Revision of the Recent species of the genus *Nemocardium* Meek, 1876 (Bivalvia, Cardiidae), with the descriptions of three new species

Jan Johan ter Poorten
Field Museum of Natural History, Department of Zoology (Invertebrates), 1400 S. Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.
Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands; terpoorten@chello.nl

The genus *Nemocardium* Meek, 1876, is traditionally considered a relic of the past. Morphometric and morphological analyses reveal that the well-known species *N. bechei* (Reeve, 1847) is in need of taxonomic reconsideration. In this paper, five species are recognized, three of which are new to science: *N. bechei* from Taiwan, Philippines and Indonesia; *N. probatum* (Iredale, 1927) from northern Australia; *N. australojaponicum* spec. nov. from southern Japan and Korea; *N. enigmaticum* spec. nov. from the South West Pacific and *N. fulvum* spec. nov. from Mozambique, Madagascar, Seychelles, India, Philippines and Vanuatu. All but the last species seem to occur perfectly parapatrically. With *N. fulvum* spec. nov., which is not confined to the Central Indo-Pacific but covers large parts of the Indian Ocean as well, the longitudinal range of *Nemocardium* is much wider than hitherto thought. A substitute lectotype is designated for *Cardium bechei* Reeve, 1847, and the New Zealand genus *Varicardium* Marwick, 1944, is synonymized with *Nemocardium*.

Key words: Bivalvia, Cardiidae, *Nemocardium*, taxonomy, Indo-Pacific.

Introduction

Nemocardium bechei (Reeve, 1847) has been considered by most workers (e.g. Poutiers, 1992; Schneider, 2002) to be the only extant species of the genus *Nemocardium* Meek, 1876, which dates back to the Aptian (Early Cretaceous) of Spain, Lebanon and Syria (Keen, 1950), England (Cleevely et al., 1983) and the Aptian-Albian of Japan (Hayami, 1975). Together with *Pratulum* Iredale, 1924, it is the oldest living cardiid genus (Schneider, 1995, 2002), and one of the few cardiid genera that survived the last mass extinction at the end of the Cretaceous. It flourished particularly in Europe during the Paleogene, where circa 30 nominal species are recorded (Poutiers, 1992). *Nemocardium* is known as a typical Tethyan representative (Keen, 1950) which, due to the closure of the eastern seaway to the Indo-Pacific in the late Early Miocene, became a Tethyan relic in Europe, where it became extinct in the Early Pleistocene (La Perna & D'Abramo, 2011). Nowadays *Nemocardium* occurs in rather deep water in tropical Indo-West Pacific environments. The unique appearance of *N. bechei* (Reeve, 1847) among the then known cardiids filled Reeve (1847: 25) with delight, consi-

dering it 'without exception the most striking and distinct from any hitherto known that can well be imagined'.

Nemocardium displays a characteristic strongly discrepant sculpture, with prominent ribs on the posterior part, invariably leaving the remainder of the surface almost smooth with subsurface radial markings and, in a few species, commarginal cords. Although remarkably uniform in gross morphological features, Ter Poorten (2009: 81, table 9) demonstrated that four forms are to be distinguished, based on morphometrical differences, and small distinctions in colour, periostracum and size. Lacking a systematic treatment, the status of these forms is as yet unresolved, as exemplified by Huber (2010: 684).

Due to allometric growth – the process in which the shell shape changes significantly during ontogeny – juvenile cardiids tend to be more rounded in outline, not reaching their ultimate shape until the subadult stage. *Nemocardium* is no exception, generally having a less clear-cut appearance when young, with rather uninformative morphometrics, hampering identification of juveniles (unfortunately the prevailing stage of museum expedition material). The remarkably uniform hinge characters among *Nemocardium* species and the absence of ribs and rib sculpture on most parts of the shell leads to a paucity of reliable markers. The dependence on more or less full-grown specimens, combined with their relative rarity (living in rather deep water), has hampered our understanding of the living members of the genus. This is in remarkable contrast to our knowledge of the large number of fossil representatives, many of them having been described more than a century ago.

Notwithstanding the aforementioned restrictions, morphometrical parameters (L/H ratio, W ratio and number of posterior ribs) allow the recognition of five different forms, coinciding with four seemingly parapatric distributions and one partly sympatric pair of ranges (Figs 1-2). Three are confined to regions in the central Indo-West Pacific, within the area from the East China Sea, Philippines, Indonesia, the northern half of Australia, New Caledonia, the Loyalty Islands to the Kermadec Islands. The fourth one is strictly extra-tropical, restricted to southern mainland Japan and South Korea, whereas the fifth one has a much wider tropical longitudinal distribution, ranging from Vanuatu across the Indian Ocean to Madagascar and Mozambique.

Several morphological differences among the aforementioned forms (shell outline, coloration, rib sculpture, hinge, periostracum, etc.) confirm the dissimilarities in the morphometrics and are consistent with the biogeographical patterns, justifying separation of these forms at the species level. It follows that the long-lived genus *Nemocardium* is still flourishing in the tropical Indo-West Pacific and adjacent areas, rather than being a monotypical living relict of the past. All five extant species are treated hereafter in the systematic part.

(opposite page)

Fig. 1. Distribution of *Nemocardium bechei* (blue diamonds), *N. probatum* (green squares), *N. australojaponicum* spec. nov. (red circles), *N. fulvum* spec. nov. (brown stars) and *N. enigmaticum* spec. nov. (purple triangles). Dark symbols: personally verified material; pale symbols: literature records. Bold dashed lines indicate boundaries of the Japonic – Indo-Pacific faunal province in the North; the Indo-Pacific – Australian faunal province in the Southeast and the Indo-Pacific – South African province in the Southwest.

