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Monophyly and interrelationships of Snook and Barramundi (Centropomidae *sensu* Greenwood) and five new markers for fish phylogenetics

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ABSTRACT

Centropomidae as defined by Greenwood (1976) is composed of three genera: *Centropomus, Lates,* and *Psammoperca*. But composition and monophyly of this family have been challenged in subsequent morphological studies. In some classifications, *Ambassis*, *Siniperca* and *Glaucosoma* were added to the Centropomidae. In other studies, *Lates* + *Psammoperca* were excluded, restricting the family to *Centropomus*. Recent analyses of DNA sequences did not solve the controversy, mainly due to limited taxonomic or character sampling. The present study is based on DNA sequence data from thirteen genes (one mitochondrial and twelve nuclear markers) for 57 taxa, representative of all relevant species. Five of the nuclear markers are new for fish phylogenetic studies. The monophyly of Centropomidae *sensu* Greenwood was supported by both maximum likelihood and Bayesian analyses of a concatenated data set (12,888 bp aligned). No support was found for previous morphological hypotheses suggesting that ambassids are closely allied to the Centropomidae. Putative affinities between centropomids and *Glaucosoma*, *Niphon*, or *Siniperca* were strongly rejected by topology tests. In agreement with previous molecular hypotheses, our results place Centropomidae within a group of fishes that includes carangoids (e.g., jacks, remoras, dolphinfish, roosterfish, and cobia), flatfishes, barracudas, archerfishes, billfishes, moonfish, and threadfins. The phylogeny for the extant Centropomidae is ((*Lates*, *Psammoperca*), *Centropomus*).

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1. Introduction

The family Centropomidae groups several species of freshwater, estuarine, and marine fishes that are common in tropical and subtropical regions of the world. Many species are important food and game fish, such as the common snook (*Centropomus undecimalis*) and the barramundi (*Lates calcarifer*). The composition and monophyly of this family and its relationships to the other perciform groups have been frequently debated (e.g., Greenwood, 1976; Mooi and Gill, 1995; Otero, 2004; Regan, 1913), but Centropomidae have been consistently placed among the so-called "basal percoids" because of their generalized morphology.

In early classifications, Centropomidae often included genera such as *Ambassis* and *Glaucosoma* in addition to *Centropomus, Lates,* and *Psammoperca* (Berg, 1940; Norman, 1966; Regan, 1913). In 1976, Greenwood examined the osteology of centropomids and their allies, and suggested that ambassids and glaucosomatids should be excluded. He diagnosed a more restricted Centropomidae on the basis of two synapomorphies: (1) pored lateral-line scales extending to the posterior margin of the caudal fin, and (2) an expansion of the neural spine of the second vertebra in an "anteroposterior direction." Greenwood's classification of the Centropomidae included two subfamilies: Latinae (*Lates* + *Psammoperca*) and Centropominae (*Centropomus*) (Fig. 1a). The Latinae includes nine marine, brackish, and freshwater species distributed in the Indo-West Pacific (e.g., the barramundi, *L. calcarifer*) and Africa (e.g., the Nile perch, *Lates niloticus*). The Centropominae, on the other hand, includes a single genus with 12 species that inhabit tropical and subtropical waters of the western Atlantic and eastern Pacific Oceans. Despite defining this group explicitly, Greenwood (1976) left the family's placement among perciforms unresolved.

Evidence from new morphological character systems, fossils, and molecular data collected since Greenwood's study has been used to challenge his classification. For example, based on evidence from a single anatomical system observed in more than 150 acanthomorph families, Mooi and Gill (1995) dismissed the monophyly of Greenwood's Centropomidae. According to this study, the two subfamilies differ in the association of their epaxial musculature and dorsal-fin pterygiophores, such that species in Centropominae share a "type 0 muscle-pterygiophore association" with groups such as Ambassidae, Centrarchidae, Glaucosomatidae, Moronidae, and Percichthyidae, but Latinae share a "type 1

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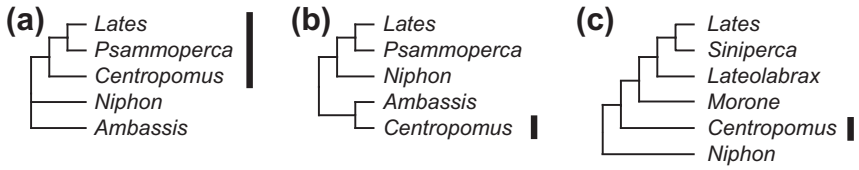

Fig. 1. Three competing hypotheses regarding the classification and phylogeny of the Centropomidae. The black bars indicate the composition of the Centropomidae proposed. (a) The Centropomidae *sensu* Greenwood (1976) is monophyletic; the interrelationships of Centropomidae amongst other percoids remains unresolved. Centropomid extant lineages include the Latinae (*Lates* + *Psammoperca*) and the monogeneric Centropominae (*Centropomus*). (b) The Centropomidae (*sensu* Greenwood, 1976) is paraphyletic: "*Ambassis* + *Centropomus*" is the sister-group of "*Niphon* + Latidae". The family "Centropomidae" is restricted to *Centropomus* (Otero, 2004). (c) The Centropomidae (*sensu* Greenwood, 1976) is polyphyletic: *Lates* is nested within a clade composed of *Lateolabrax,* †*Mioplosus*, and *Siniperca.* This latter clade plus a clade composed of *Dicentrarchus, Morone,* †*Priscacara*, and *Roccus* are the sister-group of *Centropomus* (*Ambassis* was excluded from the analysis; Whitlock, 2010).

