), placed in a polytomy with several orders. Many of these orders were formerly placed in the "Perciformes" senso lato whereas some were parts of the "Paracanthopterygii". Rather than perpetuate the myth that any evidence exists to support "Paracanthopterygii" (e. g., see Gill 1996) or "Perciformes" senso stricto as monophyletic groups, and in view of the emerging evidence that orders such as Tetraodontiformes, Pleuronectiformes, Lophiiformes, Batrachoidiformes, and even Ophidiiformes fall within "Perciformes" senso lato, we have elected to address the "current reality" in this classification (what Nelson 1989 termed "the bush at the top"). Including groups such as Pleuronectiformes, Tetraodontiformes, etc., within a series "Percaria" coordinate with Smegmamorpharia was not an option as there is no evidence for the monophyly of such a group. Two options were available to us, both of which dispense with Perciformes (and Paracanthopterygii) as presently understood (i. e., sensu Nelson 2006): 1) raise all non-smegmamorphs monophyletic groups to a rank equal to the Series Smegmamorpharia ("Percomorpharia" with 27 series), or 2) raise monophyletic suborders formerly included in Perciformes sensu lato to ordinal rank standing incertae sedis with the other currently recognized orders (Pleuronectiformes, Tetraodontiformes, etc.) within Percomorphacea. We have chosen the latter option because it best represents the fact that there is no evidence that an expanded Perciformes including such groups as Tetraodontiformes and Lophiiformes is monophyletic. We restrict "Perciformes" only to those groups that were formerly placed in the suborder Percoidei. However, we expect this to be an interim solution. We seriously doubt that "Perciformes" sensu stricto will survive rigorous phylogenetic analysis, and we have no synapomorphies to offer for the monophyly of the order.

Percomorphacea comprise the series Smegmamorpharia (seven orders) and an additional 23 orders. All 23 orders of non-smegmamorph fishes are incertae sedis within Percomorphacea and stand sedis mutabilis with series Smegmamorpharia (i. e. one vast 26-tomy). Percomorphacea are diagnosed by the following synapomorphies from Johnson & Patterson (1993):

1. Rod-like interarcual cartilage present between widely separated uncinate processes of first epibranchial and second pharyngobranchial (originally described and surveyed by Travers 1981). Absence of the interarcual cartilage in a number of percomorph groups was hypothesized to be secondary by Johnson & Patterson (1993) based on a wide separation of the tips of the uncinate processes of the first epibranchial and second pharyngobranchials, which are closely approximated in the primitive condition. Small, ovoid, non-homologous cartilages located between the two uncinate processes are found in some myctophids, melamphaids, and beryciforms s.s.
2. Second ural centrum absent (diural terminology). A separate second ural centrum is evident in adults of at least some members of all pre-percomorph lineages but lacking in adults of all members of the Percomorphacea.
3. Five or fewer hypurals. This is apparently independently derived in melamphaids, berycids, holocentrids, diretmids, and zeiforms. Batrachoidiformes, Lophiiformes, Ophidiiformes (formerly parts of Paracanthopterygii) also have five or fewer hypurals, but character conflict here is resolved by their inclusion in percomorphs.
4. Pelvic fins with fewer than six soft rays. This is a variable character hypothesized to have been acquired independently within most lineages of basal acanthomorphs. Reversals to more rays characterize the syngnathoid *Solenostomus*, and some cyprinodontoids and pleuronectiforms. Pattern of loss may clarify the homology of lost rays in these groups; see Johnson & Patterson (1993) for discussion.

5. Transforming ctenoid scales (Johnson 1983, Roberts 1993, Johnson & Patterson 1993). Several smegmamorph groups lack this character including atherinomorphs, gasterosteiforms, and synbranchiforms, as do tetraodontiforms, batrachoidiforms, lophiiforms, ophidiiforms, and many perciforms (see survey of Roberts 1993), but it does not occur below this node.
6. Free pelvic radials absent.
7. Point of origin of all but first two epineurals displaced ventrally, and distal parts of all epineurals displaced ventrally into horizontal septum. A similar pattern is found in *Aphredoderus*, one stephanoberyciform, some zeiforms, and the beryciform *Monocentrus*. This was rejected as a holacanthopterygian character by Johnson & Patterson (1993) on the grounds of parsimony.
8. Seventeen principal caudal fin rays in the pattern I,8,7,I (Fujita 1990). Further reduction in number of principal caudal fin rays is common in percomorphs, but increases are rare. Johnson & Patterson (1993) interpreted the 15 principal rays of Zeiformes as a convergence.

Percomorphacea comprise one series (Smegmamorpharia) and a number of orders that are incertae sedis. We treat the Smegmamorpharia first followed by the incertae sedis orders.

Series Smegmamorpharia Johnson & Patterson, 1993

Smegmamorpharia comprise seven orders of percomorph fishes. Four orders are incertae sedis and three orders are parts of the superorder Atherinomorphae. Atherinomorphae stand sedis mutabilis with the remaining four orders, forming a pentatomy.

Smegmamorpharia are diagnosed by a single synapomorphy. However, a number of the characters presented by Johnson & Patterson (1993) in their Table 2 are shared by most members of the group and may corroborate the monophyly of smegmamorphs or clades within it. Such a conclusion would depend on basal branching within the group. No formal analysis treating all these characters has been done. That of Springer & Orrell (2004), which rejected smegmamorph monophyly, was based on 55 characters exclusively from the gill-arch musculature and skeleton and the single uncontradicted smegmamorph synapomorphy identified by Johnson & Patterson (1993), described below. Clearly a more comprehensive analysis is needed:

1. First epineural inserting on a parapophysis or lateral process of its centrum (Johnson & Patterson 1993). The only reported convergences noted are in the carangiform *Echeneis* and the gobiiform *Gnatholepis*.

Order Elassomatiformes Johnson et Patterson, 1993, incertae sedis in Smegmamorpharia

Elassomatiformes comprise the single family Elassomatidae, characterized by a mosaic of reductive characters (Branson & Moore 1962; Johnson 1984, 1993) that have caused considerable controversy regarding their phylogenetic affinities. Johnson & Springer (1997: p. 176, abstract) presented morphological evidence suggesting a close relationship to gasterosteoids, and Springer & Johnson (2004) noted two uncommon specializations shared by these two groups: 1) anterior process of first epibranchial absent, uncinate process articulating with second pharyngobranchial; 2) first external levator inserting posterodorsally on first epibranchial and including all or part of lateral fourth of its surface. The analysis of Springer & Orrell (2004) based exclusively on gill-arch characters (and the single smegmamorph synapomorphy), retrieved *Elassoma* as the sistergroup of *Aulorhynchus* plus synbranchiforms plus gasterosteids. Synapomorphies (from Johnson 1984, 1993, unless otherwise noted) diagnosing the group include reductive characters that are not unique to elassomatids:

1. Basisphenoid absent.
2. Endopterygoid absent.
3. Ectopterygoid absent or fused to palatine.
4. Palatine with single notch-like articulation with ethmoid cartilage.
5. Full neural spine on first centrum.
6. Haemal spines on second and third preural centra not autogenous.
7. Hypurals 1-2 and 3-4-5 fused.
8. Principal caudal fin rays 14 or 15.
9. Supraneurals absent.
10. Dorsal fin originating posterior to sixth or seventh neural spine.
11. Anterior several neural spines somewhat expanded.

12. Branchiostegals five.
13. First pharyngobranchial, interarcual cartilage and fourth pharyngobranchial absent.
14. Posttemporal canal dissociated from posttemporal and posteriorly displaced or posttemporal canal absent and posterior extrascapular posteriorly displaced.
15. Numerous reductions in laterosensory system (e. g., no lateral line on body; infraorbitals absent except lacrimal; preopercular, mandibular, and angular lateralis canals absent; Branson & Moore 1962).

Order Mugiliformes Günther, 1880 incertae sedis in Smegmamorpharia

Mugiliformes comprise the single family Mugilidae. Synapomorphies diagnosing the order are those diagnosing the family, for which we cite two, the second described and recognized as synapomorphic for the first time here:

1. Pectoral girdle associated with three extrascapular bones; the third (posteriormost) extremely elongate (Stiassny 1993). See Johnson (1993: p. 17) and Johnson & Patterson (1993: p. 583) for discussions of the possible similarity of this configuration to that of *Elassoma*.
2. Distinctive configuration of dorsal fin and supports: Four dorsal spines, the first three robust and crowded; first pterygiophore inserting behind sixth or seventh neural spine, robust and much larger than succeeding ones; three very small, spineless pterygiophores between spinous and soft dorsal; all (seven) pterygiophores anterior to second dorsal fin lacking distal radials; second dorsal fin with one thin spine (segmented at its distal tip) and 7-10 soft rays.

Order Synbranchiformes sensu Gosline, 1983, incertae sedis in Smegmamorpharia

Synbranchiformes sensu Gosline (1983) comprise two suborders, Synbranchoidei and Mastacembeloidei. McAllister (1968) and Gosline (1983) suggested that these two groups are closely related, and Travers (1984b) proposed six synapomorphies corroborating this hypothesis, two of which were rejected by Britz (1996). Johnson & Patterson (1993) proposed two additional synapomorphies, and the resulting six are as follows:

1. Extension of dentary posteroventrally along ventral edge of anguloarticular (Travers 1984b).
2. Palatine sutured along posterolateral face of vomerine shaft (Travers 1984b).
3. Levator operculi inserting on dorsolateral face of opercle (Travers 1984b). This also characterizes some atherinomorphs and mugilids (Stiassny 1993, Johnson & Patterson 1993).
4. Hyohyoidei adductores dorsolaterally expanded, sealing operculum to body wall and causing restricted opercular opening (Travers 1984b).
5. Anterior surface of occipital joint of first vertebra convex, forming “plug-like” (synbranchoids: Rosen & Greenwood 1976) or “ball and socket” joint (mastacembeloids: Travers 1984a, Johnson & Patterson 1993).
6. Anterior vertebrae with distinctive configuration (Johnson & Patterson 1993: fig. 16).

