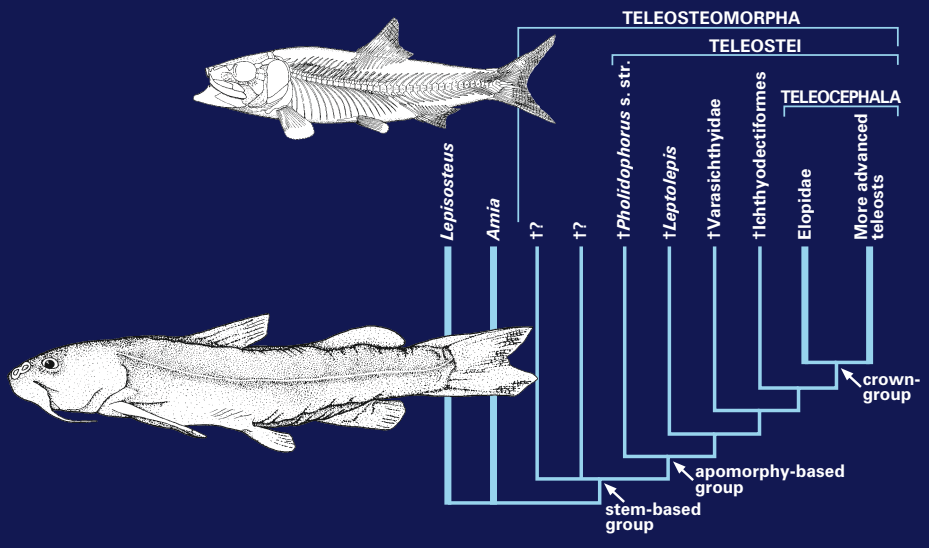
Origin and Phylogenetic Interrelationships of Teleosts

Honoring Gloria Arratia

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



Verlag Dr. Friedrich Pfeil · München

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Origin and Phylogenetic Interrelationships of Teleosts
J. S. Nelson, H.-P. Schultze & M. V. H. Wilson (eds.): pp. 431-470, 8 figs., 3 tabs., 3 apps.
 – ISBN 978-3-89937-107-9

Evolutionary relationships of the Aulopiformes (Euteleostei: Cyclosquamata): a molecular and total evidence approach

Matthew P. Davis

Abstract

Evolutionary relationships of the Aulopiformes (Euteleostei: Cyclosquamata) are investigated from a molecular and total evidence approach that includes previous morphological datasets. Molecular and total evidence analyses recover Aulopiformes as monophyletic and sister to a monophyletic Ctenosquamata, supporting the monophyly of Eurypterygii with molecular data. Monophyly of recently considered aulopiform suborders is tested, and Chlorophthalmoidei are deemed paraphyletic. The recently described genus *Paraulopus* is recovered outside *Chlorophthalmus* based on molecular and total evidence analyses, but is not recovered as the basal member of the Synodontoidei. Giganturoidei are recovered as the sister group of an ipnopid clade, rather than the sister group to Alepisauroidei. Molecular analyses strongly support a clade consisting of the family Scopelarchidae and chlorophthalmoid taxa, but total evidence analyses recover scopelarchids as the basal lineage of Alepisauroidei. A sister-group relationship between Evermannellidae and Scopelarchidae is not supported, and the family Paralepididae is deemed paraphyletic. Systematic placement of taxa within the monophyletic and paraphyletic suborders, revised classification, and evidence supporting previously unrecognized clades are discussed.

Introduction

The extreme habitats of the deep sea have produced fascinating evolutionary events among the 2000 species of marine fishes that have invaded this realm. This study focuses on one such lineage, the marine order Aulopiformes (Euteleostei: Cyclosquamata), which includes 44 genera and 236 species of lizardfishes and their allies (Nelson 2006). Aulopiform fishes include some of the most bizarre deep-sea fishes, as well as key coral-reef predators, with members of the group exhibiting diverse evolutionary adaptations, such as bioluminescence, tubular eyes, and synchronous hermaphroditism (Fig. 1). Recent work on previously unrecognized fossil taxa supports a middle to Late Cretaceous origin for the order (e.g., Rosen 1973, Fielitz 2004) in a marine environment. Aulopiformes are classified within the Superorder Cyclosquamata, and are currently divided into four monophyletic suborders as shown in Figure 2 (Baldwin & Johnson 1996, Sato & Nakabo 2002).

Hypotheses regarding aulopiform relationships have been controversial since the proposal of the order by Rosen (1973), with as many as seven distinct classifications proposed during the last 40 years (Gosline et al. 1966, Rosen 1973, Sulak 1977, R. K. Johnson 1982, Rosen 1985, Hartel & Stiassny 1986, Baldwin & Johnson 1996, Sato & Nakabo 2002). All previous hypotheses of aulopiform relationships have been based solely on morphological data. Disagreement and confusion regarding aulopiform morphological characters have resulted in a lack of consensus regarding relationships among aulopiform fishes as seen in Figure 3 (Rosen 1973, R. K. Johnson 1982, Rosen 1985, Hartel & Stiassny 1986, Johnson et al. 1996, Baldwin & Johnson 1996, Sato & Nakabo 2002), as well as confusion regarding the order's monophyly and placement among lower euteleostean fishes (Rosen 1973, R. K. Johnson 1982, Rosen 1985, Hartel & Stiassny 1986, G. D. Johnson 1992, Patterson & Johnson 1995, Baldwin & Johnson 1996, Sato & Nakabo 2002) as seen in Figure 4.

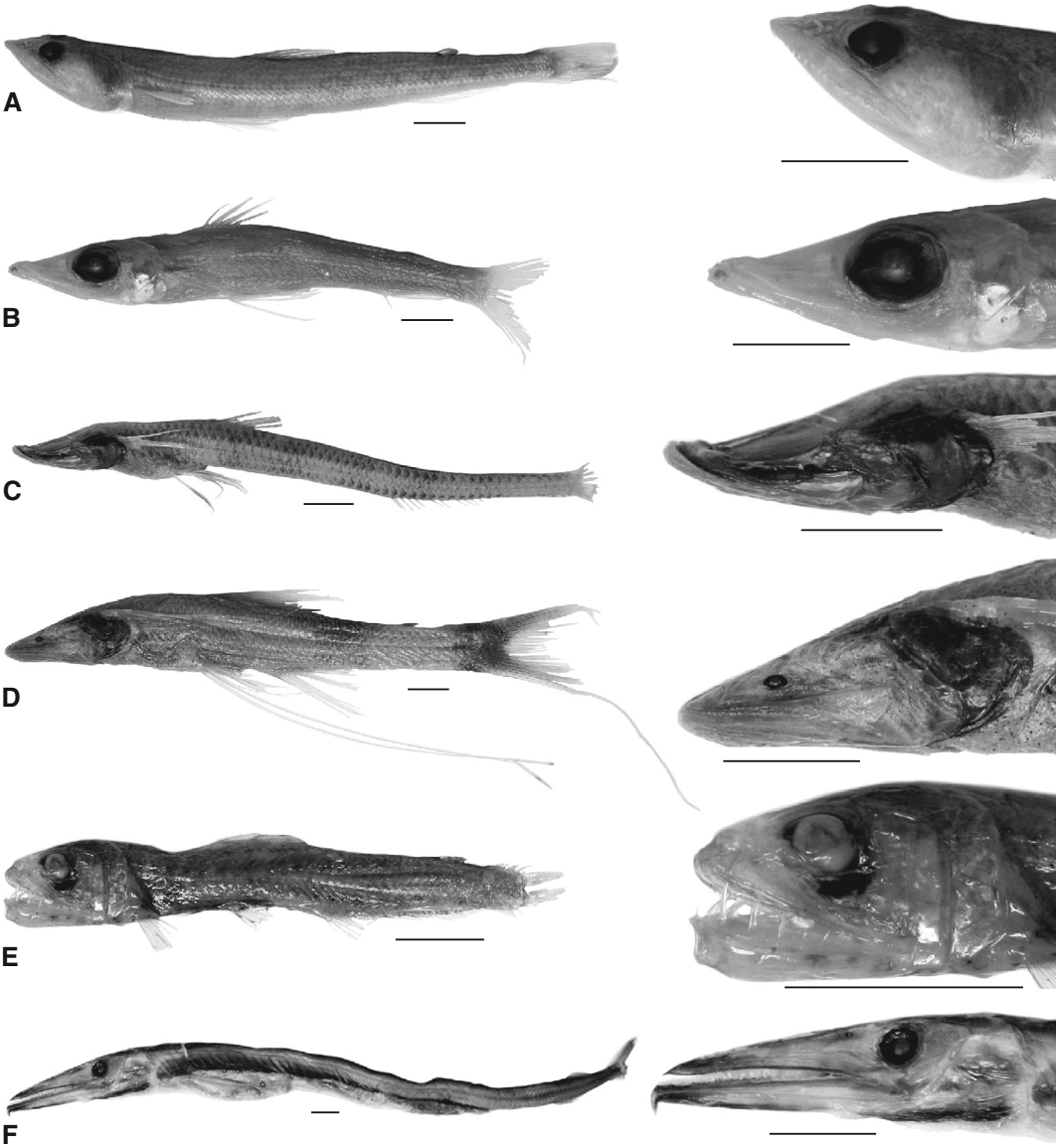

Fig. 1.
Representatives of aulopiform diversity. **A,** *Synodus foetens*, KU 18066; **B,** *Parasudis truculenta*, VIMS 03261; **C,** *Ipnops murrayi*, KU CI-182; **D,** *Bathypterois viridensis*, VIMS 6149; **E,** *Evermannella indica*, SIO 73-148; **F,** *Anotopterus pharao*, KU 28218. Scale bars denote 10 mm.

Prior to the proposal of the order Aulopiformes (Rosen 1973), aulopiform fishes were classified within the order Iniomi, which also included members of the order Myctophiformes (lanternfishes) (e. g., Regan 1911, Gosline et al. 1966). Rosen (1973) erected the order Aulopiformes from all previously recognized iniomous fishes *sans* the Myctophiformes, based primarily on the shared presence of an elongated uncinate process on the second epibranchial located within the gill arches of aulopiform fishes. Rosen (1973) further separated Myctophiformes from aulopiform fishes, and proposed a monophyletic Ctenosquamata based on the presence of ctenoid scales and advanced pharyngobranchial elements that lanternfishes share with members of the Acanthomorpha (spiny-rayed fishes) (Fig. 4A).

Baldwin & Johnson (1996)

Order Aulopiformes
- Suborder Synodontoidei
  - Family Aulopidae *(Aulopus)*
  - Family Pseudotrichonotidae *(Pseudotrichonotus)*
  - Family Synodontidae *(Harpadon*, *Saurida*, *Synodus*, *Trachinocephalus)*
- Suborder Chlorophthalmoidei
  - Family Chlorophthalmidae *(Chlorophthalmus*, *Parasudis)*
  - Bathysauropsis *(B. gracilis*, *B. malayanus)*
  - Family Notosudidae *(Ahliesaurus*, *Luciosudis*, *Scopelosaurus)*
  - Family Ipnopidae *(Bathymicrops*, *Bathypterois*, *Bathytyphlops*, *Discoverichthys*, *Ipnops)*
- Suborder Alepisauroidei
  - Family Alepisauridae *(Alepisaurus*, *Omosudis)*
  - Family Paralepididae *(Anotopterus*, *Arctozenus*, *Dolichosudis*, *Lestidiops*, *Lestidium*, *Lestrolepis*, *Macroparalepis*, *Magnisudis*, *Notolepis*, *Paralepis*, *Stemnosudis*, *Sudis*, *Uncisudis)*
  - Family Evermannellidae *(Coccorella*, *Evermannella*, *Odontostomops)*
  - Family Scopelarchidae *(Benthalbella*, *Rosenblattichthys*, *Scopelarchoides*, *Scopelarchus)*
- Suborder Giganturoidei
  - Bathysauroides gigas
  - Family Bathysauridae *(Bathysaurus)*
  - Family Giganturidae *(Gigantura)*

Sato & Nakabo (2002)

Order Aulopiformes
- Suborder Synodontoidei
  - Family Paraulopidae *(Paraulopus)*
  - Family Aulopidae *(Aulopus)*
  - Family Pseudotrichonotidae *(Pseudotrichonotus)*
  - Family Synodontidae *(Harpadon*, *Saurida*, *Synodus*, *Trachinocephalus)*
- Suborder Chlorophthalmoidei
  - Family Bathysauroididae *(Bathysauroides)*
  - Family Chlorophthalmidae *(Chlorophthalmus*, *Parasudis)*
  - Family Bathysauropsidae *(Bathysauropsis)*
  - Family Notosudidae *(Ahliesaurus*, *Luciosudis*, *Scopelosaurus)*
  - Family Ipnopidae *(Bathymicrops*, *Bathypterois*, *Bathytyphlops*, *Discoverichthys*, *Ipnops)*
- Suborder Alepisauroidei
  - Family Alepisauridae *(Alepisaurus*, *Omosudis)*
  - Family Paralepididae *(Anotopterus*, *Arctozenus*, *Dolichosudis*, *Lestidiops*, *Lestidium*, *Lestrolepis*, *Macroparalepis*, *Magnisudis*, *Notolepis*, *Paralepis*, *Stemnosudis*, *Sudis*, *Uncisudis)*
  - Family Evermannellidae *(Coccorella*, *Evermannella*, *Odontostomops)*
  - Family Scopelarchidae *(Benthalbella*, *Rosenblattichthys*, *Scopelarchoides*, *Scopelarchus)*
- Suborder Giganturoidei
  - Family Bathysauridae *(Bathysaurus)*
  - Family Giganturidae *(Gigantura)*

Fig. 2.
Recent classifications of aulopiform interrelationships. Genera within each family are listed.

The hypothesis of aulopiform monophyly has been rejected multiple times (R. K. Johnson 1982, Rosen 1985, Hartel & Stiassny 1986). R. K. Johnson (1982) rejected aulopiform monophyly in favor of an iniomous hypothesis of relationships (Figs. 3B, 4B). He argued that the presence of an elongated uncinate process on the second epibranchial was not unique to Aulopiformes and is a primitive iniomous trait shared with the Myctophiformes. Additionally, he proposed a clade within his iniomous Myctophiformes in which lanternfishes are closely related to his chlorophthalmoids based on the shared presence of an enlarged gap between the occipital region of the neurocranium and the first centrum. Rosen (1985) proposed a revised hypothesis of euteleostean relationships that left Aulopiformes paraphyletic (Fig. 4C). He proposed that the genus *Aulopus* shared derived features with ctenosquamates (e.g., the presence of a median rostral cartilage) and placed the genus within Ctenosquamata along with his chlorophthalmids. Stiassny (1986) and Hartel & Stiassny (1986) corroborated this hypothesis, and placed the aulopiform genera *Aulopus*, *Parasudis*, and *Chlorophthalmus* together as the sister group to the ctenosquamates (Fig. 4D).

Hypotheses of aulopiform paraphyly (Rosen 1985, Hartel & Stiassny 1986) were challenged by G. D. Johnson (1992), who proposed an additional gill-arch aulopiform synapomorphy (cartilaginous condyle absent on third pharyngobranchial), and provided further support for the monophyly of Rosen's (1973) Eurypterygii (Aulopiformes + Ctenosquamata) and for Ctenosquamata (Myctophiformes + Acanthomorpha) (Fig. 4A). Baldwin & Johnson (1996) disagreed with R. K. Johnson's (1982) observation that Myctophiformes posses an uncinate process on the second epibranchial, and proposed that he incorrectly identified the anterior portion of the second epibranchial as an uncinate process in the myctophiform genus *Neoscopelus*. Currently, nine morphological synapomorphies support the hypothesis of a monophyletic Aulopiformes (Baldwin & Johnson 1996, Sato & Nakabo 2002): presence of an enlarged uncinate proc-

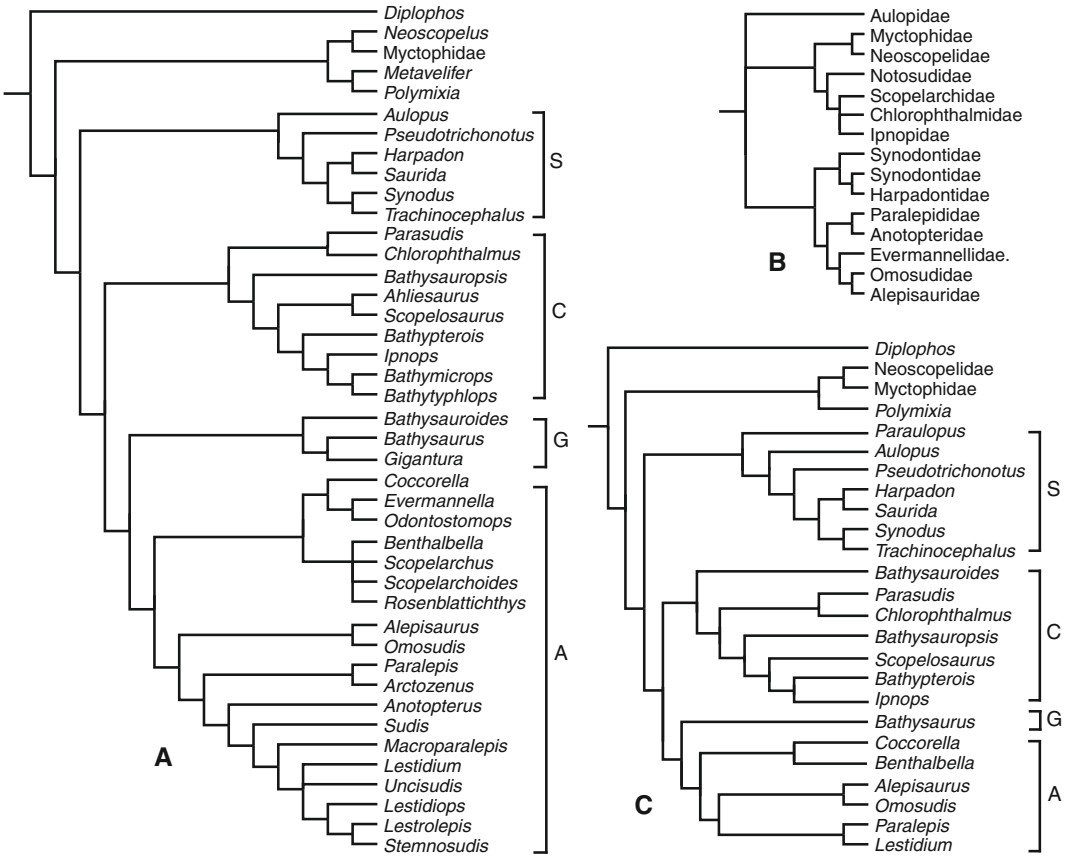

Fig. 3.
Previous phylogenetic hypotheses of aulopiform interrelationships from Baldwin & Johnson (1996; **A**); R. K. Johnson (1982; **B**) and Sato & Nakabo (2002; **C**). Suborders include A, Alepisauroidei; C, Chlorophthalmoidei; G, Giganturoidei; and S, Synodontoidei.

ess on second epibranchial (Rosen 1973), absence of cartilaginous condyle on third pharyngobranchial (G. D. Johnson 1992), epipleural bones extending to second or first vertebra (Patterson & Johnson 1995), absence of swimbladder (Marshall 1954), presence of peritoneal pigment in larvae (R. K. Johnson 1982), medial processes of pelvic girdle joined medially by cartilage (Baldwin & Johnson 1996), presence of fifth epibranchial (Baldwin & Johnson 1996), one or more epipleurals displaced dorsally into horizontal septum (Patterson & Johnson 1995), and palatine not expanded laterally (Sato & Nakabo 2002). Aulopiform monophyly has not been tested with molecular data utilizing the broad taxon sampling of the previous morphological studies.

Relationships within the Aulopiformes have undergone major revisions with essentially every study that has examined them. For an in-depth review of aulopiform classifications and phylogenetic studies prior to 1996, refer to the morphological study of Baldwin & Johnson (1996). Recent hypotheses of aulopiform relationships are illustrated in Figure 3. Baldwin & Johnson (1996) proposed a strict consensus phylogeny of nine equally parsimonious trees from 118 morphological characters that supported four major aulopiform clades as seen in Figure 3A. Sato & Nakabo (2002) investigated the systematic placement of a previously unrecognized genus *Paraulopus* within a *Chlorophthalmus* species complex. Their analysis utilized 101 morphological characters, 80 from Baldwin & Johnson (1996), with revisions to 13 characters, and the addition of 21 newly considered morphological characters. While their analysis did not include all of the same taxa as Baldwin & Johnson (1996), they also recovered four major aulopi-

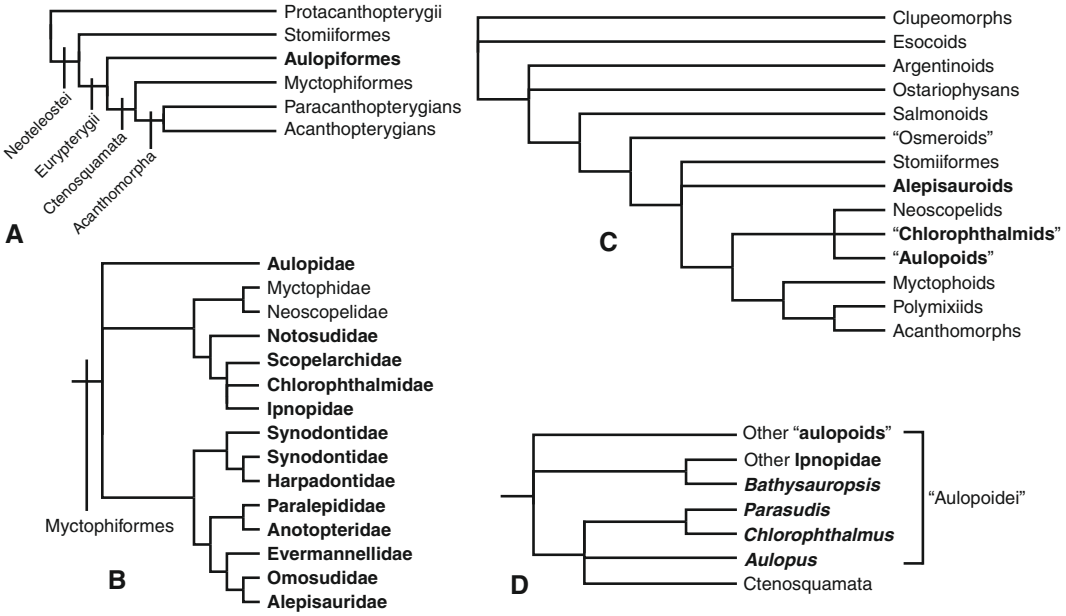

Fig. 4.
Previous phylogenetic hypotheses of aulopiform monophyly Rosen (1973; **A**); and paraphyly R. K. Johnson (1982; **B**); Rosen (1985; **C**); Hartel & Stiassny (1986; **D**). Aulopiform taxa are bolded.

form clades (Fig. 3C) with a single most parsimonious tree, and made a number of small revisions to the phylogeny proposed by Baldwin & Johnson (1996) including: the recovery of *Bathysauroides* as the basal member of Chlorophthalmoidei, rather than as a member of Giganturoidei (Baldwin & Johnson 1996), and placement of the newly diagnosed genus *Paraulopus* as the basal member of Synodontoidei. Changes to the classification of Baldwin & Johnson (1996) included elevation of the genera *Bathysauropsis* and *Bathysauroides* to family level (Bathysauropsidae and Bathysauroididae respectively).

