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An iconography of extant *Gibberulus* Jousseaume, 1888 (Mollusca, Gastropoda, Strombidae), and the introduction of a new species from the southwestern Pacific

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Abstract.—The gastropod family Strombidae has sparked the recent interest of taxonomists as early revisions of the family are re-examined, with a plethora of new species and genera being described. This has brought a greater understanding of the level of diversity within the family, which has assisted in conceptualizing its evolutionary intergeneric relationships. However, gaps in the revisions remain. This paper examines the extant members of the genus *Gibberulus* after half a century of neglect. After examination of type material and original descriptions, the species are recircumscribed, and a new species, *G. dekkersi*, new species, is presented, bringing the total number of species in the genus to four. In addition, information of the geographic range of each species is provided. We suggest that, as further revisions of the Strombidae are conducted, particularly of those species with large fragmented distributions, a greater diversity of species will be found and described.

Keywords: *Gibberulus dekkersi*, morphology, new species, Queensland, taxonomy.

There has been a renaissance in the taxonomy of the gastropod family Strombidae. The re-examination of the superfamily-group taxonomic relationships within the Stromboidae resulted in the reinstatement of the relationships between Strombidae, Seraphsidae, Rostellariidae, and their sister taxa Struthiolariidae and Aporrhaidae, with the epifamily Neostromboidae described and defined (Maxwell 2019, Maxwell et al. 2019a), in the nomenclature. Similarly, within the family Strombidae, the internal relationships have been revised and new family-group level taxonomic entities created to bring a greater understanding of the evolutionary relationships between genera (Dekkers & Maxwell 2020a, Maxwell et al. 2020a). At the generic level, internal revisions demonstrated that previous studies were overly conservative in their assessment of the species diversity in the Strombidae and Seraphsidae (Maxwell et al. 2018a, 2018b, 2019b, 2020b, 2020c; Dekkers et al. 2019, Dekkers & Maxwell 2020b). This paper adds a new page to the revisions with an examination of extant members of the genus *Gibberulus*.

There has not been a taxonomic revision of the genus *Gibberulus* for over half a

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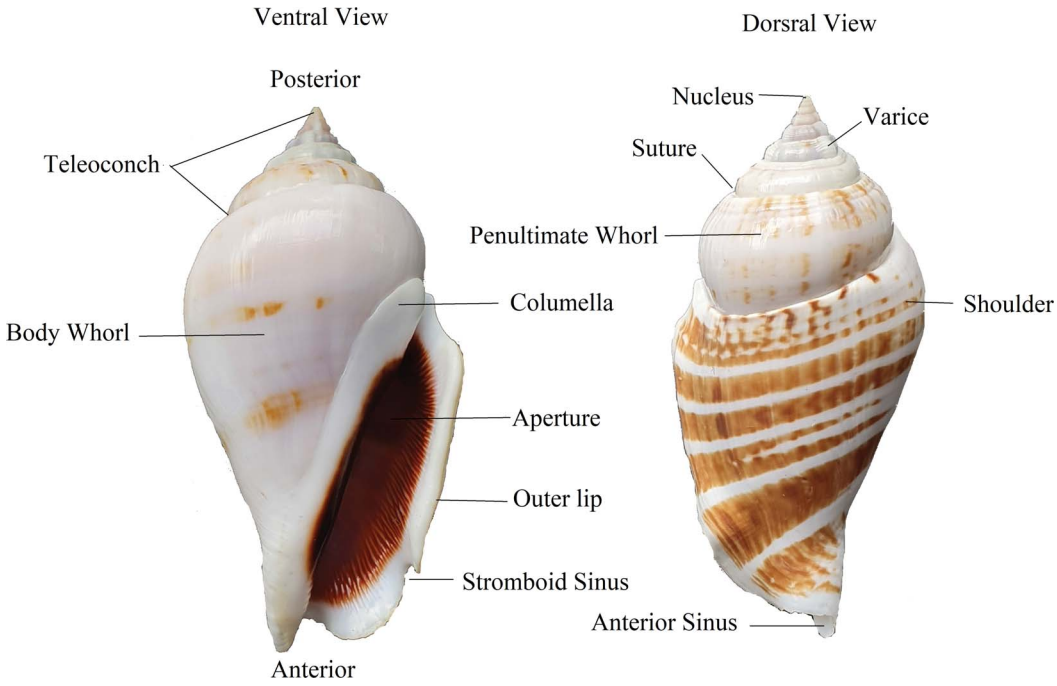


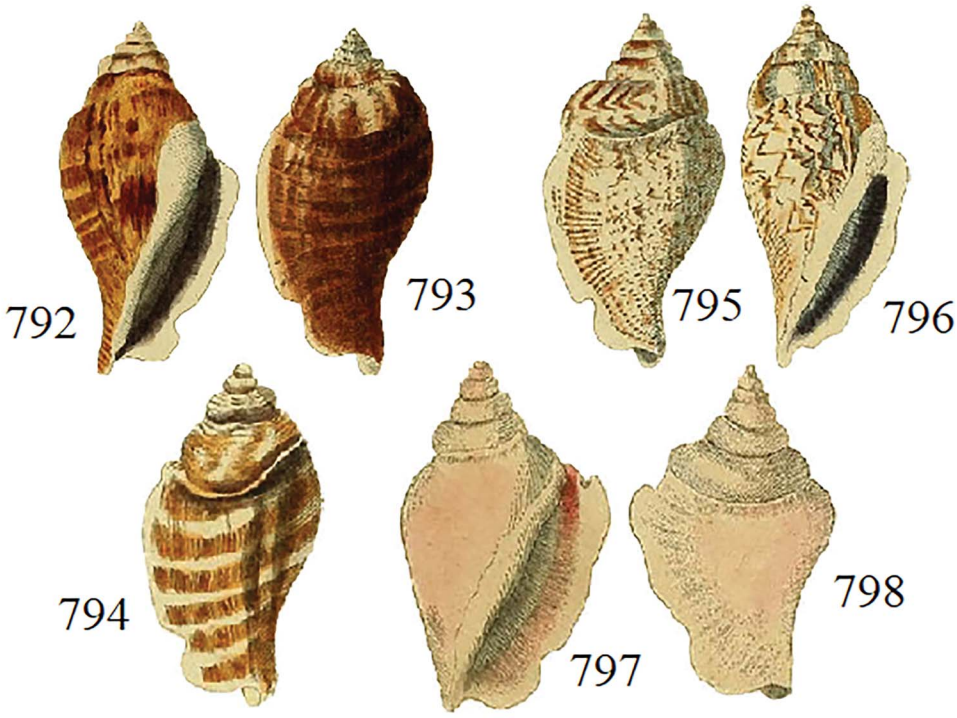
Fig. 1. The structural elements of the shell used in descriptions of species.

century (Abbott 1960), and the last published population survey was carried out even earlier (Abbott 1949). At present, *Gibberulus* is considered to contain one species, and this was subdivided into three subspecies. We now considered these to be full species (*G. albus*, *G. gibberulus*, and *G. gibbosus*). In addition, we describe a fourth new species.

Materials and Methods

This study used shell morphology and size range to guide the discernment of different species (Fig. 1). Size ranges were based on the current world records (wrs-shell.com), with location of the record used as a guide to distinguish which species with which the record was associated, either one of the existing *Gibberulus* or *G. dekkersi*. Where records for size were not available, or the material examined set a new record, the size records were used.

We compared and contrasted the type material contained within museums and also the literary works that contain the references to images that are used as types (Röding 1798, Mörch 1850) with *G. dekkersi*. In particular, we treat the Martini (1777) text as the original descriptions for the known species of *Gibberulus*, although he did not provide names for them, as they were referred to by the authors of both *G. gibbosus* and *G. albus* (Fig. 2). In addition, Martini (1777) also provides text for *G. gibberulus*, which was the first text post Linné (1758) to offer a description for that species. Literal translations of Martini (1777) were carried out by Dr. Michael Underdown, a specialist in Early German. These descriptions lack the distinguishing characteristics needed to distinguish the species. There are some interesting points that need to be clarified in the translations. Martini (1777) used the Zoll, which until 1877 was slightly larger than the English inch of 2.54 cm, being 2.615475 cm. Dr. Underdown also noted that the exact work Martini (1777) used referred to an animal inside the shell and



792-798. Figur.

