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Revision of the systematics of the cardinalfishes (Percomorpha: Apogonidae) based on molecular analyses and comparative reevaluation of morphological characters

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Abstract

Molecular analyses were conducted based on 120 of the estimated 358 species of the family Apogonidae with 33 of 40 genera and subgenera, using three gobioids and one kurtid as collective outgroups. Species of *Amioides*, *Apogon*, *Apogonichthyoides*, *Apogonichthys*, *Archamia*, *Astrapogon*, *Brephamia*, *Cercamia*, *Cheilodipterus*, *Fibramia* n. gen., *Foa*, *Fowleria*, *Glossamia*, *Gymnapogon*, *Jaydia*, *Lachneratus*, *Nectamia*, *Ostorhinchus*, *Paroncheilus*, *Phaeoptyx*, *Pristiapogon*, *Pristicon*, *Pseudamia*, *Pterapogon*, *Rhabdamia*, *Siphamia*, *Sphaeramia*, *Taeniamia*, *Verulux*, *Vincentia*, *Yarica*, *Zapogon* and *Zoramia* were present in the molecular analyses; species of *Bentuviaichthys*, *Holapogon*, *Lepidamia*, *Neamia*, *Paxton*, *Pseudamiops* and *Quinca* were absent from the analyses. Maximum-likelihood (ML), Bayesian (BA), and Maximum parsimony (MP) analyses based on two mitochondrial (12S rRNA-tRNA^{Val}-16S rRNA, ca. 1500 bp; COI, ca. 1500 bp) and two nuclear DNA (RAG1, ca. 1300 bp; ENC1, ca. 800 bp) fragments reproduced two basal clades within the monophyletic family: one including a single species, *Amioides polyacanthus*, and the other comprising species of *Pseudamia*. All the other apogonid species formed a large well-established monophyletic group, in which almost identical 12 major clades were reproduced, with phylogenetic positions of four species (*Glossamia aprion*, *Ostorhinchus margaritophorus*, *Pterapogon kauderni*, and *Vincentia novaehollandiae*) left unsettled. *Apogon sensu lato* and recent *Ostorhinchus* (excepting *O. margaritophorus*) were divided into six and three major clades, respectively. Each of the recognized clades in the family was then evaluated for morphological characters to identify synapomorphies. Based on the results of the molecular analyses and the reevaluation of morphological characters, four subfamilies were proposed within the family: Apogoninae (including most of the species in the family), Amioidinae new subfamily (including *Amioides*, and based on morphology, *Holapogon*), Paxtoninae new subfamily (including *Paxton*, based only on morphology) and Pseudamiinae (including *Pseudamia*). Within the largest subfamily Apogoninae, twelve new tribes were proposed based on the 12 molecular clades and associated morphology: Apogonichthyini, Apogonini (mainly including species of *Apogon sensu stricto*), Archamiini, Cheilodipterini, Gymnapogonini, Ostorhinchini (including striped species of recent *Ostorhinchus*), Pristiapogonini, Rhabdamiini, Sphaeramiini (mainly including barred species of traditional *Ostorhinchus*, such as *Apogonichthyoides*, *Jaydia* and *Nectamia*), Siphamiini, Veruluxini, and Zoramiini. Two additional tribes are proposed based only on morphology: Glossamiini and Lepidamiini. For each of the 14 tribes, morphological characters were described. One new genus, *Fibramia*, type species *Apogon thermalis*, recently in *Ostorhinchus*, was described supported by morphology and molecular trees. A key to all genera is provided and all valid and uncertain status species are allocated to tribes and genera.

Key words: molecular phylogeny, subfamilies, tribes, morphological diagnoses, new genus

Introduction

Cardinalfishes (Apogonidae) are one of the numerically dominant reef fish families, cryptic during daylight and active at night. Many species have documented males known to mouth brood eggs. Apogonids are widely distributed from warm temperate to tropical areas in the Pacific, Indian and Atlantic Oceans. Most species occur in coral or rocky reefs, while some species inhabit seagrass and coralline algal meadows, soft-bottom communities, estuaries and lowland freshwater. Eschmeyer & Fong (2014) report 347 valid species from the listings in the Catalog of Fishes. There are 66 available nominal genera with 32 as valid genera in the listings (Eschmeyer 2014). A summarized accumulation of available nominal and valid genus and species (Fig. 1) shows that new generic names seem to be approaching an asymptote with species names continuing to climb. Lines for available nominal and valid genera after about 1961 will probably parallel each other. The shape of the species lines after 1961 suggest many more valid species can be expected in the future. Perhaps two valid species description per year based on the past 75 years should be expected.

The family has been traditionally divided into two subfamilies: Apogoninae including most of the species (327 species), and Pseudamiinae including only 21 species (Eschmeyer & Fong 2014). Baldwin & Johnson (1999) included the following four genera in the latter subfamily: *Gymnapogon* Regan 1905, *Paxton* Baldwin & Johnson 1999, *Pseudamia* Bleeker 1865, and *Pseudamiops* Smith 1954. Two recent molecular papers, however, proposed that the genus *Gymnapogon* was nested within the clade of the Apogoninae (Thacker & Roje 2009; Cowman & Bellwood 2011).

The generic composition of the subfamily Apogoninae also varies depending on the author. Fraser (1972) provided a comprehensive family classification based on the osteological characters, in which 19 genera and 15 subgenera were recognized. At that time, the genus *Apogon* Lacepède 1801, with 10 subgenera and at least 100 valid species, was considered as the largest and likely not a monophyletic genus. Bergman (2004), in an

unpublished dissertation, performed a cladistic analysis of characters relating to the cephalic lateralis system, and concluded that the genus *Apogon sensu lato* was not monophyletic. Based on the results, she recommended elevating the subgenera within the genus to genera. Some recent authors elevated some of the subgenera to genera (for example, Randall 2005; Allen & Erdmann 2012). About 35 species formerly in the genus *Apogon* have been placed in the genera *Zoramia* Jordan 1917, *Nectamia* Jordan 1917, and *Apogonichthyoides* Smith 1949 (Greenfield *et al.* 2005; Fraser 2008; Fraser & Allen 2010). Recent molecular papers (Mabuchi *et al.* 2006; Thacker & Roje 2009; Cowman & Bellwood 2011), furthermore, demonstrated non-monophyly of the largest subgenus, *Ostorhinchus* Lacepède 1802 [referred to as a subgenus *Nectamia* in Fraser (1972): for the taxonomic details, see Gon 1987]. Mabuchi *et al.* (2006) showed that the various species of *Ostorhinchus* were arrayed into three groups distinguished by color pattern: the group with vertical bars, those with horizontal stripes, and those without either pattern. The results of these works indicate that the revision of the genus/subgenus systematics should be pursued.

To test the genus/subgenus systematics in the family, we conducted a molecular phylogenetic analysis with the broadest taxon sampling to date (Table 1), using 120 species representing about 33 of 40 genera/subgenera. Seventy-eight species of *Apogon sensu lato*, representing 13 subgenera, are included in this study (Table 1). The monophyly of apogonid systematics from family to subgenus is evaluated based on mitochondrial and nuclear DNA sequence data using three gobioids and one kurtid as collective outgroups.

TABLE 1. A comparison of previous and present molecular phylogenetic studies that sample apogonids widely. Genera formally classified as subgenera of *Apogon*, *Pterapogon*, and *Rhabdamia* are indicated with (A.), (P.), and (R.), respectively. Dash = no species sampled.

	Valid Species	Mabuchi <i>et al.</i> 2006	Thacker & Roje 2009	Cowman & Bellwood 2011	This study
Molecular markers		Mt	Mt	Mt	Mt/Nucl
Nucleotide lengths		ca. 1500 bp	ca. 3500 bp	Mostly ca. 1500 or ca. 3500 bp*	ca. 4500 bp
Genus or Subgenus					
PSEUDAMIINAE					
<i>Gymnapogon</i>	7	-	1	1	1
<i>Paxton</i>	1	-	-	-	-
<i>Pseudamia</i>	7	-	1	1	3
<i>Pseudamiops</i>	5	-	-	-	-
APOGONINAE					
<i>Amioides</i>	1	-	-	-	1
<i>Apogon</i> (A.)	50	4	3	8	19
<i>Apogonichthyoides</i> (A.)	24	4	-	4	4
<i>Apogonichthys</i>	4	-	-	-	1
<i>Archamia</i>	1	-	-	-	1
<i>Astrapogon</i>	3	-	1	2	1
<i>Bentuviaichthys</i> (R.)**	1	-	-	-	-
<i>Brephamia</i> (A.)***	1	-	-	-	1
<i>Cercamia</i>	2	-	1	1	1
<i>Cheilodipterus</i>	17	-	3	3	5
<i>Fibramia</i> (A.)	3	2	1	3	3
<i>Foa</i>	8	-	-	-	1
<i>Fowleria</i>	8	2	4	4	5
<i>Glossamia</i>	11	-	1	1	1
<i>Holapogon</i>	1	-	-	-	-

.....continued on the next page

TABLE 1. (Continued)

	Valid Species	Mabuchi <i>et al.</i> 2006	Thacker & Roje 2009	Cowman & Bellwood 2011	This study
<i>Jaydia</i> (A.)	17	3	-	3	3
<i>Lachneratus</i>	1	-	-	-	1
<i>Lepidamia</i> (A.)	4	-	-	-	-
<i>Neamia</i>	4	-	-	-	-
<i>Nectamia</i> (A.)	9	2	-	2	2
<i>Ostorhinchus</i> (A.)	92****	23	6	24	34
<i>Paroncheilus</i> (A.)	1	-	-	-	1
<i>Phaeoptyx</i>	3	-	1	3	2
<i>Pristiapogon</i> (A.)	7	3	2	3	4
<i>Pristicon</i> (A.)	3	2	1	2	2
<i>Pterapogon</i> (P.)	1	-	1	1	1
<i>Quinca</i> (P.)	1	-	-	-	-
<i>Rhabdamia</i> (R.)	4*****	-	-	-	2
<i>Siphamia</i>	23	-	1	2	5
<i>Sphaeramia</i>	2	-	1	2	2
<i>Taeniamia</i>	15	-	2	2	6
<i>Verulux</i> (R.)	1	-	1	1	1
<i>Vincentia</i>	5	-	-	-	1
<i>Yarica</i> (A.)	2	-	-	-	1
<i>Zapogon</i> (A.)	2	-	-	-	1
<i>Zoramia</i> (A.)	6	2	1	3	3
Total	358	47	33	76	120

*ca. 1500 bp for most *Apogon sensu lato*, ca. 3500 for most non-*Apogon sensu lato*

**subgenus *Bentuviaichthys* under genus *Rhabdamia* in Appendix A

***subgenus *Brephamia* under genus *Ostorhinchus* in Appendix A

****not including *Ostorhinchus (Brephamia) parvula*

*****not including *Rhabdamia (Bentuviaichthys) nigrimentum*

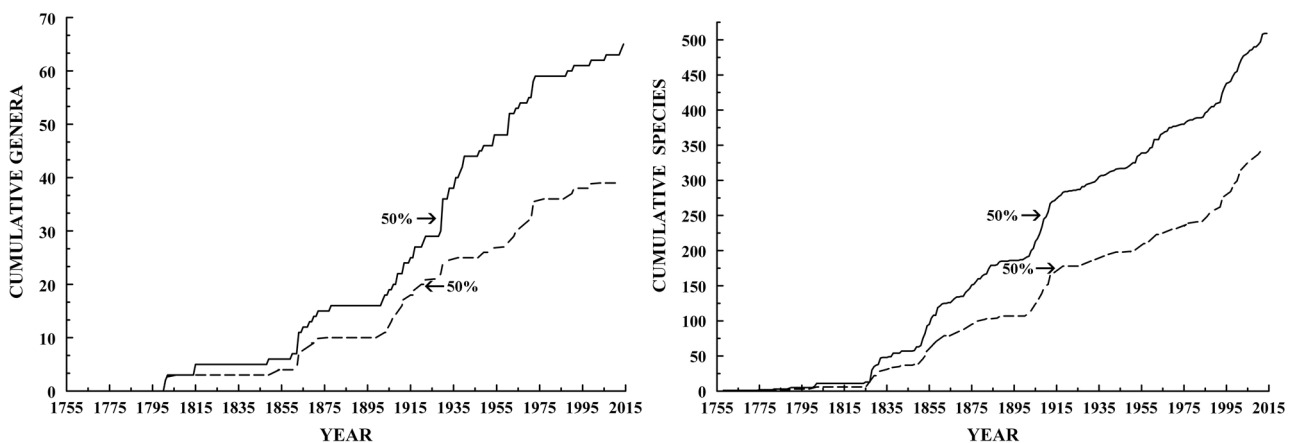


FIGURE 1. Family Apogonidae. The history of genera and species from Linnaeus (1758) to February 2014 described in the literature. Fifty percent of the nominal genera/subgenera were described after 1932. Fifty percent of the nominal species were described after 1911 (solid lines). Fifty percent of the valid genera and species were both described after 1917 (dashed lines). The data are based on information in Eschmeyer (2014): <http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>. accessed 4 February 2014, and from unpublished information by T.H. Fraser.

Based on the results of the molecular analyses and reevaluation of the known morphological data, we elevated the subgenera to genera, and proposed a new subfamily/tribe systematics. Although the present study included about one third of the recognized species, two thirds were not included yet. In addition to it, the present molecular analyses left most of the phylogenetic relationships unresolved other than the monophylies of the new subfamilies, tribes, and genera (for example, relationships among tribes remained unclear). Because of these circumstances, we focused here only on the taxonomic framework of this family, not on evolution of various interesting morphologies, such as visceral bioluminescence systems (Thacker & Roje 2009) and black guts (Fishelson *et al.* 1997). To deal with the evolution of various characters reliably, a much more resolved phylogeny with more comprehensive taxon sampling is necessary.

Material and methods

Molecular analyses

Taxon sampling. Fishes of the Apogonidae used in this study came from a number of sources, including collection by hand- and gill-nets, SCUBA diving, angling, and from museum collections (see Fricke & Eschmeyer 2014 for online museum abbreviations). One hundred twenty four individuals representing 120 species of apogonids were sequenced (Table 2). The 120 species represent 33 of 40 genera/subgenera, the following seven genera/subgenera being not included in the present molecular analyses: *Paxton* and *Pseudamiops* from the subfamily Pseudamiinae; *Bentuviaichthys* Smith 1961, *Holapogon* Fraser 1973, *Lepidamia* Gill 1863, *Neamia* Smith & Radcliffe in Radcliffe 1912, and *Quinca* Mees 1966 from the subfamily Apogoninae (see Table 1). The following four transparent species of Apogoninae ranging widely in the Pacific or Indo-Pacific were respectively represented by two individuals (#1 and 2) from distantly distributed populations: *Cercamia cladara* Randall & Smith 1988, *Gymnapogon vanderbilti* Fowler 1938, *Rhabdamia gracilis* (Bleeker 1856a), and *Verulux cypselurus* (Weber 1909) (Table 2). One voucher specimen (USNM334735; head only), was identified from a color photograph as *Fowleria* sp. from Tonga (Table 2), but this identification is considered suspect. We show it as *Fowleria* sp. in Table 2 and Figures 2–6. The specimen might represent a species of *Neamia*. DNA sequences for outgroups were all from Database (Table 2). Following the results of recent large-scale molecular analyses (Betancur-R *et al.* 2013; Near *et al.* 2013), gobioid fishes were used as outgroups. A representative of the Kurtidae is also included in the present analyses as an outgroup. A more focused search for the nearest family relationships was not part of this study.

DNA extraction, polymerase chain reaction, and sequencing. DNA extraction, amplification protocols and primers basically followed previous studies (Mabuchi *et al.* 2006; Kawahara *et al.* 2009). Two mitochondrial and two nuclear DNA fragments were sequenced: ca. 1500 bp fragment of the mitochondrial genome, including the posterior half of 12S rRNA (ca. 450 bp), entire tRNA^{Val} (ca. 70 bp) and anterior half of the 16S rRNA (ca. 1000 bp) genes (hereinafter referred to as "rRNAs" region, collectively); entire ca. 1500 bp of the mitochondrially encoded cytochrome oxidase subunit 1 (COI) gene; ca. 1300 bp of nuclear-encoded recombination activating protein 1 (RAG1) gene; ca. 800 bp of nuclear-encoded ectodermal-neural cortex 1-like protein (ENC1) gene. Eight primers were newly designed for the mitochondrial COI and two nuclear markers. Nested PCR were conducted for the nuclear DNA fragments that we could not amplify or sequence with first PCR primers. Primer sequences and PCR conditions used in this study is all presented in Table 3. Double-stranded short PCR products were purified using an Exosap-IT enzyme reaction (GE Healthcare Bio-Sciences Corp., Piscataway, NJ, USA). These were subsequently used for the direct cycle sequencing with dye-labeled terminators (BigDye terminator ver. 3.1, Applied Biosystems, Foster City, CA, USA) and using the same primers as those used in the last PCR steps. All sequencing reactions were carried out according to the manufacturer's instructions. Labeled fragments were analyzed on an ABI PRISM 3130 xl Genetic Analyzer (Applied Biosystems).

Sequence editing and alignment. Sequence editing was conducted with the computer program ATSQ ver. 5.1 (Genetyx Corp., Richmond, CA, USA). The newly determined sequences were deposited in DDBJ under the accession numbers AB889608-889686 (rRNAs), AB890002-890121 (COI), AB893355-893471 (RAG1), AB893472-893593 (ENC1) (Table 2). The obtained nucleotide sequences for "rRNAs" regions were aligned using ProAlign ver. 0.5 software (Löytynoja & Millinkovitch 2003) with default parameter settings. Regions with posterior probabilities $\leq 70\%$ were excluded from the subsequent phylogenetic analyses. Sequences for three protein-coding gene regions (mitochondrial COI and nuclear RAG1 and ENC1) were aligned using MAFFT online version (<http://mafft.cbrc.jp/alignment/server/>) and edited by eye on MacClade (Maddison & Maddison 2000), guided by the inferred amino acids from conceptual translation.

TABLE 2. Taxa included in the phylogenetic analyses, with corresponding museum numbers, collecting localities, and accession numbers.

Species	Museum no.	Locality	Mt_rRNAs	Mt_COI	Nucl_RAG1	Nucl_ENCI
Outgroup taxa						
GOBIOIDEI						
ODONTOBUTIDAE						
<i>Odontobutis potamophila</i>	—	—	ND	AY722174.1	ND	JX188987.1
<i>Percottus gleni</i>	—	—	KC292213.1	KC292213.1	JX189917.1	JX188988.1
ELEOTRIDAE						
<i>Eleotris pisonis</i>	—	—	ND	AY722157.1	JX189918.1	ND
KURTIDAE						
<i>Kurtus gulliveri</i>	—	—	ND	EU381031.1	JX190873.1	ND
Ingroup taxa						
APOGONIDAE						
PSEUDAMIINAE						
<i>Gymnapogon vanderbilti</i> #1	YCM-P45344	Japan: Ryukyu Is.	AB889608	AB890002	AB893355	AB893472
<i>Gymnapogon vanderbilti</i> #2	KU 31903	Fiji: Viti Levu	AB889609	AB890003	AB893356	AB893473
<i>Pseudamia amblyuroptera</i>	FAKU78688	Japan: Ryukyu Is.	AB889610	AB890004	AB893357	AB893474
<i>Pseudamia gelatinosa</i>	KU 31845	Fiji: Vanua Levu	AB889611	AB890005	AB893358	AB893475
<i>Pseudamia zonata</i>	ROM85488	Palau: Hatohobei	AB889612	AB890006	AB893359	AB893476
APOGONINAE						
<i>Amioides polyacanthus</i>	BPBM40786	Vanuatu	AB889613	AB890007	AB893360	AB893477
<i>Apogon atradorsatus</i>	(SIO 00-154)	Equador: Galapagos Is.	AB889614	AB890008	AB893361	AB893478
<i>Apogon aurolineatus</i>	KU30144	USA: Texas	AB889615	AB890009	AB893362	AB893479
<i>Apogon campbelli</i>	SAIAB78203	Seychelles: Mahe	AB889616	AB890010	AB893363	AB893480
<i>Apogon crassiceps</i>	USNM404711	French Polynesia	AB889617	AB890011	AB893364	AB893481
<i>Apogon doryssa</i>	NSMT-P66577	Japan: Aquarium shop	AB206128	AB890012	AB893365	AB893482
<i>Apogon dovii</i>	(SIO 00-154)	Equador: Galapagos Is.	AB889618	ND	AB893366	AB893483
<i>Apogon guadalupensis</i>	(SIO 08-59)	USA: San Clemente I.	AB889619	AB890013	AB893367	AB893484
<i>Apogon imberbis</i>	No voucher	Japan: Tokyo Sea Life Park	AB889620	ND	AB893368	AB893485

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TABLE 2. (Continued)