Baldwin & Johnson's (1996) study recovered a monophyletic Synodontoidei as the basal aulopiform lineage, with the genus *Aulopus* as the basal aulopiform taxon within the suborder. The placement of *Aulopus* within the suborder supports the findings of Johnson et al. (1996), but contradicts many previous hypotheses (Rosen 1973, R. K. Johnson 1982, Rosen 1985, Hartel & Stiassny 1986). Sato & Nakabo's (2002) revision of relationships recovered *Paraulopus* as the basal synodontoid. A novel hypothesis of a Notosudidae + Ipnopidae clade was proposed by Baldwin & Johnson (1996) within their monophyletic Chlorophthalmoidei. Notosudidae have previously been aligned with chlorophthalmoid taxa (Rosen 1973, Bertelsen et al. 1976, R. K. Johnson 1982) and have also been said to have a close relationship to the family Scopelarchidae (R. K. Johnson 1982, Patterson & Johnson 1995).

Another novel hypothesis from Baldwin & Johnson (1996) was the recovery of a monophyletic Alepisauroidei + Giganturoidei clade. The phylogenetic placement and classification of members within the bathypelagic suborder Giganturoidei *(Bathysaurus*, *Gigantura)* has been traditionally difficult because of highly modified morphological features. Previous studies placed *Gigantura* in its own order (e.g., Regan 1925, Walters 1961), and Rosen (1973) suggested that *Gigantura* was most closely related to members of the currently recognized family Synodontidae *(Synodus*, *Trachinocephalus*, *Harpadon*, *Saurida)*. Patterson & Johnson (1995) provided support for *Gigantura* as an aulopiform and suggested *Bathysaurus* as the sister group to the genus. This result contradicts previous hypotheses that *Bathysaurus* is most closely related to synodontids (Sulak 1977, R. K. Johnson 1982). Baldwin & Johnson (1996) also included their newly described genus *Bathysauroides* as the basal giganturoid; however, Sato & Nakabo (2002) revised this relationship and found *Bathysauroides* to be the basal chlorophthalmoid.

Baldwin & Johnson's (1996) study recovered a Scopelarchidae + Evermannellidae clade sister to the remaining alepisauroid taxa (Alepisauridae + Paralepididae) which form the monophyletic suborder

Alepisauroidei. Phylogenetic position and classification of Scopelarchidae have been problematic because of morphological adaptations that are potentially examples of convergence in the deep sea rather than synapomorphies. Evermannellids and scopelarchids both posses highly modified tubular eyes, and R. K. Johnson (1982) suggested that this feature is only seemingly related in the two groups. He proposed that scopelarchids are more closely related to chlorophthalmoids than evermannellids based on the shared presence of an enlarged gap between the cranium and the first centrum. Baldwin & Johnson (1996) proposed that the tubular eyes of scopelarchids and evermannellids are a synapomorphy of that clade, although they did not further investigate the morphological characteristics of the eyes to examine the possibility of convergent structures. Evolution of tubular eyes is a common adaptation among fishes in the deep sea (Helfman et al. 1997), and tubular eyes also occur with a different morphology in *Gigantura*. Baldwin & Johnson's (1996) study supported a monophyletic Alepisauridae *(Omosudis + Alepisaurus)*, and a monophyletic family Paralepididae, which also included the genus *Anotopterus*. These results concur with the findings of R. K. Johnson (1982).

An increasing number of works has demonstrated the utility of molecular data in providing additional insight into evolutionary relationships within and among groups that have diverse morphological variation (e.g., Holcroft 2004, Smith & Wheeler 2004, López et al. 2004). Presently, there are no robust phylogenies of Aulopiformes that utilize molecular data. Such phylogenies will provide further support for hypotheses of aulopiform relationships that have been traditionally problematic (e.g., phylogenetic position and relationships of giganturids and scopelarchids). Kawaguchi et al. (2001) sequenced the whole mitochondrial genome for a single species, *Aulopus japonica*, and a rudimentary phylogeny was presented, but poor taxon sampling of both outgroup and ingroup taxa prevented any definitive statements about the systematic position of Aulopiformes or their interrelationships. Molecular studies have recovered Aulopiformes as monophyletic (e.g., Miya et al. 2001, Miya et al. 2003) and paraphyletic (López et al. 2004) although in each case aulopiform taxon sampling was extremely limited, making strong inferences about aulopiform monophyly problematic.

Morphological characters have often been ignored in systematic studies that utilize large amounts of molecular characters, especially when maximum likelihood and Bayesian methods are employed, because of skepticism surrounding the use of models with morphological data. With the increase of model development and exploration with morphological data (Lewis 2001, Nylander et al. 2004), this is no longer the case. A number of recent studies have demonstrated that morphological data can have a significant impact on hypotheses of evolutionary relationships when combined with multi-gene datasets (e.g., Nylander et al. 2004, Glenner et al. 2004, Danforth et al. 2006).

Five protein coding gene regions have been targeted and sequenced for analysis: the single-copy nuclear genes RAG1, zic1, ENC1, plagl2, and the mitochondrial gene COI. RAG1 has been demonstrated to lack paralogs and provide phylogenetic resolution among teleost groups (Holcroft 2004, López et al. 2004, Li & Ortí 2006). Nuclear genes zic1, ENC1, and plagl2 are part of a suite of gene regions recently described by the Ortí Laboratory that additionally produce phylogenetic resolution in teleost groups (Li et al. 2007). Finally, the mitochondrial gene COI is included because the fast rate of mitochondrial sequence evolution is ideal for inferring relationships among species where divergence is more recent (Moritz et al. 1987, Hillis et al. 1996), allowing for increased resolution at the tips of the ingroup analysis. In an effort to fully explore the evolutionary relationships of the Aulopiformes from a total evidence approach, the morphological matrices of Baldwin & Johnson (1996) and Sato & Nakabo (2002) have been incorporated into this analysis. The goals of this study include a reexamination of (1) the systematic position of the Order Aulopiformes within Euteleostei utilizing data from nuclear gene RAG1, (2) aulopiform relationships using nuclear and mitochondrial gene sequence data and a total-evidence approach that combines a multi-gene data set with previous morphological data. These datasets (RAG1, nucDNA + mtDNA, DNA + morphology) are used to test the following hypotheses: (1) aulopiform monophyly, (2) aulopiform relationships within Euteleostei, and (3) aulopiform interrelationships.

Materials and Methods

Institutional abbreviations: KU, Division of Ichthyology, Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, Kansas; **SIO**, Scripps Institution of Oceanography, San Diego, California; **VIMS**, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia.

Taxon sampling

Taxonomic sampling for RAG1 analysis includes 18 aulopiform species representing all 4 suborders and 11 of 14 aulopiform families. Outgroup sampling includes 54 species representing 28 actinopterygiian orders (Table 1). Outgroups were chosen in order to maintain a broad taxonomic sampling of groups hypothesized to be basal or closely related to Aulopiformes (e. g., Rosen 1973, G. D. Johnson 1992, Arratia 2004) including members of the following groups (Nelson 2006): Neopterygii, Osteoglossomorpha, Elopomorpha, Otocephala, Protacanthopterygii, Sternopterygii, Ateleopodomorpha, Scopelomorpha, and Acanthomorpha. Where possible, RAG1 sequences were obtained from previous phylogenetic analyses from GenBank. RAG1 data collected in the Wiley Lab by N. Holcroft *(Caranx latus*, *Sphyraena argentea*, and *Scomber scombrus)* and E. O. Wiley *(Psettodes erumei)* were donated to this study.

Taxon sampling for multi-gene DNA analysis (nucDNA + mtDNA) includes tissue samples for 43 ingroup species representing 32 of 44 aulopiform genera and every family with the exception of the recently elevated Bathysauropsidae and Bathysauroididae (Sato & Nakabo 2002). Outgroup sampling includes tissue samples for 15 species representing 13 actinopterygiian orders (Table 1). Outgroups were chosen in order to maintain a broad sampling of groups hypothesized to be basal to or closely related to Aulopiformes (e. g., Rosen 1973, G. D. Johnson 1992, Arratia 2004) including members of the following groups (Nelson 2006): Neopterygii, Osteoglossomorpha, Otocephala, Protacanthopterygii, Sternopterygii, Ateleopodomorpha, Ctenosquamata, and Acanthomorpha. A list of tissue samples included in this analysis is located in Table 1. Total evidence analyses included 8 additional aulopiform genera that have data for morphology only (Baldwin & Johnson 1996; Sato & Nakabo 2002) (Table 1). Outgroups used in Baldwin & Johnson (1996) and Sato & Nakabo (2002) that were also sequenced for DNA included *Diplophos taenia* (Stomiiformes), *Neoscopelus macrolepidotus* (Myctophiformes), *Polymixia japonicus* (Polymixiiformes), and *Metavelifer multiradiatus* (Lampriformes). For all analyses, the only taxon designated as an outgroup was *Amia calva* (Amiiformes).

DNA extraction, amplification, and sequencing

DNA was extracted with a Guanidine Thiocyanate protocol from tissue samples frozen and stored at –70 °C, with some samples being initially preserved in 95 % ethanol. Polymerase chain reaction procedures (PCR) (Saiki 1990) were used to amplify an approximately 1500-bp region of RAG1, 900-bp regions of zic1, ENC1, and plagl2, and a 900-bp region of the mitochondrial gene COI. Amplification of RAG1 was performed using a 25 µL PCR cocktail which included approximately 10-60 ng template DNA, 1× PuReTaq Ready-To-Go PCR Beads, and 200 pmol of each primer (López et al. 2004, Holcroft 2004). Nested-PCR was used to amplify RAG1 in taxa that did not amplify with the first PCR. Products of the first PCR were diluted 100 times, and used as the template for the Nested-PCR. Primers that were internal to the primers from the first PCR were used for the Nested-PCR. The thermal cycling profile used to amplify RAG1 fragments for both rounds of PCR is as follows: 10 cycles of 94 °C denaturing for 45 s, 53-58 °C annealing for 45 s, 72 °C extension for 1 m 15 s, followed by 30 cycles of 94 °C denaturing for 45 s, 50-53 °C annealing for 45 s, and 72 °C extension for 1 m 15 s followed by a final extension step of 72 °C for 7 m.

Amplification of nucDNA gene fragments zic1, ENC1, plagl2, and mtDNA gene fragment COI was performed using a 10 µL PCR cocktail including approximately 1-60 ng template DNA, 1× TaKaRa Ex Taq PCR buffer, 200 pmol of each dNTP, 6.4 pmol of each primer (Miya & Nishida 2000, Inoue et al. 2001, Li et al. 2007), and 0.25 units of TaKaRa Ex Taq (TaKaRa). Nested-PCR was used to amplify these genes in taxa that did not amplify with the first PCR, and followed the same procedure as discussed above. The thermal cycling profile used to amplify zic1, ENC1, and plagl2 fragments for both rounds of PCR is as follows: 30 cycles of 98 °C denaturing for 10 s, 53-61 °C annealing for 30 s, and 72 °C extension for 1 m followed by a final extension step of 72 °C for 5 m. The thermal cycling profile used to amplify COI fragments for both rounds of PCR is as follows: 35 cycles of 95 °C denaturing for 15 s, 53-55 °C annealing for 15 s, and 72 °C extension for 55 s followed by a final extension step of 72 °C for 7 m.

Purification of PCR products was done using ExoSAP-IT (USB) following instructions given by the manufacturer. Light and Heavy strands of PCR products were sequenced at the University of Kansas DNA Sequencing Laboratory using an Applied Biosystems 3130XL automated sequencer. Primers used for sequencing included the amplification primers. The program Sequencher was used to inspect sequences and create a consensus sequence from the light and heavy strands. All sequences used in this analysis are available on GenBank (Table 1).

Table 1
List of species examined in this study. Classification follows Nelson (2006) with GenBank accession numbers. Species are labeled for morphology if different from species sequenced. **NA**, not applicable, species or genus was not utilized in previous morphological study or molecular analysis; *, multiple species of the same genus were examined in previous morphological study; –, morphology not coded for species in total evidence data set or DNA data not collected; **, species only used in RAG1 analysis.

Taxon		Baldwin & Johnson (1996)	Sato & Nakabo (2002)	Catalog Number	Accession Numbers				
					RAG1	zic1	ENC1	plagl2	COI
Order Amiiformes									
Family Amiidae	*Amia calva*	NA	NA	Various	AY430199	EF032909	EF032974	EF033013	AB042952
Order Hiodontiformes									
Family Hiodontidae	*Hiodon alosoides*	NA	NA	Various	AY430200	EU366766	–	–	AP004356
Order Elopiformes									
Family Megalopidae	*Megalops atlanticus***	NA	NA		AY430204	–	–	–	–
Order Clupeiformes									
Family Engraulidae	*Coilia mystus***	NA	NA		DQ912126	–	–	–	–
	*Engraulis encrasicolus***	NA	NA		DQ912103	–	–	–	–
Family Clupeidae	*Dorosoma cepedianum*	NA	NA	KU T7841	DQ912099	EU366767	–	–	EU366583
	*Harengula jaguana***	NA	NA		DQ912122	–	–	–	–
Order Gonorynchiformes									
Family Chanidae	*Chanos chanos***	NA	NA		AY430207	–	–	–	–
Order Cypriniformes									
Family Cyprinidae	*Danio rerio*	NA	NA	Various	U71093	EF032910	EF032975	EF033014	NC002333
	*Pimephales promelas***	NA	NA		AY430210	–	–	–	–
Order Characiformes									
Family Characidae	*Catoprion mento***	NA	NA		AY430212	–	–	–	–
Order Siluriformes									
Family Ictaluridae	*Pylodictis olivaris***	NA	NA		DQ492619	–	–	–	–
Order Gymnotiformes									
Family Gymnotidae	*Gymnotus* sp.**	NA	NA		DQ492427	–	–	–	–
Order Argentiniformes									
Family Argentinidae	*Argentina sialis*	NA	NA	KU T519	AY430228	EU366773	EU366634	EU366680	–
Order Osmeriformes									
Family Osmeridae	*Thaleichthys pacificus*	NA	NA	KU T3135	AY380537	EU366774	EU366635	EU366681	–
	*Salangichthys microdon***	NA	NA		AY380539	–	–	–	–
	*Mallotus villosus***	NA	NA		DQ836486	–	–	–	–
Order Salmoniformes									
Family Salmonidae	*Oncorhynchus mykiss*	NA	NA		U15663	EF032911	EF032976	EF033015	NC001717

Order Esociformes									
Family Esocidae	*Esox americanus***	NA	NA		AY380541	–	–	–	–
Order Stomiiformes									
Family Gonostomatidae	*Diplophos taenia*		*D. orientalis*	KU T3781	EU366724	EU366768	EU366630	EU366676	EU366584
	*Gonostoma bathyphilum***	NA	NA		AY438703	–	–	–	–
Order Ateleopodiformes									
Family Ateleopodidae	*Ijimaia antillarum*	NA	NA	KU T5411	EU366725	EU366769	EU366631	EU366677	EU366585
Order Aulopiformes									
Suborder Synodontoidei									
Family Paraulopidae	*Paraulopus oblongus*	NA		CBM-ZF T99-109	EU366709	EU366752	EU366615	EU366664	EU366568
Family Aulopidae	*Aulopus filamentosus*		*A. japonicus*	USNM T3816	EU366688	EU366733	EU366593	EU366642	EU366546
	Aulopus japonicus			CBM-ZF T99-124	EU366687	EU366732	EU366592	EU366641	EU366545
	Hime sp.	–	–	SIO T02-68	EU366701	EU366746	EU366606	EU366654	EU366559
Family Pseudotrichonotidae	*Pseudotrichonotus altivelis*			CBM-ZF T99-156	EU366711	EU366754	EU366617	–	EU366570
Family Synodontidae	*Synodus kaianus*	–	–	CBM-ZF T99-128	EU366719	EU366761	EU366625	EU366672	EU366578
	Synodus variegatus		*S. ulae**	KU T6901	EU366720	EU366762	EU366626	EU366673	EU366579
	Synodus intermedius	–	–	KU T5219	EU366721	EU366763	EU366627	EU366674	EU366580
	Trachinocephalus myops			KU T5225	EU366723	EU366765	EU366629	–	EU366582
	Saurida undosquamis		*S. gracilis**	CBM-ZF T99-162	EU366712	EU366755	EU366618	EU366665	EU366571
	Harpadon microchir	*H. nehereus**	*H. nehereus*	CBM-ZF T99-148	EU366700	EU366745	EU366605	EU366653	EU366558
Suborder Chlorophthalmoidei									
Family Bathysauroididae	*Bathysauroides*			NA	NA	NA	NA	NA	NA
Family Chlorophthalmidae	*Chlorophthalmus agassizi*			KU T3759	EU366695	EU366740	EU366600	–	EU366553
	Parasudis truculenta			KU T959	EU366710	EU366753	EU366616	–	EU366569
Family Bathysauropsidae	*Bathysauropsis*			NA	NA	NA	NA	NA	NA
Family Notosudidae	*Ahliesaurus berryi*		NA	KU T5285	EU366685	EU366731	EU366590	EU366639	EU366544
	Scopelosaurus harryi	–	–	KU T3244	EU366713	EU366756	EU366619	EU366666	EU366572
	Scopelosaurus lepidus	*S. argenteus**		KU T3641	EU366714	EU366757	EU366620	EU366667	EU366573
Family Ipnopidae	*Bathypterois grallator*	*B. pectinatus**	*B. atricolor**	KU T5935	EU366690	EU366735	EU366595	EU366644	EU366548
	Bathypterois mediteraneus	–	–	CBM-ZF T99-139	EU366691	EU366736	EU366596	EU366645	EU366549
	Bathypterois phenax	–	–	KU T3625	EU366692	EU366737	EU366597	EU366646	EU366550
	Ipnops sp.	*I. murrayi**	*I. murrayi*	CBM-ZF T99-144	EU366702	EU366747	EU366607	EU366655	EU366560
	Bathymicrops		NA	NA	NA	NA	NA	NA	NA
	Bathytyphlops		NA	NA	NA	NA	NA	NA	NA
Suborder Alepisauroidei									
Family Scopelarchidae	*Benthalbella dentata*			KU T3239	EU366693	EU366738	EU366598	EU366647	EU366552
	Benthalbella macropinna		*B. dentate*	KU T926	EU366694	EU366739	EU366599	EU366648	EU366552
	Scopelarchus sp.	*S. analis*	NA	KU T3783	EU366715	EU366758	EU366621	EU366668	EU366574
	Scopelarchoides		NA	NA	NA	NA	NA	NA	NA
	Rosenblattichthys		NA	NA	NA	NA	NA	NA	NA

Table 1. (continued)

Taxon		Baldwin & Johnson (1996)	Sato & Nakabo (2002)	Catalog Number	Accession Numbers				
					RAG1	zic1	ENC1	plagl2	COI
Family Evermannellidae	*Coccorella atlantica*			KU T5314	EU366696	EU366741	EU366601	EU366649	EU366554
	Evermannella indica		NA	KU T3790	EU366697	EU366742	EU366602	EU366650	EU366555
	Odontostomops sp.	*O. normalops*	NA	CBM-ZF T99-129	EU366706	EU366749	EU366612	EU366661	EU366565
Family Alepisauridae	*Alepisaurus brevirostris*		*A. ferox*	KU T5258	EU366684	EU366730	EU366589	EU366638	EU366543
	Alepisaurus ferox	–	–	KU T5395	EU366683	EU366729	–	EU366637	EU366542
	Omosudis lowei			KU T5909	EU366707	EU366750	EU366613	EU366662	EU366566
Family Paralepididae	*Anotopterus pharao*		NA	KU T2305	EU366686	–	EU366591	EU366640	–
	Lestidiops jayakari	*L. affinis**	NA	KU T3792	EU366705	–	EU366610	EU366658	EU366562
	Lestidiops ringens	–	–	SIO T93-297	–	–	–	EU366659	EU366563
	Lestidium atlanticum			KU T3544	EU366703	–	EU366608	EU366656	EU366561
	Lestrolepis intermedia		NA	KU T3557	EU366704	–	EU366609	EU366657	–
	Macroparalepis johnfitchi	*M. affine*	NA	SIO T94-266	EU366722	EU366764	EU366628	EU366675	EU366581
	Magnisudis atlantica	NA	NA	KU T5928	–	EU366748	EU366611	EU366660	EU366564
	Paralepis coregonoides			KU T3719	EU366708	EU366751	EU366614	EU366663	EU366567
	Stemonosudis macrurus	*S. rothschildi**	NA	KU T93-238	EU366716	–	EU366622	EU366669	EU366575
	Sudis atrox		NA	KU T3107	EU366717	EU366759	EU366623	EU366670	EU366576
	Sudis sp.	–	–	KU T3798	EU366718	EU366760	EU366624	EU366671	EU366577
	Arctozenus		NA	NA	NA	NA	NA	NA	NA
	Uncisudis		NA	NA	NA	NA	NA	NA	NA
Suborder Giganturoidei									
Family Bathysauridae	*Bathysaurus ferox*		*B. mollis*	KU T5934	EU366689	EU366734	EU366594	EU366643	EU366547
Family Giganturidae	*Gigantura chuni*		NA	KU T6533	EU366698	EU366743	EU366603	EU366651	EU366556
	Gigantura indica		NA	KU T5270	EU366699	EU366744	EU366604	EU366652	EU366557
Order Myctophiformes									
Family Neoscopelidae	*Neoscopelus macrolepidotus*			KU T3297	EU366727	EU366771	EU366632	EU366678	EU366587
Family Myctophidae	*Benthosema glaciale*	*L. cuprarius**		KU T3734	EU366728	EU366775	–	–	–
	Nannobrachium lineatum	–	–	KU T3634	EU366726	EU366770	–	–	EU366586
	*Diaphus effulgens***	NA	NA		EU477496	–	–	–	–
	*Lampanyctus macdonaldi***	NA	NA		EU477497	–	–	–	–
	*Notoscopelus kroyeri***	NA	NA		AY430221	–	–	–	–
	*Notoscopelus caudispinosus***	NA	NA		EF094948	–	–	–	–
	*Hygophum hygomii***	NA	NA		EF094947	–	–	–	–
Order Polymixiiformes									
Family Polymixiidae	*Polymixia japonicus*	*P. lowei*		KU T258	AY308765	EU366776	EU366636	EU366682	AB034826

Order Lampriformes									
Family Veliferidae	*Metavelifer multiradiatus*		NA	KU T1252	EF094949	EU366772	EU366633	EU366679	EU366588
Family Lampridae	*Lampris guttatus***	NA	NA		AY308764	–	–	–	–
Order Ophidiiformes									
Family Ophidiidae	*Neobythites stigmosus***	NA	NA		EF033043	–	–	–	–
	*Petrotyx sanguineus***	NA	NA		AY308782	–	–	–	–
Order Mugiliformes									
Family Mugilidae	*Mugil curema***	NA	NA		AY308783	–	–	–	–
Order Atheriniformes									
Family Atherinopsidae	*Menidia menidia***	NA	NA		AY430225	–	–	–	–
Order Cyprinodontiformes									
Family Fundulidae	*Fundulus heteroclitus***	NA	NA		EF033040	–	–	–	–
Order Beryciformes									
Family Holocentridae	*Sargocentron vexillarium***	NA	NA		AY308770	–	–	–	–
	*Sargocentron punctatissimum***	NA	NA		AY430223	–	–	–	–
Order Zeiformes									
Family Oreosomatidae	*Allocyttus verrucosus***	NA	NA		AY308781	–	–	–	–
Family Grammicolepididae	*Grammicolepis brachiusculus***	NA	NA		AY308780	–	–	–	–
Family Zeidae	*Zenopsis conchifer***	NA	NA		AY308778	–	–	–	–
Order Scorpaeniformes									
Family Peristediidae	*Peristedion miniatum***	NA	NA		AY308774	–	–	–	–
Order Perciformes									
Family Percidae	*Perca flavescens***	NA	NA		AY308768	–	–	–	–
Family Moronidae	*Morone chrysops*	NA	NA	Various	AY308767	EF032917	EF032982	EF033021	–
Family Carangidae	*Caranx latus***	NA	NA		EU477492	–	–	–	–
Family Pomacanthidae	*Holacanthus bermudensis***	NA	NA		EF530081	–	–	–	–
Family Elassomatidae	*Elassoma evergladei***	NA	NA		AY308784	–	–	–	–
Family Ephippidae	*Chaetodipterus faber***	NA	NA		AY308773	–	–	–	–
Family Sphyraenidae	*Sphyraena argentea***	NA	NA		EU477494	–	–	–	–
Family Scombridae	*Scomber scombrus***	NA	NA		EU477493	–	–	–	–
Order Pleuronectiformes									
Family Psettodidae	*Psettodes erumei***	NA	NA		EU477495	–	–	–	–

Sequence alignment and analysis

Alignment was accomplished by creating a separate NEXUS file for each gene, and sequences were aligned by eye with comparison to published GenBank sequences as an alignment template. Consensus sequences from Sequencher were checked in order to verify the existence of observed differences from the alignment template (e.g., insertion/deletion events, heterozygosities). Aligned RAG1 and nucDNA + mtDNA datasets are available upon request.

