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Bodianus atrolumbus (Valenciennes 1839), a valid species of labrid fish from the southwest Indian Ocean

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Abstract

Bodianus atrolumbus (Valenciennes 1839), a labrid fish of the southwest Indian Ocean (type locality Mauritius), was placed in the synonymy of *B. perditio* (Quoy & Gaimard), antitropical in the Pacific Ocean (type locality Tonga), by Smith (1949) who reported the first record for southern Africa. Juveniles of both species are mostly the same in color, featuring a white bar in the middle of the body, followed dorsally by a large black area. The white bar develops into an oval yellow area dorsally on the body in *B. perditio*, whereas it narrows to a spindle-shaped whitish to pink mark on the upper body that extends below the lateral line in *B. atrolumbus*. An analysis of the mitochondrial DNA barcode sequence (COI) from specimens collected from all quadrants of the the species' range reveals that the two species are 3.91% different (K2P minimum interspecific distance), while intraspecific variation is no more than 0.34%. A phenetic tree of barcode sequences for twenty *Bodianus* species is presented, showing that pairwise species differences range from 1.97% to 21.74%, with Indian/Pacific sibling-species pairs accounting for the lower range of divergences (1.97% to 4.64%). A modal difference in the count of gill rakers and the distinctly shorter pectoral fins of *B. atrolumbus* additionally differentiate it from *B. perditio*.

Key words: Labridae, coral reef fishes, phylogenetics, DNA barcoding, biogeography, taxonomy, sibling species

Introduction

The labrid fish genus *Bodianus* is represented by at least 44 species in the tropical to warm temperate seas of the world, making it the third largest genus of the family Labridae, following *Halichoeres* and *Cirrhilabrus*. Only five species of *Bodianus* are reported from the Atlantic Ocean and two for the eastern Pacific, while at least 37 occur in the rest of the Indo-Pacific. The species range in size from the diminutive *Bodianus bimaculatus* Allen, of which the largest specimen measures 59 mm standard length, to *B. macrognathos* (Morris), reported to 595 mm SL.

The genus was ably revised and beautifully illustrated by Gomon (2006), whose experience with the genus dates to 1979 when it was the subject of his PhD thesis at the University of Miami in Florida (the first author was a reviewer of the thesis). Gomon (2006) has now divided *Bodianus* into 10 subgenera, seven of them taking names of generic synonyms. Eight species were described as new. Distribution maps are provided for all species.

Gomon's Figure 54 is a distribution map that includes *Bodianus perditio* (Quoy & Gaimard), with a disjunct population: KwaZulu-Natal, Mauritius, Réunion, and St. Brandon's Shoals in southwest Indian Ocean, and antitropical in the Pacific from southern Japan in the north to southern Queensland, New South Wales and Lord Howe Island in the south. It ranges east in the South Pacific to New Caledonia, Tonga (type locality), Rapa, and Mangareva in the Tuamotu Archipelago. The very similar *Bodianus solatus*, described as new by Gomon from Western Australia, is reported from "between the Monte Bello Islands and the Houtman Abrolhos", hence within the latitudes of 20° and 30°S. However, his distribution map includes one symbol for *B. solatus* at the northernmost point of Western Australia. This is evidently intended for the record of *B. solatus* from the Northwest Shelf of Australia, misidentified as *Bodianus perditio* by Gloerfelt-Tarp and Kailola (1984: 233, fig. on adjacent plate) and by Sainsbury *et al*. (1984: 256, fig. on adjacent plate). An additional specimen of *B. solatus* was collected in 1995 in the nearby Arafura Sea at about 10 °S (AMS I.37182).

The distributions of both *Bodianus perditio* and its W. Indian Ocean sibling species are noteworthy in lacking any low-latitude records. Smith (1949: 287, pl. 52, fig. 776) reported what he believed to be the first record of *B. perditio* for southern Africa at Delagoa Bay (now Maputo Bay), Mozambique (26°S). Randall (1986: 688, fig. 221.10, pl. 90) added records from Natal (KwaZulu-Natal) and St. Brandon's Shoals in the Indian Ocean at 16–17°S. In the Pacific, *B. perditio* is almost antitropical, with no record south of Taiwan at 22°N (Shao 2013), and none north of Efate, Vanuatu at 17.8°S (collected by Grant Norton). The present distribution and DNA sequence data indicate that *B. perditio* of the Pacific has been isolated from the southwestern Indian Ocean population for a very long time.

Juveniles in both the SW Indian Ocean and Pacific populations are similar in color, with a narrow white bar from the base of the ninth dorsal spine extending down to the front of the anal fin, followed by a large black area dorsally on the body and extending onto most of the scaly basal sheath posteriorly on the dorsal fin. Adults in the Indian Ocean replace the white bar of the juvenile on midside of body with a lanceolate, pale pink streak extending well below the lateral line. Adults in the Pacific lose the ventral part of the white bar of the juvenile, the upper part enlarging to an oval, pale yellow spot, mostly above the lateral line.

