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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

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

noeahollandiae (Valenciennes 1832) vertebrae 10+15

punctata (Klunzinger 1879)

macrocauda Allen 1987