

The genus *Frigidocardium* Habe, 1951 in the Red Sea (Bivalvia, Cardiidae)

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Frigidocardium centumliratum (Melvill in Melvill & Standen, 1907), *F. helios* ter Poorten & Poutiers in ter Poorten, 2009, and *F. kiranum* Sakurai & Habe, 1966, are for the first time reported from the Red Sea. Former Red Sea records of *F. exasperatum* (G.B. Sowerby II, 1839) and *F. torresi* (E.A. Smith, 1885) are considered misidentifications and, lacking any other records, are excluded from the Red Sea malacofauna. The type material of *F. centumliratum* is a composite of three species, hence a lectotype is designated to settle the taxonomic confusion.

Key words: Cardiidae, *Frigidocardium*, distribution, Red Sea, misidentifications, range extensions, lectotype designation.

INTRODUCTION

At present, ten extant species belonging to the genus *Frigidocardium* Habe, 1951, are recognized (Bouchet & ter Poorten, 2016), seven of which are extensively discussed by ter Poorten (2009). The relatively small size, deep water occurrence (sublittoral to upper bathyal) and wrong labelling of old collection material, has contributed to misinterpretations of several species. A well-known example is *F. centumliratum* (Melvill in Melvill & Standen, 1907) that has often been synonymized with *F. torresi* (E.A. Smith, 1885), assuming that the former would be the adult stage of the latter (Prashad, 1932). Recently, the taxonomic confusion has partly been elucidated (Poutiers, 2006; Huber & ter Poorten, 2007; ter Poorten, 2009). The aim of present research is to analyze Red Sea material from

various institutions and private collections, combined with a critical re-examination of literature records and the material treated in these works. It revealed many misidentifications of Red Sea *Frigidocardium* taxa, exemplary of the fact that the genus is still poorly understood and has received little scientific attention. As a result of this investigation, alleged Red Sea occurrences of two *Frigidocardium* species are herein rejected. Additionally, Red Sea range extensions of three other congeners are reported, all of which are treated systematically hereafter and compared with the rejected species.

MATERIAL AND METHODS

The Red Sea *Frigidocardium* material examined for this study originates primarily from the HUJ/SMNH collections. Additional samples are from NHMW (*Pola* Expedition), SMF (*Meteor* 5 and 31 Expeditions) and the collections of H. Blatterer (Austria) and S. Hobbs (U.S.A.). The German *Valdivia* Expeditions did not yield any cardiids (pers. comm. Marco Taviani, 16.11.2015). Supplementary non Red Sea *Frigidocardium* material is from MNHN, NHMUK, NMW, RMNH, ZMA (now in RMNH) and various private collections. For the distributional data, the campaigns during which material has been encountered are added after the acronym of the respective institution. These samples have all been verified by the authors.

The chresonomy is not meant to be exhaustive: it mainly relates to the Red Sea occurrences and includes the original descriptions of the treated species.

The height is measured along an axis perpendicular to the hinge, and the length is the greatest distance

between the anterior and posterior ends, parallel to the hinge line. In the captions only the largest dimension is given (either L or H).

Acronyms of institutions and repositories: HUJ = Hebrew University of Jerusalem, Israel; JJTP = Colln J.J. ter Poorten, Hilversum, The Netherlands; MNHN = Museum national d'Histoire naturelle, Paris, France; NHMUK = Natural History Museum, London, United Kingdom; NHMW = Naturhistorisches Museum Wien, Vienna, Austria; NMW = National Museum of Wales, Cardiff, United Kingdom; RMNH = Naturalis Biodiversity Center, Leiden, The Netherlands; SMF = Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany; SMNH = the Steinhardt Museum of Natural History – Israel National Center for Biodiversity Studies, Tel Aviv University, Tel Aviv, Israel (formerly: TAU); ZMA = Zoological Museum Amsterdam, now part of NBC Naturalis, Leiden, The Netherlands.

Abbreviations: CP = beam trawl (chalut à perche); DW = Warén dredge (drague Warén); fr. = fragment(s); GKG, Box corer (Großkastengreifer); H = height; L = length; p.v. = paired valves; s.v. = single valve(s).

SYSTEMATIC PART

Cardiidae Lamarck, 1809

Frigidocardium

Erigidocardium [misspelling of *Frigidocardium*] Habe, 1951: 152
(as a subgenus of *Nemocardium*)

Type species by original designation: *Cardium (Fragum?) eos* Kuroda, 1929: 93, pl. 3 fig. 5. Recent, Kii peninsula, Wakayama Pref., Honshū, Japan

Frigidocardium centumliratum (Melvill in Melvill & Standen, 1907) (Figs 1-9, 30)

Cardium exasperatum Sow. — Sturany, 1899: 267.
Cardium (?Fragum) centumliratum Melvill in Melvill & Standen, 1907: 839-840, pl. 53, fig. 2 (question-mark by Melvill).
Frigidocardium eos Kuroda, 1929 — Fischer-Piette, 1977: 68 [in part].
? *Nemocardium exasperatum* Moosleitner in Vine, 1986: 176.
Frigidocardium exasperatum (Sowerby, 1841) — Von Rützen-Kositzkau, 1999: 139.
? *Microcardium torresi* — Dekker & Orlin, 2000: 12.
Nemocardium centumliratum (Melvill & Standen, 1906) — Hylleberg, 2004: 900, syntypes.
Frigidocardium torresi (E.A. Smith, 1885) — Singer & Menis, 2009: 8, pl. 1, unnumbered fig.
NOT: *Microcardium centumliratum* (Melvill & Standen, 1907) — Oliver, 1995: 245, fig. 1087 [= *Frigidocardium torresi*, NMW 1955.158.01010].

Type locality — 'Persian Gulf: Gulf of Oman. Lat 24°, 58' N., long. 56°, 54' E.; 156 fathoms. Also off Mussandam, 50 fathoms. M.C. [Mekran Coast]. Very rare off Charbar, at 40 fathoms.' [Leg. F.W. Townsend].

Type material: NHMUK 1907.5.3.6, two syntypes (s.v.); NMW 1955.158.01009, eight syntypes (s.v.), NMW 1955.158.01010, one syntype (p.v.), NMW 1955.158.01011, eight syntypes (s.v.).