muscle-pterygiophore association" with groups such as the Niphonidae, Percidae, and Serranidae. In Another study, Otero (2004) presented a more extensive phylogenetic analysis using 29 morphological characters from fossil and extant species that recovered a polyphyletic Centropomidae, in agreement with Mooi and Gill's (1995) conclusions. Otero (2004) listed three synapomorphies that unite *Ambassis* and *Centropomus*, and eight that unite *Lates* and *Psammoperca* with *Niphon* to the exclusion of "*Ambassis* + *Centropomus*." As a result, she restricted Centropomidae to *Centropomus* (Fig. 1b). However, both Otero (2004) and Whitlock (2010) noted that nearly half of the diagnostic characters described by Otero (2004) were not uniquely found among the taxa examined by those two studies. Essentially all of the proposed synapomorphies can be found elsewhere among other perciform taxa. In spite of this, most modern classifications recognize a separate family Latidae and a monogeneric Centropomidae (Froese and Pauly, 2010; Nelson, 2006). Whitlock's (2010) study, however, examined the interrelationships of †*Mioplosus* and †*Priscacara* among the "percoids"/moronoids, providing a different perspective on the limits and relationships of the Centropomidae. Whitlock recovered *Lates* in a clade with *Lateolabrax,* †*Mioplosus*, and *Siniperca*, which was sister to a clade composed of *Dicentrarchus*, *Morone*, †*Priscacara*, and *Roccus* (Fig. 1c). Together, these two clades were recovered as the sister group of Centropomidae (*sensu stricto*). In addition to these three competing hypotheses (Fig. 1), other anatomical studies have proposed alternatives (summarized in Table 1), including the placement of *Niphon* and/or *Siniperca* in Centropomidae (Rivas and Cook, 1968; Waldman, 1986).

While the classification of centropomids remains contentious among morphological studies, no analyses of molecular data have been designed to solve the controversy so far. Based solely on mitochondrial evidence, Tringali et al. (1999) inferred relationships among the 12 species of *Centropomus*. Using a combination of mitogenomic data and three nuclear markers, Little et al. (2010) found a close relationship between *Lates calcarifer* and the Carangidae; however, no species of *Centropomus* were examined in their study. One molecular study, aimed at inferring the interrelationship of gerreid fishes using two nuclear and two mitochondrial markers (Chen et al., 2007), has recovered the clade *Lates* + *Centropomus*. However, taxonomic sampling was limited, both within Centropomidae (two species, one for each genus) and among percomorphs (excluding most of the controversial taxa such as *Niphon, Glaucosoma*, and *Siniperca*). Three large-scale molecular studies that examined nuclear sequences (<5 loci) from a large number of acanthomorph species included only a handful of representatives of *Lates* and *Centropomus* (Li et al., 2009; Smith and Craig, 2007; Smith and Wheeler, 2006). While none of these studies recovered a monophyletic Centropomidae, *Lates* and *Centropomus* were placed relatively close in their topologies. Most noteworthy, these large molecular phylogenies have shown that centropomids are unexpectedly nested in a group ("clade L" sensu Chen et al., 2003; or "Carangiomorpha" sensu Li et al., 2009) that contains more "derived percoid" or unrelated "percomorph" taxa such as Pleuronectiformes (flatfishes), Sphyraenidae (barracudas), Toxotidae (archerfishes), Xiphiidae (swordfish), Leptobramidae (Beachsalmon), Menidae (moonfishes), Polynemidae (threadfins) and Carangoidea *sensu* Smith-Vaniz (1984; including the families Carangidae, Echeneidae, Coryphaenidae, Rachycentridae, and Nematistidae).

In contrast to previous morphological and molecular analyses, the present study combines dense taxon sampling within Centropomidae and related taxa with extensive molecular character sampling with the goal of testing the monophyly of Greenwood's (1976) Centropomidae and assessing the placement of this family among percomorphs. In total, sequence data from 13 genes (12,888 aligned bp), including mitochondrial 16S and twelve nuclear markers (five new developed for this study) were analyzed to investigate the limits and relationships of the centropomids. Specifically, our objectives are (1) to delimit the Centropomidae and test previous hypotheses about the composition of the Centropomidae and (2) to investigate the interrelationships between the Centropomidae and the other percomorphs in a broad taxonomic-sampling scheme.

2. Material and methods

2.1. Taxon sampling

Within Centropomidae, three species of *Lates*, *Psammoperca waigiensis,* and four species of *Centropomus* were sampled (Table 2). Three species of *Ambassis*, two specimens of *Niphon spinosus, Glaucosoma,* and *Siniperca* were included to test previous morpho-

Table 1
Alternative definitions of the Centropomidae and its interrelationships.

Hypothesis	Literature
The Centropomidae is monophyletic, with its phylogeny as ((*Lates*, *Psammoperca*), *Centropomus*)	(Greenwood, 1976; Nelson, 1994)
The Centropomidae is polyphyletic; *Lates* and *Psammoperca* belong to a separate family, Latidae	(Mooi and Gill, 1995; Otero, 2004; Smith and Craig, 2007)
Centropomus is grouped with *Ambassis*; and *Lates* is closely related to *Niphon*	(Otero, 2004)
Ambassis and *Glaucosoma* also are members of the Centropomidae in addition to *Lates*, *Psammoperca* and *Centropomus*	(Norman, 1966; Regan, 1913)
Ambassis belongs to *Centropomidae*, but *Glaucosoma* belongs to a monotypic family of its own	(Berg, 1940; Greenwood et al., 1966; Nelson, 1984)
Niphon spinosus is placed in the Centropomidae	(Rivas and Cook, 1968)
Siniperca also is a member of the Centropomidae	(Waldman, 1986)

Table 2
Taxon sampling and sequences collected.