Suborder Mastacembeloidei: Mastacembeloidei comprise two families, Mastacembelidae and Chaduriidae. Britz & Kottelat (2003) reviewed the 18 putative mastacembeloid synapomorphies proposed by Travers (1984b), concluded that only two (1 and 2 below) of those are valid, and added three (3-5 below) more:

1. Tooth plate fused to hypobranchial 3.
2. Long anterior process of membrane bone on prootic extending anteriorly into orbital.
3. Presence of elongate rostral cartilage that has lost its usual function during jaw protrusion, but instead rests on anteroventral tip of vomer and projects into median skin fold at the tip of snout.
4. Anterior nostrils at tip of tube-like extensions, i. e., presence of nasal tentacles.
5. Interarcual cartilage absent.

Suborder Synbranchoidei: Synbranchoidei comprise the single family Synbranchidae. Synapomorphies diagnosing both the suborder and the family are from Rosen & Greenwood (1976):

1. Paired fins, pelvic girdle and scapulocoracoids absent in adults.
2. Dorsal and anal fins represented by rayless rods and caudal fin greatly reduced or absent.
3. Gill membranes united and continuous around isthmus.
4. Scales absent or reduced and confined to caudal region (widely homoplastic among teleosts).
5. Region between prootic and posterior wall of orbit greatly expanded anteroposteriorly.
6. Frontals and basisphenoid united and forming posterior articulation for palatoquadrate.

7. First vertebra with articular plug and lateral flanges.
8. Basihyal ankylosed with first basibranchial.
9. Enlarged and ossified interarcual cartilage between first epibranchial and second pharyngobranchial.
10. First pharyngobranchial absent and second pharyngobranchial reduced to tiny ossicle.
11. Heart posterior, ventral aorta originating from level of ninth to twentieth vertebrae.
12. Atrium of heart with large auriculae cordis.
13. Right internal jugular vein reduced or absent.

Order Gasterosteiformes Gill, 1872, incertae sedis in Smegmamorpharia

Gasterosteiformes comprise two suborders, Gasterosteoidei and Syngnathoidei, and are diagnosed by the following synapomorphies from Johnson & Patterson (1993) (some may change depending on sistergroup relationships basally within the order):

1. Cartilaginous fifth basibranchial articulating with tips of fifth ceratobranchial. This is widespread within the group, but not universal.
2. Baudelot's ligament absent.
3. Coracoid with posteroventral extension. Pelvic bone without anterior process (Stiassny & Moore 1992).
4. Pelvic girdle with no anterior processes.
5. Full neural spine on preural centrum 2.
6. Haemal arch of preural centra 2 and 3 fused to respective centra.
7. Hypural plate single (parhypural and five hypurals not autogenous) and fused to terminal centrum. Centriscids and *Aulostomus* are exceptions (however Eocene aulostomids have the full fusion).
8. Dorsal spines, when present, not joined by membrane.
9. Scales, when present, represented by plates or scutes, except in *Aulostomus*, where Johnson & Patterson (1993) interpreted peripheral ctenoid scales as secondarily derived.

Suborder Gasterosteoidei: Gasterosteoidei comprise the families Gasterosteidae, Aulorhynchidae, Indostomidae, and Hypoptychidae following Britz & Johnson (2002). Johnson & Patterson (1993) suggested that the monotypic Hypoptychidae are the sistergroup of the aulorhynchid, *Aulichthys*, rendering the Aulorhynchidae polyphyletic (the two families are sistergroups in Pietsch 1978). Four characters from the gill arches support Johnson & Patterson's (1993) hypothesis (Springer & Orrell 2004). Synapomorphies diagnosing the suborder are from Britz & Johnson (2002):

1. Separate pectoral radials never develop and pectoral radial plate fuses as single unit to scapulocoracoid during development.
2. All or most of unpaired body plates in dorsal and ventral series formed from expanded proximal-middle radials of dorsal- and anal-fin pterygiophores.
3. Lateral body plates, when present, represented by single series of lateral dermal ossifications.
4. Paired pelvic plates arising as membranous outgrowths of pelvic girdle.

Suborder Syngnathoidei: Syngnathoidei comprise the families Sygnathidae, Pegasidae, Solenostomidae, Aulostomidae, Fistulariidae, Centriscidae, and Macroramphosidae; see classification in Pietsch (1978). Neither Pietsch (1978) nor Johnson & Patterson (1993) provided synapomorphies for the suborder and monophyly is questionable. We have identified the following two potential synapomorphies based on the distribution of characters identified and listed in Table 1 of Johnson & Patterson (1993):

1. Three to six anteriormost vertebrae elongate and with some degree of suturing.
2. Head and trunk more or less encased in bony embedded plates of exclusively dermal origin (*Aulostomus* is exceptional in having deciduous, peripheral ctenoid scales, interpreted as secondarily derived by Johnson & Patterson 1993).

Superorder Atherinomorphae (= Atherinomorpha Greenwood et al., 1966)

Atherinomorphae comprise the orders Atheriniformes, Cyprinodontiformes, and Beloniformes. The list of diagnostic synapomorphies was refined by Parenti (1993, 2005) and does not include certain characters appearing in Rosen & Parenti (1981) that have either problematic or wider distributions (L. Parenti pers. comm.). The list is long and diverse, but surprisingly Springer & Orrell (2004) identified only three synapomorphies (all homoplasious) from the gill arch skeleton and musculature. The clade is diagnosed here by the following synapomorphies:

1. Spermatogonia forming only at blind end of tubule near tunica albuginea (Rosen & Parenti 1981, Grier 1981, Parenti 1993).
2. Large demersal egg with long and short chorionic filaments and many lipid globules that coalesce at vegetal pole (Rosen & Parenti 1981, Parenti 1993).
3. Coupling during mating (Parenti 1993; observed by earlier workers).
4. Prolonged developmental period, typically one to two weeks (Parenti 1993; originally proposed as a synapomorphy of Cyprinodontiformes, Parenti 1981).
5. Separation of afferent and efferent circulation during development (Rosen 1964, Rosen & Parenti 1981, White et al. 1984, Parenti 1993).
6. Single or double disclike mesethmoid ossification(s) (Rosen 1964, Tigano & Parenti 1988, Parenti 1993). This is also found in *Elassoma* (Johnson 1984), but homology there was questioned by Parenti (1993).
7. Infraorbital series represented by lacrimal, dermosphenotic, and two or fewer anterior infraorbital bones (Rosen & Parenti 1981, Parenti 1993). Johnson & Patterson (1993) observed that reduction of infraorbitals is common among smegmamorphs as well as in a number of "higher" percomorph groups (see Springer 1983, Winterbottom 1993a).
8. Lateral process of pelvic bone and distal end of rib in close association and sometimes connected by a ligament (Parenti 1993).
9. Supracleithrum reduced or absent (Parenti 1993).
10. Dorsal gill arches with large fourth epibranchial and lacking fourth pharyngobranchial (Rosen & Parenti 1981, Parenti 1993).
11. Medial hook-like projection and ventral flange on fifth ceratobranchial bone (Stiassny 1990, Parenti 1993).
12. Supraneurals absent (Stiassny 1990, Parenti 1993).
13. Superficial (A1) division of adductor mandibulae with two tendons, one inserting on maxilla, second inserting on lacrimal (Parenti 1993).
14. Olfactory sensory epithelium arranged in sensory islets (Yamamoto 1982, Parenti 1993). Islet organization is found sporadically in other groups (Parenti 1993).
15. Restricted lobular testes (Parenti & Grier 2004).
16. Fluid versus granular egg yolk (Parenti & Grier 2004, Parenti 2005).
17. Saccus vasculosus absent (Parenti 2005).

Order Atheriniformes Rosen, 1964

Atheriniformes comprise the families Atherinidae, Bedotiidae, Isonidae, Melanotaenidae s.l. (including pseudomugilids), Phallostethidae, and Telmatherinidae. They are diagnosed by the following synapomorphies, some of which were questioned by Parenti (2005) and thus require more study:

1. Preanal length of flexion larvae short, comprising 33 % of body length (White et al. 1984). There is a single exception within the group, *Odontesthes debueni* (Atherinidae). A short preanal length is found in more derived members of the Percomorphacea and among gadids.
2. Larvae with single row of melanophores developing on dorsal midline of body. Parallel acquisition of this character is required for adrianichthyoid beloniforms (White et al. 1984, Parenti 2005).
3. Vomerine ventral face concave (Dyer & Chernoff 1996).
4. Adductor mandibulae A1 with long tendon to lacrimal (Dyer & Chernoff 1996).
5. Two anterior infraorbital bones (Dyer & Chernoff 1996; variation and interpretation discussed by Parenti 2005).
6. Pelvic-rib ligament present (Dyer & Chernoff 1996).
7. Pelvic plate not extending to anterior tip of longitudinal shaft (Dyer & Chernoff 1996).
8. Second dorsal-fin spine flexible (Dyer & Chernoff 1996).

Cyprinodontoidei Dyer & Chernoff, 1996 (Division II of Rosen & Parenti 1981)

Cyprinodontoidei, not formally classified herein, comprise Cyprinodontiformes and Beloniformes. Monophyly has been corroborated by many studies, both morphological and molecular (Rosen & Parenti 1981, Stiassny 1990, Saeed at al. 1994, Dyer & Chernoff 1996, Wiley et al. 2000, Li 2001, Parenti 2005). However, at what hierarchical level to recognize the two clades has been controversial (see Parenti 2005 for review). We have maintained the listing convention until such time as atheriniform workers agree on the formalities of rank. The clade is monophyletic, diagnosed by the following synapomorphies:

1. Second infraorbital absent (Rosen & Parenti 1981).
2. Pharyngobranchial 1 absent (Rosen & Parenti 1981).
3. Epibranchials 2 and 3 distinctly smaller than epibranchials 1 and 4 (Rosen & Parenti 1981).
4. Stomach, pyloric caeca and pneumatic duct absent (Li 2001).