In order to test for the amount of saturation as a result of substitutions, sequences were analyzed using pair-wise Tamura-Nei distances (Tamura & Nei 1993) for each gene (all positions) and third positions. Tamura-Nei distances were calculated with PAUP*4.0b10 (Swofford 2002). If saturation is not present, a linear relationship is expected between the absolute observed number of nucleotide substitutions and the Tamura-Nei distances.

The presence of heterogeneous base composition can result in misleading phylogenetic signals across taxa. Base compositional stationarity was analyzed with the Chi-square test in PAUP*4.0b10 (Swofford 2002). GC content was determined using the program CodonW (Peden 2005) for each gene (all positions) and third positions. This program was also used to measure Wright's (1990) ENC (effective number of codons), which helps identify codon bias across taxa (e.g., 20 is high codon bias, 61 is no bias) for each gene (all positions) and third positions.

Phylogenetic analyses, hypothesis testing, and data partitioning of RAG1 data set

Bayesian analyses of the RAG1 nucDNA data set were carried out in MrBayes v3.1 (Ronquist & Huelsenbeck 2003). The program MrModeltest v2.0 (Nylander 2004) was used to determine the best-fit model for each data partition using the Akaike information criterion (AIC). The data set was partitioned by codon position with a total of 3 partitions. A GTR+I+G model was selected by MrModeltest v2.0 (Nylander 2004) for all 3 RAG1 codon position partitions. Gaps were coded as missing rather than a fifth character state for all methods (Bayesian, Maximum Likelihood). Four simultaneous runs were conducted utilizing four chains for 10 million generations with a tree and parameter sampling frequency of every 100 generations. Trees sampled before stationarity (the first 10,000 trees) were excluded as burn-in, with the remaining 360,000 post-burn-in trees used to compute the consensus tree and posterior probabilities. A priori alternative phylogenetic hypotheses of aulopiform relationships were tested (Table 2). Topological constraint trees were produced with the program Treeview 1.6.6. (Page 1996). Posterior probabilities of the constraint tree hypothesis were then calculated. Post burn-in trees were loaded into PAUP*4.0b10 (Swofford 2002) and filtered to keep only trees consistent with the constraint topology. The total number of trees remaining was then divided by the total number of post stationarity trees (360,000), resulting in the posterior probability of the constraint hypothesis.

Maximum likelihood (ML) analyses were carried out in GARLI v0.95 (Zwickl 2006). Codon partitions were not incorporated in the ML analyses, and a GTR+I+Γ model was used. Ten independent analyses were conducted, with tree searching concluding if either of the two criteria were reached: a maximum of 5 million generations were generated, or when no significance between tree likelihood scores was obtained for a maximum of 10,000 generations. The tree with the best likelihood score from the ten independent runs was used to evaluate evolutionary relationships. A nonparametric bootstrap analysis was performed for 100 random pseudoreplicates using the recommended default settings in the GARLI manual. Bootstrap support values for the ML topology are shown in Fig. 5, with a bootstrap value of $\geq$70 regarded as significantly supported. Alternative hypotheses were tested with a one-tailed Shimodaira-Hasegawa (SH) test with 1000 RELL bootstrap replicates (Shimodaira & Hasegawa 1999) (Table 2). SH tests were performed in PAUP*, and GARLI v0.95 was used to obtain the best tree that corroborated the constraint topology for each alternative hypothesis. Topologies recovered from the 100 random pseudoreplicates (nonparametric bootstrap) were included in all SH tests, along with topologies representing alternative hypotheses of aulopiform placement (Table 2).

Phylogenetic analyses, hypothesis testing, and data partitioning of nucDNA and mtDNA data set

Bayesian analyses of the nucDNA and mtDNA concatenated data set were carried out in MrBayes v3.1 (Ronquist & Huelsenbeck 2003). The program MrModeltest v2.0 (Nylander 2004) was used to determine the best-fit model for each data partition using the Akaike information criterion (AIC). The concatenated data set was partitioned by both gene and codon position for the five genes, with a total of 15 partitions.

A total of four models were selected by MrModeltest v2.0 (Nylander 2004) for the following 15 codon position partitions: GTR+I+G, RAG1 (1st, 2nd, 3rd), zic1 (1st), COI (1st, 2nd), ENC1 (1st); GTR+G, zic1 (2nd), ENC1 (3rd), plagl2 (2nd, 3rd); HKY+G, zic1 (3rd), COI (3rd), ENC1 (2nd); HKY+I+G, plagl2 (1st). Gaps were coded as missing rather than as a fifth character state for all methods (Bayesian, Maximum Parsimony, Maximum Likelihood). Four simultaneous runs were conducted utilizing four chains for 10 million generations with a tree and parameter sampling frequency of every 100 generations. Trees sampled before stationarity (the first 10,000 trees) were excluded as burn-in, with the remaining 360,000 post-burn-in trees used to compute the consensus tree and posterior probabilities. A priori alternative phylogenetic hypotheses of aulopiform relationships were tested (Table 3) following the same procedure described for the RAG1 analysis.

Maximum likelihood (ML) analyses were carried out in GARLI v0.95 (Zwickl 2006). Data partitions were not incorporated in the ML analyses, and a GTR+I+Γ model was used. Ten independent analyses were conducted, with tree searching concluding if either of the two criteria were reached; a maximum of 5 million generations were generated, or when no significance between tree likelihood scores was obtained for a maximum of 10,000 generations. The tree with the best likelihood score from the ten independent runs was used to evaluate evolutionary relationships. A nonparametric bootstrap analysis was performed for 100 random pseudoreplicates using the recommended default settings in the GARLI manual. Alternative hypotheses were tested with a one-tailed Shimodaira-Hasegawa (SH) test with 1000 RELL bootstrap replicates (Shimodaira & Hasegawa 1999) following the same procedure described for the RAG1 analysis (Table 3).

Maximum parsimony analyses were conducted on the concatenated data set of all five genes with PAUP*. Heuristic searches were replicated 100 times with a step-wise addition using tree-bisection-reconnection (TBR) branch swapping. All characters were unweighted. Statistical support was estimated using a bootstrap analysis with 1000 replicates, each with 30 random step-wise addition sequence replicates, to generate bootstrap values (Felsenstein 1985). Alternative hypotheses were tested using Wilcoxon signed-ranks (WS-R) tests performed in PAUP* (Table 3). Heuristic parsimony searches were used to generate the most parsimonious topology that fit the alternative hypothesis constraint.

Phylogenetic analysis of concatenated morphological data set

The concatenated morphological data set included 118 characters from Baldwin & Johnson (1996), and 21 newly considered characters from Sato & Nakabo (2002). Sato & Nakabo (2002) made revisions to 13 characters (App. 1: 1, 15, 18, 52, 53, 69, 71, 79, 81, 96, 104, 105, 113) from Baldwin & Johnson (1996) with revisions incorporated into the concatenated data set. For a detailed description of all characters and revisions, refer to Baldwin & Johnson (1996) and Sato & Nakabo (2002). An abbreviated list of characters can be found in Appendix 1.

Maximum parsimony analysis of the concatenated morphological data set was performed in PAUP*. Parsimony tree searching procedures and bootstrap replicates followed the same guidelines as the nucDNA and mtDNA analysis. Polymorphisms were not ordered. The concatenated morphological data set can be found in Appendix 2.

Table 2.
List of a priori maximum likelihood Shimodaira-Hasegawa tests (**SH**) and Bayesian posterior probabilities (**PP**) based on RAG1 nucDNA analyses.

		RAG1 Analyses	
Hypothesis Tested	References	PP%	SH
Order Iniomi (Aulopiformes + Myctophiformes) Monophyly	Gosline et al. (1966)	2.289	0.245
Aulopiformes Monophyly	Rosen (1973)	100.0*	1.000
Aulopiform Paraphyly	Rosen (1985)	0.000	0.000**
Ateleopodiformes + Lampriformes + Myctophiformes	Miya et al. (2003)	0.000	0.013**
Aulopus + *Chlorophthalmus* + *Parasudis* sister to Ctenosquamata	Hartel & Stiassny (1986)	0.000	0.000**

* Significant PP Support at $p \geq 95$ %
** Significant difference at $p < 0.05$ (SH)

Table 3.
List of a priori maximum parsimony Wilcozon-signed-ranks tests (**WS-R**), maximum likelihood Shimodaira-Hasegawa tests (**SH**), and Bayesian posterior probabilities (**PP**) based on combined nucDNA and mtDNA and total evidence analyses.

		DNA Only		Total Evidence		
Hypothesis Tested	References	WS-R	SH	PP%	WS-R	PP%
Order Iniomi (Aulopiformes + Myctophiformes) Monophyly	Gosline et al. (1966)	0.2504	0.381	0.00	0.3110	0.00
Aulopiformes Monophyly	Rosen (1973)	1.0000	1.000	99.80**	1.00	99.95**
Aulopiformes Interrelationships	Rosen (1973)	<0.0001*	0.000*	0.00	<0.0001*	0.00
Order Myctophiformes Interrelationships (includes Aulopiformes)	R. K. Johnson (1982)	<0.0001*	0.000*	0.00	<0.0001*	0.00
Aulopiform Paraphyly	Rosen (1985)	<0.0001*	0.000*	0.00	<0.0001*	0.00
Aulopiform Interrelationships	Baldwin & Johnson (1996)	<0.0001*	0.000*	0.00	0.0001*	0.00
Aulopiform Suborder Interrelationships	Baldwin & Johnson (1996)	<0.0001*	0.000*	0.00	<0.0001*	0.00
Aulopiform Interrelationships	Sato & Nakabo (2002)	<0.0001*	0.000*	0.00	<0.0001*	0.00
Aulopiform Suborder Interrelationships	Sato & Nakabo (2002)	<0.0001*	0.000*	0.00	0.0043*	0.00
Synodontoidei Monophyly	Baldwin & Johnson (1996)	0.4255	0.047*	67.28	0.4311	99.44**
Synodontoidei Monophyly	Sato & Nakabo (2002)	0.5842	0.310	0.00	0.7679	0.81
Chlorophthalmoidei Monophyly	Baldwin & Johnson (1996)	0.0078*	0.000*	0.00	0.0006*	0.00
Chlorophthalmoidei Monophyly	Sato & Nakabo (2002)	0.0078*	0.000*	0.00	<0.0001*	0.00
Giganturoidei Monophyly	Baldwin & Johnson (1996)	0.2059	0.148	58.07	0.3020	78.69
Giganturoidei Monophyly	Sato & Nakabo (2002)	0.2059	0.148	58.07	0.3692	39.61
Alepisauroidei Monophyly	Baldwin & Johnson (1996)	0.0610	0.130	0.00	1.0000	97.52**
Alepisauroidei Monophyly	Sato & Nakabo (2002)	0.0610	0.130	0.00	1.0000	97.52**
Synodontidae Monophyly	Baldwin & Johnson (1996)	1.0000	0.185	0.02	1.0000	90.99
Aulopidae Monophyly	Baldwin & Johnson (1996)	1.0000	1.000	30.24	1.0000	55.67
Chlorophthalmidae Monophyly	Baldwin & Johnson (1996)	0.1917	0.234	0.00	1.0000	98.65**
Notosudidae Monophyly	Baldwin & Johnson (1996)	1.0000	1.000	99.99**	1.0000	99.95**
Ipnopidae Monophyly	Baldwin & Johnson (1996)	0.8981	0.140	54.00	1.0000	94.34**
Scopelarchidae Monophyly	Baldwin & Johnson (1996)	0.1917	0.139	0.05	1.0000	99.14**
Alepisauridae Monophyly	Baldwin & Johnson (1996)	1.0000	1.000	99.98**	1.0000	99.98**
Paralepididae Monophyly	Baldwin & Johnson (1996)	0.0092*	0.222	0.00	0.4194	0.00
Evermannellidae Monophyly	Baldwin & Johnson (1996)	1.0000	1.000	99.98**	1.0000	100.00**
Giganturoidei + Alepisauroidei	Baldwin & Johnson (1996)	0.0039*	0.002*	0.00	0.0002*	0.00
Paraulopus + Synodontidae	Sato & Nakabo (2002)	0.1567	0.311	0.00	0.3930	0.78
Scopelarchidae + Evermannellidae	Baldwin & Johnson (1996)	0.0136*	0.012*	0.00	0.2023	0.00
Notosudidae + Ipnopidae	Baldwin & Johnson (1996)	0.0003*	0.002*	0.00	0.0693	0.00
Alepisauridae + Paralepididae	Baldwin & Johnson (1996)	0.0092*	0.222	0.00	0.6295	0.00
Anotopterus + "Paralepididae"	Baldwin & Johnson (1996)	<0.0001*	0.000*	0.00	0.0121*	0.00
Evermannella + *Odontostomops*	Baldwin & Johnson (1996)	0.0076*	0.005*	0.00	0.1246	0.00
Ateleopodiformes + Lampriformes + Myctophiformes	Miya et al. (2003)	0.5410	0.271	0.00	0.4688	0.00

* Significant difference at $p < 0.05$ (WS-R, SH)
** Significant PP Support at $p \geq 95$ %

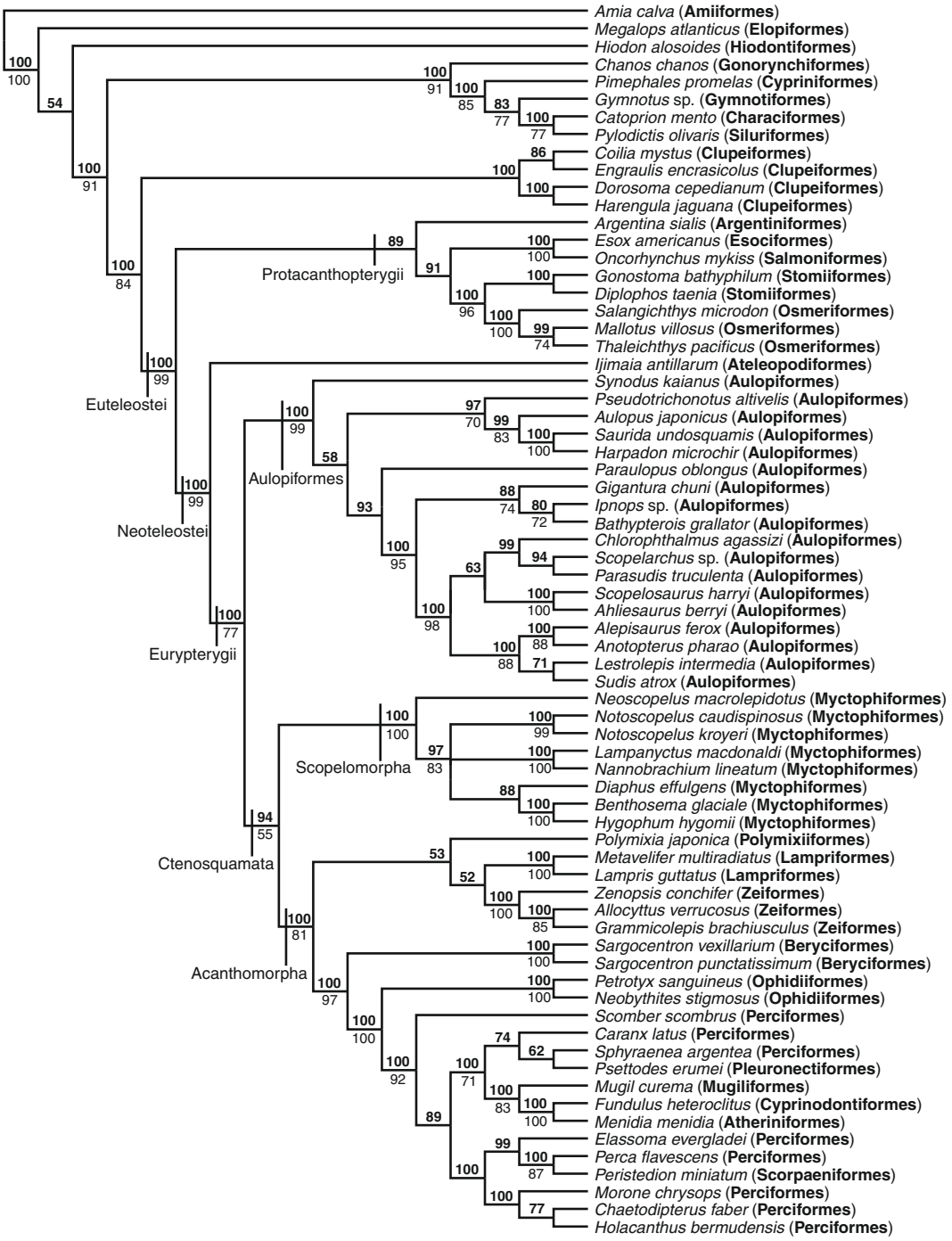

Fig. 5.
Systematic placement of the Aulopiformes based on Bayesian and Maximum Likelihood analysis of nuclear gene RAG1. Bayesian posterior probabilities denoted by bold numbers above node, with significant support ≥95. Likelihood bootstrap support values denoted by numbers below node, with significant support ≥70. Likelihood values below 70 not shown.

Phylogenetic analyses, hypothesis testing, and data partitioning of total evidence data set

Morphological data sets from Baldwin & Johnson (1996) and Sato & Nakabo (2002) were concatenated with the five gene molecular data set. Where possible, morphological data were matched to the same species used for DNA sequences. For cases where multiple species of the same genus were examined with molecular data, only species that matched a species used in previous morphological studies were coded for morphological characters. For example, as seen in Table 1, *Synodus variegatus* was examined in Baldwin & Johnson (1996), so morphological data were coded for that species, but not for *Synodus kaianus* or *Synodus intermedius* since they were not examined in either previous morphological study. In instances where an exact match was not possible, morphological data from a close relative (e.g., the same genus) were utilized following the recommendations of Nylander et al. (2004) (Table 1). The morphological studies of Baldwin & Johnson (1996) and Sato & Nakabo (2002) presented their results at the level of genera for ingroup taxa, and did not identify differences in transformation series for each species examined. For the outgroup member of the family Myctophidae, morphological data from the myctophid genera *Lampanyctus* and *Myctophum* (Baldwin & Johnson 1996) were concatenated to the molecular data for the genus *Benthosema* (Table 1) as morphological data for Myctophidae were generalized to the level of family in Baldwin & Johnson (1996). All other outgroup taxa with morphological data were either concatenated with the same species, or a member from the same genus.

Bayesian analyses of the total evidence data set utilized the same partitions and models for the five gene fragments as the nucDNA and mtDNA data set. Morphological data were analyzed within a single partition, and a MK (Markov) model was implemented as recommended by Lewis (2001) and Nylander et al. (2004). All morphological characters were unweighted, with coding sites variable and equal rates employed. Polymorphisms are treated as uncertainties in Bayesian analysis. Four simultaneous runs were conducted utilizing four chains for 15 million generations with tree and parameter sampling frequencies of every 100 generations. Trees sampled before stationarity (the first 15,000 trees) were excluded as burn-in, with the remaining 540,000 post-burn-in trees used to compute the consensus tree and posterior probabilities. Bayesian hypothesis testing followed the same procedures as outlined previously (Table 3).

Maximum parsimony analyses and morphological character distributions (App. 3) of the total evidence data set were performed in PAUP*. Phylogenetic analysis and hypothesis testing followed the same procedures as the nucDNA and mtDNA analysis. Maximum Likelihood analyses were not performed on the total evidence data set.

Results

Sequence analysis and data partitions of RAG1 dataset

The RAG1 data matrix included the 1479 base positions. Mutational site saturation was not apparent across codon positions when all three positions were analyzed together, but the third codon position alone did show slight saturation for transversions and transitions. All codon positions were included in all analyses based on the recommendations of Källersjö et al. (1999), where saturated data were demonstrated to provide phylogenetic signal.

The null hypothesis of base compositional stationarity was not rejected for the first ($\chi^2 = 79.28$, df = 213, $P = 1.000$) and second ($\chi^2 = 26.01$, df = 213, $P = 1.000$) codon positions of RAG1, but it was rejected for the third position ($\chi^2 = 1396.77$, df = 213, $P = 0.000$). The average GC content of RAG1 was 56.41 % with a range from 47.6 % in *Pylodictis olivaris* to 68.2 % in *Coilia mystus*.

Nuclear gene RAG1 possessed little codon bias, with an average ENC coefficient of 49.33. Of the 11 taxa out of 72 with ENCs < 45, 4 were Clupeiformes, 3 were Osmeriformes, and the remaining four were from various orders (Argentiniformes, Stomiiformes, Ateleopodiformes, and Myctophiformes).

Phylogenetic analysis of RAG1 data set and a priori hypothesis tests

The Bayesian analysis produced a majority-rule consensus topology as shown in Figure 5, where posterior probabilities (PP) are considered significant if PP ≥ 95 %. The four simultaneous runs reached convergence (PSRF = 1.009-1.000, s.d. = 0.01-0.00), with each run obtaining the same consensus tree topology. Of the 67 nodes represented in the analysis, 49 were significantly supported (PP ≥ 95 %). The PP of a priori hypotheses is shown in Table 2. The only a priori hypothesis that was significantly supported (PP ≥ 95 %) was monophyly of the order Aulopiformes.