Species	Museum no.	Locality	Mt_rRNAs	Mt_COI	Nucl_RAG1	Nucl_ENCI
<i>Apogon maculatus</i>	KU 30207	USA: Texas	AB889621	AB890014	AB893369	AB893486
<i>Apogon pacificus</i>	(SIO 08-61)	Mexico: La Playita	AB889622	AB890015	AB893370	AB893487
<i>Apogon phenax</i>	USNM349044	Belize: Carrie Bow Cay	AB889623	AB890016	AB893371	AB893488
<i>Apogon planifrons</i>	USNM 351286	Bermuda: St. George	AB889624	AB890017	AB893372	AB893489
<i>Apogon pseudomaculatus</i>	USNM349045	Belize: Carrie Bow Cay	AB889625	ND	AB893373	AB893490
<i>Apogon retrosella</i>	(SIO 06-55-S)	Mexico: Bahía de Los Angeles	AB889626	AB890018	AB893374	AB893491
<i>Apogon seminigraeaudus</i>	FAKU 73060	Japan: Ehime Pref.	AB206129	AB890019	AB893375	AB893492
<i>Apogon semiornatus</i>	NSMT-P66576	Japan: Aquarium shop	AB206130	AB890020	AB893376	AB893493
<i>Apogon talboti</i>	CAS 219297	Fiji: Viti Levu	AB889627	AB890021	AB893377	AB893494
<i>Apogon townsendi</i>	USNM349046	Belize: Carrie Bow Cay	AB889628	AB890022	AB893378	AB893495
<i>Apogon unicolor</i>	FAKU 73056	Japan: Kochi Pref.	AB206127	AB890023	AB893379	AB893496
<i>Apogonichthyoidea cathetogramma</i>	FAKU 70752	Japan: Ehime Pref.	AB206143	AB890024	AB893380	AB893497
<i>Apogonichthyoidea melas</i>	FAKU 73129	Japan: Ryukyu Is.	AB206154	AB890025	AB893381	AB893498
<i>Apogonichthyoidea niger</i>	FAKU 70753	Japan: Ehime Pref.	AB206155	AB890026	AB893382	AB893499
<i>Apogonichthyoidea umbratilis</i>	FAKU 73710	Japan: Ehime Pref.	AB206166	AB890027	AB893383	AB893500
<i>Apogonichthys perdix</i>	USNM404723	French Polynesia	AB889629	AB890028	AB893384	AB893501
<i>Archamia bleekeri</i>	ASIZP0802132	Taiwan: Wanli	AB889630	AB890029	AB893385	AB893502
<i>Astrapogon punctulatus</i>	USNM 327993	Belize: Carrie Bow Cay	AB889631	AB890030	AB893386	AB893503
<i>Brephamia parvula</i>	FAKU 73110	Japan: Ryukyu Is.	AB889632	AB890031	AB893387	AB893504
<i>Cercamia cladara #1</i>	USNM399590	French Polynesia	AB889633	AB890032	AB893388	AB893505
<i>Cercamia cladara #2</i>	(ROM_T04050)	Palau: Hatohobei	AB889634	AB890033	AB893389	AB893506
<i>Cheilodipterus artus</i>	SAIAB 77076	Seychelles: Mahe	AB889635	AB890034	AB893390	AB893507
<i>Cheilodipterus intermedius</i>	YCM-P41580	Japan: Ryukyu Is.	AB889636	AB890035	AB893391	AB893508
<i>Cheilodipterus isostigmus</i>	KU 31915	Fiji: Viti Levu	AB889637	AB890036	ND	AB893509
<i>Cheilodipterus macrodon</i>	FAKU 73086	Japan: Ehime Pref.	AB889638	AB890037	AB893392	AB893510
<i>Cheilodipterus quinquelineatus</i>	ASIZP0912738	Taiwan: Penghu	AB889639	AB890038	AB893393	AB893511
<i>Fibramia amboinensis</i>	NSMT-P68198	Japan: Ryukyu Is.	AB206138	AB890039	AB893394	AB893512
<i>Fibramia lateralis</i>	KU 31867	Fiji: Viti Levu	AB889640	AB890040	AB893395	AB893513
<i>Fibramia thermalis</i>	FAKU 73133	Japan: Ryukyu Is.	AB206162	AB890041	AB893396	AB893514

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TABLE 2. (Continued)

Species	Museum no.	Locality	Mt_rRNAs	Mt_COI	Nucl_RAG1	Nucl_ENCI
<i>Foa leisi</i>	USNM399549	French Polynesia	AB889641	AB890042	AB893397	AB893515
<i>Fowleria aurita</i>	SAIAB76469	Seychelles: Mahe	AB889642	AB890043	AB893398	AB893516
<i>Fowleria isostigma</i>	YCM-P41602	Japan: Ryukyu Is.	AB206125	AB890044	AB893399	AB893517
<i>Fowleria</i> sp.	USNM334735	Tonga: Tongatapu Group	AB889643	AB890045	AB893400	AB893518
<i>Fowleria vatulae</i>	SAIAB76404	Seychelles: Mahe	AB889644	AB890046	AB893401	AB893519
<i>Fowleria variegata</i>	FAKU 73055	Japan: Ehime Pref.	AB206126	AB890047	AB893402	AB893520
<i>Glossamia aprion</i>	I.33454-001	Australia: Western Australia	AB889645	AB890048	AB893403	AB893521
<i>Jaydia carinatus</i>	FAKU 73706	Japan: Kochi Pref.	AB206142	AB890049	AB893404	AB893522
<i>Jaydia truncata</i>	FAKU 73386	Japan: Kochi Pref.	AB206148	AB890050	AB893405	AB893523
<i>Jaydia lineata</i>	FAKU 77532	Japan: Hiroshima Pref.	AB206153	AB890051	AB893406	AB893524
<i>Lachneratus phasmaticus</i>	BPBM 39919	Fiji: Viti Levu	AB889646	AB890052	AB893407	AB893525
<i>Nectamia fusca</i>	FAKU 72023	Japan: Ryukyu Is.	AB206150	AB890053	AB893408	AB893526
<i>Nectamia savayensis</i>	FAKU 73141	Japan: Ryukyu Is.	AB206163	AB890054	AB893409	AB893527
<i>Ostorhinchus angustatus</i>	FAKU 78681	Japan: Ryukyu Is.	AB206139	AB890055	AB893410	AB893528
<i>Ostorhinchus apogonoides</i>	FAKU 73085	Japan: Kochi Pref.	AB206140	AB890056	AB893411	AB893529
<i>Ostorhinchus aureus</i>	FAKU 78665	Japan: Ryukyu Is.	AB206141	AB890057	AB893412	AB893530
<i>Ostorhinchus compressus</i>	FAKU 73108	Japan: Ryukyu Is.	AB206144	AB890058	AB893413	AB893531
<i>Ostorhinchus cookii</i>	FAKU78676	Japan: Ryukyu Is.	AB206145	AB890059	AB893414	AB893532
<i>Ostorhinchus cyanosoma</i>	FAKU 73152	Japan: Ryukyu Is.	AB206146	AB890060	AB893415	AB893533
<i>Ostorhinchus dispar</i>	BPBM 39845	Fiji: Viti Levu	AB889647	AB890061	AB893416	AB893534
<i>Ostorhinchus doederleini</i>	FAKU 70744	Japan: Ehime Pref.	AB206147	AB890062	AB893417	AB893535
<i>Ostorhinchus endekataenia</i>	FAKU 70759	Japan: Ehime Pref.	AB206149	AB890063	AB893418	AB893536
<i>Ostorhinchus fasciatus</i>	I.34397-057	Australia: Queensland	AB889648	AB890064	AB893419	AB893537
<i>Ostorhinchus flagelliferus</i>	SAIAB65236	South Africa: KwaZulu-Natal	AB889649	AB890065	ND	AB893538
<i>Ostorhinchus fukuui</i>	BPBM 39917	Fiji: Viti Levu	AB889650	AB890066	ND	ND
<i>Ostorhinchus gularis</i>	SAIAB 82213	Off Mozambique	AB889651	AB890067	ND	AB893539
<i>Ostorhinchus hoevenii</i>	YCM-P45346	Indonesia: Sulawesi I.	AB889652	AB890068	ND	ND
<i>Ostorhinchus holotaenia</i>	SAIAB77950	Seychelles: Mahe	AB889653	AB890069	AB893420	AB893540
<i>Ostorhinchus ishigakiensis</i>	FAKU 73137	Japan: Ryukyu Is.	AB206151	AB890070	AB893421	AB893541

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TABLE 2. (Continued)

Species	Museum no.	Locality	Mt_rRNAs	Mt_COI	Nucl_RAG1	Nucl_ENCI
<i>Ostorhinchus kiensis</i>	FAKU 73707	Japan: Kochi Pref.	AB206152	ND	AB893422	AB893542
<i>Ostorhinchus luteus</i>	KU32488	USA: Saipan	AB889654	AB890071	AB893423	AB893543
<i>Ostorhinchus margaritophorus</i>	NSMT-P66575	Japan: Aquarium shop	AB889655	AB890072	AB893424	AB893544
<i>Ostorhinchus moluccensis</i>	FAKU 73700	Japan: Ehime Pref.	AB206169	AB890073	AB893425	AB893545
<i>Ostorhinchus neotes</i>	ROM85485	Palau: Hatohebei	AB889656	AB890074	AB893426	AB893546
<i>Ostorhinchus nigrofasciatus</i>	FAKU 73166	Japan: Ryukyu Is.	AB206156	AB890075	AB893427	AB893547
<i>Ostorhinchus notatus</i>	FAKU 70738	Japan: Ehime Pref.	AB206157	AB890076	AB893428	AB893548
<i>Ostorhinchus novemfasciatus</i>	NSMT-P68199	Japan: Ryukyu Is.	AB206158	AB890077	AB893429	AB893549
<i>Ostorhinchus properuptus</i>	FAKU 73708	Japan: Ehime Pref.	AB206159	AB890078	AB893430	AB893550
<i>Ostorhinchus rubrimacula</i>	CAS217460	Fiji: Viti Levu	AB889657	AB890079	AB893431	AB893551
<i>Ostorhinchus rueppellii</i>	I.33460-023	Australia: Western Australia	AB889658	AB890080	AB893432	AB893552
<i>Ostorhinchus sealei</i>	ROM85533	Palau: Hatohebei	AB889659	AB890081	AB893433	AB893553
<i>Ostorhinchus selas</i>	FAKU 73150	Japan: Ryukyu Is.	AB206164	AB890082	AB893434	AB893554
<i>Ostorhinchus semilineatus</i>	FAKU 70779	Japan: Ehime Pref.	AB206165	AB890083	AB893435	AB893555
<i>Ostorhinchus</i> sp.1	FAKU 73093	Japan: Kochi Pref.	AB206160	AB890084	AB893436	AB893556
<i>Ostorhinchus</i> sp.2	NSMT-P62210	Japan: Ogasawara Is.	AB206168	AB890085	AB893437	AB893557
<i>Ostorhinchus</i> sp.3	YCM-P41584	Japan: Ryukyu Is.	AB206161	AB890086	AB893438	AB893558
<i>Ostorhinchus taeniophorus</i>	FAKU 73709	Japan: Ehime Pref.	AB206167	AB890087	AB893439	AB893559
<i>Paroncheilus affinis</i>	No voucher?	USA: off Florida	AB889660	AB890088	AB893440	AB893560
<i>Phaeoptyx conklini</i>	USNM 327577	Belize: Carrie Bow Cay	AB889661	AB890089	AB893441	AB893561
<i>Phaeoptyx pigmentaria</i>	KU 29730	Bermuda: St. George	AB889662	AB890090	AB893442	AB893562
<i>Pristiapogon exostigma</i>	FAKU 73132	Japan: Ryukyu Is.	AB206131	AB890091	AB893443	AB893563
<i>Pristiapogon fraenatus</i>	FAKU 73175	Japan: Ryukyu Is.	AB206132	AB890092	AB893444	AB893564
<i>Pristiapogon kallopterus</i>	FAKU 73163	Japan: Ryukyu Is.	AB206133	AB890093	AB893445	AB893565
<i>Pristiapogon taeniopterus</i>	USNM404676	French Polynesia	AB889663	AB890094	AB893446	AB893566
<i>Pristicon rhodopterus</i>	FAKU 73146	Japan: Ryukyu Is.	AB206134	AB890095	AB893447	AB893567
<i>Pristicon trimaculatus</i>	FAKU 73180	Japan: Ryukyu Is.	AB206135	AB890096	AB893448	AB893568
<i>Pterapogon kauderni</i>	No voucher	Japan: Tokyo Sea Life Park	AB889664	AB890097	AB893449	AB893569
<i>Rhabdamia gracilis</i> #1	FAKU 97600	Japan: Ryukyu Is.	AB889665	AB890098	AB893450	AB893570

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TABLE 2. (Continued)

Species	Museum no.	Locality	Mt_rRNAs	Mt_COI	Nucl_RAG1	Nucl_ENCI
<i>Rhabdamia gracilis</i> #2	CAS 217455	Fiji: Vanua Levu	AB889666	AB890099	AB893451	AB893571
<i>Rhabdamia spilota</i>	YCM-P45345	Japan: Ryukyu Is.	AB889667	AB890100	AB893452	AB893572
<i>Siphamia jebbi</i>	(Tissue #4631)	Fiji: Watering Bay	AB889668	AB890101	AB893453	AB893573
<i>Siphamia majimai</i>	FAKU78690	Japan: Ryukyu Is.	AB889669	AB890102	AB893454	AB893574
<i>Siphamia roseigaster</i>	I.41858-030	Australia: New South Wales	AB889670	AB890103	ND	AB893575
<i>Siphamia</i> sp.	YCM-P45343	Japan: Ryukyu Is.	AB889671	AB890104	AB893455	AB893576
<i>Siphamia tubulata</i>	FAKU 73087	Japan: Kochi Pref.	AB889672	AB890105	AB893456	AB893577
<i>Sphaeramia nematoptera</i>	FAKU 73103	Japan: Ryukyu Is.	AB889673	AB890106	AB893457	AB893578
<i>Sphaeramia orbicularis</i>	No voucher	Japan: Aquarium shop	AB889674	AB890107	AB893458	AB893579
<i>Taeniamia biguttata</i>	KU32567	Fiji: Viti Levu	AB889675	AB890108	AB893459	AB893580
<i>Taeniamia biruensis</i>	KU 31928	Fiji : Viti Levu	AB889676	AB890109	AB893460	AB893581
<i>Taeniamia fucata</i>	CAS225043	Fiji : Viti Levu	AB889677	AB890110	AB893461	AB893582
<i>Taeniamia kagoshimanus</i>	FAKU 73504	Japan: Kochi Pref.	AB889678	AB890111	AB893462	AB893583
<i>Taeniamia sansibaricus</i>	SAIAB78070	Seychelles: Mahe	AB889679	AB890112	AB893463	AB893584
<i>Taeniamia zosterophora</i>	FAKU 73131	Japan: Ryukyu Is.	AB889680	AB890113	AB893464	AB893585
<i>Verulux cypselurus</i> #1	FAKU 97599	Japan: Ryukyu Is.	AB889681	AB890114	AB893465	AB893586
<i>Verulux cypselurus</i> #2	SAIAB78256	Seychelles: Ile du Nord	AB889682	AB890115	AB893466	AB893587
<i>Vincentia novaehollandiae</i>	I.40867-013	Australia: New South Wales	AB889683	AB890116	ND	AB893588
<i>Yarica hyalosoma</i>	ASIZP0910242	Taiwan: Pingtung	AB889684	AB890117	AB893467	AB893589
<i>Zapogon evermanni</i>	ROM85492	Palau: Hatohobei	AB889685	AB890118	AB893468	AB893590
<i>Zoramia fragilis</i>	KU 31970	Fiji: Vanua Levu	AB889686	AB890119	AB893469	AB893591
<i>Zoramia gilberti</i>	FAKU 73139	Japan: Ryukyu Is.	AB206137	AB890120	AB893470	AB893592
<i>Zoramia leptacantha</i>	FAKU 73114	Japan: Ryukyu Is.	AB206136	AB890121	AB893471	AB893593

TABLE 3. Primers used in this study and optimized PCR conditions.

Gene	Primers	Sequences	Anneal. Temp. °C	PCR step*	References**
rRNAs (1st half)	L1083-12S	5'-ACAAACTGGGATTAGATAC-3'	55		1
	H1903-16S	5'-GTAGCTCGTYTAGTTCCGGG-3'	55		1
rRNAs (2nd half)	L1803-16S	5'-AGTACCGCAAGGAAAGCTGAAA-3'	55		1
	H2590-16S	5'-ACAAGTGATTGGGCTACCTT-3'	55		1
COI (1st half)	ApCOI12	5'-CCTRCAAAMTCTTAGTTAACAGC-3'	48		This study
	ApCOIH1	5'-GCYATCATVGCYCAVACATNCC-3'	48		This study
COI (2nd half)	ApCOI2	5'-CTYTAACAACACCTATTCTGATTCCT-3'	48		This study
	ApCOIH2	5'-GGTTATGTGRYTGCTTGAAAC-3'	48		This study
RAG1	RAG1F1	5'-CTGAGCTGCAGTCAGTACCATAAGATGT-3'	55	1st	2
	RAG1R1	5'-CTGAGTCCTTGTGAGCTTCCATRAAYTT-3'	55	1st	2
ENC1	RAG1_Apg_F1	5'-CACCAGTTTGAATGGCAGCC-3'	55	1st/2nd	This study
	RAG1_Apg_R1	5'-ACTGGCGYGCRITTCATYTTCCCG-3'	55	1st/2nd	This study
	ENC1_F85	5'-GACATGCTGGAGTTTCAGGA-3'	55	1st	3
	ENC1_R982	5'-ACTTGTTRGCMACCTGGGTCAAA-3'	55	1st	3
	ENC1_F88	5'-ATGCTGGAGTTTCAGGACAT-3'	62	2nd	3
	ENC1_R975	5'-AGCMACTGGGTCAAACTGCTC-3'	62	2nd	3
ENC1_Apg_F1	ENC1_Apg_F1	5'-GAAAACYCYCAACCRTCTAACTGTC-3'	53	1st/2nd	This study
	ENC1_Apg_R1	5'-GGKAGGCATCCRGTTGCTGC-3'	53	1st/2nd	This study

*1st and 2nd are primers for the first and nested rounds of PCR, respectively.

**1, Miya & Nishida (2000); 2, Lopez *et al.* (2004); 3, Li *et al.* (2007).

Phylogenetic analyses. Maximum parsimony (MP), partitioned maximum-likelihood (ML) and Bayesian (BA) analyses were used to infer phylogenetic trees from the aligned DNA sequences. Maximum parsimony analysis was implemented in PAUP* 4.0b10 (Swofford 1998) using heuristic search methods with 1000 pseudoreplicate bootstraps, tree-bisection-reconnection branch swapping, and random addition of taxa. All sites were treated equally. Fifty percent majority-rule consensus trees were generated from all shortest trees obtained.

Partitioned maximum-likelihood (ML) analyses were performed with RAxML 7.2.6 (Stamatakis 2006), a program implementing a novel, rapid-hill-climbing algorithm. Before running the program, optimal partition model was determined for the concatenated sequence data including six data partitions using the computer program Kakusan4 (Tanabe 2011). The six partitions included those from the 12S rRNA, tRNA^{Val}, 16S rRNA, COI, RAG1, and ENC1 genes. Under the Akaike Information Criterion (AIC; Akaike 1974), the program selected "Separate_CodonNonpartitioned" as the best partition model. A rapid bootstrap analysis (-f a) and search for the best-scoring ML tree were conducted in one single program run of the RAxML, under the GTR + Gamma model with the best partition model selected by Kakusan4. The rapid bootstrap analyses were conducted with 1000 replications, with four threads running in parallel. The program finally conducted ML optimization for every 5th bootstrapped tree to search for the best-scoring ML tree.

Partitioned Bayesian (BA) analyses were conducted with MrBayes5D (available from <http://www.fifthdimension.jp/products/mrbayes5d/>), which is "fifthdimension edition" of MrBayes (Ronquist & Huelsenbeck 2003) by Akifumi S. Tanabe. Before running the program, optimal partition & substitution model was determined for the concatenated sequence data including three data partitions [because of the limitation of computer power, three (not six) partitions were used in this analyses] using the computer program Kakusan4 (Tanabe 2011). The three partitions included those of nuclear protein-coding (RAG1 and ENC1), mitochondrial protein-coding (COI), and mitochondrial RNA-coding (12S rRNA, tRNA^{Val}, and 16S rRNA) gene regions. Under the Bayesian Information Criterion (BIC), the program selected "Proportional_CodonNonpartitioned" as the best partition model with the nucleotide substitution model for each of the three partitions as follows: RAG1+ENC1, K80 + Gamma; COI, GTR + Gamma; and 12S rRNA + tRNA^{Val} + 16S rRNA, GTR + Gamma. The Markov chain Monte Carlo (MCMC) process was set so that four chains (three heated and one cold) ran simultaneously. Two independent runs were conducted for each analysis and continued for 3,000,000 cycles, with one in every 100 trees being sampled. "Stationarity" (lack of improvement in the likelihood score) was checked graphically using Tracer ver. 1.5 (available from <http://tree.bio.ed.ac.uk/software/tracer/>) and all trees and parameters before stationarity were discarded as "burn-in." All post "burn-in" trees from the two runs were pooled, and posterior probabilities of phylogenies and their internal branches were estimated on the basis of these pooled trees. Four independent analyses with the MrBayes5D were conducted, and the phylogeny with the best likelihood (lnL) was adopted as BA tree.

Based on the results of the MP, ML, and BA analyses, a strict consensus tree was constructed with Mesquite 2.75 (Maddison & Maddison 2011).

Testing alternative phylogenetic hypotheses. Alternative tree topologies were compared to the best-scoring ML tree obtained using the likelihood-based AU test (Shimodaira 2002). We first created constraint topologies considering the monophyly of alternative hypotheses using MacClade (Maddison & Maddison 2000) and conducted ML analyses using RAxML with those constraints. The resulting constrained ML trees were used to compute the per-site log likelihoods using RAxML (-f g option), and outputs were subjected to AU tests using CONSEL (Shimodaira & Hasegawa 2001). A $p < 0.05$ was considered significantly different.

Morphological examination

For each of the clades that were newly recognized by the present molecular analyses, we (principally Fraser) reevaluated morphological characters as known, and identified candidate synapomorphies for recovered clades. Some uncertainty existed for lineages not sampled and for species conflicting with morphological information. These species, subgenera and genera were identified and provisionally allocated to tribes. Morphological characters from the following published studies were used for the reevaluation: Baldwin & Johnson (1999); Bergman (2004); Fraser (1972, 1973, 2008, 2013a, 2013b, unpublished observations); Fraser & Allen (2010); Fraser & Lachner (1985); Gon (1993, 1995, 1996); Gon & Allen (2012); Gon & Randall (2003); Randall *et al.*

(1985); Vagelli (2011) and citations from these articles. Diagnoses were provided for the family, subfamilies and tribes. Keys to apogonid subfamilies and genera were presented. All valid species of apogonids were listed in Appendix A by subfamily, tribe and genus, alphabetically, along with notations for some species that have uncertain status or associated subgeneric names using Eschmeyer (2014) as a primary guide and reflect Fraser's information. A number of old names were excluded from this list as too poorly described to associate with existing names or gain the status of valid species.

Nomenclatural issues

The historical use of family, subfamily and tribal names has been recently the focus of research (van der Laan *et al.* 2013). Use of historical names and their use in modern times yield some conflict with maintaining stability and meaning. We have chosen to follow the priority guide in the online Code by the International Commission on Zoological Nomenclature (iczn.org/code) with two exceptions. Family and subfamily names used in cardinalfishes have been uneven. In the case of *Apogon* and *Gymnapogon* we have chosen to base the family and tribe names on the oldest valid genera not the oldest family names. Thus Apogonidae, the modern prevailing use, supplants Cheilodipteridae. Gymnapogonidae supplants Henicichthyidae (used once). There are detailed discussions in the remarks sections for Apogonidae and Gymnapogonini.

Results

Molecular phylogenies. The final concatenated alignments included six gene regions (four mitochondrial and two nuclear) with 4555 sites for 128 taxa. The four mitochondrial gene regions, 16S rRNA, 12S rRNA, tRNA^{Val} and COI, had 589, 305, 58 and 1554 bp, respectively, and the nuclear RAG1 and ENC1 gene regions contributed a further 1290 and 759 bp, respectively. In the each gene region, 248, 95, 31, 655, 387 and 208 bp were parsimony-informative sites, respectively. In total, 1624 bp (36% of all nucleotide sites) were parsimony-informative.