Order Beloniformes Berg, 1937

Beloniformes comprise the suborders Adrianichthyoidei and Exocoetoidei (Belonoidei). They are diagnosed by the following synapomorphies from Rosen & Parenti (1981) and Parenti (2005, 2008).
1. Interarcual cartilage absent.
2. Second and third epibranchials relatively small.
3. Second pharyngobranchial vertically reoriented.
4. Dorsal hypohyal absent.
5. Interhyal absent.
6. Lower lobe of caudal fin with more principal fin rays than upper lobe.
7. Parietals extremely small or absent (Parenti 2008).

Comments: Parenti (2005) reviewed relationships within the order and Parenti (2008) updated the synapomorphies for the order.

Suborder Adrianichthyoidei: Adrianichthyoidei comprise the single family Adrianichthyidae, diagnosed by the following synapomorphies as reviewed and analyzed by Parenti (2008):
1. Vomer absent (Parenti 2008).
2. Articular surface of fourth epibranchial greatly expanded (Rosen 1964, Rosen & Parenti 1981).
3. Cartilaginous ceratobranchial epiphysis complexly branched (Rosen 1964, Rosen & Parenti 1981).
4. Tooth plate on the fourth ceratobranchial bone absent (Parenti 2008).
5. Autopalatine head expanded into cup-like structure that articulates with maxilla (or premaxilla) via dense ligament (Parenti 2008).
6. Rostral cartilage absent (Parenti 2008).
7. Meckel's cartilage about one-half length of dentary (Parenti 2008).
8. Articular bone oriented dorsally relative to body axis (Parenti 2008).
9. Jaw symphysis cartilaginous (Parenti 2008).
10. Metapterygoid absent (Parenti 2008).
11. Pterygoquadrate cartilage enlarged dorsally (Parenti 2008).
12. Mandibulo-lacrimal ligament absent (Dyer & Chernoff 1996, Parenti 2008).
13. Dermosphenotic lying lateral or posterior to sphenotic (Parenti 2008).
14. Supracleithrum absent (Parenti 2008).
15. Postemporal bone simple (not forked) (Parenti 2008).
16. Anterior ramus of coracoid broad and without cartilage (Parenti 2008).
17. Ventral accessory bone present in caudal skeleton (see Parenti 2008 for discussion).
18. Lateral branch of posterior lateral-line nerve in adults ventral rather than mid-lateral in position (Parenti 2008).

Li (2001) asserted that adrianichthyoids lack an elongate jaw, like cyprinodontiforms, whereas Parenti (2005) rejected the alignment of andrianichthyoids with cyprinodontiforms based on her interpretation that large-bodied adrianichthyids from Sulawesi have elongate jaws (Parenti 1987).

Suborder Exocoetoidei: Exocoetoidei comprise the families Belonidae, Scomberesocidae, Exocoetidae, and Hemiramphidae and are diagnosed by the following synapomorphies:
1. Lower pharyngeal tooth plate single (Rosen 1964, Rosen & Parenti 1981).
2. Basioccipital with vertical, plate-like process (Rosen & Parenti 1981).
3. Lower jaw elongate at some stage in development (Nichols & Breder 1928, Rosen & Parenti 1981).
4. Branchiostegal rays more than three (Rosen 1964, Rosen & Parenti 1981).
5. One narial opening on each side (Burne 1909, Rosen & Parenti 1981).

Order Cyprinodontiformes sensu Parenti, 1981

Cyprinodontiformes comprise the suborders Aplocheiloidei, and Cyprinodontoidei (Parenti 1981, Costa 1998). Parenti (2005) reviewed hypotheses of relationships for the clade and included a number of morphological and molecular studies. Cyprinodontiformes are diagnosed by the following synapomorphies:

1. Caudal fin endoskeleton with one epural symmetrically opposing parhypural (Parenti 1981, Rosen & Parenti 1981).
2. Caudal fin unlobed (Parenti 1981, Rosen & Parenti 1981).
3. First rib attached to second rather than third vertebra (Parenti 1981).
4. Pectoral fin set low on body, with large scale-like postcleithrum (Parenti 1981, Rosen & Parenti 1981).
5. Elongate interarcual cartilage joining expanded base of first epibranchial with shaft of second pharyngobranchial (Rosen & Parenti 1981).

Li (2001) challenged cyprinodontiform monophyly without inclusion of Adrianichthyoidei (see above). Parenti (2005) reviewed hypothesis of relationships within the order.

Suborder Aplocheiloidei sensu Parenti, 1981: Aplocheiloidei comprise two families, Aplocheilidae and Rivulidae, and are diagnosed by the following synapomorphies from Parenti (1981):

1. Orbital rims attached to frontals.
2. Mesethmoid cartilaginous.
3. Pelvic fin girdles closely set.
4. Lacrimal narrow and twisted.
5. Basihyal with broad anterior end.
6. Anterior nares tubular.
7. Cephalic sensory pore pattern reduced.
8. Males more elaborately pigmented than females.
9. Posterior extension of vomer dorsal to anterior arm of parasphenoid.

Suborder Cyprinodontoidei sensu Parenti, 1981: Cyprinodontoidei comprise the families Profundulidae, Fundulidae, Valenciidae, Anablepidae, Poeciliidae, and Cyprinodontidae and are diagnosed by the following synapomorphies from Parenti (1981):

1. Basibranchials two.
2. Dorsal hypohyal absent.
3. Interarcual cartilage one-half length of that in aplocheiloids.
4. Anterior extension of autopalatine sharply bent and hammer-shaped.
5. Extension of the autopalatine forms anterior covering of quadrate.
6. Metapterygoid absent.
7. Alveolar arm of premaxilla S-shaped.
8. Dentary robust and expanded medially.
9. Ethmomaxillary ligament absent.
10. Ligament that normally runs from interior arms of maxillae to middle of rostral cartilage absent.
11. Meniscus between premaxilla and maxilla absent.
12. Anteriormost fin ray absent resulting in articulation of "first" dorsal fin ray with first and second proximal radials.

Percomorphacea, incertae sedis orders

The following orders are incertae sedis within Percomorphacea. Some lack synapomorphies and are so noted using the shudder quote convention of Wiley (1979, 1981). All are listed in alphabetical order with no attempt to imply relationships. This represents our present state of knowledge about the groups.

Order Acanthuriformes Jordan, 1923, incertae sedis in Percomorphacea

Acanthuriformes comprise the families Siganidae, Luvaridae, Zanclidae, and Acanthuridae (from Tyler et al. 1989) and are diagnosed by the following synapomorphies, from Tyler et al. (1989) unless noted:

1. First neural spine fused to centrum.
2. Branchiostegal rays four or five.

3. Second infraorbital loosely articulated with or not contacting lacrimal.
4. First dorsal pterygiophore interdigitating anterior to second interneural space.
5. Supracleithral sensory canal absent, main trunk of lateral line canal communicating directly with posttemporal canal.
6. Maxillae and premaxillae tightly bound into single functional unit.
7. Anguloarticular much smaller than dentary. This requires a reversal in *Luvarus* which shows the condition in those outgroups examined by Tyler et al. (1989).
8. Supraoccipital not in contact with exoccipitals ventrally.
9. Supraoccipital crest reduced to low, short, ridge. Requires reversal in *Zanclus* (loc. cit.).
10. Supraneurals absent. Requires independent reversal in *Zanclus* and *Prionurus* (loc. cit.).
11. Narrow fourth pharyngeal tooth plate oriented longitudinally such that tooth rows are approximately parallel to, rather than perpendicular with, body axis. Requires reversal in *Luvarus* (loc. cit.).
12. During development, second or third *(Zanclus)* dorsal and pelvic spines are first rays to form and rapidly become enlarged and serrate.

The following seven (originally described by Johnson & Washington (1987) characterize only larval stages:
1. Pelvic girdle with unique T-shaped configuration.
2. Thin, slightly curved spine projecting ventrally from posteroventral corner of angular (= retroarticular), below insertion of interoperculomandibular ligament, and being first part of angular to ossify.
3. Low serrate ridge on supraoccipital. This is present in some percoid larvae (Johnson 1984).
4. Two serrate ridges on each frontal. This requires secondary loss in *Paracanthurus* and *Zebrasoma*. Similar ridges are found in pomacanthids (loc. cit.) and several families of percoids (Johnson 1984).
5. Trough-shaped nasal bone bearing serrations along one (siganids) or both edges. Similar ridges are found in pomacanthids (loc. cit.) and several families of percoids (Johnson 1984).
6. Serrate, ventrolateral, longitudinal ridge on angular. This is also found in pomacanthids.
7. Laterally directed, partially exposed ridge on each lateral ethmoid. This requires a loss in *Luvarus*.

Comment: Polarity decisions by Tyler et al. (1989) were based on a specific set of outgroup taxa. Scatophagidae (hypothesized sistergroup) and Ephippididae (second outgroup) share a number of synapomorphies with acanthuroids (see Tyler et al. 1989). Winterbottom (1993a) used this suite of characters to analyze relationships within the clade. Inclusion of Siganidae as the basal clade of the order was corroborated by Tang et al. (1999) using mitochondrial ribosomal genes but challenged by Holcroft & Wiley (2008) using nuclear protein-coding genes. Holcroft & Wiley's analysis strongly supported the inclusion of *Luvarus imperialis* in Acanthuriformes but found (with statistically significant support) that scatophagids and siganids are more closely related to their samples of lophiiform, tetraodontiform, and caproid fishes.