Of the 10 independent maximum likelihood analyses performed, all 10 topologies were identical with likelihood scores ranging from –33440.787 to –33440.798. Topology likelihood scores were verified with PAUP*. The likelihood topology was identical to the Bayesian majority-rule consensus topology as seen in Figure 5. The following a priori hypotheses of evolutionary relationships were rejected by SH tests ($p \leq 0.05$); aulopiform paraphyly (Rosen 1985), an *Aulopus*, *Chlorophthalmus* + *Parasudis* clade, and Cteno-osquamata polytomy (Hartel & Stiassny 1986), and a sister-group relationship between Myctophiformes and an Ateleopodiformes + Lampriformes clade within Scopelomorpha (Miya et al. 2003). An a priori hypothesis of Order Iniomi (Aulopiformes + Myctophiformes) failed to be rejected by SH tests (Gosline et al. 1966, R. K. Johnson 1982) as seen in Table 2.

Sequence analysis and data partitions of nucDNA and mtDNA dataset

The five-gene data matrix included the following 4898 base positions; RAG1 (1498 bp), zic1 (916 bp), ENC1 (845 bp), plagl2 (858 bp), and COI (781). A total of 1947 characters were parsimony-informative. As a result of amplification and sequencing difficulties, data were not obtained for a few taxa with regards to certain genes (Table 1). The data for these taxa were coded as missing in the five-gene data matrix, and these taxa were not excluded from any analyses following the recommendation of Wiens (2003, 2006).

Mutational site saturation was not apparent across all codon positions for any of the sequenced gene regions (RAG1, zic1, ENC1, plagl2, and COI). Nuclear gene RAG1 showed slight saturation for transversions and transitions in only the third codon position. The third codon position of COI and plagl2 showed evidence of transitional saturation. All codon positions were included in all analyses based on the recommendations of Källersjö et al. (1999), where saturated data were demonstrated to provide phylogenetic signal.

The null hypothesis of base compositional stationarity was not rejected for the following first and second codon positions of all genes; RAG1 1st ($\chi^2 = 53.47$, df = 165, $P = 1.000$), RAG1 2nd ($\chi^2 = 20.54$, df = 165, $P = 1.000$), zic1 1st ($\chi^2 = 18.19$, df = 150, $P = 1.000$), zic1 2nd ($\chi^2 = 2.37$, df = 150, $P = 1.000$), ENC1 1st ($\chi^2 = 15.45$, df = 153, $P = 1.000$), ENC1 2nd ($\chi^2 = 3.04$, df = 153, $P = 1.000$), plagl2 1st ($\chi^2 = 74.09$, df = 150, $P = 0.999$), plagl2 2nd ($\chi^2 = 37.67$, df = 150, $P = 1.000$), COI 1st ($\chi^2 = 4.01$, df = 153, $P = 1.000$), and COI 2nd ($\chi^2 = 24.20$, df = 153, $P = 1.000$). Base compositional stationarity was rejected for the following third codon positions; RAG1 3rd ($\chi^2 = 897.52$, df = 165, $P = 0.000$), zic1 3rd ($\chi^2 = 674.54$, df = 150, $P = 0.000$), ENC1 3rd ($\chi^2 = 799.01$, df = 153, $P = 0.000$), plagl2 3rd ($\chi^2 = 710.41$, df = 150, $P = 0.000$), and COI 3rd ($\chi^2 = 468.67$, df = 153, $P = 0.000$).

The ranges of GC content varied in each gene. The average GC content of RAG1 was 57.45 %, with a range from 49.1 % in *Danio rerio* to 66.9 % in *Coccorella atlantica*. For zic1, the average GC content was 57.85 %, ranging from 50.5 % in *Hiodon alosoides* to 66.9 % in *Metavelifer multiradiatus*. For ENC1, the average GC content was slightly higher at 58.2 %, with a range of 51 % in *Metavelifer multiradiatus* to 66.7 % in *Diplophos taenia*. For plagl2, the average GC content was the highest at 61.32 %, ranging from 53.1 % in *Danio rerio* to 67.1 % in *Diplophos taenia*. Finally, for COI, the average GC content was lower than all other genes at 48.96 %, with a range of 39.7 % in *Danio rerio* to 53.9 % in *Gigantura indica*.

Nuclear gene RAG1 possessed some codon bias, with an average ENC coefficient of 47.98. Of the ten taxa out of 56 with ENCs < 45, two were from the family Evermannellidae, four from the family Paralepididae, and the remaining four taxa included various orders (Salmoniformes, Argentiniformes, Ateleopodiformes, and Myctophiformes). ENC was higher overall for zic1, with an average ENC of 53.33. Seven taxa out of 52 possessed ENCs < 45 *(Metavelifer multiradiatus*, *Paralepis coregonoides*, *Scopelosaurus lepidus*, *Scopelosaurus harryi*, *Benthosema glaciale*, *Paraulopus oblongus*, and *Harpadon microchir)* although codon bias was not limited to any particular order or family with the exception of the genus *Scopelosaurus*. The ENC1 gene possessed some codon bias with an average ENC across taxa of 46.74. From the 14 taxa out of 52 with ENCs < 45, two were from the family Scopelarchidae, three from family Evermannellidae, three from the family Notosudidae, and three were from the family Paralepididae, suggesting codon bias was limited to these particular families. Only three taxa had ENCs < 40, *Thaleichthys pacificus* (31.18), *Oncorhynchus mykiss* (33.68), and *Argentina sialis* (37.8), demonstrating strong codon bias among the protacanthopterygian taxa included in this analysis. Codon bias was most prevalent with the plagl2 gene, with an average ENC of 45.01 across taxa. Of the 50 taxa sequenced for ENC1, 20 had ENCs < 45, with the strongest bias appearing in *Synodus indicus* (29.35) and *Evermannella indica* (29.66). Mitochondrial gene COI also possessed some codon bias with an average ENC of 47.25. From the 11 taxa out of 52 with ENCs < 45 only two had ENCs < 40, *Danio rerio* (39.24) and *Lestidum atlanticum* (39.33).

Phylogenetic analysis of nucDNA and mtDNA data set and a priori hypothesis tests

The Bayesian analysis produced a majority-rule consensus topology as shown in Figure 6, where posterior probabilities (PP) are considered significant if PP ≥ 95 %. The four simultaneous runs reached convergence (PSRF = 1.008-1.000, s.d. = 0.01-0.00), with each run obtaining the same consensus tree topology. Of the 54 nodes represented in the analysis, 47 were significantly supported (PP ≥ 95 %). The PP of a priori hypotheses is shown in Table 3. The following four hypotheses were significantly supported (PP ≥ 95 %): monophyly of Aulopiformes (Rosen 1973), monophyly of Notosudidae (Baldwin & Johnson 1996), monophyly of Alepisauridae (Baldwin & Johnson 1996), and monophyly of Evermannellidae (Baldwin & Johnson 1996).

Of the ten independent maximum-likelihood analyses performed, nine topologies were identical with likelihood scores ranging from –72686.62 to –72687.96. The one differing topology had the worst likelihood score of –72692.205. Topology likelihood scores were verified with PAUP*. The topology of the group composed of the nine best likelihood scores was identical to the Bayesian majority-rule consensus topology, with a few exceptions involving taxa within the suborder Synodontoidei. The clade comprised of Baldwin & Johnson's (1996) Synodontoidei, which was not significantly supported in the Bayesian analysis, was not recovered in the ML topology. The ML topology recovered a *Synodus* + *Trachinocephalus* clade as the basal aulopiform lineage, with a clade containing the genera *Harpadon*, *Saurida*, *Pseudotrichonotus*, *Aulopus*, and *Hime* being sister to all remaining aulopiform taxa. Additionally, the family Aulopidae *(Aulopus* + *Hime)* was monophyletic in the ML topology. Bootstrap support values for the ML topology are shown in Figure 6, with a bootstrap value of ≥70 regarded as significantly supported.

Maximum parsimony analysis obtained two equally parsimonious trees of 15774 steps (CI = 0.2853, HI = 0.7147, RI = 0.3858, RC = 0.1101). Clade bootstrap support values were considered significant if ≥70, following the recommendation of Hillis & Bull (1993). The parsimony consensus topology, not presented here, differed in a few relationships from the Bayesian and ML topologies. Unlike the Bayesian and ML topologies, the family Synodontidae *(Synodus*, *Trachinocephalus*, *Harpadon*, and *Saurida)* was recovered as monophyletic, but with no significant bootstrap support (<70). The genus *Paraulopus* was recovered as the sister taxon of *Pseudotrichonotus*, rather than of all remaining aulopiforms, but also with no significant bootstrap support (<70). A clade consisting of the family Aulopidae sister to all remaining aulopiform taxa was recovered with no significant bootstrap support (<70). Also unlike the Bayesian and ML topologies, the family Evermannellidae was not recovered as the basal member of the suborder Alepisauroidei, but was obtained within a clade consisting of the genera *Lestidiops*, *Lestidium*, *Lestrolepis* and *Stemnosudis*. This clade was significantly supported by bootstrap values (84), but may be an artifact of strong codon bias evident in these taxa for nuclear genes RAG1 and plagl2. Finally, the clade consisting of *Paralepis* + *Macroparalepis* was recovered as the sister group of the *Anotopterus* + *Magnisudis* clade, with that clade sister to the family Alepisauridae. This grouping was significantly supported (94) and may also be an artifact of codon bias, as the genera *Paralepis*, *Macroparalepis*, *Anotopterus*, and *Magnisudis* all demonstrated strong codon bias in nuclear genes ENC1 and plagl2.

As seen in Table 3, both WS-R and SH tests failed to reject the following a priori hypotheses not recovered in ML or MP analyses ($p \geq 0.05$): Order Iniomi monophyly (Gosline et al. 1966), a clade of Ateleopodiformes + Lampriformes sister to Myctophiformes (Miya et al. 2003), monophyly of Synodontoidei (Sato & Nakabo 2002), monophyly of Giganturoidei (Baldwin & Johnson 1996), monophyly of Alepisauroidei (Baldwin & Johnson 1996), monophyly of Chlorophthalmidae (Baldwin & Johnson 1996), monophyly of Scopelarchidae (Baldwin & Johnson 1996), and *Paraulops* as the basal member of the Synodontoidei (Sato & Nakabo 2002). The following a priori hypotheses of evolutionary relationships were rejected by both WS-R and SH tests ($p \leq 0.05$): interrelationships of Aulopiformes (Rosen 1973), Order Myctophiformes and interrelationships (R. K. Johnson 1982), aulopiform paraphyly (Rosen 1985), aulopiform interrelationships (Baldwin & Johnson 1996), aulopiform suborder relationships (Baldwin & Johnson 1996), aulopiform interrelationships (Sato & Nakabo 2002), aulopiform suborder relationships (Sato & Nakabo 2002), monophyly of Chlorophthalmoidei (Baldwin & Johnson 1996, Sato & Nakabo 2002), a Giganturoidei + Alepisauroidei clade (Baldwin & Johnson 1996), a Notosudidae + Ipnopidae clade (Baldwin & Johnson 1996), an *Anotopterus* + Paralepididae clade (Baldwin & Johnson 1996), and an *Evermannella* + *Odontostomops* clade (Baldwin & Johnson 1996). Monophyly of Synodontoidei (Baldwin & Johnson 1996) was rejected by SH, but not WS-R. The hypotheses of a monophyletic Paralepididae (Baldwin & Johnson 1996) and an Alepisauridae + Paralepididae clade (Baldwin & Johnson 1996) were rejected by WS-R, but not SH tests.

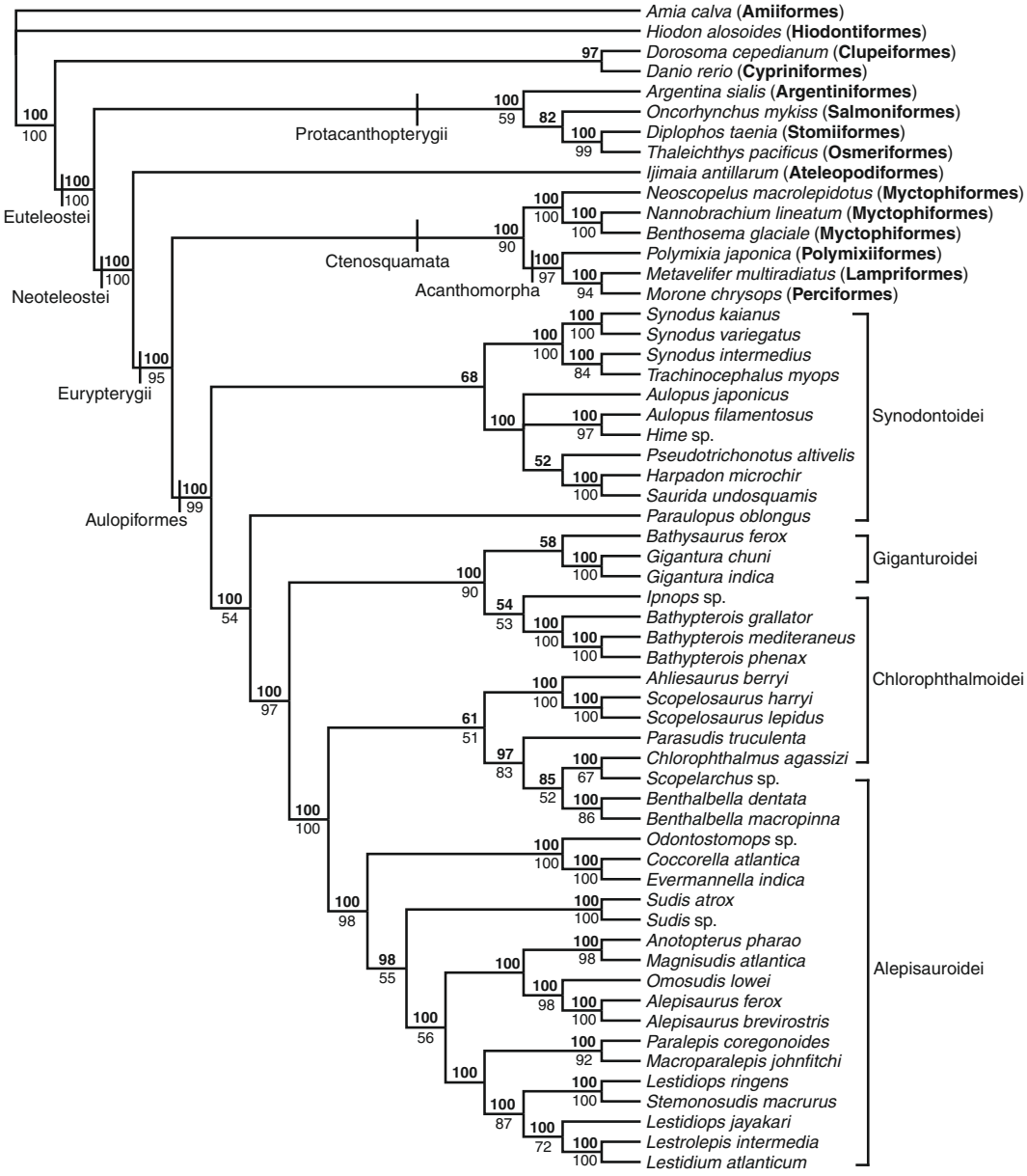

Fig. 6.
Relationships of the Aulopiformes based on Bayesian and Maximum Likelihood analysis of five genes (RAG1, zic1, ENC1, plagl2, COI). Bayesian posterior probabilities denoted by bold numbers above node, with significant support ≥95. Likelihood bootstrap support values denoted by numbers below node, with significant support ≥70. Values below 50 not shown. Bars denote aulopiform suborders as described by Baldwin & Johnson (1996) and Sato & Nakabo (2002).

Phylogenetic analysis of morphological data set

Maximum parsimony analysis of the concatenated morphological data set from Baldwin & Johnson (1996) and Sato & Nakabo (2002) generated eleven equally parsimonious trees of 485 steps (CI = 0.4928, HI = 0.5381, RI = 0.7659, RC = 0.3774). All 139 characters were parsimony informative. The MP consensus tree, not presented here, differed from the relationships presented by Baldwin & Johnson (1996) and Sato & Nakabo (2002) in the following ways: Giganturoidei is the sister group to Chlorophthalmoidei (sensu Sato & Nakabo 2002) although without significant bootstrap support; a Scopelarchidae + Evermannellidae clade is less resolved, and Scopelarchidae are no longer monophyletic with the scopelarchid + evermannellid clade forming a polytomy among *Benthalbella*, Evermannellidae, and a *Scopelarchus* + *Scopelarchoides* + *Rosenblattichthys* clade.

Phylogenetic analyses of total evidence data set and a priori hypothesis tests

The Bayesian majority consensus topology is shown in Figure 7. The four simultaneous runs reached convergence (PSRF = 1.022-1.000, s.d. = 0.08-0.00), with each run generating the same consensus tree topology. Of the 64 clades present in the analysis, 47 had significant support (PP ≥ 95 %). Clades of a priori hypotheses that possessed significant support (PP ≥ 95 %) include the following (Table 3): monophyly of Aulopiformes (Rosen 1973), monophyly of Synodontoidei (Baldwin & Johnson 1996), monophyly of Alepisauroidei (Baldwin & Johnson 1996, Sato & Nakabo 2002), monophyly of Chlorophthalmidae (Baldwin & Johnson 1996), monophyly of Notosudidae (Baldwin & Johnson 1996), monophyly of Ipnopidae (Baldwin & Johnson 1996), monophyly of Scopelarchidae (Baldwin & Johnson 1996), monophyly of Alepisauridae (Baldwin & Johnson 1996), and Evermannellidae monophyly (Baldwin & Johnson 1996).

Maximum-parsimony analysis generated five equally parsimonious trees of 16358 steps (CI = 0.2902, HI = 0.7107, RI = 0.4016, RC = 0.1165). Of the 5036 included characters (4898 DNA, 138 morphological), 2086 characters were parsimony informative. Differences among the five equally parsimonious trees involved the phylogenetic relationships and placement of the genera *Lestidium*, *Lestrolepis*, and *Uncisudis*. The strict consensus parsimony tree, not presented here, differed from the Bayesian reconstruction of relationships in a few ways. The same differences discussed previously between the Bayesian and maximum parsimony consensus topologies for the nucDNA and mtDNA data set were observed in the total evidence analyses, with no significant bootstrap support values (≥70) for any discrepant parsimony clades. Unlike the Bayesian analysis, the genus *Bathysauroides* was not recovered within the suborder Giganturoidei, and instead was recovered as the sister group to the Alepisauroidei, although with no significant bootstrap support (≥70). Additionally, in the parsimony analysis the genus *Bathysauropsis* was sister to a clade consisting of Chlorophthalmidae, Bathysauroididae, and Alepisauroidei, with no significant bootstrap support. Clades with significant bootstrap support (≥70) that are congruent with the Bayesian majority consensus topology are presented in Figure 7.

The WS-R test failed to reject the following a priori hypotheses not recovered in the MP analysis ($p \geq 0.05$) as seen in Table 3: monophyly of Order Iniomi (Gosline et al. 1966), a Mytophiformes + Ateleopodiformes + Lampriformes clade (Miya et al. 2003), monophyly of Synodontoidei (Baldwin & Johnson 1996), monophyly of Synodontoidei (Sato & Nakabo 2002), monophyly of Giganturoidei (Baldwin & Johnson 1996), monophyly of Giganturoidei (Sato & Nakabo 2002), monophyly of Paralepididae (Baldwin & Johnson 1996), a *Paraulopus* + Synodontoidei clade (Sato & Nakabo 2002), a Scopelarchidae + Evermannellidae clade (Baldwin & Johnson 1996), a Notosudidae + Ipnopidae clade (Baldwin & Johnson 1996), an Alepisauridae + Paralepididae clade (Baldwin & Johnson 1996), and an *Evermannella* + *Odontostomops* clade (Baldwin & Johnson 1996). The following a priori hypotheses of evolutionary relationships were rejected by WS-R tests ($p \leq 0.05$): Aulopiformes interrelationships (Rosen 1973), Order Myctophiformes and interrelationships (R. K. Johnson 1982), aulopiform paraphyly (Rosen 1985), aulopiform interrelationships (Baldwin & Johnson 1996), aulopiform suborder relationships (Baldwin & Johnson 1996), aulopiform interrelationships (Sato & Nakabo 2002), aulopiform suborder relationships (Sato & Nakabo 2002), monophyly of Chlorophthalmoidei (Baldwin & Johnson 1996), monophyly of Chlorophthalmoidei (Sato & Nakabo 2002), a Giganturoidei + Alepisauroidei clade (Baldwin & Johnson 1996), and an *Anotopterus* + Paralepididae clade (Baldwin & Johnson 1996).

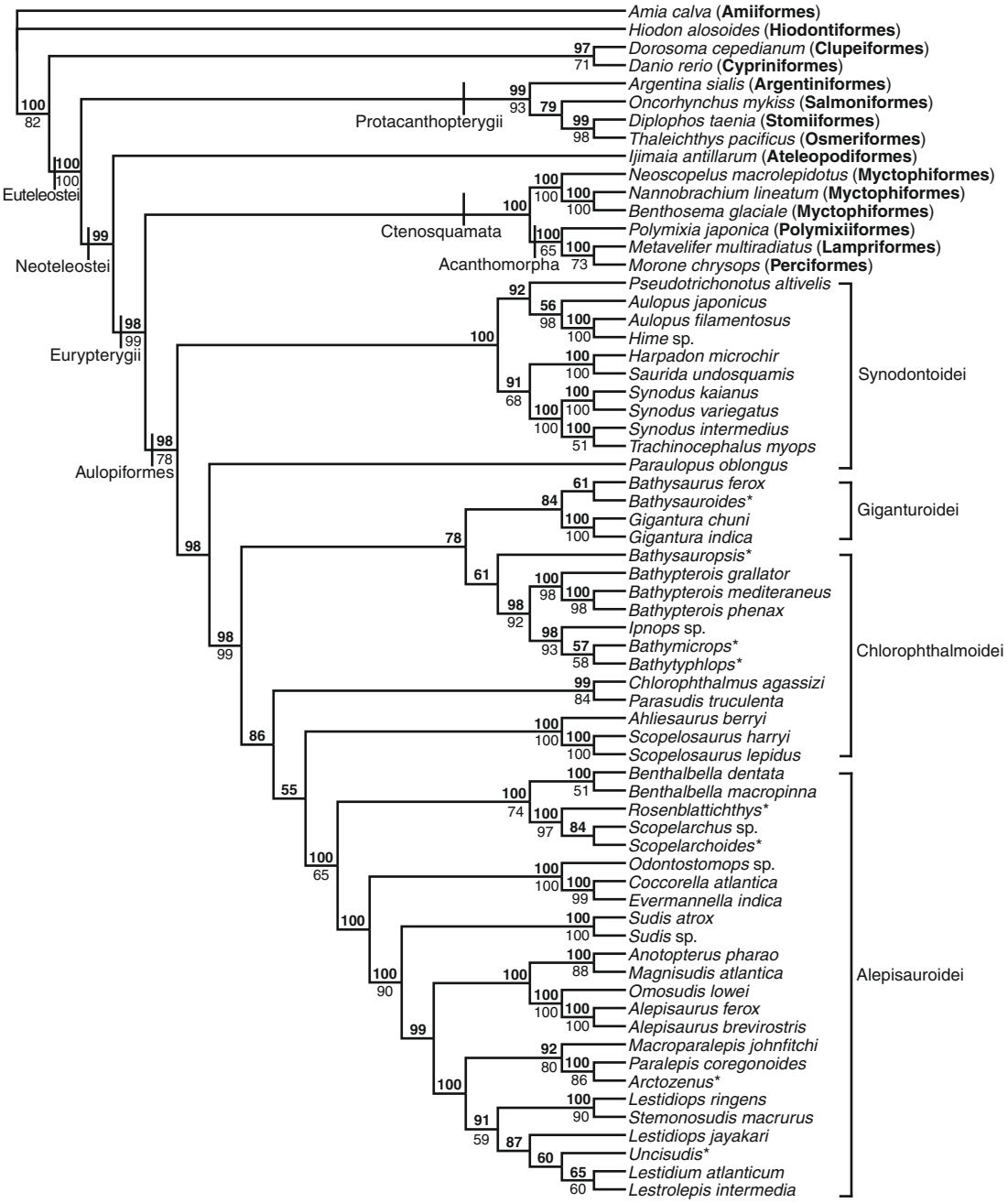

Fig. 7.
Relationships of the Aulopiformes based on Bayesian analysis of five genes (RAG1, zic1, ENC1, plagl2, COI) and 138 morphological characters (Baldwin & Johnson 1996; Sato & Nakabo 2002). Bayesian posterior probabilities denoted by bold numbers above node, with significant support ≥95. Parsimony bootstrap support values denoted by numbers below node, with significant support ≥70. Values below 50 not shown. Bars denote aulopiform suborders as described by Baldwin & Johnson (1996) and Sato & Nakabo (2002). * indicates taxa represented by morphological data only.