Family	Genus	Species	16S	ficd	KBTBD4	KIAA1239	myh6	plagl2	RAG1	RIPK4	sidkey	SLC10A3	sreb2	zic1	znf536
Cyprinidae	*Danio*	*rerio*	NC_002333	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl
Polymixiidae	*Polymixia*	*japonica*	NC_002648	This study			EU001926	EU366682	AY308765	This study	This study	This study	This study	EU001893	
Gasterosteidae	*Gasterosteus*	*aculeatus*	NC_003174	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl
Tetradontidae	*Takifugu*	*rubripes*	NC_004299	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl
Tetradontidae	*Tetraodon*	*nigroviridis*	NC_007176	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl	Ensembl
Glaucosomatidae	*Glaucosoma*	*hebraicum*	This study	This study	This study	This study		This study	This study	This study	This study	This study	This study	This study	This study
Howellidae	*Howella*	*brodiei*	This study	This study	This study	This study	GU368868	GU368849	GU368831	This study	GU368811	This study	GU368776	GU368719	This study
Lateolabracidae	*Lateolabrax*	*japonicus*	This study	This study	This study	This study	GU368853	GU368835	GU368815		GU368798	GU368780	GU368761	GU368704	
Moronidae	*Dicentrarchus*	*labrax*	This study	This study	This study	This study	GU368857	GU368839	GU368819	This study	GU368802	GU368784	GU368765	GU368708	This study
Moronidae	*Morone*	*chrysops*	This study	This study	This study	This study	EF032930	EF033021	GU368823	This study	GU368806	GU368788	GU368768	EF032917	This study
Percichthyidae	*Percichthys*	*trucha*	This study	This study	This study	This study	GU368852	GU368834	GU368814	This study	GU368797	GU368779	GU368760	GU368703	This study
Sinipercidae	*Siniperca*	*chuatsi*	This study	This study	This study	This study	GU368862	GU368843	GU368825	This study	GU368808	GU368790	GU368770	GU368713	
Percidae	*Perca*	*flavescens*	This study		This study	This study	GU368859	GU368840	GU368821	This study	GU368804	GU368786	GU368766	GU368710	This study
Centrarchidae	*Micropterus*	*dolomieu*	This study	This study	This study	This study	GU368856	GU368838	GU368818	This study	GU368801	GU368783	GU368764	GU368707	This study
Centrarchidae	*Micropterus*	*salmoides*	This study	This study	This study	This study	GU368870	GU368851	GU368833	This study	GU368813	GU368796	GU368778	GU368721	This study
Sciaenidae	*Sciaenops*	*ocellatus*	This study	This study	This study		GU368869	GU368850	GU368832	This study	GU368812	GU368795	GU368777	GU368720	This study
Priacanthidae	*Pristigenys*	*alta*	This study	This study	This study	This study	GU368860	GU368841	GU368822	This study	GU368805	GU368787	GU368767	GU368711	This study
Epinephelidae	*Epinephelus*	*maculatus*	This study	This study	This study	This study	This study	This study	This study	This study		This study	This study	This study	This study
Epinephelidae	*Grammistes*	*sexlineatus*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Epinephelidae	*Liopropoma*	*rubre*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Niphonidae	*Niphon*	*spinosus – 00-1743*	This study	This study	This study		This study	This study	This study	This study		This study	This study	This study	This study
Niphonidae	*Niphon*	*spinosus – 00-1749*	This study							This study		This study	This study		
Serranidae	*Anthias*	*nicholsi*	This study		This study			This study	This study	This study		This study		This study	
Serranidae	*Holanthias*	*chrysostictus*	This study		This study	This study	GU368854	GU368836	GU368816	This study	GU368799	GU368781	GU368762	GU368705	
Serranidae	*Serranus*	*baldwini*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Ambassidae	*Ambassis*	*agrammus*	This study		This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Ambassidae	*Ambassis*	*interrupta*	This study	This study	This study	This study	This study	This study	This study	This study		This study	This study	This study	This study
Ambassidae	*Ambassis*	*macleayi*	This study		This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Soleidae	*Solea*	*solea*	This study	This study	This study	This study		This study	EF095644	This study	This study		This study	This study	
Carangidae	*Caranx*	*crysos*	This study		This study	This study	This study		This study	This study	This study	This study	This study	This study	This study
Coryphaenidae	*Coryphaena*	*hippurus*	This study	This study	This study	This study	This study	This study	EU167822	This study	This study		This study	This study	
Menidae	*Mene*	*maculata*	This study	This study	This study	This study	This study		This study	This study	This study	This study	This study	This study	This study
Polynemidae	*Polydactylus*	*octonemus*	This study	This study	This study		This study	This study	EU167863	This study	This study		This study		This study
Rachycentridae	*Rachycentron*	*canadum*	This study		This study	This study	This study	This study	This study	This study		This study	This study	This study	This study
Channidae	*Channa*	*striata*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Sphyraenidae	*Sphyraena*	*putnamae*	This study	This study		This study		This study	This study	This study	This study	This study			This study
Toxotidae	*Toxotes*	*chatareus*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Xiphioidei	*Istiophorus*	*platypterus*	This study		This study				This study	This study	This study	This study	This study	This study	This study
Anabantidae	*Ctenopoma*	*acutirostre*	This study		This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Citharidae	*Citharus*	*linguatula*	This study			This study			This study	This study					This study
Nematistiidae	*Nematistius*	*pectoralis*	This study	This study	This study		This study		EU167755	This study		This study	This study	This study	
Psettodidae	*Psettodes*	*erumei*	This study	This study	This study	This study	This study	This study	This study	This study	This study		This study	This study	This study
Centropomidae	*Centropomus*	*armatus – KU8522*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Centropomus*	*rmatus – KU8523*	This study	This study	This study		This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Centropomus*	*ensiferus – KU5843*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Centropomus*	*ensiferus – ODU480*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Centropomus*	*medius – KU8498*	This study	This study	This study	This study	This study	This study	This study	This study		This study	This study	This study	This study
Centropomidae	*Centropomus*	*medius – ODU592*	This study		This study		This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Centropomus*	*undecimalis – KU37*	This study	This study	This study	This study	This study	GU368837	GU368817	This study	GU368800	GU368782	GU368763	GU368706	This study
Centropomidae	*Lates*	*calcarifer – B10.78*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Lates*	*calcarifer – B6.28*	This study	This study	This study	This study		This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Lates*	*calcarifer – GO481*	This study		This study	This study	GU368858	This study	GU368820	This study	GU368803	GU368785		GU368709	

(*continued on next page*)

Table 2 (*continued*)

