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Redescription of *Bathymodiolus septemdierum* Hashimoto and Okutani, 1994 (Bivalvia, Mytilida, Mytilidae), a mussel broadly distributed across hydrothermal vent locations in the western Pacific and Indian Oceans

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Abstract

Mussels of the genus *Bathymodiolus* Kenk & Wilson belong to the foundation fauna at hydrothermal vents in the global deep sea. In the western Pacific and Indian oceans, the three nominal taxa *B. septemdierum* Hashimoto and Okutani, *B. brevior* Cosel, Métivier & Okutani and *B. marisindicus* Hashimoto are currently recognized as separate species despite morphological and genetic evidence for their conspecificity. All three are listed with the International Union for Conservation of Nature Red List based on highly restricted ranges. We compile and supplement existing morphometric and molecular data to revise the *Bathymodiolus septemdierum* species group. We redescribe *B. septemdierum* as a single species with *B. brevior* and *B. marisindicus* recognized as junior synonyms. Given the exceptionally broad range of *B. septemdierum*, we propose removal of these three taxa from the IUCN Red List.

Key words: Bathymodiolinae, species delimitation, morphological taxonomy, molecular barcoding, cytochrome *c* oxidase subunit I, *COI,* NADH dehydrogenase subunit 4, *ND4*

Introduction

With the growing interest in metals sequestered in hydrothermal vent deposits, prospecting has begun at vent sites in the western Pacific within state territorial waters, while exploration contracts are active at vent sites on international seabed in the Atlantic and Indian oceans under the International Seabed Authority. Concern has mounted around the consequences of mining for the unique fauna of the vent ecosystems that occupy tiny, discrete sites coincident with metalliferous deposits (Van Dover *et al.* 2018). Key issues are i) the very high levels of endemicity of animals dependent on chemosynthetic productivity and ii) disruption of connectivity among scattered populations by removing stepping stone habitats. Several approaches to conservation are currently in development, one of which is to use the criteria erected by the International Union for Conservation of Nature (IUCN) to assign vulnerability status to vent species with limited distributions (Sigwart *et al.* 2019). This Red List approach is particularly useful as it is easily communicated to the public and to decision-makers. To date, well over 150 molluscs that inhabit hydrothermal vents are entered in the database (https://www.iucnredlist.org; accessed June 13, 2022). In their assessment of the applicability of the IUCN criteria for listing, Thomas *et al.* (2022) decide that geographic range is the single most important criterion for endemic vent species: the smaller the range, the more vulnerable the species.

Mussels of the genus *Bathymodiolus* Kenk & Wilson, 1985, are important foundation species in hydrothermal vent and cold seep ecosystems of the Pacific, Indian and Atlantic oceans; here, they form high biomass beds reliant on chemosynthetic production from bacterial symbionts. Since the description of the first species of the new subfamily (Bathymodiolinae) and genus from the vents of the Eastern Galapagos Spreading Center (Kenk & Wilson 1985), taxonomists have designated 20 additional species. Several more species are transferred to an allied genus *Gigantidas* Cosel & Marshall, 2003, following Thubaut *et al.* (2013). *Bathymodiolus* species on the IUCN Red List include *B. marisindicus* Hashimoto, 2001 (Thomas *et al.* 2019), *B. brevior* Cosel, Métivier and Hashimoto, 1994 (Thomas & Sigwart 2020a) and *B. septemdierum* Hashimoto and Okutani, 1994 (Thomas & Sigwart 2020b). The

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first two are assigned "Vulnerable" status, while the last has an "Endangered" status based on apparent restriction to vents on a few seamounts in the Izu-Bonin Arc southeast of Japan. We note there are prior records of broader distributions for *B. septemdierum* in the Northwest Pacific (Mariana Arc) based on morphology (Tunnicliffe *et al.* 2009; Watanabe *et al.* 2019) and genetics (Breusing *et al.* 2015). *Bathymodiolus septemdierum* was described from the Northwest Pacific in 1994 (Hashimoto & Okutani 1994), then Cosel *et al.* (1994) published *B. brevior* a month later with specimens from the Lau and North Fiji basins in the Southwest Pacific. In 2001, Hashimoto (2001) described *B. marisindicus* from a newly discovered vent site in the Indian Ocean. This latter study notes the morphological similarity of the three species and presents a comparison of features to distinguish them. Most characters are located on the shell, and many relate to shell shape and position of muscle scars.

Several studies illustrate the genetic similarities of these three species in the last 20 years, beginning in 2003, with a short comparison of *COI* sequences between *B. septemdierum* and *B. marisindicus* (Shintaku 2003). Kyuno *et al.* (2009) find evidence of gene flow among all three "species" over distances of 5000 km using one mitochondrial gene, and Miyazaki *et al.* (2010) use two genes to construct a tree that does not differentiate the three species, including specimens from NW Eifuku Seamount (Mariana Arc). Similar analyses led to the proposal that the three species be amalgamated (Vrijenhoek 2009; Thubaut *et al.* 2013). Breusing *et al.* (2015) find no significant genetic differentiation among mussel populations across the western Pacific. Although they note that the Indian Ocean population represented by *B. marisindicus* appears to diverge, the overall genetic difference is insufficient to designate a separate species. More recently, a phylogenetic study defining a new species of *Gigantidas* from the Indian Ocean uses a five-gene consensus tree that finds *B. brevior* and *B. marisindicus* to be almost identical (Jang *et al.* 2020).

The objective of our study is to assimilate the known genetic and morphological information, augment with new data and support the redefinition of a single species with a very wide range (Fig. 1). We amend the description of *B. septemdierum* and indicate both *B. brevior* and *B. marisindicus* as junior synonyms.

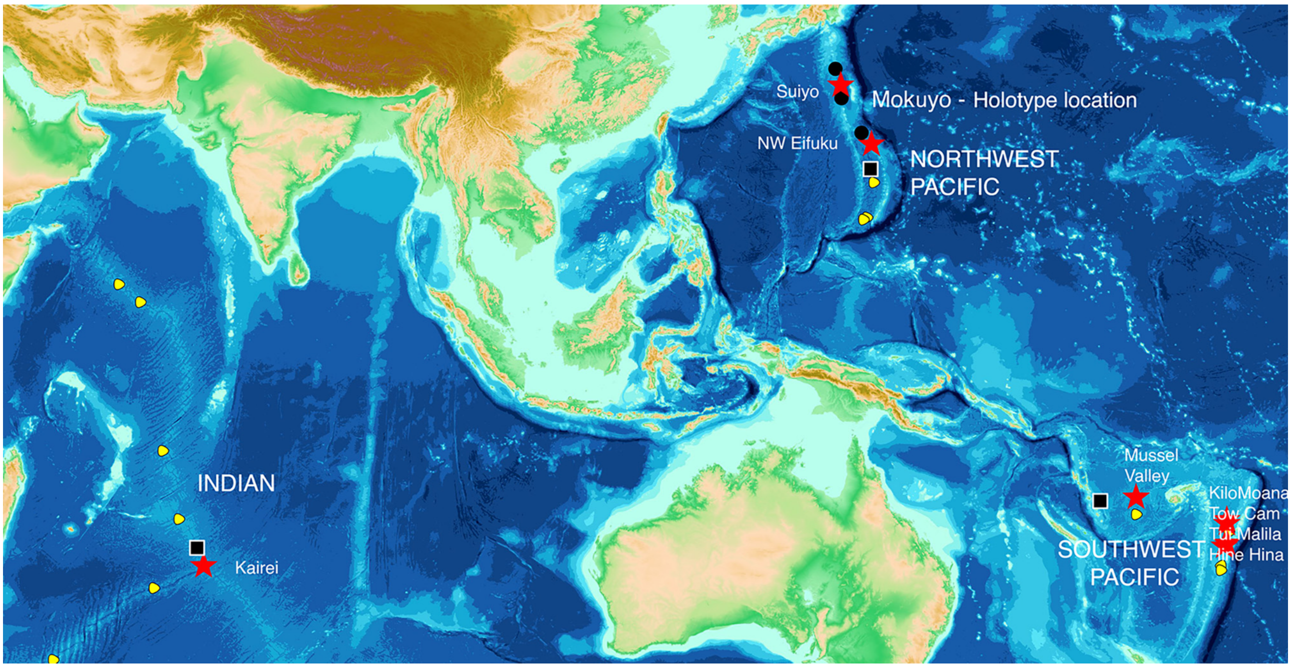

FIGURE 1 Distribution of *Bathymodiolus septemdierum* in the western Pacific and Indian oceans. Red stars indicate sites for which both genetic and morphological data are used in this study; black squares for genetic data only; black circles for morphological data only. Yellow symbols are additional sites at which this species occurs. Indian Ocean sites extended from records in Zhou *et al*. (2022).

Materials and methods

Genetic analyses. Publicly available sequences for mitochondrial cytochrome *c* oxidase subunit I (*COI*) and NADH dehydrogenase subunit 4 (*ND4*) of *B. septemdierum*, *B. brevior* and *B. marisindicus* were retrieved from GenBank (Appendix 1 and 2). New sequences for *COI* are deposited under accession numbers ON799000–ON799015. Specimens from type locations are included in the analysis, however, type material was not sequenced as specimens were fixed in formalin before transfer to ethanol. Instead, we ensured that sequences were available from collections at the holotype locations. Sequences for each gene were aligned in GENEIOUS PRIME (https://www.geneious.com) with MAFFT (Katoh *et al.* 2002). Alignments were imported to POPART (Leigh & Bryant 2015) for haplotype network construction via the median joining algorithm (Bandelt *et al.* 1999). Nucleotide sequence divergence and haplotype diversities were estimated based on Kimura's 2-parameter model (Kimura 1980) and the method by Nei & Tajima (1981), respectively, with the APE and PEGAS packages in R (Paradis 2010; Paradis & Schliep 2019; R Core Team 2022).