Discussion

Monophyly of the Aulopiformes and their systematic placement within Euteleostei

Monophyly of the Aulopiformes as first proposed by Rosen (1973) was strongly supported in all analyses (RAG1, nucDNA + mtDNA, morphology only, DNA + Morphology) (Figs. 5, 6, 7). This result is in disagreement with the works of R. K. Johnson (1982), Rosen (1985), and Hartel & Stiassny (1986), but corroborates recent studies based on morphological data alone (G. D. Johnson 1992, Patterson & Johnson 1995, Johnson et al. 1996, Baldwin & Johnson 1996, Sato & Nakabo 2002). While an a priori hypothesis of iniomous relationships (Gosline et al. 1966) could not be significantly rejected, an aulopiform + myctophiform clade was not recovered in any analysis, and an iniomous hypothesis of relationships possessed a 0 % posterior probability for Bayesian topologies (nucDNA + mtDNA, DNA + morphology). Aulopiform relationships as proposed by R. K. Johnson (1982) and Rosen (1985) were significantly rejected for all analyses. Aulopiform monophyly is supported by fourteen morphological synapomorphies in this study (App. 3: 1-1, 2-1, 16-2, 18-1, 58-1, 59-1, 69-1, 70-1, 89-1, 93-1, 104-1, 120-1, 133-1, 137-1), including six recovered in both ACCTRAN and DELTRAN optimizations; presence of an enlarged second epibranchial uncinate process (1-1), presence of a fifth epibranchial (18-1), lateral expansion of the palatine absent (58-1), palatinad cartilaginous facet for articulation with lateral ethmoid located on posterior portion of palatine (59-1), posterior processes of pelvic girdle elongate and widely separated (104-1), and absence of swimbladder (133-1).

Aulopiformes were recovered as the sister group to a monophyletic Ctenosquamata (Myctophiformes + Acanthomorpha) in all analyses (RAG1, nucDNA + mtDNA, DNA + morphology) with high statistical support for the nucDNA + mtDNA and total evidence analyses (Figs. 6, 7). The sister-group relationship with ctenosquamates supports the monophyly of Rosen's (1973) Eurypterygii. Miya et al. (2003) also found support for a monophyletic Eurypterygii with whole mitochondrial genomes; however, their Ctenosquamata consisted of a Myctophiformes + Ateleopodiformes + Lampriformes clade sister to the remaining Acanthomorpha. In all analyses (RAG1, nucDNA + mtDNA, DNA + morphology), Ateleopodiformes were recovered as the sister group to the eurypterygians with strong statistical support (Figs. 5, 6, 7). This result partially corroborates the placement by Olney et al. (1993) of Ateleopodiformes in a trichotomy with Stomiiformes and Eurypterygii. An a priori hypothesis of a Myctophiformes + Ateleopodiformes + Lampriformes clade (Miya et al. 2003) was not significantly rejected with the nucDNA + mtDNA dataset across parsimony (WS-R) and likelihood analyses (SH), but possessed a 0 % posterior probability among Bayesian topologies (nucDNA + mtDNA, DNA + Morphology), and was additionally significantly rejected with the RAG1 dataset likelihood analysis (SH).

Monophyly of Rosen's (1973) Ctenosquamata was strongly supported across all nucDNA + mtDNA and total evidence analyses, with high statistical support for a monophyletic Scopelomorpha (Myctophiformes) sister to a strongly supported Acanthomorpha (Figs. 6, 7). Within the monophyletic Myctophiformes, the family Neoscopelidae was recovered as sister to a strongly supported clade comprised of species within the family Myctophidae (Fig. 5). This result corroborates previous myctophiform morphological studies (e. g., Paxton 1972, Stiassny 1996) but contradicts the findings of Rosen (1985) in which Neoscopelidae formed a clade with aulopoid and chlorophthalmoid aulopiforms as the sister group to Ctenosquamata including the family Myctophidae. While 11 of the 20 orders of Acanthomorpha (Nelson 2006) were sampled in the RAG1 analysis (Fig. 5), a discussion on the phylogenetic relationships of acanthomorphs is beyond the scope of this study and would require greater taxon sampling of this extremely diverse group.

Of the included taxa within this analysis, monophyly of Neoteleostei was highly supported with the exception of the Order Stomiiformes, which was recovered as the sister group to Osmeriformes within Protacanthopterygii with high statistical support across all analyses (RAG1, nucDNA + mtDNA, DNA + morphology) (Figs. 5-7). The RAG1 analysis included representatives of two stomiiform families, Gonostomatidae and Diplophidae (Nelson 2006), while the combined DNA and total evidence analyses included only *Diplophos taenia*. While this result is in disagreement with the vast majority of morphological studies (e. g., Rosen 1973, G. D. Johnson 1992, Johnson & Patterson 1993), it corroborates other recent molecular studies examining protacanthopterygian relationships (e. g., López et al. 2004), which recovered Stomiiformes closely related to Osmeriformes. While the mitochondrial study of Miya et al. (2003) recovered a more traditional Neoteleostei with Stomiiformes sister to the eurypterygians, their analysis did not include any Osmeriformes.

Monophyly of aulopiform suborders

Relationships within the order Aulopiformes have recently been classified in four monophyletic suborders (Synodontoidei, Chlorophthalmoidei, Alepisauroidei, and Giganturoidei) following the studies of Baldwin & Johnson (1996) and Sato & Nakabo (2002). The results of the nucDNA + mtDNA only analyses do not support the monophyly of either the Chlorophthalmoidei or Alepisauroidei as described by Baldwin & Johnson (1996) and Sato & Nakabo (2002) (Fig. 6). Bayesian reconstructions (nucDNA + mtDNA) recovered a monophyletic Synodontoidei sensu Baldwin & Johnson (1996) without any statistical support. The genus *Paraulopus* was not recovered as a member of the Synodontoidei (Sato & Nakabo 2002) in any of the DNA analyses. The suborder Giganturoidei was recovered as monophyletic with no statistical support in the nucDNA + mtDNA analyses. Total evidence (DNA + morphology) analyses recovered monophyletic suborders Synodontoidei, Giganturoidei, and Alepisauroidei sensu Baldwin & Johnson (1996) with strong statistical support for Synodontoidei and Alepisauroidei (Fig. 7). The results of the total evidence analyses and a priori hypothesis tests suggest that the suborder Chlorophthalmoidei as currently recognized is not monophyletic. Systematic placement of taxa within the monophyletic and paraphyletic suborders, revised classification, and morphological evidence supporting previously unrecognized clades are discussed below. A complete list of morphological character optimizations for each node and terminal can be found in Appendix 3.

Aulopiform relationships

The results of the molecular (nucDNA + mtDNA) and total evidence (DNA + morphology) analyses suggest that the taxa within the suborder Synodontoidei (Baldwin & Johnson 1996, Sato & Nakabo 2002), classified in this study as the Aulopoidei, are the basal lineages of aulopiform fishes (Figs. 6, 7). This result concurs with the hypotheses of Baldwin & Johnson (1996) and Sato & Nakabo (2002). The newly recognized genus *Paraulopus*, diagnosed from a *Chlorophthalmus* species complex, was not recovered in any analysis as the basal aulopoid lineage as hypothesized by Sato & Nakabo (2002). However, an a priori hypothesis of a *Paraulopus* + Aulopoidei clade was not significantly rejected for parsimony and ML analyses (Table 3). The results from the DNA and total evidence analyses suggest that *Paraulopus*, recognized here as the sole member of the suborder Paraulopoidei (sensu novo), is the sister group of a clade consisting of taxa from the suborders Chlorophthalmoidei, Alepisauroidei, and Giganturoidei sensu Baldwin & Johnson (1996), classified in this study as the suborder Alepisauroidei (sensu novo) as seen in Figure 8. This hypothesis of the systematic placement of the genus *Paraulopus* had high statistical support for nucDNA + mtDNA and total evidence analyses, and is a novel reconstruction of relationships.

Taxa within the suborder Aulopoidei were recovered as monophyletic and as the basal aulopiform lineage (Figs. 6, 7), with both strong (DNA + morphology) and weak (nucDNA + mtDNA) statistical support. Two distinct aulopoid clades were recovered with the DNA analyses. A clade comprising *Synodus* + *Trachinocephalus* was sister to a clade consisting of the genera *Aulopus*, *Hime*, *Pseudotrichonotus*, *Harpadon*, and *Saurida*. Molecular data alone did not recover a monophyletic Synodontidae *(Synodus*, *Trachinocephalus*, *Harpadon*, and *Saurida)* or Aulopidae *(Aulopus* and *Hime)* with Bayesian reconstructions. A clade consisting of *Harpadon* + *Saurida* was recovered with high statistical support corroborating many previous studies (e.g., Rosen 1973, Sulak 1977, R. K. Johnson 1982, Baldwin & Johnson 1996). Results from the total evidence analyses also suggest two aulopoid clades, although with different taxonomic composition. The family Synodontidae is monophyletic with high statistical support and sister to a clade consisting of Pseudotrichonotidae + Aulopidae. The results of the total evidence analysis concur with the nucDNA + mtDNA only analysis in recognizing a *Harpadon* + *Saurida* clade with strong statistical support.

For both nucDNA + mtDNA and total evidence analyses, a *Synodus* + *Trachinocephalus* clade was recovered where *Trachinocephalus* is placed within the genus *Synodus*, sister to *Synodus intermedius* with high statistical support. The monotypic genus *Trachinocephalus* shares all of its morphological character transformation series with *Synodus*, with one exception (Baldwin & Johnson 1996). *Trachinocephalus myops* possesses a reduced fifth epibranchial that is present as a small cartilage, with fifth epibranchials absent in *Synodus* (18-0). The results of this study suggest that *Trachinocephalus myops* is a member of the genus *Synodus*, although further study is needed that would include a broader taxonomic sampling of the approximately 36 species of *Synodus* (Nelson 2006).

The genus *Hime* was recovered within the genus *Aulopus* across both nucDNA + mtDNA (ML and

MP) and total evidence (Bayesian and MP) topologies with high statistical support (Fig. 7). The genus *Hime* is recognized by Parin & Kotlyar (1989) and Thompson (1998) to include all former species of *Aulopus* that are distributed in the Pacific Ocean (e.g., *Aulopus japonicus*, *Aulopus purpurissatus*), with Atlantic-distributed species remaining in the genus *Aulopus* (e.g., *Aulopus filamentosus*). Baldwin & Johnson (1996) rejected the use of *Hime* as a valid genus because of a lack of significant morphological differences between Atlantic and Pacific species, and *Aulopus* is the currently accepted generic name. The results of the nucDNA + mtDNA and total evidence analyses show strong support for the recognition of a single genus *Aulopus*, as the Atlantic *Aulopus filamentosus* was found to be more closely related to the specimen of *Hime sp.* collected in the Pacific Ocean than either were to the specimen of *Aulopus japonicus*, previously regarded as a member of the genus *Hime*. The nucDNA + mtDNA and total evidence analyses support the inclusion of Aulopidae within the aulopoids (e.g., Johnson et al. 1996, Baldwin & Johnson 1996), and not the sister group of the Ctenosquamata (Stiassny 1986, Hartel & Stiassny 1986) (Figs. 6, 7). The results of the total evidence Bayesian reconstruction suggest a sister-group relationship between Aulopidae and the Pacific and Indian Ocean distributed genus *Pseudotrichonotus*, which is a novel hypothesis of aulopiform relationships, although it is not statistically supported. An *Aulopus* + *Pseudotrichonotus* clade is supported by four morphological synapomorphies (60-1, 77-1, 120-1, 121-1).

The suborder Chlorophthalmoidei, including the families Chlorophthalmidae, Bathysauropsidae, Notosudidae, and Ipnopidae (Baldwin & Johnson 1996, Sato & Nakabo 2002) was not recovered as monophyletic. The results of the nucDNA + mtDNA and total evidence analyses strongly support a Giganturoidei *(Gigantura* + *Bathysaurus* + *Bathysauroides)* + Bathysauropsidae + Ipnopidae clade sister to all remaining chlorophthalmoids + Alepisauroidei taxa (Figs. 6, 7). Support for a Giganturoidei *(Bathysaurus* + *Gigantura)* + Ipnopidae *(Ipnops* + *Bathypterois)* clade was strong for nucDNA + mtDNA analyses, but weak with total evidence analyses where the genera *Bathysauroides* and *Bathysauropsis* were added with morphological data alone. A sister group relationship between giganturids and ipnopids has never been proposed, and contradicts previous placement of the suborder Giganturoidei as the sister group to the suborder Alepisauroidei (Baldwin & Johnson 1996, Sato & Nakabo 2002). A priori hypothesis tests of a Giganturoidei + Alepisauroidei clade were significantly rejected for all analyses (Table 3). A giganturid + ipnopid clade was supported by multiple morphological characters (26-1, 27-1, 113-2, 128-1, 134-1), including two recovered in both ACCTRAN and DELTRAN optimizations, the number of postcleithra (113-2), and eye morphology (128-1).

Within the giganturid + ipnopid clade, recognized in this study as the superfamily Ipnopoidea (sensu novo), the suborder Giganturoidei (Baldwin & Johnson 1996) was recovered as monophyletic in both nucDNA + mtDNA and total evidence analyses (Bayesian reconstruction), although without statistical support (Figs. 6, 7, 8). Taxa within the suborder Giganturoidei sensu Baldwin & Johnson (1996) are classified in this study within the epifamily Giganturoidae (sensu novo). A sister group relationship between *Bathysaurus* and *Gigantura*, first suggested by Patterson & Johnson (1995), was supported by molecular data, although without strong support. When the genus *Bathysauroides* was included in the total evidence analyses, it was recovered within the epifamily Giganturoidae as suggested by Baldwin & Johnson (1996), although only in Bayesian reconstructions where a clade consisting of *Bathysauroides* + *Bathysaurus* was sister to *Gigantura* (Figs. 7, 8).

The family Ipnopidae was recovered as monophyletic in all analyses with high statistical support (DNA + morphology). Relationships within the family corroborate those of Baldwin & Johnson (1996). Total evidence analyses (Bayesian) recover the genus *Bathysauropsis* as the sister group to the family Ipnopidae, a result which corroborates Hartel & Stiassny's (1986) systematic placement of the genus, and its inclusion within their Ipnopidae based on the shared presence of a small obliquely aligned basihyal. Sulak (1977) also recovered *Bathysauropsis* as the sister group to his subfamily Ipnopinae, which included all currently recognized members of Ipnopidae. Baldwin & Johnson (1996) hypothesized that *Bathysauropsis* was the sister group to a Notosudidae + Ipnopidae clade, and removed *Bathysauropsis* from the family Ipnopidae. Sato & Nakabo (2002) subsequently elevated *Bathysauropsis* to family level (Bathysauropsidae). This study concurs with the elevation of *Bathysauropsis* to family level as the *Bathysauropsis* + Ipnopidae clade is weakly supported, while the Ipnopidae clade sensu Baldwin & Johnson (1996) has strong statistical support (Figs. 7, 8). For nucDNA + mtDNA and total evidence analyses, a priori hypothesis tests of a Notosudidae + Ipnopidae clade were significantly rejected (Table 3).

Relationships among the remaining chlorophthalmoid taxa were less resolved. Molecular analyses recovered a Notosudidae + Chlorophthalmidae + Scopelarchidae clade as the sister group to all remain-

ing alepisauroid taxa with high statistical support, however the Notosudidae + Chlorophthalmidae + Scopelarchidae clade itself was weakly supported (Fig. 6). Within this clade, the family Notosudidae *(Ahliesaurus* and *Scopelosaurus)* was recovered as monophyletic and the sister group to a well supported Chlorophthalmidae + Scopelarchidae clade, where neither family was monophyletic. R. K. Johnson (1982), considered the family Scopelarchidae within his chlorophthalmoid group in a clade consisting of the families Chlorophthalmidae + Ipnopidae based on the shared presence of a gap in ossification between the first centrum and the skull (R. K. Johnson 1982: p. 40). Prior to this reconstruction, Scopelarchids had been thought to be more closely related to the family Evermannellidae (e.g., Gosline et al. 1966), and Baldwin & Johnson (1996) recovered an Evermannellidae + Scopelarchidae clade as the sister group of all remaining alepisauroid taxa. Baldwin & Johnson (1996) suggested that scopelarchids and evermannellids share five synapomorphies (82-1; 84-2; 117-1; 128-3; 135-2); however, two of these synapomorphies (128-3; 135-2) are directly related to the shared feature of tubular eyes. R. K. Johnson (1982) identified that the tubular eyes of scopelarchids and evermannellids may be a result of convergence, and that the morphological characteristics of the tubular eyes are potentially not homologous. While it is interesting that molecular data supports R. K. Johnson's (1982) hypothesis that scopelarchids are more closely related to chlorophthalmoids than alepisauroids, further molecular and morphological analysis is needed to further investigate these relationships.

Total evidence analyses recover a monophyletic Notosudidae, Chlorophthalmidae and Scopelarchidae with high statistical support for each family (Fig. 7). Systematic positions of the Chlorophthalmidae and Notosudidae are not well supported, with superfamily Chlorophthalmoidea (sensu novo) sister to a clade consisting of superfamilies Notosudoidea (sensu novo) + Alepisauroidea (sensu novo). Scopelarchidae are recovered as the basal group within the Alepisauroidea with strong statistical support, but are not recovered as the sister group of the Evermannellidae, as hypothesized by Baldwin & Johnson (1996). An a priori hypothesis test of an Evermannellidae + Scopelarchidae clade was significantly rejected for all analyses with the exception of total evidence parsimony tests (Table 3).

The results of the total evidence analyses (Bayesian reconstruction) strongly suggest that Evermannellidae are the sister group to all remaining taxa of Alepisauroidea (Sudidae, Alepisauridae, Paralepididae) (Figs. 7, 8). Under total evidence and nucDNA + mtDNA only parsimony analysis, evermannellids were recovered within a clade of paralepidids; however, this result was most likely the result of significant codon bias in these taxa for nuclear genes RAG1 and plagl2. Relationships within the Evermannellidae for both DNA and total evidence analyses corroborate those of R. K. Johnson (1982), with *Odontostomops* sister to a strongly supported *Evermannella* + *Coccorella* clade (Figs. 6, 7). The genera *Evermannella* and *Coccorella* share the possession of tubular eyes (128-3), which are absent in *Odontostomops*. Baldwin & Johnson (1996) hypothesized a sister-group relationship between *Evermannella* + *Odontostomops* that required a reversal in *Odontostomops* for possession of tubular eyes. An *Evermannella* + *Odontostomops* clade was significantly rejected in all a priori hypothesis tests with the exception of total evidence parsimony (Table 3).

A strongly supported clade consisting of the families Sudidae, Alepisauridae, and Paralepididae includes the remainder of the Alepisauroidea. The family Paralepididae sensu Baldwin & Johnson (1996; *Sudis*, *Anotopterus*, *Magnisudis*, *Paralepis*, *Macroparalepis*, *Lestidiops*, *Lestrolepis*, *Lestidium*, *Stemonosudis*, *Arctozenus*, *Uncisudis*) was recovered as paraphyletic for nucDNA + mtDNA and total evidence analyses (Figs. 6, 7, 8). This result contradicts the findings of Patterson & Johnson (1996), Baldwin & Johnson (1996), and Sato & Nakabo (2002), where an Alepisauridae + Paralepididae clade was hypothesized. Null hypotheses of an Alepisauridae + Paralepididae clade were significantly rejected for all analyses with the exception of nucDNA + mtDNA maximum likelihood, and total evidence parsimony (Table 3). The results of all analyses strongly support *Sudis* as the sister group to a clade consisting of the family Alepisauridae (sensu novo; [*Omosudis* + *Alepisaurus*] + [*Anotopterus* + *Magnisudis*]) and the remaining paralepidids (Figs. 6, 7, 8). The genus *Sudis* is re-elevated to the family Sudidae which is distinguished by multiple morphological apomorphies (App. 3), including enlarged pectoral fins in larvae (134-1), and larval head spines (136-1).

A monophyletic Alepisauridae (sensu novo) consisting of *Anotopterus* + *Magnisudis* sister to *Alepisaurus* + *Omosudis*, was recovered with strong support as sister to all remaining paralepidid taxa (Bayesian and ML topologies) (Figs. 6, 7, 8). Monophyly of the family Alepisauridae was recovered with high statistical support by both nucDNA + mtDNA and total evidence analyses. This corroborates the sister-group relationship between *Omosudis* and *Alepisaurus* first proposed by R. K. Johnson (1982), and its sister group,

the *Anotopterus* + *Magnisudis* clade, is a novel hypothesis of relationships with strong support. The genera *Anotopterus* and *Magnisudis* are recognized here within the family Alepisauridae (sensu novo), and members of this family share a third pharyngobranchial toothplate (UP3) that is restricted to the lateral edge of the ventral surface of pharyngobranchial 3 (11-1), and a supracleithrum that is equal to or longer than the cleithrum (99-1), along with other apopmorphies (App. 3). Baldwin & Johnson (1996) recovered *Anotopterus* within a monophyletic Paralepididae, corroborating the hypothesis of R. K. Johnson (1982). This relationship between *Anotopterus* and paralepidids was significantly rejected across all hypothesis tests (Table 3). The genus *Magnisudis* was not included in the studies of Baldwin & Johnson (1996) or Sato & Nakabo (2002), but had previously been hypothesized to be closely related to the paralepidid genera *Arctozenus*, *Paralepis*, and *Notolepis* (Post 1987).