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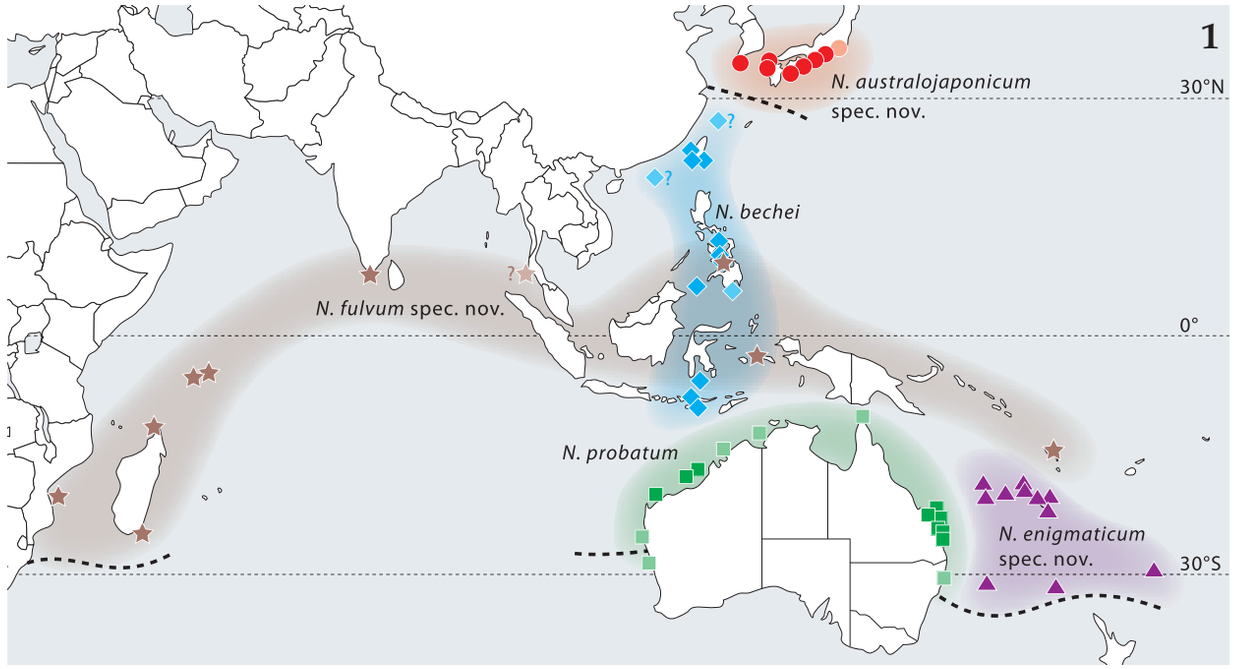
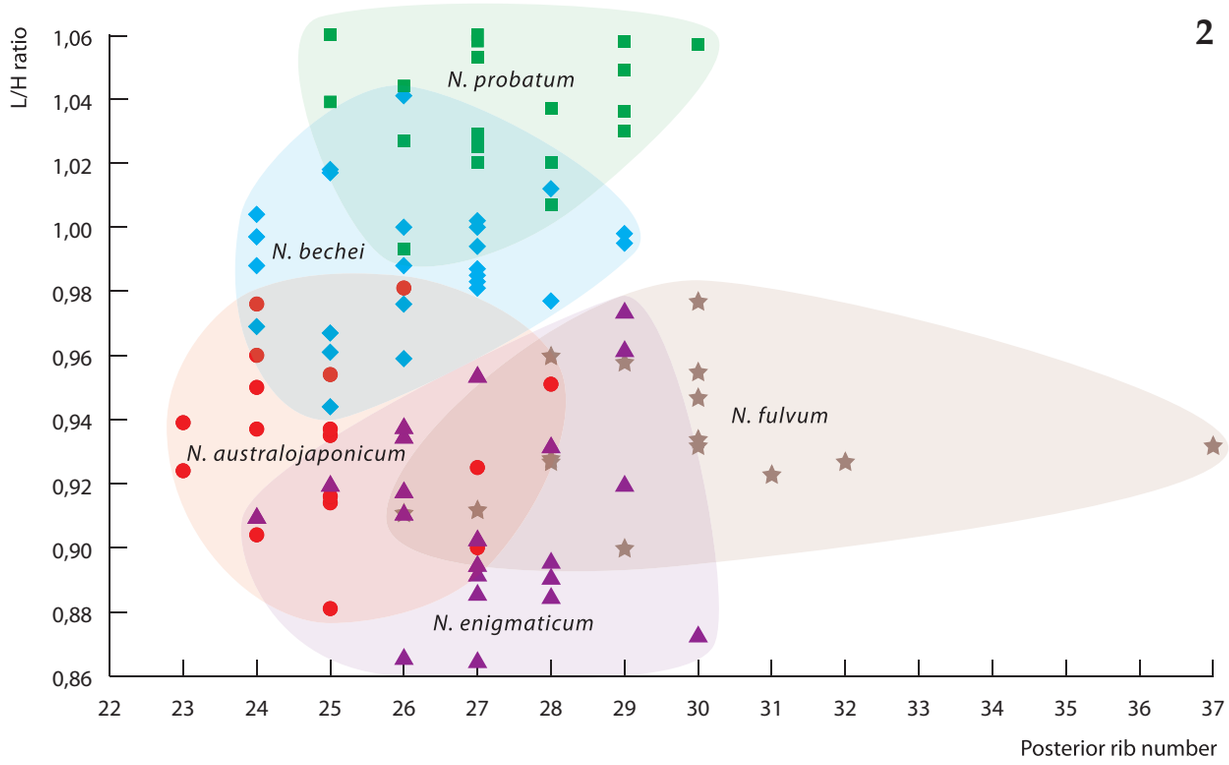
Fig. 2. A representation of the morphospace for the *Nemocardium bechei* lineage, showing the relationship between length and height and the posterior rib number in *N. bechei* (blue diamonds), n = 25, *N. probatum* (green squares, n = 20), *N. australojaponicum* spec. nov. (red circles, n = 18), *N. fulvum* spec. nov. (brown stars, n = 15) and *N. enigmaticum* spec. nov. (purple triangles, n = 21). Only (sub)adult shells are plotted, defined as all those individuals with a size of at least 40 mm. Colln FMNH, MNHN, NMNZ, NSMT, RMNH, USNM, WAM, ZMA, EK, MH and JJTP.





Abbreviations and acronyms. – AL, anterior length; H, height; L, length; LV, left valve; PL, posterior length; p.v., paired valves; RV, right valve; s.v., single valve(s); W, width.

AMS, Australian Museum Sydney, Australia; ANSP, Academy of Natural Sciences Philadelphia, U.S.A.; EK, Colln E. Kaptein, Almelo, The Netherlands; FMNH, Field Museum of Natural History, Chicago, U.S.A.; GNS, GNS Science, Lower Hutt, New Zealand; JJTP, Colln J.J. ter Poorten, Hilversum, The Netherlands; MH, Colln M. Huber, Winterthur, Switzerland; MNHN, Muséum national d'Histoire naturelle, Paris, France; MNHN.F, Muséum national d'Histoire naturelle, Collection de Paléontologie, Paris, France; NHMUK, The Natural History Museum (formerly British Museum of Natural History), London, U.K.; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; NSMT, National Museum of Nature and Science, Tokyo, Japan; PRI, Paleontological Research Institution, Ithaca, U.S.A.; RGM, Naturalis Biodiversity Center, Leiden, The Netherlands (Paleontological collection); RMNH, Naturalis Biodiversity Center, Leiden, The Netherlands (Recent collection); SH, Colln S. Hobbs, Cape May, New Jersey, U.S.A.; UMZC, University Museum of Zoology, Cambridge, U.K.; USNM, National Museum of Natural History, Smithsonian Institution, (formerly United States National Museum) Washington, DC, U.S.A.; WAM, Western Australian Museum, Perth, Australia; ZMA, Zoological Museum Amsterdam, The Netherlands (now part of NCB Naturalis, Leiden, The Netherlands).

Material and methods

The material used in this study originates from a number of institutions: AMS, ANSP, FMNH, GNS, MNHN, NHMUK, NMNZ, NSMT, RMNH, UMZC, USNM, WAM and ZMA. Fossil material has been examined in RGM, MNHN.F, PRI and USNM. Additionally, samples from private collections (EK, JJTP, MH, SH) have been taken into account. As mature shells are best suitable for morphometric study (see hereafter) and being scarcely represented in institutional expedition material, the predominantly adult samples from private collections, though originating from the shell dealer market, formed important additions.

Length (L) is defined as a line parallel to the line connecting the tip of the anterior and posterior ventral lateral tooth, which starts at the anteriormost shell margin. Height (H) is defined as the line perpendicular to L, which results in the greatest value of the dorsal height. In the captions, L or H is indicated, depending on the larger size. Anterior length (AL) is that portion of line L which is anterior of line H. Posterior length (PL) is that portion of line L which is posterior of line H. In total: AL + PL = L.

The width (W) ratio is defined by the following formula: ((L+H):2):W (extrapolated in case of single valves). The total rib number is based on counting the marginal crenulations; the posterior rib number is based on counting the actual number of sculptured ribs.

The marginal crenulations have been estimated by examining the shell interior, including the minute to indistinct crenulations close to the lunular area by using floodlight. As they often become barely perceptible towards the dorsal margin, a certain degree of subjectivity is unavoidable, and therefore no mean values were calculated.

Specimens containing parts of the dried animal or any kind of flesh remains are considered to have been taken alive and are indicated as such at the examined material section. Regrettably, due to the absence of preserved tissue material suitable for DNA extraction, this study had to be based exclusively on morphological markers.

Systematic part

Family Cardiidae Lamarck, 1809

Provisionally assigned to subfamily Laevicardiinae, see below

Nemocardium Meek, 1876

Nemocardium Meek, 1876: 167 (as a section of *Cardium*). Type species, by subsequent designation (Sacco, 1899: 56): *Cardium semiasperum* Deshayes, 1858; Lower Eocene, Paris Basin, France.

Varicardium Marwick, 1944: 266-267. Type species, by original designation: *Cardium patulum* Hutton, 1873; Miocene, New Zealand [**syn. nov.**].

Diagnosis. – Shell rather large, ovately quadrate. Sculpture heterogeneous, dividing the surface into two markedly distinct zones: anterior two-thirds consisting of numerous, completely flattened, subsurface radial ribs, lacking ornamentation; posterior one-third sharply demarcated, covered with numerous well developed and spinose radial ribs. In-

terstices of ribs devoid of spines and transverse elements. Marginal crenulations, in accordance with ribs, much wider and more strongly serrated on posterior zone. Hinge with very unequal cardinal teeth, the larger strongly curved; RV cardinals partly joined by a saddle. Lunule and escutcheon present. Periostracum well developed.

Soft parts. – Anatomical data are scarce: Nakazima (1964) discussed the nature of the crenated folds in the midgut gland. As his material has a Japanese origin, it must refer to *N. australojaponicum* spec. nov. Schneider (2002: fig. 5) figured the internal stomach morphology of *N. bechei* (USNM 747190, Indonesia, Moluccas). As in most cardiids, the right caecum is located on the right side of the stomach floor. In addition, his anatomical investigations make clear that the labial palps are relatively short, defined as less than one-third the length of the entire animal, and that the ventral ridge on the foot is moderately developed.

Distribution. – Early Cretaceous to Recent, Indo-Pacific, Japonic; sublittoral-upper bathyal. Inclusion of the intertidal zone by Wilson & Stevenson (1977: 64) is possibly based on Iredale's (1927: 333) record that 'many valves were present on the Caloundra beaches', but a littoral occurrence is not supported by the data in this study.