Only Kuiter (2010: 36) has listed *Bodianus atrolumbus* as a valid species in his pictorial review of labrid fishes. We provide here the documentation to fully establish its validity based on color pattern, morphology, and mtDNA sequence differences. The recent development of large-scale DNA sequencing programs, such as the Barcode of Life project (www.boldsystems.org), permits comparisons between and among populations and species and can assist in establishing the validity of species by assessing the degree to which populations are reproductively isolated and, along with additional genetic analyses, an estimate of the time since the populations split.

Materials and Methods

Specimens have been examined at, or obtained on loan from, the Bernice P. Bishop Museum, Honolulu (BPBM); South African Institute for Aquatic Biodiversity, Grahamstown, South Africa (SAIAB), and the United States National Museum of Natural History (USNM).

Lengths of specimens are given as standard length (SL), measured from the median end of the upper lip or upper canine teeth, whichever is more anterior, to the base of the caudal fin (posterior end of hypural plate); head length is measured from the same anterior point to the posterior end of the opercular flap, and upper-jaw length from the same anterior point to the posterior end of the maxilla; body depth is the greatest depth from the base of the dorsal spines to the ventral margin of the abdomen (correcting for any obvious malformation of preservation);

body width is taken just posterior to the gill opening; orbit diameter is the greatest fleshy diameter; interorbital width the least bony width; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and base of the caudal fin; lengths of spines and rays of median fins are measured to their extreme bases; caudal concavity is the horizontal distance between tips of the longest and shortest rays; pectoral-fin length is the length of the longest ray to the extreme base (average taken of the two fins when different); pelvic-fin length is measured from the base of the pelvic spine to the tip of the longest ray.

Counts of pectoral-fin rays include the rudimentary upper ray. Lateral-line scale counts do not include the one or two pored scales on the base of the caudal fin. Gill-raker counts include rudiments.

DNA extractions and sequencing were performed at the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Ontario, Canada, using the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. A 652-bp segment was amplified from the 5′ region of the mitochondrial COI gene using a variety of primers (Ivanova *et al.* 2007). PCR amplifications were performed in 12.5 µl volume including 6.25 µl of 10% trehalose, 2 µl of ultra pure water, 1.25 µl of 10× PCR buffer (10mM KCl, 10mM (NH4)2SO4, 20mM Tris-HCl (pH8.8), 2mM MgSO4, 0.1% Triton X-100), 0.625 µl of MgCl2 (50mM), 0.125 µl of each primer (0.01mM), 0.0625 µl of each dNTP (10mM), 0.0625 µl of *Taq* DNA polymerase (New England Biolabs), and 2 µl of template DNA. The PCR conditions consisted of 94°C for 2 min., 35 cycles of 94°C for 30 sec., 52°C for 40 sec., and 72°C for 1 min., with a final extension at 72°C for 10 min.

Specimen information, the barcode sequence data, and the phenetic tree analysis for this study were compiled using the Barcode of Life Data Systems (BOLD, www.barcodinglife.org; Ratnasingham & Hebert 2007). The sequence data used for statistics and the tree are publicly accessible on BOLD and GenBank. Sequence divergence was calculated using BOLD with the Kimura 2-parameter (K2P) model and a pairwise model. The phenetic tree was calculated from a Kimura 2-parameter (K2P) model which generated a mid-point rooted neighbor-joining (NJ) phenogram to provide a graphic representation of the species divergence.

Bodianus atrolumbus (Valenciennes *in* Cuvier & Valenciennes 1839)

Figures 1–3; Table 1

Cossyphus atrolumbus Valenciennes *in* Cuvier & Valenciennes 1839: 123 (Mauritius); Günther 1862: 105 (Mauritius); Bauchot 1963: 27 (holotype, MNHN A.8262, 183 mm SL, dried skin).

Cossyphus nigromaculatus Gilchrist & Thompson 1908: 197 (Durban).

Chaeropsodes pictus Gilchrist & Thompson 1909: 260 (Durban).

Lepidaplois perditio Smith 1949: 287, pl. 52, fig. 776 (Delagoa Bay); Baissac 1953: 224 (Mauritius); Fourmanoir & Guézé 1961: 7 (Mauritius, Réunion).

Bodianus perditio Baissac 1976: 213 (Mauritius); van der Elst 1981: 189, fig. (Mozambique to Durban); Randall 1982: 203 (antitropical); Gomon in Fischer & Bianchi 1984: unnumbered pages (Mauritius, Réunion, St. Brandon's Shoals, and Natal Coast, KwaZulu-Natal); Randall in Smith & Heemstra 1986: 688, pl. 90, fig. 220.10 (Mauritius, Réunion, St. Brandon's Shoals, and northern Mozambique to KwaZulu-Natal); Debelius 1993: 219, lower fig. (his illustration is *Bodianus perditio* from the Pacific); Lieske & Myers 1994: 90, figs. (juvenile and adult; Mozambique to South Africa and Mauritius); Fricke 1999: 400 (annotated checklist); Heemstra & Heemstra 2004: 339 (Mozambique to Aliwal Shoal, South Africa); E. Heemstra *et al*. 2004: 3325 (Rodrigues, Mascarene Islands); Gomon 2006: 87, figs 7b, 53-54, pls 8J, 9A-B (taxonomy); Taquet & Diringer 2012: 460, middle fig. (Indian Ocean).