The remaining paralepidids are recovered within a strongly supported clade in all analyses, recognized here as the family Paralepididae (sensu novo) (Figs. 6-8). A clade including the genera *Paralepis* + *Macroparalepis* was strongly recovered in nucDNA + mtDNA analyses. When the genus *Arctozenus* was included in total evidence analyses, it was recovered as the sister group to *Paralepis* within the *Macroparlepis* + *Paralepis* clade. A sister group relationship between *Paralepis* and *Arctozenus* corroborates the findings of Baldwin & Johnson (1996). In parsimony analyses (nucDNA + mtDNA and total evidence), the *Macroparalepis* + *Paralepis* + *Arctozenus* clade is recovered as the sister group to the *Anotopeterus* + *Magnisudis* clade, with this entire clade sister to Alepisauridae (sensu Baldwin & Johnson 1996). However, this parsimony relationship may be an artifact of strong codon bias as the genera *Paralepis*, *Macroparalepis*, *Anotopterus*, and *Magnisudis* all possess strong codon bias in nuclear genes ENC1 and plagl2.

The results of this study support the recovery of a clade consisting of the genera *Lestidiops*, *Stemonosudis*, *Lestrolepis*, *Lestidium*, and *Uncisudis*; this result corroborates relationships recovered by Baldwin & Johnson (1996). However, relationships within this clade differ slightly from those of their study, and resolution among the taxa was poorly supported for total evidence analyses, but strongly supported for nucDNA + mtDNA analyses (Figs. 6, 7). For nucDNA + mtDNA analyses, a sister-group relationship was recovered between *Stemonosudis* and *Lestidiops ringens*, with the genus *Lestidiops* paraphyletic. This clade was sister to a clade consisting of *Lestidiops jayakari* sister to a *Lestrolepis* + *Lestidium* clade. In total evidence analyses, the genus *Uncisudis* was recovered as the sister group to the *Lestrolepis* + *Lestidium* clade. Further work and broader taxon sampling is necessary in order to satisfactorily resolve relationships among the paralepidids.

Morphological signal in total evidence analyses

In general, concerns that morphological data would be overshadowed by a large multi-gene data set were not observed in this study. Analyses utilizing the five nuclear and mitochondrial gene data-set were well resolved, with 47 of 54 nodes significantly supported with posterior probabilities of ≥ 95 % in the Bayesian topology reconstruction. Even with well resolved topologies based on molecular data, morphological characters from Baldwin & Johnson (1996) and Sato & Nakabo (2002) were able to significantly influence aulopiform evolutionary relationships recovered by the total evidence analyses, regardless of the fact that morphological characters contributed < 3 % of the total evidence data matrix. The results of this study support the recommendations of Nylander et al. (2004) that morphological signal can contribute important information to molecular systematic analyses, and should be considered when morphological information is applicable and available.

Comment on extinct aulopiform taxa

Currently the study of Fielitz (2004), focusing on the Late Cretaceous marine enchodontids, is the only phylogenetic study that incorporates both extinct and extant aulopiform taxa. Fielitz (2004) proposed a monophyletic Superfamily †Enchodontoidea (families †Cimolichthyidae and †Enchodontidae) as the sister group to Alepisauridae sensu Baldwin & Johnson (1996), with that clade sister to Paralepididae. While fossil taxa were not included in this analysis, it is likely that the systematic position of the enchodontids would remain within Alepisauroidea, sister to Alepisauridae. Monophyly and relationships to extant taxa of the remaining aulopiform fossil taxa (e.g., Suborder †Ichthyotringoidei, Suborder †Halecoidei) are questionable (e.g., Rosen 1973, Chalifa 1989, De Figueiredo & Gallo 2005, Nelson 2006). Additional robust systematic studies that include both extinct and extant aulopiforms are needed to further elucidate the evolutionary relationships of fossil aulopiform taxa.

Classification

A new classification of extant aulopiform genera and families is presented. Asterisks indicate taxa not included in analyses. Classification follows phyletic sequence, and reflects the total evidence hypothesis of relationships (Fig. 8).

Order Aulopiformes
- Suborder Aulopoidei sensu nov.
  - Family Synodontidae *(Synodus, Trachinocephalus, Harpadon, Saurida)*
  - Family Aulopidae *(Aulopus)*
  - Family Pseudotrichonotidae *(Pseudotrichonotus)*
- Suborder Paraulopoidei taxon nov.
  - Family Paraulopidae *(Paraulopus)*
- Suborder Alepisauroidei sensu nov.
  - Superfamily Ipnopoidea sensu nov.
    - Epifamily Giganturoidae sensu nov.
      - Family Giganturidae *(Gigantura)*
      - Family Bathysauridae *(Bathysaurus)*
      - Family Bathysauroididae *(Bathysauroides)*
    - Epifamily Ipnopoidae sensu nov.
      - Family Bathysauropsidae *(Bathysauropsis)*
      - Family Ipnopidae (*Bathypterois*, *Ipnops*, *Bathymicrops*, *Bathytyphlops*, *Discoverichthys**)
  - Superfamily Chlorophthalmoidea sensu nov.
    - Family Chlorophthalmidae *(Chlorophthalmus, Parasudis)*
  - Superfamily Notosudoidea sensu nov.
    - Family Notosudidae (*Scopelosaurus*, *Ahliesaurus*, *Luciosudis**)
  - Superfamily Alepisauroidea sensu nov.
    - Family Scopelarchidae *(Benthalbella, Rosenblattichthys, Scopelarchus, Scopelarchoides)*
    - Family Evermannellidae *(Odontostomops, Coccorella, Evermannella)*
    - Family Sudidae *(Sudis)*
    - Family Alepisauridae sensu nov. *(Anotopterus, Magnisudis, Omosudis, Alepisaurus)*
    - Family Paralepididae sensu nov. (*Macroparalepis*, *Paralepis*, *Arctozenus*, *Stemonosudis*, *Lestidiops*, *Uncisudis*, *Lestrolepis*, *Lestidium*, *Dolichosudis**)

Conclusions

In summary, DNA and total evidence analyses strongly support monophyly of the Aulopiformes. Aulopiformes are recovered as the sister group to Rosen's (1973) Ctenosquamata with high statistical support. This result corroborates monophyly of Eurypterygii (e.g., Rosen 1973, Johnson 1992) with nuclear and mitochondrial gene data. Ateleopodiformes were recovered as the sister group to the Eurypterygii with high statistical support using molecular data. Within Aulopiformes, the suborders Synodontoidei and Giganturoidei sensu Baldwin & Johnson (1996) were recovered as monophyletic with DNA data, but without statistical support. Total evidence analyses recovered monophyletic suborders Synodontoidei, and Alepisauroidei sensu Baldwin & Johnson (1996) with statistical support. The suborder Chlorophthalmoidei was not recovered as monophyletic. DNA analyses recovered the following families as paraphyletic: Synodontidae (Bayesian, ML), Scopelarchidae (Bayesian, ML, MP), Chlorophthalmidae (Bayesian, ML, MP), and Paralepididae (Bayesian, ML, MP). All families were recovered as monophyletic with high statistical support in total evidence analyses with the exception of the paraphyletic Paralepididae (Bayesian, ML, MP).

DNA analyses corroborated Sato & Nakabo (2002) in recovering *Paraulopus* outside of *Chlorophthalmus*, but did not support their hypothesis that *Paraulopus* is the basal member of the suborder Aulopoidei. The genus was recovered as the sister group to all chlorophthalmoid + giganturoid + alepisauroid taxa with strong statistical support, and is recognized here as the sole member of suborder Paraulopoidei. The monotypic genus *Trachinocephalus* was recovered within the genus *Synodus* (nucDNA + mtDNA, DNA + morphology), and further research is needed to determine whether *Trachinocephalus myops* should be

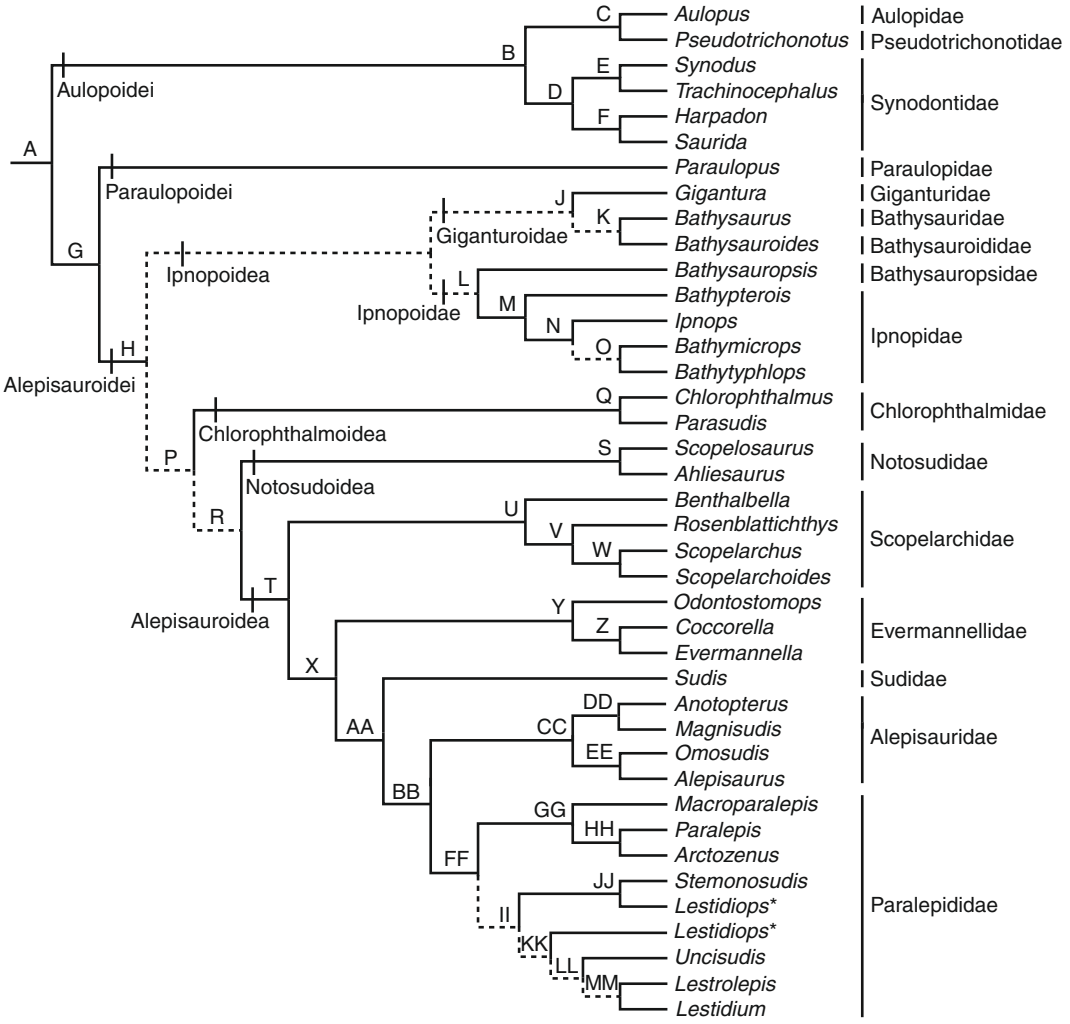

Fig. 8.
Classification of the Aulopiformes based on Bayesian total evidence topology (Fig. 7). Solid lines denote nodes with strong statistical support in either Bayesian or parsimony reconstructions. Dashed lines indicate nodes with weak support. For morphological character distributions please see Appendix 3.

assigned to *Synodus*. Recognition of the genus *Hime* was not supported by molecular data and a single genus *Aulopus* is recommended, although further research is needed to properly assess the potential of genetic and morphological diversity between Atlantic and Pacific species of the genus *Aulopus*.

Taxa within the Giganturoidae were recovered as the sister group of Ipnopoidae within the superfamily Ipnopoidea, rather than of the suborder Alepisauroidei (Baldwin & Johnson 1996; Sato & Nakabo 2002) with high statistical support. The genus *Bathysauroides* was recovered within Giganturoidae, corroborating Baldwin & Johnson (1996). The genus *Bathysauropsis* was recovered as the sister group of Ipnopidae (total evidence Bayesian, ML) without statistical support, and remains assigned to its own family Bathysauropsidae. The results of the nucDNA + mtDNA and total evidence analyses suggest that the family Notosudidae is not the sister group of the ipnopids as hypothesized by Baldwin & Johnson (1996).

DNA analyses recovered a Notosudidae + Chlorophthalmidae + Scopelarchidae clade without support. Scopelarchidae was recovered with Chlorophthalmidae within a clade where both families were paraphyletic with high statistical support for molecular data. While this result corroborates the placement of scopelarchids with chlorophthalmoids suggested by R. K. Johnson (1982), total evidence analyses recover Scopelarchidae as the basal family in the Alepisauroidea lineage. In either case, Scopelarchidae are not recovered as the sister group to Evermannellidae (Baldwin & Johnson 1996), and further research into the morphologies of these groups is needed to ascertain whether a number of derived features are truly shared (e.g., tubular eyes) or are the result of convergence in the deep sea. The systematic position of Chlorophthalmidae and Notosudidae is weakly supported for total evidence analyses, but Chlorophthalmoidea are sister to a Notosudoidea + Alepisauroidea clade.

Evermannellidae were recovered as the sister group to a clade consisting of alepisauroid taxa in the families Sudidae, Alepisauridae (sensu novo) and Paralepididae (sensu novo). Relationships within Evermannellidae corroborate R. K. Johnson (1982) in recovering *Coccorella* and *Evermannella* as sister groups. The genus *Sudis* is the sister group to a clade comprised of two distinct lineages of parelepidid and alepisaurid fishes, and is re-elevated here to the family Sudidae. The first lineage includes the family Alepisauridae, with an *Alepisaurus* + *Omosudis* clade sister to an *Anotopterus* + *Magnisudis* clade (Bayesian, ML). The genera *Anotopterus* and *Magnisudis* were previously recognized as members of the family Paralepididae, and are recognized here as belonging to the family Alepisauridae. The second distinct lineage includes the remaining genera of the family Paralepididae, including *Paralepis*, *Macroparalepis*, *Arctozenus*, *Lestidiops*, *Stemonosudis*, *Lestrolepis*, *Uncisudis*, and *Lestidium*. Resolution of this clade is strongly supported by molecular data, but weakly supported by the total-evidence analyses. Further research is needed with broader taxon sampling to further investigate relationships among the lineages of Paralepididae.

Acknowledgments

I thank the following people and institutions for providing specimens and tissue loans used in this study: E. O. Wiley and A. Bentley (University of Kansas Natural History Museum and Biodiversity Institute, Lawrence, Kansas), H. J. Walker (Scripps Institution of Oceanography, San Diego, California), K. Hartel (Museum of Comparative Zoology, Cambridge, Massachusetts), E. J. Hilton (Virginia Institute of Marine Science) and M. Miya (Natural History Museum & Institute, Chiba, Japan). Special thanks go to C. Li, Lincoln, Nebraska, for providing alignment material and PCR troubleshooting advice for the genes ENC1, zic1, and plagl2. For training in molecular techniques and PCR troubleshooting, I thank S. DeVaney and N. Holcroft, Lawrence, Kansas. Funding for this work was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (DEB 0910081), NSF Euteleost Tree of Life Grant (DEB 0732819), University of Kansas Natural History Museum and Biodiversity Institute Panorama Grants, and the Wiley Laboratory. I also thank E. Wiley and C. R. Robins, Lawrence, Kansas, for many thoughtful discussions and helpful advice. Thanks also go to F. Abe, K. Mickle, N. Holcroft, E. Wiley, all Lawrence, Kansas, L. Smith, Chicago, Illinois, and M. Ghedotti, Denver, Colorado, for suggestions and comments on this manuscript. Finally, I thank G. Arratia, Lawrence, Kansas, for countless discussions about fish morphology and systematics.

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Appendix 1
Abbreviated List of Morphological Characters

Reproduced and modified from Baldwin & Johnson (1996) and Sato & Nakabo (2002). For full descriptions and figures, please see the respective studies.

Gill Arches

1. Second epibranchial uncinate process: absent (0), present, enlarged (1), present, not enlarged, end of second pharyngobranchial displaced posterolaterally (2), present, not enlarged, end of second pharyngobranchial displaced posteriorly (3) (Baldwin & Johnson [1], 1996; Sato & Nakabo [32], 2002).
2. Cartilaginous condyle on dorsal surface of third pharyngobranchial: PB3 with cartilaginous condyle articulating with EB2 (0), PB3 without cartilaginous condyle articulating with EB2 (1) (Baldwin & Johnson [2], 1996).
3. Fourth pharyngobranchial toothplate: UP4 present (0), UP4 absent (1) (Baldwin & Johnson [3], 1996).
4. Articulation of first pharyngobranchial: PB1 articulates at distal tip of EB1 (0), PB1 articulates at proximal base of cartilaginous tip of EB1 (1) (Baldwin & Johnson [4], 1996).
5. Gill rakers or toothplates: Gill rakers long, lathlike (0), gill rakers present as toothplates (1), single elongate gill raker on EB1 (2) (Baldwin & Johnson [5], 1996).
6. Second pharyngobranchial with extra uncinate process: PB2 without extra uncinate process (0), PB2 without extra uncinate process but with expanded proximal base (1), PB2 with extra uncinate process (2) (Baldwin & Johnson [6], 1996).
7. Second pharyngobranchial toothplate: UP2 present (0), UP2 absent (1) (Baldwin & Johnson [7], 1996).
8. Second pharyngobranchial uncinate process: PB2 with short uncinate process (0), PB2 with long uncinate process (1) (Baldwin & Johnson [8], 1996).
9. Uncinate process of second epibranchial adjacent to second epibranchial: EB2 uncinate process diverges from EB2 as it approaches PB3; PB2 oriented anteromedial to posterolateral (0), EB2 uncinate process adjacent to EB2 as both approach PB3; PB2 oriented anterior to posterior (1) (Baldwin & Johnson [9], 1996).
10. Articulation between uncinate processes of first epibranchial and second pharyngobranchial: EB1 and PB2 articulate via uncinate processes (0), uncinate process of EB1 does not articulate with that of PB2 (1), uncinate process on EB1 absent (2) (Sato & Nakabo [43], 2002).
11. Third pharyngobranchial produced: PB3 not extending anteriorly beyond the tips of EB1 and PB2 (0), PB3 extending anteriorly beyond the tips of EB1 and PB2 (1) (Baldwin & Johnson [10], 1996).
12. Bony ridge on dorsal surface of third pharyngobranchial: absent (0), present (1) (Sato & Nakabo [34], 2002).
13. Distribution of PB3 teeth: UP3 covering large area of ventral surface of PB3 (0), UP3 restricted to lateral edge of ventral surface of PB3 (1), UP3 absent (2) (Baldwin & Johnson [11], 1996).
14. Size of PB3 teeth: small (0), large (1) (Baldwin & Johnson [12], 1996).
15. First pharyngobranchial: PB1 normal or reduced (0), PB1 very long (1), PB1 absent (2) (Baldwin & Johnson [13], 1996; Sato & Nakabo [38], 2002).
16. Fourth epibranchial morphology: EB4 has a slender proximal end and an uncinate process attached to the fourth levator externus (0), end of EB4 slender, but lacks an uncinate process (1), EB4 has an expanded proximal end capped with a large band of cartilage and an uncinate process at the middle (2), proximally expanded EB4 lacking an uncinate process (3) (Sato & Nakabo [44], 2002).
17. Ossification of first epibranchial and ceratobranchial: well ossified and capped by a proximally short cartilage (0), ossification weak, proximal cartilaginous portions long (1) (Sato & Nakabo [46], 2002).
18. Fifth epibranchial: EB5 absent (0), EB5 present (1) (Baldwin & Johnson [14], 1996; Sato & Nakabo [45], 2002)
19. Dentition of fifth ceratobranchial: teeth scattered all over anterodorsal surface (0), teeth restricted to medial edge of anterodorsal surface (1), teeth restricted to medial edge of anterodorsal surface (2), without teeth (3) (Baldwin & Johnson [15], 1996).
20. Shape of fifth ceratobranchial: CB5 not V-shaped (0), CB5 V-shaped, the medial limb slender (1), CB5 V-shaped, the medial limb robust (2) (Baldwin & Johnson [16], 1996).
21. Gap between the fourth basibranchial cartilage and fifth ceratobranchials: no gap (0), gap between CB5s and BB4 cartilage, CB5s not articulating with reduced BB4 (1), CB5s separated from main body of BB4 by tail or small nubbins of cartilage extending posteriorly from BB4 (2) (Baldwin & Johnson [17], 1996).
22. Third basibranchial extends beyond fourth basibranchial cartilage: BB3 terminates beneath the anterior end of BB4 cartilage (0), BB3 terminates beyond the posterior end of BB4 cartilage (1) (Baldwin & Johnson [18], 1996).
23. Fourth basibranchial ossified: cartilaginous (0), ossified (1) (Baldwin & Johnson [19], 1996).
24. Elongate first basibranchial: BB1 not elongate (0), BB1 elongate, ossified (1), BB1 usually elongate, comprising a short ossified anterior segment followed by a long posterior cartilage (2) (Baldwin & Johnson [20], 1996).
25. Elongate second basibranchial: not elongate (0), elongate (1) (Baldwin & Johnson [21], 1996).
26. Gillrakers or toothplates on third hypobranchials: present on HB3 (0), absent on HB3 (1) (Baldwin & Johnson [22], 1996).

27. Gillrakers or toothplates on basibranchials: lacking on basibranchials (0), present on BB2, sometimes BB1 and BB3 (1) (Baldwin & Johnson [23], 1996).
28. Gill rakers on medial surface of gill arches: present (0), absent on first arch only (1), present on first hypobranchial only (2), absent (3) (Sato & Nakabo [50], 2002).
29. Ligament between first hypobranchial and ventral hypohyal: not ossified (0), ossified (1) (Baldwin & Johnson [24], 1996).
30. First hypobranchial with ventrally directed processes: without ventrally directed processes (0), with a ventrally directed process (1) (Baldwin & Johnson [25], 1996).
31. Second hypobranchial with ventrally directed process: without ventrally directed processes (0), with a ventrally directed process (1) (Baldwin & Johnson [26], 1996).
32. Third hypobranchials fused ventrally: not fused (0), fused (1) (Baldwin & Johnson [27], 1996).

Hyoid Arch

33. Ventral ceratohyal cartilage: anterior ceratohyal without autogenous ventral cartilage (0), anterior ceratohyal with autogenous cartilage along ventral margin (1) (Baldwin & Johnson [28], 1996).
34. Number of branchiostegals on the posterior ceratohyal: four or fewer (0), five (1), six or more (2) (Baldwin & Johnson [29], 1996).
35. Number of branchiostegals on the anterior ceratohyal: five or more (0), four or fewer (1) (Baldwin & Johnson [30], 1996).
36. Proximity of posteriormost tow branchiostegals: all branchiostegals on posterior ceratohyal evenly spaced (0), two posteriormost branchiostegals close, inserting on ventral margin of posterior ceratohyal (1), two posteriormost branchiostegals close, inserting on posteroventral corner of posterior ceratohyal (2) (Baldwin & Johnson [31], 1996).
37. 3+1 arrangement of branchiostegals on the anterior ceratohyal: branchiostegals on anterior ceratohyal evenly spaced (0), branchiostegals on anterior ceratohyal arranged in "3+1" pattern (1) (Baldwin & Johnson [32], 1996).
38. Hypohyal branchiostegals: no branchiostegals on ventral hypohyal (0), anteriormost branchiostegal on ventral hypohyal (1), anteriormost three branchiostegals on ventral hypohyal (2) (Baldwin & Johnson [33], 1996).
39. Basihyal morphology: basihyal oriented horizontally (0), basihyal oriented obliquely (1), basihyal oriented at 90° angle to BB1 (2) (Baldwin & Johnson [34], 1996).
40. Basihyal teeth: absent or unmodified (0), present as large, posteriorly curved structures (1) (Baldwin & Johnson [35], 1996).