Family	Genus	Species	16S	ficd	KBTBD4	KIAA1239	myh6	plagl2	RAG1	RIPK4	sidkey	SLC10A3	sreb2	zic1	znf536
Centropomidae	*Lates*	*japonicus*	This study	This study	This study	This study		This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Lates*	*microlepis*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Psammoperca*	*waigiensis – B5.28*	This study		This study		This study	This study	This study	This study	This study	This study	This study	This study	This study
Centropomidae	*Psammoperca*	*waigiensis – ODU597*	This study	This study	This study	This study		This study		This study	This study	This study	This study	This study	
Centropomidae	*Psammoperca*	*waigiensis – WFC04-001*	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study
Percentage of missing data (%)	0	25	9	21	18	11	4	4	18	11	7	9	19		

Notes: Codes appended to the species name, such as "KU8522" are sample identifications used for the purpose of distinguishing different specimens of the same species. Ensembl indicates sequences retrieved from the Ensembl database. Sequences collected in this study are lodged in GenBank (accession numbers HQ731077–HQ731438). Sequence alignments can be obtained from the Supplementary online material.

logical hypotheses on the limits of Centropomidae. Whenever possible, multiple specimens of the same species were included to help detect potentially misidentified samples as well as cross -contamination, and for resolving species-tree gene-tree discordance. Three serranids and three epinephelids were also included to further test centropomid monophyly. Representatives of all major lineages of the serranids (*sensu* Johnson, 1983) were sampled because the centropomids have historically been allied with the serranids (Gosline, 1966; Greenwood et al., 1966; Norman, 1966; Regan, 1913) and the "serranids" been historically and recently combined and split numerous times (Jordan, 1923; Smith and Craig, 2007). Finally, 27 additional percomorphs, including the potential close relatives to the centropomids as suggested by recent molecular studies (Li et al., 2009; Little et al., 2010; Smith and Craig, 2007) were also included for the purpose of testing interrelationships. *Danio rerio* and *Polymixia japonica* were used as outgroups. In total, 57 samples were analyzed in this study (Table 2).

2.2. Molecular markers

One mitochondrial locus, 16S, and twelve nuclear gene markers were analyzed in the present study. Multiple nuclear genes could provide independent tests for results obtained with mitochondrial genes alone (Curole and Kocher, 1999). Seven of the included nuclear markers have been reported previously (Li et al., 2008; Li and Ortí, 2007; Li et al., 2007; Li et al., 2010), including recombination activating gene 1 (rag1), zic family member 1 (zic1), cardiac muscle myosin heavy chain 6 alpha (myh6), pleiomorphic adenoma protein-like 2 (plagl2), brain super conserved receptor 2 (sreb2) gene, si:dkey-174m14.3 (sidkey), and zgc:85947 (SLC10A3). The PCR conditions for these seven markers followed reports in previous studies. In addition, five new markers were developed for this study: (1) FIC domain-containing protein (ficd), (2) kelch repeat and BTB (POZ) domain containing 4 (KBTBD4), (3) LOC562320 (KIAA1239), (4) receptor-interacting serine–threonine kinase 4 (RIPK4), and (5) novel zinc finger protein Fragment (znf536). Primers and PCR annealing temperatures for these new markers are listed in Table 3.

2.3. Data collection

The DNA samples were extracted from ethanol-preserved muscle or gill tissues using the DNeasy tissue kit (Qiagen, Valencia, CA, USA). Nested-PCR was used to amplify the target genes if the first round of PCR failed to generate a clean product. In these cases, the products of the first-round PCR were diluted 20–100 times and used as template for a second PCR with a set of primers nested within the product of the first PCR. The reactions were performed in a total volume of 20 μl, including 0.1 μl TaKaRa Taq^{TM} (Takara, Mountain View, CA, USA), 2.0 μl 10 × PCR buffer (+ $MgCl_2$), 1.6 μl dNTP Mixture (2.5 mM each dNTP), 0.64 μl forward and reverse primers respectively, 0.8 μl DNA template and 14.22 μl distilled water. The PCR program consisted of a 95 °C initial heating for 30 s, 15 cycles of 98 °C for 10 s, the first annealing temperature (Tm) for 30 s and 72 °C for 45 s, 15 cycles of 98 °C for 10 s, the second Tm for 30 s and 72 °C for 45 s, followed by a final extension at 72 °C for 5 min. The PCR products were visualized on agarose gels to check the quality and size of amplification before sequencing. The DNA sequences were determined directly on the PCR products at the High-Throughput Genomics Unit (HTGU), University of Washington, using standard sequencing protocols.

Sequences were edited and assembled using software Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). Because these markers are partial exons of nuclear protein-coding genes, they were translated into amino acid sequences for quality control and for alignment using Clustal W, implemented in MEGA 4

Table 3
New nuclear markers developed for this study, with primer sequences and PCR annealing temperatures (Tm).

Marker_primer name	Primer sequence	Tm	PCR*
ficd_F166	GTSGTCCARGCGGAYCACCTCTA	6058	1st
ficd_R965	GTGCATTTGGCKATRAATCGRA		
ficd_F169	GTCCARGCGGAYCACCTCTACA	6058	2nd
ficd_R965	GTGCATTTGGCKATRAATCGRA		
ficd_F186	CTACACTAARGCCYTSGCCATCTC	6058	2nd
ficd_R941	AAGGGTCGAACRTCSCCCTCRTT		
KIAA1239_F273	GAGGCTCGAAARCTNTGGTGGCT	6058	1st
KIAA1239_R2079	GTCCACAGAARGCRTACATYCCATC		
KIAA1239_F558	GAGGTTGTTCAYTGGAGRTCKCA	6058	2nd
KIAA1239_R1719	GTCTGCTCTCAACATCCCANGTRCT		
KIAA1239_F567	CACTGGAGRTCKCACAARGATGT	6058	2nd
KIAA1239_R1609	AGCGGCAATCTYTCWGGRCTGTAGGT		
kbtbd4_F79	TGTGAYGAGGACGAYGCSATCAG	6058	1st
kbtbd4_R861	TCAGGCCAGWACRAACTGCCAGT		
kbtbd4_F85	GAGGACGAYGCSATCAGYGT	6058	2nd
kbtbd4_R847	ACTGCCAGTTYGTRAGSAGGATTTT		
kbtbd4_F97	ATCAGTGTGMGCGGNCAGAACAG	6058	2nd
kbtbd4_R776	AAAGTGTTCGCRTCNCCTTTCTT		
znf536_F1	ATGGAGGACTCYAGTTTGTG	5452	1st
znf536_R1532	AGGAGCGATCGYTTYTCATTTTC		
znf536_F9	CTCCAGTTTGTGTCTYGGYGT	5553	2nd
znf536_R1469	TTTCCTAACATTTCYTTYTCCTTCAT		
znf536_F78	AAACGGCCGCTATCCNATMAG	5553	2nd
znf536_R1243	CCARCTTGTTGAGATGNACCTTCAT		
RIPK4_F57	GCCAAGTTGATGAAGATCCTVCAG	5452	1st
RIPK4_R880	CCCTCTTCTATCAGCATYTTRACTGT		
RIPK4_F65	GATGAAGATCCTVCAGCCTCA	5856	2nd
RIPK4_R766	AGACGAGARGTGCTGGTGTG		