Order Anabantiformes sensu Britz 1995 (= Labyrinthici Regan, 1909)

Anabantiformes comprise two suborders, Anabantoidei and Channoidei. The labyrinth fishes have been recognized as a natural group since Cuvier & Valenciennes (1831), but most modern works have retained them as separate perciform suborders (e. g., Nelson 2006). Herein we follow Britz (1995, 2003, 2004) in recognizing a single clade at the ordinal level based on 7 synapomorphies (and acknowledge his personal assistance in describing and assigning these to the appropriate levels):
1. Suprabranchial organ (= accessory air-breathing organ) present comprising suprabranchial chamber housing expanded, modified first epibranchial (labyrinth) (Cuvier & Valenciennes 1831, Henninger 1908, Bader 1937, Peters 1978, Britz 1995).
2. Blood supply of suprabranchial organ by first two afferent branchial arteries (Bader 1937; Wu & Chang 1946; Munshi et al. 1986, 1994; Olson et al. 1986; Ishimatsu et al. 1979). This was recognized as synapomorphic by Britz (2003, 2004).
3. Efferent blood vessels from suprabranchial organ joining anterior cardinal vein, not dorsal aorta (Bader 1937; Munshi et al. 1986, 1994; Olson et al. 1986; Ishimatsu et al. 1979). This was recognized as synapomorphic by Britz (2003, 2004).
4. Double ventral aorta, anterior branch splitting into first two afferent branchial arteries supplying suprabranchial organ; posterior branch supplying two posterior afferent branchial arteries (Ishimatsu et al. 1979; Munshi et al. 1986, 1994; Olson et al. 1986). This was recognized as synapomorphic by Britz (2003, 2004).

5. Basioccipital with paired articular processes forming diarthrosis with upper pharyngeal jaws (Britz 1995, 2003, 2004).
6. Gas bladder extending posteriorly to parhypural (Britz 1995).
7. Larvae with bilateral pair of oil vesicles as floating device (Peters 1947, Cambray 1990). This was recognized as synapomorphic by Britz (1995, 2004).

Suborder Anabantoidei: Anabantoidei (sensu Britz 2003, Springer & Johnson 2004) comprise the families Luciocephalidae, Anabantidae, Helostomatidae, Osphronemidae, and Belontiidae and are diagnosed by the following synapomorphies:

1. Suprabranchial air chamber clearly separated from buccal cavity and respiratory air confined to suprabranchial cavity (Lauder & Liem 1983).
2. Distinct foramen exoccipitale covered by tympanum-like membrane present in exoccipital (Lauder & Liem 1983).

Britz (1994, 1995) reviewed the morphological evidence for the monophyly of the suborder and the relationships of *Luciocephalus* to other members of the clade. Rüber et al. (2006) presented an analysis of intrarelationships based on mitochondrial and nuclear gene sequences using channoids as the outgroup.

Suborder Channoidei: Channoidei comprise the family Channidae and are diagnosed by the following synapomorphies.

1. Otic bulla for sacculith mostly contained in prootic (Lauder & Liem 1983).
2. Metapterygoid with anterodorsal uncinate process approaching neurocranium (Lauder & Liem 1983) or articulating with it (Bhimachar 1932, Berg 1947, Britz pers. comm.).
3. Accessory breathing organs with respiratory nodules on first and second epibranchials, hyomandibular, and parasphenoid (Liem 1980).
4. An autogenous elongate bone (like a detached hemal spine) between hemal spines of PU2 and PU3, first figured and mentioned by Day (1914), maybe should be termed "Day's bone" from now on (R. Britz, pers. comm.).
5. Absence of fin spines in all fins (R. Britz, pers. comm.).

Order Batrachoidiformes Berg, 1937, incertae sedis in Percomorphacea

Batrachoidiformes comprise the family Batrachoididae. They have been removed herein from "Paracanthopterygii" (see discussion in introduction to Percomorphacea) and placed incertae sedis in Percomorphacea based on mitochondrial DNA sequence studies (Wiley et al. 2000, Miya et al. 2005, and others). Regan (1912: p. 279) held a similar belief, suggesting that except for pecularities of the form of the caudal fin, both batrachoidiformes and Lophiiformes would be considered "highly specialized percoids". Although traditionally allied to Lophiiformes (Regan 1912, Rosen & Patterson 1969, Patterson & Rosen 1989), that hypothesis has been questioned (Pietsch 1984, Pietsch & Grobecker 1987, and numerous molecular studies, including Miya et al. 2005). Patterson & Rosen (1989) suggested that batrachoidiform monophyly is likely, given various "peculiarities" cited by Regan (1912). Lauder & Liem (1983) proposed two synapomorphies diagnosing the order, endopterygoid unossified and the form of the dorsal fin. The former makes no sense, as the endopterygoid is a dermal bone, and lack of ossification would indicate absence – it is not absent. The latter might be reflected in Regan's diagnosis: "Spinous dorsal post-cephalic of 2 to 4 pungent spines, with fixed basalia", and we believe the configuration of the dorsal spine/pterygiophore is indeed unique. The most recent analysis of batrachoidid relationships based on 50 osteological characters (Greenfield et al. 2008) surprisingly offered no character support for monophyly of the group. We propose the following batrachoidiform synapomorphies:

1. Larvae with enormous yolk sac bearing adhesive disc on its ventral surface (Breder & Rosen 1966) – recognized as synapomorphic here.
2. Unique "crowded" configuration of dorsal spine/pterygiophore complex (see Monod 1960: fig. 13, Regan 1912).
3. First epineural hypertrophied, robust and ligamentously bound to medial surface of cleithrum (pers. obs., GDJ). This bone was erroneously labeled "endocleithrum" in Greenfield et al. (2008: fig. 50), wherein the bone labelled exoccipital is actually that bone plus the broad neural arch of the first vertebra, on which the robust first epineural inserts.

4. Five pectoral radials, the uppermost unossified in some species, the lowermost the largest and with a somewhat condylar association with the coracoid (see Monod 1960: figs. 19, 80, and Greenfield al. 2008: fig. 60).
5. Supracleithrum with condylar articulation with ankylosed posttemporal (pers. obs., GDJ).
6. Parietals absent (Rosen & Patterson 1969). As summarized by Winterbottom (1993a), parietals are also absent in tetraodontiforms (Tyler 1980), several acanthuroids (Tyler et al. 1989), some smegmamorphs (Parenti 1981, 1984), and gobioids (Regan 1911b, Birdsong 1975, Springer 1983, Winterbottom 1993a, Johnson & Brothers 1993).
7. Pelvic fin with one very short spine and two soft rays. Gosline (1970) reported two or three soft rays, and Greenfield et al. (2008) reported only three. We have observed only two pelvic soft rays in batrachoidiforms and believe that reports of three are erroneous.
8. Mesethmoid unossified (Gosline 1970).
9. Swimbladder with distinctive configuration (Sorensen 1884, Gosline 1970), "roughly heart-shaped with an anterior division into two lobes and the intrinsic musculature in bands along the lateral surface of each lobe" (Collette & Russo 1981).

Blenniiformes sensu Springer, 1993, incertae sedis in Percomorphacea

Blenniiformes sensu Springer, 1993, comprise the families Tripterygiidae, Dactyloscopidae, Clinidae, Blenniidae, Chaenopsidae, and Labrisomidae. Springer (1993) listed synapomorphies grouped into five character complexes and discussed distributional exceptions. We have listed each character separately, but make no claims for independence of characters.

1. First pharyngobranchial absent or cartilaginous (Springer 1993).
2. Second and fourth pharyngobranchials absent (Springer 1993).
3. First epibranchial with no uncinate process or associated interarcual cartilage (Springer 1993).
4. Neural spines lacking on first and several subsequent vertebrae (Johnson 1993). A few other perciforms lack a neural spine on the first vertebra (see Johnson 1993).
5. "Blennioid pelvic girdle" present. Position, shape and association of pelvic girdle are unique among percomorphs (Springer 1993).
6. Unique configuration of caudal skeleton. Springer (1993: p. 477) described the least specialized state for the blennioid caudal skeleton, various more specialized conditions, and noted that "with rare exceptions, one can recognize a blennioid fish based only on the structure of its caudal fin".
7. Roughly fan-shaped, anterior slip of epaxial muscle bundle inserting on distal portions of anterior dorsal-fin pterygiophores and extending forward to skull (Mooi & Gill 1995: p. 130).
8. First external levator and fourth transversus ventralis absent (Springer & Orrell 2004).

Order "Caproiformes", sensu Rosen, 1984, incertae sedis in Percomorphacea

Caproiformes comprise the family Caproidae and two genera, *Antigonia* and *Capros*. Rosen (1984: p. 31) diagnosed the family with a single synapomorphy: posterior pelvic processes sutured together in the midline and flared laterally into wing-like plates. He noted that a similar condition is found in holocentrids, where parsimony dictates that it must be independently derived. In their considerably more detailed analysis of zeiform relationships, Tyler et al. (2003) did not find this character in either genus and found no convincing synapomorphies to support the monophyly of this group. We recognize "Caproiformes" here only for convenience and agree with Johnson & Patterson (1993) that the two are not closely related, nor is either closely related to zeiforms as suggested by several previous authors (e. g., Rosen 1984, Tyler et. al. 2003).

Order Carangiformes Jordan, 1923, incertae sedis in Percomorphacea

Carangiformes comprise the families Nematistiidae, Coryphaenidae, Rachycentridae, Echeneididae, and Carangidae (see Smith-Vaniz 1984 for phylogenetic analysis of the families). The order is diagnosed by the following synapomorphies:

1. One or two tubular ossifications (prenasals) around extension of nasal canal (Freihofer 1978, Smith-Vaniz 1984, Johnson 1984; found elsewhere only in Toxotidae of "Perciformes").
2. Presence of small adherent cycloid scales (Smith-Vaniz 1984, Johnson 1984).