Morphometric analyses. We accessed specimens (total number = 224) from several locations for *B. septemdierum* and *B. brevior;* only one location was available for *B. marisindicus* (see Material Examined). In all cases, these include specimens from the holotype and/or paratype locations. Our study focusses on the characters that appear to differ in the original species descriptions: general shape, shell height to length, shell height to width (tumidity), position of beak, relative length of the dorsal shell ligament, size of pedal retractor muscle, and positions of the anterior retractor and the anterior adductor muscle scars. Analyses included information from the original type specimens. For statistical analyses, data were first tested for normality; in all cases, non-parametric tests were necessary. Not all type material was available at the time of inquiry; however, data assembled here include the measurements presented in the original descriptions of the three species. As one author (J. Hashimoto) contributed to each description, there is consistency across the papers on the measures presented.

Our genetic work was executed in 2014 for another study (Breusing et al. 2015). As there was no expectation of a future systematic study, shells were separated from the body without identity tracking of individuals. Thus, figured specimens from the SW Pacific and NW Eifuku in the NW Pacific are not linked to genetic sequences, although they do come from the sequenced collections. While figured specimens from Suiyo and Mokuyo (NW Pacific) and from Kairei (Indian Ocean) were not sequenced, sequences are available from these sites. All figured specimens are deposited with the Scripps Institution of Oceanography (SIO) Invertebrate Collection under accession numbers M19389 to M19395, M19397, M19399 (https://scripps.ucsd.edu/benthic-invertebrate-collection).

Results

Genetics. Mitochondrial *COI* and *ND4* sequence data consist of 63 and 97 haplotypes, with neighbouring haplotypes being separated by not more than three mutations (Fig. 2). Overall gene diversities are 0.91±0.01 for *COI* and 0.90±0.02 for *ND4* (Table 1). Nucleotide sequence divergences within oceanic regions range from 0.24–0.89% for *COI* and 0.27–0.74% for *ND4*, while sequence divergences between regions are slightly higher (*COI*: 0.59–1.24%, *ND4*: 0.45–0.93%), with the strongest difference being observed for the NW Pacific and Indian Ocean pairs (Table 1). In accordance with patterns of genetic divergence, haplotypes are broadly grouped into an Indian and western Pacific cluster (Fig. 2), while no structuring is evident between NW and SW Pacific.

TABLE 1. Haplotype diversity and genetic divergence for mitochondrial *COI* and *ND4* sequences of *B. septemdierum* across the Indo-Pacific Ocean. H = Number of haplotypes, Hd = Haplotype/gene diversity, K2P divergence = Kimura-2-parameter divergence.

Gene	H	Hd (SD)	K2P divergence (SD)					
			NW Pac.	SW Pac.	Indian	NW Pac.—SW Pac.	NW Pac.—Indian	SW Pac.—Indian
COI	63	0.9126 (0.0126)	0.0089 (0.0072)	0.0024 (0.0018)	0.0065 (0.0049)	0.0059 (0.0054)	0.0124 (0.0061)	0.0080 (0.0027)
ND4	97	0.8998 (0.0164)	0.0061 (0.0035)	0.0027 (0.0023)	0.0074 (0.0046)	0.0045 (0.0032)	0.0093 (0.0039)	0.0089 (0.0034)

Morphology. The overall shell shape tends to be modioliform, although many specimens from the SW Pacific tend to have a higher postero-dorsal angle. However, within both single collections and geographic regions, a range of shapes is present (Figs 3–7). Size reaches 151.5 mm length, but the limited specimens from the Indian Ocean do not exceed 95.4 mm (Table 2). We note that Copley *et al.* (2016) figure a mussel from another Indian Ocean vent site of about 120 mm length. The height/length relationship (Fig. 8) is a power curve with shells becoming more elongate with size. Using the overlapping size range (48 to 145 mm) between NW and SW Pacific shells and detrending the curve, a Mann-Whitney test detects a significantly higher height to length ratio for the southwest specimens, although much overlap occurs. In the NW Pacific, shells from NW Eifuku are more fragile and more elongate than those from the Izu-Bonin Arc sites further north. Measures of height to width (tumidity) are also size dependent ($H/W = -0.3\ln(L) + 2.8$); a Kruskal-Wallis two-tailed test detected no differences among ocean regions.

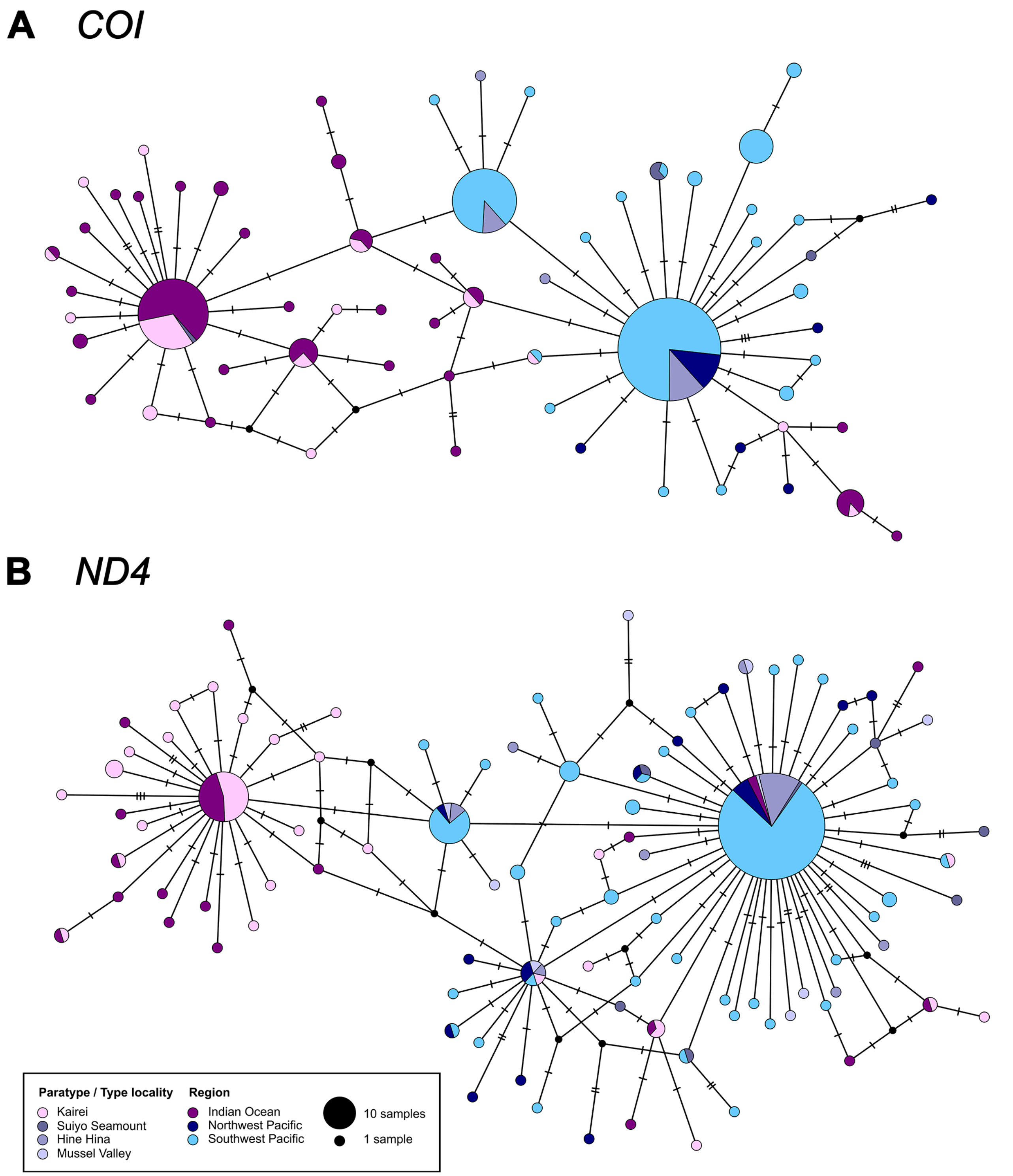

FIGURE 2 Haplotype networks for mitochondrial *COI* and *ND4*, with haplotypes coloured by broader geographic region or type / paratype locality. Dot sizes are proportional to haplotype frequency. Dashes on connecting branches indicate number of mutations between haplotypes. Despite shared genetic variation among geographic regions, haplotypes can be broadly grouped into an Indian and western Pacific cluster.

TABLE 2. Range of dimensions (mm) measured for *Bathymodiolus septemdierum* described from the Northwest Pacific, Southwest Pacific ("brevior") and Indian ("marisindicus") oceans. Data include measurements in original descriptions.

Region	Morphotype	N	Length		Height		Full Width	
			Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
NW Pacific	*B. septemdierum*	111	4.7–151.5	83.9 (37.7)	3.2–68.1	40.2 (15.7)	1.2–62	33.5 (16.0)
SW Pacific	*B. brevior*	107	48.8–143.5	99.4 (20.2)	30.2–67.5	49.9 (8.4)	20.3–60.5	40.6 (8.4)
Indian	*B. marisindicus*	18	55.4–95.4	73.1 (10.1)	27.3–44.9	34.8 (4.8)	21.5–38.9	29.1 (4.5)

Only the Izu-Bonin Arc (NW Pacific) collection includes specimens under 50 mm in length. Here, the relative position of the beak is strongly related to size: distance to anterior margin = $0.2(L)^{1.35}$ ($R^2 = 0.94$; n = 41). However, the remaining specimens show a low correlation to size, with NW Eifuku (NW Pacific) ranging from 8 to 22% of length in specimens over 80 mm long. Below 40 mm length, the dorsal ligament is a notably smaller proportion of the postero-dorsal margin. We find no obvious difference among ocean regions above this size: NW Pacific (n = 66), mean of 94%; SW Pacific (n = 14) mean of 90%; Indian (n = 9), mean of 95%. The position of the anterior adductor muscle scar noted by Hashimoto (2001) was just anterior the umbo for the type collection of *B. marisindicus*. Of the 34 NW Eifuku specimens we examined, only four scars are under and the remaining are anterior to the umbo (Fig. 3). The SW Pacific specimens (n = 14) show an even mix of positions while this scar in nine Indian specimens lies anterior to the umbo. The position of the anterior retractor muscle scar is a variable mix of anterior to, or at, extreme end of umbonal cavity within specimens from each geographic region. This observation differs from Hashimoto (2001) who distinguishes *B. septemdierum* and *B. brevior* with anterior positions and *B. marisindicus* with extreme. Overall, there is pronounced morphological variability within and among ocean regions, with the greatest ranges evident in the NW Eifuku specimens (about 540 km from the Izu-Bonin Arc sites). There is scant evidence of morphological differentiation. Based on genetic congruence among the nominal species and overlap of morphological variability, we conclude that *B. brevior* and *B. marisindicus* both belong to the species designated as *B. septemdierum.*

Systematics

Order Mytilida Férussac, 1822

Family Mytilidae Rafinesque, 1815

Subfamily Bathymodiolinae Kenk & Wilson, 1985

Bathymodiolus Kenk & Wilson, 1985

Bathymodiolus septemdierum Hashimoto & Okutani, 1994

Synonymy

1994 *Bathymodiolus septemdierum* Hashimoto & Okutani, [OD], Venus 53 (2), 72, (fig. 5, pl. 1.7-8, pl. 2.1, pl. 3.4), [type locality Mokuyo Seamount, Izu-Bonin Arc]; published August 31, 1994; **holotype** (NSMT Mo-70035) and **paratypes** as designated by Hashimoto & Okutani (1994), amended herein.