Die buklichte Kanarienschnekke.

Fr. Ailée à spirales bossues.

Holl. Gebande en gebulde Kanary.

Engl. Girdled Kanary.

Fig. 792-798.

Ex Mus. nostro.

Cochlis subalata, laevis fasciata & maculata, spiris varie gibbosis, ore striato ex violaceo nigrescente. Fig. 792. ad 798.

Alata Canarium gibbosum.

b) Fig. 794. Die dunkelrostfarbig und breitbandirten Kanarienschnekken, mit violetter Mündung und einem Brandflekt an der innern schwülichten Lefze. 1½ - 1¾ Zoll lang.

c) Das gesprenkelte kanarische Rebhuhn, mit violetter Mündung und weisen Lefzen. Fig. 795. 796. mit feinen zerrißnen Zikzakfiguren und starken Streifen. Aus Mauritien.

d) Die weise buklichte Kanarienschnekke Fig. 797. 798. mit reizend rosenrother Mündung. Aus Ostindien. S. *Rumph.* p. 87. n. 13. Leßer p. 343. III) *Gualt.* T. 32. c.

Ihre Benennung haben diese und folgende Kanarienschnekken der Aehnlichkeit einer gewissen Kanarienfrucht, nach Rumphs Berichte zu danken. Die Stumpfchen davon S. Fig. 863. 864.

Fig. 2. Extracts form Martini (1777) plate 72 figures related to the *Gibberulus* complex, showing that there has been a recognition of three distinct taxa: figure 794 is the type for *Gibberulus gibbosus* [Röding, 1798; figures 795 and 796 are *Gibberulus gibberulus* (Linné, 1758)], figures 792 and 793 are also this species; and figures 797 and 798 is the type for *Gibberulus albus* (Mörch, 1850). (Images from www.strombidae.de, accessed 29 October 2020, with permission.)

not the shell, but he erred on the side of convenience in translation, using shell in the translation. The term "canary" in the Martini (1777) description refers not to the bird, but to a fruit alluded to by the Rumph works he had at hand. Given that, the descriptions of Martini (1777) allow for the distinguishing of the three species based on the coloration or locations provided. We take this further and provide a redescription of the morphological characteristics of each species to provide clarity and to assist the discernment of novel taxa. Martini (1777) also offers references to other images, the "blunt {ones} of them see fig. 863. 864," which are juvenile members of *Gibberulus*.

The following specimens, and their locations contained under each species, were examined: *G. albus*—50 specimens from 16 locations; *G. gibberulus*—74 specimens from 24 locations; *G. gibbosus*—160 specimens from 22 locations; *G dekkersi*—737 specimens from 70 locations.

Abbreviations.—AD, Aart M. Dekkers Collection, The Netherlands. BC, Barbra Collins Collection, Cairns, Queensland. SM, Stephen Maxwell Collection, Cairns, Queensland. VC, Valda Cantamessa Collection, Proserpine, Queensland. VL, Virgilio Liverani Collection, Faenza, Italy. YC, Trevor and Marguerite Young Collection, Cannonvale, Queensland.

Systematics

Superfamily Stromboidea Rafinesque, 1815

Epifamily Neostromboidae Maxwell, Dekkers, Rymer, & Congdon, 2019

Family Strombidae Rafinesque, 1815

Gibberulus Jousseaume, 1888

Gibberulus Jousseaume, 1888:174.

Type species.—*Strombus gibberulus* Gmelin = *Strombus gibberulus* Linné, 1758.

Strombus (*Gibberulus*) Jousseaume Abbott, 1960:141.

Type species.—*Strombus gibberulus* Linné, 1758.

Type species.—*Strombus gibberulus* Gmelin, 1791 = *Strombus gibberulus* Linné, 1758:744, no. 433.—Jousseaume, 1888:174.

Description.—The shell is asymmetrical, varices, when present, are broad and wide. The body whorl is laterally compressed. There is no basal peg on the marginal teeth.

Gibberulus albus Mörch, 1850
Fig. 3

Strombus gibberulus Gmelin, 1791:3514, no. 17, in part.—Duclos, 1844, Figs. 5, 6.

Strombus albus "Martini" Mörch, 1850:11, no. 264.—Mörch, 1852:62.

Strombus gibberulus rhodostomus "Mörch": von Martens, 1869:64.

Strombus gibberulus rhodostomus Mörch: Tryon, 1885:121, 143.

Strombus gibberulus albus Mörch: Mastaller, 1978:131.—Oliver & Nicholls, 1975:80, 81.—Abbott & Dance, 1982:81.

Strombus (*Gibberulus*) *gibberulus albus* Mörch: Abbott, 1960:144, pl. 14, Fig. 27.—Mienis, 1984:560.—Walls, 1980:145, 146.—Kreipl et al., 1999:13, 54, pl. 118.

Gibberulus albus Mörch: Kronenberg & Vermeij, 2002:51.

Type material.—Holotype – Martini, 1777, vol. 3, Figs. 797, 798, designated Mörch, 1850:11, no. 264, Fig. 2.

Type locality.—Red Sea (Abbott 1960:144).

Material examined.—Red Sea (SM 51.001 × 1, VC x 5); Gulf of Aden (SM 51.003 × 6); Egypt (VC x 1, AD STR0109/STR1621 × 2); Abu Dabab Reef (YC x 1); Dahab, Sinai (51.005 x1); Hurghada (SM 51.002 × 1, AD STR0520-STR0522 × 3, VC x 1); Ras Mohamed (YC x 2); Safaga

Fig. 3. Variations of *Gibberulus albus* (Mörch, 1850) Gulf of Aden, collected 1991 (SM 51.003).

(AD STR0110 × 1); Sharm el Sheikh (SM 51.004 × 1, BC x 3, VC x 4); Soma Bay (AD STR1630, STR1632 × 2); Eritrea Masawa (YC x 1); Oman (AD STR0653 × 1); Al Masirah (AD STR0653/STR1981 × 2); Mirbat (AD STR2308 × 1, VL 1000-14 × 2); Sur (VL 1000-13 × 7); Saudi Arabia (AD STR1663 × 1).

Original description.—Martini (1777, 96d, Figs. 797, 798) provided the following transliteral description as "the white hunchback canary snail. Fig. 797.798.