Remarks. – La Perna & D'Abrama (2011) state that the type species, *Cardium semiasperum* Deshayes, 1858, was designated originally by Meek (1876), not subsequently by Sacco (1899). This is incorrect as Meek (1876: 167) did not explicitly designate a nominal species as the type species but only mentioned a species (ICZN, 1999: Art. 67.5, 68.2). *Nemocardium semiasperum* (Figs 3-4) is a rather rare species, poorly represented in collections. It is relatively small (L 40 mm), fragile, rather inflated, with erect, pronounced tubercles placed on up to circa 20 posterior ribs and has a wide lunule.

The subfamilial assignment has a rather complex history. Traditionally, *Nemocardium*, together with a number of Mesozoic and Cenozoic genera were assigned to Protocardiinae Bronn, 1849 (Keen, 1980; Poutiers, 1992). Schneider's (1992, 1995) phylogenetic analyses made clear that Protocardiinae as construed so far was paraphyletic and that it should be restricted to a Mesozoic group consisting of *Protocardia* Von Beyrich, 1845, *Leptocardia* Meek, 1876, *Pachycardium* Conrad, 1869 and *Tamilicardia* Chiplonkar & Tapaswi, 1976; with the remaining genera and subgenera to be placed in Lahilliinae (*Cryptocardia* Palmer, 1974, *Globocardium* Hayami, 1965, *Integricardium* Rollier, 1912, *Onestia* McLearn, 1933, *Tendagurium* Salisbury, 1934, *Yokoyamaina* Hayami, 1958), Laevicardiinae (*Arctopratulum* Keen, 1954, *Brevicardium* Stephenson, 1941, *Discors* Deshayes, 1858, *Divaricardium* Dollfus & Dautzenberg, 1886, *Frigidocardium* Habe, 1951, *Fulvia* J.E. Gray, 1853, *Habecardium* Glibert & Van de Poel, 1970, *Keenaea* Habe, 1951, *Laevicardium* Swainson, 1840, *Lophocardium* P. Fischer, 1887, *Microcardium* Thiele, 1934, *Nemocardium* Meek, 1876, *Pratulum* Iredale, 1924, *Trifaricardium* Kuroda & Habe in Habe, 1951, *Varicardium* Marwick, 1944) and Cardiidae incertae cedis (*Jurassicardium* Cossmann, 1906). Instead of a sister-group relationship with *Nemocardium*, Schneider (1995: 341) postulated an alternative scenario in which Laevicardiinae was derived in some form from *Nemocardium*. Therefore its true phylogenetic relationship would lie within *Nemocardium*, not as a sister taxon. Lacking a more detailed phylogenetic analysis of the involved taxa, this possibility was left open.

Recent extensive species-level phylogenetic analysis (Herrera, et al., in prep.) has shown that Laevicardiinae

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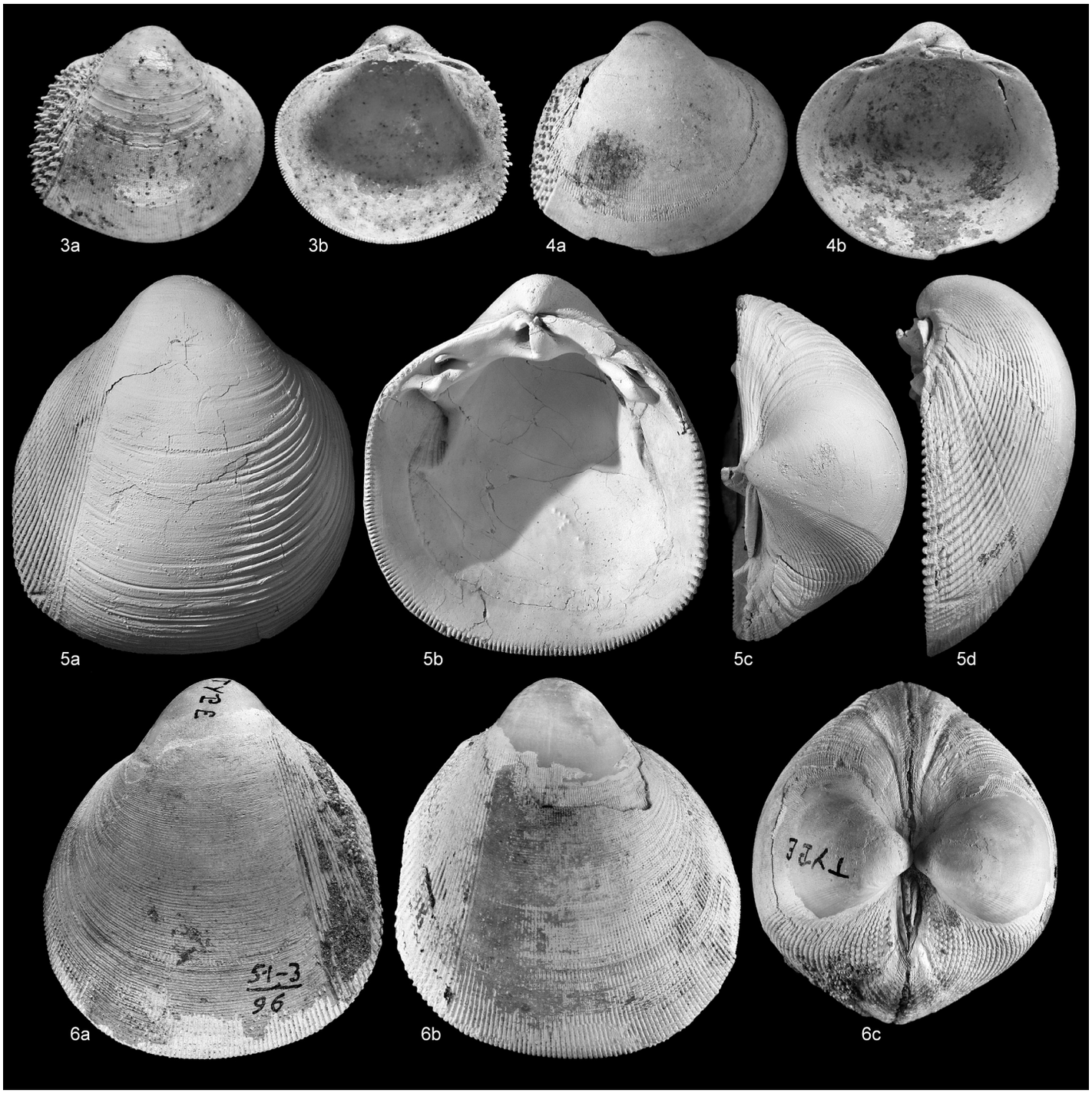
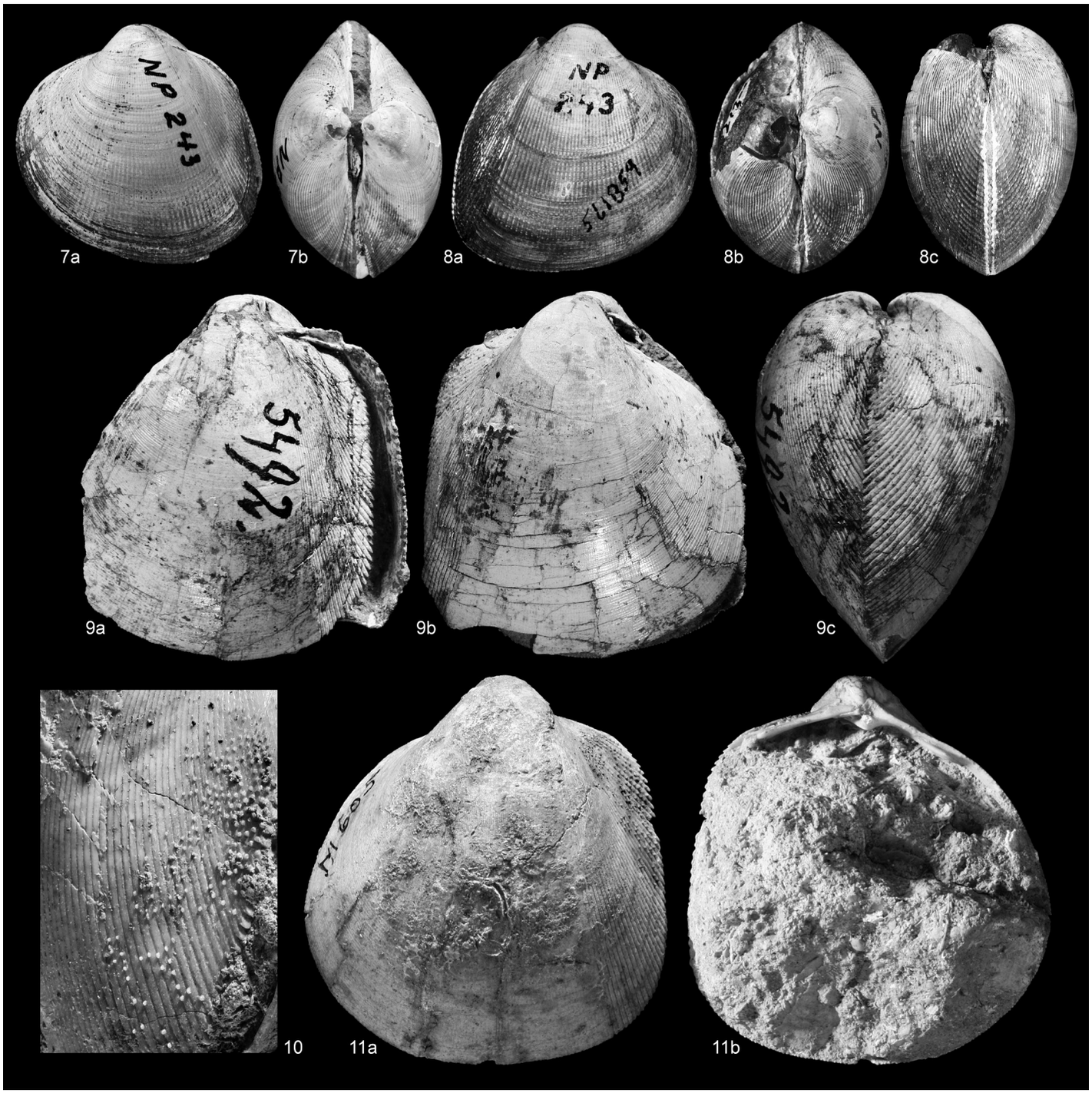
Figs 3-6. Cenozoic *Nemocardium* species. **3-4.** *Nemocardium semiasperum* (Deshayes, 1858), type species of *Nemocardium* Meek, 1876. **3a-b**, France, Picardie, Aisne, Aizy-Jouy. Eocene, Ypresian. MNHN.F.A47046, topotype, coll. Morlet, L 18.0 mm (a: RV exterior, b: RV interior). **4a-b**, Same locality, ex Cossmann & Pissarro, 1905: pl. 19 fig. 72-7. MNHN.F.J07335, L 23.2 mm (a: RV exterior, b: RV interior). **5a-d.** *Nemocardium patulum* (Hutton, 1873), type species of *Varicardium* Marwick, 1944. New Zealand, North Canterbury, Weka Pass, Weka Creek. Middle Miocene, Lillburnian NZ local Stage. GS9566, M34/f9083, H 95.7 mm (a: RV exterior, b: RV interior, c: dorsal view, d: posterior view. Specimen whitened; photos courtesy Marianna Terezow, GNS Science). **6a-c.** *Nemocardium auberti* (Abrard, 1946). Vanuatu, Epi (Baie de Foreland). Upper Miocene. MNHN.F.A26990, holotype, H 52.0 mm (a: LV exterior, b: RV exterior, c: dorsal view).