Description. — Shell relatively large (H up to 20-28 mm), inflated, ovate-quadrangular and almost equilateral. Length about equals height. Circa 120-135 radial ribs, mostly sculptured on rib flanks or occasionally in interstices with a radial row of spines, regularly interchanging with rib flanks or interstices lacking sculpture, nature of sculpture changing from spoon-shaped anteriorly to more pointed posteriorly and rows of spines of alternating strength. Regularly placed well developed cross bars present in interstices that are lacking sculpture. On juveniles, the radial rows with primary sculpture are often relatively prominent (Fig. 7); spines projecting, rather distantly placed and rows of secondary sculpture poorly developed, if present at all. Lunular heart well defined, yellow or orange coloured and generally broader in right valve (Figs 1d, 2d: arrows). Lunular area very weakly sculptured and sharply delimited. Exterior white, posterior slope and margins sometimes yellowish brown or light orange, interior white except for occasionally orange coloured margins and pale yellow umbonal cavity. Periostracum rather thin, rust-brown to olive-green, mainly preserved in marginal area.

Remarks. — The oldest Red Sea record that could be traced appears to be from Sturany (1899: 267, as *Cardium exasperatum* Sow., one s.v., Gulf of Aqaba, 350 m). Examination of photos of this Austrian Pola Expedition sample (1895-1898, NHMW 84341, Fig. 3a-b) makes clear that it belongs to *F. centumliratum*. Remarkably, it is the only (and one of the most northern) record of this pioneer expedition (see Janssen & Taviani, 2015: fig. 1 for a map showing the deep-water Pola Expedition records). This Gulf of Aqaba occurrence has recently been reported by Singer & Menis (2009, as *F. torresi*). *F. exasperatum* (G.B. Sowerby II, 1839) does not occur in the Red Sea nor in the Indian Ocean; its distribution is limited to southern Japan, China and Vietnam (Huber & ter Poorten, 2007). Examination of all TAU (now SMNH) samples from the Red Sea identified in 1975 by Fischer-Piette as *Frigidocardium eos* Kuroda or *Trigoniocardia eos* (Kuroda) and published under the former genus (Fischer-Piette, 1977), leads us to conclude that these identifications relate to a composite of three species: *F. centumliratum*, *F. helios* and *F. kiranum*. *F. eos* is restricted to the tropical central Indo-West Pacific, ranging from S. Japan to N.W. Australia (ter Poorten, 2009) and the Solomon Is-

Species	Max. size (L or H)	Rib number	Number of primary sculptured rows	Secondary sculptured rows present	Lunular heart (LH)	Predominant exterior colouration	Geographic range
					Lunular area (LA)		
<i>F. centumliratum</i>	25-28 mm (Height)	120-135	30-45	Limited to posterior part, at times also on median part	LH well defined, rather broad, elevated LA weakly sculptured	White, posterior slope/margin/ LH often yellowish-orange	Red Sea, Mozambique, Madagascar, Réunion, Seychelles, Gulf of Oman, W. Thailand
<i>F. helios</i>	5-9.5 mm (Length)	130-175	44-66	Generally limited to antero-dorsal part	LH small but broad and elevated LA vaguely bordered yellowish	White, often vaguely orange streaked, reddish umbonal tip	Red Sea, Madagascar, N.W. Australia, Philippines, Indonesia, New Caledonia, Vanuatu, Fiji
<i>F. kiranum</i>	15-20 mm (Height)	120-130	Highly variable strength: indeterminable	Present on whole shell	LH + LA barely defined	White, often with orange-red rays Posterior slope + umbo red	Red Sea, S. Madagascar, Mascarene Isl., S. Japan to Indonesia, New Caledonia to Northern Fiji Basin
<i>F. torresi</i>	5-9 mm (Length)	75-90	22-32	Only rarely a few present	LH narrow, smooth LA un-sculptured, not sharply bordered	White with orange-reddish umbosal tip	S.E. Africa, Persian Gulf, Gulf of Oman, W. Thailand, N. Australia, Indonesia to Vanuatu

Table 1. Comparison of morphometrical and distributional data of Red Sea *Frigidocardium* taxa, supplemented with the related *F. torresi*. Modified after ter Poorten (2009: table 7).

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lands (MNHN). It differs by its deep orange colours, often arranged in radial rows as well as commarginally streaked. Contrary to *F. centumliratum*, all rib flanks of *F. eos* are more or less prominently sculptured. Another close congener is *F. iris* Huber & ter Poorten, 2007, which is also restricted to the tropical central Indo-West Pacific from the Philippines to N.W. Australia (ter Poorten, 2009). It has a different coloration consisting of pink or red commarginally aligned bands on a white background and usually a deep yellow umbonal cavity. Close to the antero-dorsal margin, the rib sculpture is of a more coarse nature, becoming spatulate to almost knobby and very close set.

Syntypes of *F. centumliratum* are deposited in the following collections: NHMUK 1907.5.3.6 (two unmatched s.v., H 20.7 and H 19.3 mm, original label mentioning 'Persian Gulf: Gulf of Oman', 'Types', Figs 1-2); of these the right valve (Fig. 2a-d) is considered the figured syntype (Trew, 1987). Additionally, NMW 1955.158.01009 (8 juvenile s.v., largest L 5.3 mm, original label mentioning 'G. of Oman', Figs 16-19). None of the original labels accompanying these samples are as elaborate as the type description, which incorporates coordinates and depths. The NHMUK sample represents *F. centumliratum* but this complete NMW

sample is re-identified as *F. torresi* (E.A. Smith, 1885). NMW 1955.158.01010 (1 p.v., L 7.0 mm, original label mentioning 'P. Gulf', subsequent labels 'Malcolm Inlet, Arabian Gulf', Fig. 20a-c) is figured by Oliver (1995). This valve represents a relatively fine sculptured *F. torresi*. NMW 1955.158.01011 (8 s.v., original label mentioning 'G. of Oman') is a composite of three species: the largest s.v. is *F. cf. centumliratum* (L 6.2 mm, fr., NMW 1955.158.01011/a), six smaller s.v. represent *F. torresi* (Fig. 21) and the smallest s.v. is a juvenile *Timoclea* specimen (NMW 1955.158.01011/b). Lacking the word 'type' on the original labels, the NMW samples cannot be unequivocally considered syntypes.

In order to put an end to the taxonomic confusion, a lectotype is herein selected, viz. the smallest of the two NHMUK 1907.5.3.6 valves (H 19.3; L 19.6; $\frac{1}{2}W$ 7.7 mm; Fig. 2a-d), a right valve that best fits the dimensions and type figure of Melvill & Standen (1907: 840, pl. 53 fig. 2), the remaining syntypes becoming paralectotypes, irrespective of their current taxonomic identity.