The partitioned maximum-likelihood (ML) analysis resulted in a single tree shown in Fig. 2. The result of the partitioned Bayesian (BA) analyses was summarized into a 50% majority-rule consensus tree shown in Fig. 3. Four independent searches for the BA trees resulted in four trees with the likelihood scores of $\ln L = -78150.019$, -78148.984 , -78148.927 , and -78149.880 . For each trees, likelihood values converged after 2,000,000, 500,000, 1,500,000, and 300,000 generations, respectively. The tree with the best score (-78148.927) was adopted here as the BA tree as shown in Fig. 3. The maximum parsimony (MP) analysis resulted in five most parsimonious trees, which were summarized into the two strict consensus trees shown in Figs. 4 and 5 (hereafter referred to as MP tree-A and -B, respectively). The two MP trees were largely different in the positions of *Pterapogon kauderni* Koumans 1933 and *Vincentia novaehollandiae* (Valenciennes 1832). A strict consensus tree of all the ML, BA, and MP trees is shown in Fig. 6.

In spite of many differences in topology, all of these ML, BA, and MP trees showed almost identical basal relationships and higher level groupings as clearly shown in the strict consensus tree of all the trees (Fig. 6). All of the three analyses resolved *Kurtus gulliveri* Castelnau 1878 as the sister lineage of all apogonids, and reproduced two basal clades within the apogonid clade: one including a single species, *Amioides polyacanthus* (Vaillant 1877), and the other comprising species of *Pseudamia*. All the other apogonid species formed a large well-established monophyletic group, in which almost identical 12 clades (clades I–XII in Figs. 2–6; summarized in Table 4) were reproduced, with phylogenetic positions of four species [*Glossamia aprion* (Richardson 1842), *Ostorhinchus margaritophorus* (Bleeker 1855), *Pterapogon kauderni*, and *Vincentia novaehollandiae*] left unsettled (summarized in Table 5).

The results of the statistical tests for alternative phylogenetic hypotheses (H01–16) are provided in Table 6.

Morphological synapomorphies for recovered clades. For each of the basal or major clades in the molecular trees, morphological synapomorphies were found as described later in the description of each corresponding taxon.

TABLE 4. Major clades reproduced in ML, BA and MP analyses with its support values [bootstrap probabilities (BPs) for ML and MP analyses, Bayesian posterior probabilities (PPs) for BA analysis], genera included, and correspondence to the tribes that were morphologically defined in this study.

	ML (BP)	BA (PP)	MP (BP)	Genera included	Correspondence to tribes
Clade I	100	100	97	<i>Cercamia</i> , <i>Gymnapogon</i> , <i>Lachneratus</i>	Gymnapogonini
Clade II	100	100	99	<i>Apogon</i> -1, 2, 3, <i>Astrapogon</i> , <i>Paroncheilus</i> , <i>Phaeoptyx</i> , <i>Zapogon</i>	Apogonini
Clade III	100	100	94	<i>Apogonichthys</i> , <i>Foa</i> , <i>Fowleria</i>	Apogonichthyini (minus <i>Vincentia</i>)
Clade IV	80	99	<50	<i>Apogonichthyooides</i> , <i>Jaydia</i> , <i>Nectamia</i> , <i>Ostorhinchus</i> -1, 2, <i>Sphaeramia</i>	Sphaeramini (plus <i>Ostorhinchus</i> -2)
Clade V	100	100	100	<i>Verulux</i>	Veruluxini
Clade VI	62	96	56	<i>Pristiapogon</i> , <i>Pristicon</i>	Pristiapogonini
Clade VII	99	100	78	<i>Siphamia</i>	Siphamini
Clade VIII	100	100	100	<i>Ostorhinchus</i> -4 (new genus <i>Fibramia</i>), <i>Zoramia</i>	Zoramini
Clade IX	99	100	80	<i>Rhabdamia</i> , <i>Yarica</i>	Rhabdamiini (plus <i>Yarica</i>)
Clade X	100	100	100	<i>Cheilodipterus</i>	Cheilodipterini
Clade XI	100	100	100	<i>Archamia</i> , <i>Taeniamia</i>	Archamiini
Clade XII	<50	—*	<50	<i>Brephamia</i> , <i>Ostorhinchus</i> -5	Ostorhinchini

*Clade XII was divided into the two clades, Clade XII-i and -ii, in the BA tree (see Fig. 3)

TABLE 5. Phylogenetic positions (sister clades or species) of four apogoninae species in the ML (Fig. 2), BA (Fig. 3) and MP (Figs. 4 and 5) trees. These species were included in none of the 12 major clades summarized in Table 4.

Species	Sister clade or species			MP tree-B (Fig. 5)
	ML tree (Fig. 2)	BA tree (Fig. 3)	MP tree-A (Fig. 4)	
<i>Glossamia aprion</i>	Clade II	Clade II	Clade II	<i>V. novaehollandiae</i>
<i>Ostorhinchus margaritophorus</i>	Clade VII + <i>P. kauderni</i>	polytomy with <i>P. kauderni</i> and three clades*	<i>P. kauderni</i>	Clade VII
<i>Pterapogon kauderni</i>	Clade VII	polytomy with <i>O. margaritophorus</i> and three clades*	<i>O. margaritophorus</i>	nested within Clade XII
<i>Vincentia novaehollandiae</i>	Clade III	Clade III	Clade III	<i>G. aprion</i>

* Clades VII, VIII and a large clade including clades IX, X, XI, XII-i, and XII-ii.

TABLE 6. Statistical likelihood-based AU tests between unconstrained and constrained trees.

	Alternative hypotheses tested	-ln L	Δln L	Remarks
	Unconstrained (ML tree)	93218.0486	0.0	
H01	Clade XII (<i>Ostorhinchus</i> -5 + <i>Brephamia</i>) + <i>Ostorhinchus</i> -3	93270.3625	52.3	<i>Ostorhinchus</i> -3 = <i>O. margaritophorus</i>
H02	Clade IV (Sphaeramini + <i>Ostorhinchus</i> -2) + <i>Pterapogon</i>	93272.4866	54.4	
H03	Clade XII (<i>Ostorhinchus</i> -5 + <i>Brephamia</i>) + <i>Pterapogon</i>	93281.7260	63.7	3 of the 5 MP trees (Fig. 5)
H04	<i>Glossamia</i> + <i>Vincentia</i>	93288.6390	70.6	3 of the 5 MP trees (Fig. 5)
H05	<i>Rhabdamia</i> + <i>Verulux</i>	93313.5251	95.5	Genus <i>Rhabdamia</i> in Fraser (1972)
H06	<i>Glossamia</i> + <i>Yarica</i>	93317.3888	99.3	Tribe Glossamiini
H07	Clade XII (<i>Ostorhinchus</i> -5 + <i>Brephamia</i>) + <i>Ostorhinchus</i> -2	93383.7841	165.7*	<i>Ostorhinchus</i> -2 = <i>O. hoevenii</i> , <i>O. ishigakiensis</i> , and <i>O. rueppellii</i>
H08	Clade XII (<i>Ostorhinchus</i> -5 + <i>Brephamia</i>) + <i>Ostorhinchus</i> -4	93387.1617	169.1*	<i>Ostorhinchus</i> -4 = species of new genus <i>Fibramia</i>
H09	Kurtidae (<i>Kurtus</i>) + Archamiini (<i>Archamia</i> and <i>Taentamia</i>)	93393.8116	175.8*	Prokofiev (2006)
H10	<i>Apogon sensu stricto</i> (<i>Apogon</i> -1, 2, and 3)	93407.5464	189.5*	Subgenus <i>Apogon</i> in Fraser (1972)
H11	Clade XII (<i>Ostorhinchus</i> -5 + <i>Brephamia</i>) + <i>Ostorhinchus</i> -1	93434.9751	216.9*	<i>Ostorhinchus</i> -1 = <i>Apogonichthyoides melas</i>
H12	<i>Brephamia parvula</i> + <i>Ostorhinchus neotes</i>	93439.9040	221.9	<i>O. neotes</i> is a possible <i>Brephamia</i> species
H13	Amioiinae (<i>Amioides</i>) + Cheilodipterini (<i>Cheilodipterus</i>)	93533.4964	315.4*	Smith (1961)
H14	<i>Pseudamia</i> + <i>Gymnapogon</i>	93627.6566	409.6*	Subfamily Pseudamiinae in Fraser (1972)
H15	<i>Apogon sensu lato</i>	93641.5842	423.5*	Genus <i>Apogon</i> in Fraser (1972)
H16	Recent <i>Ostorhinchus</i> (<i>Ostorhinchus</i> -1, 2, 3, 4, and 5)	94122.7441	904.7*	

Statistically significant differences $p < 0.001$ denoted by asterisks.



FIGURE 2. Phylogenetic tree from the partitioned maximum-likelihood (ML) analysis. Numbers besides internal branches indicate bootstrap probabilities (BPs) from 1000 replicates (only those of > 50% shown). Species names of recent *Ostorhinchus* [we included here *Apogonichthyoides melas* as a possible *Ostorhinchus*, following Mabuchi *et al.* (2006)] were blue, those of *Apogon sensu lato* [genus *Apogon* in Fraser (1972)] excepting the *Ostorhinchus* red, and those of genus *Rhabdamia* in Fraser (1972) green. The names of the twelve major clades (clades I to XII) within the Apogoninae were indicated on the left of the corresponding clades. Four species, which phylogenetic positions were largely different among the ML, Bayesian (BA: Fig. 3), and most parsimonious (MP: Figs. 4 and 5) trees, were indicated by arrows with asterisks.

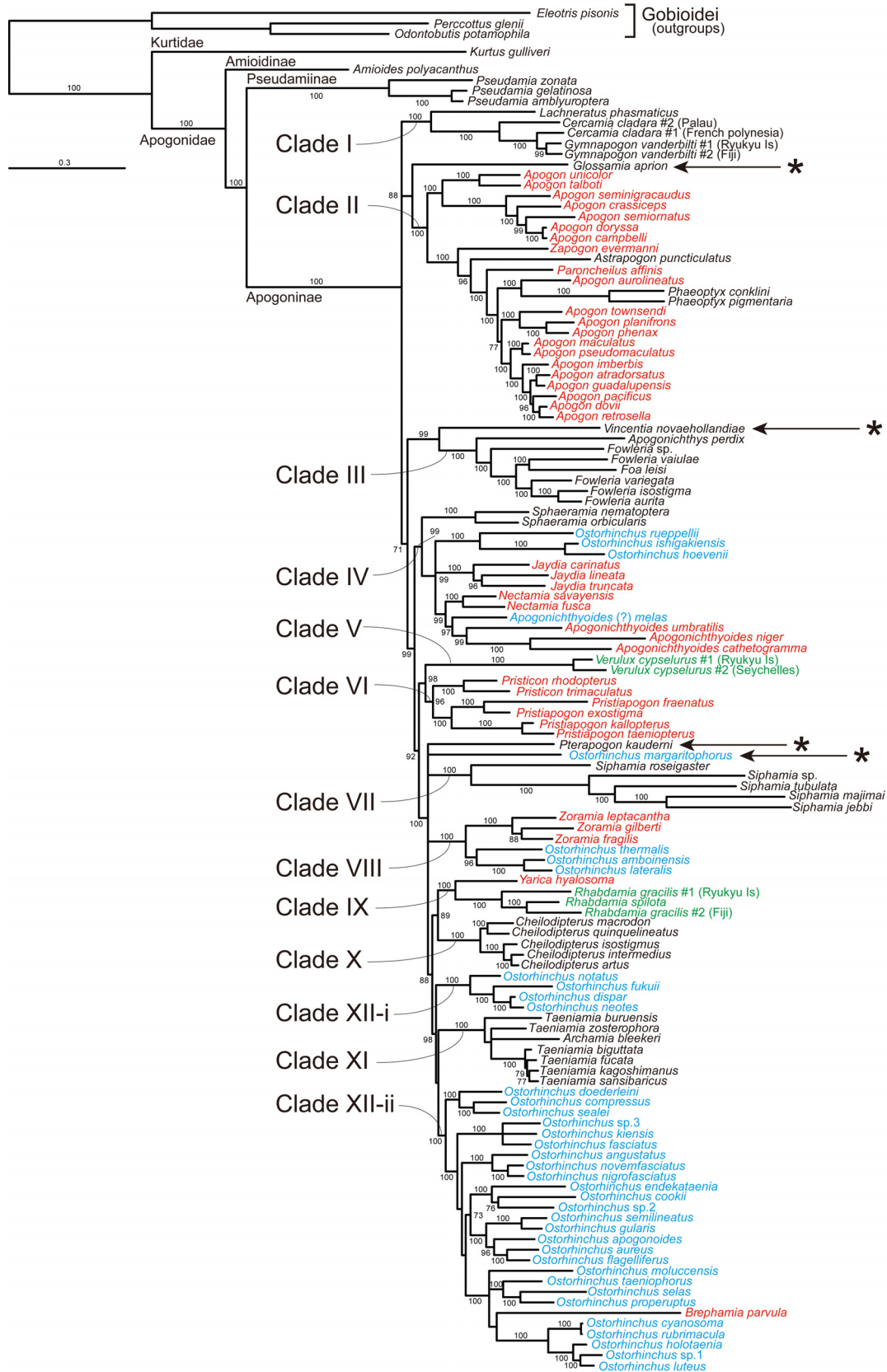


FIGURE 3. Phylogenetic tree (50% majority-rule consensus tree) from the partitioned Bayesian (BA) analysis. Numbers besides internal branches indicate Bayesian posterior probabilities (PPs: shown as percentages, only those of > 50% shown). Species names were colored as in Figure 2. The names of the twelve major clades were indicated as in Figure 2. Four species, which phylogenetic positions were largely different among the ML (Fig. 2), BA (Fig. 3), and most parsimonious (MP: Figs. 4 and 5) trees, were indicated by arrows with asterisks.

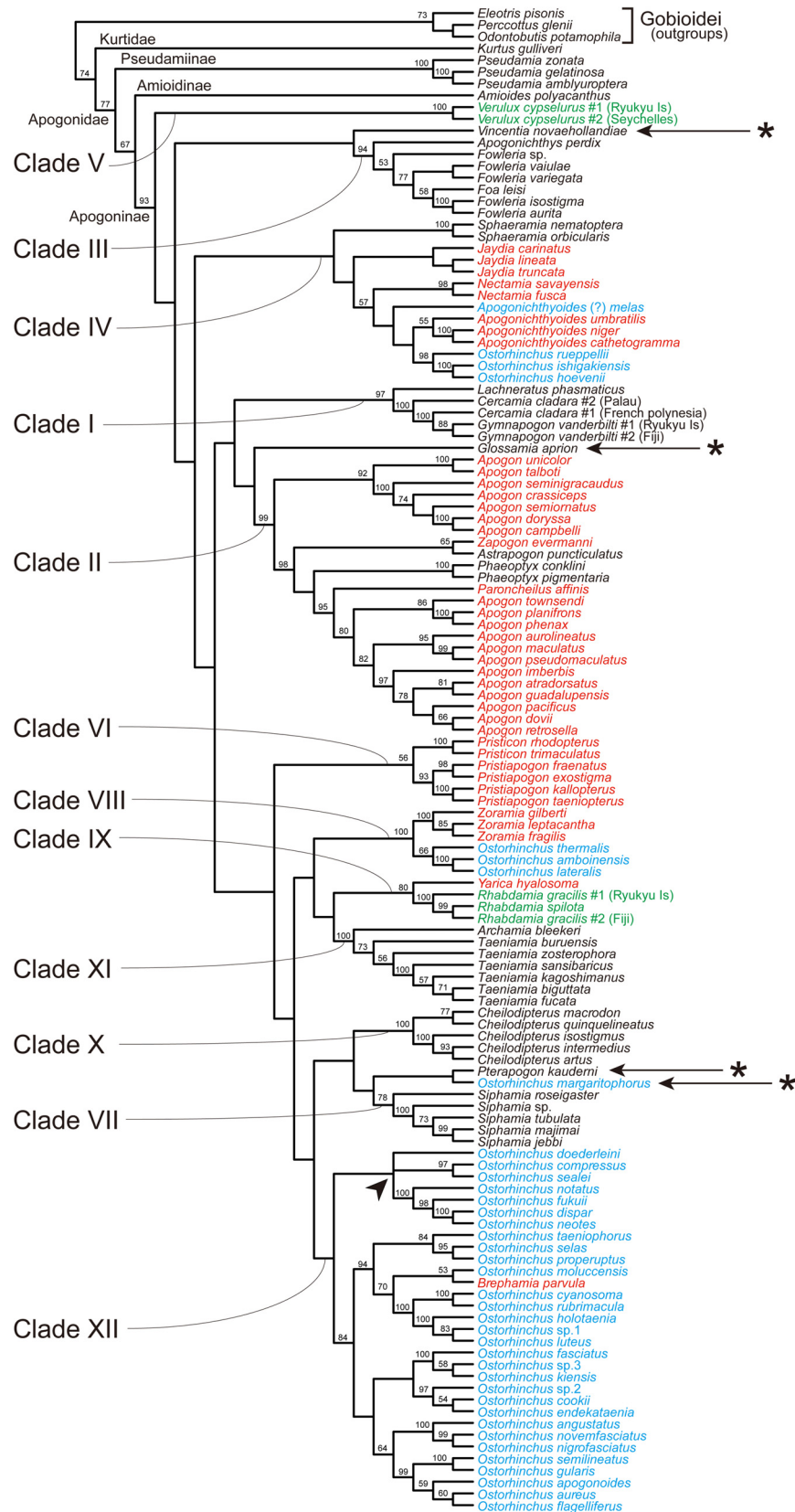


FIGURE 4. Strict consensus tree of two of the five most parsimonious (MP) trees (MP tree-A). Numbers besides internal branches indicate bootstrap probabilities (BPs) from 1000 replicates (only those of > 50% shown). Topological incongruity between the two MP trees denoted by an arrowhead. Four species, which phylogenetic positions were largely different among the ML (Fig. 2), BA (Fig. 3), and MP (Figs. 4 and 5) trees, were indicated by arrows with asterisks. Species names were colored as in Figure 2. The names of the twelve clades were indicated as in Figure 2.

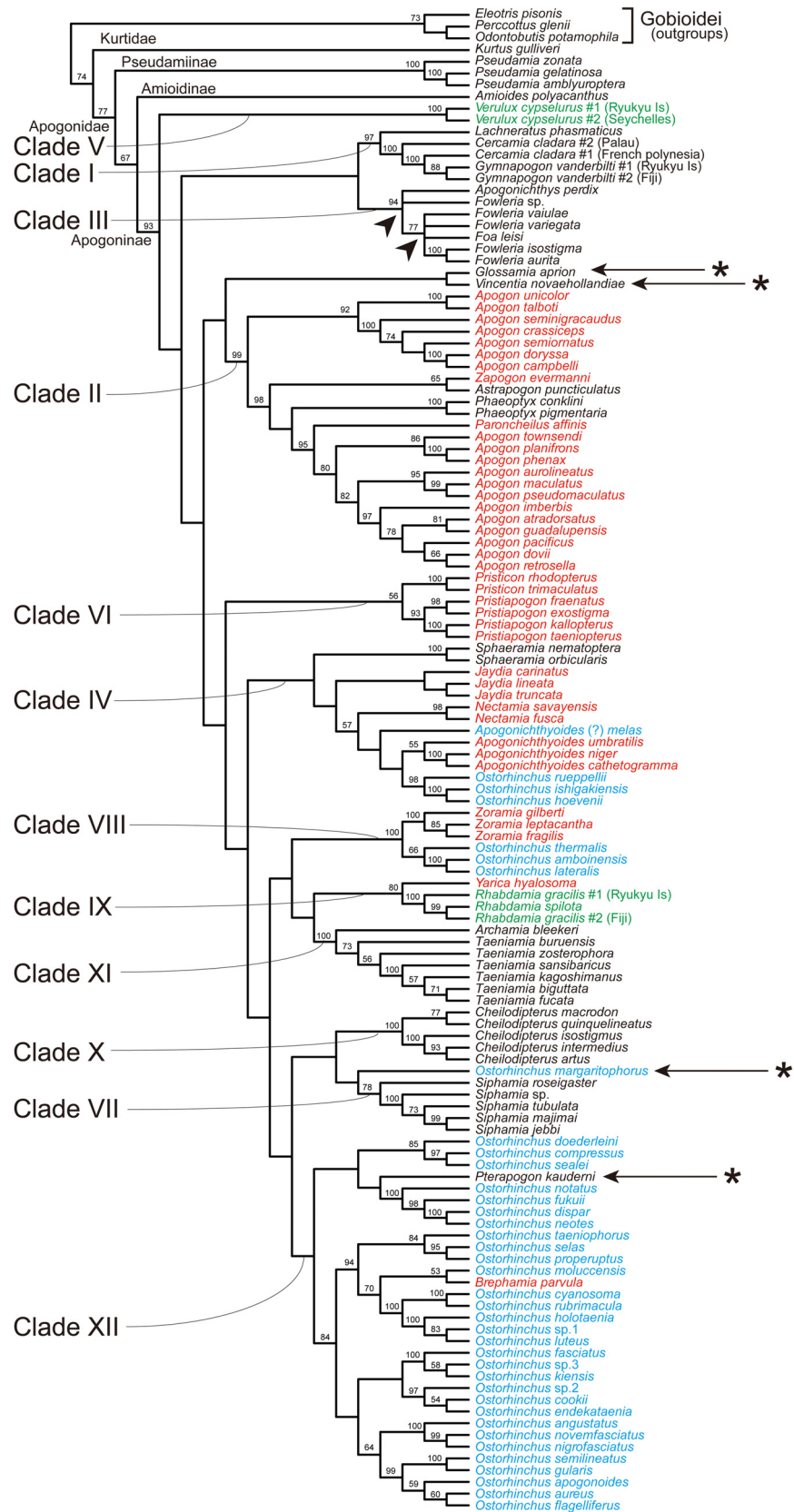


FIGURE 5. Strict consensus tree of the remaining three of the five most parsimonious (MP) trees (MP tree-B). Topological incongruities between the three MP trees denoted by arrowheads. Four species, which phylogenetic positions were largely different among the ML (Fig. 2), BA (Fig. 3), and MP (Figs. 4 and 5) trees, were indicated by arrows with asterisks. This tree was largely different from the MP tree-A (Fig. 4) in the positions of *Pterapogon kauderni* and *Vincentia novaehollandiae*.