sensu Schneider (1995) is polyphyletic; that *Frigidocardium, Lophocardium, Microcardium,* and *Trifaricardium* form a clade basal to all other living cardiids sequenced to date; and that Laevicardiinae is sister to Trachycardiinae, representing the youngest lineages in the family. Unfortunately, due to the unavailability of *Nemocardium* and *Pratulum* tissue material, the phylogenetic placement of these taxa is still not fully resolved, for which reason I refrain from erecting a new subfamily for *Nemocardium*.

Nemocardium has traditionally been subdivided into a large number of subgenera (Keen, 1980; Schneider, 1995); many of them have been raised to generic level by most modern taxonomists: *Discors, Frigidocardium, Habecardium, Lophocardium, Lyrocardium* Meek, 1876, *Microcardium, Pratulum* and *Trifaricardium*. The status of some alleged subgenera is discussed hereafter.

Varicardium Marwick, 1944 was described to accommodate *Cardium patulum* Hutton, 1873 (Fig. 5a-d) from the Upper Oligocene - Middle Miocene of New Zealand. Subsequent workers either treated it as genus (Boreham, 1965) or as subgenus of *Nemocardium* (Keen, 1980; Beu & Maxwell, 1990; Maxwell, 1992; Schneider, 1995; Beu & Raine, 2009). It resembles *Nemocardium* in size and outline but is separated by the presence of commarginal undulating ridges on the anterior part on the shell, gradually becoming weaker on the median part. Additionally, the about 30 posterior ribs bear only very tiny tubercles on the anterior edges (visible on well-preserved juveniles) and the hinge is more prominent. However, it should be noted that within *C. patulum* the strength of the commarginal ridges is rather variable. Although more weakly developed, some extant *Nemocardium* species (especially *N. enigmaticum* spec. nov. and *N. fulvum* spec. nov.) possess similar ridges. A fossil example is the Oligocene *N. bhagothorense* (Vredenburg, 1928) from Pakistan. The Middle Eocene *N.* (*N.*) *carteri* Maxwell, 1992, an earlier Cenozoic *Nemocardium* species from New Zealand, has well-developed commarginal ridges, too, leading Maxwell (1992) to discuss whether placement in *Nemocardium* (s.s.) or *N.* (*Varicardium*) would be more appropriate. Yet *N. carteri* also displays pronounced tubercles on the posterior ribs, a typical *Nemocardium* feature. It seems likely that *C. patulum* has descended from *N. carteri* (A. Beu, GNS Science, pers. comm. 15.11.2010). All in all, there is little reason to retain *Varicardium,* either as genus or subgenus; it is therefore herein considered synonymous with *Nemocardium*.

Pratulum Iredale, 1924 (type species *Cardium striatulum* var. *thetidis* Hedley, 1902; New South Wales, Australia) is given full generic rank, following Poutiers (1992), Beu & Raine (2009) and Spencer et al. (2009). It differs from *Nemocardium* by the following characters: '[...] the outer surface has two clearly differentiated areas as in *Nemocardium* s.s. but, in *Pratulum*, radial ribbing is not confined to the posterior area. Moreover, the anterior and median areas of *Pratulum* spp. have a fine secondary sculpture of irregularly commarginal anastomosing threads crossing the radial ribs. The marginal crenulations are not clearly stronger posteriorly as they are in *Nemocardium*, but as in that genus, the crenulations do correspond with the radial sculpture.' (Poutiers, 1992: 142). Additionally, *Pratulum* remains much smaller than *Nemocardium*. Unlike *Nemocardium*, it does not appear to represent a Tethyan Indo-Pacific element (Poutiers, 1992), but is restricted to the temperate waters of the southern half of Australia (extending well up the eastern and western coasts) and New Zealand.

Arctopratulum Keen, 1954 (type species *Nemocardium* (*Arctopratulum*) *griphus* Keen, 1954; U.SA., Washington, Middle Miocene; Figs 7-8) and *Keenaea* Habe 1951 (type species *Cardium* (*Nemocardium*) *samarangae* Makiyama, 1934; *nomen*

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Figs 7-11. Cenozoic *Arctopratulum* and *Nemocardium* species. **7-8.** *Nemocardium* (*Arctopratulum*) *griphus* Keen, 1954. **7a-b**, United States, Washington, Grays Harbor County, N. of Aberdeen, Standford Univ. loc. NP-243. Leg. Harrold Hannibal, 1912. Middle Miocene, Astoria formation. PRI 24545, paratype, L 32.0 mm (a: LV exterior, b: dorsal view). **8a-c**, Same locality, USNM 561859, paratype, L 33.5 mm (a: RV exterior, b: dorsal view, c: posterior view). **9-11.** *Nemocardium* spec. **9a-c**, Indonesia, Java, Ngampel. Lower Miocene. RGM 5492, H c. 38.5 mm (a: LV exterior, b: RV exterior, c: posterior view). **10**, Indonesia, Java, Sedan. Lower Miocene. RGM 794164, H 54.4 mm, detail of posterior slope. **11a-b**, Same locality, ex Pannekoek, 1936: pl. 4 figs 50, 50a. RGM 794164, H 35.2 mm (a: LV exterior, b: LV interior).

novum for *Cardium modestum* A. Adams & Reeve, 1850, non Philippi, 1849; 'Eastern Seas' [Japan]) share with *Pratulum* the homogeneous marginal crenulations, a strong argument for generic separation from *Nemocardium*. Both taxa have not recently been defined critically. I prefer to treat them as separate genera.