Interestingly, Melvill in Melvill & Standen (1907: 840) states that 'the form of the shell [*centumliratum*] is almost identical with that of the much smaller

C. (*Fragum*) *torresi* E. A. Sm., from the Torres Straits'. This may have invoked Prashad (1932) to synonymise *F. centumliratum* with *F. torresi*, possibly induced by the assumption of E.A. Smith (1885) that the types of *F. torresi* were probably juveniles. Collection research by the senior author in the ZMA led to the conclusion that the Siboga specimens identified by Prashad (1932) as *F. torresi* are a composite of no less than four species: *Frigidocardium eos* (Kuroda, 1929), *F. sancticaroli* ter Poorten & Poutiers, 2009, *F. helios* ter Poorten & Poutiers, 2009 and *F. torresi* (E.A. Smith, 1885).

Distribution (Fig. 30). — *Frigidocardium centumliratum* is known from various offshore localities throughout the Indian Ocean: Madagascar (MNHN, ATIMO VATAE 2010 and MIRIKY 2009, Figs 8-9); S. Mozambique (MNHN, MAINBAZA 2009); Réunion (MNHN, Marion Dufresne 32, 1982; Bigot, 2006; Bigot et al., 2006); Seychelles (Lewis & Taylor, 1966); Gulf of Oman (type material in NHMUK and NMW) and Thailand, Andaman Sea (Collin J. Hylleberg, ex Phuket Marine Biological Center and 5th Thai-Danish Expedition to the Andaman Sea, 1966). Given the known distributional patterns, Tantanasiriwong's (1979) record of '*Nemocardium exasperatum*' from W. Thailand most probably involves *F. centumliratum*. The same counts for a similar record from the Andaman and Nicobar Islands (Ramakrishna & Dey, 2010).

The HUJ/SMNH/SMF records of the present species, 27 samples, originate from a wide bathymetric range of 37-700 m and 101-600 m when exclusively based on p.v. Two of these samples contain the dried animal or parts thereof and are from a depth of 329-403 m (SMNH MO 6738) and 600 m (SMNH MO 27449, Fig. 6). The possibility that part of the material has been transported from shallow water environments is likely, given the very steep offshore profile in the Gulf of Aqaba. This is especially probable for empty collected samples, but much less obvious for the two samples with the dried animal preserved inside the shell. Therefore, *F. centumliratum* is considered an eurybathic species with a wide bathymetric range. So far, this finding is not confirmed by the known bathymetric range in other parts of its distribution. For instance, of 18 live samples from Mozambique (MNHN, MAINBAZA) and Madagascar (MNHN, MIRIKY and ATIMO VATAE, Figs 8-9), all but one (DW3245: '90-257 m') originate from a depth of 50-153 m, while numerous stations (out of 580 in total) hit depths of 200 to well over 1000 m.

Material examined — **Israel**, Gulf of Aqaba, Elat Electric Plant, 320 m, grab. Leg. D. Zalcman, 09.02.1970. (SMNH MO 27450, 1 p.v., juv., def. and fresh); Elat Lighthouse, 300 m. Leg. D. Zalcman, 11.02.1970. (SMNH MO 27444, 2 s.v., juv., def., rather

fresh); Elat Marine Biol. Stat., 600 m. Leg. D. Zalcman. (SMNH MO 27449, 4 p.v., all juv. to very juv., alive); Elat Old Port, 420 m, grab. Leg. D. Zalcman, 13.02.1970. (SMNH MO 27447, 2 s.v., juv.); Elat Zarhin Plant, 167 m. Leg. D. Zalcman, 16.09.1968. (SMNH MO 27453, 4 s.v., juv., 1 fr.); Elat, 215 m. Leg. D. Zalcman. (SMNH MO 27412, 8 s.v., juv., some def./fr.); Elat, 316 m, grab. Leg. D. Zalcman, 17.11.1969. (SMNH MO 27428, 2 s.v., juv.); Elat, 62-81 m. Leg. Ch. Lewinsohn, 07.09.1966. (SMNH MO 27437, 3 s.v., juv./def.); Elat, border station, 242 m. Leg. D. Zalcman, 12.11.1969. (SMNH MO 27417, 1 s.v., juv.); Elat, Electric Plant, 320 m. Leg. D. Zalcman, 09.02.1970. (SMNH MO 27484, 5 s.v., juv., one fr.); Elat, Marine Biol. Stat., 400 m, grab. Leg. D. Zalcman, 11.02.1970. (SMNH MO 26976, 2 s.v., juv.); Elat, Marine Biol. Stat., 400-450 m, Menzies trawl. Leg. D. Zalcman. (SMNH MO 27424, 2 s.v., juv.); Elat, New Port, 220 m, grab. Leg. D. Zalcman, 16.09.1968. (SMNH MO 27446, 3 s.v., subadult-juv.); Elat, Old Port, 121 m. Leg. D. Zalcman, 10.09.1968. (SMNH MO 27448, 11 s.v., most juv., few fr.); Elat, RS 9, 280-300 m. 21.08.1965. (HUJ 37906, 1 p.v., adult); Oil port, 350 m, grab. Leg. D. Zalcman, 16.09.1968. (SMNH MO 27413, 3 s.v., juv.).

Egypt, Gulf of Aqaba, Maras Murach, + Fractures 92 m, 08.11.1969. (SMNH MO 27479, 6 s.v., subadult-juv.); Marsa Abu Samra, Centre, 132-137 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 27420, 7 s.v., juv.-subadult); Marsa Murach, 92 m, angular dredge, st. 35, 06.10.1969. (SMNH MO 41424, 1 s.v., juv.); Nuweiba El Museina, 329-403 m. Leg. Ch. Lewinsohn, 08.10.1969. (SMNH MO 6738, 1 p.v., subadult, def., with dried animal); Nuweiba El Tarabin, 137-146 m. Leg. Ch. Lewinsohn, 08.10.1969. (SMNH MO 27427, 21 s.v., subadult-juv.); Nuweiba South, 550-700 m. Leg. D. Zalcman. (SMNH MO 27421, 2 s.v., juv.); Nuweiba, 137-146 m, triangular dredge. Leg. Ch. Lewinsohn, 08.10.1969. (SMNH MO 27481, 2 s.v., subadult); Nuweiba, 329-403 m, triangular dredge. Leg. Ch. Lewinsohn, 08.10.1969. (SMNH MO 27439, 1 s.v., juv., rather fresh)

N Gulf of Aqaba, 29°13.5'N, 34°47.8'E, 17.04.1896. 350 m, mud. Pola Exp. Red Sea, st. 96 [15/1] (NHMW 84341, 1 s.v., juv.).

Sudan, off Suakin, 18°57.5'N, 38°15.8'E, 90 m, mud, 27.02.1995. Meteor Exp. st. Me31/2-100 GKG 8 (SMF 347560, 5 s.v., subadult-juv.); off Suakin, 18°57.5'N, 38°15.7'E, 101 m, mud, 27.02.1995. Meteor Exp. st. Me31/2-100 GKG 9 (SMF 347561, 1 p.v., juv., 5 s.v., subadult-juv.).