* PCR: 1st indicates primers for the first-round PCR; 2nd denotes primers for the nested-PCR.

(Tamura et al., 2007). Subsequently, the aligned sequences were back-translated to nucleotide sequences for further analysis.

The size of the alignment, number of variable site, number of parsimony informative sites, and average *p*-distance among all taxa for each gene were calculated using MEGA 4. The homogeneity of base composition was tested for each gene using Chi-square test implemented in PAUP* (Swofford, 2003).

2.4. Phylogenetic methods

Maximum likelihood tree searches were conducted with TreeFinder (Jobb, 2008) and RAxML (Stamatakis et al., 2005). Bootstrap analysis with 1000 pseudo replicates was performed to assess the statistical support for each node in the resulting phylogeny. Both partitioning by gene and codon position and by codon position only were applied to the nuclear genes while the 16S locus was not partitioned. Because the different partitioning schemes did not affect the optimal topology, no further data partitioning methods (e.g., Li et al., 2008) were tested for this dataset. The evolutionary models for each data partition were selected using ModelTest (Posada and Crandall, 1998). Bayesian analyses were carried out using MrBayes 3.1.2 (Nylander et al., 2004). The same partitioning scheme and similar models were applied in Bayesian analyses. Two independent runs, with 20 Markov Chain Monte Carlo (MCMC) chains for each run were carried out for Bayesian analyses. The heating parameter was set as "temp = 0.1" and "nswaps = 5" to improve the mixing of the MCMC chains. The runs were terminated after 10 million generations. Parameter states were sampled every 1000 generations (10,000 trees saved for each run). The majority-rule 50% consensus tree was summarized from the sampled trees after discarding the burn-in samples before reaching stationarity. Two approaches were taken to evaluate the convergence of the runs. First, the average standard deviation of split frequencies between two independent runs was monitored. A standard deviation below 0.01 was considered indicative of convergence of the two independent runs to the same stationary phase. Second, AWTY (Nylander et al., 2008) was used to evaluate the results from MCMC runs. To test different phylogenetic hypotheses, the alternative topologies were evaluated by one tailed Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa, 1999) with 50,000 RELL bootstrap replicates as implemented in TreeFinder.

In addition to analyzing all 13 genes together, ML tree searches were also performed for each individual gene to check the congruence among the gene trees and to assess the support for the limits and relationships of centropomids from each gene.

3. Results

3.1. Characterization of the sequences

Sequences were determined for most samples; only 12% of the total fragments were missing across the whole dataset, and only 0–25% of the fragments were missing for any particular gene (Table 2). The length of each marker, the number of variable sites, and the number of parsimony informative sites are listed in Table 4. The length of individual gene sequences ranged from 624 bp to 1563 bp, totaling 12,888 bp in the concatenated alignment. Among all loci tested, zic1 gene had the slowest rate of molecular evolution, while 16S had the fastest rate of evolution as assessed by their average *p*-distance. The five newly developed markers had moderate to fast rates of molecular evolution compared to the previously described nuclear markers. Chi-square test could not reject the stationarity of base composition in all markers except for sidkey ($p < 0.05$) (Table 4).

3.2. Phylogeny based on concatenated dataset

The model selected for each partition was GTR + Γ. Maximum likelihood searches using TreeFinder and RAxML as well as Bayesian analyses all resulted in the same tree except for the resolution of a few poorly supported branches outside of the Centropomidae (Fig. 2). The monophyly of the Centropomidae (*sensu* Greenwood, 1976) was supported with a bootstrap support (BS) value of 63 and a posterior probability (PP) of 0.74. The Centropomidae included the monophyletic genus *Centropomus* (BS = 100, PP = 1.0) and a clade consisting of the sister-group pairing of *Lates* and *P. waigiensis* (BS = 100, PP = 1.0). The intrarelationships among centropomid genera are congruent with Greenwood's subfamilial classification. A clade composed of the barracuda, *Sphyraena putnamae*, plus the psettodoidei flatfish, *Psettodes erumei*, was found to be the

Table 4
Characterization of the 13 molecular markers used in this study.

Markers	# bp	# var	# PI	*p*-Dis	*p* (Chi-sq)
16S	1563	921	730	0.193	0.9
myh6	792	335	258	0.099	0.9
plagl2	870	365	261	0.080	0.97
rag1	1527	794	637	0.105	0.62
sidkey	1179	560	375	0.107	0.01
SLC10A3	783	357	267	0.113	1.0
sreb2	1014	311	224	0.060	1.0
zic1	870	259	171	0.045	1.0
ficd	**705**	**303**	**230**	**0.103**	**1.0**
KBTBD4	**624**	**242**	**185**	**0.084**	**1.0**
kiaa1239	**1068**	**422**	**314**	**0.090**	**1.0**
RIPK4	**801**	**387**	**290**	**0.124**	**0.98**
znf536	**1092**	**489**	**386**	**0.092**	**1.0**

Note: #bp is the number of base pairs; #var is the number of variable sites; #PI is the number of parsimony informative sites; p-Dis is the average p-distance among all taxa; *p* (Chi-sq) is the *p*-value of Chi-square test on homogeneity of base composition. The markers in bold font were newly developed in this study.