1994 *Bathymodiolus brevior* Cosel, Métivier & Hashimoto, The Veliger 37 (4), 375, (figs 1-10, 26, 30-34, 37, 38), [type locality Vailili vent site, Lau Basin]; published October 4, 1994.

2001 *Bathymodiolus marisindicus* Hashimoto, Venus 60, 142, (figs 2-9, 12), [type locality Kairei vent site, Central Indian Ridge].

Material Examined. Type material not examined for the three species for reasons presented in the Materials and Methods.

Northwest Pacific: Whole specimens of 41 mussels from the Izu-Bonin Arc: Mokuyo Seamount (type locality), Suiyo Seamount and Myojin Knoll (both paratype localities). Valves of 64 mussels from the Mariana Volcanic Arc: NW Eifuku and Nikko Seamounts. Whole specimens of 32 mussels from NW Eifuku Seamount.

Southwest Pacific: Valves of 67 mussels from four vent sites in the Lau Basin: Hine Hina (paratype locality for *B. brevior*), Tow Cam, Tu'i Malila, and Kilo Moana. Eleven valves from one site in the North Fiji Basin: White Lady (material in *B. brevior* description).

Indian Ocean: Whole specimens of nine mussels from one site on the Central Indian Ridge: Kairei (type locality).

Description. *Shell* (Fig. 2). Modioliform shell of variable fragility: very thin to strongly calcified dependent on habitat. Size up to 151 mm in length; height to length ratio decreases with size varying from 0.40 to 0.55 in large specimens. Similarly, tumidity (height/width) varies from 1.0 to 1.3. Juveniles are more oval and slender. Ventral margin may be slightly convex, straight or slightly concave, with a population showing all three forms. Anterior margin broadly to narrowly rounded; posterior margin may be fully rounded or forming a sharp angle at the dorsal junction (Fig. 3). Beak subterminal positioned at about 15% of shell length but ranging from 8% to 22% in larger specimens.

Exterior smooth with largely intact glossy golden brown periostracum that may accumulate mineral deposits from vent fluids. Inner aragonite layer may show variable growth lines or signs of reabsorption/deposition, while outer calcite layer has distinct daily growth bands. Larval shell about 400 µm (Cosel *et al.* 1994, figs 30-33). Hinge edentulous. Ligament opisthodetic extending 90 to100% of the posterodorsal margin in large specimens.

Body. Anterior adductor muscle scar usually situated anterior to umbo but may overlap; shape variable around an oval (Fig. 3); anterior retractor muscle scar usually under middle or forward end of the umbonal cavity. Anterior bundle scar of the posterior pedal/byssal retractor muscle located under ligament at half to two-thirds of its length. Posterior bundle of this muscle forms a bilobed scar with the posterior adductor muscle (Fig. 3). These muscle insertions can vary somewhat in position partly dependent on shell size.

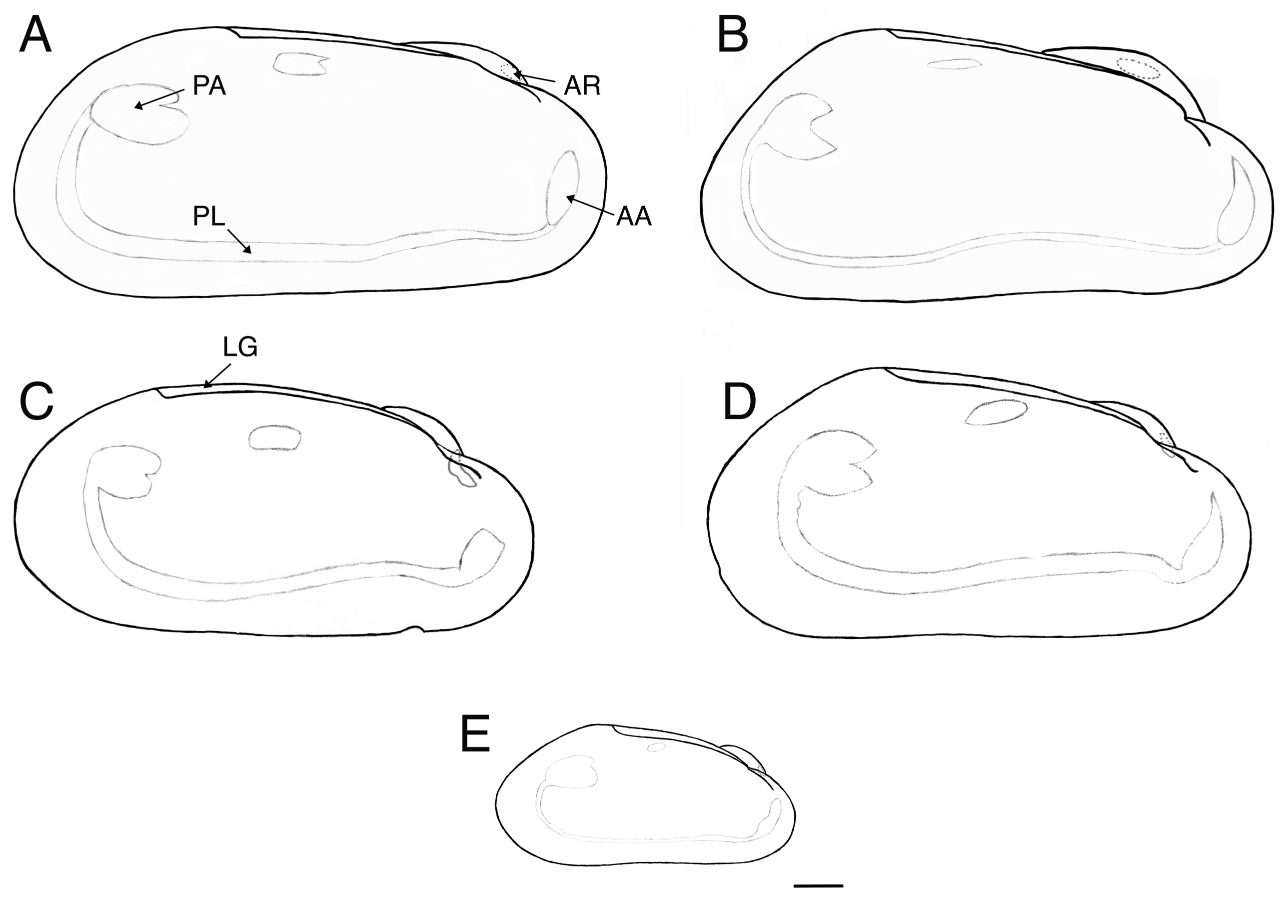

FIGURE 3 Outline sketches of *Bathymodiolus septemdierum* shells illustrating variability in shape and positions of the anterior retractor and anterior adductor muscle scars. AR: anterior retractor muscle scar; PA: posterior adductor muscle scar; PL: pallial line; AA: anterior adductor scar; LG: ligament. Scale bar is 10 mm and applies to all specimens. A and B: NW Eifuku site, Northwest Pacific; shells are predominantly rounded as in A. C and D: Tu'i Malila site, Lau Basin; shells are predominately angular as in D. E: Kairei site, Central Indian Ridge; redrawn from Hashimoto (2001) holotype. Here, we correct the scale applied to this drawing in the original. The specimen is 55.7 mm long. (A: SIO accession # M19392; B: SIO accession # M19393; C: SIO accession # M19391; D: SIO accession # M19389; E: paratype JAMSTEC #032386).