Jaws, Suspensorium, and Circumorbitals

41. Dominant tooth-bearing bone: premaxilla (or premaxilla and maxilla) (0), premaxilla and palatine (1), palatine (2) (Baldwin & Johnson [36], 1996).
42. Quadrate with produced anterior limb: quadrate fan-shaped (0), quadrate with produced anterior limb (1) (Baldwin & Johnson [37], 1996).
43. Quadrate with two distinct cartilaginous heads: quadrate with single large cartilage on dorsal border (0), quadrate cartilage separated into tow condyles (1) (Baldwin & Johnson [38], 1996).
44. Large concavity in dorsal margin of quadrate: no concavity (0), concavity between anterior and posterior cartilaginous condyles (1) (Baldwin & Johnson [39], 1996).
45. Posterior cartilaginous condyle of quadrate articulates with hyomandibular: posterior portion of quadrate articulates dorsally with metapterygoid (0), posterior cartilaginous condyle of quadrate articulates dorsally with hyomandibular (1) (Baldwin & Johnson [40], 1996).
46. Metapterygoid produced anteriorly: metapterygoid overlies quadrate (0), metapterygoid extends anteriorly over posterior portion of ectopterygoid (1) (Baldwin & Johnson [41], 1996).
47. Metapterygoid free of hyomandibular: metapterygoid bound to hyomandibular (0), metapterygoid free from hyomandibular (1) (Baldwin & Johnson [42], 1996).
48. Ectopterygoid teeth: without teeth (0), teeth on ventral margin of ectopterygoid (1) (Sato & Nakabo [20], 2002).
49. Endopterygoid teeth: present (0), absent (1) (Sato & Nakabo [21], 2002).
50. Hyomandibular and opercle oriented horizontally: hyomandibular oriented vertically or subvertically, opercle posterior to suspensorium (0), hyomandibular oriented ca. horizontally, opercle rotated dorsally to lie above hyomandibular (1) (Baldwin & Johnson [43], 1996).
51. Hyomandibular condyle for articulation with skull: two condyles for articulation with skull (0), one condyle for articulation (1) (Sato & Nakabo [19], 2002).
52. Ossification of palatine prong: well developed cartilaginous head overhanging the proximal portion of the maxilla in adult (0), mostly ossified, capped by cartilage only at its dorsal tip (1), palatine prong absent (2) (Baldwin & Johnson [44], 1996; Sato & Nakabo [5], 2002).

53. Dorso-medially directed premaxillary process: premaxilla without dorso-medially directed process medial edge (0), premaxilla with dorso-medially directed process on medial edge (1) (Baldwin & Johnson [45], 1996).
54. Number of infraorbitals: six (0), seven (1), eight (2), five (3), three (4), none (5) (Baldwin & Johnson [46], 1996).
55. Long snout: snout length less than 50 percent head length (0), snout length greater than 50 percent head length (1) (Baldwin & Johnson [47], 1996).
56. Premaxillary fenestra: no premaxillary fenestra (0), anterior premaxilla with fenestra (1) (Baldwin & Johnson [48], 1996).
57. Palatine articulates with premaxilla: palatine without process for articulation with premaxilla (0), palatine with long process for articulation with premaxilla (1) (Baldwin & Johnson [49], 1996).
58. Palatine morphology: ventral portion of the palatine expanded laterally (0), lateral expansion absent (1) (Sato & Nakabo [23], 2002).
59. Position of palatinad cartilaginous facet for articulation with lateral ethmoid: facet located anteriorly (0), facet located on the posterior portion of palatine (1), absent (2) (Sato & Nakabo [24], 2002).
60. Maxillary palatinad facet on maxilla: present (0), absent (1) (Sato & Nakabo [7], 2002).
61. Lacrimal oriented horizontally on snout: lacrimal bordering orbit anteriorly (0), lacrimal anterior to orbit, oriented horizontally (1) (Baldwin & Johnson [50], 1996).
62. Maxilla reduced: maxilla well developed with posterior end expanded (0), maxilla intact but slender, posterior end not expanded (1), maxilla present as posterior remnant (2), maxilla present as anterior remnant (3) (Baldwin & Johnson [51], 1996).
63. Outer tooth patch on tip of lower jaw: absent (0), outer tooth patch exposed to the outside on tip of lower jaw (1), outer tooth patch separated from the inner tooth patch, becomes elongated along the margin of lower jaw (2) (Sato & Nakabo [8], 2002).
64. Mandibulohyoid ligament: present (0), absent (1) (Sato & Nakabo [22], 2002).
65. Cheek muscle: discrete A1 and A2 muscle elements (0), A1 and A2 components of the adductor mandibulae fused (1), A1 component is absent (2) (Sato & Nakabo [25], 2002).

Cranium

66. Frontal expanded laterally over orbit: frontal not expanded laterally (0), frontal expanded laterally (1) (Baldwin & Johnson [52], 1996).
67. Sphenotic process: sphenotic without anterior process (0), sphenotic with anterior process (1) (Baldwin & Johnson [53], 1996).
68. Exoccipital pocess: absent (0), present (1) (Sato & Nakabo [3], 2002).

Intermuscular bones and ligaments

69. Epipleurals extend anteriorly to first or second vertebra: epipleurals originate on V3, do not extend to V1 or V2 (0), epipleurals originate on V2 (1), epipleurals originate on V1 (2), absent (3) (Baldwin & Johnson [54], 1996; Sato & Nakabo [59], 2002).
70. One or more epipleurals displaced dorsally into horizontal septum: all epipleurals beneath the horizontal septum (0), one or more epipleurals displaced dorsally into horizontal septum (1) (Baldwin & Johnson [55], 1996).
71. Abrupt transition of epipleurals in and beneath the horizontal septum: no epipleurals displaced dorsally into the horizontal septum or the transition between epipleurals in and beneath the horizontal septum is gradual (0), abrupt transition between epipleurals in and beneath the horizontal septum (1) (Baldwin & Johnson [56], 1996).
72. One or more epipleurals forked distally: epipleurals not forked distally (0), epipleurals forked distally at transition of epipleurals in and beneath the horizontal septum (1) (Baldwin & Johnson [57], 1996).
73. Epipleurals on first and second vertebrae fused to centrum: epipleurals on V1 and V2 autogenous (0), epipleurals on V1 and V2 fused to centrum (1) (Baldwin & Johnson [58], 1996).
74. Epipleurals not attached to axial skeleton: most or all epipleurals attached to axial skeleton (0), most epipleurals not attached to axial skeleton (1), most epipleurals are free dorsal branches (2) (Baldwin & Johnson [59], 1996).
75. Reduced number of epipleurals: long series of epipleurals (0), epipleurals not extending posteriorly beyond V5 (1) (Baldwin & Johnson [60], 1996).
76. Origin of epineurals: all epipleurals originate on neural arch (0), some epineurals originate on the centrum or parapophysis, these flanked anteriorly and posteriorly by epineurals originating on the neural arch (1), most or all epineurals originate on centrum, epineurals not reascending to neural arch posteriorly (2) (Baldwin & Johnson [61], 1996).
77. First one to three epineurals with distal end displaced ventrally: distal end of epineurals not displaced ventrally (0), distal end of first one to three epineurals displaced ventrally (1) (Baldwin & Johnson [62], 1996).

78. Some epineurals and epipleurals forked proximally: no epineurals or epipleurals forked proximally (0), epineurals and epipleurals from about V12-V15 to near end of series forked proximally (1), epineurals and epipleurals on about V1-V5 forked proximally (2), *"Gigantura"* pattern of branching (3) (Baldwin & Johnson [63], 1996).
79. Epineurals fused to neural arch: epineurals not fused to axial skeleton (0), epineural fused to neural arch on V1 (1), epineurals fused to neural arch on V1-V5 (2), epineurals fused to neural arch on V1-V10 (3), most epineurals fused to centrum (4), fused to neural arch on V3-V6 (or V9) (5) (Baldwin & Johnson [64], 1996; Sato & Nakabo [66], 2002).
80. Epineurals attached to axial skeleton: most or all epineurals attached to axial skeleton (0), most epineurals unattached (1), all epineurals unattached (2), unattached epineurals represent only free ventral branches of forked epineurals (3) (Baldwin & Johnson [65], 1996).
81. Epicentrals: epicentrals ligamentous (0), epicentrals ossified (1), epicentrals absent (2), epicentrals cartilaginous anteriorly, ligamentous posteriorly (3), ossified anteriorly, ligamentous posteriorly (4) (Baldwin & Johnson [66], 1996; Sato & Nakabo [68], 2002).
82. Anterior epicentrals closely applied to distal end of epipleurals: all epicentrals attached to centrum or parapophyses (0), anterior epicentrals attached to distal end of epipleurals (1) (Baldwin & Johnson [67], 1996).

Postcranial axial skeleton

83. Number of supraneurals: three or more supraneurals (0), two supraneurals (1), one supraneural (2), no supraneurals (3) (Baldwin & Johnson [68], 1996).
84. Number of caudal vertebrae: <25 % caudal vertebrae (0), 40-60 % caudal vertebrae (1), >60 % caudal vertebrae (2) (Baldwin & Johnson [69], 1996).
85. Accessory neural arch: accessory neural arch absent (0), accessory neural arch present (1) (Baldwin & Johnson [70], 1996).
86. First neural arch with brush-like growth: no brush-like growth on first neural arch (0), brush-like growth on first neural arch (1) (Baldwin & Johnson [71], 1996).
87. Number of open neural arches: many neural arches open dorsally (0), neural arches open on V1 and sometimes V2-V4 (1), all neural arches closed dorsally (2) (Baldwin & Johnson [72], 1996).
88. Origin of first rib: first rib originates on V3 (0), first rib originates on V4 (1), first rib originates on V5 (2), first rib originates on V2 (3), first rib originates on V1 (4), ribs absent (5) (Baldwin & Johnson [73], 1996).
89. Ossification of ribs: all ribs ossify in cartilage (0), some ribs ossify in membrane bone (1), all ribs ossify in membrane bone (2), ribs absent (3), some or all ribs ligamentous (4) (Baldwin & Johnson [74], 1996).
90. Origin of Baudelot's ligament: Baudelot's ligament originates on V1 (0), Baudelot's ligament originates on more than one vertebra (1), Baudelot's ligament originates on V1 and the occiput (2) (Baldwin & Johnson [75], 1996).
91. Ossification of Baudelot's ligament: Baudelot's ligament is ligamentous (0), Baudelot's ligament is ossified (1), Baudelot's ligament is absent (2) (Baldwin & Johnson [76], 1996).
92. Condition of ventral parapophyses on first vertebra: parapophyses with enlarged base (0), parapophyses without enlarged base (1) (Sato & Nakabo [58], 2002).

Caudal Fin and Rays

93. Modified proximal segmentation of caudal-fin rays: proximal portion of principal caudal-fin rays not modified (0), proximal portion of most principal caudal rays with modified segment (1) (Baldwin & Johnson [77], 1996).
94. Segmentation begins on distal half of each caudal ray: segmentation begins on proximal half of each caudal ray (0), segmentation begins on distal half of each caudal ray (1), caudal rays not segmented (2) (Baldwin & Johnson [78, 1996).
95. Median caudal cartilages: two CMCs, about equal in size (0), two CMCs, the dorsal one minute (1), one CMC (2), no CMC (3) (Baldwin & Johnson [79], 1996).
96. Urodermal: no urodermal (0), small urodermal in upper caudal lobe (1) (Baldwin & Johnson [80], 1996).
97. Expanded neural and haemal spines on posterior vertebrae: posterior neural and haemal spine no expanded (0), neural arch and haemal spines of PU2 expanded (1), neural arch and haemal spines of PU2 and PU3 expanded (2) (Baldwin & Johnson [81], 1996).
98. Number of hypurals: six hypurals (0), five hypurals, the sixth lost or fused (1), five hypurals, the first and second not differentiated (2), four hypurals, the first and second not differentiated, the sixth lost or fused (3), two hypurals (4) (Baldwin & Johnson [82], 1996).
99. Number of epurals: adults with two or three epurals, if two, one split (0), adults with two epurals, neither split (1), adults with one epural (2) (Baldwin & Johnson [83], 1996).
100. Fusion of adjacent pterygiophores: no fusion of pterygiophores of dorsal or anal fin (0), adjacent posterior anal-fin pterygiophores fused (1), adjacent dorsal-fin pterygiophores fused (2) (Baldwin & Johnson [84], 1996).

101. Pterygiophores of dorsal fin triangular proximally: pterygiophores of anal fin not triangular proximally (0), anterior pterygiophores of anal fin triangular proximally (1), posterior pterygiophores of anal fin triangular proximally (2) (Baldwin & Johnson [85], 1996).
102. Pterygiophores of anal fin triangular proximally: pterygiophores of anal fin not triangular proximally (0), anterior pterygiophores of anal fin triangular proximally (1), posterior pterygiophores of anal fin triangular proximally (2) (Baldwin & Johnson [86], 1996).

Pelvic and Pectoral Girdles and Fins

103. Medial processes of the pelvic girdle joined medially by cartilage: medial processes not joined medially (0), medial processes joined medially by cartilage (1) (Baldwin & Johnson [87], 1996).
104. Posterior processes of pelvic girdle elongate and widely separated: posterior pelvic processes small (or absent) (0), posterior pelvic processes elongate, widely separated (1) (Baldwin & Johnson [88], 1996).
105. Posterior processes of pelvic girdle absent: ossified posterior processes of pelvic girdle present (0), posterior processes are cartilaginous (1), posterior processes of pelvic girdle absent (2) (Baldwin & Johnson [89], 1996).

Appendix 2.

Morphological Data Matrix. See Appendix 1 for abbreviated list of characters. Y = (01), L = (12), M = (02), N = (13).

	1	11111 11112	22222 22223	33333 33334	44444 44445	55555 55556	66666 66667
	12345 67890	12345 67890	12345 67890	12345 67890	12345 67890	12345 67890	12345 67890
Diplophos	00100 01000	00000 00?00	00000 00100	00000 00110	00000 00000	12000 00000	00000 00000
Myctophidae	00000 00000	00000 00000	1000Y 11000	00000 00200	00000 00000	01000 00000	00010 00000
Neoscopelus	00000 00000	00000 00000	10000 10000	00000 00000	00000 00100	01000 00000	00010 00000
Metavelifer	0000Y 0000?	0?000 ??000	00000 10?00	10001 00000	00000 00??0	??050 00???	00??? 00?3?
Polymixia	00000 00000	00000 00000	10000 10000	00001 00000	00001 00100	00000 00000	00010 00000
Aulopus	11000 00000	01000 20100	20000 10000	00120 00000	00000 00100	00000 00111	00000 00011
Pseudotrichonotus	11100 01002	00002 30100	00000 00000	00100 00000	00000 00010	02000 00121	00010 00011
Synodus	11111 00001	00000 10002	20000 00001	10120 00000	01111 10010	01000 00120	01000 00011
Trachinocephalus	11111 00001	00000 10102	20000 00001	10120 00000	01111 10010	01000 00120	01000 00011
Harpadon	11101 00000	10110 10102	21000 00001	10120 00000	01100 10100	01000 0011?	02010 00011
Saurida	11101 00000	00110 10102	21000 00Y01	10120 00000	01100 10100	01000 00110	01010 00011
Bathypterois	21000 21000	00000 30100	00000 11100	00010 00010	00000 01Y10	00100 00110	00200 11110
Bathymicrops	11100 2000?	0?000 ??100	00101 11?10	00000 00010	00000 01??1	??150 00???	00??? 11?10
Bathytyphlops	11002 2100?	0?000 ??100	00001 11?10	00000 00010	00000 01??1	??130 00???	00??? 11?11
Ipnops	11000 21000	00000 30100	00100 11100	00000 00010	00000 01010	00130 00120	00200 ??10?
Scopelosaurus	11000 20000	00000 00100	00011 11000	00000 00100	00100 00010	02110 00110	00210 00011
Ahliesaurus	11000 2000?	0?000 ??100	00011 11?00	00000 00100	00100 00??0	??110 00???	00??? 00?11
Chlorophthalmus	11000 10000	00000 00100	00000 00101	00001 00000	00000 00010	11100 00111	00101 00111
Parasudis	11000 10000	00000 00100	00000 10100	00001 00000	00000 00010	11100 00111	00101 00110
Bathysauropsis	11000 10000	00000 20100	00000 11100	00000 00010	00000 00110	00100 00000	00200 00111
Omosudis	11001 01100	10112 01020	01000 00300	0000? ?0000	20000 00010	02020 00100	00010 00021
Alepisaurus	11001 01000	10112 01020	01000 00300	00001 00000	20000 00010	02020 00100	00010 00021
Coccorella	11001 01100	10112 01031	00001 00200	00001 00020	20000 00010	02020 00100	00012 00021
Odontostomops	11001 0110?	0?110 ??021	00001 00?00	01001 10020	20000 00??0	??020 00???	00??? 00?21
Evermannella	11001 0110?	0?110 ??021	00001 00?00	01001 10020	20000 00??0	??020 00???	00??? 00?21
Scopelarchus	11001 0100?	0?112 ??020	00000 00?00	00001 00001	20000 00??0	??000 00???	00??? 00?21
Scopelarchoides	11001 0100?	0?112 ??010	00000 00?00	00001 00001	20000 00??0	??000 00???	00??? 00?21
Benthalbella	11001 00000	00110 01010	00000 00300	00001 00001	20000 00010	02000 00100	00012 00121
Rosenblattichthys	11001 0100?	0?110 ??010	00000 00?00	00001 00001	20000 00??0	??000 00???	00??? 00?2?
Paralepis	11001 01000	00110 00020	00020 10000	00001 21000	20000 00010	02021 11110	10012 00021
Arctozenus	11001 0100?	0?110 ??020	00020 10?00	01001 21000	20000 00??0	??021 11???	10??? 00?21
Lestrolepis	11001 0101?	0?2?0 ??020	00020 00?00	00001 21000	20000 00??0	??021 11???	10??? 00?21
Lestidium	31001 01010	002?0 00020	00020 00300	00001 21000	20000 00010	02021 11110	10002 00021
Stemonosudis	11001 0101?	0?2?0 ??020	00020 00?00	00001 21000	20000 00??0	??021 11???	10??? 00?21
Uncisudis	11001 0101?	0?2?0 ??023	30020 00?00	00001 21000	20000 00??0	??021 11???	10??? 00?2?
Macroparalepis	11001 0101?	0?2?0 ??020	00020 00?00	00001 21000	20000 00??0	??021 11???	10??? 00?21
Lestidiops	11001 0101?	0?2?0 ??020	00020 00?00	00001 21000	20000 00??0	??021 11???	10??? 00???
Sudis	11001 0100?	0?2?0 ??020	00020 00?00	00001 20000	20000 00??0	??0?1 11???	?0??? 00?21
Anotopterus	11101 0100?	1?2?0 ??020	00020 00?00	00001 00000	20000 00??0	??001 11???	11??? 00?21
Bathysauroides	11001 00000	00011 00100	00000 10100	00001 00000	20000 00010	00100 00110	00100 00121
Bathysaurus	11001 00000	00011 10100	00000 11001	00001 00000	10000 00010	01000 0010?	03010 00021
Gigantura	1100? 0?00?	0?0?? ?????	00??? ????0	??00? 0?000	?0000 00??0	??000 00???	?2??? 00?21
Paraulopus	10000 0?0?1	01?00 201?0	00??? ??0??	??000 00?0?	00000 0000?	000?? 00111	00000 ?0000

106. Lateral pelvic processes: lateral pelvic processes small (0), lateral pelvic processes large, sometimes ossifying in adults (1) (Baldwin & Johnson [90], 1996).
107. Autogenous pelvic cartilages: autogenous pelvic cartilages absent (0), autogenous pelvic cartilages present (1) (Baldwin & Johnson [91], 1996).
108. Ventrally directed posterior cartilage of the pelvic fin: cartilage between medial processes, if present, not terminating in ventrally directed process (0), cartilage between medial processes terminating in ventrally directed process (1) (Baldwin & Johnson [92], 1996).
109. Posterior pelvic cartilage elongate: cartilage extending posteriorly from between medial processes, if present, not elongate (0), cartilage extending posteriorly from between medial processes elongate (1) (Baldwin & Johnson [93], 1996).
110. Ventral surface of pelvic girdle: ventral surface of pelvic girdle is smooth (0), the pelvic girdle has a transverse keel dividing the ventral surface of the medial process area (1) (Sato & Nakabo [84], 2002).
111. Position of pectoral and pelvic fins: pectoral fins set high on body, pelvics subthoracic (0), pectoral fins set low on body, pelvics abdominal (1) (Baldwin & Johnson [94], 1996).