Brevicardium Stephenson, 1941 (type species *Brevicardium fragile* Stephenson, 1941; U.S.A., Mississippi, Upper Cretaceous) is essentially distinguished from *Nemocardium* 'by the position of the spines which, on *Brevicardium*, occupy the channels between the ribs, whereas in *Nemocardium* they stand upon the crest of the ribs', which 'probably indicates a fundamental generic difference' (Stephenson, 1941: 203). *Laevicardium bechei* Reeve sensu Pannekoek (1936) from the Lower Miocene of Java, Indonesia has an identical positioning of the spines to that in *Brevicardium*, but otherwise perfectly matches *Nemocardium*, although it is probably an undescribed species (Figs 9-11). Another example is the Italian Early Pliocene to Early Pleistocene species *Nemocardium italicum* La Perna & D'Abramo, 2011. The similar positioning of the spines could be an example of convergence. The small size of the American representatives of *Brevicardium* (none exceeding 8 mm in length) and the conspicuous development of sinuous, commarginal lines readily separate it from *Nemocardium*. Additionally, the anterior and median radial ribs, though low, cannot be considered subsurface. The last three mentioned characters point to a closer relationship to *Pratulum* than to *Nemocardium,* as seen in Schneider's (1995: fig. 22) preferred cladogram.

Overall, there seems little reason to maintain the classic concept of *Nemocardium* subdivided into a number of subgenera. It is unlikely that these taxa, representing such a different biogeography and age, are monophyletic. Hence, this concept is abandoned herein.

Nemocardium bechei (Reeve, 1847)
(Figs 1-2, 12-16, 39)

Cardium bechei Reeve, 1847: 25-26; A. Adams & Reeve, 1850: 78, pl. 22 fig. 12.

Laevicardium beechei [sic!] (Adams & Reeve) – H. Adams & A. Adams, 1857: 457.

Cardium (*Nemocardium*) *bechei* Reeve, 1847 – Otuka, 1937: 135-136, fig. 49a-b.

Nemocardium bechei (Reeve, 1840) – Wilson & Stevenson, 1977: pl. 1 figs 18-19 [non figs 15-17].

Keenaea bechei (Reeve, 1847) – Bernard et al., 1993: 72 [pars].

Nemocardium bechei (Reeve) – Hu & Tao, 1995: 183, pl. 104 fig. 1.

Nemocardium (*Nemocardium*) *bechei* (Reeve, 1847) – Higo et al., 1999: 473 [pars]; Ter Poorten, 2009: table 9, pl. 20 fig. 11, pl. 22 fig. 5a-c [non fig. 4]; Huber, 2010: 306, unnumbered fig.; Ter Poorten in Poppe, 2011: 232, pl. 1111 figs 1-2; La Perna & D'Abrama, 2011: fig. 1.

Nemocardium bechei (Reeve, 1847) – Robin, 2011, 197 fig. 2.

Type locality: 'Sooloo Seas, between the islands of Borneo and Mindanao' [Philippines, Sulu Sea], 40 fm [73 m] and Yellow Sea, Korean Archipelago. Leg. Capt. E. Belcher & A. Adams on Samarang, 1843-1846.
Type repository: NHMUK 1971.031, lectotype (designated by Wilson & Stevenson, 1977: 15, pl. 1 figs 18-19. Philippines, Ticao, coll. Cuming) [invalid]; UMZC i.100445, syntype (Bishop & Way, 1976: 44), herein designated as substitute lectotype (Fig. 12).

Description (modified after Ter Poorten, 2009: 80-81). – Shell rather large (L 45-66 mm), L about equals H (mean L/H ratio 0.99, range 0.94-1.04, n = 29), inflated (mean W ratio 1.37, range 1.32-1.43, n = 26), solid, ovately quadrate, and

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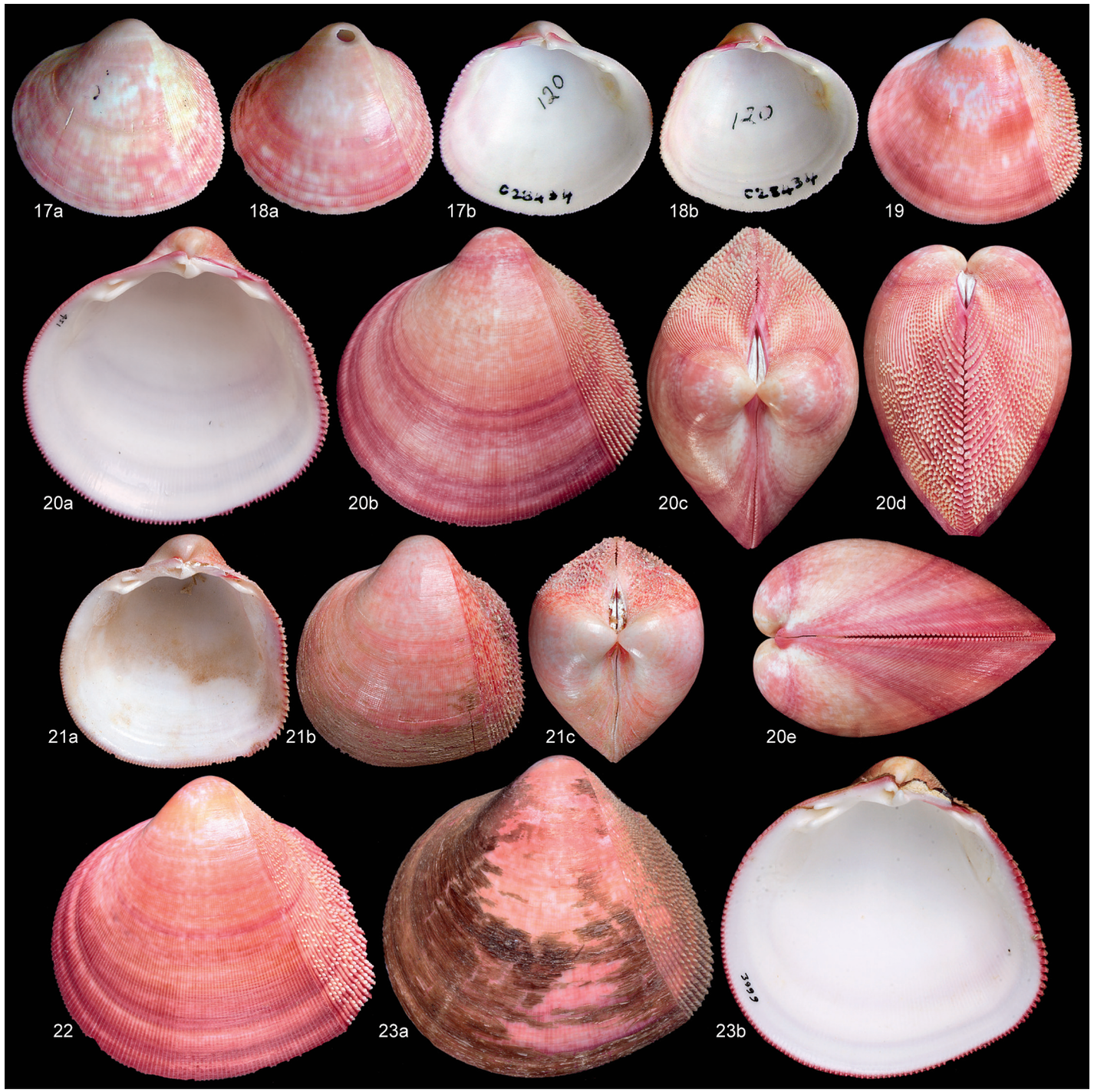
Figs 12-16. *Nemocardium bechei* (Reeve, 1847). **12a-d**, 'Sooloo Seas, between the islands of Borneo and Mindanao' [Philippines, Sulu Sea], 40 fm [73 m], Leg. E. Belcher & A. Adams, *Samarang*, 1843-1846. UMZC i.100445, lectotype, H 50.8 mm (a: RV exterior, b: RV interior, c: posterior view, d: UMZC label. Photos: courtesy Jamie Gundry). **13a-c**, Unknown provenance, ex Wilson & Stevenson, 1971: pl. 1 figs 18-19. NHMUK 1971.031, H 41.3 mm (a: LV exterior, b: posterior view, c: dorsal view. Photos courtesy Harry Taylor, NHMUK). **14**, Philippines, Balicasag Island, tangle nets, 80 m, 04.2008, ex Ter Poorten, 2009: pl. 22 fig. 5a-c. JJTP 3602, H 62.0 mm, LV exterior. **15**, Philippines, Panglao Island, tangle nets, 50-100 m, 04.2013. JJTP 4236, H 50.3 mm, LV exterior. **16a-c**, Philippines, Bantayan Island, local fishermen, c. 10-15 m, 2008. JJTP 3666, L 65.5 mm (a: LV exterior, b: RV exterior, c: RV interior).