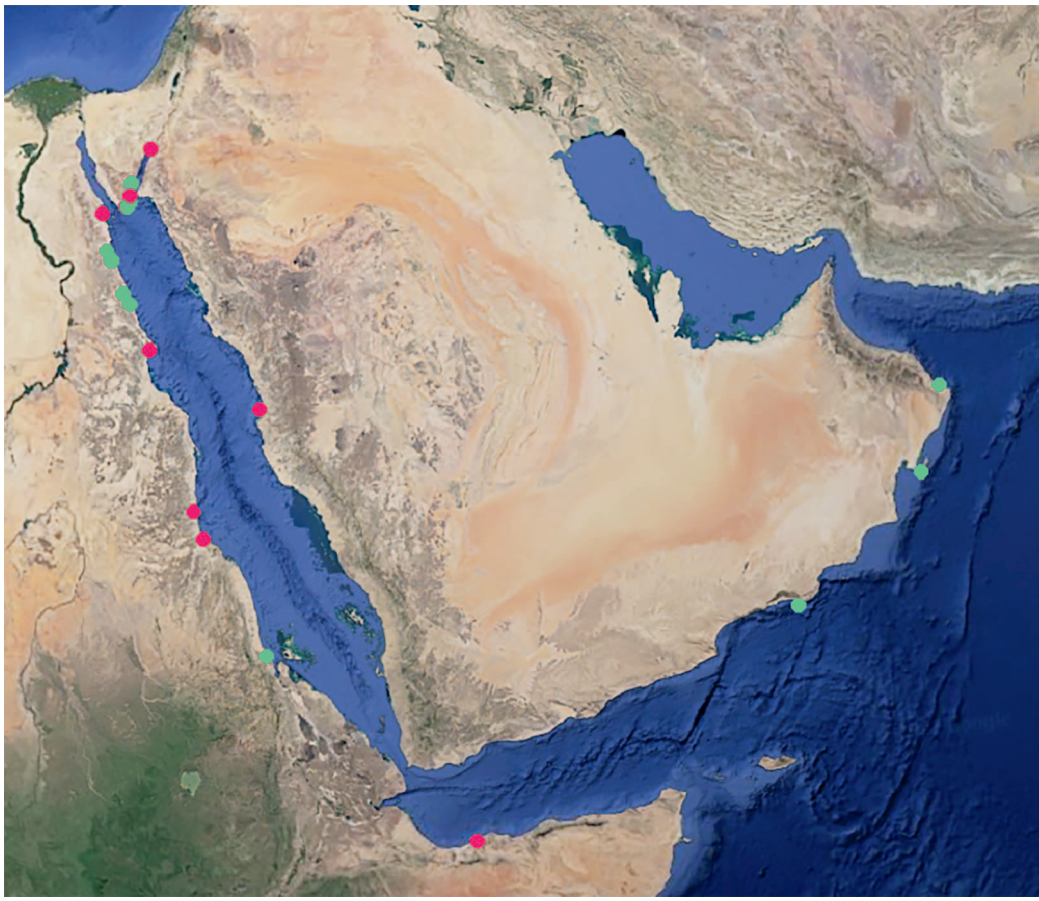


Fig. 4. Locality data map of *Gibberulus albus* (Mörch, 1850) centered on the Red Sea and Gulf of Aden, showing literary references (pink) and material examined (green). (Base Map: Google 2021; Imagey 2021 NASA; TereMetrics Map Data 2021, accessed 16 March 2021).

With attractive rose red opening. From the East Indies. S Rump. p. 87 n. 13. Lister p. 343. III) Gualt. T.32.c." Note: We understand this to be the white shell with a distorted body whorl and with a rose red aperture, Figs. 797 and 798, from Indonesia. The color form of *G. albus* is not known from Indonesia, with the distributional evidence indicating a restricted range to the Red Sea and Arabian Peninsula. Martini (1777) provides three literary references: 1) the Rumphius reference is problematic with the *Thesaurus Imaginum*... (1711) and *D'Amboinsche Rariteitkamer* ... (1705, 1741) all not showing a p. 87. n. 13 *Gibberulus*; 2) similarly, the Lister (1688) *Historiae sive Synopsis Methodicae Conchyliorum* does not show *Gibberulus* on p. 343; 3) the Gualtieri (1742) *Index Testarvm Conchyliorvm* ... plate 32, figure C, is clear and resembles *G. albus*.

Diagnosis.—Shell shows distinctive angulate shoulders and rose red/pink aperture.

Redescription.—The shell is obovate, ranging in size from 26.5 mm (Red Sea) to 68.8 mm (Red Sea). The nuclear whorls are rounded, not acute, and are smooth with three whorls. The early teleoconch whorls are rounded with distinctive evenly spaced uniform fine spiral lines; the first

Fig. 5. Holotype of *Strombus gibberulus* Linné, 1758. Online Linnaean Collection Reference: Box number: LSL.431; Dance label image ref: G–M 0010013 (accessed 4 September 2020).

spiral line below the suture being wider than the others; whorls typically with three evenly spaced distinctive varices, commencing on the second post nuclear whorl; these varices do not interrupt the continuity of the spiral lines; the sutures are moderately incised. The later teleoconch shows moderately stepped rounded whorls, becoming more angulate as the shell develops; the incised lines evidenced on earlier whorls diminish, becoming obsolete by the penultimate whorl; the subsutural incised line may continue, forming a subsutural chord that becomes obsolete by the penultimate whorl. The smooth round penultimate whorl shows a distinctive angulate shoulder; the whorl being widest at the shoulder and being distinctly narrower at the suture on the body whorl; the subsutural incised line may form a chord that is lost by the formation of the ventral body whorl. Ventral body whorl is spathulate and somewhat flattened centrally, with a largely thickened left side, forming an axial bulge at the dorsal margin; the acute shoulder is smooth, showing only faint, wide, evenly spaced spiral lines on the lower third. On the dorsal body, the lower spiral lines continue from the ventral side being more defined and raised toward the aperture; fine spiral raised lines commence from the second half of the body whorl and become stronger and more defined toward the outer lip, but do not reach it. There is a distinctive step that forms a wide ridge along the edge of the aperture to the commencement of the stromboid sinus. Outer lip is apically quadrate and not thickened, becoming axial parallel, thickened and blunt being calloused more apically; stromboid sinus is well formed; the posterior lip is not callused and is rather sharp; joining the shell well below the shoulder, forming a shallow sinus with the columella. The labrum is smooth toward the edge with inner fine raised spiral lirae that do not continue into the shell. The columella is smooth and thickened extending above the join of the outer lip to below the shoulder. The inner aperture is smooth. The siphonal canal is dorsally open, extending well past the dorsal shell margins. The coloration of early whorls is uniformly white pinkish; later teleoconch whorls becoming white or with a tingeing of light tan banding, often with a darkening below the suture; the body whorl is dorsally white, or pink, which may have tan bands that cover the shell; the dorsum with a distinctive short subsutural dark band that does not reach the outer lip; the columella is white, but may have a pink hue internally, particularly apically; the inner aperture white with a distinctive pink/rose red band the entire length in the area of the lirae; this does not reach the outer edge, nor continues to the inner aperture of the shell.

Distribution.—This species is known from the upper reaches of the Red Sea and Arabian coast into the Gulf of Oman (Fig. 4).

Literature records.—Egypt, Gulf of Suez (Abbott 1960); Ras Banas (Abbott 1960); Sinai (Mienis 1984); Saudi Arabia 20 miles north of Jeddah (Abbott 1960); Somalia Berber a (Abbott 1960); Sudan Port Sudan

Fig. 6. Variations of *Gibberulus gibberulus* (Linné, 1758) Sakala Island, Kangean Islands, Indonesia, collected 2020, highlighting the variability in pattern and form (SM 50.005).

(Abbott 1960, Mastaller 1978); Suakin (Mastaller 1978); Israel Eilat ('Hadar' *in* Abbott 1960).

Remarks.—This species is not known to be sympatric with any other species in the *Gibberulus* complex. However, during the veliger stage, members of the Strombidae are able to cover large distances and are recruited into populations away from the point of spawning (Delgado et al. 2008, Paris et al. 2008, Pérez-Enriquez et al. 2011). Therefore, it is highly probable that