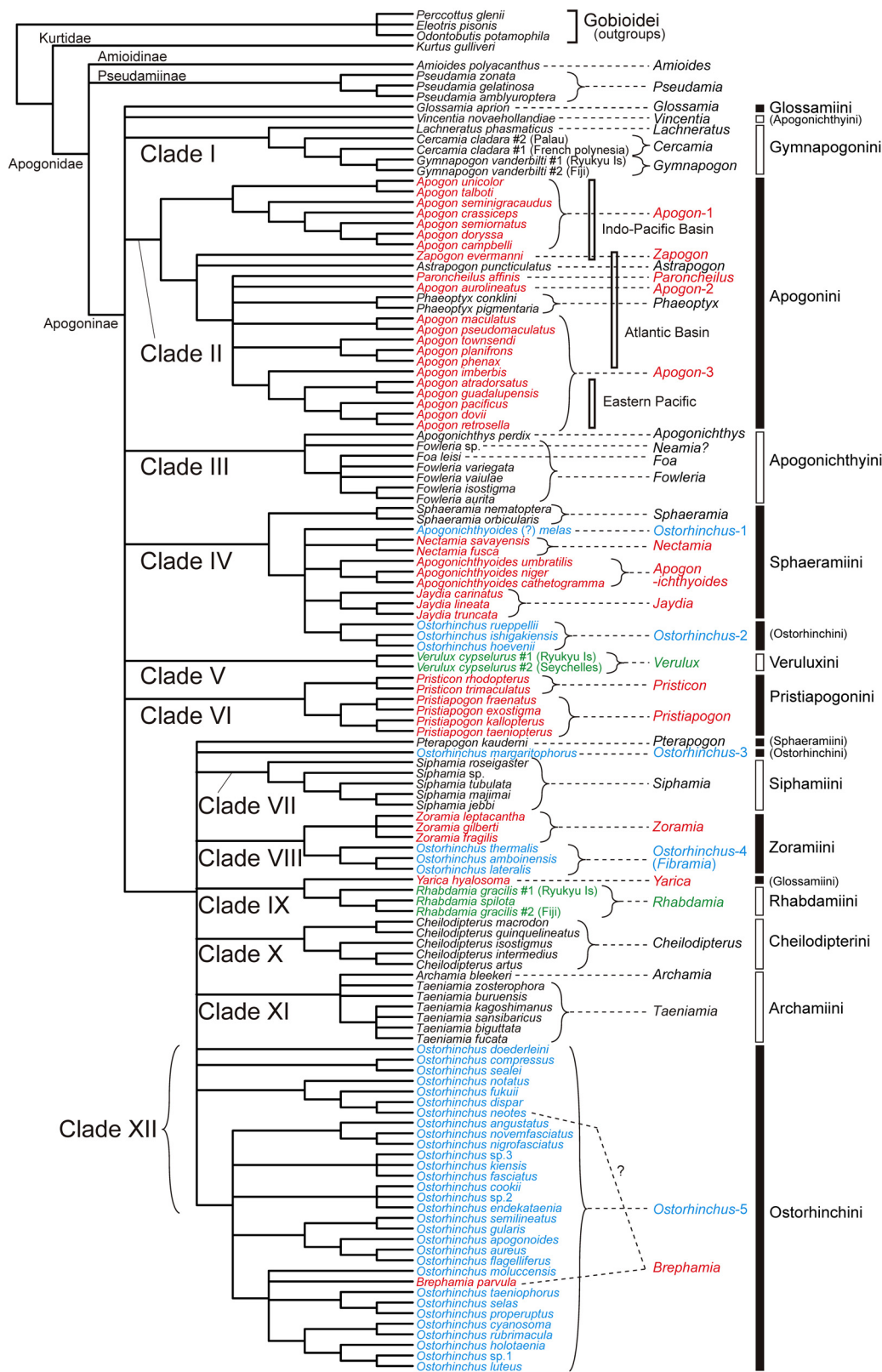


FIGURE 6. Strict consensus tree of the ML, BA and MP trees shown in Figures 2-5. Species names were colored as in Figures 2-5. The names of the twelve major clades (clades I to XII) within the Apogoninae were indicated besides the corresponding clades, while the names of the thirteen tribes (defined based on morphological characters) on the right of corresponding major and minor clades. The tribe Lepidamiini is not in the tree. Tribes with solid bars include species of *Apogon sensu lato*, and those with open bars do not include it. Geographic ranges were indicated on the right of the clades only for the species of clade II (Apogonini), all the other apogonids occurring on Indo-Pacific Basin. For the revised genus names of some species, see Appendix A.

Discussion

Basal and major clades in the molecular trees. The present molecular analyses repeatedly reproduced two basal clades within apogonid clade (Fig. 6). One was the clade of *Amioides*, and the other was that of *Pseudamia*. The phylogenetic position of *Amioides* within the family was firstly revealed in this study (there has been no molecular study on it until this study). Basal placement of *Pseudamia* within this family has, however, been already indicated in the recent two molecular studies (Thacker & Roje 2009; Cowman & Bellwood 2011).

Within the large clade of the remaining apogonids, almost identical 12 major clades were repeatedly reproduced mostly with high statistical supports (Table 4). Most of the multi-genus major clades were firstly recognized here, being only partly recognized in the previous molecular studies (Table 1).

Clade I included the species of *Cercamia*, *Gymnapogon* and *Lachneratus*, their monophyly being supported by high statistical values [100% bootstrap probability (BP) in ML analysis, 100% posterior probability (PP) in BA analysis, and 97% BP in MP analysis]. Thacker & Roje (2009) showed monophyly of the former two genera, but *Lachneratus* was absent from the analysis.

Clade II included the species of *Apogon sensu stricto*, *Astrapogon*, *Paroncheilus*, *Phaeoptyx*, and *Zapogon*, their monophyly being supported by high statistical values (100% BP, 100% PP, and 99% BP). Thacker & Roje (2009) showed monophyly of three Caribbean (and West Atlantic) species of *Apogon sensu stricto*, one species of *Phaeoptyx*, and one species of *Astrapogon* (*Paroncheilus* and *Zapogon* were absent from the analysis). In the present study, Indo-pacific species of *Apogon sensu stricto* were included, demonstrating an interesting phylogeographic pattern within the clade (Fig. 6). For details, see the remarks of the tribe Apogonini.

Clade III included the species of *Apogonichthys*, *Foa*, and *Fowleria*, their monophyly being supported by high statistical values (100% BP, 100% PP, and 94% BP). Thacker & Roje (2009) and Cowman & Bellwood (2011) showed monophyly of four species of *Fowleria*. Monophyly of the three genera was, however, firstly recognized in this study by reliable molecular data.

Clade IV included the species of *Apogonichthyoides*, *Jaydia*, *Nectamia*, and *Sphaeramia*, as well as three species of *Ostorhinchus* (*O. hoevenii*, *O. ishigakiensis*, and *O. rueppellii*) [for genus name of "*Apogonichthyoides* (?) *melas*", see the remarks of the tribe Sphaeramiini]. Although support values were partly low (80% BP, 99% PP, and <50% BP), their monophylies were recovered through all the three analyses. Among these genera, *Apogonichthyoides*, *Jaydia*, and *Nectamia* were formerly classified under *Ostorhinchus*. These traditional and recent *Ostorhinchus* species correspond to the "barred group" of *Ostorhinchus* (*Ostorhinchus* II) in Mabuchi *et al.* (2006). Considering their body colorations, monophyly between these *Ostorhinchus* species and *Sphaeramia* [absent from Mabuchi *et al.* (2006)] seems reasonable.

Clade V included only one genus, *Verulux*, which was a subgenus of *Rhabdamia* in Fraser (1972). Monophyly of the two specimens of *Verulux cypselurus* from two distantly distributed populations was supported by high statistical values (100% BP, 100% PP, and 100% BP).

Clade VI included the species of *Pristiapogon* and *Pristicon*. Although support values were not high (62% BP, 96% PP, and 56% BP), their monophyly was recovered through all the three analyses in the present study. In addition to it, it was reproduced in the three previous molecular studies (Mabuchi *et al.* 2006; Thacker & Roje 2009; and Cowman & Bellwood 2011).

Clade VII included only one genus, *Siphamia*. Monophyly of five species of the genus was supported by high statistical values (99% BP, 100% PP, and 78% BP).

Clade VIII included three species of *Ostorhinchus*, which are described as a new genus *Fibramia* below, as well as three species of *Zoramia*. Their monophyly was supported by high statistical values (100% BP, 100% PP, and 100% BP). This clade corresponds to "*Ostorhinchus* I + *Zoramia*" clade in Mabuchi *et al.* (2006).

Clade IX included species of *Rhabdamia sensu stricto* and *Yarica*, their monophyly being supported by high statistical values (99% BP, 100% PP, and 80% BP). Close relationship between the two genera was firstly recognized here, but we failed to find sound morphological evidence (for details, see the remarks of the tribes Glossamiini and Rhabdamiini).

Clade X included only one genus, *Cheilodipterus*. Monophyly of five species of the genus was supported by high statistical values (100% BP, 100% PP, and 100% BP).

Clade XI included the species of *Archamia* and *Taeniamia*, their monophyly was supported by high statistical values (100% BP, 100% PP, and 100% BP). All the members of the clade were formerly classified under *Archamia* until Fraser (2013b).

Clade XII included species of *Ostorhinchus* and *Brephamia*. This clade was shown not as a complete monophyletic, but as a partly paraphyletic group in the strict consensus tree (Fig. 6). It was clearly because this clade included Clade XI in the BA tree (Fig. 3), and *Pterapogon kauderni* in the MP tree-B (Fig. 5). The species of the Clade XII were, however, completely monophyletic in the remaining two trees, ML tree (Fig. 2) and MP tree-A (Fig. 4). Although supporting values for the monophyly of this clade was low (<50% BP both in ML and MP analyses), we are treating this group as a single clade, based on the typical color pattern (stripes on body and/or head) shared by most of the included species. This clade corresponds to the "striped group" of *Ostorhinchus* (*Ostorhinchus* III) in Mabuchi *et al.* (2006) [*Brephamia* was absent from the previous study].

Cowman & Bellwood (2011), the latest molecular study covering apogonids widely, failed to produce many major clades obtained in the present study. This previous analysis, including 76 apogonid species, was almost completely based on the sequence data from the two previous studies, Mabuchi *et al.* (2006) including 47 species and Thacker & Roje (2009) including 33 species. The two studies covered different taxa (mainly the species of *Apogon sensu lato* in the former study, while those of non-*Apogon sensu lato* in the latter study: for details, see Table 1), and used different mitochondrial genes (12S and 16S rRNA genes in the former study, while CO1, ND1, and ND2 genes in the latter study). Combining of such different datasets conducted in Cowman & Bellwood (2011) might bring many topological differences between their and our results.

Comparison with traditional subfamilial and genus/subgenus systematics. The resulting phylogenetic relationships significantly disagreed with the traditional subfamilial and genus/subgenus systematics. In particular, *Apogon sensu lato* and recent *Ostorhinchus* were divided into six (clades II, IV, VI, VIII, IX, and XII) and three (clades IV, VIII, and XII) major clades, respectively (Fig. 6), with the phylogenetic positions of *Ostorhinchus margaritophorus* left unsettled (Table 5). Monophyly of *Apogon sensu lato* (H15) and that of recent *Ostorhinchus* (H16) were both significantly rejected by the AU test (Table 6). Based on these results of the molecular analyses and reevaluation of the known morphological data (see below in details), we elevated the traditional subgenera of *Apogon sensu lato* (including *Ostorhinchus*) to genera, except for *Brephamia*. For the traditional subgenera of genus *Rhabdamia sensu* Fraser (1972), see the remarks of the tribes Rhabdamiini and Veruluxini, and for *Brephamia*, those of the tribe Ostorhinchini.

Monophyly of the subfamily Pseudamiinae in Fraser (1972) (*Pseudamia* + *Gymnapogon*) (H14) and that of *Amioides* Smith & Radcliffe in Radcliffe 1912 and *Cheilodipterus* Lacepède 1802 (H13) were both significantly rejected by the AU test (Table 6). Based on these results and the phylogenetic positions of them (Fig. 6), we proposed two new subfamilies for *Amioides* and *Pseudamia*. For details, see the remarks of the subfamilies Amioidinae and Pseudamiinae.

Proposal of a new classification system. By evaluating all previously used morphological characters, we found synapomorphies supporting newly recognized clades. Except for three of the 12 major clades (clades III, IV, and IX), each of the three basal (*Amioides*, *Pseudamia* and other apogonids) and the remaining nine of the 12 major clades had well-defined synapomorphies (for details, see below the description of each corresponding taxon). We propose a new subfamily/tribe classification system for them: the basal three clades are ranked as subfamilies (Amioidinae, Pseudamiinae and Apogoninae), and nine of the 12 major clades are recognized using tribal names as a new level of classification. The remaining three of 12 major clades also are given new tribe names with some morphologically different species excluded (clades IV and IX) or a morphologically similar and phylogenetically related species included (clade III). For details, see the remarks of the tribes Sphaeramiini, Rhabdamiini, and Apogonichthyini, respectively. In addition to the 12 new tribes (see the right column of Table 4), two new tribes (Glossamiini and Lepidamiini) are tentatively proposed for *Glossamia* Gill 1863, *Yarica* Whitley 1930 and *Lepidamia* mostly based on shared morphological characters (*Yarica* included in Glossamiini based only on morphology, while it did not form a monophyletic group with *Glossamia* in the molecular trees. For details, see the remarks of the two tribes.). Paxtoninae is also tentatively proposed to accommodate an enigmatic genus *Paxton* based only on morphology. We describe below these new taxa, discussing some of the significant findings, and refer to the results of the present molecular analyses. A new genus *Fibramia* is described for three species (formerly in *Ostorhinchus*) recovered as sister to species of *Zoramia*, both placed into the tribe Zoramiini (clade VIII). *Brephamia* is placed under the genus *Ostorhinchus* as a subgenus, and *Bentuviaichthys* under the genus *Rhabdamia*.

The new subfamily/tribe systematics with included genera was as summarized below. For the correspondences between the new tribes and major clades in molecular trees, see Fig. 6 and Table 4. Keys to all the subfamilies and

genera were provided below, and all valid and uncertain status species are allocated to tribes and genera in an Appendix A.

Family Apogonidae (38 genera)

Subfamily Amioidinae (2 genera: *Amioides*, *Holapogon*)

Subfamily Apogoninae (34 genera)

Tribe Apogonichthyini (5 genera: *Apogonichthys*, *Foa*, *Fowleria*, *Neamia*, *Vincentia*)

Tribe Apogonini (5 genera: *Apogon*, *Astrapogon*, *Paroncheilus*, *Phaeoptyx*, *Zapogon*)

Tribe Archamiini (2 genera: *Archamia*, *Taeniamia*)

Tribe Cheilodipterini (1 genus: *Cheilodipterus*)

Tribe Glossamiini (2 genera: *Glossamia*, *Yarica*)

Tribe Gymnapogonini (4 genera: *Cercamia*, *Gymnapogon*, *Lachneratus*, *Pseudamiops*)

Tribe Lepidamiini (1 genus: *Lepidamia*)

Tribe Ostorhinchini (1 genus *Ostorhinchus* including subgenus *Brephamia*)

Tribe Pristiapogonini (2 genera: *Pristiapogon*, *Pristicon*)

Tribe Rhabdamiini (1 genus: *Rhabdamia* including subgenus *Bentuviaichthys*)

Tribe Siphamiini (1 genus: *Siphamia*)

Tribe Sphaeramiini (6 genera: *Apogonichthyoides*, *Jaydia*, *Nectamia*, *Pterapogon*, *Quinca*, *Sphaeramia*)

Tribe Veruluxini (1 genus: *Verulux*)

Tribe Zoramiini (2 genera: *Fibramia*, *Zoramia*)

Subfamily Paxtoninae (1 genus: *Paxton*)

Subfamily Pseudamiinae (1 genus: *Pseudamia*)

Family, subfamily and tribal morphological diagnoses, general distribution and remarks

1. FAMILY

Family **Apogonidae** Günther 1859

Type genus *Apogon* Lacepède 1801

The following is a summary of known apogonid characteristics. Those in italics are known for almost all genera and species and expected where the general state is unknown.

Diagnosis. *One or two anal spines, first spine usually small, supernumerary in position, second spine or first anal ray in serial association with first distal and proximal-middle radials; first segmented anal ray unbranched or branched, 7–18 rays; dorsal spines VI–IX; first segmented dorsal ray unbranched, 8–19 rays; supernumerary dorsal spines 1–2; supraneurals 0–3; principal caudal fin-rays 9+8, 13–17 branched and segmented; procurrent rays unbranched and segmented or spinous; six infraorbitals, perforated openings for passage of nerve trunks to large neuromasts, lower edge of large 1st infraorbital (lachrymal) smooth, serrated or smooth along upper edges of 2nd and 3rd infraorbitals, 3rd to 5th infraorbitals with internal shelves present or absent; preopercle ridge smooth or serrate, preopercle edges smooth, serrate or with unossified lower portion; basisphenoid present, reduced or absent; vertebrae 9–10+14–16; epineurals on first two vertebrae; ribs on 3rd to 10th vertebrae or absent on 10th vertebrae; epineurals present on ribs of 3rd to 9th vertebrae or absent on some, 6th to 9th vertebrae, or absent on all ribs; ribs rod-like or variably expanded proximally; PU2 with neural crest; PU2 and PU3 with autogenous haemal spines or fused; hypurals 1–5 present, not fused or various combinations of 1+2, 3+4 or 1–4 fused, may fuse to terminal centrum, hypural 5 splint-like or absent; parhypural free or fused to hypurals 1+2; second epibranchial articulating with third pharyngobranchial; prootic included as part of the inner orbit ring or excluded by the pterosphenoids and parasphenoid; pterosphenoids medially separate; parietal separated by supraoccipital; anterior and posterior ceratohyals sutured together by a few interdigitating struts medially or without struts; perforated anterior ceratohyal or not; seven branchiostegals, anterior three ventrally followed by two on distal side of anterior ceratohyal, two on distal side of posterior ceratohyal; swim bladder simple without anterior or posterior*

modifications, a dorsal oval and ventral gas glands either simple or complex; free neuromasts on head, body and caudal fin; free medial extrascapular or fused with lateral extrascapular; scales ctenoid, spinoid, cycloid or absent; single lateral-line present from posttemporal to base of caudal fin either as pored, pitted or grooved scales, or if without scales, with linear free neuromasts; secondary lateral-line scales or linear free neuromasts on lower body present or absent; if scales on body then scales on cheek, opercle, subopercle, interopercle and urohyal regions of head, predorsal scales present or absent, scales on cheek, opercle, subopercle, interopercle and gular regions of head; if body with scales then no scales on snout, interorbit, temporal region of head, supramaxilla or maxilla; no scales extending out on pectoral, pelvic, first and second dorsal and anal fins, a few scales on base of caudal fin, a scale sheath at base of second dorsal fin or not; males mouth brooding fertilized eggs; simple filaments present around the micropyle.

Distribution. Apogonids are found predominately in tropical and subtropical marine waters of all oceans from near shore to about a depth of 300 m. Many fewer shallow-water apogonids are found in fresh, estuarine, or warm-temperate waters.

Remarks. This family's diagnosis is inclusive for four subfamilies, and is believed to exclude all other percomorph families in parts or combinations of characters. Fraser (2013b) examined the literature relating to the living Kurtidae as well as morphological characters of both species. He concluded that there were only two possible synapomorphies shared by both families but neither is exclusive of other families. Kurtid morphology has many derived characters compared with other percomorphs including apogonids (for the relationship between the Kurtidae and apogonid genera *Archamia* Gill 1863 and *Taeniamia* Fraser 2013b, see the remarks of the tribe Archamiini). Neither this study nor Fraser (2013b) focused on the question about which family is the closest sister. An answer to family relationships awaits a different focus with groups that have characters more in common with the basal apogonids *Amioides* and *Holapogon* (for the relationship between *Amioides* and *Cheilodipterus*, see the remarks of the tribe Cheilodipterini).

In the absence of well-defined sister families analyzed using *Amioides* and *Holapogon* as the basal apogonids, the following characters are proposed as likely synapomorphies for the Apogonidae: 1) a single supernumerary anal spine with the following spine or ray in serial association with the first distal and proximal radials, 2) mouth brooding of fertilized eggs, 3) simple filaments around the micropyle of the egg, 4) swim bladder with a dorsal or anterodorsal oval and ventral gas glands, no anterior projections to skull or posterior connections with first anal pterygiophore.

Apogon, the first genus in the family, was described by Lacepède (1801) in page priority before he described *Cheilodipterus* the second genus. Cheilodipteroidei was erected by Bleeker (1856b) prior to Günther's Apogonina in 1859. Gill (1862) used Apogoninae and Bleeker in his 1874 revision of apogonids used Apogonini. Gill (1893) in his list of families and subfamilies used Cheilodipteridae referring to Bleeker's Cheilodipteroidei in 1859. Günther (1859) changed *Cheilodipterus* to *Chilodipterus* and that variant later appeared as a family name. Both generic based names have been used variably as family stem names though about the 1960s. Virtually, all systematic publications have used Apogonidae since the 1970s. Gon (1993), in his revision of *Cheilodipterus*, did not comment on family names, using Apogonidae. He noted Smith's (1961) use as Cheilodipterinae, now a tribe we recognize. We believe that the prevailing use of Apogonidae should be kept for stability at the family level.

2. SUBFAMILIES

Key to the subfamilies of Apogonidae

- 1 Two dorsal fins, I,8–13 in second dorsal fin; first dorsal spines all with uneven lengths 2
- Single dorsal fin, VI,19; spines III–VI similar lengths Paxtoninae
- 2 Supramaxilla small or absent, if large, dorsal fin VI–I,9–10 3
- Supramaxilla large, dorsal fin VII or VIII–I,9–10 Amioidinae
- 3 A single lateral line when scales present or absent; if scales absent, lateral line composed of free neuromasts Apogoninae
- Double lateral lines, first pored or notched from posttemporal, second abdominal with only notched scales. Pseudamiinae

Amioidinae new subfamily Fraser & Mabuchi

Type genus *Amioides* Smith & Radcliffe in Radcliffe 1912

Diagnosis. Incomplete, based on radiographs and external characters: Two dorsal fins VIII or IX dorsal spines deeply divided as VII or VIII+I,9–10; anal fin II,7–8; internal support of spines by serial proximal-middle radials closely associated, 6th and 7th elements broadening at fin division; two supernumerary dorsal spines; three supraneurals; first anal proximal-middle radial straight; 15 branched caudal fin-rays, upper and lower unbranched; preopercle ridge smooth, preopercle edges serrate; large supramaxilla; basisphenoid present; vertebrae 10+14; rod-like ribs on 3rd to 10th vertebrae; epineurals present on ribs of 3rd to 8th vertebrae; PU2 and PU3 with autogenous haemal spines; two pairs of uroneurals; hypurals 1–5 present, not fused; parhypural free; three epurals; perforated anterior ceratohyal; posttemporal serrate or one or two large spines on edge; cephalic pore system complex with many small pores and canal flutes; multiple pores in lateral-line scales, many free neuromast on lateral-line scales; lateral-line scales large, 24–25, ctenoid; mouth brooding of eggs unknown.

Distribution. *Amioides* is a deep-dwelling (77–267 m) genus known from limited material. The collection sites support the conclusion that it is widespread from continental locations and islands of the Indo-Pacific of East Africa to Japan and Vanuatu (Fraser 2013a). *Holapogon* is a deeper-dwelling (38–100 m) genus known from limited material from the Andaman Islands and in the Arabian Sea along the west coast of India and Oman. It should be expected along the coast of Yemen and possibly Somalia.