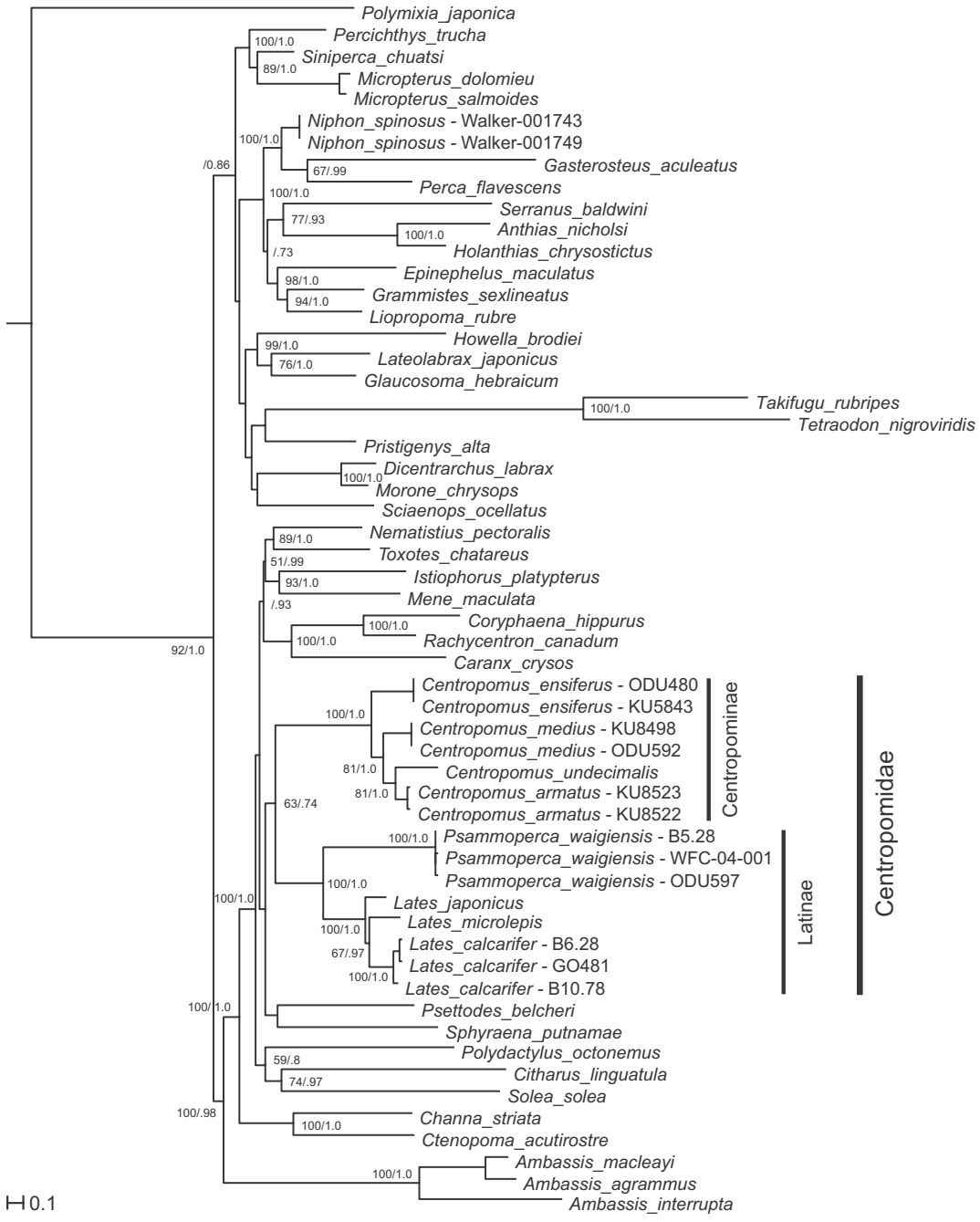

Fig. 2. The maximum likelihood tree of the Centropomidae and its putative relatives reconstructed on 13 concatenated genes (12,888 bp) using RAxML (Stamatakis et al., 2008). The tree is rooted with the outgroup *Danio rerio* (not shown). Numbers on the nodes represent bootstrap support values/posterior probabilities. Only nodes with high support values (BS > 50 and PP > 0.7) are labeled. Bayesian and TreeFinder maximum likelihood analyses resulted in an identical tree topology within Centropomidae (not shown); only a few poorly supported branches outside the Centropomidae are incongruent among different reconstruction methods.

sister group of the Centropomidae, but the support values were weak (BS < 50, PP < 70).

The SH topology test for Otero's (2004) hypothesis implying a sister-group relationship between the Latinae and *Niphon* plus the closely related *Centropomus* and *Ambassis*, was significantly rejected ($p < 0.01$; Table 5). Similarly, the previous hypotheses that suggested *Glaucosoma*, *Niphon* and/or *Siniperca* are centropomids were also significantly rejected ($p < 0.01$; Table 5). Instead, *Glaucosoma* grouped with *Lateolabrax* (BS = 76, PP = 1.0), whereas *Siniperca* was close to *Micropterus* and *Percichthys* (BS = 100, PP = 1.0). The sister-group relationship between the Ambassidae and Centropomidae also was rejected ($p < 0.05$; Table 5). The separation of *Niphon* from the serranids and epinephelids (Craig and Hastings, 2007; Smith and Craig, 2007; Whitlock, 2010) was supported. In contrast to those studies, this study recovered a clade composed of Serranidae + Epinephelidae. However, the current study did not include any scorpaenoids to test Smith and Craig's (2007) hypothesis.