nearly equilateral (AL slightly larger than PL). In adult specimens, ventral margin just anterior of radial ribbing commonly straight or slightly concave (Fig. 16). In RV, angle formed by tip of ventral laterals and posterior margin more than 90°. Anterior and median zone covering 70-75% of the shell, nearly smooth with numerous subsurface radial ribs and irregular commarginal striae (Fig. 39b); posterior zone with c. 26 radial ribs (mean 26.31, range 24-29, n = 30), carrying ventral-dorsally elongate spines (Fig. 39a); interstices smooth, rather broad and deep. Margins with c. 139-160 marginal crenulations, changing abruptly in size at postero-ventral junction, posteriorly wider and strongly serrate. Hinge typical for the genus, ventral anterior lateral tooth not or only slightly pointed downwards (Fig. 39c). In RV, ventral anterior lateral and posterior lateral approximately equidistant from posterior cardinal tooth. Lunule large and broad, lunular heart small, elevated and flattened on top, having transverse furrows in juveniles; escutcheon long and narrow. Exterior colour orange-brown or pink, darker towards the margins and on lunular heart, spines somewhat lighter. Interior white, umbonal cavity pale orange, posterior margin pink. Periostracum well developed and silky, consisting of commarginal lamellae, restricted to anterior zone and along postero-dorsal margin.

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Figs 17-23. *Nemocardium probatum* (Iredale, 1927). **17a-b**, Australia, New South Wales, Trial Bay [30°53'S, 153°4'E], 1908. AMS C28434, syntype, L 29.9 mm (a: LV exterior. b: LV interior). **18a-b**, Same locality, AMS C28434, syntype, L 27.0 mm (a: LV exterior, b: LV interior. Photos 17-18: courtesy AMS). **19**, Australia, Queensland, Bundaberg, trawled, 20 fm [36 m]. JJTP 3577, L 30.0 mm, LV exterior. **20a-e**, Australia, Queensland, Keppel Bay. JJTP 451, L 69.7 mm (a: RV interior, b: LV exterior, c: dorsal view, d: posterior view, e: anterior view). **21a-c**, Australia, Western Australia, off Mermaid Reef, 17°46'6S, 120°43'E, 97-109 m, 20.06.2007. Leg. C. Whisson & O. Gomez, CSIRO RV 'Southern Surveyor' Cruise, st. SS0507/097. WAM S32861, H 37.5 mm (a: RV interior, b: LV exterior, c: dorsal view). **22**, Australia, S. Queensland, off Mooloolabah, trawled, 150 m. JJTP 4043, L 63.1 mm, LV exterior. **23a-b**, Australia, N. Queensland, trawled, 80 m. JJTP 3999, L 72.2 mm (a: LV exterior, b: RV interior).

Distribution (Fig. 1). – Taiwan, Philippines and Indonesia. Bathymetric range: 10-155 m (dead; 10 m record based on dealer specimen). Records of Bernard et al. (1993) and Higo et al. (1999) from the South and East China Seas (no figures included) most probably refer to the currently defined concept of *N. bechei*, although Zhongyan (2004) and Xu & Zhang (2008) do not report the species from this area, nor do Hylleberg & Kilburn (2003) and Thach (2005, 2012) from Vietnam.

Remarks. – Petit (2007) demonstrated that the species should be attributed to Reeve (1847), rather than A. Adams & Reeve (1850).

Assuming that the two localities ('Sooloo Seas, between the islands of Borneo and Mindanao' [Sulu Sea, Philippines] and 'Yellow Sea, thirty degrees north, at one of the islands of the Korean Archipelago' mentioned in Reeve's (1847: 25-26) type description are correct, his two valves are a composite of two species, viz. *N. bechei* and *N. australojaponicum* spec. nov., respectively. Wilson & Stevenson (1977: 15, pl. 1 figs 18-19) designated NHMUK 1971.031 valve (L 40.6; H 41.3 mm; Fig. 13a-c) as lectotype of *Cardium bechei* Reeve: 'Lectotype (here selected) B.M.(N.H.) Cuming Collection. Ticao, Philippines. (x ¾)'; subsequently erroneously termed 'holotype' (Wilson & Stevenson, 1977: 62). However, this locality is not given by Reeve (1847), as Ticao Island is located north of Masbate Island in the central Philippines. From the title of Reeve's (1847) paper it follows that the material was collected by 'Capt. Sir Edward Belcher and Mr. [A.] Adams during the voyage of H.M.S. Samarang' and not by the famous Hugh Cuming (1791-1865). Lacking any data regarding the provenance, the NHMUK 1971.031 valve cannot be formally traced to the original publication (ICZN, 1999: Art. 74.2). Hence, Wilson & Stevenson's (1977) lectotype designation is considered invalid. The subadult, rather worn valve, in all probability represents *N. bechei*. The image given by Adams & Reeve (1850: pl. 22 fig. 12), although roughly in agreement, is not necessarily identical, judging the positions of the darker colored commarginal bands.

In addition, UMZC i.100445 represents an alleged syntype to which the Philippine locality does fit: 'Sooloo Seas between Mindanao and Borneo', written in pencil inside the

shell. It originates from the collection of Jane Saul (1807-1895) and it is additionally inscribed within in pencil 'Belcher /21.3.48.' in her handwriting, indicating that it was purchased from Sir Edward Belcher and so is an original specimen collected during the Samarang expedition. Dance (1966: 212) recorded the sale of some of Belcher's shells to Reeve, and Saul presumably bought some also. The specimen was bequeathed to the UMZC collection in 1895 (Bishop & Way, 1976). In order to settle the taxonomic confusion, the UMZC i.100445 syntype is herein designated as a substitute lectotype of *Cardium bechei* Reeve, 1847, representing a right valve (H 50.8, L 49.1 mm, 25 posterior ribs; Fig. 12a-c).

Nemocardium bechei proves to be confined to a relatively small area in the tropical West Pacific, not occurring up to central Japan as hitherto believed. It therefore can no longer be considered a tropical 'bridge species' (Jablonski et al., 2013), referring to an evolutionary lineage that straddles the boundary between the tropics and temperate neighboring regions.

Material examined. – **Taiwan** (JJTP 2256, 1 p.v.); Peng Hu Isls., by local diver, 2006 (JJTP 3852, 1 p.v.); 01.1973, colln L. De Lanoy-Meijer de Geer (RMNH. MOL.119654, 1 p.v.); SE. part, trawled offshore, on sand (EK 73.1, 2 p.v.); SW. part, trawled, 20-40 m (EK 2433.2, 2 p.v.). **Philippines**, Masbate Isl. (JJTP 67, 1 p.v.; 2658, 1 p.v.); Bantayan Isl., trawled offshore, 40-50 m (EK 1297.3, 3 p.v.); Bantayan Isl., by local fishermen, c. 10-15 m, 2008 (JJTP 3666, 1 p.v.); Bantayan Isl., 10-50 m (MH QQ258, 1 p.v.); Leyte Isl., offshore, trawled, 50-60 m (EK 1298.1, 1 p.v.); Cebu Isl., by local people, 12.1999 (JJTP 1106, 3 p.v.); Panglao Isl., tangle nets, 50-100 m, 04.2013 (JJTP 4236, 2 p.v.); Panglao Isl., trawled, 60 m (EK 841.3, 3 p.v.); Bohol Isl., Balicasag Isl., tangle nets, 80 m, 04.2008 (JJTP 3602, 1 p.v.); Bohol Isl., Balicasag Isl., tangle nets (MH QQ258.1, 1 p.v.); Sulu? (ZMA.MOLL.24272, ex coll. Samia Martin, 1 p.v.). **Indonesia**, N.E. Taka bone Rate (Tiger Isls.), S. of Pulau Tarupa Kecil, 6°31.6'S, 121°07.5'E, sandy bottom with calcareous nodules, 58 m, 3.5 m Agassiz trawl, 17.10.1984, 'Tyro' Indonesian-Dutch Snellius-II Exped. st. S4.234 (RMNH.MOL.80866, 1 s.v.); E. of Komodo, Teluk Slawi, 8°36.8'S, 119°30.7'E, coarse yellow sand with shell gravel, 65 m, van Veen grab, 17.ix.1984, 'Tyro' Indonesian-Dutch Snellius-II Exped. st. S4.075 (RMNH.MOL.119652, 1 s.v.); 8°29'S 119°38.2'E, small calcareous nodules, echinoderms, sponges, 81 m, rectangular dredge, 19.ix.1984, 'Tyro' Indonesian-Dutch Snellius-II Exped. st. S4.099 (RMNH.MOL.119653, 1 s.v.); NE. coast of Sumba, E. of Melolo, 9°54'S, 120°44.8'E, many calcareous stones & nodules, 125 m, rectangular dredge, 14.09.1984, 'Tyro' Indonesian-Dutch Snellius-II Exped. st. S4.056 (RMNH.MOL.119650, 1 s.v.); 9°54'S, 120°45'E, shells, scarce epifauna, 145-155 m, rectangular dredge, 15.09.1984, 'Tyro' Indonesian-Dutch Snellius-II Exped. st. S4.063 (RMNH.MOL.119651, 1 s.v.).