Bodianus atrolumbus Kuiter 2010: 36, 4 figs. (Indian Ocean, Mozambique to Aliwal Shoal, Mauritius, and Réunion).

Diagnosis. Dorsal rays XII,10; anal rays III,11; pectoral rays 17; lateral line smoothly curved, following dorsal contour of body, the pored scales 30 or 31; scales above origin of lateral line to origin of dorsal fin 8; predorsal scales small, becoming embedded anteriorly, ending in posterior interorbital; a patch of very small scales on cheek posterior to center of eye, except for the broad naked flange of the preopercle; no scales on lower jaw; a broad sheath of scales basally on median fins; total gill rakers 18–21; dorsal profile of snout to above eye straight, becoming smoothly convex on nape; snout length 2.7–3.0 in head length; orbit diameter varying from 4.7 in head length in an 88-mm specimen to 9.3 in a 430-mm specimen; mouth slightly oblique, forming an angle of about 20° to horizontal axis of body, the maxilla reaching to below anterior half of eye; front of jaws with two pairs of canine teeth that interdigitate when mouth closed, the middle pair of upper jaw and lateral pair of lower jaw largest and recurved, the middle pair of lower jaw about half length of lateral pair; side of jaws with a dental ridge of coalesced teeth bearing a row of small, stout, close-set, conical teeth, of which a series of five or six in middle of jaws are largest; no teeth on palate; labial flaps well-developed; dorsal spines progressively longer, the last spine 2.0–2.2 in head length, the membranes deeply incised; seventh or eighth dorsal soft ray longest, 2.0–2.1 in head length; third anal spine longest, about 2.0–2.4 in head length; caudal fin of juveniles truncate, of adults double emarginate with long pointed lobes; pectoral fins relatively short, 3.9–4.25 in SL; pelvic fins just reaching anus in 88-mm juvenile, reaching beyond third anal spine in a 360-mm adult. Diagnostic color differences from *B. perditio* include the central white bar of the juvenile narrowing to a spindle-shaped whitish to pink mark on the upper body extending below the lateral line (vs. a dorsal oval yellow spot) and the caudal peduncle of the juvenile with a white bar extending full width (vs. a central white patch surrounded by dark)(Figures 1–3). Reaches 57 cm.

Remarks. *Bodianus atrolumbus* is known from the three Mascarene Islands (type locality, Mauritius), St. Brandon's Shoals, KwaZulu-Natal, and southern Mozambique. It was placed in the synonymy of *B. perditio* (Quoy & Gaimard) by Smith (1949), followed by Gomon in Fischer and Bianchi (1984) and by Gomon (2006) in his revision of the genus.

Van der Elst (1981: 189) reported this species as a common fish of deeper rock and coral reefs of South Africa. He gave the diet as mainly sea urchins, crabs, gastropod mollusks, and other hard-shelled invertebrates, which are crushed in the powerful pharyngeal plates that are studded with large molariform teeth.

The usual common names for *Bodianus perditio* in the Pacific are Goldspot Wrasse, as indicated by Grant (1982: pl. 288), Goldspot Hogfish (Randall *et al*. 1990: 301), Golden-spot Pigfish (Kuiter 1993: 269), and Golden Spot Hogfish, the FAO English name (Westneat in Carpenter & Niem 2001: 3412). Van der Elst (1981: 189) used Goldsaddle Hogfish as the common name in South Africa, followed by Randall in Smith and Heemstra (1986: 339) and Heemstra and Heemstra (2004: 339). However, this is not appropriate, because the equivalent marking in adult *B. atrolumbus* is not yellow or golden but whitish to pale pink, nor does it reach the dorsal edge of the body. We propose the common name Palebar Hogfish for *B. atrolumbus*.

Gomon (2006: 89) wrote: "Three specimens at the MNHN are listed as syntypes of *C. atrolumbus* in the collection catalogue. MNHN A.8262 is here designated lectotype to affix the name should the Indian Ocean and Pacific Ocean populations prove to be taxonomically separate." However, Bauchot (1963: 27) already listed MNHN A.8262, a dried specimen 183 mm SL, as the holotype of *Cossyphus atrolumbus*.

Material of *Bodianus atrolumbus*. Mauritius, BPBM 20293, 195 mm. St. Brandon's Shoals, USNM 217848, 87.5 mm. South Africa, KwaZulu-Natal, Sodwana Bay, SAIAB 7397, 238 mm; Durban, SAIAB 43687, 2: 204-233 mm; Park Rynie, SAIAB 189242, 307 mm.

TABLE 1

Total gill-raker counts for specimens of *Bodianus*

	18	19	20	21	22	23
B. atrolumbus	1	3	4	2		
B. perditio			3	5	3	1

Figure 1. *Bodianus atrolumbus*, top: small juvenile, Sodwana Bay, KwaZulu-Natal, South Africa (D. King); middle: juvenile, Réunion (A. Diringer); bottom: 9 cm TL, KwaZulu-Natal, South Africa (D. King).