Order Cottiformes, new rank, sensu Imamura & Yabe, 2002, incertae sedis in Percomorphacea

Imamura & Yabe (2002) rejected Scorpaeniformes sensu lato as a monophyletic group and aligned cottoids with zoarcoids and scorpaenoids with serranoids based on a suite of morphological characters. Although not entirely congruent, molecular analysis by Smith & Wheeler (2004) also placed zoarcoids close to cottoids (but also Gasterosteoidei which were aligned with cottoids and zoarcoids in other molecular studies: Chen et al. 2003, Miya et al. 2003). Incorporation of zoarcoids into a new Cottiformes obviously affects previous classifications. Shinohara (1994) recognized several suborders of cottoids s. s. Many are monofamilial. As an alternative, we propose that Cottiformes comprise two suborders, Cottoidei and Zoarcoidei. This serves to unite the two lineages without introducing a superorder at this stage in the development of percomorph classification. One consequence is that Shinohara's cottoid suborders would be become superfamilies if we make the ordinal cut as one that unites the cottoid lineage sensu Imamura & Shinohara (1998) with the former Zoarciformes (Imamura & Yabe 2002). Synapomorphies diagnosing the order are taken from Imamura & Yabe (2002); many of these were previously considered cottoid synapomorphies (cf. Shinohara 1994) and have been reanalyzed as cottiform (Cottoidei + Zoarcoidei) synapomorphies. Several of these characters are variable within Cottiformes, and many are found outside the group and thus may be synapomorphies at a higher level, but for now are optimized as cottiform synapomorphies by Imamura & Yabe (2002), who provided a discussion of variability.

1. Parasphenoid connected with pterosphenoids (Quast 1965, Yabe 1985, Shinohara 1994, Imamura & Yabe 2002).
2. Branchiostegal rays six (Imamura & Yabe 2002).
3. Third epibranchial without tooth plate (Shinohara 1994, Imamura 1996).
4. Lateral extrascapulars comprising two elements (Imamura & Yabe 2002).
5. Supraneurals absent (Shinohara 1994, Imamura & Yabe 2002).
6. Dorsal pterygiophores arranged singly in each neural space (Shinohara 1994, Imamura & Yabe 2002).
7. Anal fin spines with robust pterygiophores absent (Shinohara 1994, Imamura & Yabe 2002).
8. Adductor mandibulae section 3 located on medial surface of levator arcus palatini (Anderson 1994, for zoarcoids; Imamura & Yabe 2002, for cottoids).
9. Levator operculi composed of two elements with origins on pterotic and posttemporal respectively (Imamura & Yabe 2002).
10. Circular elements of transversus dorsalis anterior present (Imamura & Yabe 2002).
11. Adductors I-III present (Imamura & Yabe 2002).
12. Gas bladder absent (Iwami 1985, Imamura 2000, Imamura & Yabe 2002).
13. Parietal sensory canal without spines (Imamura & Yabe 2002: fig. 15).

Suborder Cottoidei: Cottoidei comprise a series of former suborders (Shinohara 1994) that are ranked here as superfamilies. Each is followed by the family or families in parentheses: Anoplopomatoidea (Anoplopomatidae), Zaniolepididoidea (Zaniolepididae), Hexagrammoidea (Hexagrammidae), Cottoidea (Rhamphocottidae, Ereuniidae, Cottidae, Hemitripteridae, Agonidae, Psychrolutidae, Abyssocottidae, Comephoridae, Cyclopteridae, Liparididae, and problematically, Normanichthyidae and Bathylutichthyidae (see Imamura & Shinohara 1998). We note that molecular analysis is largely congruent with Shinohara's hypothesis of relationships within the suborder (Smith & Wheeler 2004). Synapomorphies diagnosing the suborder are:

1. Suborbital stay originating from third infraorbital (Imamura & Yabe 2002; homoplasious by parsimony with suborbital stays in other groups).
2. Extrinsic gas bladder muscle derived from epaxialis musculature (Imamura 1996, 2000).

Suborder Zoarcoidei: Zoarcoidei comprise the families Zoarcidae, Bathymasteridae, Stichaeidae, Cryptacanthodidae, Pholididae, Anarhichadidae, Ptilichthyidae, Zaproridae, and Scytalinidae. Synapomorphies diagnosing the suborder are from Anderson (1994) and the analysis of Imamura & Yabe (2002).

1. Basisphenoid absent (Anderson 1994).
2. Nostrils single (Anderson 1994).
3. Absence of dorsal and anal fin stays (Imamura & Yabe 2002).

Order Dactylopteriformes Jordan, 1923, incertae sedis in Percomophacea

Dactylopteriformes comprise the single family Dactylopteridae. Whereas monophyly of this group has never been questioned, its relationship to other percomorphs remains controversial. Although traditionally placed in the Scorpaeniformes, Berg (1940, 1947) rejected that hypothesis and treated it as a separate order, a placement recognized by many subsequent authors (see Imamura 2000 for authors recognizing each hypothesis). Imamura (2000) reviewed and rejected the scorpaeniform hypothesis and placed dactylopterids within the perciform family Malacanthidae. Of the eight putative synapomorphies he proposed for his expanded Dactylopteridae, Springer & Johnson (2004) noted that the most significant would appear to be fused nasal bones. However, as shown in Imamura's figure 4 the architecture and relationship of the fused nasals to other skull bones differs significantly in the two groups, as does the architecture of the entire neurocranium, also shown (only in dorsal view) in that figure. Such trenchant differences, not discussed or coded by Imamura (2000) argue against close relationship. Furthermore, as pointed out by Springer & Johnson (2004), Imamura's (2000) synapomorphies 2-6, and 8 (see Springer & Johnson for problems with the seventh) are widespread and variable among percomorphs, and need to be considered in a much broader sampling of taxa and characters (including a much more detailed comparative examination of larval morphology), if such an extraordinarily unlikely hypothesis is going to be taken seriously. We note also that to date no molecular analyses that include malacanthids and dactylopterids have recovered the two as closely related. We reject Imamura's (2000) hypothesis and list the following putative synapomorphies of dactylopteriforms, several considered here as such for the first time:

1. Nasals fused in adults (Allis 1909), also in the gasterosteiform pegasids (Pietsch 1978).
2. Five infraorbitals, a posteriorly directed stay on second (Imamura 2000), attaching to preopercle by apparently unique "hinge bone" involved in lateral movement and locking of long preopercular spine (Eschmeyer 1997).
3. Large, horseshoe-shaped swimbladder (Regan 1913, Eschmeyer 1997).
4. Intrinsic swimbladder drumming muscle present (Eschmeyer 1997). Imamura (2000) reported it to be absent in *Dactyloptena*.
5. First three vertebrae sutured together along neural arches and centra in a pattern considered nonhomologous with that of gasterosteiforms (Pietsch 1978, Johnson & Patterson 1993).
6. First vertebra sutured to occiput (Johnson & Patterson 1993).
7. Vertebrae 22 (Eschmeyer 1997).
8. Pelvic fin with one spine and four soft rays (Eschmeyer 1997).
9. Dorsal soft rays eight; anal soft rays six (Eschmeyer 1997).
10. Dorsal spines flexible, first one or two fully or partly separate from remaining spinous fin (Eschmeyer 1997).
11. Pectoral fins extremely elongate, inserted horizontally, with anteriormost 5-7 rays somewhat separate (Eschmeyer 1997).
12. Neural spines absent on first three vertebrae (pers. obs., GDJ; illustrated but not described by Imamura 2000: fig. 12C,D).
13. Body encased in distinctive keel-like scales (Pietsch 1978, Eschmeyer 1997, and numerous earlier authors).
14. Two enlarged, modified scales on each side of body at base of caudal fin; two to seven enlarged, modified scales on either side ventrally anterior to caudal fin (Eschmeyer 1997).
15. Head encased in bony armor, with uniquely conspicuous, very large, flattened, triangular, posterior extensions of the posttemporals (curiously as "suprascapulars" by Allis 1909) and preopercles ending as spines (Eschmeyer 1997), a distinctive pattern unique to this group (pers. obs., GDJ).

Order Gobiesociformes Gill, 1872, incertae sedis in Percomorphacea

Gobiesociformes comprise the suborders Gobiesocoidei and Callionymoidei and are diagnosed by the following synapomorphies:

1. Pelvic fin attached to anterior side of pectoral fin base by skin fold (Böhlke & Robins 1970, Gosline 1970).
2. Metapterygoid absent (Gosline 1970).
3. Infraorbital series represented only by lacrimal (Gosline 1970).
4. Scales absent (Gosline 1970).

5. First epineural absent, ribs absent (callionymids) (Johnson & Patterson 1993) (= "ribs start on second vertebra", Gosline 1970).
6. Strongly developed symplectic forming dorsal strut of palatoquadrate between hyomandibular and quadrate (Winterbottom 1993a).
7. Basipterygia transversely oriented (Winterbottom 1993a).
8. Free cartilaginous radial present at base of pelvic spine (Johnson & Patterson 1993).

Suborder Gobiesocoidei: Gobiesocoidei comprise the family Gobiesocidae and are diagnosed by the following synapomorphies:
1. Abdominal adhesive disc present (Gosline 1970, Springer & Fraser 1976), shown by Parenti & Song (1996) to comprise exclusively elements of the pelvic fin.
2. Supracleithrum with shallow, concave process at distal end articulating with convex condyle on anterior surface of cleithrum (Springer & Fraser 1976).
3. Proximal part of parhypural absent. This is also found in gobioids (Winterbottom 1993a).
4. Ribs inserting on epineurals anteriorly (Johnson & Patterson 1993). (= "two sets of ribs from the third vertebra" of Gosline 1970).

In their paper synonymizing Cheilobranchidae with Gobiesocidae, Springer & Fraser (1976) listed 32 specializations (most reductive and osteological) of gobiesocids, a number of which were also listed by Gosline (1970), whose work was inadvertently not cited by Springer & Fraser (1976).

Suborder Callionymoidei: Callionymoidei comprise the families Callionymidae and Draconettidae and are diagnosed by the following synapomorphies:
1. Frontals fused, anterior portion restricted and replaced in part by mesethmoid (Gosline 1970).
2. Abdominal vertebrae seven or fewer, total vertebrae 23 or fewer (Gosline 1970).