Remarks. This subfamily contains two genera, two species: *Amioides polyacanthus* and *Holapogon maximus* (Boulenger 1888). Although the latter species was absent from the present molecular analyses, it is placed in this subfamily based on the morphology (see Fraser 1973). Among cardinalfishes the presence of a deeply divided spinous dorsal fin with IX dorsal spines, a visible, but small, eighth dorsal spine, a large supramaxilla shaped lacking an slender antero-proximal point, multiple pores in lateral-line scales with multiple free neuromasts on the lateral-line scales, serrated preopercular edge, perforated anterior ceratohyal, caudal skeleton (three epurals, two pairs of uroneurals, five free hypurals a free parhypural), ribs on 3rd to 10th vertebrae, nine epineurals and vertebrae arrangement with median fins are all plesiomorphic family characters. These characters plus other family characters possessed by this subfamily should be very useful in the hunt for close family relatives. The cephalic arrangement of pores and flutes are likely synapomorphies that united these two large, relatively deep-dwelling genera (Bergman 2004). Other possible synapomorphies await more detailed studies. The osteology of both species has not been studied with cleared and counter stained small specimens. No small specimens, < 80 mm SL exist in collections, only large adults up to 198 mm SL (Fraser 2013a).

Subfamily Apogoninae Günther 1859

Type genus *Apogon* Lacepède 1801

Diagnosis. Two dorsal fins, VII to IX dorsal spines deeply divided as VI, VII, VII(I), VIII+I,9–13; anal fin II,8–18; internal support of spines by serial proximal-middle radials closely associated, 6th and 7th elements broadening at fin division or wide separation between dorsal fins; internal support of dorsal spines by serial proximal-middle radials not in close articulation, far apart at 6th between and 7th elements; one or two supernumerary dorsal spines; 0–3 supraneurals; first anal proximal-middle radial straight; 13–15 branched, upper and lower unbranched; basisphenoid present, reduced or absent; preopercle ridge smooth or serrate, preopercle edges smooth, serrate or with unossified lower portion; vertebrae 9–10+14–16; rod-like or proximally expanded ribs on 3rd to 10th vertebrae; epineurals present on ribs of 3rd to 8th or 9th vertebrae; PU2 and PU3 with autogenous haemal spines; anterior pair of uroneurals absent, posterior pair of uroneurals reduced or absent; 0–3 epurals; hypural 1–5 present, free or combinations of fusion by hypurals 1–4 or with terminal centrum, hypural 5 always free, splint-like; parhypural free or fused to hypurals 1+2; prootic included as part of the inner orbit ring; anterior and posterior ceratohyals sutured together by a few interdigitating struts medially or without struts; free medial extrascapular or fused with lateral extrascapular; scales ctenoid, spinoid, cycloid or absent; a scale sheath at base of second dorsal fin or not; single lateral-line present from posttemporal to base of caudal fin either as pored, pitted or grooved scales, or if without scales, with linear free neuromasts; secondary lateral-line scales or linear free neuromasts on lower body present or absent; cephalic pore system complex with many small pores and canal flutes, two or more pores in single row of lateral-line scales; pored lateral-line scales 3–48.

Distribution. Members of the Apogoninae are known from the eastern Pacific, Atlantic basin and the Indo-Pacific. The distribution is complete in the tropics and subtropical coastal zones down to nearly 300 meters.

Remarks. This subfamily contains most of the species in the family and has the greatest diversity of body shapes and sizes, color patterns (internal and external), habitats occupied and the only subfamily with bioluminescent species. Diversity is expressed in the molecular analysis by the clades that are consistent with morphology. The presence of a small, slender supramaxilla is a synapomorphy for some of the genera relative to the large supramaxilla found in the Amioiidae. Absence of a supramaxilla, another possible synapomorphy, is shared by a portion of the Apogoninae and the two other subfamilies. No single morphological synapomorphy has been identified that is inclusive of all members of this subfamily. Many are partial synapomorphies, shared across tribes as characters trending to fusion, reduction and loss (see tables in Fraser 2013b; remarks under tribes).

See Appendix A for species allocation in tribes. Distribution is described under each tribe.

Paxtoninae new subfamily Fraser & Mabuchi

Type genus *Paxton* Baldwin & Johnson 1999

Diagnosis. One continuous dorsal fin, VI,19; anal fin I,15–16; internal support of spines by serial proximal-middle radials in near articulation with gaps between each spine, similar distance between 6th and 7th elements; sixth proximal-middle radial without serial spine or ray; fifth and seventh proximal-middle radials with serial spine and ray respectively; one supernumerary dorsal spine; supraneurals absent; first anal proximal-middle radial curved; 9+8 branched principal caudal fin-rays; caudal fin truncate or slightly rounded; vertebrae 10+14; epineurals on first two vertebrae; rod-like ribs on 3rd to 10th vertebrae; epineurals present on ribs of 3rd to 9th vertebrae; supramaxilla and basisphenoid absent; six infraorbitals, without shelf on third, only first and second in contact, third sixth not in contact and all small; medial and lateral extrascapular absent; preopercle ridge smooth and edge with single large spine at angle, preopercle, including spine, covered by skin; prootic excluded along internal orbit ring by pterosphenoids and parasphenoid; parietal separated by supraoccipital; a unique postfrontal bone; uroneurals absent; two epurals; haemal spines for PU3 and PU4 each fused to centra; parhypural fused to hypurals 1+2; terminal centrum fused with hypurals 3+4; hypural 5 absent; second epibranchial articulating with third pharyngobranchial; anterior and posterior ceratohyals sutured together by a few interdigitating struts medially; anterior ceratohyal not perforated; seven branchiostegals, anterior three ventrally followed by two on distal side of anterior ceratohyal, two on distal side of posterior ceratohyal; single postcleithrum.

Distribution. This monotypic subfamily is known only from northwestern Western Australia, collected by trawls in 40–80 m. Only six specimens known (Baldwin & Johnson 1999; Atlas of Living Australia <http://www.ala.org.au/australias-species/>).

Remarks. This subfamily contains one genus, one species: *Paxton concilians* Baldwin & Johnson 1999. Because the species was absent from the present molecular analyses, this tribe is proposed based only on morphology. *Paxton* is characterized by a series of morphological apomorphies not found in any other apogonid (Baldwin & Johnson 1999; Fraser 2013b). These apomorphies include: VI dorsal spines; a continuous dorsal fin as VI,19 without a notched division or expanded pterygiophores at the transition from spines to branched, segmented fin-rays (all other apogonids have deeply divided dorsal fins and unbranched segmented first fin-ray); sixth pterygiophore without a serial spine or ray or subdermal remnants (unique for a continuous dorsal fin?); dorsal spines IV–VI subequal, longer than spines I–II (all other apogonids have unequal first dorsal-spines); anal fin with I,15–16, the spine in supernumerary position, with the first branched, segmented ray in series and supported by the first pterygiophore (all other apogonids have 2 anal spines); entire margin of preopercle covered by skin (all other apogonids have exposed preopercular edges); third epibranchial toothplate lacking (all other apogonids have a toothplate); fifth hypural absent (all other apogonid have a splint-like fifth hypural); anterior and posterior pelvic-girdle processes lacking; an autogenous wishbone-shaped cartilage present between proximal bases of left and right pelvic fins; medial and lateral extrascapular absent (all other apogonids have a lateral extrascapular and *Gymnapogon* has both); principal caudal fin-rays 9+8, all branched (all other apogonids have the upper-most and lower-most principal caudal fin-rays unbranched and some *Gymnapogon* species have additional unbranched principal caudal fin-rays); and postfrontal bones. Bergman's (2004) figures and descriptive text shows that *Paxton*

has a much reduced number of cephalic pores associated with canals compared with *Gymnapogon*, *Pseudamiops*, *Cercamia* or *Lachneratus*. She followed up with ..."The cephalic lateralis of *Paxton*, despite its simple canal structure, few perforations and, lack of secondary canal development, is characterized by an extensive network of sensory papillae. This characteristic, in combination with the lack of perforation, distinguishes *Paxton* from all other apogonids." Baldwin & Johnson's analysis provided a convincing list of synapomorphic characters with other pseudamine fishes and therefore did not to recognize a separate family or subfamily. They hypothesized that *Gymnapogon* and *Paxton* are sister genera. *Paxton*, *Cercamia* and *Gymnapogon* share a fused parhypural with fused hypurals 1 and 2 (see these publications for characters among these genera: Fraser 1972; Hayashi 1991; Baldwin & Johnson 1999). Larval stages may prove useful in determining if there is more than one sequence of fusing these elements. *Gymnapogon* has a single preopercular spine and *Cercamia* has 2–3 serrations near the angle and a single serration on the ridge. The preopercle of *Paxton* is unexposed, covered by skin with a single, unexposed spine. An infraorbital shelf is present in *Gymnapogon* and *Cercamia* and all six infraorbitals have contiguous relationships, whereas only the first two infraorbitals are contiguous for *Paxton*. *Cercamia* has some weak ctenoid scales but no pored or pitted lateral line. We conclude that *Gymnapogon* and *Cercamia* are sister genera (see remarks for the tribe Gymnapogonini) and that the fusion of the parhypural with fused hypurals 1 and 2, preopercular spine and other shared reductive characters occurred independently in *Paxton*. *Paxton* is given subfamily recognition.

Subfamily **Pseudamiinae** Smith 1954

Type genus *Pseudamia* Bleeker 1865

Diagnosis. Two separate dorsal fins, VII dorsal spines as VI+I,8–9; anal fin II,8–10; wide separation between dorsal fins; internal support of dorsal spines by serial proximal-middle radials not in close articulation, far apart at 6th between and 7th elements; one supernumerary dorsal spine; 1–2 supraneurals; first anal proximal-middle radial straight; 9+8 principal caudal fin-rays, 15 branched, upper and lower unbranched, caudal fin rounded or rhomboid, mid-line fin-ray longest; supramaxilla and basisphenoid absent; preopercle ridge smooth, edge serrated at angle or smooth; prootic narrowed along internal orbit rim, not quit excluded by pterosphenoid and parasphenoid; anterior pair of uroneurals absent, posterior pair of uroneurals reduced or absent; two epurals; hypurals 1–2 fused, 3–4 fused, separate from urostyle; hypural 5 free; parhypural free; free medial extrascapular; neuromasts reduced to a simple cross-hatch on head, linear and vertical rows on body, present on caudal fin; cephalic pore system simple without canal flutes; lateral-line scales 23–43, first few scales pored, followed by notched scales, a lower lateral line of notched scales begins on abdomen; cycloid scales on body.

Distribution. Members of the Pseudamiinae are found along the continental coasts and islands of the Red Sea, Persian Gulf, Indian Ocean, Western Pacific out to Japan, Palmyra, Tahiti, Austral Islands and Australia. They can be found in shallow water down to about 64 meters.

Remarks. This subfamily contains one genus, 7 species: *Pseudamia amblyroptera* (Bleeker 1856c), *P. gelatinosa* Smith 1956, *P. hayashii* Randall, Lachner & Fraser 1985, *P. nigra* Allen 1992, *P. rubra* Randall, Lachner & Fraser 1985, *P. tarri* Randall, Lachner & Fraser 1985, *P. zonata* Randall, Lachner & Fraser 1985. The molecular analyses support a separate subfamily for species of *Pseudamia* (see Figs. 2–6). Morphological information associated *Gymnapogon* and *Pseudamiops* with *Pseudamia* (Smith, 1961; Fraser 1972; Baldwin & Johnson 1999; Bergman 2004) as belonging in this subfamily. However, Thacker & Roje's (2009), Cowman & Bellwood's (2011), and the present molecular analyses placed *Pseudamia* outside the rest of the Apogonidae with *Gymnapogon* nested into the latter large clade (*Pseudamiops* was absent from these studies). Corresponding to such phylogenetic relationship, monophyly between *Pseudamia* and *Gymnapogon* (H14) was significantly rejected by the AU test based on the present molecular data (Table 6). All *Pseudamia* have two scaled lateral lines on the body, hypurals 1 and 2 fused, urostyle over hypurals 3 and 4, one reduced pair of uroneurals in anterior position, all possible synapomorphies. The comparative morphological features of *Pseudamia* are reductive, fusion and loss of bones (Baldwin & Johnson, 1999). Many of these reductive features are held in common with *Gymnapogon*, *Cercamia* Randall & Smith 1988, *Lachneratus* Fraser & Struhsaker 1991 and *Pseudamiops*. The latter four genera are all translucent when alive unlike most (all?) species of *Pseudamia*. Body shapes of *Gymnapogon*, *Cercamia* and *Lachneratus* include forked caudal fins and the latter two genera have large scales and

lack pored lateral-line scales. *Pseudamiops* was not part of this study and is removed from the Pseudamiinae to the Gymnapogonini based on its body being translucent, having large scales without pored lateral-line scales. The conflict between using molecular and morphological information independently supporting differing hypotheses remains confounding for these five genera.

Living pseudamine fishes have virtually no morphological characters that are considered basal for apogonids as restricted here. All are derived characters from those states present in the Amioidinae and in the basal Apogoninae. Baldwin & Johnson (1999) listed plesiomorphic characters for the expanded pseudamine fishes. They did not include *Lachneratus* or *Cercamia* as part of the pseudamine group.

3. APOGONINAE TRIBES ALL NEW

Tribe **Apogonichthyini** Snodgrass & Heller 1905

Type genus *Apogonichthys* Bleeker 1854a

Diagnosis. Members of the Apogoninae: dorsal fin VII(I) or VIII+I,7–10; anal fin II,7–9; head and body with ctenoid scales; pored lateral-line scales, 3–24, scales not pored with groove or pit in scale; preopercle smooth on ridge, serrate or smooth on edges, where smooth a narrow weakly ossified to unossified flap; three supraneurals; supramaxilla narrow, reduced or absent; basisphenoid reduced or absent; one pair of uroneurals present; three epurals; five free hypurals or 1–2 fused and 3–4 fused, one or more fused to terminal centrum; free parhypural; caudal fin emarginate, truncate or rounded; head and body reddish, brownish or blackish without stripes, often with pale or dark spots on body.

Other characteristics. two supernumerary spines; branched first segmented dorsal and anal ray; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scale on opercle and onto base of caudal fin; pored lateral-line scales simple with one pore on upper side and one on lower side; pectoral fin-rays 11–16; three supraneurals; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; teeth on premaxilla, dentary, vomer, palatine, all villiform (one species present on ectopterygoid) or absent on palatine; six infraorbitals, bony shelf on third infraorbital; supramaxilla absent; basisphenoid present, reduced or absent; anterior ceratohyal smooth or notched; 10+14 or 10+15 (*Vincentia*) vertebrae; 8 ribs; 8–9 epineurals; low crest on PU2.

Distribution. *Apogonichthys*, *Foa* Jordan & Evermann in Jordan & Seale 1905, are widespread throughout the Indo-Pacific from the Red Sea, East Africa to Japan, Hawaii and French Polynesia; *Fowleria* Jordan & Evermann 1903 and *Neamia* from the Red Sea, East Africa to Japan and French Polynesia; and *Vincentia* known from warm-temperate Australia.

Remarks. This tribe contains five genera, *Apogonichthys*, *Neamia*, *Foa*, *Fowleria* and *Vincentia*, almost corresponding to the clade III in the molecular trees (Figs. 2–6, Table 4). The last genus, *Vincentia*, was tentatively included in this tribe, because it was sister to the clade III in the trees of Figs. 2, 3 and 4. Members are morphologically defined by the following characters: the smooth preopercle edges, rounded caudal fin, a reduced supramaxilla, and 10+14 vertebrae. *Vincentia* does not show these morphological features, and was sister not to the clade III, but to *Glossamia* in tree in Fig. 5. Thus, *Vincentia* may not belong to this tribe. Species of *Neamia* were not part of the molecular analysis, but thought to belong to this tribe through morphological synapomorphies (smooth preopercle edges, reduced supramaxilla, rounded caudal fin and color patterns).

Apogonichthyidae has been used several times first by Snodgrass & Heller (1905) with two species of Eastern Pacific *Apogon*, then by Jordan & Evermann (1905) with *Apogonichthys* and other apogonids and again by Jordan & Seale (1905) with *Amia* Gronow in Gray 1854a an unavailable name for *Apogon* and other apogonids. No type genus was mentioned by any of these authors. Jordan and co-workers had previously used Apogonidae. The stem of Apogonichthyidae is Apogonichthy. We use the tribal name in conjunction with *Apogonichthys* Bleeker 1854a the source of the stem.

Tribe **Apogonini** Günther 1859

Type genus *Apogon* Lacepède 1801

Diagnosis. Members of the Apogoninae: dorsal fin VI+I,9; anal fin II,8; developed gill rakers 9–19; posttemporal edge smooth or weakly serrate; anterior nare with low rim and flap; preopercle smooth on ridge, serrate to smooth on vertical edge, horizontal edge an unossified large flap; head and body with ctenoid or cycloid scales; pored lateral-line scales 23–25, scales with one pore above center and one below central pore; intestine and stomach pale (except two species); head and body reddish with or without blackish markings or head and body brownish without bars or stripes, both color patterns may be translucent in some species.

Other characteristics. one supernumerary spine; branched first segmented dorsal and anal ray; ctenoid or cycloid scales on predorsal, cheek, breast, two pelvic scales, and body; cycloid scale on opercle and onto base of caudal fin; pored lateral-line scales simple with one pore on upper side and one on lower side; pectoral fin-rays 11–16; 0–3 supraneurals; pored lateral-line scales from posttemporal to base of caudal fin; caudal fin forked or rounded; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; teeth on premaxilla, dentary, vomer, palatine, all villiform (except one species canine-like on premaxilla and dentary) or absent on palatine; six infraorbitals, bony shelf on third infraorbital; supramaxilla absent; basisphenoid present, reduced or absent; anterior ceratohyal notched; 10+14 vertebrae; 8 ribs; 8–9 epineurals; uroneurals absent; three epurals; five free hypurals, 1–2 fused and 3–4 fused, 1–2 fused and 3–4 fused to terminal centrum; free parhypural; low crest on PU2.

Distribution. *Apogon sensu stricto* is found in all tropical regions, *Zapogon* Fraser 1972 in the Atlantic and Indo-Pacific, *Phaeoptyx* Fraser & Robins 1970 and *Paroncheilus* Smith 1964 in the Eastern and Western Atlantic Ocean and *Astrapogon* Fowler 1907 confined to the Western Atlantic Ocean.

Remarks. This tribe contains five genera, *Astrapogon*, *Apogon sensu stricto*, *Phaeoptyx*, *Paroncheilus* and *Zapogon*, corresponding to the clade II in the molecular trees (Figs. 2–6, Table 4). Members have a large, unossified preopercular flap (a proposed synapomorphy), simple pore arrangement on lateral-line scales, six first dorsal spines and color patterns. Monophyly of *Apogon sensu stricto* (H10) was, however, statistically rejected by AU test (Table 6). In the molecular trees, *Apogon sensu stricto* was divided into three (*Apogon*-1, 2, and 3) or two (*Apogon*-1 and 2+3) lineages. One of the two or three lineages, *Apogon*-1, was sister to the clade including all the other members of this tribe. This basal dichotomy agrees with geographic distributions: species of the former clade (*Apogon*-1) distributed in Indo-Pacific Basin and those of the latter clade basically in Atlantic Basin with a small group of *Apogon*-3 within it occurring in Eastern Pacific. These molecular results suggest that species of Apogonini have been firstly separated between the Atlantic and Indo-Pacific regions and then an Atlantic species invaded to Eastern Pacific. *Asperapogon* Smith 1961 is an available name for some or all of the Indo-Pacific species (*Apogon*-1) as a genus or subgenus. A morphological diagnosis for *Asperapogon* awaits determination of species composition. Type species of *Apogon* is *Apogon ruber* Lacepède 1801, a synonym of *A. imberbis* (Linnaeus 1758) from the Eastern Atlantic Basin and the Mediterranean Sea. No other subfamilies or tribes occur in the Atlantic Basin or Eastern Pacific.

Tribe **Archamiini** new name Fraser & Mabuchi

Type genus *Archamia* Gill 1863

Diagnosis. Members of the Apogoninae: VI+I,9 or VII+I,9; anal fin II,12–19; head and body with ctenoid scales; pored lateral-line scales 24–25; preopercle ridge smooth, edges serrate; three supraneurals; supramaxilla absent; basisphenoid present; one pair of uroneurals present or absent; three epurals; five free hypurals, 1–2 fused and 3–4 fused to terminal centrum; free parhypural; caudal fin forked; body translucent without bars and head tinged greenish yellow and small dark basicaudal spot or with dark or yellowish to reddish bars on body, dark basicaudal spot, small or large, compact or diffuse or head and body with one or two narrow yellowish to dark stripes.

Other characteristics. one or two supernumerary dorsal spines; branched first segmented dorsal and anal ray; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scale on opercle and onto base of caudal fin; pored lateral-line scales with multiple pores; pectoral fin-rays 11–16; three supraneurals; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; teeth on premaxilla, dentary, vomer, palatine, all villiform (one species present on ectopterygoid) or absent on palatine; six infraorbitals, bony shelf on third infraorbital; anterior ceratohyal smooth or notched; developed gill rakers 15–23; 10+14 vertebrae; 8 ribs; 8 epineurals; stomach and intestine blackish, peritoneum silvery with melanophores; low crest on PU2.

Distribution. *Archamia* and *Taeniamia* are widespread throughout the Indo-Pacific from the Red Sea, East Africa to Japan and Samoa.

Remarks. This tribe contains two genera, *Archamia* and *Taeniamia*, corresponding to the clade XI in the molecular trees (Figs. 2–6, Table 4). All the members of the clade were formerly classified under *Archamia*, but Fraser (2013b) redescribed *Archamia* as monotypic and recognized a new genus, *Taeniamia* for the remaining species. The history of this species is given by Gon & Randall (2003). Our molecular results did not disagree with the idea of recognizing two species (*Taeniamia kagoshimanus* Döderlein in Steindachner & Döderlein 1883 and *T. sansibaricus* Pfeffer 1893) that has been long confused with *Taeniamia fucata* (Cantor 1849) (Fraser 2013b). This idea is supported also by the geographic variation in gill raker counts reported by Gon & Randall (2003). Prokofiev (2006) indicated a possible close relationship between the species of "*Archamia*" (*Archamia* + *Taeniamia*) and *Kurtus gulliveri* based on morphological characters. But their monophyly was significantly rejected by the AU test based on the present molecular data (H09; Table 6).

Archami- is the stem for this new tribe.

Tribe **Cheilodipterini** Bleeker 1856b

Type genus *Cheilodipterus* Lacepède 1801

Diagnosis. Members of the Apogoninae: VI+I,9; anal fin II,8; head and body with ctenoid scales; pored lateral-line scales 24–26; canine teeth on premaxilla and dentary; preopercle ridge smooth, edges serrate; three supraneurals; reduced supramaxilla; one pair of uroneurals; three epurals; five free hypurals; free parhypural; caudal fin forked or emarginate; dark stripes on head and body, no stripes in second dorsal or anal fin, basicaudal dark spot, band or no spot.