Djibouti, Bab-al-Mandab Strait, 12°43.5'N, 43°14.8'E, 214-237 m, 05.03.1987. Meteor Exp. st. Me5-Stat. 230 KD2, (SMF 347559, 1 s.v., subadult).

Frigidocardium helios
Ter Poorten & Poutiers in ter Poorten, 2009
(Figs 10-15, 31)

Frigidocardium eos Kuroda, 1929 — Fischer-Piette, 1977: 68 [in part].

Frigidocardium centrumliratum [sic!] (Melvill & Standen, 1907) — Von Rützen-Kositzkau, 1999: 139.

? *Microcardium torresi* — Dekker & Orlin, 2000: 12.

Frigidocardium helios ter Poorten & Poutiers in ter Poorten, 2009:

64-65, pl. 18 figs 1-6, pl. 19 fig. 2, pl. 20 fig. 1.
Frigidocardium torresi — Edelman-Furstenberg & Faershtein,
2010: 10, 32-34, 37-39, 41-43, pl. 7 fig. 54a-b.

Type locality.— Vanuatu, SE corner of Santo, SANTO 2006, Stn FB94 (exact locality data not recorded), 09/10.2006, alive

Type material. — MNHN-IM-2000-22978 (sequenced MNHN-IM-2007-30161), holotype (p.v., Fig. 9a-d)

Description (modified after ter Poorten, 2009). — Shell relatively small (L up to 9.5 mm) and thin, moderately inflated, ovate-quadrangular and slightly inequilateral. L/H ratio 0.98-1.08 (mean 1.03, n = 17). Anterior and ventral margins regularly rounded, posterior margin truncate, nearly straight, dorsal half often widely convex and oblique. Inner margins finely crenulated. Circa 130-175 delicate low riblets and about 44-66 primary radial rows of tiny spines, originating from the interstices, which are nearly as wide as the ribs. Spiny rows alternate with the remaining interstices that carry minute thin crossbars, more prominent on the posterior slope, in some specimens extending over the rib margins and interconnected. Secondary sculptured rows restricted to antero-dorsal part, limited to 1-3 rows, if present at all. Lunular area finely sculptured with a few radial rows of minute tubercles, not sharply delimited, margin a little sinuous. Lunular heart small, broad and elevated, forming a glossy process reflected over the valve margin and expanding on umbo. Hinge plate arched, umbonal angle between cardinal and lateral teeth about 155°; hinge rather finely built with two very unequal cardinals, the more ventral cardinal being large and thick and the more dorsal one small, in right valve not clearly joined by a saddle. Lateral teeth approximately equidistant from cardinals. Shell exterior milky white, often vaguely radially and commarginally streaked orange with a reddish-orange stain near postero-dorsal margin; umbonal tip reddish and lunular area with a distinct yellow-orange hue; interior same colouration because of the translucency of the shell.

Remarks. — The SMNH samples from the Red Sea identified by Fischer-Piette (1977) as *Frigidocardium eos* Kuroda are a composite of three taxa: *F. helios*, *F. centumliratum* and *F. kiranum*. The holotype of *F. helios* (Fig. 10a-d) has been used for molecular phylogenetic analysis by Herrera et al. (2015) and was grouped in a subclade together with *F. torresi* in the maximum-likelihood phylogram of the concatenated dataset for H3, 16S and 28S genes. Also when the shell morphology is analysed, *F. torresi* is the most closely related species. It has a similar size and a roughly similar outline but *F. helios* differs by a more finely built, thinner shell; a L/H ratio that is approximately 1 in adults (whereas L

clearly exceeds H in adult *F. torresi*); a higher rib number (130-175 versus 75-90, Table 1); less prominent crossbars in the interstices; secondary sculpture present on the antero-dorsal part of the shell (occasionally also on the median part) and a more colorful shell, fresh material often containing a reddish-orange stain near the postero-dorsal margin and, not uncommonly, a similarly coloured umbonal cavity.

Some of the Gulf of Aqaba specimens show more variation in the number of sculptured ribs, the strength of the rib sculpture and the mutual distance between the spines than the type material. This renders identification of a few samples problematic (Fig. 15a-d). Whether indeed a higher intraspecific plasticity is involved or taxonomic separation at species level is needed, cannot be resolved solely on basis of this material but requires an integrative approach with samples throughout the distribution range.

Distribution (Fig. 31). — *Frigidocardium helios* is widely distributed in the tropical Indo-West Pacific, recorded from S. Madagascar (MNHN, MIRIKY 2009 and ATIMO VATAE 2010); Philippines (MNHN, PANGLAO 2004); Indonesia (ZMA, Siboga, Kepulauan Seribu Expedition); Vanuatu (MNHN, SANTO 2006); New Caledonia (MNHN, MONTROUZIER) and Fiji (MNHN, SUVA 2).

The numerous HUJ/SMNH/SMF records of the

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Figs 1-9. *Frigidocardium centumliratum* (Melvill in Melvill & Standen, 1907). **1-2**, Persian Gulf, Gulf of Oman [Leg. F.W. Townsend]. NHMUK 1907.5.3.6. **1**, paralectotype, H 20.7 mm (a: LV exterior, b: LV interior, c: dorsal, d: lunular heart indicated by arrow). **2**, lectotype, L 19.6 mm (a: RV exterior, b: RV interior, c: dorsal, d: lunular heart indicated by arrow and partly broken off cardinal). **3**, Egypt, N Gulf of Aqaba, 29°13.5'N, 34°47.8'E, mud, 350 m, 17.04.1896. Pola Exp. Red Sea, st. 96 [15/1]. NHMW 84341, L 15.1 mm (a: LV exterior, b: LV interior). **4**, Israel, Elat, RS 9, 280-300 m. 21.08.1965. HUJ 37906, H 22.5 mm (a: RV exterior, b: LV exterior, c: LV interior, d: RV interior. Specimen figured by Singer & Mienis, 2009: pl. 1). **5**, Egypt, Nuweiba, 137-146 m, triangular dredge. Leg. Ch. Lewinsohn, 08.10.1969. SMNH MO 27481, H 11.0 mm (a: LV exterior, b: LV interior). **6**, Israel, Elat Marine Biol. Stat., 600 m, alive with dried animal. Leg. D. Zalcman. SMNH MO 27449, L 7.0 mm (RV exterior). **7**, Sudan, off Suakin, 18°57.5'N, 38°15.7'E, sandy mud, 101 m, 27.02.1995. Meteor Exp., st. Me31/2-100 GKG 9. SMF 347561, L 5.2 mm (RV exterior). **8-9**, Madagascar, in front of Baie de Nazendry, 14°31'S, 47°25'E, 50-107 m, alive. Leg. P. Bouchet & Y. Kantor, 06.07.2009. MIRIKY st. DW3237. **8**, MNHN IM-2009-9803 (genotyped specimen), L 13.5 mm (LV exterior). **9**, MNHN IM-2009-9786 (genotyped specimen), H 23.5 mm (a: RV exterior, b: LV interior, c: dorsal).