Order Gobiiformes Günther, 1880, incertae sedis in Percomorphacea

Gobiiformes comprise the families Rhyacichthyidae, Odontobutidae, Eleotrididae, Gobiidae, Kraemeriidae, Xenisthmidae, Microdesmidae, and Schindleriidae and are diagnosed by the following synapomorphies:
1. Pelvic intercleithral cartilage present (Springer 1983).
2. Ventral intercleithral cartilage present (Springer 1983).
3. Sagittae and lapilli with distinctly elongate primordia (Brothers 1984, Johnson & Brothers 1993).
4. Sperm-duct glands well developed (Miller 1992, Johnson & Brothers 1993).
5. Hypurals 1 and 2 fused; hypurals 3 and 4 fused to each other and to urostyle (Johnson & Brothers 1993, see Winterbottom 1993b for discussion of variation in other taxa).
6. Neural and haemal arches and associated spines developing as membrane bones with little or no cartilaginous precursors (Johnson & Brothers 1993). This character is uncommon in acanthomorphs; see Johnson & Brothers (1993) for some exceptions.
7. First neural arch fused to first centrum at its earliest appearance in ontogeny (Johnson & Brothers 1993).
8. Dorsalmost pectoral ray articulating with posterior margin of dorsal-most actinost (or radial cartilage) rather than with scapula; medial part of ray lacking enlarged articular base, and, in early ontogeny, not embracing ovoid cartilage lying at posterodorsal corner of scapulocoracoid cartilage (Johnson & Brothers 1993).
9. Interhyal not articulating at junction between symplectic and hyomandibular (Springer 1983, Johnson & Brothers 1993).
10. Parietals absent (Regan 1911b, Birdsong 1975, Springer 1983, Winterbottom 1993a, Johnson & Brothers 1993). As summarized by Winterbottom (1993a), parietals are also absent in tetraodontiforms (Tyler 1980), several acanthuroids (Tyler et al. 1989), some smegmamorphs (Parenti 1981, 1984), and batrachoidiforms (Rosen & Patterson 1969).
11. Basisphenoid absent (Springer 1983, Johnson & Brothers 1993). A basisphenoid is also absent in various other perciforms (e.g., zoarcoids, gobiesocids, Springer 1993).
12. Two or fewer infraorbitals (Springer 1983, Johnson & Brothers 1993).
13. Supraneurals absent (Springer 1983, Johnson & Brothers 1993). They are also absent in various other perciforms (see e.g., Johnson 1986, 1993).

14. Basibranchial 1 cartilaginous (Springer 1983). This is also seen in gobiesocids (Winterbottom 1993a). Springer noted two exceptions among gobioids where basibranchial 1 is ossified – neither is a basal member of the suborder.

See Birdsong (1975), Springer (1983), Winterbottom (1993a), Hoese & Gill (1993), and Johnson & Brothers (1993) for further discussions of gobiiform characters and character distributions of gobiiforms and/or their possible relatives. See Hoese & Gill (1993) for a hypothesis of relationships within the order.

Order Icosteiformes Berg, 1937, incertae sedis in Percomorphacea

Icosteiformes comprise a single species, *Icosteus aenigmaticus* in the monotypic Icosteidae. Most authors refer to the uniqueness of body form and integument, and the skeleton is largely cartilaginous. Because there is only one species, the order is technically "monophyletic" as it comprises a single lineage. Its treatment as an order here only reflects our ignorance about its closest relatives. For an extensive discussion of possible relationships, see Springer & Johnson (2004). In that discussion, Springer concluded that *Icosteus* "occupies a pre-percomorph position among the acanthomorphs" and tentatively placed it "near the Stephanoberyciformes". Johnson strongly disagrees and believes, based on available evidence, that *Icosteus* is well nested within the percomorphs.

Order Labriformes sensu Kaufman & Liem, 1982, incertae sedis in Percomorphacea

Labriformes sensu Kaufman & Liem (1982) comprise the families Labridae, Scaridae, Odacidae, Embiotocidae, Cichlidae, and Pomacentridae. Although long recognized and presently diagnosed by synapomorphies, the monophyly of this group has been challenged. As pointed out by several authors (e. g., Johnson 1993, Springer & Johnson 2004, Springer & Orrell 2004, Mabuchi et al. 2007), monophyly rests on a single complex of functionally related characters. The formal cladistic analysis of Springer & Orrell (2004), based on gill-arch musculature and skeletal characters, found the group to be paraphyletic without the inclusion of the family Pholidichthyidae but noted that molecular studies "are still needed, as are morphological studies based on more than gill-arch anatomy". Accordingly, we follow the conclusion of Springer & Johnson (2004), that "The relationships of the Pholidichthyidae remain unresolved" (see Britz 2006 for additional insights into the possible affinites of this family). Although each disagrees to a greater or lesser extent, no molecular phylogenetic analyses to date have recovered the labriformes as monophyletic but, rather, polyphyletic (Streelman & Karl 1997, Sparks & Smith 2004, Mabuchi et al. 2007). There are two problems. (1) None of the molecular phylogenies agree in detail, perhaps due to incongruency among the gene phylogenies or to inadequate taxon sampling. (2) Refutation of the eight synapomorphies has not been forthcoming although several authors (most recently Mabuchi et al. 2007) have pointed to the fact that not one of the eight synapomorphies is unique to labriform fishes, as noted below. The synapomorphies claimed to corroborate labriform monophyly are listed below:

1. Blade-like keel on lower pharyngeal jaw correlated with shift in insertion of part to all of transversus ventralis onto that keel (Stiassny & Jensen 1987). This is also found in exocoetoid atherinomorphs (loc. cit).
2. Third subdivision of transversus dorsalis anterior, m. transversus pharyngobranchialis 2 present (Stiassny & Jensen 1987). The plesiomorphic condition in perciforms is hypothesized to be two subdivisions (m. cranio-pharyngobranchialis 2 and m. transversus epibranchialis 2. Embiotocids and labrids lack m. cranio-pharyngobranchialis 2 but have m. transversus pharyngobranchialis 2. Embiotocids lack both m. cranio-pharyngobranchialis 2 and m. transversus pharyngobranchialis 2. Thus, interpretation of the muscle as a labroid synapomorphy requires that its absence in embiotocids is due to loss (Stiassny & Jensen 1987).
3. Transversus dorsalis anterior and transversus dorsalis posterior do not completely overlie raised articular bony facets of third pharyngobranchial, leaving facets exposed and creating a true diarthrosis (Kaufman & Liem 1982, Stiassny & Jensen 1987).
4. Neurocranium with characteristically ventrally projected and rounded neurocranial apophysis formed by parasphenoid and supported dorsally by ventral margins of prootics (Stiassny & Jensen 1987). In cichlids and embiotocids basioccipitals may also contribute to articular surface.
5. Sphincter oesophagi with no subdivision (Stiassny & Jensen 1987). Subdivision of this muscle is also absent in exocoetid and reduced in scomberesocid atherinomorphs, and it is absent in a number of nonlabroid perciforms (Johnson 1993).

6. Insertion of levator externus 4 shifted from epibranchial 4 to ceratobranchial 5 (Stiassny & Jensen 1987). Pomacentrids are polymorphic (loc. cit.). A similar muscle sling is known in a number of atherinomorphs (Stiassny & Jensen 1987, Johnson 1993) and perciforms (Johnson 1993).
7. Fifth ceratobranchials united to form single unit (Stiassny & Jensen 1987). This also characterizes some other percomorphs with hypertrophied fifth ceratobranchials. Stiassny & Jensen (1987) suggested that this is a synapomorphy of labroids because it occurs there even in the absence of hypertrophy.
8. First basibranchial elongate, cylindrical and displaced dorsoventrally to lie below basihyal axis (Stiassny & Jensen 1987). A similar condition is found in the kyphosid *Girella*. Rosen (in Rosen & Patterson 1990) suggested that this character defined a larger group of perciform fishes, including gerreids and kyphosids, whereas Johnson (1993) could see no clear-cut difference in the condition of labroids and several percoids he examined.

Order Lophiiformes Garman, 1899, incertae sedis in Percomorphacea

Lophiiformes comprise the suborders Lophioidei, Antennarioidei, Chaunacoidei, Ogcocephaloidei, and Ceratioidei (Pietsch 1981, 1984, Pietsch & Grobecker 1987). Relationships among the suborders were detailed most recently in Pietsch & Grobecker (1987, based on Pietsch 1981, 1984). The order is diagnosed by the following characters from Pietsch (1981, 1984):

1. Spinous dorsal fin number primitively six, with first three spines cephalic in position and modified into luring apparatus; correlated with other modifications.
2. Epiotics separated from parietals and meeting on midline posterior to supraoccipital.
3. Gill openings restricted to small, elongate, tube-like opening situated near the pectoral fin base.
4. First and second ural centra fused to first preural centrum to form plate emanating from single, complex, half-centrum (Rosen & Patterson 1969).
5. Pectoral radials narrow and elongate, ventral-most considerably expanded distally.
6. Eggs spawned in double, scroll-shaped sheath (Rasquin 1958).

Suborder Lophioidei: Lophioidei comprise the single family Lophiidae (Pietsch 1981). Although considered monophyletic, there is no analysis of synapomorphies for the family.

Suborder Antennarioidei: Antennarioidei comprise the families (in phylogenetic sequence; Pietsch 1984, Pietsch & Grobecker 1987) Brachionichthyidae, Lophichthyidae, Tetrabrachiidae, and Antennariidae. Synapomorphies diagnosing the clade are listed below.

1. Interhyal with medial, posteriorly directed process that makes contact with preopercle (Pietsch 1981).
2. Illicial pterygiophore and pterygiophore of third dorsal spine with highly compressed, blade-like, dorsal expansions (Pietsch 1981).

Relationships of Antennarioidei to the remaining suborders listed below are detailed by Pietsch & Grobecker (1987) based on Pietsch (1981, 1984).

Suborder Chaunacoidei: Chaunacoidei comprise the single family Chaunacidae. The suborder is undoubtedly monophyletic, but no formal list of synapomorphies has been proposed. Pietsch & Grobecker (1987) provided a traditional diagnosis.

Suborder Ogcocephaloidei: Ogcocephaloidei comprise the family Ogcocephalidae. The suborder is undoubtedly monophyletic, but no formal list of synapomorphies has been proposed. Pietsch & Grobecker (1987) provided a traditional diagnosis.