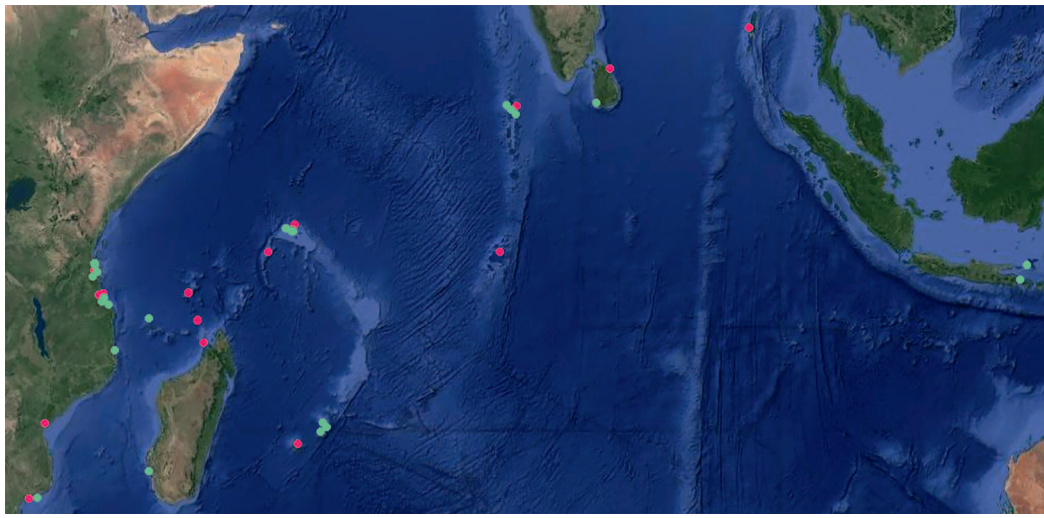


Fig. 7. Locality data map of *Gibberulus gibberulus* (Linné, 1758) centered on the Indian Ocean, showing literary references (pink) and material examined (green). (Base Map: Google 2021; Imagey 2021 NASA; TereMetrics Map Data 2021, accessed 16 March 2021.)

within some populations of *G. albus* there may occur the occasional vagrant *G. gibberulus*. There are no hybrids recorded for this species (Maxwell et al. 2019c). This study extends the distribution of this species into the Gulf of Oman, and it is highly likely that this species is also found along the Iranian coast. That area, however, remains currently unknown within the literature in terms of its species of Strombidae.

Gibberulus gibberulus Linné, 1758
Fig. 6

Strombus luhuanus Linné, 1758, 10th ed., p. 744, no. 432, in part.

Strombus gibberulus Linné, 1758, 10th ed., p. 744, no. 433, 1767:1210, no. 501.—Gmelin, 1791:3514, no. 17, in part.—Born, 1778:275.—Dillwyn, 1817:666.—Kiener, 1843:37, pl. 28, Fig. 1, pl. 33, Fig. 5.—Duclos, 1844, Figs. 1–3.—Hanley, 1856:123, pl. 25, Fig. 20.—Reeve, 1860:93.—Woodward, 1880:211.—Pilsbry, 1920:321.—Adam & Leloup, 1938:110.—Dodge, 1956:265.—Fischer, 1961:106, 1962:44–46.—Dance, 1974:83.—McClanahan, 1989, 2002:1490.—Drivas & Jay, 1998:12.—Kronenberg & Vermeij, 2002.—Barnard, 1900:88, pl. 11, Fig. 22.—Braithwaite et al., 1973:324.—Hughes & Gamble, 1977:353.

Lambis gibberula Röding, 1798:62, nos. 782–785.

Strombus labiatus Perry, 1811, pl. 12, Fig. 3.

Harpago gibberulus Linné: Hanley, 1860:73.

Canarium gibberulum Linné: Newton, 1900:509, pl. 20, Fig. 2.

Alata pictus Humphrey: Dodge, 1956:266.

Strombus (*Gibberulus*) *gibberulus gibberulus* Linné: Abbott, 1960:141, pl. 14, Fig. 28, pl. 114, Figs. 5–7, pl. 115, Fig. 5.—Walls, 1980:143–144.—Kreipl et al., 1999:13, 54, pl. 117, pl. 130, Fig. 2.—Dharma, 2005:74, pl. 12, Fig. 8a–d.

Strombus gibberulus gibberulus Linné: Oliver & Nicholls, 1975:80, 81.—Abbott & Dance, 1982:81.—Agombar et al., 2003:15.

Gibberulus gibberulus Linné: Kronenberg & Vermeij, 2002:51.

Material examined.—Comoro Islands (VC x 1); Indonesia Sakala Island, Kan-

Fig. 8. Variations of *Gibberulus gibbosus* (Röding, 1798) form the type location of Cebu Island, Philippines, collected 2011 (SM 49.002).

gean Islands (SM 50.005 × 15); Sumberkima, Bali (SM 50.006 x1); *Kenya* Funzi Bay (AD STR1671 × 1); Mombasa (YC x 2, AD STR0517/STR1647 × 2); Mbuyu Beach (AD STR1646 × 1); Madagascar (SM 50.004 × 2); Toliara (AD STR3235-STR3244 × 9); Maldives Alif Alif Atoll (AD STR3272 × 1); Lhaviyami Atoll (AD STR0879/STR0880 × 2); Rasdu Atoll (AD STR0531/STR0515 × 2); Mauritius (YC x 2, AD STR0516/STR0518/STT0519 × 3, SM 50.002 × 2); Bambous Virieux (SM

50.007 × 1); Black River (SM 50.003 × 3); Mahebourg Lagoon (AD STR904 × 1); Mozambique Inhaca Is (AD STR0513/STR1241 × 2); Nacala Bay (SM 50.001 × 4); Seychelles Anse Boileau (AD STR0512 × 1); Mahe (AD STR1641 × 1); Sri Lanka Unawatana (AD STR0514 × 10); Tanzania Chwaka Beach (AD STR0108 × 1); Makundichii, Zanzibar (AD STR3161 × 1); Michawvi, (AD STR2206 × 1); Zanzibar (AD STR0107/STR0658 × 2).

Type material.—Holotype–Linnaean Collection Box number: LSL. 431; Dance label image ref: G–M 0010013 (Fig. 5).

Type locality.—Zanzibar (Abbott 1960:143).

Original description.—Martini (1777, 96c, Figs. 795, 796) was the first to distinguish this shell from both *G. gibbosus* and *G. albus*, transliterally describing the shell as "the sprinkled canary partridge, with a violet opening and white lips. Fig. 795.796. with fine torn apart zigzag figures and strong stripes. From Mauritius." Note: We interpret this to be: the spotted shell from Mauritius with a dark aperture bordered with white, with fine broken zigzag lines and spiral banding, see Figs. 795, 796.

Diagnosis.—Shell has rounded shoulders, a constantly violet aperture and only weak spiral lines on the spire.

Redescription.—The shell is ovately-fusiform ranging in size from 26.2 mm (Mauritius) to 74.6 mm (Tanzania). There are three nuclear whorls that are smooth and rounded. The teleoconch is triangulate with a distinctive subsutural cord and diminished spiral lines, which are typically only on the upper part of the whorls; these lines may be obsolete in some specimens, and are typically absent in later whorls; usually three broad flat varices on each whorl. The penultimate whorl is broad, somewhat triangulate, typically smooth and may have one or two broad varices. The ventral body whorl with a rounded shoulder; moderately flattened with only a mild axial shoulder on the dorsal border; lower third with faint spiral lines. Dorsal body whorl smooth with developing fine spiral raised lines, from the last one-third of the body whorl or continue on from the ventral side, along the length of the shell body whorl; these lines do not extend to the edge of the outer lip; there is a broad step prior to the aperture between the apical end to the stromboid sinus. The outer lip is spirally thin before turning, thickening, and running axially to the well-formed stromboid sinus, the edge of which is not thickened; the lower outer lip is thin and sharp. The columella is thickened, even, broad and is the aperture; the columella forms with the outer lip a well-defined posterior sinus that exposes the body whorl that separates the two sides. The inner aperture is smooth at the edge, with inner lirae the length of the aperture that do not extend into the shell. The siphonal canal extends beyond the dorsal edge of the shell. The base coloration of the shell is light tan to cream with axial brown banding and may have axial wavy lines, there may be a dark subsutural band on the dorsum and some areas of the spire; the columella is white with an inner tinge of violet; the aperture is white, but is tinged violet where lirate.

Distribution.—The species ranges from the east coast of Africa to the Kangean Islands and surrounds of Indonesia (Fig. 7).