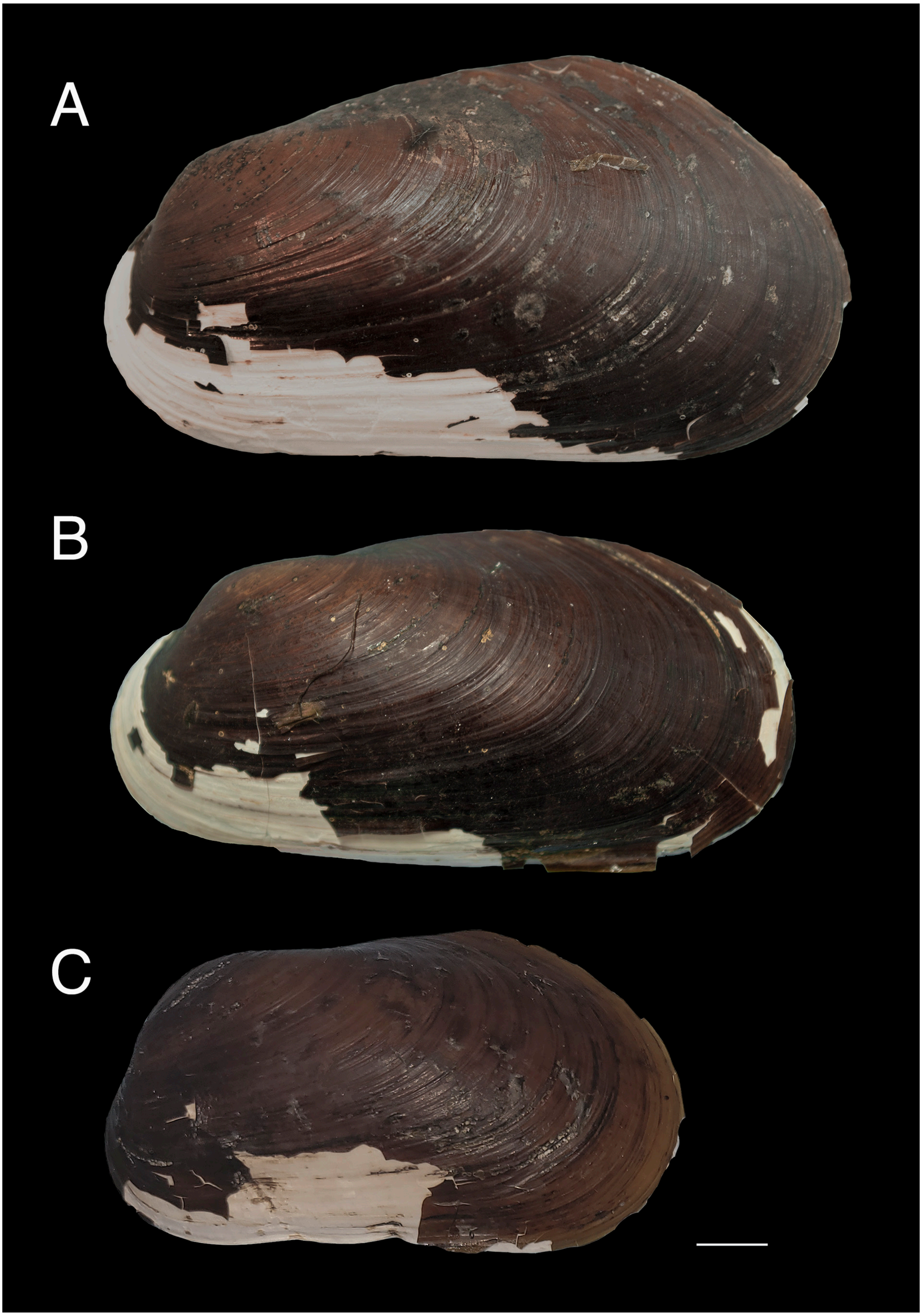

FIGURE 4. Shells of *Bathymodiolus septemdierum* from Lau Basin (Southwest Pacific), sites listed as 'other material' for original description of *B. brevior*. Shell shape variability includes posterior angularity and beak position relative to anterior margin. Dark brownish periostracum largely intact but detaching where dried. Scale bar is 10 mm. (A: SIO accession #M19389; B:SIO accession # M19391; C: SIO accession # M19390).

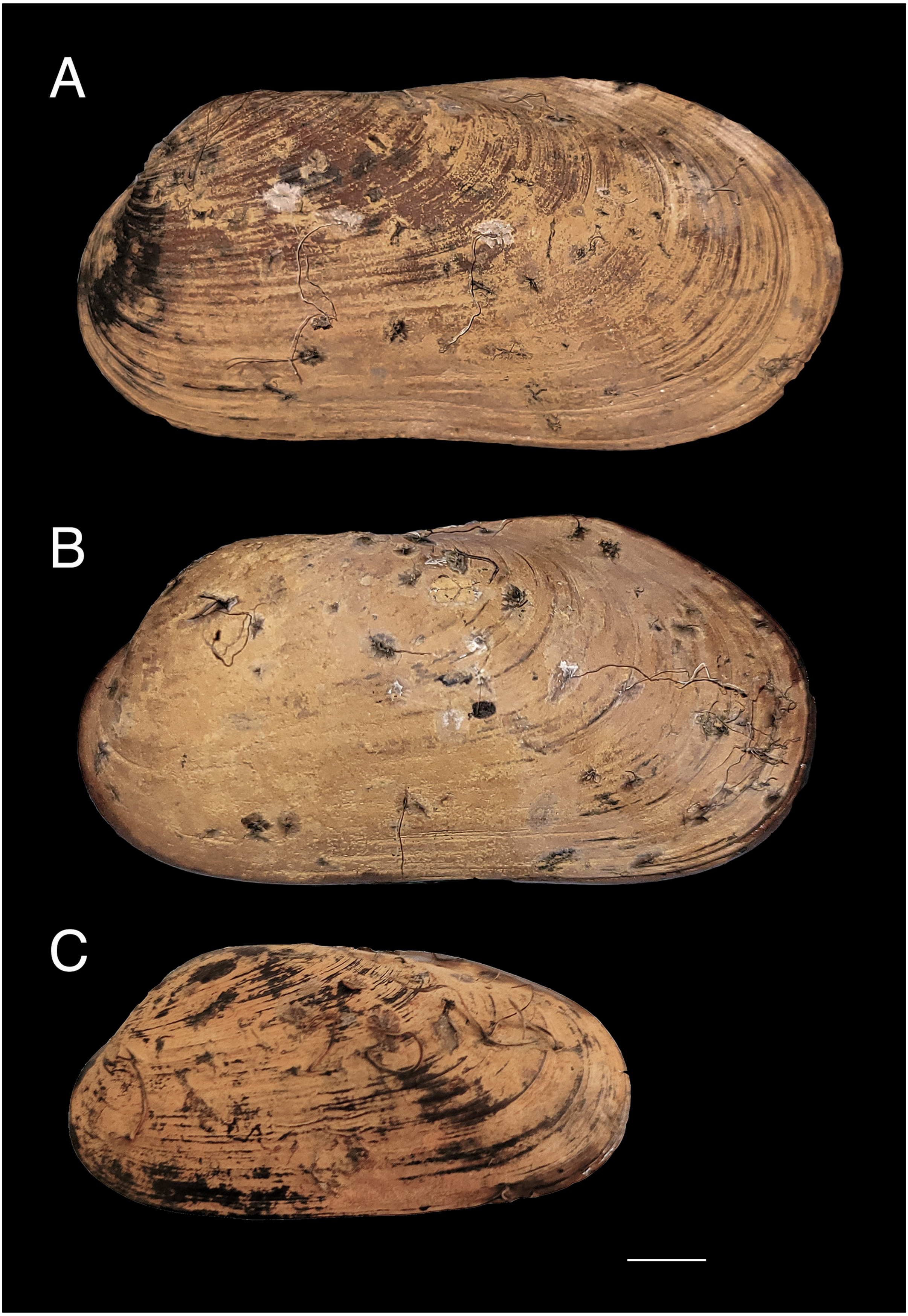

FIGURE 5. Shells of *Bathymodiolus septemdierum* from Kairei, Central Indian Ridge, holotype site for original description of *B. marisindicus.* Shells have an oxidized mineral coating over the periostracum and black stains where byssal threads from other individuals attached. Scale bar is 10 mm. (A, B and C: SIO accession # M19395).

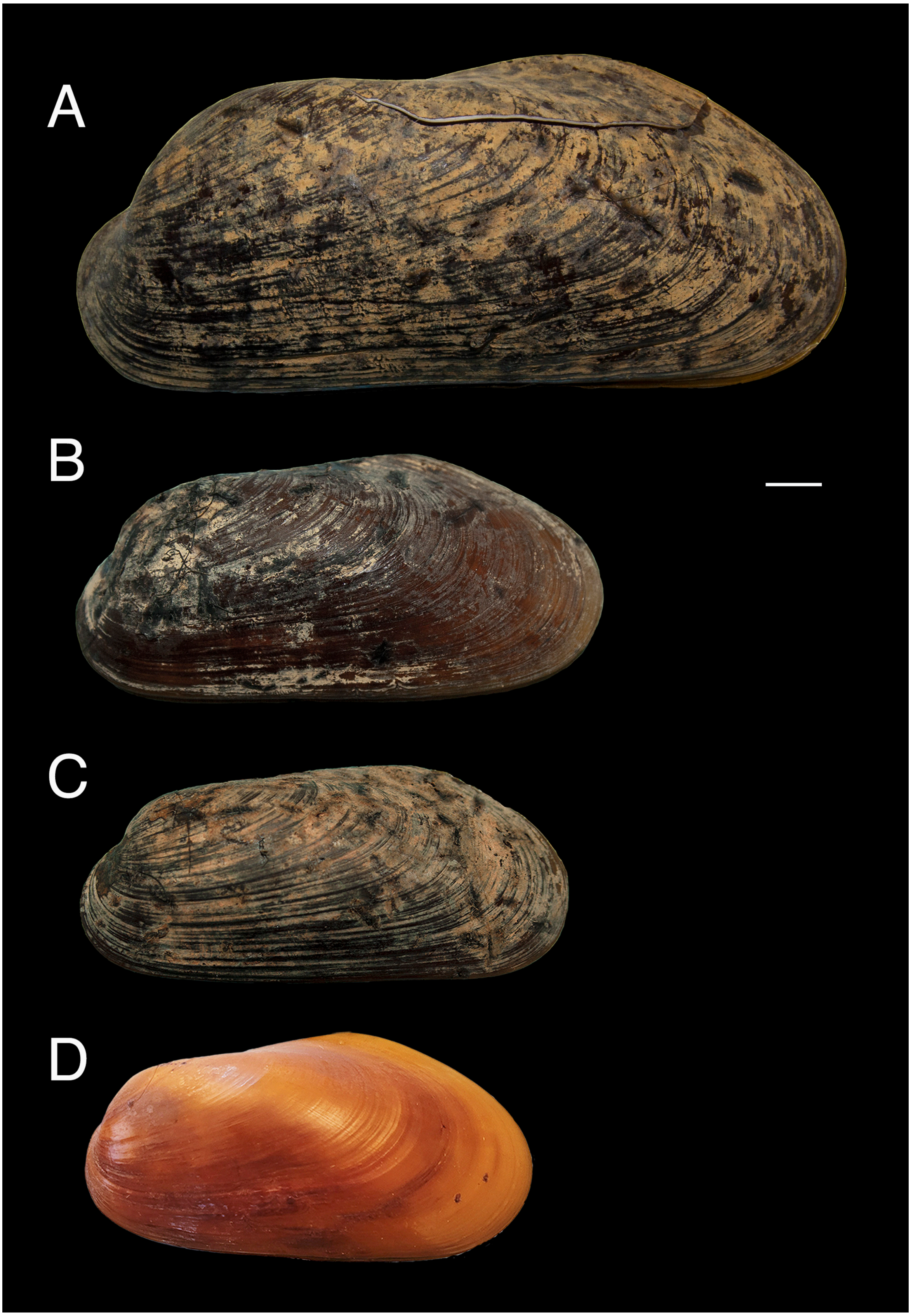

FIGURE 6. Shells of *Bathymodiolus septemdierum* from Izu-Bonin Arc (Northwest Pacific). A, B, C: From paratype location, Suiyo Seamount; colour differences due to mineral deposits. D: From type location (Mokuyo Seamount) of first description of the species; specimen shows clean periostracum. Scale bar is 10 mm. (A, B and C: SIO accession # M19397; D: SIO accession #M19399).