Suborder Ceratioidei: Ceratioidei comprise the families Caulophrynidae, Neoceratiidae, Himantolophidae, Oneirodidae, Thaumatichthyidae, Centrophrynidae, Ceratiidae, and Linophrynidae (Bertelsen 1951, 1984; Pietsch 1972). Pietsch (1979) and Bertelsen (1984) presented alternative proposals for the relationships among families. Pietsch & Orr (2007) presented a detailed series of phylogenetic analyses based on characters of different sexes and life stages. Unique and unreversed synapomorphies listed in Pietsch & Orr (2007: p. 23-24) are listed below, with appropriate analysis noted).

1. Palatines reduced or absent (metamorphosed female anlaysis).
2. Basihyal absent (metamorphosed female anlaysis).
3. Pelvic fins absent (metamorphosed female anlaysis).
4. Extreme sexual dimorphism with dwarf males (metamorphosed male and female and larva analysis: noted at least since Regan 1925)

5. Denticular bones in dwarf males (metamorphosed male and female and larva analysis: noted at least since Regan 1912).

Order Nototheniiformes Jordan, 1923, incertae sedis in Percomorphacea

Nototheniiformes comprise the families Nototheniidae, Bovichthyidae, Harpagiferidae, Bathydraconidae, Channichthyidae, and Artedidraconidae. Hastings (1993) hypothesized that Nototheniiformes might be embedded in what would be a paraphyletic Trachinoidei sensu Pietsch (1989). If so, then the single nostril of notothenioids is a synapomorphy of this larger group and its rank would have to be adjusted to render Trachiniformes monophyletic. Nototheniiformes are diagnosed by the following synapomorphies.

1. Floating posterior ribs present (Eakin 1981, Hastings 1993).
2. Pectoral fin radials in adults three (Hastings 1993). A fourth radial is found in juvenile bovichthyids (Andriashev 1987, cited in Hastings 1993) and apparently fuses to the scapula during ontogeny.
3. Nasal accessory organs present (Iwami 1986).

Order "Ophidiiformes", Berg, 1937, incertae sedis in Percomorphacea

The relationships and monophyly of ophidiiform fishes are problematic. Hypotheses range from relating cuskeels to Gadiformes (Rosen & Patterson 1969, Cohen & Nielsen 1978) to including them in Percomorphacea (Gosline 1968, 1971; Miya et al. 2005; molecular). Rosen (1985) and Howes (1992) could find no suite of synapomorphies for the order and Nielsen et al. (1999) concluded that evidence of monophyly is lacking. Given that Lophiiformes have joined the Percomorphacea, we expect that additional molecular and morphological evidence will corroborate the mitochondrial genomic results of Miya et al. (2005) and placed this nominal order within Percomorphacea.

Suborder "Ophidioidei" sensu Cohen & Nielsen, 1978: No convincing synapomorphies have been found to diagnose ophidioid fishes as monophyletic (Gordon et al. 1984, Rosen 1985, Patterson & Rosen 1989). As currently recognized (Nielsen et al. 1999), "Ophidioidei" comprise the families Carapodidae and Ophidiidae.

Suborder Bythitoidei sensu Cohen & Nielsen, 1978: Bythitoidei comprise the families Bythitidae and Aphyonidae and are diagnosed by a single complex synapomorphy: viviparity and morphology associated with this reproductive mode (Patterson & Rosen 1989, Nielsen et al. 1999).

Order "Perciformes" sensu stricto, incertae sedis in Percomorphacea

Perciformes sensu lato included most of the clades now raised to ordinal rank within Percomorphacea. We restrict the order to the former Percoidei sensu Johnson (1984), except for members of that group that show affinities elsewhere (e. g., Serranidae moved to Scorpaeniformes). As circumscribed here, "Perciformes" comprise some 90 families and incertae sedis genera (see Johnson 1984).

Order Pholidichthyiformes sensu Springer & Johnson, 2004, incertae sedis in Percomorphacea

Pholidichthyiformes comprise the single family Pholidichthyidae, variously aligned with Blenniiformes (Springer & Freihofer 1976), Labriformes (Stiassny & Jensen 1987), and Trachiniformes (Nelson 1994, but not 2006). Springer & Johnson (2004) noted that pholidichthyids "share specializations with a diverse group of fishes" and concluded that their relationships are unresolved. The following pholidichthyiform synapomorphies are from Springer & Freihofer (1976):

1. Septal bone present
2. Paraspenoid without ascending process.
3. Metapterygoid large and "complex".
4. Infraorbital lateralis organs apparently freed and displaced dorsally in gap area, which is partially invaded by free lateralis organs innervated by ramus buccalis accessorius facialis of truncus hyomandibularis.
5. Free lateralis organs present along horizontal septum anteriorly ventral to dorsal longitudinal collector lateral-line nerve.

Order Pleuronectiformes Bleeker, 1859, incertae sedis in Percomorphacea

Pleuronectiformes comprise two suborders, Psettodoidei (one family), and Pleuronectoidei (10 families) and are diagnosed by the following synapomorphies from Chapleau (1993):

1. Ontogeny characterized by migration of one eye (Brewster 1987, Chapleau 1993).
2. Dorsal fin anteriorly placed, minimally overlapping neurocranium (Chapleau 1993).
3. Recessus orbitalis (Chapleau 1993, and earlier references therein).

Suborder Psettodoidei: Psettodoidei comprise the family Psettodidae, with one genus and three species, diagnosed by a single synapomorphy: pseudomesial bar, an autogenous bone, between blind-side lateral ethmoid and blind-side frontal (Chabanaud 1934, Amaoka 1969, Chapleau 1993).

Suborder Pleuronectoidei sensu Chapleau & Keast, 1988: Pleuronectoidei comprise the remaining 10 flatfish families: Citharidae, Bothidae, Achiropsettidae, Scophthalmidae, Paralichthyidae, Pleuronectidae, Samaridae, Achiridae, Soleidae, and Cynoglossidae. The suborder is diagnosed by the following synapomorphies from Chapleau (1993).

1. Palatine teeth absent.
2. Basihyal without tooth plates.
3. Basisphenoid absent.
4. Spines on median fins absent.
5. Urohyal with distinct and often elongate sciatic portion.
6. Uroneurals reduced or absent.
7. Second pharyngobranchial of various sizes (absent in Cynoglossidae, Chapleau 1993).
8. Supramaxilla vestigial or absent.

Order Scombriformes sensu Johnson, 1986, incertae sedis in Percomorphacea

Scombriformes sensu Johnson, 1986, comprise the families Scombrolabracidae, Sphyraenidae, Gempylidae, Trichiuridae, Scombridae, Istiophoridae, and Xiphiidae. Considerable controversy surrounds this order, and inclusion or exclusion of Istiophoridae and Xiphiidae within Scombriformes. Based on morphology, Collette et al. (1984) hypothesized that billfishes and scombroids are sistergroups whereas Johnson (1986) argued that the scombrid, *Acanthocybium*, is the sistergroup of the billfishes, and this clade was thus embedded within scombroids sensu Collette et al. (1984). In molecular analyses billfishes and scombroids have either been related as sistergroups (Finnerty & Block 1995) or separated by several other percomorph families (Orrell et al. 2006). Given the relatively low statistical support in the Orrell et al. (2006) study, until additional molecular or morphological data challenge the hypothesis that billfishes and scombroids are at least sistergroups (regardless of the position of wahoos and billfishes within the clade), the options are reduced to the level in the hierarchy at which to express sistergroup relationships. We choose the ordinal level, with suborder allocation to be determined after the distribution of apomorphies (both morphological and molecular) is better understood. Synapomorphies of Scombriformes are from Johnson (1986):

1. Horizontal fronto-sphenotic shelf with sharp edge; fossa occupied mainly by an enlarged dilitator operculi.
2. Second epibranchial articulates with third pharyngobranchial via curved cartilaginous rod that extends medially well beyond lateral margin of third pharyngobranchial to articulate with small cartilaginous condyle (occasionally absent) at anterior tip of longitudinally oriented bony column on mid-dorsal surface of third pharyngobranchial.
3. Fourth pharyngobranchial cartilage absent, and fourth epibranchial articulating directly with relatively extensive posterior cartilaginous portion of third pharyngobranchial, which fills concave dorsal surface of fourth pharyngeal tooth plate usually occupied by fourth pharyngobranchial.
4. Third pharyngobranchial and fourth pharyngeal tooth plate notably elongate and “streamlined”.
5. Upper jaw complex tightly bound and non-protrusible; rostral cartilage providing pivot point for dorsoventral rotation of premaxillae.
6. Fifth branchiostegal borne posterior to anterior ceratohyal.

Scorpaeniformes sensu Imamura & Yabe, 2002, new usage, incertae sedis in Percomorphacea

Scorpaeniformes sensu Imamura & Yabe, 2002, comprise two suborders, Scorpaenoidei and Serranoidei. The inclusion of the serranids, traditionally placed in Percoidei, represented the first steps of disassembling the artificial assemblage herein named “Perciformes” s. s., formerly Percoidei of Perciformes. We note that molecular results of Smith & Wheeler (2004) support the dismemberment of “Perciformes” but are not congruent with the monophyly of Scorpaeniformes sensu Imamura & Yabe, 2002; serranoids are basal to a polyphyletic Scorpaenoidei. The order sensu Imamura & Yabe, 2002, is diagnosed by the following synapomorphies, some of which are questioned by Smith & Wheeler (2004):

1. Backwardly directed opercular spine (Imamura 1996). This is homoplastic with a similar condition in *Sphyraenops* (Epigonidae), *Bembrops* (Percophidae), Trachinidae and Channichthyidae (Johnson 1983, Iwami 1985, Imamura & Yabe 2002). Interpretation by Smith & Wheeler (2004) depends on their tree topology.
2. Adductor dorsalis present (Imamura & Yabe 2002. This is inferred by a parsimony argument. This muscle is widespread among percomorph fishes but absent in Cottiformes, the former sistergroup. The character was questioned by Smith & Wheeler (2004).
3. Larvae with single postocular spine in subocular region (sensu Moser & Ahlstrom 1978, Imamura & Yabe 2002). The wider distribution of this character in other “Perciformes” was noted by Imamura & Yabe (2002, also see Johnson 1984, and Baldwin & Johnson 1993). Only some serranoid species have this character; thus its status as synapomorphic for scorpaeniform fishes is problematic; see discussion by Imamura & Yabe (2002: p. 112).