Literature records.—Andaman Islands (Abbott 1960); Chagos Archipelago ('Melvill' in Abbott 1960). Kenya (McClanahan 2002); Mombasa (Fischer 1962); Madagascar Gloriosa Island (Abbott 1960); Nossi-bé (Abbott 1960); Maldives Malé (Abbott 1960); Mozambique Inhaca Island, Delagoa Bay (Abbott 1960); Mozambique City (Abbott 1960); Réunion (Drivas & Jay 1998); Seychelles Aride Island Beach (Agombar et al. 2003); Aldabra Atoll (Hughes & Gamble 1977); Ile des Roches, Amirante Isles ('Smith' in Abbott 1960); Sri Lanka Powder Bay,

Trincomalee (Abbott 1960); Tanzania Zanzibar (Abbott 1960).

Remarks.—*Gibberulus gibberulus* is sympatric in its Indonesian range with *G. gibbosus*. There are known putative hybrids between *G. gibberulus* and *Conomurex decorus* (Röding, 1798) (Dekkers & Maxwell 2018); inter-generic hybrids are well known in Strombidae (Maxwell et al. 2020a).

Gibberulus gibbosus Röding, 1798
Figs. 8–10.

Strombus gibberulus Gmelin, 1791:3514, no. 17 in part.—Duclos, 1844, Fig. 4.—Reeve, 1850, pl. 8, Fig. 15.

Lambis gibberula Gmelin: Röding, 1798:62, no. 786–788.

Strombus (*Gibberulus*) *gibberulus gibbosus* Röding: Abbott, 1960:143.—Springsteen & Leobrera, 1986:74; pl. 17, Fig. 18.—Okutani, 2000:183, Fig. 13.

Strombus (*Gibberulus*) *gibberulus gibbosus* Linné: Dharma, 2005:74, pl. 12, Fig. 9a–d.

Gibberulus gibbosus Röding: Wilson, 1993:158, pl. 21, Fig. 12.—Poppe, 2008:53, pl. 214, Figs. 2–4, 6, 8.

Strombus gibberulus gibbosus Röding: Zhongyan, 2003:50, pl. 23, Fig. c.—Thach, 2005:16, Fig. 19.

Strombus gibberulus albus Mörch: Thach, 2005:16, Fig. 25.

Type material.—Holotype–Martini (1777) pl. 72, Fig. 794 designated Röding, 1798:62; no. 786–788, Fig. 2.

Material examined.—Indonesia Sorong (VC x 1); Java (SM 49.005 × 1); Sakala Island, Kangean Islands (SM 49.003 × 104); Sumberkima, Bali (SM 49.004 × 2); Japan (AD STR0106 × 1); New Caledonia (VC x 2); Palau (YC x 2); Papua New Guinea Madang (VC x 2); Rabaul (SM 49.007 × 2, VC x 5); Philippines Balabac Is, Palawan (AD STR3226/STR3227 × 2); Bantayan Island (SM 49.006 × 1); Bohol Island (AD STR0526/STR0614/STR3232-STR3234 × 6, SM 49.001 × 2); Cebu Island (SM 49.002 × 10); Dinagat Island (AD STR0860/STR3224 × 2); Masbate (AD STR2730 × 1); Olango Is (AD STR2076/STR3228/STR3229 × 3); Paritoba Is, Palawan (AD STR3225 × 1); Polango, Palawan (AD STR3230/STR3232 × 2); Siargao Island (AD STR3221/STR3040 × 2); Solomons (SM 49.008 × 1); Bellona Reef (VC x 4); South China Sea (AD STR1669 x1).

Type locality.—Cebu Island, Philippines (Abbott 1960:144, Fig. 8)

Original description.—Martini (1777, 96b, Fig. 794) transliterally described the shell as "the dark red colored and wide-banded canary snail, with violet opening and a burn mark on the inner swollen-like aperture. 1½ to 1¾ inches long". Note: We interpret this as: the shell is dark red colored with wide banding, the aperture is violet, and the columella has a dark stain, 1½ to 1¾ inches long.

Diagnosis.—The spire of the shell is not distorted and the rounded penultimate whorl typically with pronounced broad varices give a triangulate appearance when viewed axially. The early teleoconch whorls are transected by strong spiral lirae, from suture to suture on earlier whorls.

Redescription.—The shell shape is variable in this species ranging from ovately elliptic to fusiform, and ranging in size from 19.2 mm (Philippines) to 66.2 mm (Philippines). There are three nuclear whorls that are smooth, rounded and somewhat acute in appearance. The evenly developing teleoconch has deeply incised sutures; with the whorls combining to give a moderately stepped and convex form that varies greatly from extended and lanceolate, to moderately raised and elliptic in appearance. The moderately convex early teleoconch has distinct evenly spaced spiral incised lines that cross the broad low varices that number three per whorl; varices give the whorls a slight triangulate appearance. The spiral lines diminish in strength on later whorls, remaining pronounced only on the broad raised varices.

Fig. 9. Variations of *Gibberulus gibbosus* (Röding, 1798) Sakala Island, Indonesia, collected 2020, highlighting the variability in pattern and form of the purple phenotype (SM 49.003).

The last varix typically appearing on the now smooth rounded penultimate whorl mid-dorsally; this varix still retains the distinct spiral incised lines, even if those on the body have become obsolete; the shoulder of the body whorl is moderately defined; and the penultimate whorl is not distorted or greatly inflated, along with the varices combine on the round whorls to giving a triangulate appearance. The ventral body whorl is flattened, smooth with only faint anterior spiral incised lines developing on the lower third; there is a strong broad dorso-ventral shoulder that

Fig. 10. Variations of *Gibberulus gibbosus* (Röding, 1798) Sakala Island, Indonesia, collected 2020, highlighting the variability in pattern and form of the orange phenotype (SM 49.003).

extends from the suture to the middle of the whorl, then diminishes anteriorly. The dorsal body whorl is smooth, developing faint raised spiral lines on the last part of the dorsal surface near the broad step prior to the edge of aperture between the posterior to the stromboid sinus, these lines do not reach the margin of the outer lip; the stromboid sinus is well formed and not thickened at the edge; the lower outer lip is thin and sharp. The posterior edge of the outer lip is thin and spirally stepped, before turning and thickening from the base of the step to the stromboid sinus; this

thickened area is axially wavy with four slight concave indentations; the edge becomes thin at the stromboid sinus to the base of the shell; the columella combines with the outer lip to form a well-defined posterior sinus that exposes the body whorl and separates the two. The columella is thickened, raised and extends the entire length of the aperture. The aperture is smooth with a band of uniform reticulated raised lirae that do not extend into the shell or to the outer lip. The siphonal canal extends slightly past the dorsal body whorl forming an open canal. The color is variable, with two distinct color morphs: first, a purple patterned shell with a white margined aperture and columella, both of which possess an inner deep violet coloration, that may continue deeply into the aperture in some specimens; and second, an orange colored shell that has a white aperture and columella, which may have occasional staining of orange. Integrations of both color forms are known, but these color examples are considered rare. The base cream shell has a high degree of variability in the pattern in both color forms ranging from zig zag lines, solid color, to maculations and spots; this pattern is broken by axial bands that reveal the base color of the shell; the dorsal body whorls are typically more patterned and colored than the teleoconch and ventral body whorl; there is often a strong band of color below the last suture dorsally.

Distribution.—This species is centered on the Philippines and eastern Indonesian Archipelago but ranges sporadically to the east into northeastern Papua New Guinea and associated Island chains (Fig. 11).

Literature records.—Australia Cocos Keeling (Abbot 1960, Wilson 1993); Scott Reef (Wilson 1993); Indonesia (Cernohorsky 1965); Ambonia (Abbott 1960); Batjan Island (Abbott 1960); Bouro Island (Abbott 1960); Halmahera Island (Abbott 1960); Marissa, Celebes Island (Abbott 1960); Mollucca Islands (Abbott 1960); Japan Okinawa Island (Abbott 1960); Ryukyu Islands (Cernohorsky 1965); Palau Helen Reef (Abbott 1960); Philippines (Cernohorsky 1965); Balabac Island (Abbott 1960); Busuanga Island (Abbott 1960); Catanduanes Island (Abbott 1960); Caubian Island (Poppe 2008); Cebu Island (Abbott 1960); Cuyo Island (Abbott 1960); Luzon Island (Abbott 1960); Marinduque Island (Abbott 1960); Palawan Island (Abbott 1960); Panay Island (Abbott 1960); Samar Island (Abbott 1960); Sanga Sanga Island (Abbott 1960); Siquijor (Poppe 2008); Taiwan Kurun ('Kuroda' in Abbott 1960); Vietnam Con Son Island (Thach 2005); Ninh Thuan (Thach 2005).