Other characteristics. one supernumerary dorsal spine; branched first segmented dorsal and anal ray; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scale on opercle and onto base of caudal fin; pored lateral-line scales with multiple pores; pectoral fin-rays 11–14; three supraneurals; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; villiform teeth on vomer and palatine; six infraorbitals, bony shelf on third infraorbital; basisphenoid present; anterior ceratohyal smooth or notched; 10+14 vertebrae; 8 ribs; 7–8 epineurals; stomach and intestine pale with pale peritoneum; low crest on PU2.

Distribution. *Cheilodipterus* is widespread throughout the Indo-Pacific from the Red Sea, East Africa to Japan and French Polynesia following Gon (1993). There have been several short-lived efforts to subdivide this genus with several names proposed (*Cheilodipterops* Schultz 1940; *Desmoamia* Fowler & Bean 1930; *Paramia* Bleeker 1863). More molecular analysis among the 17 species should provide insight to relationships not apparent in the five species we sampled.

Remarks. This tribe contains one genus, *Cheilodipterus*, corresponding to the clade X in the molecular trees (Figs. 2–6, Table 4). Canine or caninoid teeth on the premaxilla and dentary, a reduced supramaxilla, a single supernumerary dorsal spine, stripes on body and a diffuse or solid basicaudal spot in most species often with some surrounding yellow are characteristics of this tribe. Cheilodipteroidei, as a family, was recognized by Bleeker (1856b). Schultz (1940) recognized the Cheilodipteridae, but as a broad grouping of a number of families. Smith (1961) and Norman (1966) recognized this group as a subfamily Cheilodipterinae including *Coranthus* Smith 1961 (now *Amioides*) and *Paramia* Bleeker 1863 (now *Cheilodipterus*). Monophyly of *Amioides* and *Cheilodipterus* was significantly rejected by AU test (H13; Table 6). The shape and position of the reduced supramaxilla (see Fraser 1972) and canine or caninoid teeth are synapomorphies.

Tribe **Glossamiini new name** Fraser & Mabuchi

Type genus *Glossamia* Gill 1863

Diagnosis. Members of the Apogoninae: dorsal fin VI+I,8–10; anal fin II,8–10; pored lateral-line scales 24–50; preopercle ridge smooth edges smooth to serrate; three supraneurals; large supramaxilla present; basisphenoid

present, reduced or absent; anterior pair of uroneurals; three epurals; five free hypurals; parhypural separate; two autogenous haemal spines; one supernumerary dorsal spine; caudal fin emarginate, truncate or rounded.

Other characteristics. first dorsal ray unbranched and first anal ray branched and segmented; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; head and body with ctenoid scales or cycloid on nape, cheek, opercle, anterior pored lateral-line scales, ctenoid on breast, grading from cycloid to ctenoid posteriorly; pored lateral-line scales simple with one pore on upper side and one on lower side; pectoral fin-rays 13–16; developed gill rakers 7–15; 10+14 vertebrae; 8 ribs; 9 epineurals; teeth in multiple rows on premaxilla, dentary, vomer, palatine, all villiform, present or absent on ectopterygoid; six infraorbitals, bony shelf on third infraorbital; stomach and intestine pale with pale peritoneum; low crest on PU2.

Distribution. Species of *Glossamia* are found in tidal and flowing freshwaters of Australia and the island of New Guinea. One species is known from Australia (perhaps a species complex) and the rest on the island of New Guinea. The only described species of *Yarica* is found in tidal streams, flowing freshwater and lowland lakes from Myanmar, Andaman and Nicobar Islands, Thailand, Malaysia, Indonesia, Philippines, Australia, New Guinea, Solomon Islands to New Caledonia and out to Saipan.

Remarks. In the present molecular analyses, *Glossamia* did not form a robust monophyletic group with any other apogonines (see Figs. 2–6 and Table 5). For this genus, we gave tribe status. We included *Yarica* (Fig. 7A) in this tribe based solely on morphological data. The present molecular analyses reproduced a relatively robust sister relationship between *Yarica* and *Rhabdamia* (clade IX). Species of *Rhabdamia* have a smaller mouth and slender translucent body with a forked caudal fin (Fig. 7B) consistent with their marine reef pelagic habitat preferences and differ in their osteological characteristics as follows: 1 or 2 supraneurals; fused hypurals plate consisting of hypurals 1+2+3+4 to the terminal centrum; 1–2 rows of villiform teeth on premaxilla or some canine, 1 row of villiform teeth on dentary, vomer and palatine; 7 epineurals on ribs 1–7; shelf on third infraorbital reduced or absent; uroneurals reduced or absent; supramaxilla absent. The cephalic pores are much more complex for *Rhabdamia* and free neuromasts much less numerous than for *Yarica* (Bergman 2004, Figs. 11, 29–30). Support for combining *Glossamia* and *Yarica* are similar body shapes, freshwater habitat preferences, a large supramaxilla of similar shape, a single supernumerary dorsal spine and 9 epineurals. In spite of non-monophyly in the obtained trees, AU test did not reject the monophyly of *Glossamia* and *Yarica* (H06, see Table 6). The wide spread distribution of *Yarica* indicates that this species has euryhaline characteristics imbedded in its life history.

Tribe *Gymnapogonini* Whitley 1941

Type genus *Gymnapogon* Regan 1905

Diagnosis. Members of the Apogoninae: VI+I,8–13; anal fin II,8–16; head and body naked or with large weakly ctenoid or cycloid scales; lateral-line scales 23–24 or lateral line a series of free neuromasts to base of caudal fin, interrupted mid-line lateral line present or absent; preopercle ridge smooth, edge with one or more spines at angle; 0–2 ossified supraneurals; supramaxilla, paired uroneurals and basisphenoid absent; 2–3 epurals; hypurals 1–2 fused, 3–4 separate or fused to urostyle; parhypural separate or fused to hypurals 1–2; caudal fin forked or rounded; pterospheneid and parasphenoid joined excluding prootic from internal orbit rim.

Other characteristics. one supernumerary dorsal-fin spine; unbranched or branched first segmented dorsal-fin ray, branched first anal-fin ray; cycloid or weakly ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; cycloid scale on opercle and onto base of caudal fin; pectoral-fin rays 10–14; 9+8 segmented principal caudal rays, 13–15 branched, upper one or two and lower one or two unbranched; unbranched procurrent rays, longest segmented; some enlarged teeth on premaxilla and dentary, canine or villiform on vomer, villiform on palatine; six infraorbitals, bony shelf on third infraorbital present or absent; 1–2 postcleithra; anterior ceratohyal smooth or notched; 10+14 or 9+15 (*Cercamia*) vertebrae; 7–8 ribs; 0–6 epipleurals; low crest on PU2.

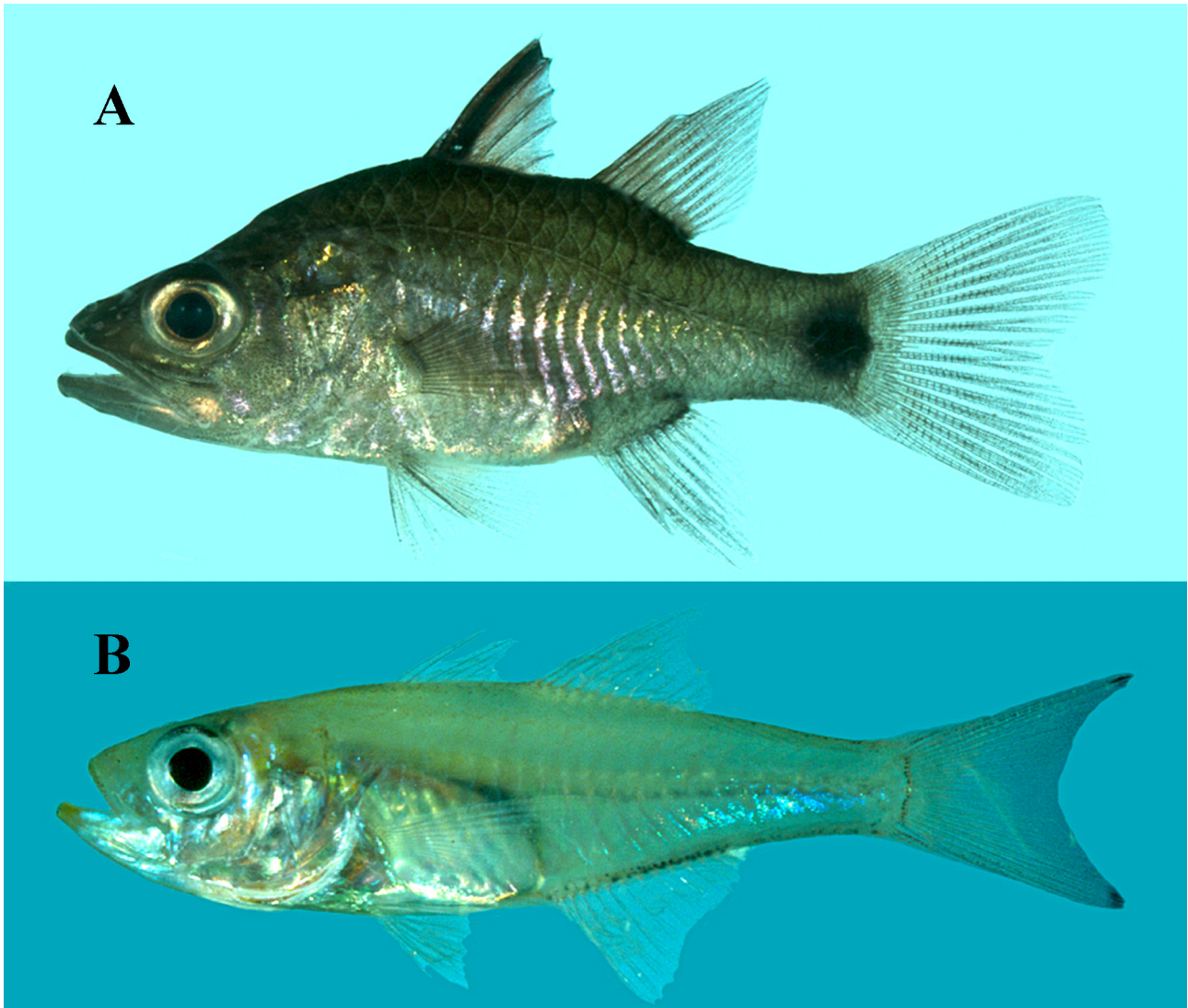


FIGURE 7. A. *Yarica hyalosoma*, ROM 65737, 58.0 mm SL, New Caledonia, by R. Winterbottom. B. *Rhabdamia gracilis*, ROM 65791, 47.5 mm SL, New Caledonia, by R. Winterbottom.

Distribution. *Pseudamiops* East Africa to Japan, Hawaii and French Polynesia, *Gymnapogon* widespread from the Red Sea, East Africa to Japan and French Polynesia, *Lachneratus* from East Africa to Hawaii and Tonga and *Cercamia* from the Eastern Indian Ocean to Japan and French Polynesia.

Remarks. This tribe contains four genera, *Cercamia*, *Gymnapogon*, *Lachneratus* and *Pseudamiops*, corresponding to the clade I in the molecular trees (Figs. 2–6, Table 4). Species of the included genera are all translucent with many reductive morphologic characters. Although *Pseudamiops* was absent from the present analyses, we tentatively associated this genus with the *Gymnapogonini* based on its translucent body and the reductive morphological characters. Bergman (2004) noted: "...The cephalic lateralis system of *Gymnapogon* is very similar to that of *Pseudamiops*. A notable exception being that the preopercular and mandibular canal portions are confluent in *Gymnapogon* species." *Pseudamiops*, with scales, lacks pored, notched or pitted lateral-line scales. *Cercamia* and *Lachneratus* have not previously been associated with *Gymnapogon*. Both genera have deciduous scales and both lack pored, notched or pitted lateral-line scales. *Gymnapogon* and *Pseudamiops* were formerly classified under Pseudamiinae, together with *Pseudamia*. As mentioned above in the remarks of the subfamily Pseudamiinae, the present molecular data significantly rejected their monophyly (H14 in Table 6). In our molecular trees, two individuals of *Cercamia cladara* from two distantly distributed populations (French Polynesia and Palau) were paraphyletic to *Gymnapogon* and genetically distant from each other, which may indicate needs of taxonomical revisions of them.

Tanaka (1915) described the new family Henicichthyidae for the new genus and single new species

Henicichthys foraminosus. Tanaka's family name has been used only in the original publication. Whitley (1941) created the family Gymnapogonidae with Regan's genus as the type species. He noted that the oldest genus name '...becomes the root for the family name.' Whitley's (1941) synonymy of the literature for *Henicichthys* has the last published use of this genus in 1939. Whitley (1941) recognized that *Henicichthys foraminosus* and *Austalaphia annona* Whitley 1936 are synonyms of *Gymnapogon*. The sole use of *Gymnapogon* has been continuous since 1941. Fowler (1944) and Lindberg (1971) used Gymnapogonidae. We regarded Gymnapogonini as an easily recognized tribal name among apogonids and is its preferred use.

Tribe **Lepidamiini** new name Fraser & Mabuchi

Type genus *Lepidamia* Gill 1863

Diagnosis. Members of the Apogoninae: dorsal fin VII(I)-I,9 or VIII-I,9; anal fin II,8; head and body with ctenoid scales; pored lateral-line scales 35–48; preopercle ridge smooth, edges serrate; three supraneurals; supramaxilla absent; basisphenoid present; one pair of reduced uroneurals present; three epurals; five free hypurals; parhypural separate; two autogenous haemal spines; two supernumerary dorsal spines, caudal fin forked.

Other characteristics. first fin ray in second dorsal fin branched and segmented; first anal-fin ray branched and segmented; ctenoid scales on predorsal, cheek, breast, four pelvic scales, and body; ctenoid scales on opercle and onto base of caudal fin; pored lateral-line scales with multiple pores; 15 branched, upper and lower unbranched; developed gill rakers 8–17; unbranched procurrent rays, longest segmented; 10+14 vertebrae; 8 ribs; 9 epipleurals; teeth in multiple rows on premaxilla, dentary, vomer, palatine, all villiform; six infraorbitals, bony shelf on third infraorbital; stomach and intestine pale, peritoneum pale; low crest on PU2.

Distribution. *Lepidamia* with four species has been collected only from continental marine waters from South Africa to China (Gon 1995). Members of this tribe have not been collected in Australia or New Guinea. One specimen (USNM 175754, 96 mm SL) was collected in 1909 from Manila Bay, Luzon, Philippines. None have been reported elsewhere in the Philippines or again from Manila Bay. Perhaps the location is erroneous.

Remarks. We did not have tissue from any species. Based on known morphological characters including color patterns of the juveniles and adults, body shape and small body scales, we recognized *Lepidamia* in its own tribe for the present.

Tribe **Ostorhinchini** Whitley 1959

Type genus *Ostorhinchus* Lacepède 1802

Diagnosis. Members of the Apogoninae: dorsal fin VI+I,9 or VII+I,9; anal fin II,8–9; head and body with ctenoid scales; pored lateral-line scales 6–26; preopercle ridge smooth, edges serrate; 2–3 supraneurals; supramaxilla absent; basisphenoid present; one pair of reduced uroneurals present or absent; three epurals; five free hypurals or 1–2 fused; parhypural separate; caudal fin forked; head and/or body with one or more light or dark stripes, bars rarely present, basicaudal spot or broad mark present or absent.

Other characteristics. one or two supernumerary dorsal spines; branched first segmented fin ray in second dorsal-fin; first anal-fin ray branched and segmented; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scale on opercle and onto base of caudal fin; pored lateral-line scales with multiple pores; pectoral fin-rays 11–16; three supraneurals; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; teeth in one or multiple rows on premaxilla, dentary, vomer, palatine, all villiform or absent on palatine, sometimes enlarged, but not canine on side of dentary; six infraorbitals, bony shelf on third infraorbital; anterior ceratohyal smooth or notched; developed gill rakers 10–26; 10+14 vertebrae; 8 ribs; 8 epipleurals; blackish stomachs and intestines; low crest on PU2.

Distribution. The restricted *Ostorhinchus* is widespread throughout the Indo-Pacific from the Red Sea, East Africa to Japan, Hawaii, Easter Island and French Polynesia.

Remarks. Monophyly of recent *Ostorhinchus* (species indicated by blue in Figs. 2–6) was significantly rejected by AU test (H16 in Table 6). This tribe, however, corresponds to one of the five lineages of the recent

Ostorhinchus, clade XII. It included most species of the recent *Ostorhinchus*: many striped species of *Ostorhinchus* (species of *Ostorhinchus*-5) and *Brephamia parvula* Smith & Radcliffe in Radcliffe 1912 (Figs. 2–6, Table 4). Other species of the recent *Ostorhinchus* were divided into four lineages, *Ostorhinchus*-1, 2, 3 and 4. They were all placed far from the clade XII. Except for *Ostorhinchus*-3 (*O. margaritophorus*), monophyly between this tribe (clade XII) and each of the remaining lineages was rejected by AU tests (H07, 08 and 11 in Table 6). Although the bootstrap values supporting the clade XII were not so high (< 50%) both in the ML (Fig. 2) and MP (Figs. 4 and 5) trees (Table 4), and further the clade was divided into two separate clades in the BA tree (Fig. 3), we are treating this group as a single genus, based on the typical color pattern (stripes on body and/or head) shared by most of the included species. This group corresponds to the "striped group" of *Ostorhinchus* (*Ostorhinchus* III) in Mabuchi *et al.* (2006). One of the other recent *Ostorhinchus* lineages, *O. margaritophorus*, has long stripes, short bars between two long stripes on body and fused hypurals 1+2. Phylogenetic position of this species remains unsettled in the molecular trees (Table 5), but monophyly between this species and the members of this tribe was not rejected by AU test (H01 in Table 6). Based on its featured color pattern, we tentatively included this species in this tribe. *Apogon* (*Brephamia*) *parvula* has a very similar species within this tribe. It is *Ostorhinchus neotes*. Although they were not sister to each other in the molecular trees, their monophyly was not rejected by AU test (H12 in Table 6). While recognition of *Brephamia* Jordan in Jordan & Jordan (1922) as a subgenus or genus needs further evaluation, we synonymized it under the restricted *Ostorhinchus* for the present. Likely synapomorphies may include color pattern groupings, probably at the subgenus level. At the genus level, with the exception of the loss of tiny first dorsal-fin spines, all species have 7 visible first dorsal spines, a serrated preopercular edge and most have blackish stomachs and intestines.

There are two available names (*Gronovichthys* Whitley 1929; *Lovamia* Whitley 1930) which could be used in the future. There are at least 93 species in the group. We have sampled 31 species. Whitley (1959) first used the present name at family level Ostorhinchidae. The name appeared once. We use the name at the tribal level.

Tribe **Pristiapogonini** new name Fraser & Mabuchi

Type genus *Pristiapogon* Klunzinger 1870

Diagnosis. Members of the Apogoninae: dorsal fin VI+I,9 or VII+I,9; anal fin II,8; head and body with ctenoid scales; pored lateral-line scales 23–25; preopercle ridge serrate, edges serrate; infraorbitals serrate; three supraneurals; supramaxilla absent; basisphenoid present; one pair of uroneurals or absent; three epurals; five free hypurals; parhypural separate; one or two supernumerary dorsal spines; caudal fin forked.

Other characteristics. first segmented fin-ray in second dorsal-fin branched, first anal-fin ray branched and segmented; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scales on opercle and onto base of caudal fin; pored lateral-line scales with multiple pores; pectoral fin-rays 12–16; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; teeth in one or multiple rows on premaxilla, dentary, vomer, palatine, all villiform or absent on palatine; six infraorbitals, bony shelf on third infraorbital; anterior ceratohyal smooth or notched; developed gill rakers 10–19; 10+14 vertebrae; 8 ribs; 8 epipleurals; low crest on PU2.

Distribution. *Pristiapogon* is wide spread from East Africa, Red Sea, Indian Ocean Islands, Indonesia, Philippines, Pacific islands to Hawaii, Japan, French Polynesia and Australia. One species of *Pristicon* Fraser 1972 is restricted to the West Pacific. Another species reaches out to some islands on the Pacific Plate. One species of *Pristicon* has been reported from the west coast of India, with a gap between India and Indonesia (Suresh & Thomas 2007).

Remarks. This tribe contains two genera, *Pristiapogon* and *Pristicon*, corresponding to the clade VI in the molecular trees (Figs. 2–6, Table 4). Although bootstrap values supporting the tribe were not so high (62 and 56% BPs in ML and MP analyses, respectively), this tribe is morphologically well-defined: relatively large body with serrations on the preopercle ridge (a likely synapomorphy), edges and infraorbitals (a likely synapomorphy). Species of *Pristiapogon* usually have a darkish single stripe and/or a variable basicaudal spot while *Pristicon* have bars or saddles under the dorsal fins and spots at the base of the caudal fin or on the opercle.

Tribe **Rhabdamiini** new name Fraser & Mabuchi

Type genus *Rhabdamia* Weber 1909

Diagnosis. Members of the Apogoninae: dorsal fin VI+I,9 or VII+I,10–11; anal fin II,11–13; head and body with weakly ctenoid or cycloid; pored lateral-line scales 23–24; preopercle ridge smooth, edges smooth; two supraneurals; supramaxilla absent; basisphenoid present or absent; anterior pair of uroneurals reduced or absent; three epurals; hypurals 1+2+3+4 fused, the plate fused to terminal centrum; parhypural separate; no autogenous haemal spines; 1–2 supernumerary dorsal spines; caudal fin forked.

Other characteristics. first segmented fin-ray in second dorsal-fin branched, first anal-fin ray branched and segmented; pectoral-fin rays 13–17; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; developed gill rakers 17–31; unbranched procurrent rays, longest segmented; villiform teeth in one or two rows on premaxilla, or with a few canines (*Bentuviaichthys*), one villiform row on dentary and vomer, one villiform row or absent on palatine; six infraorbitals, bony shelf reduce or absent on third infraorbital; stomach and intestine pale with melanophores and silvery peritoneum with melanophores; 10+14 vertebrae; low crest on PU2.

Distribution. No reviews of the species have been made, but members have been reported from East Africa, the Red Sea, islands in the Indian Ocean, the West Pacific and out onto the Pacific Plate.