FIGURE 7. Shells of *Bathymodiolus septemdierum* from Mariana Arc to illustrate more variation in shells of sequenced individuals. B and C have accumulations of iron oxide over the periostracum. Scale bar is 10 mm. (A: SIO accession # M19394; B and C: SIO accession # M19392).

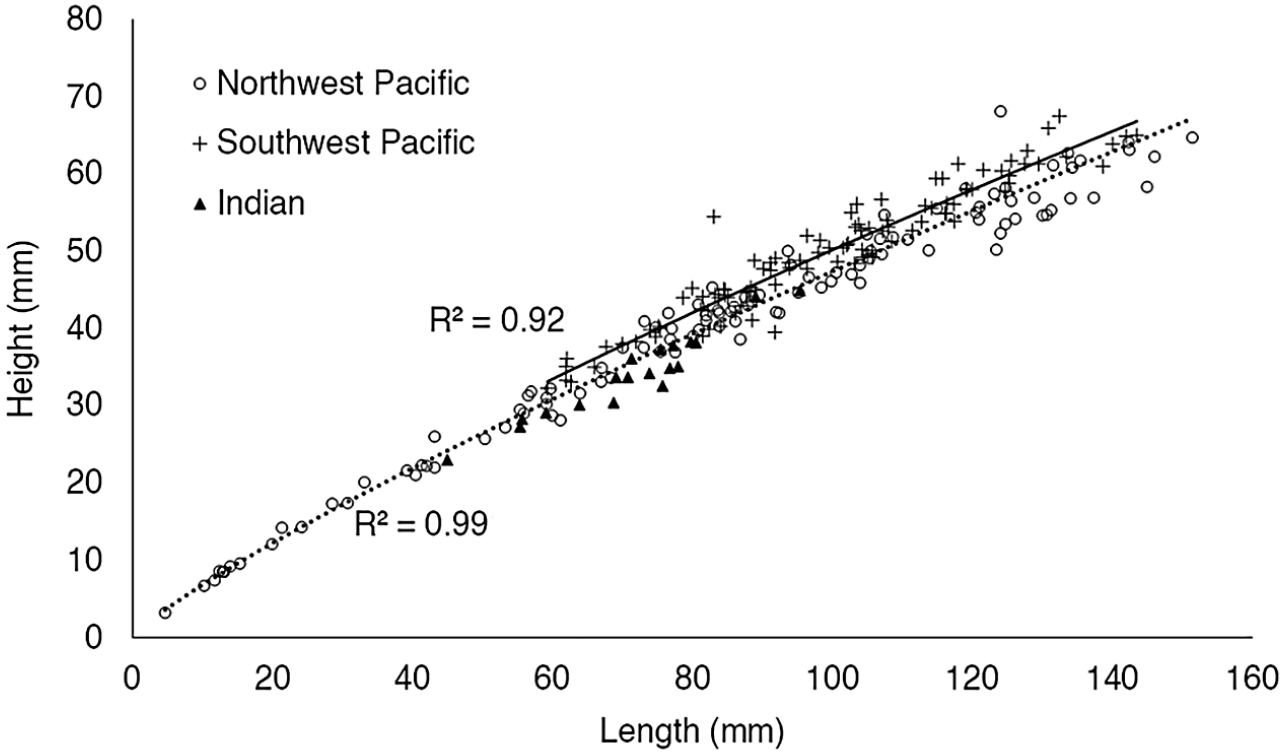

FIGURE 8. Height to length proportions of *Bathymodiolus septemdierum* shells from three ocean regions with regression lines shown for Northwest Pacific sites (dotted) and Southwest Pacific sites (solid).

Ctenidia large from two-thirds to five-sixths length of shell, variable within a population. Inner and outer demibranchs more or less equal length with the former attached to mantle anteriorly but detached posteriorly. Valvular siphonal membrane narrow, terminating at postero-ventral margin; papilla absent.

Mantle lobes separate along ventral margin usually with fluted edging. Mantle folds extend dorsally over anterior adductor muscle, along anterior margin, then down and posteriorly under the anterior adductor muscle. Foot somewhat variable in breadth with ventral byssal groove about two-thirds the length.

Posterior byssus retractor muscles arise from foot-byssus muscle complex to attach as two muscle bundles (anterior and posterior) on dorsal and postero-dorsal shell interior. Posterior pedal retractors stout rising from base of foot to join with anterior bundle of the posterior byssus retractor muscles. Anterior retractor muscles of the complex rising forward to attach on anterior wall of umbo.

Habitat and Distribution. Known only from hydrothermal vents of the western Pacific and Indian oceans (Fig. 1). Hosts thiotrophic bacterial symbionts in gills, thus requires access to sulphide-rich vent fluids. Usually forms dense clusters around diffuse fluid flows, attached by byssal threads to rocks or other shells. Where currents disperse concentrated fluids over the seabed, can form extensive areas of high biomass. Shells very thin where fluid pH low.

This mussel species has a wide range: Northwest Pacific in Izu-Bonin Volcanic Arc, Mariana Volcanic Arc and Mariana Back-arc spreading ridge; in the Southwest Pacific, in the New Hebrides Arc, North Fiji Basin, Lau Basin, Tonga-Tofua Arc, and Kermadec Arc; in the Indian Ocean on the Southwest Indian Ridge and the Central Indian Ridge. Thus, *B. septemdierum* occurs in mid-ocean ridge, back-arc ridge and volcanic arc settings.

Remarks. Given both the phenotypic variability and the wide geographic spread, it is not surprising that separate species were described from three ocean regions. Hashimoto (2001) provides a table of distinguishing characters among these species; however, we find that the noted shell differences are encompassed by larger samples from both NW and SW Pacific; relative position of the beak is one example. Within samples from one site, shell and scar characters may also vary as noted by Cosel *et al.* (1994) for ratio of height to length.

Discussion

Bathymodiolus septemdierum represents the first described taxon within a complex that includes three species-level designations. Although previous phylogenetic and population genetic work questions the species delimitations of these taxa (Vrijenhoek 2009; Thubaut *et al.* 2013; Breusing *et al.* 2015; Jang *et al.* 2020), a taxonomic revision was not formally conducted. Using new and existing molecular and morphological evidence, we confirm that *B. septemdierum*, *B. brevior* and *B. marisindicus* encompass a single, broadly distributed species, recognized by the prior synonym *B. septemdierum*. Mitochondrial sequence divergence among mussel populations across the Indo-Pacific Ocean was less than 2%—a commonly applied threshold for species delimitation based on the *COI* marker gene (Hebert *et al.* 2003). Nevertheless, Indian and western Pacific populations were genetically distinct, indicating existence of dispersal barriers and/or differential adaptations to local habitat conditions among these regions.

Morphologically, *B. septemdierum* shows high variability in shell proportions among all examined populations, although the predominant shape in the Southwest Pacific tends to be a more angular posterior margin leading to a higher height to length ratio. Most shell characters are size-related, thus can manifest differently when comparing larger to smaller specimens. Use of a wide range of animal sizes in designating taxa in this subfamily would help to define ontogenetic changes. Environmental factors also influence phenotypic expression. Tumidity may reflect size of the largest organ in the body—the gills, the condition of which is dependent on access to dissolved sulphides (Rossi & Tunnicliffe 2017). Similarly, Tunnicliffe *et al.* (2009) show that shell fragility is a function of pH in the vent water flowing over the mussels. Ecophenotypic variability manifests in other mytilids in response to predation (Leonard *et al.* 1999), substratum (Owada 2015) and geographic range (Osores *et al.* 2017), among other factors.

The maximum size of the Indian Ocean specimens is 95.4 mm (mean length 72 mm). Both our specimens and those from the type collection derive from one vent site, Kairei, on the Central Indian Ridge. We suggest that the small size of mussels at Kairei likely reflects a young population. Measures of growth lines in the shell of *B. septemdierum* support formulation of length/age growth models (Schöne & Giere 2005) that predict the large NW Eifuku mussels may live to 40 years (Tunnicliffe *et al.* 2009). Specimens from more sites in the Indian Ocean are necessary to evaluate regional variability and genetic diversity.

McCowin *et al.* (2020) note that the likely sister species to *B. septemdierum* is *B. nancyschneiderae* from East Pacific cold seeps. This species differs in its highly elongate, curving shell with a beak near the anterior margin. Hashimoto and Okutani (1994), Cosel *et al.* (1994) and Hashimoto (2001) provide details on the differences of *B. septemdierum* from several others of the genus. Cosel *et al.* (1994) also describe another species, *B. elongatus,* from one site in the North Fiji Basin, noting that the key differences with *B. brevior* relate to the shell, whereas soft parts are similar. Given the variability of *B. septemdierum* already mentioned, it is likely this additional species is another junior synonym. *Bathymodiolus brevior* and *B. elongatus* (one specimen) are identical in ITS2 sequences (Olu-Le Roy *et al.* 2007). We were unable to extract usable DNA from the borrowed museum specimen. New material from the original site is required.

Bathymodiolus septemdierum has a notably broad range for a species endemic to hydrothermal vents (Fig. 1) where most species are restricted to a biogeographic region (e.g., Rogers *et al.* 2012). Very long-range dispersal of larvae may support the infrequent connectivity of distal populations. Similar trans-oceanic distributions occur in two pairs of *Bathymodiolus* species at cold seeps on both sides of the Atlantic Ocean (Olu-Le Roy *et al.* 2007). We agree with Thomas *et al.* (2022) that limited biogeographic range is a key factor in placing vent species on the IUCN Red List. *Bathymodiolus septemdierum*, however, does not meet the criterion, and it should be removed (along with the junior synonyms). Attention to the remaining listed species becomes more compelling.