Figure 2. *Bodianus atrolumbus*, top: KwaZulu-Natal (D. Polack); middle: 15 cm TL, Rodrigues, Mascarenes, SAIAB 69529 (P. Heemstra); bottom: 28 cm TL, KwaZulu-Natal (D. King).

Figure 3. *Bodianus atrolumbus*, top: 30 cm TL, KwaZulu-Natal (D. King); middle: Réunion (A. Diringer); bottom: Réunion (A. Diringer).

Bodianus perditio (Quoy & Gaimard 1834)

Figures 4–6; Table 1

Labrus perditio Quoy & Gaimard 1834: 702, pl. 20, fig. 4 (Tongatapu); Bauchot 1963: 93 [holotype, 7 *pouces* (= 189.5 mm) has been lost].

Cossyphus perditio Valenciennes *in* Cuvier & Valenciennes 1839: 125 (Tongatapu).

Cossyphus atrolumbus [*non* Valenciennes] Günther 1862: 105, in part (Tongatapu, Minerva Reef, Saumarez Reefs, and Aneiteum); Günther 1881: 241 (same localities, except error for Zanzibar); Ogilby 1889: 66 (Lord Howe Island).

Trochocopus sanguinolentus De Vis 1883: 287 (Hutchinson Shoal, Cape Moreton, Queensland).

Cossyphus aurifer De Vis 1884: 146 (Moreton Bay, Queensland).

Cossyphus latro De Vis 1885: 878 (Moreton Bay, Queensland).

Lepidaplois perditio Jordan & Snyder 1902: 618, fig. 2 (Saikasaki, Wakanoura, Honshu, Japan); Jordan & Seale 1906: 293 (Tonga, Saumarez Reefs, Aneiteum, and Japan); Ogilby 1916: 184 (Snapper Banks off Moreton Bay, Queensland); Fowler & Bean 1928: 206 (Riu Kiu Islands); Chen, J.T.F. 1952: 104 (Taiwan).

Lepidaplois perdito Jordan, Tanaka & Snyder 1913: 198, fig. 144 (near Wakanoura, Japan); Fowler & Bean 1928: 328 (New Caledonia).

Bodianus perditio Matsubara 1964: 888, 892 (Japan); Yu 1968: 20, fig. 9 (Taichung, Pescadores, and Tainan, Taiwan); Masuda, Araga & Yoshino 1975: 295, pl. 102 E, F (Sagami Bay southward, Japan); Allen *et al*. 1976: 418 (Lord Howe Island); Grant 1982: 561, pl. 288 (southern Queensland, Australia); Randall 1982: 203 (*B. perditio* antitropical in the western and south Pacific); Yamakawa in Masuda *et al*. 1984: 203, pl. 196 B, C (Sagami Bay southward, Japan); Randall in Smith & Heemstra 1986: 688, pl. 90, fig. 220-10; Allen & Swainston 1988: 112, fig. 729 (Western Australia: Abrolhos northward); Randall, Allen & Steene 1990: 301, upper fig; Francis 1991: 214, fig. 30 (Norfolk Island); Kuiter 1993: 269, upper two figs. (southeast Australia; juveniles to rocky estuaries in New South Wales); Masuda & Kobayashi 1994: 249, figs. 6–8 (Ogasawara Islands and Izu Peninsula, Honshu, Japan); Kulbicki & Williams 1997: 19 (Ouvéa Atoll, Loyalty Islands); Okamura & Amaoka 1997: 470, middle column of figs. (Ogasawara Islands, Kochi Prefecture, and Amami-Oshima, Japan); Laboute & Grandperrin 2000: 351, 3 lower figs. (New Caledonia); Parenti & Randall 2000: 6 (antiequatorial: islands of southern Oceania and Taiwan to southern Japan); Randall 2005: 394 (western and southern Pacific); Bacchet, Zysman & Lefèvre 2006: 369, lower fig. (French Polynesia); Gomon 2006: 87, figs. 7b, 53-54, plates 8J, 9A & 9B (western and southern Pacific); Chen *et al*. 2010: 177, figs. G, H, and I (Kenting National Park, southern tip of Taiwan); Kuiter 2010: 37, 5 figs. (southern Japan to eastern Australia, ranging to Central Pacific); Nishiyama & Motomura 2012: 26-27, 7 figs. (Japan).

Diagnosis. The morphological diagnosis for *Bodianus perditio* is essentially the same as *B. atrolumbus*, and need not be repeated here. Diagnostic color differences from *B. atrolumbus* include the central white bar of the juvenile diminishing to an oval yellow spot above the lateral line (vs. a spindled whitish to pink mark extending below the lateral line) and the caudal peduncle of the juvenile with a central white patch surrounded by dark (vs. a white bar extending full width)(Figures 4–6). We have found one meristic difference to partially separate the two species: the number of gill rakers is 20–23 in *B. perditio* vs. 18–21 in *B. atrolumbus* (Table 1). Van der Elst (1981: 189) gave the gill-raker counts of South African material of *B. atrolumbus* as 17–20. Evidently he did not include the small rudiment at each end of the series of gill rakers. Furthermore, we have found a difference in the length of the pectoral fins of the two species. Nine specimens of *B. perditio* from the South Pacific, 159–320 mm SL, have a pectoral-fin length 3.4–3.8 in the standard length, the fin length proportionately longer with growth. In comparison, four specimens of *B. atrolumbus* within the same size range from South Africa have a pectoral-fin length 3.9–4.25 in the standard length. The pectoral-fin length of *B. atrolumbus* in Fig. 220.10 of Smith and Heemstra (1986: 688) also falls within this range. Reaches 53 cm (Grant 1982: 561).