Remarks. This tribe contains one genus *Rhabdamia* (including two subgenera *Rhabdamia* and *Bentuviaichthys sensu* Fraser 1972). There are six names (Appendix A). Three species are streamlined apogonines exploiting the near pelagic zone of coral reefs for food. Likely synapomorphies include smooth preopercle ridge and edges, reduced dentition, fused hypurals, and two supraneurals. All species are mostly translucent. In the present molecular analyses, they formed a robust monophyletic group (clade IX) with *Yarica hyalosoma* (Figs. 2–6, Table 4) (see also Fig. 7), but it is very unlikely based on morphological evidence (for details, see the remarks of the tribe Glossamiini). In Fraser (1972), subgenus *Rhabdamia* was classified under the genus *Rhabdamia* together with the subgenera *Bentuviaichthys* and *Verulux* Fraser 1972. The last lineage, *Verulux* (clade V), was placed far from the first lineage, *Rhabdamia*, in the present molecular trees (Figs. 2–6). Although monophyly between the two lineages was not rejected by AU test (H05 in Table 6), we recognized each of them in its own tribe for the present (for *Verulux*, see the tribe Veruluxini). The present molecular analyses did not include *Bentuviaichthys*, but it was included in this tribe based on the following morphological characters: fused hypurals 1+2+3+4, epipleurals absent on last three ribs, single row of teeth on dentary, two supraneurals, slender, mostly translucent body and forked caudal fin. Two individuals of *Rhabdamia gracilis* from two distantly distributed populations (Fiji and Ryukyu Islands) were paraphyletic to *R. spilota* Allen & Kuitert 1994 and genetically distant from each other, which may indicate needs of taxonomical revisions of them.

Tribe **Siphamiini** Smith 1955

Type genus *Siphamia* Weber 1909

Diagnosis. Members of the Apogoninae: dorsal fin VI–VII + I,7–11; anal fin II,7–11; pored lateral-line scales 0–24; preopercular ridge smooth, edges smooth to serrate; supraneurals 1–2; supramaxilla absent; basisphenoid absent; uroneurals absent; two epurals; hypurals 1+2 and 3+4 fused into two plates, upper plate fused to terminal centrum; parhypural separate; one or two supernumerary dorsal spines; caudal fin emarginate or forked; bacteria bioluminescent system from hyal region to along body above or past anal-fin base.

Other characteristics. first segmented fin-ray in second dorsal-fin branched, first anal-fin ray branched and segmented; ctenoid, cycloid or spinoid scales; median predorsal scales 0–6; pectoral rays 11–16; segmented principal caudal rays 9+8, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; villiform teeth in one or multiple rows on premaxilla, dentary, vomer, palatine, or absent on palatine; developed gill rakers 6–18; lateral-line scales usually with a vertical row of free neuromasts; six infraorbitals, bony shelf on third infraorbital; anterior ceratohyal smooth or notched; developed gill rakers 10–26; 10+14 vertebrae; 8 ribs; 8 epipleurals; stomach, intestine and peritoneum generally pale with variously sized melanophores; low crest on PU2.

Distribution. Representatives of the tribe are found from East Africa, Red Sea, islands in the Indian Ocean, throughout the West Pacific to Japan, onto the Pacific Plate to French Polynesia and Australia (Gon & Allen 2012).

Remarks. This tribe contains one genus *Siphamia*, corresponding to the clade VII in the molecular trees (Figs. 2–6, Table 4). All species of *Siphamia* have bioluminescent bacteria in a specialized organ (a synapomorphy for the species) unique among apogonines. Smith (1955) proposed placing species of *Siphamia* in its own subfamily Siphamiinae. Our results based on analysis of five of the twenty-three species suggest that *Siphamia roseigaster* Ramsay & Ogilby 1887 could be recognized in its own genus *Adenapogon* McCulloch 1921, because it was placed relatively far from the remaining species. Gon & Allen's (2012) results based on morphology suggest that two other Australian species belong in *Adenapogon* and that *Fodifoa* Whitley 1936 is available for another group of species. We defer to Ofer Gon who is continuing to work on relationships within this tribe (Gon & Allen 2012).

Tribe **Sphaeramiini** new name Fraser & Mabuchi

Type genus *Sphaeramia* Fowler & Bean 1930

Diagnosis. Members of the Apogoninae: dorsal fin VII+I,9–10, VII(I)+I,9–14 or VIII+I,9–10 with eighth spine reduced to a tiny visible spine or a nubbin hidden under skin supported by a free sixth distal radial; anal fin II,8–13; head and body with ctenoid scales; pored lateral-line scales 23–27; preopercle ridge smooth, edges serrate; 2–3 supraneurals; supramaxilla absent; basisphenoid present; one pair of uroneurals; three epurals; five free hypurals or 1+2 fused and 3+4 fused with 3+4 fused to terminal centrum; parhypural separate; two autogenous haemal spines; two supernumerary dorsal spines; caudal fin forked, emarginate or truncate.

Other characteristics. first segmented fin-ray in second dorsal-fin branched, first anal-fin ray branched and segmented; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scales on opercle and onto base of caudal fin; 1–3 predorsal scales cycloid or ctenoid; pored lateral-line scales with multiple pores; pectoral-fin rays 13–17; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; developed gill rakers 7–38; unbranched procurent rays, longest segmented or spinous; third or fourth dorsal spine longest; 10+14 or 10+15 vertebrae; 8 ribs; 8–9 epipleurals; teeth in one or multiple rows on premaxilla, dentary, vomer, palatine, all villiform; six infraorbitals, bony shelf on third infraorbital; stomach and intestine pale or black with pale peritoneum; low crest on PU2.

Distribution. Species of *Apogonichthyoides* are found throughout the Indo-West Pacific from East Africa, Red Sea, India, some island of the Indian Ocean, throughout Indonesia, Philippines to Japan, New Guinea, Australia and the Solomon Islands. Some species have restricted distribution and some are rare in collections. Species of *Jaydia* Smith 1961 have a more continental distribution, mostly caught in trawls, and are widespread from Africa to Japan, New Guinea, Australia and larger islands in the Coral Sea. Representatives of *Nectamia* are found on reef habitats from East Africa, Red Sea, islands in the Indian Ocean, throughout the West Pacific to Japan, onto the Pacific Plate out to the Line Islands and French Polynesia. *Sphaeramia*, represented by two species, one found in mangrove habitats and one on coral reefs, also have wide distribution in the Indo-West Pacific. *Quinca*, represented by a single species, is known from northwestern coast of Australia.

Remarks. This tribe contains six genera, *Apogonichthyoides*, *Jaydia*, *Nectamia*, *Pterapogon* Koumans 1933, *Quinca* and *Sphaeramia*, almost corresponding to the clade IV in the molecular trees (Figs. 2–6, Table 4). First three of the six genera were formerly classified under *Ostorhinchus*, corresponding to "barred group" of *Ostorhinchus* (*Ostorhinchus* II) in Mabuchi *et al.* (2006). Two of the remaining three genera (*Pterapogon* and *Sphaeramia*) have distinct bar(s) on body. In addition to the six genera, corresponding molecular clade included three species of *Ostorhinchus*-2 (*O. hoevenii* Bleeker 1854b, *O. ishigakiensis* Ida & Moyer 1974, and *O. rueppellii* Günther 1859). But there are no morphological characters that support this association. We defer taxonomical action on this possible relationship for the present. This clade further included another species of the former *Ostorhinchus* (*Ostorhinchus*-1). For this species, the latest authors (Allen & Erdmann 2012) provisionally used *Apogonichthyoides* as its genus name, and we followed it here, but such application of the name made this genus paraphyletic in our molecular trees. Based on its morphological features, we tentatively included it [*Apogonichthyoides* (?) *melas*] in this tribe, but further study including more Sphaeramiini species will be needed to clarify its taxonomic status. In the present molecular analyses, phylogenetic position of *Pterapogon* remained unsettled (Table 5). It was sister to the clade VII (Siphamiini) in ML tree (Fig. 2), sister to *Ostorhinchus margaritophorus* in MP tree-A (Fig. 4), and nested within the clade XII (Ostorhinchini) in the MP tree-B (Fig. 5). It

formed a polytomy with *O. margaritophorus*, clade VII, clade VIII, and a large clade including clades IX–XII in BA tree (Fig. 3). *Pterapogon* has, however, a synapomorphy (spinous procurent caudal rays) uniquely held with *Sphaeramia* as well as similarities in color patterns and body shape, but differs with fused hypurals 1+2 and 3+4. Based on these morphological features, we tentatively included this species in the tribe Sphaeramiini. Monophyly of them was not rejected by AU test (H02 in Table 6), although its inclusion within Ostorhinchini was also not rejected (H03 in Table 6). We had no good DNA extracts from tissue of *Quinca*. This monotypic genus has morphological characteristics and color pattern suggestive of a relationship with *Apogonichthyoides*, and was provisionally placed in the Sphaeramiini.

Tribe **Veruluxini** new name Fraser & Mabuchi

Type genus *Verulux* Fraser 1972

Diagnosis. Members of the Apogoninae: dorsal fin VI–I,9; anal fin II,9; head and body with weakly ctenoid or cycloid scales; pored lateral-line scales 24; preopercle ridge smooth, edges smooth; one supraneural; supramaxilla absent; basisphenoid present; uroneurals absent; two epurals; fused hypurals 1+2+3+4, fused to terminal centrum; no autogenous haemal spines; one supernumerary dorsal spine; bioluminescent organ under cleithrum; caudal fin forked.

Other characteristics. first segmented fin-ray in second dorsal-fin branched, first anal fin-ray branched and segmented; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; developed gill rakers 12–15; unbranched procurent rays, longest segmented; pectoral fin-rays 14–16; 10+14 vertebrae; 8 ribs; 5–6 epipleurals; teeth in one row on premaxilla, dentary, vomer, palatine, all villiform, or absent on palatine; six infraorbitals, bony shelf absent on third infraorbital; stomach and intestine black with silvery peritoneum; low crest on PU2.

Distribution. The single described species is known from East Africa, Red Sea, islands in the Indian Ocean, throughout the West Pacific to Japan, onto the Pacific Plate to Marshall Islands, Vanuatu, New Caledonia and Australia.

Remarks. This tribe contains only one species, *Verulux cypselurus*, corresponding to the clade V in the molecular trees (Figs. 2–6, Table 4). Representatives of *Verulux* (two individuals from Ryukyu Islands and Seychelles) were monophyletic separated by a moderate genetic distance, which may indicate presence of cryptic species. This lineage was recovered far from *Rhabdamia* (tribe Rhabdamiini), although their monophyly (genus *Rhabdamia sensu* Fraser 1972) was not rejected by AU test (H05 in Table 6). The single described species has a bioluminescent organ under cleithrum unlike *Rhabdamia*.

Tribe **Zoramiini** new name Fraser & Mabuchi

Type genus *Zoramia* Jordan 1917

Diagnosis. Members of the Apogoninae: dorsal fin VI–I,9; anal fin II,8–9; head and body with ctenoid scales; pored lateral-line scales 24; preopercle ridge smooth, edges serrate; three supraneurals; supramaxilla absent; basisphenoid present; anterior pair of uroneurals; three epurals; five free hypurals; parhypural separate; two autogenous haemal spines; one supernumerary dorsal spine; caudal fin forked.

Other characteristics. first segmented fin-ray in second dorsal-fin branched, first anal-fin ray branched and segmented; second dorsal spine longest, very long and filamentous in some species of both genera; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; ctenoid scales on opercle and onto base of caudal fin; cycloid or ctenoid predorsal scales 1–3; pored lateral-line scales simple with one pore above and one below midline; pectoral-fin rays 13–17; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; developed gill rakers 7–38; unbranched procurent rays, longest segmented; 10+14 vertebrae; 8 ribs; 7–8 epipleurals; teeth in one, two or multiple rows on premaxilla, dentary, vomer, palatine, all villiform; six infraorbitals, bony shelf absent or on third infraorbital; stomach and intestine black with silvery peritoneum; low crest on PU2.

Distribution. Species of *Zoramia* are known from East Africa, Red Sea, islands in the Indian Ocean, throughout the West Pacific to Japan, onto the Pacific Plate to Marshall Islands, Samoa, Tonga, Solomon Islands, New Caledonia and Australia. Species of *Fibramia* are known from East Africa, some islands in the Indian Ocean, Sri Lanka, throughout the West Pacific to Philippines, Solomon Islands, Santa Cruz Islands, Fiji, Vanuatu, New Caledonia, Australia, Samoa and Tonga.

Remarks. This tribe contains two genera, a new genus *Fibramia* described below and *Zoramia*, corresponding to the clade VIII in the molecular trees (Figs. 2–6, Table 4). Both genera have species with elongate second dorsal spine, a single supernumerary dorsal spine, and can be found in tidal fresh and brackish water, near shore waters and in lagoons. *Fibramia* corresponds to the clade of *Ostorhinchus*-4 in the present study, and that of *Ostorhinchus* I in Mabuchi *et al.* (2006).

4. GENERA

Key to the genera of Apogonidae

Note this key uses external characters where possible to afford more use. Where the key is inclusive of all genera in a subfamily or a tribe that half of the couplet is so indicated.

1	Some pored lateral-line scales on body	3
-	No pored lateral-line scales or scales absent on body	2
2	Single dorsal fin, six spines [Paxtoninae]	<i>Paxton</i>
-	Two dorsal fins, seven spines (Gymnapogonini)	4
3	One pored lateral line, sometimes partially pored followed by pits or grooves	7
-	Two inconspicuous lateral-line scales, one dorsal (pored then notched), one ventral (notched) [Pseudamiinae]	<i>Pseudamia</i>
4	Scales present	5
-	Scales absent	<i>Gymnapogon</i>
5	Second dorsal fin I,8–9	6
-	Second dorsal fin I,12–13	<i>Lachneratus</i>
6	Anal rays 11–13	<i>Cercamia</i>
-	Anal rays 8 or 9	<i>Pseudamiops</i>
7	Silver or blackish band (bioluminous in life) along ventral side from hyal region extending past abdomen onto caudal peduncle (Siphamiini)	<i>Siphamia</i>
-	No such bioluminous bands	8
8	Longest procurrent caudal-fin rays segmented	10
-	Longest procurrent caudal-fin rays spinous, not segmented	9
9	Dorsal-fin rays 9; anal-fin rays 9	<i>Sphaeramia</i>
-	Dorsal-fin rays 13–15; anal-fin rays 12–14	<i>Pterapogon</i>
10	Dorsal-fin rays 8–13	11
-	Dorsal-fin rays 14–15; anal-fin rays 13–14	<i>Quinca</i>
11	Lateral-line scales less than 29	12
-	Lateral-line scales greater than 32 (Lepidamiini)	<i>Lepidamia</i>
12	Preopercular ventral edge ossified, serrated, crenulated or smooth	13
-	Preopercular ventral edge with unossified flap (Apogonini)	15
13	First three infraorbitals with upper edges smooth to crenulated	19
-	First three infraorbitals with upper edges strongly serrated (Pristiapogonini)	14
14	Dorsal fin VI–I,9; Dark spot on body below lateral line under first dorsal fin; dark spot(s) under posterior base of second dorsal fin; No stripe from snout onto opercle through eye	<i>Pristicon</i>
-	Dorsal fin VII–I,9; No spots on body below dorsal fins; Stripe from snout onto opercle through eye, may continue on body.	<i>Pristiapogon</i>
15	Predorsal scaled	16
-	Predorsal without scales along the center line to origin of first dorsal fin	<i>Astrapogon</i>
16	Anal-fin rays 8	17
-	Anal-fin rays 9	<i>Paroncheilus</i>
17	Stomach and intestine pale	18
-	Stomach and intestine black	<i>Zapogon</i>
18	Preopercular flap not extends past vertical edge	<i>Apogon</i>
-	Preopercular flap extends past vertical edge	<i>Phaeoptyx</i>
19	Supramaxilla large, easy to detect	20

-	Supramaxilla small difficult to detect or absent	23
20	First dorsal spines 7 or 8 [Amioidinae]	21
-	First dorsal spines 6 (Glossamiini)	22
21	Anal-fin rays 8; canine teeth; basicaudal bar	<i>Amioides</i>
-	Anal-fin rays 7; villiform teeth; spots on body	<i>Holapogon</i>
22	Preopercle edges serrate; only a basicaudal spot	<i>Yarica</i>
-	Preopercle edges smooth; body with many markings	<i>Glossamia</i>
23	Anal-fin rays 8–9	27
-	Anal-fin rays 10–19	24
24	Edge of preopercle serrated (Archamiini)	26
-	Edge of preopercle smooth (Rhabdamiini)	25
25	Anal fin rays 10–11; Dorsal fins VII–I, 10–11; Some canine teeth	<i>Rhabdamia (Bentuviaichthys)</i>
-	Anal-fin rays 12–13; Dorsal fins VI–I, 9; Villiform teeth	<i>Rhabdamia (Rhabdamia)</i>
26	Anal-fin rays 15–17; No bars or stripes on head or body; First dorsal-fin spine 1.1–1.4 in second dorsal-fin spine	<i>Archamia</i>
-	Anal-fin rays 12–19; two yellow bars on head, or 1–23 bars on body, or darkish or yellowish mid-line stripe; First dorsal spine 1.3–3.4 in second dorsal-fin spine	<i>Taeniamia</i>
27	No canine teeth; some lateral dentary teeth may be slightly enlarged	28
-	Canine and canoid teeth present (Cheilodipterini)	<i>Cheilodipterus</i>
28	First dorsal spines 6–8, if 6 spines then second dorsal-fin rays 8 or anal-fin rays 9	29
-	First dorsal spines 6; second dorsal-fin rays 9, anal-fin rays 8	<i>Fibramia</i>
29	First dorsal spines 6–8, if 6 spines then body with one or more stripes extending to caudal fin	32
-	First dorsal spines 6; no body stripes	30
30	Anal-fin rays 9; no cheek mark	31
-	Anal-fin rays 8; narrow or broad cheek mark	<i>Nectamia</i>
31	Preopercle edge serrate; caudal peduncle and/or caudal base with one small dark spot or diffuse large darkish region; no small dark snout mark	<i>Zoramia</i>
-	Preopercle edge smooth; no dark marks on caudal base or caudal peduncle; small dark snout mark	<i>Verulux</i>
32	Stomach and intestine pale; first dorsal spines 7 or 8	34
-	Stomach and intestine with melanophores to completely blackish; first dorsal spines 7	33
33	Fourth dorsal spine longer than third spine; caudal fin emarginate, truncate or rounded	<i>Jaydia</i>
-	Third dorsal spine longer than fourth, if fourth longer then caudal fin forked (Ostorhinchini)	<i>Ostorhinchus</i>
34	Edge of preopercle serrated	38
-	Edge of preopercle smooth	35
35	Palatine teeth absent	36
-	Palatine teeth present	<i>Foa</i>
36	Pored lateral-line scales from posttemporal to base of caudal fin	37
-	Pored lateral-line scales usually short, only pits present past dorsal fins	<i>Fowleria</i>
37	First dorsal fin with 8 spines, or dark mark on opercle if 7 spines	<i>Neamia and Fowleria*</i>
-	*Species of <i>Neamia</i> have fused hypurals 2 + 3 and 4 + 5; Species of <i>Fowleria</i> have 5 free hypurals	
-	No dark mark on opercle	<i>Apogonichthys</i>
38	Posttemporal serrate; basisphenoid present	<i>Apogonichthyoides</i>
-	Posttemporal smooth; basisphenoid absent	<i>Vincentia</i>

***Fibramia* new genus Fraser & Mabuchi**

Figure 8

Type species *Apogon thermalis* Cuvier in Cuvier & Valenciennes, 1829, holotype MNHN 8686; 54.7 mm SL, Sri Lanka, Trincomalee, Reynaud.

Diagnosis. A member of the Apogoninae; dorsal fin VI+I,9; anal fin II,8; developed gill rakers 16–25; posttemporal edge smooth; anterior naris tubular; black dorsal spine membranes of the first, most of the second and distal part of the third membranes with the remainder of the fin pale; discreet or diffuse dark or silvery midline body stripe ending in a basicaudal spot smaller than the pupil of the eye; intestine and stomach pale with tiny melanophores, peritoneum pale.

Other characteristics. one supernumerary dorsal spine; one supernumerary anal spine; first segmented fin-ray in second dorsal-fin branched, first anal fin-ray branched and segmented; ctenoid scales on predorsal, cheek, breast, two pelvic scales, and body; cycloid scale on opercle and onto base of caudal fin; pored lateral-line scales simple with one pore above and one below midline; caudal fin forked; 9+8 segmented principal caudal rays, 15 branched, upper and lower unbranched; unbranched procurrent rays, longest segmented; teeth on premaxilla,

dentary, vomer, palatine, all villiform; preopercle ridge smooth, preopercle edges ossified and serrated; infraorbitals smooth; six infraorbitals, bony shelf on third infraorbital; supramaxilla absent; basisphenoid present; anterior ceratohyal notched; three supraneurals; 10+14 vertebrae; 8 ribs; 8 epipleurals; 5 free hypurals, 3 epurals; reduced second pair of uroneurals; free parhypural; low crest on PU2.

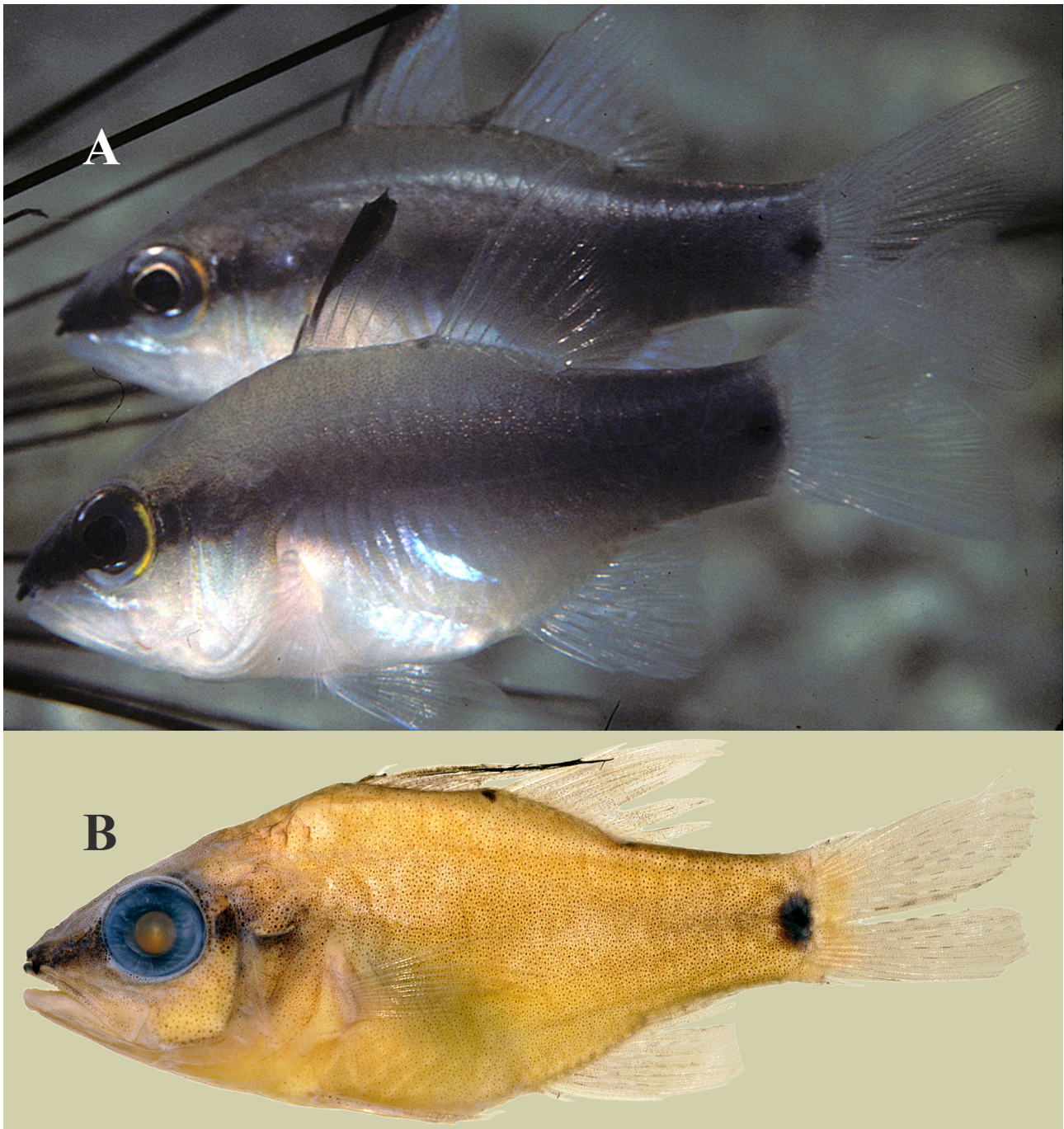


FIGURE 8. *Fibramia thermalis*. A. Live adults taken at Gilimanuk, Bali, Indonesia, about 50 mm by J.E. Randall. B. Preserved in 70% ethanol, USNM 361694, 50.2 mm SL, Vanuatu, Efate I., Emten Lagoon, by T. Fraser.