Remarks.—*Gibberulus gibbosus* is sympatric in the western side of its range with *G. gibberulus* and to the east with *G. dekkersi*. At present, there are no known hybrids with this species (Maxwell et al. 2019c). However, given the propensity for members of the family to which it belongs to hybridize, both intra- and inter-generic hybrids are expected (Maxwell et al. 2020a).

Gibberulus dekkersi, new species
urn:lsid:zoobank.org:act:F7E075FE-CCCA-413D-80F7-5DAF8C3A8BA7
Figs. 12–14

Strombus gibberulus Linné: Allan, 1950:100, pl. 17, Fig. 12.—Rippingale & McMichael, 1961:56, pl. 5, Fig 16.—Hinton, 1972:10, pl. 5, Figs. 1–3.—Berg, 1974:277.—Stone & Bawden, 1975:58, 59.—Short & Potter, 1987:34, pl. 16, Fig. 3.—Richer de Forges et al., 1988:3.—Wilson, 2002:108, 109.

Strombus (*Gibberulus*) *gibberulus gibbosus* Röding: Abbott, 1960, Indo-Pacific Mollusca, 1, pl. 14, Fig. 26; pl. 114, Figs. 1–4.—Wilson & Gillett, 1971:40; pl. 18, Fig. 9, 1979:76, pl. 14, Fig. 9.—Ladd, 1972:62; pl. 19, Fig. 9, pl. 20, Fig. 1.—Cernohorsky, 1972:83; pl. 19, Fig. 9.—Walls, 1980:145, 146.

Strombus gibberulus gibbosus Röding: Hinton, 1977a:13; no. 7, 1977b:10, no. 8.—

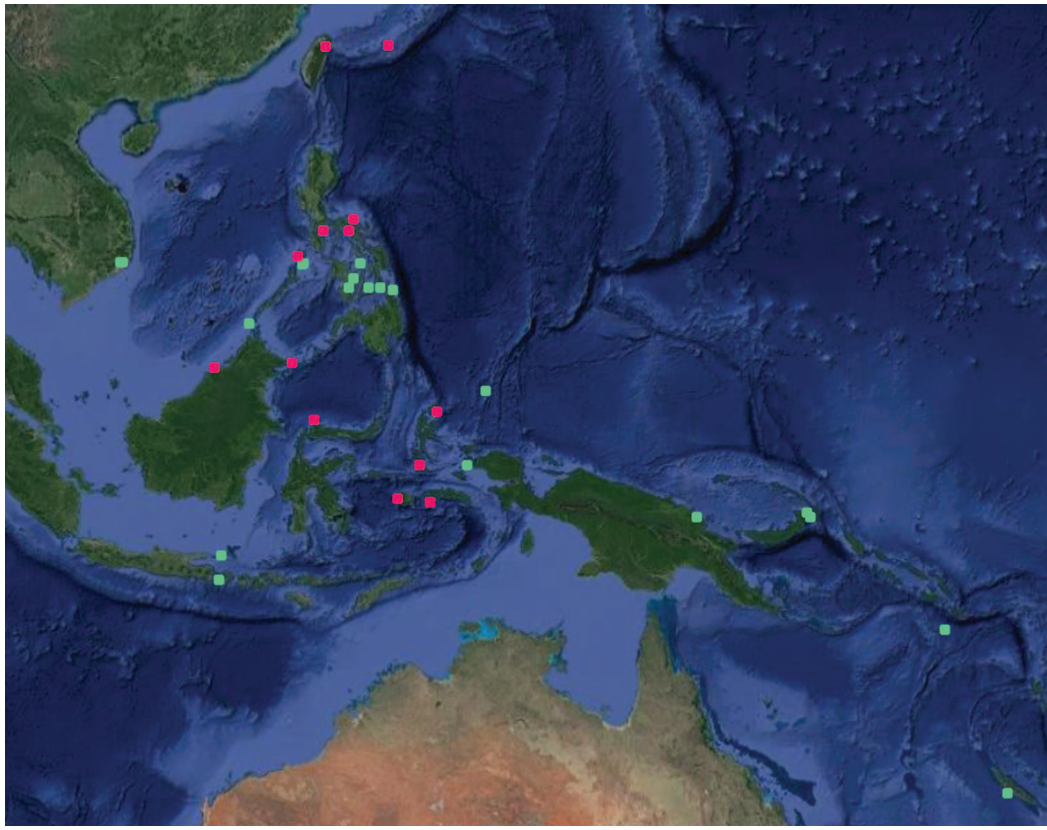


Fig. 11. Locality data map of *Gibberulus gibbosus* (Röding, 1798) centered on the central and eastern coral triangle, showing literary references (pink) and material examined (green). (Base Map: Google 2021; Imagey 2021 NASA; TereMetrics Map Data 2021, accessed 16 March 2021.)

Smith, 2003:255.—Wen, 2017:47, Fig. 135.

Strombus (*Gibberulus*) *gibberulus gibbosus* Röding: Richer de Forges et al., 1988:8.

Strombus (*Conomurex*) *gibberulus gibbosus* Linné: Cernohorsky, 1965:11, pl. 2, Fig. 10.

Gibberulus gibberulus gibbosus Röding: Brown, 2011:248.

Strombus gibberulus clergy: Cooper, 2000, not paginated.

Material examined.—Australia Archer Point (Rymer Collection x 1), Armit Island (VC x 5), Big Sandy, Swain Reefs Complex (SM 49a.019/49a040 × 39, VC x 30), Bills Reef, Swain Reefs Complex (VC x 2), Boult Reef (SM 49a.020 × 4, AMD STR820 x1), Broadhurst Reef (VC x 1), Bushy Island (SM 49a.007 × 12, VC x 8), Cairns Reef (SM 49a.044 × 2), Capricorn Bunker group trawled 1969 (SM 49a.033 × 65, Rowell Collection x 1), Dingo Beach (SM 49a.002-49a.004 × 43, VC x 34, Hernandez Duran Collection x 1), East Diamond Island (AD STR0529 × 1, VC x 1), East Little Diamond Island (AD STR0530 × 1), Endeavour Reef (SM 49a.049 × 2), Fantome Reef (SM 49a.015 × 3), Fitzroy Reef (SM 49a.014 × 4, VC x 4), Gloucester Passage (SM 49a.041 × 4, YC x 1), Gould Reef (SM 49a.048 × 1), Green Island (SM 49a.034/49a.035 × 36, VC x 12), Hall Thompson Reef (SM 49a.046 × 2), Hazelwood Island (SM 49a.011 × 4, VC x 1), Hervey Bay (VC x 2), Hope Island (SM 49a.018 × 9, VC x 4), Hydeaway Bay (SM 49a.001 × 55, VC x

Fig. 12. Type series of *Gibberulus dekkersi*, Green Island, Queenland, collected March and June 2017, E: A, Holotype—male, 38.5 mm (QM); B, Paratype 1—male, 38.5 mm (SM 49a.035a); C, Paratype 2—female, 42.5 mm (SM 49a.034a); D, Paratype 3—female, 44.5 mm (SM 49a.034b); E, Paratype 4—male, 35.0 mm (SM 49a.035b); F, Paratype 5—male, 38.5 mm (SM 49a.035c); G, Paratype 6—male, 34.5 mm (SM 49a.035d); H, Paratype 7—female, 42.5 mm (SM 49a.034c); I, Paratype 8—male, 34.0 mm (SM 49a.035e). Collected under Marine Parks and GBRMA permit number G15/37503.1.