3.3. Phylogenetic signal from individual genes

To dissect the phylogenetic signal supporting the relationships of the centropomids, ML trees resulting from the analysis of individual genes were reconstructed. The relationships of interest were examined in each of the individual gene tree. Four of the 13 gene trees had a monophyletic Centropomidae, but the genes that failed

Table 5
Results of SH-tests (Shimodaira and Hasegawa, 1999) on alternative hypotheses proposed for the classification of the Centropomidae.

Hypothesis	References	*p*-value
The Latinae is sister to *Niphon*; and *Centropomus* is related to *Ambassis*	Otero (2004)	<0.01
Ambassis is sister to the Centropomidae	Nelson (1984)	0.04
Glaucosoma belongs to the Centropomidae	Norman (1966)	<0.01
Niphon is placed within Latinae	Rivas and Cook (1968)	<0.01
Siniperca is the sister taxon of *Psammoperca* (Latinae)	Waldman (1986)	<0.01

to support the monophyly of the Centropomidae could not reject it either ($p > 0.05$; Table 6). None of the 13 gene trees placed *Ambassis* as the sister group of the Centropomidae. Also, a grouping of *Niphon*, *Glaucosoma,* and/or *Siniperca* with the centropomids was not observed in any of the 13 gene trees (Table 6).

4. Discussion

4.1. The monophyly of Centropomidae (sensu Greenwood, 1976)

Greenwood (1976) presented two synapomorphies to unite a Centropomidae. One character was the pored lateral-line scales extending onto the posterior margin of caudal fin. As noted by Greenwood (1976), the lateral-line scale character is shared with many groups, but it rarely reaches the margin of the caudal fin as it does in adult centropomids (exceptions include some sciaenids, moronids, and polynemids; Greenwood, 1976; pers. obs.). Although clearly not unique and unreversed, this feature remains rare among percomorphs, and it would diagnose the Centropomidae in our analysis. Given the close affinity of centropomids and polynemids in our topology (among other carangiomorph taxa), it also remains unclear whether this characteristic has single or independent origins in these two families. Greenwood's second proposed synapomorphy is an expansion of the neural spine of the second vertebra in an "anteroposterior direction". Mooi and Gill (1995) have questioned whether the expansion of the second neural-spine is a homologous condition in both centropomid subfamilies. They suggested that the centropomine second neural spine is broadly expanded over most of its length (resulting in a truncated tip of the spine); whereas, the second neural spine in latines is only expanded proximally (a condition Mooi and Gill (1995:129) describe as found in "various basal perciforms"). Similarly, Otero (2004) viewed the variation of this character as continuous and dismissed the synapomorphy. Despite our analyses recovering a monophyletic Centropomidae, we agree with Mooi and Gill (1995) and Otero (2004) that this proposed synapomorphy is poorly defined, and its homology and evidentiary value is minimally suspect, if not entirely void.

In arguing against a monophyletic Centropomidae (*sensu* Greenwood, 1976), Mooi and Gill (1995) focused on the differences in the association of the epaxial musculature and dorsal-fin pterygiophores that corresponded with the two centropomid subfamilies. Their only corroboration for the proposed taxonomic changes came from their rejection of Greenwood's (1976) proposed synapomorphies rather than the addition of compelling evidence contradicting this relationship. Unfortunately, this variation in the association of the epaxial musculature and dorsal-fin pterygiophores within Centropomidae was just one example from five families, out of approximately 60 examined families, that had variation in this association when multiple species within a family were examined. Mooi and Gill (1995) did not reject the monophyly of any of the other four families that were polymorphic for the association of epaxial musculature and dorsal-fin pterygiophores. Recently, Otero (2004) supported Mooi and Gill's (1995) separation of the Centropominae and Latinae in a phylogenetic study based on 29 morphological characters (21 of which differed between *Centropomus* and the extant latines). It is noteworthy that Otero's major assemblages were consistent with Mooi and Gill's (1995) muscle-pterygiophore association pattern. Following these two studies, the latest ichthyological consensus has been to treat these two clades as distinct families (Froese and Pauly, 2010; Nelson, 2006). More recently, broad-scale molecular studies with fewer genes sampled, more outgroups, and limited centropomid sampling (Li et al., 2009; Smith and Craig, 2007) have recovered a polyphyletic Centropomidae (but see Chen et al., 2007) grouping these taxa within a greater caragoid and pleuronectiform assemblage. No clear pattern of Mooi and Gill's (1995) muscle-pterygiophore association in relation to the results of these previous molecular studies were obvious among the centropomids and their close allies. Finally, Whitlock (2010), in a phylogenetic study of fossil and extant basal perciforms, recovered a polyphyletic Centropomidae (*sensu* Greenwood, 1976) that was not consistent with either Mooi and Gill's (1995) muscle-pterygiophore association or with any previous morphological or molecular phylogenies with regard to the relationships of the Centropominae and Latinae.

While only four out of thirteen single-partition analyses recover the monophyly of the Centropomidae, interestingly, the concatenated dataset in this study compellingly supports Greenwood's hypothesis. Although the analysis of the remaining nine individual genes did not result in a monophyletic Centropomidae, in all cases the topology tests failed to reject a sister-group relationship between latines and centropomines (Table 6). This suggests limited phylogenetic signal in these nine loci, rather than gene-tree/organismal-tree discordance. Finally, the Centropomidae provides a good case study emphasizing the increasing need for phylogenomic approaches to resolve the so-called "percomporh bush" (Smith and Craig, 2007; Li et al., 2009; Negrisolo et al., 2010).

4.2. Comments on the relationships of the centropomids and non-centropomid percomorphs

As noted above, *Glaucosoma, Niphon, Siniperca,* and/or ambassids have historically been placed in or allied with the Centrop-

Table 6
Phylogenetic signal in individual genes and their support for alternative centropomid definitions.