present species, all empty, originate from a depth range of 37-700 m; limited to 49-215 m when exclusively based on p.v. As for *F. centumliratum*, down-slope transportation is likely to have occurred. Life taken samples are known from the Philippines, 83-102 m (MNHN, PANGLAO 2004); New Caledonia, 90-115 m (MNHN, MONTROUZIER, 1993) and Madagascar, 48-54 m (MNHN, MIRIKY 2009). The possibility that *F. helios* is an eurybathic species is not supported by these data.

Material examined. — **Israel**, Gulf of Aqaba, Elat Lighthouse, 300 m. Leg. D. Zalcman, 11.02.1970. (SMNH MO 78894, 1 s.v., def., worn); Elat Marine Biol. Stat., 600 m. Leg. D. Zalcman. (SMNH MO 78899, 4 s.v., juv.); Elat New Port, 170-270 m, Ockelman dredge. Leg. D. Zalcman, 13.02.1970. (SMNH MO 27451, 22 s.v., worn, few fr.); Elat Old Port, 420 m, grab. Leg. D. Zalcman, 13.02.1970. (SMNH MO 78896, 17 s.v., partly juv./def.); Elat Zarhin Plant, 167 m. Leg. D. Zalcman, 16.09.1968. (SMNH MO 78900, 89 s.v., some juv., def./fr.); Elat, 215 m. Leg. D. Zalcman. (SMNH MO 78883, 1 p.v.; 10 s.v., some def./fr. and juv.); Elat, 316 m, grab. Leg. D. Zalcman, 17.11.1969. (SMNH MO 78890, 1 s.v., rather worn); Elat, 40-46 m. Leg. Ch. Lewinsohn, 07.09.1966. (SMNH MO 27418, 1 s.v., much worn); Elat, 40-49 m.

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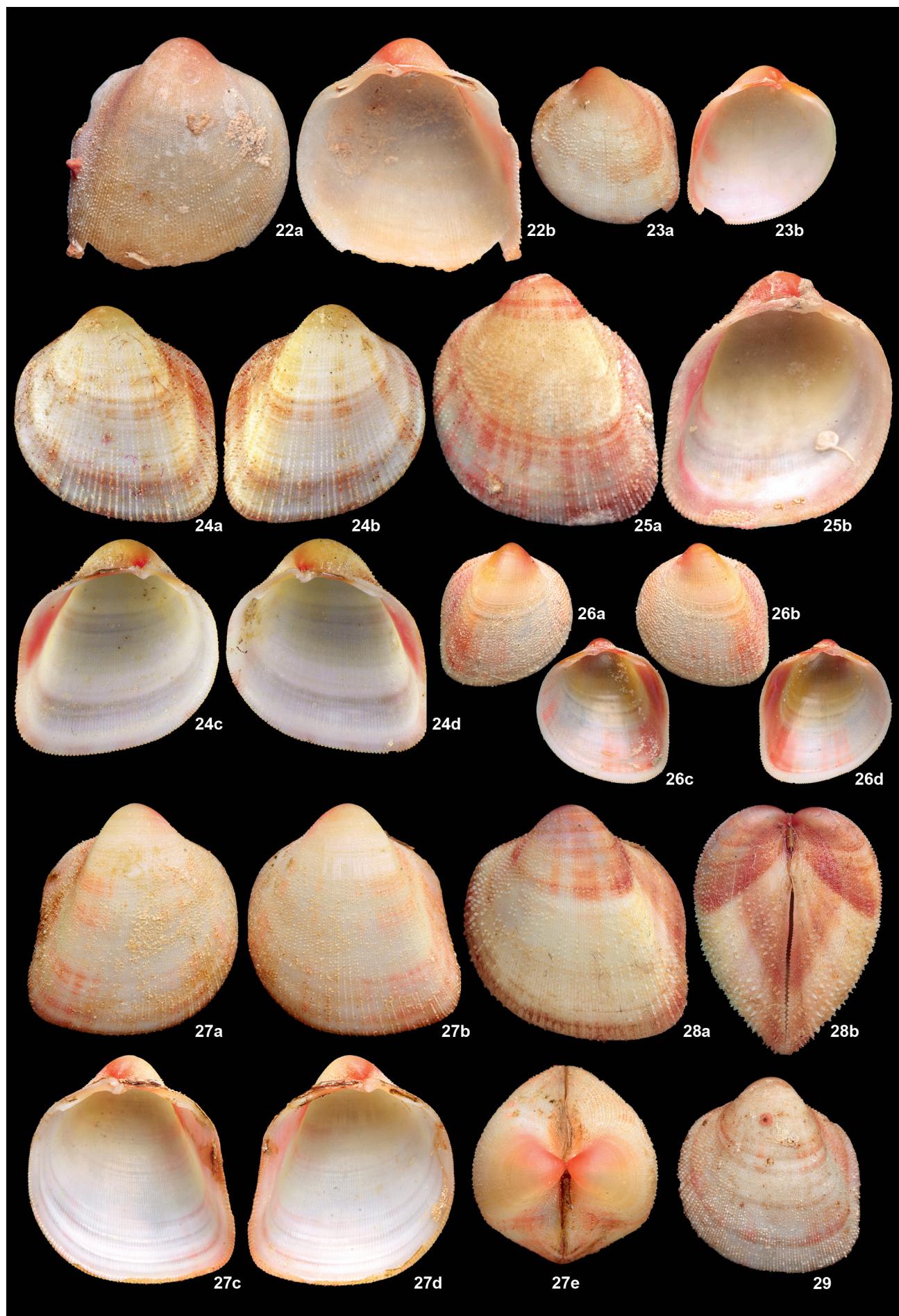
Figs 10-21. *Frigidocardium helios* ter Poorten & Poutiers in ter Poorten, 2009, *Frigidocardium torresi* (E.A. Smith, 1885), possible syntypes of *Cardium* (*?Fragum*) *centumliratum* Melvill in Melvill & Standen, 1907. *Frigidocardium helios* ter Poorten & Poutiers, **10**, Vanuatu, SE corner of Santo, SANTO 2006, Stn FB94 (exact locality data not recorded), 09/10.2006, alive MNHN-IM-2000-22978 (sequenced as MNHN-IM-2007-30161), holotype, L 7.3 mm (a: RV exterior, b: LV exterior, c: LV interior, d: RV interior); **11-12**, Egypt, Gulf of Aqaba, Marsa Abu Samra, Centre, 132-137 m, rock dredge. Leg. Ch. Lewinsohn, 08.10.1969. SMNH MO 78886. **11**, L 6.8 mm (a: RV exterior, b: RV interior); **12**, L 5.1 mm (a: RV exterior, b: interior); **13-14**, Egypt, Gulf of Aqaba, Nuweiba El Tarabin, 137-146 m. Leg. Ch. Lewinsohn, 08.10.1969. SMNH MO 78889; **13**, L 5.9 mm (a: RV exterior, b: RV interior); **14**, L 6.9 mm (a: RV exterior, b: RV interior). **15**. *Frigidocardium* cf. *helios* ter Poorten & Poutiers in ter Poorten, 2009. Egypt, Gulf of Aqaba, Marsa Abu Samra, centre, 49-55 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. SMNH MO 27416, L 7.6 mm (a: LV exterior, b: LV interior, c: dorsal). **16-21**, *Frigidocardium torresi* (E.A. Smith, 1885); **16-19**, Gulf of Oman [Leg. F.W. Townsend]. NMW 1955.158.01009, largest L 5.3 mm (exteriors of RV, LV); **20**, Arabian Gulf, Malcolm Inlet [Leg. F.W. Townsend]. NMW 1955.15801010, L 7.0 mm (a: RV exterior, b: LV exterior, c: RV interior. Specimen figured by Oliver, 1995: fig. 1087); **21**, Gulf of Oman [Leg. F.W. Townsend]. NMW 1955.158.01011/b, L 5.1 mm (LV exterior).