Fig. 13. Type series of *Gibberulus dekkersi*: A, Archer Point (Rymer Collection); B, Dingo Beach (Hernandez Duran Collection); C, Gloucester Passage (YC); D, Swain Reefs (VC); E, Thursday Island (AMD STR819); F, Boult Reef (AMD STR820); G, Trawled, Capricorn Bunker group (Rowell Collection).

30), Ingrim Reef (VC x 1), Lady Musgrave Island (SM 49a.045 × 1), Langford Reef (SM 49a.010 × 4), Lavers Cay, Swain Reefs Complex (SM 49a.006 × 14), Little Trunk Reef (SM 49a.030 × 10), Low Isles (SM 49a.005 × 13, VC x 3), Mackerel Bay (SM 49a.017 × 6, VC x 33), North Reef (SM 49a.043 × 2), North West Reef (VC x 8), Perfect Reef, Swain Reefs Complex (AD STR1238 × 1, SM 49a.008 × 42, VC x 2), Pickers Gill Reef (SM 49a.009 × 44, VC x 15), Port Douglas (AD STR1871 × 1),

Fig. 14. Variations of *Gibberulus dekkersi*, Perfect Reef, Swain Reefs Complex, Queensland, collected 2008 (SM 49a.008).

Prong II Reef, Swain Reefs Complex (SM.042 × 1), Prong Reef (SM 49a.047 × 3), Rudder Reef (SM 49a.016 × 3), Shute Harbour (VC x 2), Stonehaven Bay (VC x 2), Stradbroke Island (VC x 1), Swain Reefs Complex (AD STR0531/STR0989-0990 × 3, SM 491.012 × 5, VC x 12), Thursday Island (SM 49a.013 × 5, VC x 4, AMD STR819 × 1); Cook Islands Rarotonga (AD STR0659); Fiji (SM 49a.051 × 2), between Thuvu and Naevueve (AD STR0112-STR0114 × 3), Momi Bay, Viti Livi (SM 49a.021 × 3), Mosquito Island (SM 49a.027 × 3), Plantation Is (SM

49a.050 × 2), Yanuca Island (AD STR3245-STR3251 × 6); French Polynesia Mataiva Atoll (AD STR3264 × 1), Matira Point (AD STR3415 × 1); Marianas Guam (SM 49a.038 × 1, VC x 1); Marshall Islands Kwajalein (SM 49a.022 × 6); Moorea (AD STR3038 × 1, SM 49a.037 × 11), Raiatia Island (SM 49a.028 × 1), Tautira (SM 49a.036 × 3); New Caledonia (AD STR0524/STR0525/STR1660 × 3, SM 49a.023 × 7), Chesterfield Reef (VC x 1), Poindimie (VC x 2); Palau (YC x 1); Papua New Guinea Kokopo (SM 49a052 × 5), Port Moresby (VC x 4), Rabaul (SM 49a.024 × 3); Tonga (AD STR0922 × 1), Pangai Beach (SM 49a.026 × 3); Vanuatu (AD STR2306 × 1), Erakor (SM 49a.0390 × 1), Port Vila (SM 49a.039 × 6).

Type material.—Holotype–Green Island, Queensland, Queensland Museum no. MO 85757 (Fig. 12a); Paratype 1, Green Island, Queensland (SM. 49a.035a); Paratype 2, Green Island, Queensland (SM. 49a.034a); Paratype 3, Green Island, Queensland (SM. 49a.034b); Paratype 4, Green Island, Queensland (SM. 49a. 035b); Paratype 5, Green Island, Queensland (SM. 49a.035c); Paratype 6, Green Island, Queensland (SM. 49a.035d); Paratype 7, Green Island, Queensland (SM. 49a.034c); Paratype 8, Green Island, Queensland (SM. 49a.035e).

Type locality.—Green Island, Queensland (16°45′S, 145°58′E).

Diagnosis.—The penultimate whorl is disproportionately large compared to other whorls of the spire and typically without varices, the dorsal region prior to the edge of the outer lip typically is smooth, lacking the distinctive spiral raised lines in other species.

Description.—The shell is obovate when viewed ventrally, and ranges in size from 25 mm (Moorea, French Polynesia, SM 49a.037) to 61 mm (Perfect Reef, Queensland, SM 49a.008).

The nuclear whorls, numbering up to four, are translucent, smooth. The early teleoconch is acute with fine incised spiral lines that are evenly spaced, and extend from suture to suture. The penultimate whorl, and its immediate precursory whorl, mark the fading of these spiral lines into obsolescence, leaving one that forms a subsutural chord with the deeply incised sutures, which also fades before the formation of the body whorl; these later whorls develop rapidly, becoming bulbiform inflated and rounded; the penultimate whorl is irregularly rounded and typically without varices. The ventral body whorl is smooth somewhat spathulate, and the anterior spiral lines, when present, are diminished; the dorsal ventral interface is rounded and not shouldered. The dorsal body whorl is smooth and the step prior to the outer lip above the stromboid sinus is well formed. The outer lip is thin and is spirally stepped often reflecting anteriorly forming a keel, before sharply turning and thickening as it runs axially to the commencement of the stromboid sinus where the lip becomes thin and sharp again; the edge of the thickened area is wavy with four or five wide shallow convex depressions that may be obsolete; the anterior canal extends past the dorsal body whorl, forming an open canal. The columella is smooth and thickened and partially callused posteriorly. The inner aperture is smooth; there is a band of faint reticulated raised lirae that runs parallel to the length of the aperture but does not extend to the outer lip or into the inner aperture. There are two distinct color forms of this shell that fall on a white to off-white background: first, a dark form, being purple, brown, chocolate or tan, and having a white aperture and columella that are stained purple within; second, a pale orange to red form with an aperture and columella that are white, and rarely with tinges of orange. Both these color forms vary in pattern from maculations, broken axial lines, solid color, all of which are intersected by a number of irregularly spaced spiral bands of the shells base color. There may be a distinctive band

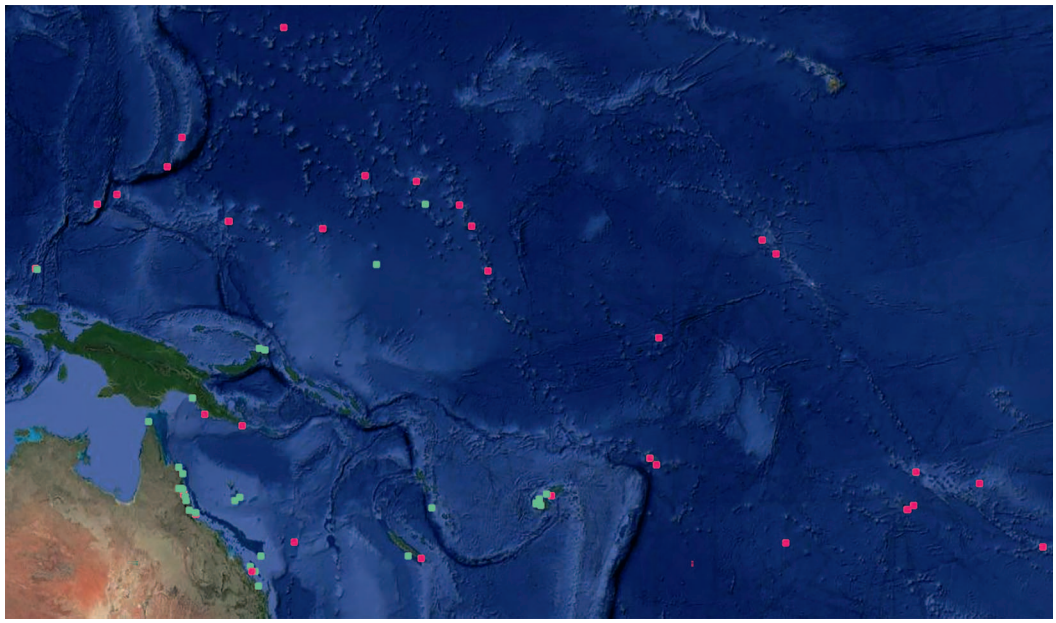


Fig. 15. Locality data map of *Gibberulus dekkersi* centered on the central and western Pacific, showing literary references (pink) and material examined (green). (Base Map: Google 2021; Imagey 2021 NASA; TereMetrics Map Data 2021, accessed 16 March 2021.)

below the suture of the dorsal body whorl that takes the color form of the shell being either dark purple or orange.