Phylogenetic relationships supported	16S	ficd	KBTBD4	kiaa1239	myh6	plagl2	rag1	RIPK4	sidkey	SLC10A3	sreb2	zic1	znf536
Is Centropomidae monophyletic?	N	N	Y	Y	N	N	Y	N	N	Y	N	N	N
p-value of SH-test on Monophyletic Centropomidae	0.15	0.09	–	–	0.07	0.17	–	0.25	0.06	–	1	0.09	0.09
Is Ambassis the sister-group of the Centropomidae?	N	N	N	N	N	N	N	N	N	N	N	N	N
Is Niphon related to the Latinae?	N	N	N	N/A	N	N	N	N	N/A	N	N	N	N
Does Glaucosoma belong in the Centropomidae?	N	N	N	N	N/A	N	N	N	N	N	N	N	N
Is Siniperca a member of the Centropomidae?	N	N	N	N	N	N	N	N	N	N	N	N	N/A

Notes: Y, indicates relationship observed in gene tree; N, indicates relationship not observed in gene tree. N/A, indicates relationship not applicable due to missing data.

omidae (Berg, 1940; Norman, 1966; Regan, 1913). In this study, *Glaucosoma* was placed with *Lateolabrax* with high support (BS = 76, PP = 1.0; Fig. 2). The SH-test also rejected the close relationship of *Glaucosoma* and the centropomids ($p < 0.01$). Waldman (1986) suggested that *Siniperca* should be included in the Centropomidae, and specifically pointed to affinities with the Latinae. He also listed a suite of characters associated with the antero-posterior expansion of the second neural spine, unique ornamentation of the preopercle, enclosure of the preopercular portion of the preoperculo-mandibular canal by bone, and a derived form of the symplectic. However, this proposed relationship between *Siniperca* and the centropomids was strongly rejected in this analysis ($p < 0.01$). In this study, *Siniperca* was found to be the sister taxon to the centrarchids and the percichthyids (Fig. 2), which is consistent with previous molecular studies (Li et al., 2010). Greenwood (1976) found no evidence to support a close relationship between centropomids and ambassids (Otero, 2004). Likewise, our results provide no support for Otero's (2004) hypothesis. Finally, the enigmatic *N. spinosus* was placed near *Lates* in the Centropomidae by Rivas and Cook (1968). Greenwood (1976) rejected this hypothesis, arguing that most of the diagnostic features listed by Rivas and Cook were symplesiomorphic. Later, Johnson (1983) provided four characters (most notably a unique first dorsal-spine pterygiophore) to link *Niphon* with his Epinephelinae; this relationship was supported in the molecular study of Li et al. (2009). However, it is noteworthy that the sole sequence of *Niphon* included in Li et al. (2009; rhodopsin GenBank accession number EU637934) was collected in Vanuatu and noted in the GenBank file as, "thought to be an Ambassidae [sic]; most similar to *Epinephelus*; identified as juvenile *Niphon spinosus* Santo 2006." The identification of this specimen as *Niphon* is dubious given its provisional identification, its contradictory phylogenetic position relative to all other molecular studies, and, most importantly, that *Niphon spinosus* is not known from Vanuatu, specifically, and the southern hemisphere, generally.

Otero (2004) proposed eight apomorphic characters grouping latids and *Niphon*, but she noted that many of these features are found in other perciforms as well. More recently, Craig and Hastings (2007), Smith and Craig (2007), and Whitlock (2010) have all recovered *Niphon* in a clade with the percids and notothenioids. In the present study, The SH-test significantly rejected a close relationship between *Niphon* and the centropomids ($p < 0.01$). *Niphon* was found to be the sister taxon to *Perca*, and, together with *Gasterosteus,* formed the sister clade to the serranids + epinephelids (Fig. 2). A broader taxon sampling is required to test this hypothesis.

Given the strong signal and robust results from this molecular study, future work will need to focus on increasing the taxon sampling (both within Centropomidae and among allied percomorphs) using both morphological and molecular data. In particular, it would be valuable to examine the distribution of the characters highlighted in Otero (2004) and Whitlock (2010) in a broader phylogenetic study. This is particularly relevant given the lack of variation within centropomids suggested by other broad-scale "one-system" morphological studies. For example, neither Freihofer (1963) nor Johnson (1984) reported variation in several of their examined systems (e.g., RLA pattern 9, procurrent spur presence, and interarcual cartilage presence). Further, Springer and Orrell (2004) recovered Centropominae and Latinae as a clade in their in-depth analysis of the gill-arch data described by Springer and Johnson (2004). Clearly, the most decisive step would be to complete complementary morphological and molecular datasets to examine congruence and conflict among the various data partitions to further investigate this longstanding phylogenetic question.

In our molecular phylogeny, *S. putnamae* and *P. erumei* form a clade close to the centropomids, but this relationship is marginally supported. Nonetheless, in agreement with previous molecular hypotheses, centropomids were placed within the Carangiomorpha sensu Li et al. (2009), a diverse group of percomorph fishes that, in addition to shyraenids and *Psettodes*, include the carangoids, pleuronectoidei flatfishes, toxotids, istiophorids plus *Xiphias*, *Mene*, *Leptobrama*, and polynemids (see also Clade L in Chen et al., 2003; Smith and Craig, 2007; Smith and Wheeler, 2006). The relationships among major carangiomorph groups are poorly supported and deserve further investigation.

5. Conclusions

The delimitation of the Centropomidae *sensu* Greenwood (1976), including his proposed subfamilial classification (i.e., Centropominae plus Latinae), was fully congruent with our multilocus phylogenetic assessment using 13 DNA markers (12,888 bp). Our results do not support previous suggestions that ambassids, *Glaucosoma*, *Niphon*, and/or *Siniperca* are closely allied to the Centropomidae. All these alternative hypotheses were significantly rejected by the topology tests ($p < 0.01$). Instead, our results are consistent with previous molecular studies that place the centropomids among the carangiomorphs (sensu Li et al., 2009), a well-supported clade of percomorph fishes that includes the carangoids, pleuronectiforms, sphyraenids, toxotids, istiophorids (and expectedly xiphiids), menids, and polynemids. The phylogeny for the extant Centropomidae is ((*Lates*, *Psammoperca*), *Centropomus*).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.05.004.

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