Figure 4. *Bodianus perditio*, top: 3 cm, New Caledonia (J.E. Randall); middle: 4.5 cm, New Caledonia (J.E. Randall); bottom: 7.5 cm, New Caledonia (J.E. Randall).

Figure 5. *Bodianus perditio*, top: 25 cm, Mangareva (J.E. Randall); middle: 30 cm, Mangareva (J.E. Randall); bottom: 36 cm, New Caledonia (J.E. Randall).

Figure 6. *Bodianus perditio*, The bright yellow juvenile sold in the aquarium trade, frequently shipped out of Vanuatu (photo by Milan Kořínek, http://www.biolib.cz/en).

Genetics. DNA sequences were obtained from all quadrants of the range for the two sibling species: from South Africa for *Bodianus atrolumbus* and, for *B. perditio*, from Taiwan in the northern-Pacific antitropical range and in the southern Pacific from the western edge of the range in Queensland, Australia to the central population in New Caledonia and the easternmost population in Mangareva, in the Gambier Islands of French Polynesia. The barcode mitochondrial DNA sequences (COI) for the two species are 3.91% divergent (K2P minimum interspecific distance; 3.78% pairwise), compared to a maximum intraspecific distance of 0.34%. *B. solatus* Gomon, the W. Australian sibling species recently separated from *B. perditio*, is much more distant genetically, despite occupying the intervening geographic range between the two species (11.96% divergent from *B. perditio* (10.94% pairwise)).

The interspecific distance is well within the range of divergences found between other species of *Bodianus*. The neighbor-joining phenetic tree based on 85 COI mtDNA sequences of twenty species in the genus (about half of the known species), following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database), shows deep divergences between species and, in most cases, only minimal variation within species (Fig. 7). The exception to the low variation within species is the 2.86% different sequence for Indian vs. Pacific Ocean specimens of *B. anthioides* (Bennett) (2.74% pairwise); Gomon (2006) found a meristic difference but a closer look at the phylogeography of the species is certainly warranted. The differences between pairs of *Bodianus* species range from 1.87% to 21.74%, with a mean of 17.3% (minimum interspecific distances by K2P; pairwise values are 1.84% to 18.59%, mean of 15.19%). Interestingly, the lower range of interspecific distances occur between Indian/Pacific Ocean sibling species and Hawaiian endemic vs. widespread Indo-Pacific sibling species: the former ranging from 1.87% between *B. rubrisos* Gomon and *B. trilineatus* (Fowler)(W. Indian/W. Pacific) to 4.64% between *B. diana* (Lacepède) and *B. dictynna* Gomon (Indian/W. Pacific) and 3.01% between the Hawaiian endemic *B. albotaeniatus* (Valenciennes) and Indo-Pacific *B. bilunulatus* (Lacepède) (1.64%, 4.45%, and 2.92% pairwise distances, respectively). These results confirm that the splitting of sibling species from the Indian and Pacific Ocean basins is based on evidence of long-standing reproductive isolation and, for the genus *Bodianus* at least, there is no evidence for pan-Indo-Pacific species with uninterrupted gene flow. COI divergences of 3% indicate more than a million years of separation by most estimates of the molecular clock (Bermingham *et al*. 1997).

Remarks. The color figures of *Bodianus atrolumbus* (Figs. 1–3) and *B. perditio* (Figs. 4 & 5) are arranged in the order of the total length (measured for specimens, but only estimated for fish photographed underwater). The relative size of the eye is helpful in arranging photographs of fishes according to size when the length is not known, the smaller individuals having a relatively larger eye. However, a surprising exception was found in the collection of specimens of *B. perditio* by the first author at the island of Mangareva in the Tuamotu Archipelago. Seven specimens, 217–320 mm SL, were caught by hook and line from 92 m, and one of 189 mm SL was collected at the same island from less than one meter depth. The 189-mm fish (25 cm TL) would be expected to