Suborder Scorpaenoidei sensu Imamura & Shinohara, 1998: Scorpaenoidei sensu Imamura & Shinohara, 1998, comprise two superfamilies, Scorpaenoidea and Platycephaloidea. The superfamilies have the same limits as the previously recognized suborders Scorpaenoidei and Platycephaloidei of Imamura & Shinohara (1998). We note that Smith & Wheeler (2004) did not find a monophyletic Scorpaenoidei or a monophyletic Platycephaloidea. Scorpaenoidei herein are diagnosed by the following synapomorphies:

1. Suborbital stay on third infraorbital (Imamura & Yabe 2002). This is homoplasious by parsimony with suborbital stays in other groups.
2. Extrinsic gas bladder muscle derived from obliquus superioris.

Suborder Serranoidei Imamura & Yabe, 2002: Serranoidei comprise the family Serranidae (with three subfamilies; e. g. Baldwin & Johnson 1993, Nelson 2006), diagnosed currently by the following reductive synapomorphies from Johnson (1983) (additional analyses are needed to diagnose serranoids within the scorpaeniform context):

1. Posterior uroneural absent.
2. Procurrent spur absent.
3. Fourth preural interhaemal spine cartilage absent.

Order Stromateiformes Jordan, 1923, incertae sedis in Percomorphacea

Stromateiformes comprise the families Amarsipidae, Centrolophidae, Nomeidae, Tetragonuridae, and Stromateidae. Prior to the discovery of *Amarsipus carlsbergi*, stromateoids were united by the presence of toothed sacculuar outgrowths posterior to the last gill arch (Haedrich 1967). These pharyngeal pouches are lacking in *Amarsipus*. As discussed by Springer & Johnson (2004), Haedrich (1969) justified his inclusion of *Amarsipus* in his Stromateoidei based on several characters it shares with them. Johnson & Fritzsche (1989) rejected the validity of one of these, the pons moultoni (described in more detail by Haedrich 1971), as a stromateoid synapomorphy, based upon its wider distribution among percomorphs. Springer & Johnson (2004) rejected all but one of the others on similar grounds, as they did the three proposed by Horn (1984). Springer & Johnson (2004) did not discuss Haedrich’s (1969) remaining stromateoid character (subdermal canal system), and Springer concluded that “’we’ find no reason to consider *Amarsipus*, closely related to the stromateoids”. Johnson, on the other hand, finds no reason to question its validity as the single unique synapomorphy of Stromateiformes:

1. Extensive subdermal canal system communicating to the surface through small pores scattered over body (Haedrich 1967, 1969). See Konovalenko & Piotrovskiy (1989) for a description of the subdermal canal system in *Amarsipus*.

In a cladistic analysis based on 28 morphological characters, Douichi et al. (2004) identified eight putative synapomorphies for stromateoids and found *Amarsipus* to be deeply embedded within the group, despite lacking two of these (one being the pharyngeal sac). Because most of their stromateoid characters are widespread among percomorphs, and the status of these as synapomorphic is thus highly dependent on choice of outgroups *(Kyphosus* and *Arripis)*, we recognize here the only unique one shared by *Amarsipus* and the remaining taxa (noted above). Unfortunately the molecular analyisis of Douichi & Nakabo (2006) did not include *Amarsipus*.

Order Tetraodontiformes Berg, 1937
(= Plectognathes Cuvier, 1816), incertae sedis in Percomorphacea

Tetraodontiformes sensu Tyler, 1980, comprise three suborders with 10 extant families: Triacanthoidei (Triacanthodidae and Triacanthidae), Balistoidei (Balistidae, Monacanthidae, Aracanidae, and Ostraciidae), and Tetraodontoidei (Triodontidae, Tetraodontidae, Diodontidae, and Molidae). Winterbottom (1974), in his myological treatise, recognized only eight families, treating monocanthids and aracanids as subfamilies of Balistidae and Ostraciidae, respectively. Fossil diversity is significant and their incorporation into phylogentic analyses has significantly changed our concept of basal tetraodontiform synapomorphies. Tyler & Sorbini (1996) analyzed relationships and recognized 16 fossil and extant families. Santini & Tyler (2003) presented another analysis of relationships, recognizing additional fossil families. Relationships among several families remain controversial (e. g., see Leis 1984, Britz & Johnson 2005, Johnson & Britz 2005). Holcroft (2005) reviewed the history and presented a phylogenetic hypothesis based on DNA sequencing data. Relationships of tetraodontiforms to other acanthomorph fishes are also controversial. Rosen (1984), based on morphology, considered Tetraodontiformes to be basal acanthomorphs related to Zeiformes and Caproiformes, a hypothesis tentatively accepted and expanded by Tyler & Sorbini (1996) and Tyler et al. (2003). Tyler & Sorbini (1996) used Zeiformes as the outgroup to hypothesize diagnostic synapomorphies for the order. Analysis of DNA sequences, both mitochondrial and nuclear (Holcroft 2004) placed Tetraodontiformes as well as Caproiformes within Percomorphacea and close to a number of other groups traditionally considered allied to Tetraodontiforms (e. g., Acanthuriformes; Winterbottom 1974, Tyler 1980) and groups usually considered basal to percomorphs (Lophiiformes; Holcroft 2004). No molecular phylogenetic analysis has placed the order near Zeiformes (Chen et al. 2003, Miya et al. 2003, Holcroft 2004). Given this controversy, it is inevitable that diagnostic synapomorphies that are dependent on outgroup argumentation (as opposed to being unique or rare) will remain problematic. We acknowledge Jim Tyler for his advice and recommendations and accordingly list the following synapomorphies for fossil and extant taxa from Tyler & Sorbini (1996), a number of which were previously noted by Tyler (1980):

1. Vertebrae 21 or fewer.
2. Anal-fin spines absent.
3. Pelvic fin with no more than one spine and two soft rays.
4. Posterior processes of pelvic basipterygia sutured medially or fused.
5. Parietals absent.
6. Small, slit-like gill opening just anterior to pectoral fin base.
7. Ribs absent (except one species of monacanthid and Triodontidae).
8. Caudal fin with 12 or fewer principal rays.
9. Nasal bones absent.
10. Extrascapulars absent.

Order "Trachiniformes Bertin et Arambourg, 1958", (Trachinoidei sensu Pietsch, 1989), incertae sedis in Percomorphacea

Pietsch (1989) recognized Trachinoidei as comprising the families Chiasmodontidae, Champsodontidae, Pinguipedidae, Cheimarrhichthyidae, Trichonotidae, Creediidae, Percophididae, Leptoscopidae, Trachinidae, and Uranoscopidae. Pietsch & Zabetian (1990) added the family Ammodytidae. The monophyly of this group was supported by two derived characters of questionable value: presence of a pelvic spur and small, and short, wide pectoral radials. The monophyly of this group was challenged by Johnson (1993), Hastings (1993), Mooi & Johnson (1997), and Mooi & Johnson (2003). The major problem is variability in both characters among other percomorph groups coupled with variability within trachiniforms

(Johnson 1993). This does not, necessarily preclude these characters from diagnosing a monophyletic Trachiniformes, but it does require careful outgroup argumentation that, in turn, requires more knowledge of the relationships of percomorph fishes generally. In addition, Mooi & Johnson (1997) argued that the affinities of Champsodontidae lie with scorpaeniform or cottiform fishes, and Hastings (1993) pointed out that Nototheniiformes could easily be nested among the trachiniform families. Until such time as a more comprehensive phylogenetic analysis is performed, we treat this group as nominal and probably paraphyletic.

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The origin and the phylogenetic interrelationships of teleosts have been controversial subjects ever since Greenwood, P. H., Rosen, D. E., Weitzman, S. H. and Myers, G. S. in 1966 presented a revision of teleost phylogeny. Different taxa (*Amia*, *Lepisosteus*, *Amia* + *Lepisosteus*, †Pycnodontiformes, †*Dapedium*, †Pachycormiformes, and others) have been proposed as the sister group of teleosts. Tremendous advances have occurred in our knowledge of Neopterygii, basal to teleosts, and in their major component the teleosts over the past 40 years. Many new key fossils have been studied, and many extant teleost clades have been traced back to the Jurassic in detailed studies by Gloria Arratia in 1987, 1996, and 2000. In addition to new fossils, a large number of new morphological and molecular characters have been incorporated in recent phylogenetic analyses, adding to our arsenal of approaches. This book gives a modern view of these approaches. It includes a compilation of synapomorphies of numerous teleostean taxa with a new proposal of their classification, a proposal that pycnodonts are the fossil sister group of teleosts, a phylogeny based on mitochondrial genome sequences, separate analyses of basal teleostean taxa (Osteoglossomorpha, Clupeiformes, Gonorynchiformes, Cypriniformes, Characiformes, Siluriformes, Salmoniformes, Esociformes) and the euteleostean Aulopiformes, karyological studies of Cyprinodontidae, and morphological analyses of the posterior part of the neurocranium. A biography of Gloria Arratia is also presented.

The book represents contributions to the symposium “Origin and phylogenetic interrelationships of teleosts” sponsored by the American Society of Ichthyologists and Herpetologists (ASIH) and organized by the three editors of this volume and held at the Society’s annual meeting in St. Louis, Missouri, on 14 July 2007. At the same meeting, Gloria Arratia was honored with the Robert H. Gibbs, Jr. Memorial Award, 2007, for her outstanding contributions to systematic ichthyology. The volume presents the current state of phylogenetic knowledge of the origin of teleosts and the interrelationships of teleost groups, both key issues in fish systematics, based on both morphological (of extant and fossil taxa) and molecular evidence. The many contributors to the volume present and evaluate progress in studying both characters and taxa and in establishing databases (morphological and molecular) that will be of use in future.

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