Etymology. A combination of the feminine Latin *fibra* meaning thread or filament and the feminine Greek *amia* often applied as an ending for some cardinalfish genera as well as an incorrect past usage as a cardinalfish genus. The name refers to two characteristics of the species in this genus, an elongate second dorsal spine in one species and the narrow, pale or dark mid-line on the body of two species.

Remarks. Three recognized species, *Apogon amboinensis* Bleeker 1853, *Apogon lateralis* Valenciennes 1832 and *Apogon thermalis* Valenciennes 1832, all described in *Apogon* belong in the new genus. There is one or

possibly two new species in this group. Fraser (1972) treated these three species in the subgenus *Nectamia*. Gon (1987) revived *Ostorhinchus* which replaced *Nectamia*. Fraser (2008) later recognized *Nectamia* as a genus for a different group of apogonids. Mabuchi *et al.* (2006, Fig. 2) using a molecular analysis, hypothesized that these species (*Apogon thermalis* and *A. amboinensis* were included with the former species referred to as *Apogon sangiensis*) were related to species of *Zoramia* Jordan 1971 as *Ostorhinchus* I. That hypothesized relationship holds for the molecular analyses reported here (clade VIII in the molecular trees).

The dorsal and anal fins of these three species share a VI+I,9 in the dorsal fin and II,8 in the anal fin. Species of *Zoramia* shares the VI+I,9 dorsal fins but have one more anal ray II,9. Adults of *thermalis* have a somewhat elongated second dorsal spine similar to some species of *Zoramia*. All species of *Fibramia* have black dorsal spine membranes of the first, most of the second and distal part of the third membranes with the remainder of the fin pale. No species of *Zoramia* has a black mark in the first dorsal fin (Fraser & Lachner 1985; Kuitert & Kozawa 1999; Greenfield *et al.* 2005). All species of *Fibramia* have a discreet or diffuse midline body stripe ending in a basicaudal spot smaller than the pupil of the eye. No species of *Zoramia* has a midline stripe, rather those species with body markings have bars while the others have no bars or stripes. The intestine and stomach are pale for species of *Fibramia* and blackish for all species of *Zoramia*. Species of *Fibramia* have an ossified shelf on the third infraorbital while species of *Zoramia* lack this shelf. Species of *Fibramia* have 16–25 developed gill rakers while species of *Zoramia* have 24–32 developed gill rakers.

Fibramia and *Zoramia* are sister genera recognized in the new tribe Zoramiini.

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APPENDIX A. A list of valid species in Apogonidae allocated to subfamilies, tribes and genera in alphabetical order. Known undescribed species are not included. Some species have uncertain status and are so noted. Break down to subgenera or species groups is not provided. Junior synonyms are not shown. The authors and dates are given but not cited in the literature section. For complete citations see Catalog of Fishes online (<http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>)

Subfamily Amioidinae (2 genera, 2 species)

Amioides Smith & Radcliffe in Radcliffe 1912 (1 species)

polyacanthus (Vaillant 1877)

Holapogon Fraser 1973 (1 species)

maximus (Boulenger 1888)

Subfamily Apogoninae (34 genera, 348 species)

Tribe Apogonichthyini (5 genera, 29 species)

Apogonichthys Bleeker 1854 (4 species)

landoni Herre 1934

ocellatus (Weber 1913)

perdix Bleeker 1854

waikiki Jordan & Evermann 1903 status uncertain

Foa Jordan & Evermann in Jordan & Seale 1905 (8 species)

albimaculosa (Kailola 1976) new genus, in press

brachygramma (Jenkins 1903)

fo Jordan & Seale 1905

hyalina (Smith & Radcliffe in Radcliffe 1912)

leisi Fraser & Randall 2011

longimana Weber 1909 - status uncertain

madagascariensis Petit 1931

nivosa Fraser & Randall 2011

Fowleria Jordan & Evermann 1903 (8 species)

aurita (Valenciennes in Cuvier & Valenciennes 1831)

flammea Allen 1993

isostigma (Jordan & Seale 1906)

marmorata (Alleyne & Macleay 1877)

polystigma (Bleeker 1854)

punctulata (Rüppell 1838)

vaiulae (Jordan & Seale 1906)

variegata (Valenciennes 1832)

Neamia Smith & Radcliffe in Radcliffe 1912 (4 species)

articycla Fraser & Allen 2006

notula Fraser & Allen 2001

octospina Smith & Radcliffe in Radcliffe 1912

xenica Fraser 2010

Vincentia Castelnau 1872 (5 species)

badia Allen 1987

conspersa (Klunzinger 1872) vertebrae 10+15

noaehollandiae (Valenciennes 1832) vertebrae 10+15

punctata (Klunzinger 1879)

macrocauda Allen 1987

Tribe Apogonini (5 genera, 59 species)

Apogon Lacepède 1801 (50 species)

americanus Castelnau 1855
atradorsatus Heller & Snodgrass 1903
atricaudus Jordan & McGregor in Jordan & Evermann 1898
aurolineatus (Mowbray in Breder 1927)
axillaris Valenciennes 1832
binotatus (Poey 1867)
campbelli Smith 1949
cardinalis (Seale 1910) uncertain if a senior synonym
caudicinctus Randall & Smith 1988
coccineus Rüppell 1838
crassiceps Garman 1903
dammermani Weber & de Beaufort 1929
deetsie Randall 1998
dianthus Fraser & Randall 2002
doryssa (Jordan & Seale 1906)
dovii Günther 1862
erythrinus Snyder 1904
erythrosoma Gon & Randall 2003
gouldi Smith-Vaniz 1977
guadalupensis (Osburn & Nichols 1916) may be junior to *atricaudus*
hypselonotus Bleeker 1855 - uncertain if a senior synonym
imberbis (Linnaeus 1758)
indicus Greenfield 2001
kautamea Greenfield & Randall 2004
kominatoensis Ebina 1935 uncertain if a senior synonym
lachneri Böhlke 1959
lativittatus Randall 2001
leptocaulus Gilbert 1972
maculatus (Poey 1860)
marquesensis Greenfield 2001
mosavi Dale 1977
pacificus (Herre 1935)
phenax Böhlke & Randall 1968
pillionatus Böhlke & Randall 1968
planifrons Longley & Hildebrand 1940
posterofasciatus Allen & Randall 2002
pseudomaculatus Longley 1932
quadrisquamatus Longley 1934
retrosella (Gill 1862)
robbyi Gilbert & Tyler 1997
robinsi Böhlke & Randall 1968
rubellus (Smith 1961)
rubrifuscus Greenfield & Randall 2004
seminigracaudus Greenfield 2007
semiornatus Peters 1876
susanae Greenfield 2001
talboti Smith 1961
townsendi (Breder 1927)
tricinctus (Allen & Erdmann 2012)
unicolor Steindachner & Döderlein 1883

Astrapogon Fowler 1907 (3 species)

alutus (Jordan & Gilbert 1882)
puncticulatus (Poey 1867)
stellatus (Cope 1867)

Paroncheilus Smith 1964 (1 species)

affinis (Poey 1875)

Phaeoptyx Fraser & Robins 1970 (3 species)

conklini (Silvester 1915)

pigmentaria (Poey 1860)

xenus (Böhlke & Randall 1968)

Zapogon Fraser 1972 (2 species)

evermanni (Jordan & Snyder 1904)

isus (Randall & Böhlke 1981)

Tribe Archamiini (2 genera, 16 species)

Archamia Gill 1863 (1 species)

bleekeri Günther 1859)

Taeniamia Fraser 2013 (15 species)

ataenia (Randall & Satapoomin 1999)

biguttata (Lachner 1951)

bilineata (Gon & Randall 1995)

buruensis (Bleeker 1856)

flavofasciata (Gon & Randall 2003)

fucata (Cantor 1849)

kagoshimamus (Döderlein in Steindachner & Döderlein 1883)

leai (Waite 1916)

lineolata (Cuvier in Cuvier & Valenciennes 1828)

macroptera (Cuvier in Cuvier & Valenciennes 1828)

melasma (Lachner & Taylor 1960)

mozambiquensis (Smith 1961)

pallida (Gon & Randall 1995)

sansibaricus (Pfeffer 1893)

zosterophora (Bleeker 1856)

Tribe Cheilodipterini (1 genus, 17 species)

Cheilodipterus Lacepède 1801 (17 species)

alleni Gon 1993

arabicus (Gmelin 1789)

artus Smith 1961

intermedius Gon 1993

isostigmus (Schultz 1940)

lachneri Klausewitz 1959

macrodon (Lacepède 1802)

nigrotaeniatus Smith & Radcliffe in Radcliffe 1912

novemstriatus (Rüppell 1838)

octovittatus Cuvier in Cuvier & Valenciennes 1828

parazonatus Gon 1993

persicus Gon 1993

pygmaios Gon 1993

quinquelineatus Cuvier in Cuvier & Valenciennes 1828

singaporensis Bleeker 1860

subulatus Weber 1909

zonatus Smith & Radcliffe in Radcliffe 1912

Tribe Glossamiini (2 genera, 13 species)

Glossamia Gill 1863 (11 species)

abo (Herre 1935)

aprion (Richardson 1842)

argumi Hadiaty & Allen 2011

beauforti (Weber 1907)

gjellerupi (Weber & de Beaufort 1929)

heurni (Weber & de Beaufort 1929)

narindica Roberts 1978

sandei (Weber 1907)

timika Allen, Hortle & Renyaan 2000

trifasciata (Weber 1913)
wichmanni (Weber 1907)

Yarica Whitley 1930 (2 species)
hyalosoma (Bleeker 1852)
torresiensis (Castelnau 1875) species uncertain

Tribe Gymnapogonini (4 genera, 15 species)

Cercamia Randall & Smith 1988 (2 species)
cladara Randall & Smith 1988
eremia (Allen 1987) vertebrae 9+15

Gymnapogon Regan 1905 (7 species)

africanus Smith 1954
annona (Whitley 1936)
foraminosus (Tanaka 1915)
japonicus Regan 1905
melanogaster Gon & Golani 2002
philippinus (Herre 1939)
vanderbilti (Fowler 1938) *urosipilotus* (Lachner 1953) is a junior synonym or cryptic species complex

Lachneratus Fraser & Struhsaker 1991 (1 species)
phasmaticus Fraser & Struhsaker 1991

Pseudamiops Smith 1954 (5 species)

diaphanes Randall 1998
gracilicauda (Lachner 1953)
pellucidus Smith 1954
phasma Randall 2001
springeri Gon, Bogorodsky & Mal 2013

Tribe Lepidamiini (1 genus, 4 species)

Lepidamia Gill 1863 (4 species)
kalosoma (Bleeker 1852)
multitaeniata (Cuvier in Cuvier & Valenciennes 1828)
natalensis (Gilchrist & Thompson 1908)
omanensis (Gon & Mee in Gon 1995)

Tribe Ostorhinchini (1 genus, 93 species)

Ostorhinchus Lacepède 1802 (93 species)
angustatus (Smith & Radcliffe 1912)
aphanes Fraser 2012
apogonoides (Bleeker 1856)
aroubiensis (Hombron & Jacquinot in Jacquinot & Guichenot 1853)
aterrimus (Günther 1867)
atrogaster (Smith & Radcliffe in Radcliffe 1912)
aureus (Lacepède 1802)
brevispinis (Fraser & Randall 2003)
bryx (Fraser 1998)
capricornis (Allen & Randall 1993)
cavitensis (Jordan & Seale 1907)
chalcus (Fraser & Randall 1986)
cheni (Hayashi 1990)
chrysopomus (Bleeker 1854)
chrysotaenia Bleeker 1851
cladophilos (Allen & Randall 2002)
compressus (Smith & Radcliffe in Radcliffe 1912)
cookii (Macleay 1881)
cyanosoma (Bleeker 1853)
cyanotaenia (Bleeker 1853)
dispar (Fraser & Randall 1976)
diversus (Smith & Radcliffe 1912)

doederleini (Jordan & Snyder 1901)
endekataenia (Bleeker 1852)
fasciatus (Shaw in White 1790)
flagelliferus Smith 1961
flavus (Allen & Randall 1993)
fleurieu Lacepède 1802
franssedai (Allen Kuitert & Randall 1994)
fukuii (Hayashi 1990)
gularis (Fraser & Lachner 1984)
griffini (Seale 1910) may be junior to *urostigmus*
hartzfeldii (Bleeker 1852)
heptastygma (Cuvier in Cuvier & Valenciennes 1828)
hoevenii (Bleeker 1854)
holotaenia (Regan 1905)
ishigakiensis (Ida & Moyer 1974)
jenkinsi (Evermann & Seale 1907)
kiensis (Jordan & Snyder 1901)
komodoensis (Allen 1998)
leptofasciatus (Allen 2001)
leslie Schultz & Randall 2006
limenus (Randall & Hoese 1988)
lineomaculatus (Allen & Randall 2002)
luteus (Randall & Kulbicki 1998)
maculiferus (Garrett 1864)
magnifica (Seale 1910) status uncertain
margaritophorus (Bleeker 1854)
melanoproctus (Fraser & Randall 1976)
melanopterus (Fowler & Bean 1930) uncertain if valid
microspilos (Allen & Randall 2002)
moluccensis (Valenciennes 1832)
monospilus (Fraser Randall & Allen 2002)
multilineatus (Bleeker 1874)
mydrus (Jordan & Seale 1905) status uncertain
nanus (Allen Kuitert & Randall 1994)
neotes (Allen Kuitert & Randall 1994) uncertain subgenus *Brephamia*
nigricans (Day 1875) - status uncertain
nigripes (Playfair in Playfair & Günther 1867)
nigrocinctus (Smith & Radcliffe in Radcliffe 1912)
nigrofasciatus (Lachner 1953)
norfolcensis (Ogilby 1888)
notatus (Houttuyn 1872)
noumeae (Whitley 1958)
novemfasciatus (Cuvier & Valenciennes 1828)
ocellicaudus (Allen Kuitert & Randall 1994)
oxina (Fraser 1999)
oxygrammus (Allen 2001)
parvula (Smith & Radcliffe in Radcliffe 1912) subgenus *Brephamia*
pallidofasciatus (Allen 1987)
pleuron (Fraser 2005)
popur (Montrouzier 1857) status uncertain
properuptus (Whitley 1964)
pselion (Randall Fraser & Lachner 1990)
quinquestriatus (Regan 1908)
radcliffei (Fowler 1918)
regula (Fraser & Randall 2003)
relativus (Randall 2001)
rubrimacula (Randall & Kulbicki 1998)
rueppellii (Günther 1859)
rufus (Randall & Fraser 1999)
schlegeli (Bleeker 1854)
sealei (Fowler 1918)

selas (Randall & Hayashi 1990)
semilineatus (Temminck & Schlegel 1842)
septemstriatus (Günther 1880)
sinus (Randall 2001)
spilurus (Regan 1905)
taeniophorus (Regan 1908)
urostigmus (Bleeker 1874)
victoriae (Günther 1859)
wassinki (Bleeker 1861)
wilsoni (Fowler 1918)

Tribe Pristiapogonini (2 genera, 10 species)

Pristiapogon Klunzinger 1870 (7 species)
abrogramma (Fraser & Lachner 1985)
exostigma (Jordan & Starks in Jordan & Seale 1906)
fraenatus (Valenciennes 1832)
kallopterus (Bleeker 1856)
menesemus (Jenkins 1903) status uncertain
taeniopterus (Bennett 1836)
unitaeniatus (Allen 1995) generic placement uncertain, 10+16 vertebrae

Pristicon Fraser 1972 (3 species)

rhodopterus (Bleeker 1852)
rufus (Randall & Fraser 1999)
trimaculatus (Cuvier in Cuvier & Valenciennes 1828)

Tribe Rhabdamiini (1 genus, 5 species)

Rhabdamia Weber 1909 (5 species)
clupeiformis Weber 1909
gracilis (Bleeker 1856)
nigrimentum (Smith 1961) subgenus *Bentuviaichthys*
nuda (Regan 1905) *mentalis* (Evermann & Seal 1907) may be a junior synonym
spilota Allen & Kuitert 1994

Tribe Siphamiini (1 genus, 23 species)

Siphamia Weber 1909 (23 species)
arabica Gon & Allen 2012
argentea Lachner 1953
brevilux Gon & Allen 2012
cephalotes (Castelnau 1875)
corallicola Allen 1993
cuneiceps Whitley 1941
cyanophthalma Gon & Allen 2012
elongata Lachner 1953
fistulosa (Weber 1909)
fraseri Gon & Allen 2012
fuscolineata Lachner 1953
goreni Gon & Allen 2012
guttulatus (Alleyne & Macleay 1877)
jebbi Allen 1993
majimai Matsubara & Iwai 1958
mossambica Smith 1955
randalli Gon & Allen 2012
roseigaster (Ramsay & Ogilby 1887)
senoui Gon & Allen 2012
spinicola Gon & Allen 2012
stenotes Gon & Allen 2012
tubifer Weber 1909
tubulata (Weber 1909)

Tribe Sphaeramiini (6 genera, 54 species)

Apogonichthyoides Smith 1949 (24 species)

atripes (Ogilby 1916)
brevicaudatus (Weber 1909)
cantoris (Bleeker 1851)
cathetogramma (Tanaka 1917)
chrysurus (Ogilby 1889)
enigmaticus Smith 1961
erdmanni Fraser & Allen 2011
euspilotus (Fraser 2006)
gardineri (Regan 1908)
heptastygma (Cuvier in Cuvier & Valenciennes 1828)
niger (Döderlein in Steindachner & Döderlein 1883)
nigripinnis (Cuvier in Cuvier & Valenciennes 1828)
maculipinnis (Regan 1908)
melas (Bleeker 1848) uncertain placement
miniatus Fraser 2010
opercularis (Macleay 1878)
pharaonis (Bellotti 1874)
pseudotaeniatus (Gon 1986)
regani (Whitley 1951)
sialis (Jordan & Thompson 1914)
taeniatus (Cuvier in Cuvier & Valenciennes 1828)
timorensis (Bleeker 1854)
uninotatus (Smith & Radcliffe in Radcliffe 1912)
umbratilis Fraser & Allen 2010

Jaydia Smith 1961 (17 species)

albomarginatus (Smith & Radcliffe in Radcliffe 1912)
argyrogaster (Weber 1911)
carinatus (Cuvier in Cuvier & Valenciennes 1828)
catalai (Fourmanoir 1973)
hungi (Fourmanoir & Do-Thi 1965)
lineata (Temminck & Schlegel 1842)
melanopus (Weber 1911)
novaeguineae (Valenciennes 1832)
photogaster (Gon & Allen 1998)
poecilopterus (Cuvier in Cuvier & Valenciennes 1828)
quartus (Fraser 2000)
queketti (Gilchrist 1903)
smithi Kotthaus 1970
striata (Smith & Radcliffe in Radcliffe 1912)
striatodes (Gon 1997)
tchefouensis (Fang 1942) status not clear if senior to *striatodes* or junior to *lineata*
truncata (Bleeker 1854) *elliotti* (Day 1875) is a junior synonym

Nectamia Jordan 1917 (9 species)

annularis (Rüppell 1829)
bandanensis (Bleeker 1854)
fusca (Quoy & Gaimard 1825)
ignitops Fraser 2008
luxuria Fraser 2008
savayensis (Günther 1872)
similis Fraser 2008
viria Fraser 2008
zebrinus (Fraser Randall & Lachner 1999)

Pterapogon Koumans 1933 (1 species)

kauderni Koumans 1933

Quinca Mees 1966 (1 species)

mirifica Mees 1966

Sphaeramia Fowler & Bean 1930 (2 species)
orbicularis (Cuvier in Cuvier & Valenciennes 1828)
nematoptera (Bleeker 1856)

Tribe Veruluxini (1 genus, 1 species)

Verulux Fraser 1972 (1 species)
cypselurus (Weber 1909)

Tribe Zoramiini (2 genera, 9 species)

Fibramia Fraser & Mabuchi 2014 (3 species)
amboinensis (Bleeker 1853)
lateralis (Valenciennes 1832)
thermalis (Cuvier in Cuvier & Valenciennes 1829)

Zoramia Jordan 1917 (6 species)

flebila Greenfield Langston & Randall 2005
fragilis (Smith 1961)
gilberti (Jordan & Seale 1905)
leptacantha (Bleeker 1856-57)
perlita (Fraser & Lachner 1985)
viridiventer Greenfield Langston & Randall 2005

Subfamily Paxtoninae (1 genus, 1 species)

Paxton Baldwin & Johnson 1999 (1 species)
concilians Baldwin & Johnson 1999

Subfamily Pseudamiinae (1 genus, 7 species)

Pseudamia Bleeker 1865 (7 species)
amblyuroptera (Bleeker 1856)
gelatinosa Smith 1956
hayashii Randall, Lachner & Fraser 1985
nigra Allen 1992
rubra Randall & Ida 1993
tarri Randall, Lachner & Fraser 1985
zonata Randall, Lachner & Fraser 1985