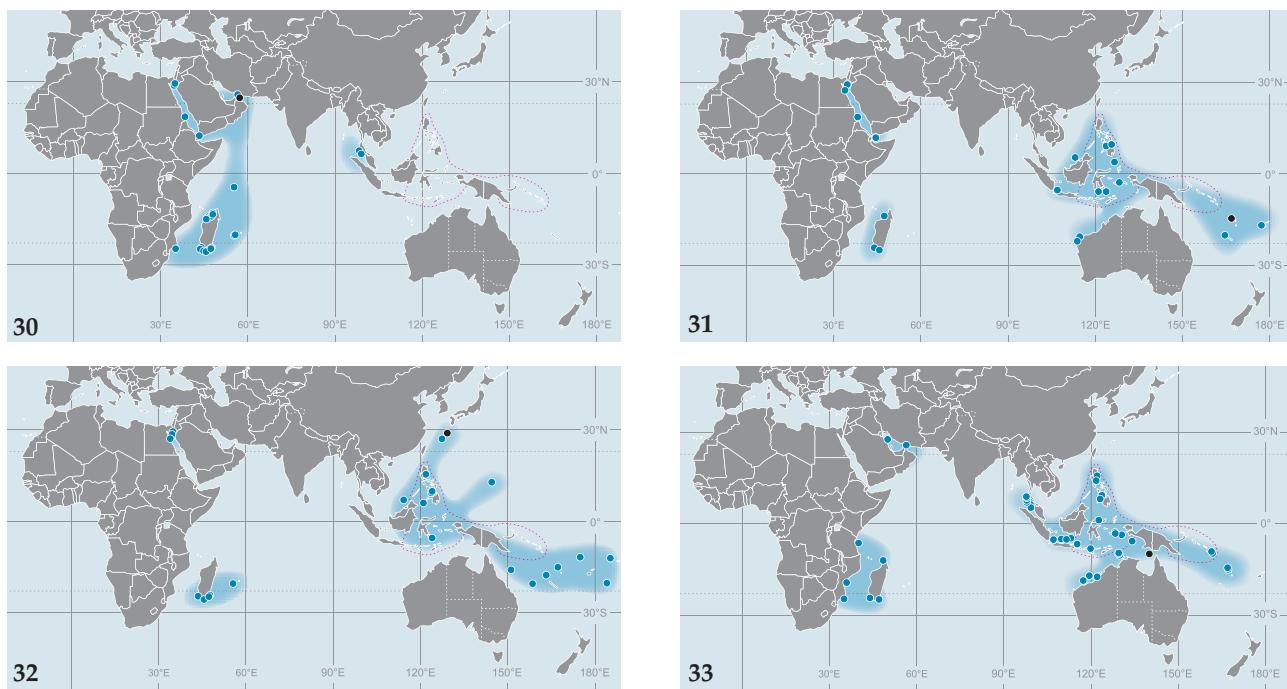
Leg. Ch. Lewinsohn, 05.09.1966. (SMNH MO 27440, 2 s.v., much worn); Elat, 62-81 m. Leg. Ch. Lewinsohn, 07.09.1966. (SMNH MO 78891, 3 p.v., subadult; > 100 s.v., juv.-adult, some def.); Elat, 62-81 m. Leg. Ch. Lewinsohn, 07.09.1966. (SMNH MO 78902, 1 p.v.; c. 162 s.v., worn); Elat, 64-92 m. Leg. Ch. Lewinsohn, 05.09.1966. (SMNH MO 27436, 1 p.v.; 32 s.v., some juv.); Elat, border station, 242 m. Leg. D. Zalcman, 12.11.1969. (SMNH MO 78885, 11 s.v., rather worn); Elat, Marine Biol. Stat., 400-450 m, Menzies trawl. Leg. D. Zalcman. (SMNH MO 78888, 1 s.v.); Elat, New Port, 220 m, grab. Leg. D. Zalcman, 16.09.1968. (SMNH MO 78895, 13 s.v., mostly worn/juv./def./fr.); Elat, Old Port, 121 m. Leg. D. Zalcman, 10.09.1968. (SMNH MO 78897, 36 s.v., most def./fr. and juv.); Elat, RS 15, 70 m, grab, 08.10.1965. (HUJ 1852, 32 s.v., partly worn / def.); New Port, 270 m. Leg. D. Zalcman, 13.02.1970. (SMNH MO 27423, c. 25 s.v., many broken/def.); oil port, 350 m, grab. Leg. D. Zalcman, 16.09.1968. (SMNH MO 78884, 3 s.v., subadult-juv.); Taba, 55-90 m, Ockelman dredge. Leg. D. Zalcman, 14.12.1967. (SMNH MO 27452, 15 s.v.).