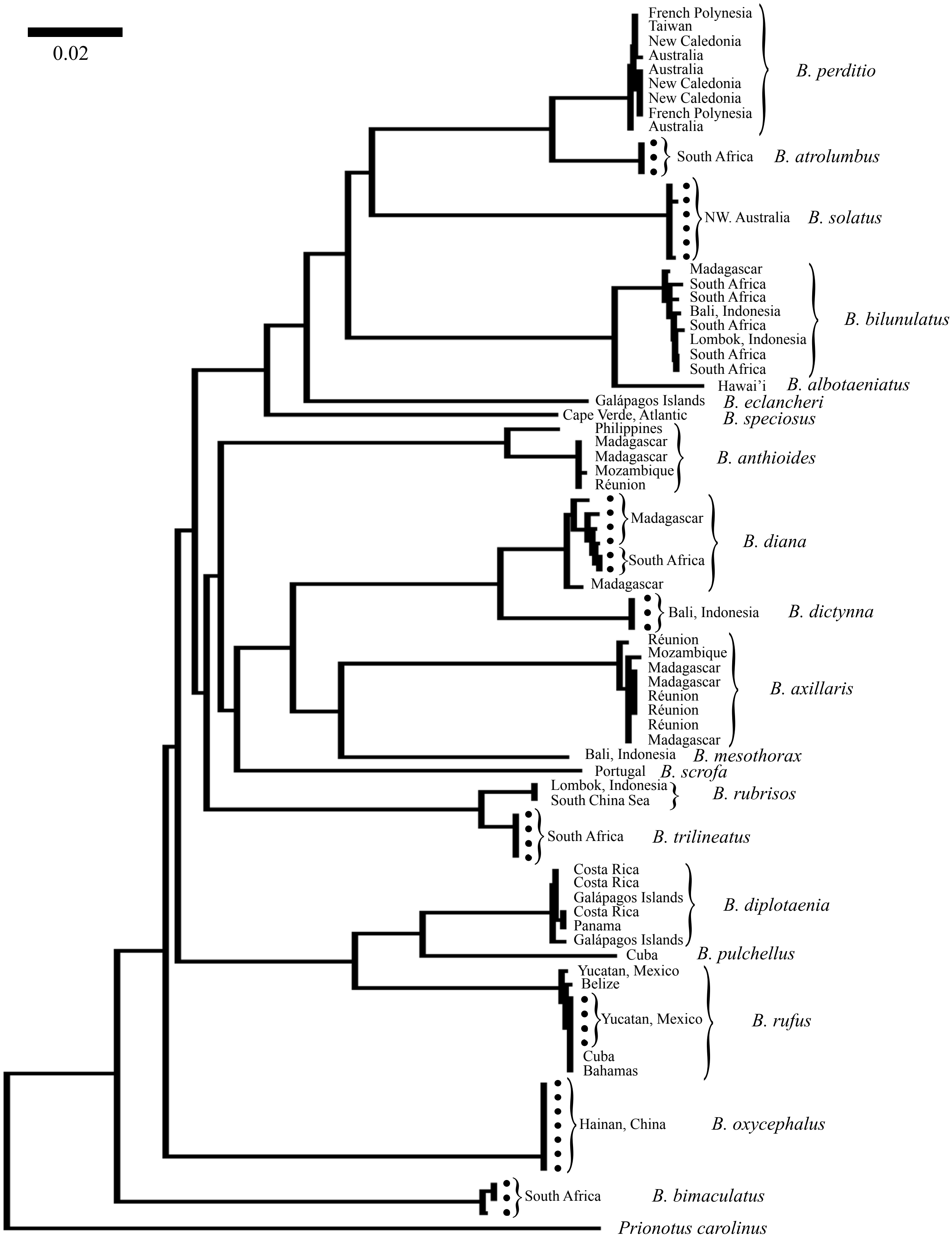

Figure 7. The neighbor-joining phenetic tree based on 85 COI mtDNA sequences of 20 species of *Bodianus* following the Kimura two-parameter model (K2P) generated by BOLD (Barcode of Life Database). The scale bar at left represents a 2% sequence difference. Collection locations for specimens are indicated, and *Prionotus carolinus* is used as an outgroup. GenBank accession numbers and collection data for the sequences in the tree are listed in Appendix 1.

have a relatively larger eye than the 250-mm specimen (30 cm TL). Instead it has a distinctly smaller eye than the fish from 92 m (compare Fig. 5 top and middle). The same unexpected larger eye was found in photographs of *B. atrolumbus* dominated by red, inferring capture from relatively deep water. Like many reef fishes that are found from shallow water to moderate depths, the species of *Bodianus* have more red color in the deeper water (presumed to make them less visible, as the red end of the spectrum is lost first with increasing depth). Note the larger eye of the mainly red *B. atrolumbus* of the middle image of Fig. 2 placed in the order of total length, but now out of order on eye size. The first author also found a larger eye in a specimen of the Hawaiian goby *Opua nephodes* Jordan collected in 130 m, compared to ones from about 15 m. We postulate that prejuvenile fishes that recruit to deeper water may develop a relatively larger eye than those that settle out in the shallows.

Material of *Bodianus perditio* examined. Tuamotu Archipelago, Gambier Group, Mangareva, BPBM 14275, 189 mm; BPBM 14293, 7: 217–320 mm. Rapa, Hiri Bay, BPBM 12968, 268 mm. New Caledonia, Bulari Pass, BPBM 27157, 35 mm. Australia, N.S.W., Sydney, BPBM 14961, 2: 30–47 mm. Vanuatu, Erromango, USNM 360098, 159 mm. Japan, Wakanoura, USNM 71782, 230 mm; USNM 71783, 132 mm.

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*note text in blue were revisions for final publication.