Etymology.—Named to honor Aart M. Dekkers for contributions that have led to a greater understanding of molluscan diversity represented by the naming of many new species, and in particular, his work on the phylogeny and radiation of the Strombidae that spans many decades.

Distribution.—Figure 15.

Literature records.—American Samoa Tutuila Island (Abbott 1949, Brown 2011); Vatia Wharf (Cernohorsky 1972); Australia (Cernohorsky 1965), Low Isles (Abbott 1960), One Tree Reef (Jones et al. 1990), Palm Island (Rippingale & McMichael 1961); Cook Islands (Abbott 1960); Federated States of Micronesia Ponhapei (Abbott 1960), Truk Island ('Gallemore' in Abbott 1960), Ulithi (Abbott 1960), Yap (Abbott 1960); Fiji (Cernohorsky 1965), Markin (Abbott 1960); French Polynesia Borabora (Abbott 1960), Marutea ('Dautzenberg & Bouge' in Abbott 1960), Moorea Atoll Tahiti (Abbott 1960), Raroia, Tuamotu (Abbott 1960), Tahiti (Cernohorsky 1965), Takume, Tuamotu (Abbott 1960), Tikahau, Tuamotu (Abbott 1960); Japan Marcus Island, Minamitorishima, Ogasawara (Abbott 1960), Kiribati (Cernohorsky 1965), Fanning Atoll (Berg 1974), Kanton Island (Abbott 1960), Palmyra (Abbott 1960); Marianas Guam (Smith 2003), Agana Bay, Guam Island (Abbott 1949), Majuro (Abbott 1960), Pago Bay, Guam Island (Vermeij & Zipser 1986), Saipan (Abbott 1960), Wotje (Abbott 1960); Marshall Islands Bikini Atoll (Abbott 1960), Eniwetok Atoll (Berg 1974), Igurin Island, Eniwetok (Abbott 1949, 1960), Rongalap (Abbott 1960); New Caledonia (Abbott 1960), South West Lagoon (Richer de Forges et al. 1988); Papua New Guinea Port Moresby (Hinton 1972), Samarai (Hinton 1972); Samoa Toloa Point, Upolu Island (Abbott 1960).

Remarks.—*Gibberulus dekkersi* is readily distinguished from the partially sympat-

ric *G. gibbosus* in not having the typical broad varices on the last body whorl, and the distinctive raised spiral lines on the dorsum prior to the outer lip of that species. Another difference is the shape and form of the spire, with *G. dekkersi* having penultimate and sub-penultimate whorls being greatly inflated. However, these two species share similarities in pattern and coloration with both species having distinctive color morphs of a light and dark form. *Gibberulus dekkersi* shares some similarities with the geographically isolated *G. albus* in having the inflated penultimate whorl but differs in apertural coloration and also lacks the strong dorsal raised spiral lines of that species. *Gibberulus gibberulus* differs from *G. dekkersi* in the shape and form of the spire, with *G. gibberulus* lacking the inflated penultimate whorl and having spiral lines from suture to suture not found in that species. There are anatomical differences in penial structures between species, with *G. dekkersi* having a prongless verge, in contrast to that of *G. gibberulus* with a distinct distal prong on the lobe (Abbott 1960).

From our observation of the study material, *G. gibberulus* and *G. dekkersi* come in a variety of colors and patterns, whereas *G. gibberulus* tends to vary on a smaller color scheme, and *G. albus* species lack variability. Furthermore, coastal and near coastal *G. dekkersi* have a greater color variability than those on the outer Great Barrier Reef, which are greatly reduced in variability (Figs. 12, 14).

Cooper (2000) produced a brief unpaginated report of expeditions that were carried out to the Swain Reefs, in which it was noted: "*Gibberulus gibberulus* CLERGYI were in great abundance only to find the black line of the collar of the rarer ones, hence the name CLERGYI very distinct collar. Colour of the collar vary from orange to black." It is clear from the text throughout that this name was to be applied to the particular color form, and not intended to formally name that shell as a new species; no types were declared, nor was a description or comparative text offered; furthermore, in the species list presented, only *Strombus gibberulus* was listed in relation to this complex. From the material examined, the Swain Reefs, and outer reefs of Queensland have a much paler and less varied range of color forms and patterns than the coastal and near coastal forms (Fig. 14). We, therefore, argue that the name "*clergyi*" has a role in distinguishing these color morphs, such that it should now be shifted to form *Strombus dekkersi f. clergyi.*

Discussion

Historically, *Gibberulus* was considered to contain one species, but this was subdivided into three subspecies. We now consider these to be full species (*G. albus*, *G. gibberulus* and *G. gibbosus*), and herein we introduce *G. dekkersi*, increasing the species count to four. In recognizing these as species, and not subspecies, we follow Maxwell & Dekkers (2019) in which a species is defined as an organism where there is a physically observable point of differentiation. Maxwell & Dekkers (2019) argue that the rank subspecies should be reserved for phenetic gene sequence differences. This avoids the arbitrariness in the application of the rank subspecies by authors (Páll-Gergely et al. 2019).

The *Gibberulus* fossil record of this group indicates an arrival during the Pliocene (Abbott 1960), with the only named species *Strombus praegibberulus* Abrard, 1947 from the Pliocene of Vanuatu. The teleoconch sculpture of *Gibberulus praegibberulus* (Abrard, 1947) indicates a close relationship with modern *G. gibbosus*, being with fine raised spiral lines from suture to suture but lacks the large flattened varices and a teleoconch that has regularly increasing whorls. *Gibberulus praegibberulus* lacks the inflation in latter

whorls of *G. dekkersi* and *G. albus* and the spiral striations that do not reach suture to suture in *G. gibberulus*. It may be the case that the genus arose in what is now the coral triangle and radiated out into the Indian and Pacific Oceans. We concur with Ladd (1972) that *G. praegibberulus* is a valid species and reject the synonymizing of that species under Abbott (1960) based on geological time and lack of broad varices, being smaller and more pronounced in *G. praegibberulus*.

There is only limited knowledge on the population structure of most members of the *Gibberulus* group. The group members are a gregarious species, living in large colonies where they are often encountered intertidally down to a depth of 10 fathoms (Abbott 1960). Furthermore, in *G. dekkersi* there is significant sexual bias in favor of females (60% of the population, Guam, Abbott 1949). Abbott (1949) also noted that those small average populations come from atolls and areas lacking in high nutrient levels. In *G. dekkersi* the sex of the animal did not have a determination on the color or pattern of the shell (Abbott 1949).

Conclusion

This paper demonstrates that the continuing revision of the historical taxonomy will result in an increase in the diversity of the complex of the Strombidae as more neglected genera are revised. In contrast to *Laevistrombus* and other generic revisions, *G. dekkersi* arose after the examination of a species with a large range that had not been tested for regional distinctiveness. It is expected that, as further revisions into the Strombidae are carried out, particularly of those species with large fragmented distributions, more species will be described within the complex.

This work has been registered in ZooBank with the registration number urn:lsid:zoobank.org:pub:202C254F-5928-4AB3-AA9E-AF11E5310799.

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Erratum

An iconography of extant *Gibberulus* Jousseaume, 1888 (Mollusca, Gastropoda, Strombidae), and the introduction of a new species from the southwestern Pacific—ERRATUM

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In the original version of this article, Figure 11 is incorrect. The error has been rectified in the print and online PDF copies of this article.

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