Egypt, Gulf of Aqaba, Elat, 37-49 m. Leg. Ch. Lewinsohn, 06.09.1966. (SMNH MO 27443, 20 s.v., most worn, some juv./def.); Gazirat Fara'un, 64-73 m, triangular dredge. Leg. Ch. Lewinsohn, 09.10.1969. (SMNH MO 27419, 1 s.v., very fresh); Marsa Murach, 73-82 m. Leg. Ch. Lewinsohn, 09.10.1969. (SMNH MO 7650, 1 s.v., def.); Maras Murach, + Fractures 92 m, 08.11.1969. (SMNH MO 78901, 5 s.v., most subadult); Marsa Abu Samra North, 46-49 m. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 27442, 34 s.v., adult-juv., some def./fr.); Marsa Abu Samra North, 51-53 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 27414, 24 s.v., many fresh, few def.); Marsa Abu Samra North, 51-53 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 27483, 1 s.v., adult, worn); Marsa Abu Samra North, 37-53 m, rock dredge. 06.10.1969. (SMNH MO 41723, 1 s.v., adult); Marsa Abu Samra, Centre, 132-137 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 78886, 20 s.v., some very fresh + several fr.); Marsa Abu Samra, Centre, 49-55 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 27422, 1 p.v.; 33 s.v.); Marsa Murach, 81-82 m, triangular dredge. Leg. Ch. Lewinsohn, 09.10.1969. (SMNH MO 27441, 2 s.v., fresh); Marsa Murach, 92 m, angular dredge, 06.10.1969. (SMNH MO 27482, 2 s.v., rather worn); Nuweiba El Tarabin, 137-146 m. Leg. Ch. Lewinsohn, 08.10.1969. (SMNH MO 78889, > 100 s.v., adult-juv.); Nuweiba South, 550-700 m. Leg. D. Zalcman. (SMNH MO 78887, 1 s.v., adult, rather fresh); Hurghada area, Shaab Umm Qammar, 27°19'59"N, 33°54'59"E, 65-87 m (Colln S. Hobbs, 1 p.v., adult).

Sudan, off Suakin, 19°00.2'N, 38°22.1'E, 669 m, mud, 27.02.1995. Meteor Exp. st. Me31/2-100 GKG 6 (SMF 347562, 3 s.v., subadult-juv.); off Suakin, 18°57.5'N, 38°15.8'E, 90 m, mud, 27.02.1995. Meteor Exp. st. Me31/2-100 GKG 8 (SMF 347563, 1 s.v., fr., juv.); off Suakin, 18°57.5'N, 38°15.7'E, 101 m, mud, 27.02.1995. Meteor Exp. st. Me31/2-100 GKG 9 (SMF 347564, 2 s.v., juv.).

Yemen, Gulf of Aden, off Aden, 12°27.6'N, 44°25.3'E, 71 m, coarse sand, 04.03.1995. Meteor Exp. st. Me31/3-105 GKG 1





Figs 30-31. Indo-West Pacific distributions of *Frigidocardium* species as currently known. Coral Triangle indicated in red dotted line, type localities with black circle. **30.** *F. centumliratum* (based on 85 verified samples). **31.** *F. helios* (based on 78 verified samples); **32.** *F. kirandum* (based on 39 verified samples); **33.** *F. torresi* (based on 128 verified samples). Material mainly originating from MNHN, NHMUK, RMNH, SMF, SMNH, ZMA, JJTP and S. Hobbs.

(SMF 347565, 6 s.v., adult-juv.); Gulf of Aden, off Aden, 12°22.8'N, 44°31.5'E, 321 m, sand, 04.03.1995. Meteor Exp. st. Me31/3-105 GKG 3 (SMF 347566, 3 s.v., juv.).

Frigidocardium spec. aff. *helios*. — **Egypt**, Gulf of Aqaba, Marsa Abu Samra, centre, 49-55 m, rock dredge. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 27416, 1 s.v., adult, fresh); Nuweiba,

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Figs 22-29. *Frigidocardium kirandum* Sakurai & Habe, 1966. **22-23**, Israel, Gulf of Aqaba, Elat, old port, 121 m. Leg. D. Zalcman, 10.09.1968. SMNH MO 27449. **22**, H 13.7 mm (a: RV exterior, b: RV interior). **23**, H 9.4 mm (a: LV exterior, b: LV interior). **24**, Egypt, Gulf of Aqaba, Dahab, dive site 'Islands', 21 m, in sand covered by some seagrass. Leg. and colln H. Blatterer, Austria, H 16.9 mm (a: LV exterior, b: RV exterior, c: LV interior, d: RV interior). **25-27**, Egypt, Hurghada area, Shaab Umm Qammar, 27°19'59"N, 33°54'59"E, 65-87 m. Colln S. Hobbs, U.S.A. **25**, H 20.0 mm (a: LV exterior, b: LV interior). **26**, H 8.6 mm (a: RV exterior, b: LV exterior, c: RV interior, d: LV interior). **27**, H 19.5 mm (a: RV exterior, b: LV exterior, c: RV interior, d: LV interior, e: dorsal). **28**, Egypt, Hurghada area, Umm Qammar, by trimix diver, 90 m. Colln S. Hobbs, U.S.A. (a: LV exterior, b: posterior view). **29**, Madagascar, S. of Faux-Cap, 26°03.2'S, 45°32.1'E, 98 m. 05.05.2010. ATIMO VATAE st. DW3550. MNHN-IM-2014-6006, H 15.7 mm (LV exterior).

329-403 m, triangular dredge. Leg. Ch. Lewinsohn, 08.10.1969. (SMNH MO 78893, 1 s.v., juv., worn).

Frigidocardium kirandum Sakurai & Habe, 1966 (Figs 22-29, 32)

Frigidocardium kirana Sakurai & Habe, 1966: 294, 296, fig. 1.

Frigidocardium kirana Sakurai & Habe, 1966 — Huber, 2010: 307, unnumbered fig.

Frigidocardium eos Kuroda, 1929 — Fischer-Piette, 1977: 68 [in part].

Type locality. — Japan, S of Kyushu, Amami Isls., Kakeroma Isl.

Type material. — NSMT-Mo 52635, holotype (s.v.)