Nemocardium probatum (Iredale, 1927) (Figs 1-2, 17-23, 40)

Laevicardium beechei [sic!] (Adams & Reeve, 1850) – Brazier, 1877: 306-307 [pars, Australian records].
Cardium (*Laevicardium*) *bechei* Ad. & Rve. – Melvill & Standen, 1899: 192.
Pratulum probatum Iredale, 1927: 333-334, pl. 46 fig. 8.
Pratulum probatum Iredale – Allan, 1950: 319, pl. 37 fig. 25; Rippingale & McMichael, 1961: 182, 187, pl. 26 fig. 8.
Nemocardium bechei (Reeve, 1840) – Wilson & Stevenson, 1977: 62-64, pl. 1 figs 15-17, text fig. 7 [non figs 18-19]; Taylor & Glover, 2004: 263.
Nemocardium (*Nemocardium*) *bechei* (Reeve, 1840) – Lamprell & Whitehead, 1992: no. 216.
Nemocardium (*Nemocardium*) *bechei* (Reeve, 1847), Australian form – Ter Poorten, 2009: 81, table 9.
Nemocardium (*Nemocardium*) *probatum* (T. Iredale, 1927) – Huber, 2010: 306, unnumbered fig.

Type locality: Australia, New South Wales, Trial Bay [30°53'S, 153°4'E], 1908.
Type repository: AMS C28434, two syntypes, unmatched valves (Hylleberg, 2004: 900, unnumbered figs; figs 17-18), L 29.9, H 26.6 mm and L 27.0, H 26.2 mm.

Description. – Shell very large (L 60-81 mm), L slightly higher than H (mean L/H ratio 1.03, range 0.99-1.06, n = 23); moderately inflated (mean W ratio 1.42, range 1.32-1.54, n = 20), almost equilateral (AL slightly larger than PL), ovately quadrate, with marked angular and pinched postero-ventral margin; relatively thin. In RV, angle formed by tip of ventral laterals and posterior margin more than 90°, often up to circa 110°. Anterior and median zone covering c. 75% of the shell, nearly smooth with numerous subsurface radial ribs and very fine, irregular commarginal striae (Fig. 40b); posterior zone with c. 28 quadrangular, prominent radial ribs

(mean 27.55, range 25-30, n = 22); carrying ventral-dorsally elongate spines (Fig. 40a), interstices smooth, rather broad and deep. Margins with c. 144-154 marginal crenulations, posteriorly wider and stronger. Hinge typical for the genus, ventral anterior lateral tooth rather thin and elongate, not pointed downwards (Fig. 40c). In RV, posterior lateral slightly closer to posterior cardinal than ventral anterior lateral tooth. Adductor muscle scars only shallowly impressed, about equal in size. Exterior colour pink, deep pink commarginal bands. marginally, with irregular patches of white in subadult stage, umbo cream or nearly white, spines yellowish. Interior, including umbonal cavity white, margins pink. Periostracum well developed, olive-green.

Distribution (Fig. 1). – Northern half of Australia, from Geraldton, Western Australia (Wilson & Stevenson, 1977) and Torres Strait, Queensland (Brazier, 1877; Melvill & Standen, 1899) to Trial Bay, northern New South Wales (syntypes of *N. probatum*). Bathymetric range: 36-150 m (dead).

Remarks. – Only a few earlier workers (i.e. Allan, 1950; Powell, 1958; Rippingale & McMichael, 1961) have considered *N. probatum* a distinct species; more recent workers (Wilson & Stevenson, 1977; Voskuil & Onverwagt, 1991; Lamprell & Whitehead, 1992; Poutiers, 1992; Schneider, 2002; Taylor & Glover, 2004) unequivocally have treated *N. probatum* as a junior synonym of *N. bechei*. However, as pointed out by Ter Poorten (2009), the two species can easily be differentiated by a series of characters, among which are differences in coloration, size, L/H ratio and inflation. The absence of records from the Northern Territory may be an artifact related to the inaccessibility of material rather than indicative of a disjunct distribution, as its continental shelf has been reasonably well collected (Ponder et al., 2002: 109, table 2.1). Notable differences in size between Western and eastern Australian populations appear to exist, with WA specimens remaining significantly smaller. According to Aaron Cosgrove-Wilke (e-mail 18.04.2013) the largest WA valves in the WAM collection, based on a sample number of 60 (the majority containing 1-2 valves), are the following: Shark Bay, N. of Dirk Hartog Island, L 54.8 mm (WAM S82698); Pilbara coast, L 54.6 mm (WAM S82699). In contrast, specimens from East Australia attain lengths of over 80 mm (SH; Iredale, 1927). This merits additional study.

Keen's (1950: 28) inclusion of *Nemocardium probatum* in subgenus *Pratulum* is remarkable and seems to have taken place inadvertently given the inclusion of '… no sharp change in sculpture at the umbonal angle or ridge' in her definition of *Pratulum* (Keen, 1950: 24). It is obvious that *N. probatum* does not belong in *Pratulum*. *Cardium* (*Protocardium*) *antisemigranulatum* McCoy, 1877 (Poutiers, 1992: fig. 2e) from the Fyansford Formation, Fyansford, central coastal Victoria, Australia may be its most direct ancestor. It is of Balcombian age (Middle Miocene, probably Langhian Stage; e-mail 19.09.2013 T. Darragh to A.G. Beu). Hedley (1902: 288) already noted that this species is 'barely separable' from *C. bechei* originating from New South Wales (= *N. probatum*).

Material examined. – **Australia, Western Australia**, Rowley Shoals, off Mermaid Reef, 17°46'6.23"S, 120°43'9.12"E to 17°45'56.87"S, 120°42'56.51"E, 97-109 m, 20.06.2007. Leg. C. Whisson & O. Gomez, CSIRO RV 'Southern Surveyor' Cruise, st. SS0507/097 (WAM S32861, 1 p.v.); Rowley Shoals, Imperieuse Reef L23, 18.4602°S, 120.1447°E to 18.462°S, 120.1447°E, 80-81 m. 19.06.2007. Leg. C. Whisson & O. Gomez, CSIRO RV 'Southern Surveyor' Cruise, st. SS0507/082 (WAM S32865, 4 s.v.); Rowley Shoals, off Mermaid Reef, 17.7605°S, 120.7111°E, 110 m, 19.06.2007. Leg. C. Whisson & O. Gomez, CSIRO RV 'Southern Surveyor' Cruise, st. SS0507/089 (WAM S32869, 1 s.v.); off Onslow, L19, 20°12'14.76"S, 115°8'20.75"E to 20°12'8.28"S, 115°8'15.71"E, 100 m, 11.06.2007. Leg. C. Whisson, CSIRO RV 'Southern Surveyor' Cruise, st. SS0507/018 (WAM S32870, 1 s.v.)

Australia, Queensland, (EK 2430.1, 1 p.v.); 27 fm. [49 m] (EK 2431.2, 2 p.v.); N. Queensland, trawled, 80 m (JJTP 3999, 1 p.v.); Yeppoon, trawled, alive (JJTP 4209, 1 p.v.); Wheeler Cay, Keppel Bay, 20 fm. [36 m] (ZMA.MOLL.214617, ex coll. P. Hessel 34228, 2 p.v.); Keppel Bay, trawled offshore, 27 fm. [49 m], 12.1972. (ZMA.MOLL.421038, ex coll. P.A. Gillissen 381, 1 p.v.); Keppel Bay, trawled offshore, (ZMA.MOLL. 421038, ex coll. J. van der Dussen, 1 p.v.); Keppel Bay, before 1980 (JJTP 451, 2 p.v.); Keppel Bay, 26 fm [48 m] (MH QQ256, 1 p.v.); Lady Musgrave Isl., trawled, 150 m (MH QQ256.1, 1 p.v.); Capricorn Channel, trawled, up to 70 fm. [128 m] (EK 1907.1, 1 p.v.); Hervey Bay, Bundaberg, trawled, 20 fm [36 m] (JJTP 3577, 3 p.v.; JJTP 3891, 2 p.v.); Fraser Isl., trawled (JJTP 4044, 1 p.v.); Tin Can Bay, trawled (SH, 1 p.v.); off Mooloolabah, trawled, 150 m (JJTP 4043, 2 p.v.)