Appendix 1. Specimen data and GenBank accession numbers for the mtDNA COI barcode sequences used to generate the phenogram in Fig. 7.

Genus	species	Collection site	Voucher	GenBank #	Collector/Source
Bodianus	*perditio*	Gambier Islands, Fr. Polynesia	GAM-556	KC684990	J. Williams *et al*.
Bodianus	*perditio*	Chenggong, Taiwan	ASIZP0800729	KC684993	P.F. Lee/K.T. Shao
Bodianus	*perditio*	New Caledonia	ecbp123	KC684989	E. Clua
Bodianus	*perditio*	Gneering Shoals, Australia	djbp124	KC684996	A. DeJong
Bodianus	*perditio*	Gneering Shoals, Australia	djbp122	KC684988	A. DeJong
Bodianus	*perditio*	Gambier Islands, Fr. Polynesia	GAM-586	KC684991	S. Planes & P. Sasal
Bodianus	*perditio*	New Caledonia	ecbp122	KC684994	E. Clua
Bodianus	*perditio*	New Caledonia	ecbp121	KC684995	E. Clua
Bodianus	*perditio*	Gneering Shoals, Australia	djbp121	KC684992	A. DeJong
Bodianus	*atrolumbus*	Park Rynie, South Africa	ADC220.10-3	JF492967	A. Connell
Bodianus	*atrolumbus*	Park Rynie, South Africa	ADC220.10-1	DQ884974	A. Connell
Bodianus	*atrolumbus*	Park Rynie, South Africa	ADC220.10-2	DQ884973	A. Connell
Bodianus	*solatus*	N.W. Australia	BW-A1221	DQ885070	A. Graham/R. Ward
Bodianus	*solatus*	N.W. Australia	NMV A 29676-006	KC684997	M. Gomon & D. Bray
Bodianus	*solatus*	N.W. Australia	CSIRO H 4041-03	DQ885069	A. Graham/R. Ward
Bodianus	*solatus*	N.W. Australia	BW-A1224	DQ885068	A. Graham/R. Ward
Bodianus	*solatus*	N.W. Australia	BW-A1220	DQ885067	A. Graham/R. Ward
Bodianus	*solatus*	N.W. Australia	BW-A1222	DQ885066	A. Graham/R. Ward
Bodianus	*bilunulatus*	Nosy Be, Madagascar	NBE1140	JF434760	N. Hubert *et al*.
Bodianus	*bilunulatus*	Park Rynie, South Africa	ADC220.7-6	JF492960	A. Connell
Bodianus	*bilunulatus*	Park Rynie, South Africa	ADC220.7-3	JF492958	A. Connell
Bodianus	*bilunulatus*	Amed, Bali, Indonesia	bal11700bl280	JQ839402	B. Victor
Bodianus	*bilunulatus*	Park Rynie, South Africa	ADC220.7-5	JF492962	A. Connell
Bodianus	*bilunulatus*	Lombok, Indonesia	BW-A10667	JN311757	W. White/R. Ward
Bodianus	*bilunulatus*	Park Rynie, South Africa	ADC220.7-1	JF492961	A. Connell
Bodianus	*bilunulatus*	Park Rynie, South Africa	ADC220.7-2	JF492959	A. Connell
Bodianus	*albotaeniatus*	Honolulu, Hawaii	08COIFishC57	KC684979	D. Carlon/A. Faucci
Bodianus	*eclancheri*	Isla Isabela, Galápagos	GA490be270	JQ839404	B. Victor
Bodianus	*speciosus*	Sao Vicente, Cape Verde	KV4	GQ341587	R. Hanel *et al*.
Bodianus	*anthioides*	Aquarium trade, Philippines	HLC-13187	FJ582899	D. Yanke/D. Steinke
Bodianus	*anthioides*	Nosy Be, Madagascar	NBE1113	JF434747	N. Hubert *et al*.
Bodianus	*anthioides*	Nosy Be, Madagascar	NBE1113	JF434746	N. Hubert *et al*.
Bodianus	*anthioides*	Pomene, Mozambique, Africa	ADC09-220.5-1	JF492957	A. Connell
Bodianus	*anthioides*	St. Gilles, Réunion, France	REU0734	JQ349800	S. Planes *et al*.
Bodianus	*diana*	Nosy Be, Madagascar	NBE1117	JF434756	N. Hubert *et al*.
Bodianus	*diana*	Nosy Be, Madagascar	NBE1118	JF434755	N. Hubert *et al*.
Bodianus	*diana*	Nosy Be, Madagascar	NBE1116	JF434757	N. Hubert *et al*.
Bodianus	*diana*	Nosy Be, Madagascar	NBE1115	JF434758	N. Hubert *et al*.
Bodianus	*diana*	Aliwal Shoal, South Africa	ADC220.8-3	JF492965	P. Heemstra/A. Connell
Bodianus	*diana*	Aliwal Shoal, South Africa	ADC220.8-2	JF492966	P. Heemstra/A. Connell
Bodianus	*diana*	Nosy Be, Madagascar	NBE0365	JF434759	N. Hubert *et al*.
Bodianus	*dictynna*	Amed, Bali, Indonesia	bal11700bd171	KC684981	B. Victor

Appendix 1. cont.