Acknowledgements

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APPENDIX 1. *COI* sequence accessions for *B. septemdierum* from the NW Pacific, SW Pacific and Indian oceans.

Sample	Morphotype	Region
AB101430	*B. septemdierum*	NW Pacific
AB101429	*B. septemdierum*	NW Pacific
AB101428	*B. septemdierum*	NW Pacific
AB101426	*B. septemdierum*	NW Pacific
AB101425	*B. septemdierum*	NW Pacific
AB101424	*B. septemdierum*	NW Pacific
AB170041	*B. septemdierum*	NW Pacific
AB170045	*B. marisindicus*	Indian Ocean
AB170044	*B. marisindicus*	Indian Ocean
AB170043	*B. marisindicus*	Indian Ocean
AB170042	*B. marisindicus*	Indian Ocean
MT067565	*B. marisindicus*	Indian Ocean
MT052845	*B. marisindicus*	Indian Ocean
MT052844	*B. marisindicus*	Indian Ocean
MT052843	*B. marisindicus*	Indian Ocean
MT052842	*B. marisindicus*	Indian Ocean
MT052841	*B. marisindicus*	Indian Ocean
MT052840	*B. marisindicus*	Indian Ocean
MT052839	*B. marisindicus*	Indian Ocean
MT052838	*B. marisindicus*	Indian Ocean
MT052837	*B. marisindicus*	Indian Ocean
MT052836	*B. marisindicus*	Indian Ocean
MT052835	*B. marisindicus*	Indian Ocean
MT052834	*B. marisindicus*	Indian Ocean
MT052833	*B. marisindicus*	Indian Ocean
MT052832	*B. marisindicus*	Indian Ocean
MT052831	*B. marisindicus*	Indian Ocean
MT052830	*B. marisindicus*	Indian Ocean
MT052829	*B. marisindicus*	Indian Ocean
MT052828	*B. marisindicus*	Indian Ocean
MT052827	*B. marisindicus*	Indian Ocean
MT052826	*B. marisindicus*	Indian Ocean
MT052825	*B. marisindicus*	Indian Ocean
MT052824	*B. marisindicus*	Indian Ocean
MT052823	*B. marisindicus*	Indian Ocean
MT052822	*B. marisindicus*	Indian Ocean
MT052821	*B. marisindicus*	Indian Ocean
MT052820	*B. marisindicus*	Indian Ocean

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APPENDIX 1. (Continued)

Sample	Morphotype	Region
MT052819	*B. marisindicus*	Indian Ocean
MT052818	*B. marisindicus*	Indian Ocean
MT052817	*B. marisindicus*	Indian Ocean
MT052816	*B. marisindicus*	Indian Ocean
MT052815	*B. marisindicus*	Indian Ocean
MT052814	*B. marisindicus*	Indian Ocean
MT052813	*B. marisindicus*	Indian Ocean
MT052812	*B. marisindicus*	Indian Ocean
MT052811	*B. marisindicus*	Indian Ocean
MT052810	*B. marisindicus*	Indian Ocean
MT052809	*B. marisindicus*	Indian Ocean
MT052808	*B. marisindicus*	Indian Ocean
MT052807	*B. marisindicus*	Indian Ocean
MT052806	*B. marisindicus*	Indian Ocean
MT052805	*B. marisindicus*	Indian Ocean
MT052804	*B. marisindicus*	Indian Ocean
MT052803	*B. marisindicus*	Indian Ocean
MT052802	*B. marisindicus*	Indian Ocean
MH202766	*B. marisindicus*	Indian Ocean
KF521937	*B. marisindicus*	Indian Ocean
AY649799	*B. septemdierum*	NW Pacific
AY275544	*B. brevior*	SW Pacific
KF521936	*B. brevior*	SW Pacific
HF545111	*B. septemdierum*	NW Pacific
ON799000	*B. septemdierum*	NW Pacific
ON799001	*B. septemdierum*	NW Pacific
ON799002	*B. septemdierum*	NW Pacific
ON799003	*B. septemdierum*	NW Pacific
ON799004	*B. septemdierum*	NW Pacific
ON799010	*B. brevior*	SW Pacific
ON799011	*B. brevior*	SW Pacific
ON799012	*B. brevior*	SW Pacific
ON799013	*B. brevior*	SW Pacific
ON799014	*B. brevior*	SW Pacific
ON799015	*B. brevior*	SW Pacific
KP879540	*B. brevior*	SW Pacific
KP879541	*B. brevior*	SW Pacific
KP879542	*B. brevior*	SW Pacific
KP879543	*B. brevior*	SW Pacific
KP879544	*B. brevior*	SW Pacific
KP879545	*B. brevior*	SW Pacific
KP879546	*B. brevior*	SW Pacific
KP879547	*B. brevior*	SW Pacific

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APPENDIX 1. (Continued)

Sample	Morphotype	Region
KP879548	*B. brevior*	SW Pacific
KP879549	*B. brevior*	SW Pacific
KP879550	*B. brevior*	SW Pacific
KP879551	*B. brevior*	SW Pacific
KP879552	*B. brevior*	SW Pacific
KP879553	*B. brevior*	SW Pacific
KP879554	*B. brevior*	SW Pacific
KP879555	*B. brevior*	SW Pacific
KP879556	*B. brevior*	SW Pacific
KP879557	*B. brevior*	SW Pacific
KP879558	*B. brevior*	SW Pacific
KP879559	*B. brevior*	SW Pacific
KP879560	*B. brevior*	SW Pacific
KP879561	*B. brevior*	SW Pacific
KP879562	*B. brevior*	SW Pacific
KP879563	*B. brevior*	SW Pacific
KP879564	*B. brevior*	SW Pacific
KP879565	*B. brevior*	SW Pacific
KP879566	*B. brevior*	SW Pacific
KP879567	*B. brevior*	SW Pacific
KP879568	*B. brevior*	SW Pacific
KP879569	*B. brevior*	SW Pacific
KP879570	*B. brevior*	SW Pacific
KP879571	*B. brevior*	SW Pacific
KP879572	*B. brevior*	SW Pacific
KP879573	*B. brevior*	SW Pacific
KP879574	*B. brevior*	SW Pacific
KP879575	*B. brevior*	SW Pacific
KP879576	*B. brevior*	SW Pacific
KP879577	*B. brevior*	SW Pacific
KP879578	*B. brevior*	SW Pacific
KP879579	*B. brevior*	SW Pacific
KP879580	*B. brevior*	SW Pacific
KP879581	*B. brevior*	SW Pacific
KP879582	*B. brevior*	SW Pacific
KP879583	*B. brevior*	SW Pacific
KP879584	*B. brevior*	SW Pacific
KP879585	*B. brevior*	SW Pacific
KP879586	*B. brevior*	SW Pacific
KP879587	*B. brevior*	SW Pacific
KP879588	*B. brevior*	SW Pacific
KP879589	*B. brevior*	SW Pacific
KP879590	*B. brevior*	SW Pacific

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APPENDIX 1. (Continued)

Sample	Morphotype	Region
KP879591	*B. brevior*	SW Pacific
KP879592	*B. brevior*	SW Pacific
KP879593	*B. brevior*	SW Pacific
KP879594	*B. brevior*	SW Pacific
KP879595	*B. brevior*	SW Pacific
KP879596	*B. brevior*	SW Pacific
KP879597	*B. brevior*	SW Pacific
KP879598	*B. brevior*	SW Pacific
KP879599	*B. brevior*	SW Pacific
KP879600	*B. brevior*	SW Pacific
KP879601	*B. brevior*	SW Pacific
KP879602	*B. brevior*	SW Pacific
KP879603	*B. brevior*	SW Pacific
KP879604	*B. brevior*	SW Pacific
KP879605	*B. brevior*	SW Pacific
KP879606	*B. brevior*	SW Pacific
KP879607	*B. brevior*	SW Pacific
KP879608	*B. brevior*	SW Pacific
KP879609	*B. brevior*	SW Pacific
KP879610	*B. brevior*	SW Pacific
KP879611	*B. brevior*	SW Pacific
KP879612	*B. brevior*	SW Pacific
KP879613	*B. brevior*	SW Pacific
KP879614	*B. brevior*	SW Pacific
KP879615	*B. brevior*	SW Pacific
KP879616	*B. brevior*	SW Pacific
KP879617	*B. brevior*	SW Pacific
KP879618	*B. brevior*	SW Pacific
KP879619	*B. brevior*	SW Pacific
KP879620	*B. brevior*	SW Pacific
KP879621	*B. brevior*	SW Pacific
KP879622	*B. brevior*	SW Pacific
KP879623	*B. brevior*	SW Pacific
KP879624	*B. brevior*	SW Pacific
KP879625	*B. brevior*	SW Pacific
KP879626	*B. brevior*	SW Pacific
KP879627	*B. brevior*	SW Pacific
KP879628	*B. brevior*	SW Pacific
KP879629	*B. brevior*	SW Pacific
KP879630	*B. brevior*	SW Pacific
KP879631	*B. brevior*	SW Pacific
KP879632	*B. brevior*	SW Pacific
KP879633	*B. brevior*	SW Pacific

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APPENDIX 1. (Continued)