			1	11111 11111	11111 11111	11111 11111	11111 1111
77777 77778	88888 88889	99999 99990	00000 00001	11111 11112	22222 22223	33333 3333	
12345 67890	12345 67890	12345 67890	12345 67890	12345 67890	12345 67890	12345 6789	
00000 00020	00011 00100	00000 00000	00000 00000	11201 00010	00000 00001	?0000 0000	
00000 00100	00010 02000	00000 Y0000	00000 01000	00000 00000	00000 00000	00Y0M 0000	
00000 00100	00010 02000	00002 10000	00000 00000	00000 00000	10000 00000	00Y00 0000	
????? 00000	00210 02012	0?003 0000?	00000 0000?	00101 00???	?0000 000?1	?0000 0000	
00000 10000	00010 02000	01003 00000	00000 00000	00000 00000	00000 00011	00000 1000	
00000 01000	00011 00020	01103 Y2000	00110 00000	00400 00001	10000 00000	00100 0100	
10000 01000	00110 00120	01103 02120	00110 00000	00000 00001	10000 00001	00100 0200	
10000 01000	00001 10220	01103 02120	00110 00000	00000 00001	00000 00000	00100 0200	
10000 01000	00001 10220	01103 02120	00110 00000	00000 00001	00000 00000	00100 0200	
00000 00030	00001 00320	11103 00110	00110 00001	00200 00100	00000 00000	00100 0200	
00000 00030	00001 00120	11103 02010	00110 00001	00000 00100	00000 00000	00100 0200	
00000 00000	00210 01310	01002 00000	00101 10001	00100 00101	?0000 0?210	10110 0Y00	
00000 00000	00220 01530	1?013 00420	0010? 1000?	00200 10???	?0000 0?2?1	10110 0000	
00000 00000	00120 01310	0?003 00010	00101 1000?	00000 10???	?0000 0?211	10110 0100	
00000 01000	00220 02310	00013 00210	00101 10000	00200 00100	00000 0?511	10110 0000	
01000 10000	00210 01010	01002 00000	00102 10001	00000 00100	00000 01110	10101 0000	
01000 10000	00210 01010	0?002 00000	00102 1000?	00000 00???	?0000 011?0	10101 0000	
00000 01100	00120 01010	00000 Y0000	00102 10001	00300 00100	00000 11000	10100 0100	
00000 00100	40210 01010	00000 00000	00102 10001	00000 00100	00000 11000	10100 0101	
00000 00000	00010 01010	00000 00000	00102 ?0000	00300 00100	00000 01100	10??? ???0	
00110 000?1	10210 01421	0100? 10101	00102 01000	10001 00010	01210 00000	11100 1101	
00100 00021	10310 01421	01000 00101	00102 01000	10?01 00010	01210 00000	11100 1101	
00000 10000	31120 01010	01000 00020	10102 01011	10401 01000	01100 00300	10102 0100	
00?00 ??0??	31120 01010	0?000 00020	11102 0101?	10301 01???	?1100 00000	10102 0100	
00000 10000	31120 01010	0?000 00020	11102 0101?	10301 01???	?1100 00300	10102 0100	
00000 10000	01020 01340	0?000 00000	00102 1010?	10001 01???	?1000 00300	10102 0100	
00000 10000	01020 01040	0?000 00000	02102 0010?	10001 01???	?1000 00300	10102 0000	
00000 10000	01020 01040	0100? 00000	00102 01000	10301 00000	01000 00300	10100 0100	
000?0 10040	0?020 01040	0?000 00000	00102 0010?	10001 01???	?1000 00300	10102 0100	
00120 00213	20110 01420	0100? 00000	00102 01001	10401 00010	01000 00000	10100 0100	
00020 00203	20110 01021	0?000 00200	00102 0100?	10001 00???	?1000 00000	10100 0100	
00001 00000	20120 01121	0?002 000?0	00102 0100?	11011 00???	?1101 00000	10100 0101	
00001 00000	20110 01021	01001 00000	00102 01001	11011 00010	01101 00000	10100 0100	
00001 00000	20110 01121	0?002 00000	00102 1100?	11011 00???	?1101 00000	10100 0101	
?0??? ?????	??110 ?1?2?	??001 00002	00102 0100?	11011 00???	?1101 00000	10100 0100	
00001 00010	20110 01221	0?000 00000	00102 0100?	11011 00???	?1101 00000	10100 0100	
?00?? 00?00	??110 01120	0?001 000?0	00102 0100?	11001 00???	?1101 00000	10100 0101	
00001 ??000	20110 0112?	??000 00000	00102 0100?	11?01 00???	?1101 00000	10110 1100	
00000 00002	20?10 013?1	0?000 ?0N20	?0102 0000?	??111 00???	?0120 00000	10100 0100	
00000 11000	00000 01010	00000 12000	00102 00000	00300 00100	00000 01100	101?? ??00	
00000 20040	20000 00310	01000 10000	00102 00000	00400 00100	00000 0010Y	10110 0110	
00000 20300	20?00 0053?	2?022 01020	00?02 0000?	10202 00???	?0200 00400	10100 0110	
0?00? 0005?	40??Y 00010	001?2 110?0	??1?? 10??0	0?0?0 ?0001	1000? 01??0	001?? ????	

112. Relative position of abdominal pelvic fins: pelvic fins subthoracic or, if abdominal, inserting beneath or behind a vertical through the origin of the dorsal fin (0), pelvic fins abdominal, inserting anterior to vertical through dorsal fin (1) (Baldwin & Johnson [95], 1996).
113. Number of postcleithra: two postcleithra (0), one postcleithra (1), postcleithra absent (2), three postcleithra, dorsalmost postcleithrum attaches to the posterolateral surface over dorsal margin of posterior strut of the cleithrum (3), three postcleithra, dorsalmost postcleithrum attaches to the medial surface of the cleithrum (4) (Baldwin & Johnson [96], 1996; Sato & Nakabo [77], 2002).
114. Cleithrum with strut extending to dorsal postcleithrum: cleithrum with small rounded posterior projection or projection absent (0), cleithrum with strut extending posteriorly to postcleithrum (1) (Baldwin & Johnson [97], 1996).
115. Orientation of pectoral-fin base: pectoral-fin base more vertical than horizontal (0), pectoral-fin base more horizontal than vertical, inserted on the ventrolateral surface of the body (1), pectoral-fin base horizontal, inserted on the dorsolateral surface of body (2) (Baldwin & Johnson [98], 1996).
116. Greatly elongated supracleithrum: supracleithrum shorter than cleithrum (0), supracleithrum equal to or longer than cleithrum (1) (Baldwin & Johnson [99], 1996).
117. Ventral limb of posttemporal not ossified: posttemporal forked, both branches ossified (0), posttemporal unforked, the ventral branch ligamentous (1) (Baldwin & Johnson [100], 1996).
118. Position of cleithrum-coracoid articulation: near the anteroventral end of the cleithrum (0), joint is shifted dorsally (1) (Sato & Nakabo [76], 2002).
119. Origin of adductor profundus: originates from the ventral or middle portion of the cleithrum (0), originates around the anterodorsal portion of the coracoid (1) (Sato & Nakabo [80], 2002).
120. Number of adductor profundus elements: single adductor profundus (0), two adductor profundus elements (1) (Sato & Nakabo [81], 2002).
121. Spur size on medial half of second ray of pectoral fin: spurs of the pectoral fin rays are almost equal in size (0), spur of the medial half of the second ray is more reduced than those of successive rays (1) (Sato & Nakabo [82], 2002).

External morphology

122. Margin of anal fin indented: margin of anal fin not indented (0), margin of anal fin indented (1) (Baldwin & Johnson [101], 1996).
123. Scales: Body and lateral-line scales present and ossified (0), body scales absent, lateral-line scales or structures at least partially ossified (1), body and lateral-line scales or structures absent (2) (Baldwin & Johnson [102], 1996).
124. Fleshy mid-lateral keel: absent (0), single fleshy mid-lateral keel on posterior portion of body (1), pair of fleshy mid-lateral keels on caudal peduncle (2) (Baldwin & Johnson [103], 1996).
125. Body transparent, glassy in life: appearance in life not transparent or glassy (0), appearance in life transparent, glassy (1) (Baldwin & Johnson [104], 1996).
126. Scale pockets in continuous flap of skin: scale pockets not in continuous flap of skin (0), scale pockets in a continuous flap of marginally pigmented skin (1) (Baldwin & Johnson [105], 1996).
127. Elliptical or keyhole aphakic space: no aphakic space (0), elliptical or keyhole shaped aphakic space (1) (Baldwin & Johnson [106], 1996).
128. Eye morphology: eyes laterally directed, round (0), eyes slightly flattened to elliptical (1), eyes minute or absent (2), eyes dorsally directed, semitubular or tubular (3), eyes anteriorly directed, telescopic (4), eyes are broad, lensless plates on dorsal surface of head (5) (Baldwin & Johnson [107], 1996).
129. Gular fold: gular fold tent-shaped (0), gular fold crescent-shaped (1) (Baldwin & Johnson [108], 1996).
130. Adipose fin: present (0), absent (1) (Baldwin & Johnson [109], 1996).
131. Mode of reproduction: separate sexes (0), synchronous hermaphrodites (1) (Baldwin & Johnson [110], 1996).
132. Thin-walled, heavily pigmented stomach: stomach not highly distensible, with thick unpigmented walls (0), stomach highly distensible, with thin heavily pigmented walls (1) (Baldwin & Johnson [111], 1996).
133. Swimbladder: present (0), absent (1) (Baldwin & Johnson [112], 1996).
134. Enlarged pectoral fins: pectoral fins not enlarged in larvae (0), pectoral fins enlarged in larvae (1) (Baldwin & Johnson [113], 1996).
135. Elongate eyes: eyes in larvae round (0), eyes in larvae elongate, the horizontal axis longer than the vertical (1), eyes in larvae elongate, the vertical axis longer than the horizontal (2) (Baldwin & Johnson [114], 1996).
136. Head spination: head spines lacking in larvae (0), head spines present in larvae (1) (Baldwin & Johnson [115], 1996).
137. Peritoneal pigment: absent in larvae (0), single or multiple unpaired peritoneal pigment sections in larvae (1), multiple paired peritoneal pigment sections in larvae (2) (Baldwin & Johnson [116], 1996).

138. Ontogenetic reduction of large maxilla: maxilla not enlarged in larva, not greatly reduced ontogenetically (0), maxilla enlarged in larva, greatly reduced ontogenetically (1) (Baldwin & Johnson [117], 1996).
139. Ontogenetic fusion of epurals: no ontogenetic fusion of epurals (0), partial ontogenetic fusion of two epurals (1) (Baldwin & Johnson [118], 1996).

Appendix 3
Morphological Character Distribution

Distributions based on the total evidence Bayesian topology (Fig. 7, 8). Results from both ACCTRAN (A) and DELTRAN (D) optimizations are provided below. The first number represents the character, while the second indicates the state.

Node A Order Aulopiformes): 1-1^{AD}, 2-1^{A}, 16-2^{A}, 18-1^{AD}, 58-1^{AD}, 59-1^{AD}, 69-1^{A}, 70-1^{A}, 89-1^{A}, 93-1^{A}, 103-1^{AD}, 120-1^{A}, 133-1^{AD}, 137-1^{A}.
Node B (Suborder Aulopoidei): 2-1^{D}, 3-1^{A}, 21-2^{A}, 33-1^{AD}, 34-2^{A}, 69-1^{D}, 70-1^{D}, 77-1^{A}, 85-1^{A}, 88-1^{A}, 89-2^{AD}, 92-1^{AD}, 93-1^{D}, 95-3^{AD}, 97-2^{AD}, 98-1^{A}, 99-2^{A}, 104-1^{AD}, 137-2^{AD}.
Node C: 60-1^{AD}, 77-1^{D}, 120-1^{D}, 121-1^{AD}.
Node D (Family Synodontidae): 3-1^{D}, 5-1^{AD}, 16-1^{AD}, 20-2^{AD}, 21-2^{D}, 30-1^{AD}, 31-1^{AD}, 34-2^{D}, 42-1^{AD}, 43-1^{AD}, 46-1^{AD}, 52-1^{AD}, 62-1^{AD}, 84-0^{AD}, 85-1^{D}.
Node E: 4-1^{AD}, 10-1^{AD}, 44-1^{AD}, 45-1^{AD}, 49-1^{AD}, 59-2^{AD}, 71-1^{AD}, 77-1^{D}, 86-1^{AD}, 88-2^{AD}, 98-1^{D}, 99-2^{D}, 120-1^{D}.
Node F: 13-1^{AD}, 14-1^{AD}, 22-1^{AD}, 48-1^{AD}, 64-1^{AD}, 77-0^{A}, 79-3^{AD}, 91-1^{AD}, 99-1^{AD}, 110-1^{AD}, 118-1^{AD}, 120-0^{A}.
Node G: 26-1^{A}, 89-1^{D}, 105-2^{A}, 106-1^{AD}, 127-1^{AD}.
Node H (Suborder Alepisauroidei): 2-1^{D}, 16-0^{A}, 28-1^{A}, 35-1^{A}, 49-1^{AD}, 53-1^{A}, 68-1^{A}, 69-1^{D}, 70-1^{D}, 87-1^{A}, 93-0^{A}, 105-1^{D}, 118-1^{AD}, 120-1^{A}, 131-1^{AD}.
Node I (Superfamily Ipnopoidea): 26-1^{D}, 27-1^{A}, 113-2^{AD}, 128-1^{AD}, 134-1^{A}.
Node J (Epifamily Giganturoidae): 5-1^{A}, 14-1^{A}, 15-1^{A}, 41-1^{A}, 53-0^{A}, 69-2^{AD}, 76-2^{AD}, 81-2^{A}, 84-0^{AD}, 87-0^{A}, 106-0^{AD}, 127-0^{A}, 137-1^{D}, 138-1^{A}.
Node K: 5-1^{D}, 14-1^{D}, 15-1^{D}, 35-1^{D}, 96-1^{AD}, 113-3^{A}.
Node L (Epifamily Ipnopoidae): 6-1^{A}, 16-2^{A}, 27-1^{D}, 28-1^{D}, 35-0^{A}, 39-1^{AD}, 53-1^{D}, 63-2^{AD}, 68-1^{D}, 87-1^{D}, 137-0^{A}.
Node M (Family Ipnopidae): 6-2^{AD}, 7-1^{AD}, 16-3^{AD}, 47-1^{AD}, 66-1^{AD}, 67-1^{AD}, 70-0^{A}, 83-2^{AD}, 88-3^{AD}, 95-2^{A}, 105-1^{AD}, 128-2^{AD}, 129-1^{AD}, 134-1^{D}.
Node N: 23-1^{A}, 54-3^{AD}, 59-2^{A}, 84-2^{AD}, 94-1^{A}, 95-3^{AD}, 99-1^{AD}, 130-1^{AD}.
Node O: 25-1^{AD}, 29-1^{AD}, 50-1^{AD}, 116-1^{AD}.
Node P: 52-1^{A}, 83-1^{A}, 87-1^{D}, 110-1^{AD}.
Node Q (Superfamily Chlorophthalmoidea; Family Chlorophthalmidae): 6-1^{AD}, 28-1^{D}, 35-1^{D}, 51-1^{AD}, 52-1^{D}, 53-1^{D}, 60-1^{AD}, 63-1^{AD}, 65-1^{AD}, 68-1^{D}, 78-1^{AD}, 126-1^{AD}, 137-1^{D}.
Node R: 28-0^{A}, 52-2^{AD}, 64-1^{AD}, 68-0^{A}, 76-1^{AD}, 92-1^{AD}.
Node S (Superfamily Notosudoidea; Family Notosudidae): 6-1^{AD}, 24-1^{AD}, 25-1^{AD}, 26-1^{D}, 27-1^{AD}, 35-0^{A}, 38-1^{AD}, 43-1^{AD}, 53-1^{D}, 54-1^{AD}, 63-2^{A}, 72-1^{AD}, 83-2^{AD}, 95-2^{AD}, 128-1^{AD}, 129-1^{A}, 135-1^{AD}, 137-0^{A}.
Node T (Superfamily Alepisauroidea): 5-1^{AD}, 7-1^{A}, 13-1^{AD}, 14-1^{AD}, 17-1^{AD}, 18-0^{AD}, 19-1^{A}, 26-0^{A}, 28-3^{AD}, 35-1^{D}, 41-2^{AD}, 53-0^{A}, 59-0^{AD}, 65-2^{AD}, 69-2^{AD}, 82-1^{A}, 84-2^{A}, 106-0^{AD}, 107-1^{A}, 111-1^{AD}, 115-1^{AD}, 118-0^{AD}, 122-1^{AD}, 127-0^{AD}, 137-1^{D}.
Node U (Family Scopelarchidae): 19-1^{D}, 40-1^{AD}, 68-1^{A}, 82-1^{D}, 83-0^{A}, 84-1^{D}, 89-4^{AD}, 110-0^{A}, 128-3^{AD}.
Node V: 7-1^{D}, 107-0^{A}, 108-1^{AD}, 117-1^{AD}, 135-2^{AD}.
Node W: 15-2^{AD}.
Node X: 7-1^{D}, 19-2^{AD}, 36-1^{A}, 54-2^{AD}, 81-2^{A}, 83-1^{D}, 107-1^{D}, 123-1^{AD}.
Node Y (Family Evermannellidae): 8-1^{AD}, 20-1^{AD}, 25-1^{AD}, 28-2^{A}, 32-1^{A}, 39-2^{AD}, 81-3^{AD}, 82-1^{D}, 84-2^{D}, 99-2^{AD}, 101-1^{AD}, 102-1^{A}, 109-1^{AD}, 113-3^{AD}, 117-1^{AD}, 135-2^{AD}.
Node Z: 128-3^{AD}.
Node AA: 13-2^{AD}, 24-2^{AD}, 36-2^{A}, 55-1^{AD}, 56-1^{A}, 57-1^{A}, 61-1^{A}, 75-1^{A}, 76-0^{A}, 81-2^{D}, 82-0^{A}, 84-1^{A}, 88-1^{A}, 89-2^{AD}, 90-1^{A}, 112-1^{A}, 119-1^{A}, 125-1^{A}.
Node BB: 76-0^{D}, 88-4^{A}, 90-1^{D}, 119-1^{D}.
Node CC (Family Alepisauridae): 11-1^{AD}, 36-0^{A}, 65-0^{A}, 75-0^{A}, 80-1^{A}, 83-2^{A}, 98-1^{AD}, 110-0^{A}, 112-0^{A}, 124-1^{A}, 125-0^{A}.
Node DD: Molecular Data Only (no morphological data for *Magnisudis*).
Node EE: 13-1^{AD}, 15-2^{AD}, 22-1^{AD}, 24-0^{AD}, 55-0^{AD}, 56-0^{A}, 57-0^{A}, 61-0^{A}, 65-0^{D}, 73-1^{AD}, 79-2^{A}, 80-1^{D}, 81-1^{AD}, 88-4^{D}, 100-1^{AD}, 110-0^{D}, 123-2^{AD}, 124-1^{D}, 132-1^{AD}, 136-1^{AD}, 139-1^{AD}.
Node FF (Family Paralepididae): 9-1^{A}, 17-0^{AD}, 36-2^{D}, 37-1^{AD}, 56-1^{D}, 57-1^{D}, 59-1^{AD}, 61-1^{D}.
Node GG: 28-0^{A}, 79-1^{A}.

Node HH: 9-0[A], 13-1[AD], 26-1[AD], 74-2[AD], 75-0[A], 78-2[AD], 80-3[AD], 112-0[A], 123-0[AD], 125-0[A].
Node II: 9-1[D], 64-0[A], 75-1[D], 88-1[AD], 95-1[AD], 112-1[D], 125-1[D], 139-1[A].
Node JJ: 139-1[D].
Node KK: Molecular Data Only.
Node LL: 114-1[AD], 139-0[A].
Node MM: Molecular Data Only.
***Alepisaurus*:** 79-2[D], 83-3[A].
***Anotopterus*:** 3-1[AD], 54-0[AD], 56-1[D], 57-1[D], 61-1[D], 62-1[AD], 80-2[AD], 88-3[AD], 99-2[AD], 107-0[AD], 113-1[AD], 114-1[AD], 122-0[AD], 124-2[AD].
***Arctozenus*:** 32-1[AD], 79-0[A], 88-0[A], 98-2[AD].
***Aulopus* (Family Aulopidae):** 3-0[A], 12-1[AD], 16-2[D], 21-2[D], 26-1[AD], 34-2[D], 48-1[AD], 85-1[D], 88-0[A], 98-0[A], 99-0[A], 113-4[AD], 137-1[AD].
***Bathymicrops*:** 3-1[AD], 7-0[AD], 23-1[D], 54-5[AD], 88-5[AD], 89-3[AD], 91-1[AD], 94-1[D], 98-4[AD], 99-2[AD].
***Bathypterois*:** 1-2[AD], 34-1[AD], 70-0[D], 92-1[AD], 95-2[D], 110-1[AD], 113-1[AD], 120-1[AD].
***Bathytyphlops*:** 5-2[AD], 23-0[A], 70-1[A], 83-1[AD], 94-0[A], 113-0[AD], 137-1[AD].
***Bathysauroides* (Family Bathysauroididae):** 27-0[A], 28-1[D], 41-2[AD], 53-1[AD], 63-1[AD], 76-1[AD], 77-1[AD], 81-0[A], 87-1[AD], 97-2[AD], 113-3[D], 127-1[A], 138-0[A].
***Bathysauropsis* (Family Bathysauropsidae):** 6-1[D], 16-2[D], 48-1[AD], 58-0[AD], 59-0[AD], 113-3[AD].
***Bathysaurus* (Family Bathysauridae):** 16-1[AD], 27-1[D], 28-0[A], 30-1[AD], 41-1[D], 52-1[AD], 59-0[AD], 62-3[AD], 64-1[AD], 68-0[A], 79-4[AD], 81-2[D], 88-3[AD], 92-1[AD], 113-4[AD], 127-0[D], 134-1[D], 138-1[D].
***Benthalbella*:** 7-0[A], 68-1[D], 107-1[D], 110-0[D], 113-3[AD].
***Chlorophthalmus*:** 26-0[A], 30-1[AD], 77-1[AD], 83-1[D], 84-2[AD], 113-3[AD].
***Coccorella*:** 11-1[AD], 15-2[AD], 19-3[AD], 28-2[D], 32-0[A], 36-0[A], 102-0[A], 113-4[AD].
***Evermannella*:** 32-1[D], 36-1[D], 102-1[D].
***Gigantura* (Family Giganturidae):** 62-2[AD], 78-3[AD], 81-2[D], 88-5[AD], 89-3[AD], 91-2[AD], 94-2[AD], 95-2[AD], 97-1[AD], 99-2[AD], 111-1[AD], 115-2[AD], 123-2[AD], 127-0[D], 128-4[AD], 134-0[A], 138-1[D].
***Harpadon*:** 11-1[AD], 62-2[AD], 88-3[AD], 97-0[AD], 98-1[D], 113-2[AD].
***Ipnops*:** 23-1[D], 59-2[D], 69-0[AD], 77-1[AD], 87-2[AD], 94-1[D], 98-2[AD], 128-5[AD].
***Lestidiops*:** 90-0[AD], 139-1[D].
***Lestidium*:** 1-3[AD], 64-0[D], 88-0[AD].
***Lestrolepis*:** 84-2[AD], 95-2[AD], 139-1[AD].
***Macroparalepis*:** 9-1[D], 75-1[D], 88-2[AD], 95-1[D], 112-1[D], 114-1[A], 125-1[D].
***Odontostomops*:** 32-1[D], 36-1[D], 102-1[D].
***Omosudis*:** 8-1[AD], 74-1[AD], 83-2[D], 96-1[AD].
***Paralepis*:** 28-0[D], 73-1[AD], 79-1[D], 88-4[D], 90-0[AD], 113-4[AD].
***Parasudis*:** 26-1[D], 70-0[AD], 81-4[AD], 83-2[AD], 139-1[AD].
***Paraulopus* (Suborder Paraulopoidei; Family Paraulopidae):** 2-0[A], 10-1[AD], 12-1[AD], 16-2[D], 60-1[AD], 69-0[A], 70-0[A], 79-5[AD], 81-4[AD], 93-1[D], 95-2[AD], 96-1[AD], 97-1[AD], 120-1[D], 121-1[AD].
***Pseudotrichonotus* (Family Pseudotrichontidae):** 3-1[D], 7-1[AD], 10-2[AD], 15-2[AD], 16-3[AD], 21-0[A], 34-0[A], 49-1[AD], 52-2[AD], 59-2[AD], 64-1[AD], 71-1[AD], 83-1[AD], 85-0[A], 88-1[D], 98-1[D], 99-2[D], 130-1[AD].
***Rosenblattichthys*:** 79-4[AD].
***Saurida*:** 88-1[D], 98-0[A].
***Scopelarchus*:** 19-2[AD], 88-3[AD], 106-1[AD].
***Scopelarchoides*:** 102-2[AD], 137-0[AD].
***Scopelosaurus*:** 63-2[D], 129-1[D].
***Sudis* (Family Sudidae):** 36-2[D], 75-1[D], 88-1[D], 112-1[D], 125-1[D], 134-1[AD], 136-1[AD].
***Synodus*:** 18-0[AD]
***Uncisudis*:** 20-3[AD], 21-3[AD], 100-2[AD].

Author's address:
Matthew P. Davis, Division of Ichthyology, Natural History Museum and Biodiversity Institute, and Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, KS 66045-7451, U.S.A.
E-mail: mpdavis@ku.edu

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.

ISBN 978-3-89937-107-9 www.pfeil-verlag.de