Bodianus	*dictynna*	Amed, Bali, Indonesia	bal11700bd123	KC684982	B. Victor
Bodianus	*dictynna*	Amed, Bali, Indonesia	bal11700bd133	KC684980	B. Victor
Bodianus	*axillaris*	St. Leu, Réunion, France	REU1617	JF434748	N. Hubert *et al*.
Bodianus	*axillaris*	Pomene, Mozambique, Africa	ADC09-220.6-1	GU805092	A. Connell
Bodianus	*axillaris*	Nosy Be, Madagascar	NBE0075	JF434753	N. Hubert *et al*.
Bodianus	*axillaris*	Nosy Be, Madagascar	NBE0356	JF434752	N. Hubert *et al*.
Bodianus	*axillaris*	St. Leu, Réunion, France	REU0995	JF434749	N. Hubert *et al*.
Bodianus	*axillaris*	Hermitage, Réunion, France	REU0775	JF434750	N. Hubert *et al*.
Bodianus	*axillaris*	Hermitage, Réunion, France	REU0735	JF434751	N. Hubert *et al*.
Bodianus	*axillaris*	Nosy Be, Madagascar	NBE0074	JF434754	N. Hubert *et al*.
Bodianus	*mesothorax*	Amed, Bali, Indonesia	bal11800bm126	JQ839406	B. Victor
Bodianus	*scrofa*	Funchal, Madeira, Portugal	LB122	GQ341586	R. Hanel *et al*.
Bodianus	*rubrisos*	Lombok, Indonesia	BW-A10666	JN311756	W. White/R. Ward
Bodianus	*rubrisos*	South China Sea	MBCSCHSY08337	FJ237633	Junbin Zhang
Bodianus	*trilineatus*	Park Rynie, South Africa	ADC220.9-1	JF492970	A. Connell
Bodianus	*trilineatus*	Park Rynie, South Africa	ADC220.9-3	JF492968	A. Connell
Bodianus	*trilineatus*	Park Rynie, South Africa	ADC220.9-2	JF492971	A. Connell
Bodianus	*trilineatus*	Park Rynie, South Africa	ADC220.9-5	JF492969	A. Connell
Bodianus	*diplotaenia*	Guanacaste, Costa Rica	JHLOW00156	KC684983	J. Lowenstein/B. Victor
Bodianus	*diplotaenia*	Guanacaste, Costa Rica	JHLOW00230	KC684987	J. Lowenstein/B. Victor
Bodianus	*diplotaenia*	Isla Fernandina, Galápagos	gal98606bd108	KC684984	B. Victor
Bodianus	*diplotaenia*	Guanacaste, Costa Rica	JHLOW00340	KC684986	J. Lowenstein/B. Victor
Bodianus	*diplotaenia*	Isla Contadora, Panama	pe821120bd600	JQ839403	B. Victor
Bodianus	*diplotaenia*	Isla Isabela, Galápagos	gal98528bd101	KC684985	B. Victor
Bodianus	*pulchellus*	Aquarium trade, Cuba	HLC-11025	FJ582902	D. Yanke/D. Steinke
Bodianus	*rufus*	Quintana Roo, Mexico	ECOCH5748-58b	GU225156	M. Valdez-Moreno
Bodianus	*rufus*	Turneffe, Belize	cn10b99	HQ987864	C. Nolan/B. Victor
Bodianus	*rufus*	Quintana Roo, Mexico	ECOCH5748-58c	GU225154	M. Valdez-Moreno
Bodianus	*rufus*	Isla Mujeres, Mexico	ECOCH7143-209	JN311758	L. Vásquez-Yeomans
Bodianus	*rufus*	Quintana Roo, Mexico	ECOCH5748-58d	GU225155	M. Valdez-Moreno
Bodianus	*rufus*	Quintana Roo, Mexico	ECOCH5748-58d	GU225155	M. Valdez-Moreno
Bodianus	*rufus*	Aquarium trade, Cuba	HLC-12307	FJ582903	D. Yanke/D. Steinke
Bodianus	*rufus*	San Salvador, Bahamas	bah91729br120	JQ839407	G. Wellington/B. Victor
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08518	FJ237628	Junbin Zhang
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08519	FJ237627	Junbin Zhang
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08515	FJ237631	Junbin Zhang
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08517	FJ237629	Junbin Zhang
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08336	FJ237632	Junbin Zhang
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08516	FJ237630	Junbin Zhang
Bodianus	*oxycephalus*	Hainan, China	MBCSCHSY08520	FJ237626	Junbin Zhang
Bodianus	*bimaculatus*	Park Rynie, South Africa	ADC220.7a-2 5	JF492963	A. Connell
Bodianus	*bimaculatus*	Park Rynie, South Africa	ADC220.7a-1	JF492964	A. Connell
Bodianus	*bimaculatus*	Sodwana Bay, South Africa	ADC12 220.7a-3	KF489507	A. Connell
Prionotus	*carolinus*	Massachusetts, USA	DAL 07-097	KC015843	P. Chase, NOAA