Sample	Morphotype	Region
KP879634	*B. brevior*	SW Pacific
KP879635	*B. brevior*	SW Pacific
KP879636	*B. brevior*	SW Pacific
KP879637	*B. brevior*	SW Pacific
KP879638	*B. brevior*	SW Pacific
KP879639	*B. brevior*	SW Pacific
KP879640	*B. brevior*	SW Pacific
KP879641	*B. brevior*	SW Pacific
KP879642	*B. brevior*	SW Pacific
KP879643	*B. brevior*	SW Pacific
KP879644	*B. brevior*	SW Pacific
KP879645	*B. brevior*	SW Pacific
KP879646	*B. brevior*	SW Pacific
KP879647	*B. brevior*	SW Pacific
KP879648	*B. brevior*	SW Pacific
KP879649	*B. brevior*	SW Pacific
KP879650	*B. brevior*	SW Pacific
KP879651	*B. brevior*	SW Pacific
KP879652	*B. brevior*	SW Pacific
KP879653	*B. brevior*	SW Pacific
KP879654	*B. brevior*	SW Pacific
KP879655	*B. brevior*	SW Pacific
KP879656	*B. brevior*	SW Pacific
KP879657	*B. brevior*	SW Pacific
KP879658	*B. brevior*	SW Pacific
KP879659	*B. brevior*	SW Pacific
KP879660	*B. brevior*	SW Pacific
KP879661	*B. brevior*	SW Pacific
KP879662	*B. brevior*	SW Pacific
KP879663	*B. brevior*	SW Pacific
KP879664	*B. marisindicus*	Indian Ocean
KP879665	*B. marisindicus*	Indian Ocean
KP879666	*B. marisindicus*	Indian Ocean
KP879667	*B. marisindicus*	Indian Ocean
KP879668	*B. marisindicus*	Indian Ocean
KP879669	*B. marisindicus*	Indian Ocean
KP879670	*B. marisindicus*	Indian Ocean
KP879671	*B. marisindicus*	Indian Ocean
KP879672	*B. marisindicus*	Indian Ocean
KP879673	*B. marisindicus*	Indian Ocean
KP879674	*B. marisindicus*	Indian Ocean
KP879675	*B. marisindicus*	Indian Ocean
KP879676	*B. marisindicus*	Indian Ocean

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APPENDIX 1. (Continued)

Sample	Morphotype	Region
KP879677	*B. marisindicus*	Indian Ocean
KP879678	*B. marisindicus*	Indian Ocean
KP879679	*B. marisindicus*	Indian Ocean
KP879680	*B. marisindicus*	Indian Ocean
KP879681	*B. marisindicus*	Indian Ocean
KP879682	*B. marisindicus*	Indian Ocean
KP879683	*B. marisindicus*	Indian Ocean
KP879684	*B. marisindicus*	Indian Ocean
KP879685	*B. marisindicus*	Indian Ocean
KP879686	*B. marisindicus*	Indian Ocean
KP879687	*B. marisindicus*	Indian Ocean
KP879688	*B. marisindicus*	Indian Ocean
KP879689	*B. marisindicus*	Indian Ocean
KP879690	*B. marisindicus*	Indian Ocean
KP879691	*B. marisindicus*	Indian Ocean
KP879692	*B. marisindicus*	Indian Ocean
KP879693	*B. marisindicus*	Indian Ocean
KP879694	*B. marisindicus*	Indian Ocean
KP879695	*B. marisindicus*	Indian Ocean
KP879696	*B. marisindicus*	Indian Ocean
KP879697	*B. marisindicus*	Indian Ocean
KP879698	*B. marisindicus*	Indian Ocean
KP879699	*B. marisindicus*	Indian Ocean
KP879700	*B. marisindicus*	Indian Ocean
KP879701	*B. marisindicus*	Indian Ocean
KP879702	*B. marisindicus*	Indian Ocean
KP879703	*B. marisindicus*	Indian Ocean
KP879704	*B. marisindicus*	Indian Ocean
KP879705	*B. marisindicus*	Indian Ocean
KP879706	*B. marisindicus*	Indian Ocean
KP879707	*B. marisindicus*	Indian Ocean
KP879708	*B. marisindicus*	Indian Ocean
KP879709	*B. marisindicus*	Indian Ocean
KP879710	*B. marisindicus*	Indian Ocean
KP879711	*B. marisindicus*	Indian Ocean
KP879712	*B. marisindicus*	Indian Ocean
KP879713	*B. marisindicus*	Indian Ocean
KP879714	*B. marisindicus*	Indian Ocean
KP879715	*B. marisindicus*	Indian Ocean
KP879716	*B. marisindicus*	Indian Ocean
KP879717	*B. marisindicus*	Indian Ocean
KP879718	*B. marisindicus*	Indian Ocean
KP879719	*B. marisindicus*	Indian Ocean

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APPENDIX 1. (Continued)

Sample	Morphotype	Region
KP879720	*B. marisindicus*	Indian Ocean
KP879721	*B. septemdierum*	NW Pacific
KP879722	*B. septemdierum*	NW Pacific
KP879723	*B. septemdierum*	NW Pacific
KP879724	*B. septemdierum*	NW Pacific
KP879725	*B. septemdierum*	NW Pacific
KP879726	*B. septemdierum*	NW Pacific
ON799005	*B. brevior*	SW Pacific
ON799006	*B. brevior*	SW Pacific
ON799007	*B. brevior*	SW Pacific
ON799008	*B. brevior*	SW Pacific
ON799009	*B. brevior*	SW Pacific
KP879727	*B. brevior*	SW Pacific
KP879728	*B. brevior*	SW Pacific
KP879729	*B. brevior*	SW Pacific
KP879730	*B. brevior*	SW Pacific
KP879731	*B. brevior*	SW Pacific
KP879732	*B. brevior*	SW Pacific
KP879733	*B. brevior*	SW Pacific
KP879734	*B. brevior*	SW Pacific
KP879735	*B. brevior*	SW Pacific
KP879736	*B. brevior*	SW Pacific
KP879737	*B. brevior*	SW Pacific
KP879738	*B. brevior*	SW Pacific
KP879739	*B. brevior*	SW Pacific
KP879740	*B. brevior*	SW Pacific
KP879741	*B. brevior*	SW Pacific
KP879742	*B. brevior*	SW Pacific
KP879743	*B. brevior*	SW Pacific
KP879744	*B. brevior*	SW Pacific
KP879745	*B. brevior*	SW Pacific
KP879746	*B. brevior*	SW Pacific
KP879747	*B. brevior*	SW Pacific
KP879748	*B. brevior*	SW Pacific
KP879749	*B. brevior*	SW Pacific
KP879750	*B. brevior*	SW Pacific
KP879751	*B. brevior*	SW Pacific
KP879752	*B. brevior*	SW Pacific
KP879753	*B. brevior*	SW Pacific
KP879754	*B. brevior*	SW Pacific

APPENDIX 2 *ND4* sequence accessions for *B. septemdierum* from the NW Pacific, SW Pacific and Indian oceans.

Sample	Morphotype	Region
AY649806	*B. marisindicus*	Indian Ocean
KF521941	*B. marisindicus*	Indian Ocean
AB485629	*B. marisindicus*	Indian Ocean
AB485628	*B. marisindicus*	Indian Ocean
AB485627	*B. marisindicus*	Indian Ocean
AB485626	*B. marisindicus*	Indian Ocean
AB485625	*B. brevior*	SW Pacific
AB485624	*B. brevior*	SW Pacific
AB485623	*B. brevior*	SW Pacific
AB485622	*B. brevior*	SW Pacific
AB485621	*B. brevior*	SW Pacific
AB485620	*B. brevior*	SW Pacific
AB485619	*B. brevior*	SW Pacific
AB485618	*B. brevior*	SW Pacific
AB485617	*B. brevior*	SW Pacific
AY046279	*B. marisindicus*	Indian Ocean
AY046278	*B. marisindicus*	Indian Ocean
AY046277	*B. brevior*	SW Pacific
AB175318	*B. septemdierum*	NW Pacific
AB175317	*B. septemdierum*	NW Pacific
AB175316	*B. septemdierum*	NW Pacific
AB175315	*B. septemdierum*	NW Pacific
AB175314	*B. septemdierum*	NW Pacific
AB175313	*B. septemdierum*	NW Pacific
AB175309	*B. septemdierum*	NW Pacific
AB175308	*B. septemdierum*	NW Pacific
AB175307	*B. septemdierum*	NW Pacific
AB175306	*B. septemdierum*	NW Pacific
AB175305	*B. septemdierum*	NW Pacific
AB175304	*B. septemdierum*	NW Pacific
AB175303	*B. septemdierum*	NW Pacific
AB242561	*B. septemdierum*	NW Pacific
AB175312	*B. marisindicus*	Indian Ocean
AB175311	*B. marisindicus*	Indian Ocean
AB175310	*B. marisindicus*	Indian Ocean
KF521943	*B. marisindicus*	Indian Ocean
AB485616	*B. marisindicus*	Indian Ocean
AB485615	*B. marisindicus*	Indian Ocean
AB485614	*B. marisindicus*	Indian Ocean
AB485613	*B. marisindicus*	Indian Ocean
AB485612	*B. marisindicus*	Indian Ocean
AB485611	*B. marisindicus*	Indian Ocean
AB485610	*B. marisindicus*	Indian Ocean
AB485609	*B. marisindicus*	Indian Ocean

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APPENDIX 2. (Continued)

Sample	Morphotype	Region
AB485608	*B. marisindicus*	Indian Ocean
AB485607	*B. marisindicus*	Indian Ocean
AB485606	*B. marisindicus*	Indian Ocean
KP881001	*B. brevior*	SW Pacific
KP881002	*B. brevior*	SW Pacific
KP881003	*B. brevior*	SW Pacific
KP881004	*B. brevior*	SW Pacific
KP881005	*B. brevior*	SW Pacific
KP881006	*B. brevior*	SW Pacific
KP881007	*B. brevior*	SW Pacific
KP881008	*B. brevior*	SW Pacific
KP881009	*B. brevior*	SW Pacific
KP881010	*B. brevior*	SW Pacific
KP881011	*B. brevior*	SW Pacific
KP881012	*B. brevior*	SW Pacific
KP881013	*B. brevior*	SW Pacific
KP881014	*B. brevior*	SW Pacific
KP881015	*B. brevior*	SW Pacific
KP881016	*B. brevior*	SW Pacific
KP881017	*B. brevior*	SW Pacific
KP881018	*B. brevior*	SW Pacific
KP881019	*B. brevior*	SW Pacific
KP881020	*B. brevior*	SW Pacific
KP881021	*B. brevior*	SW Pacific
KP881022	*B. brevior*	SW Pacific
KP881023	*B. brevior*	SW Pacific
KP881024	*B. brevior*	SW Pacific
KP881025	*B. brevior*	SW Pacific
KP881026	*B. brevior*	SW Pacific
KP881027	*B. brevior*	SW Pacific
KP881028	*B. brevior*	SW Pacific
KP881029	*B. brevior*	SW Pacific
KP881030	*B. brevior*	SW Pacific
KP881031	*B. brevior*	SW Pacific
KP881032	*B. brevior*	SW Pacific
KP881033	*B. brevior*	SW Pacific
KP881034	*B. brevior*	SW Pacific
KP881035	*B. brevior*	SW Pacific
KP881036	*B. brevior*	SW Pacific
KP881037	*B. brevior*	SW Pacific
KP881038	*B. brevior*	SW Pacific
KP881039	*B. brevior*	SW Pacific
KP881040	*B. brevior*	SW Pacific