Description (modified after ter Poorten, 2009). — Shell medium sized (H up to 20 mm) and rather thin, inequilateral with strong umbono-ventral flexure, angled postero-ventral margin and straight or slightly concave posterior margin. Length usually approximately equal to height. Numerous (circa 120-130) radial ribs, all finely sculptured. Spines tiny, of highly variable thickness, mainly arising from rib interstices though they may encroach on anterior flank of ribs on posterior half of valves, on posterior flank on anterior half of valves and even extend to top of ribs on anterior slope. The change from spines that arise on anterior as opposed to posterior flanks occurs just anterior to the umbono-ventral flexure. Lunular heart

and area barely defined. Shell with radial, orange-red lines on a white background. Umbo and posterior slope deep red. Occasionally all lemon yellow or pure white with yellow umbones. Interior with yellowish umbral cavity and reddish patch on posterior slope.

Remarks. — Van Gemert (2015) points out that the specific epithet *kirana* should be emended to *kiranum*. Type material is figured by Hasegawa & Saito (1995: 31, pl. 7 fig. 1) and Higo et al. (2001: fig. B817). This species is relatively easy to recognize because of the prominent umbral keel and inequilateral shell shape. The Red Sea occurrence is mentioned by Huber (2010), although the depicted specimen is from the Philippines, Balicasag Isl. Additional published Red Sea records could not be traced. Images of Red Sea material can be found on the website of J. Dafni (http://www.dafni.com/mollusca/spec_15.htm#Cardiid, as *Frigidocardium kirana* (Sukaria & Habe, 1996) [3x sic!]). The maximum height reported so far is 16 mm (ter Poorten, 2009; Huber, 2010); the largest observed Red Sea specimen however, attains a height of 20 mm (colln S. Hobbs, Fig. 25a-b). Given the paucity of records, it is likely that the fully adult size is a bit larger.

Distribution (Fig. 32). — Tropical Indo-West Pacific, recorded from S. Madagascar (MNHN, ATIMO VATAE 2010, Fig. 29); Réunion (Drivas & Jay, 1988, as *Laevicardium* sp.; Poutiers, 2006); S. of Japan (Sakurai & Habe, 1966); Philippines (MNHN, PANGLAO 2004, PANGLAO 2005, AURORA 2007); Malaysia, Sabah (JJTP); Indonesia (JJTP); Guam (Paulay, 2003); New Caledonia (MNHN, CONCALIS, EBISCO); Vanuatu (MNHN, SANTO 2006); Tonga (Poutiers, 2006) and Northern Fiji Basin (MNHN, MUSORSTOM 7).

The bathymetric range of the Red Sea SMNH records is 46–221 m, all empty and consisting of loose valves. Supplementary Red Sea samples show a range of 21–90 m (p.v.); life-taken material originates from a range of 65–87 m.

Material examined. — **Israel**, Gulf of Aqaba, Elat Zarhin Plant, 167 m. Leg. D. Zalcman, 16.09.1968. (SMNH MO 27445, 1 s.v., subadult); Elat, New Port, 220 m, grab. Leg. D. Zalcman, 16.09.1968. (SMNH MO 27426, 1 s.v., subadult); Elat, old port, 121 m. Leg. D. Zalcman, 10.09.1968. (SMNH MO 27415, 7 s.v., mostly subadult, def. or fr.); Elat, Old Port, 121 m. Leg. D. Zalcman, 10.09.1968. (SMNH MO 78898, 1 s.v., fr.).

Egypt, Gulf of Aqaba, Marsa Abu Samra North, 46–49 m. Leg. Ch. Lewinsohn, 06.10.1969. (SMNH MO 78892, 1 s.v., subadult and worn); Gulf of Aqaba, Dahab, dive site 'Islands', 21 m, in sand covered by some seagrass. Leg. H. Blatterer, 14.11.2007 (1 p.v., adult); Hurghada area, Shaab Umm Qammar, 27°19'59"N, 33°54'59"E, 65–87 m (Colln S. Hobbs, 5 p.v., adult-juv. alive, 16 s.v., adult-juv.); Umm Qammar, by trimix diver, 90 m (Colln S. Hobbs, 1 p.v., adult).

DISCUSSION

Records of other *Frigidocardium* species from the Red Sea are scarce. Fischer-Piette (1977: 68) reports a 2.7 by 2.5 mm TAU (now SMNH) valve of *F. exasperatum* (G.B. Sowerby II, 1839) from Eilat (now Elat). Unfortunately, this was not found among the samples from SMNH. This species is also recorded by Oliver (1992: pl. 21 figs 10a-b), who mentions a maximum size of 12 mm for the Red Sea, whereas the indicated size of the figured specimen is 26.1 mm. Huber & ter Poorten (2007) make clear that this specimen does not originate from the Red Sea proper, which is confirmed by Harriet Wood (NMW, e-mail 12.08.2013). *F. exasperatum* is restricted to the area from southern Japan – Taiwan – Vietnam; lacking any reliable records, it is concluded that it does not live in the Red Sea. It can easily be distinguished from *F. centumliratum* by its typical asymmetric, often partly orange coloured lunule, its lower rib number (80–90) and the more robust sculpture, especially on the anterior part. See ter Poorten (2009: table 7) for differences with other congeneric species.

Given the presence of *F. torresi* in the W. Indian Ocean and its occurrence in the Gulf of Oman (see above) up to the northern Persian Gulf (27°44'40"N 50°4'30"E, RMNH.MOL.33826; Fig. 33), additional sampling and research will be needed in order to get more insight in its distributional limits. It also will provide more certainty whether it can indeed be excluded from the malacofauna of the Red Sea.

Due to the scarcity of Red Sea deep water samplings, our understanding of *Frigidocardium* distributions remains poor and incomplete. Noteworthy is that practically all of the Red Sea samples in this paper have become available thanks to dredge/grab operations or specialized trimix deep sea diving techniques. Sadly enough, due to unfavourable geo-politic circumstances over the decades, systematic research covering the Red Sea deep benthos is lacking and hardly any information is available regarding deep-sea Red Sea molluscs distributed in the 200–400 m range (Janssen & Taviani, 2015). The presence of a life-taken sample of *F. centumliratum* from a depth of 600 m indicates that it has to be added to the 94 bivalve species that have been recorded below 400 m depth (Janssen & Taviani, 2015).

The Indo-West Pacific distribution of the three *Frigidocardium* species treated in this paper (Figs 30–32), as well as the related *F. torresi* (Fig. 33), has become fairly well known but is still patchy and incomplete. These seemingly disjunct distributions more likely appear to reflect a local low sampling intensity rather than range fragmentations. Supportive of this view is that throughout their ranges, the shell

morphology of the three species is rather uniform. Besides, it is apparent that particularly the deep water component of continental East Africa and the northern Indian Ocean are severely undersampled.

With four of the ten currently accepted *Frigidocardium* species having been introduced in the past ten years, it is obvious that re-examination of deep water old collection material can be very rewarding and yield unexpected results. It also shows that our present concept of this genus is far from comprehensive.

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