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APPENDIX 2. (Continued)

Sample	Morphotype	Region
KP881041	*B. brevior*	SW Pacific
KP881042	*B. brevior*	SW Pacific
KP881043	*B. brevior*	SW Pacific
KP881044	*B. brevior*	SW Pacific
KP881045	*B. brevior*	SW Pacific
KP881046	*B. brevior*	SW Pacific
KP881047	*B. brevior*	SW Pacific
KP881048	*B. brevior*	SW Pacific
KP881049	*B. brevior*	SW Pacific
KP881050	*B. brevior*	SW Pacific
KP881051	*B. brevior*	SW Pacific
KP881052	*B. brevior*	SW Pacific
KP881053	*B. brevior*	SW Pacific
KP881054	*B. brevior*	SW Pacific
KP881055	*B. brevior*	SW Pacific
KP881056	*B. brevior*	SW Pacific
KP881057	*B. brevior*	SW Pacific
KP881058	*B. brevior*	SW Pacific
KP881059	*B. brevior*	SW Pacific
KP881060	*B. brevior*	SW Pacific
KP881061	*B. brevior*	SW Pacific
KP881062	*B. brevior*	SW Pacific
KP881063	*B. brevior*	SW Pacific
KP881064	*B. brevior*	SW Pacific
KP881065	*B. brevior*	SW Pacific
KP881066	*B. brevior*	SW Pacific
KP881067	*B. brevior*	SW Pacific
KP881068	*B. brevior*	SW Pacific
KP881069	*B. brevior*	SW Pacific
KP881070	*B. brevior*	SW Pacific
KP881071	*B. brevior*	SW Pacific
KP881072	*B. brevior*	SW Pacific
KP881073	*B. brevior*	SW Pacific
KP881074	*B. brevior*	SW Pacific
KP881075	*B. brevior*	SW Pacific
KP881076	*B. brevior*	SW Pacific
KP881077	*B. brevior*	SW Pacific
KP881078	*B. brevior*	SW Pacific
KP881079	*B. brevior*	SW Pacific
KP881080	*B. brevior*	SW Pacific
KP881081	*B. brevior*	SW Pacific
KP881082	*B. brevior*	SW Pacific
KP881083	*B. brevior*	SW Pacific

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APPENDIX 2. (Continued)

Sample	Morphotype	Region
KP881084	*B. brevior*	SW Pacific
KP881085	*B. brevior*	SW Pacific
KP881086	*B. brevior*	SW Pacific
KP881087	*B. brevior*	SW Pacific
KP881088	*B. brevior*	SW Pacific
KP881089	*B. brevior*	SW Pacific
KP881090	*B. brevior*	SW Pacific
KP881091	*B. brevior*	SW Pacific
KP881092	*B. brevior*	SW Pacific
KP881093	*B. brevior*	SW Pacific
KP881094	*B. brevior*	SW Pacific
KP881095	*B. brevior*	SW Pacific
KP881096	*B. brevior*	SW Pacific
KP881097	*B. brevior*	SW Pacific
KP881098	*B. brevior*	SW Pacific
KP881099	*B. brevior*	SW Pacific
KP881100	*B. brevior*	SW Pacific
KP881101	*B. brevior*	SW Pacific
KP881102	*B. brevior*	SW Pacific
KP881103	*B. brevior*	SW Pacific
KP881104	*B. brevior*	SW Pacific
KP881105	*B. brevior*	SW Pacific
KP881106	*B. brevior*	SW Pacific
KP881107	*B. brevior*	SW Pacific
KP881108	*B. brevior*	SW Pacific
KP881109	*B. brevior*	SW Pacific
KP881110	*B. brevior*	SW Pacific
KP881111	*B. brevior*	SW Pacific
KP881112	*B. brevior*	SW Pacific
KP881113	*B. brevior*	SW Pacific
KP881114	*B. brevior*	SW Pacific
KP881115	*B. brevior*	SW Pacific
KP881116	*B. brevior*	SW Pacific
KP881117	*B. brevior*	SW Pacific
KP881118	*B. brevior*	SW Pacific
KP881119	*B. brevior*	SW Pacific
KP881120	*B. brevior*	SW Pacific
KP881121	*B. brevior*	SW Pacific
KP881122	*B. brevior*	SW Pacific
KP881123	*B. brevior*	SW Pacific
KP881124	*B. brevior*	SW Pacific
KP881125	*B. brevior*	SW Pacific
KP881126	*B. brevior*	SW Pacific

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APPENDIX 2. (Continued)

Sample	Morphotype	Region
KP881127	*B. brevior*	SW Pacific
KP881128	*B. brevior*	SW Pacific
KP881129	*B. brevior*	SW Pacific
KP881130	*B. brevior*	SW Pacific
KP881131	*B. brevior*	SW Pacific
KP881132	*B. brevior*	SW Pacific
KP881133	*B. brevior*	SW Pacific
KP881134	*B. marisindicus*	Indian Ocean
KP881135	*B. marisindicus*	Indian Ocean
KP881136	*B. marisindicus*	Indian Ocean
KP881137	*B. marisindicus*	Indian Ocean
KP881138	*B. marisindicus*	Indian Ocean
KP881139	*B. marisindicus*	Indian Ocean
KP881140	*B. marisindicus*	Indian Ocean
KP881141	*B. marisindicus*	Indian Ocean
KP881142	*B. marisindicus*	Indian Ocean
KP881143	*B. marisindicus*	Indian Ocean
KP881144	*B. marisindicus*	Indian Ocean
KP881145	*B. marisindicus*	Indian Ocean
KP881146	*B. marisindicus*	Indian Ocean
KP881147	*B. marisindicus*	Indian Ocean
KP881148	*B. marisindicus*	Indian Ocean
KP881149	*B. marisindicus*	Indian Ocean
KP881150	*B. marisindicus*	Indian Ocean
KP881151	*B. marisindicus*	Indian Ocean
KP881152	*B. marisindicus*	Indian Ocean
KP881153	*B. marisindicus*	Indian Ocean
KP881154	*B. marisindicus*	Indian Ocean
KP881155	*B. marisindicus*	Indian Ocean
KP881156	*B. marisindicus*	Indian Ocean
KP881157	*B. marisindicus*	Indian Ocean
KP881158	*B. marisindicus*	Indian Ocean
KP881159	*B. marisindicus*	Indian Ocean
KP881160	*B. marisindicus*	Indian Ocean
KP881161	*B. marisindicus*	Indian Ocean
KP881162	*B. marisindicus*	Indian Ocean
KP881163	*B. marisindicus*	Indian Ocean
KP881164	*B. marisindicus*	Indian Ocean
KP881165	*B. marisindicus*	Indian Ocean
KP881166	*B. marisindicus*	Indian Ocean
KP881167	*B. marisindicus*	Indian Ocean
KP881168	*B. marisindicus*	Indian Ocean
KP881169	*B. marisindicus*	Indian Ocean

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APPENDIX 2. (Continued)

Sample	Morphotype	Region
KP881170	*B. marisindicus*	Indian Ocean
KP881171	*B. marisindicus*	Indian Ocean
KP881172	*B. marisindicus*	Indian Ocean
KP881173	*B. marisindicus*	Indian Ocean
KP881174	*B. marisindicus*	Indian Ocean
KP881175	*B. marisindicus*	Indian Ocean
KP881176	*B. marisindicus*	Indian Ocean
KP881177	*B. marisindicus*	Indian Ocean
KP881178	*B. marisindicus*	Indian Ocean
KP881179	*B. marisindicus*	Indian Ocean
KP881180	*B. marisindicus*	Indian Ocean
KP881181	*B. marisindicus*	Indian Ocean
KP881182	*B. marisindicus*	Indian Ocean
KP881183	*B. marisindicus*	Indian Ocean
KP881184	*B. marisindicus*	Indian Ocean
KP881185	*B. marisindicus*	Indian Ocean
KP881186	*B. marisindicus*	Indian Ocean
KP881187	*B. marisindicus*	Indian Ocean
KP881188	*B. marisindicus*	Indian Ocean
KP881189	*B. septemdierum*	NW Pacific
KP881190	*B. septemdierum*	NW Pacific
KP881191	*B. septemdierum*	NW Pacific
KP881192	*B. septemdierum*	NW Pacific
KP881193	*B. septemdierum*	NW Pacific
KP881194	*B. septemdierum*	NW Pacific
KP881195	*B. brevior*	SW Pacific
KP881196	*B. brevior*	SW Pacific
KP881197	*B. brevior*	SW Pacific
KP881198	*B. brevior*	SW Pacific
KP881199	*B. brevior*	SW Pacific
KP881200	*B. brevior*	SW Pacific
KP881201	*B. brevior*	SW Pacific
KP881202	*B. brevior*	SW Pacific
KP881203	*B. brevior*	SW Pacific
KP881204	*B. brevior*	SW Pacific
KP881205	*B. brevior*	SW Pacific
KP881206	*B. brevior*	SW Pacific
KP881207	*B. brevior*	SW Pacific
KP881208	*B. brevior*	SW Pacific
KP881209	*B. brevior*	SW Pacific
KP881210	*B. brevior*	SW Pacific
KP881211	*B. brevior*	SW Pacific
KP881212	*B. brevior*	SW Pacific

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APPENDIX 2. (Continued)

Sample	Morphotype	Region
KP881213	*B. brevior*	SW Pacific
KP881214	*B. brevior*	SW Pacific
KP881215	*B. brevior*	SW Pacific
KP881216	*B. brevior*	SW Pacific
KP881217	*B. brevior*	SW Pacific
KP881218	*B. brevior*	SW Pacific
KP881219	*B. brevior*	SW Pacific
KP881220	*B. brevior*	SW Pacific
KP881221	*B. brevior*	SW Pacific
KP881222	*B. brevior*	SW Pacific