Nemocardium australojaponicum spec. nov.
(Figs 1-2, 24-27, 41)

Cardium bechei Adams et Reeve – Dunker, 1882: 212-213, pl. 15 figs 1-3.
Cardium (*Nemocardium*) *beckei* [sic!] Reeve – Hirase, 1938: 17, pl. 30 fig. 8.
Cardium (*Nemocardium*) *bechei* Reeve – Hirase & Taki, 1954: 113, pl. 30 fig. 8.
Nemocardium bechei (Reeve) – Kira, 1954: 108, pl. 54 fig. 18; Kira, 1959: 137, pl. 54 fig. 18; Kira, 1962: 155, pl. 55 fig. 18; Habe, 1970: 148, pl. 55 fig. 14.
Nemocardium bechei – Okutani & Takemura, 1967: 177, unnumbered plate, fig. 3; ? Ko et al., 2012: 213.
Nemocardium bechei (Reeve, 1947 [sic!]) – Koyama et al., 1981: 113.
Nemocardium bechei (Reeve, 1847) – Habe & Kosuge, 1970: 151, pl. 58 fig. 8; Abbott & Dance, 1982: 330, unnumbered fig.; Okutani et al., 1989: 112, unnumbered fig.; Matsukuma et al., 1991: 186, pl. 145 fig. 6; Matsukuma, 2000: 955, pl. 475 fig. 27 [juvenile figured]; Kwon et al., 2001: 249, figs 1000-1, 1000-2; ? Noseworthy et al., 2007: 97 [pars]; ? Le et al., 2010: 43.
Nemocardium (*Nemocardium*) *bechei* (Reeve, 1847) – Kuroda et al., 1971: 401, 623, pl. 88 fig. 8; Schneider, 1995: figs 9c-d; 2002: figs 6b, 16a (ANSP 252661); Higo et al., 1999: 473 [pars]; Lee & Min, 2002: 162; Min et al., 2004: 431, figs 1412-1, 1412-2.
Nemocardium (*Nemocardium*) *bechei* (Reeve, 1847), Japanese form – Ter Poorten, 2009: 81, table 9.
Nemocardium (*Nemocardium*) sp. 1 – Huber, 2010: 306, unnumbered fig.

Description. – Shell large (H 60-76 mm), L smaller than H (mean L/H ratio 0.93, range 0.88-0.98, n= 22), inflated (mean W ratio 1.36, range 1.30-1.41, n = 19) and rather inequilateral (AL much larger than PL), truncated posteriorly. In RV, angle formed by tip of ventral laterals and posterior margin just over 90°. Anterior and median zone covering 75-80% of the shell, nearly smooth with numerous subsurface radial ribs and fine, irregular commarginal striae (Fig. 41b); posterior zone circa 25 low rounded, rather well developed, radial ribs (mean 24.92, range 23-28, n = 25), carrying ventral-dorsally slightly elongate, rather blunt spines (Fig. 41a); interstices smooth and shallow. Margins with c. 141-160 marginal crenulations, posteriorly wider and stronger. Hinge typical for the genus, ventral anterior lateral tooth hardly or not pointed downwards (Fig. 41c). In RV, posterior lateral closer to posterior cardinal than ventral anterior lateral tooth. Exterior colour, including early juvenile stage, light salmon pink with darker collars. Interior white, umbonal cavity pale orange or white, posterior margin light pink. Periostracum prominent, dark olive-green.

Distribution (Fig. 1). – Southern part of Honshu, Japan, from Boso Peninsula (Koyama et al., 1981; Higo et al., 1999; Matsukuma, 2000) to Kyushu, and southern South Korea (Reeve, 1847; Kwon et al., 2001; Lee & Min, 2002; Min et al., 2004; Noseworthy et al., 2007; Le et al., 2010; Ko et al., 2012). Bathymetric range: 36-60 m (alive); 30-80 m (dead).

Etymology. – The specific epithet refers to the Latin word *australe*, meaning 'southern' and *japonicum*, a transliteration of the Latin *Iaponia*, Japan, the country from where the species is principally reported.

Remarks. – The largest recorded specimen has a height of 76 mm (Hirase, 1938: 17, pl. 30 fig. 8; Hirase & Taki, 1954: 113, pl. 30 fig. 8). Le et al. (2010: 43) reported *N. bechei* from Jeju Island, Korea where it lives 'in sandy areas at a subtidal depth of 20-40 m. The shell, which has a length of about 7 cm, is orange with one side having sharp, well-developed projections. The mantle cavity and thick foot are also orange.' The figures in Kwon et al. (2001) and Min et al. (2004), originating from Jeju Island, confirm that they refer to *N. australojaponicum* spec. nov.
Apart from *Nemocardium bechei*, Keen (1973) mentioned the following 5 fossil Japanese species attributed to *Nemocardium* (s.s.), type material of most of these has been figured

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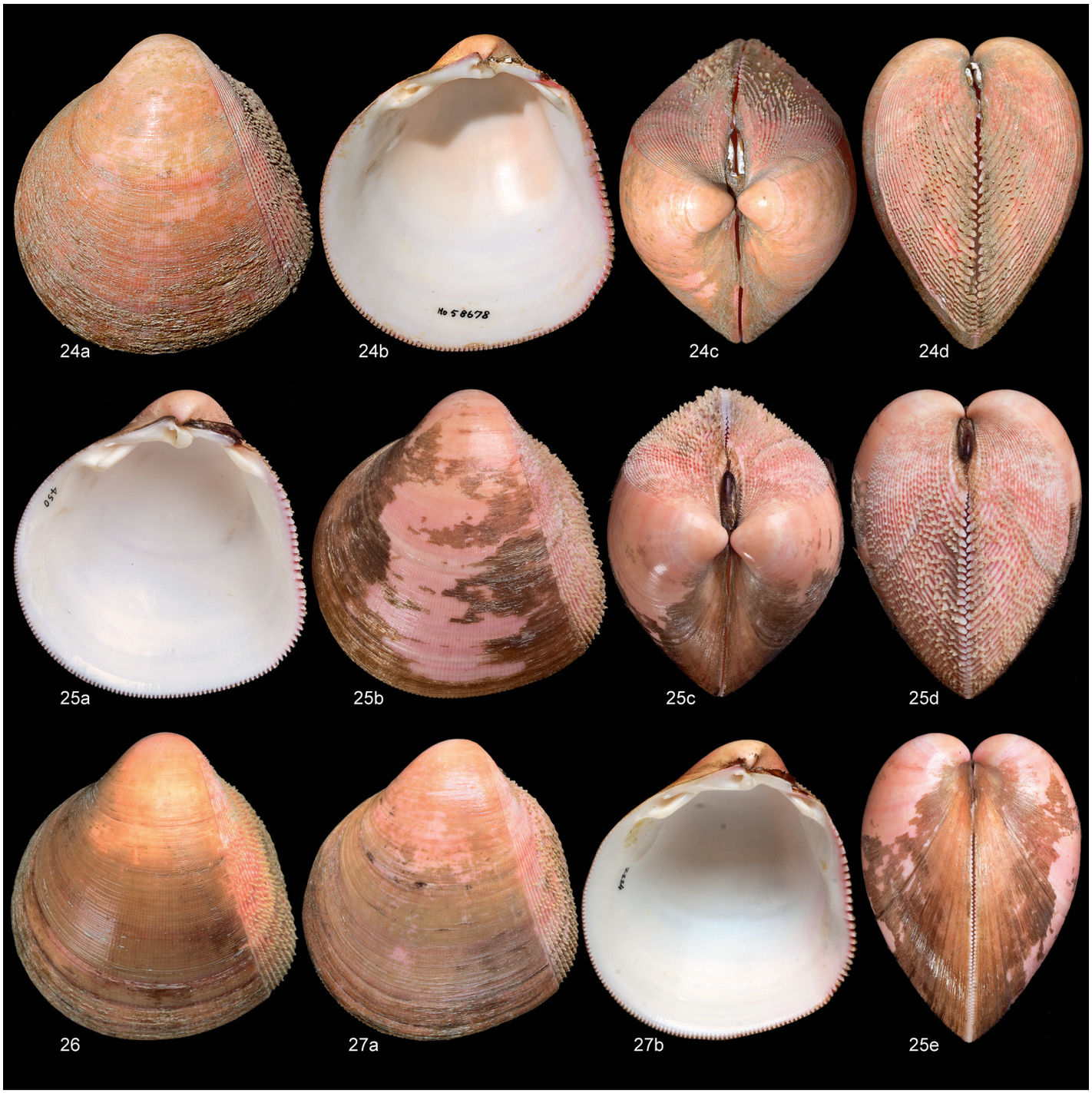
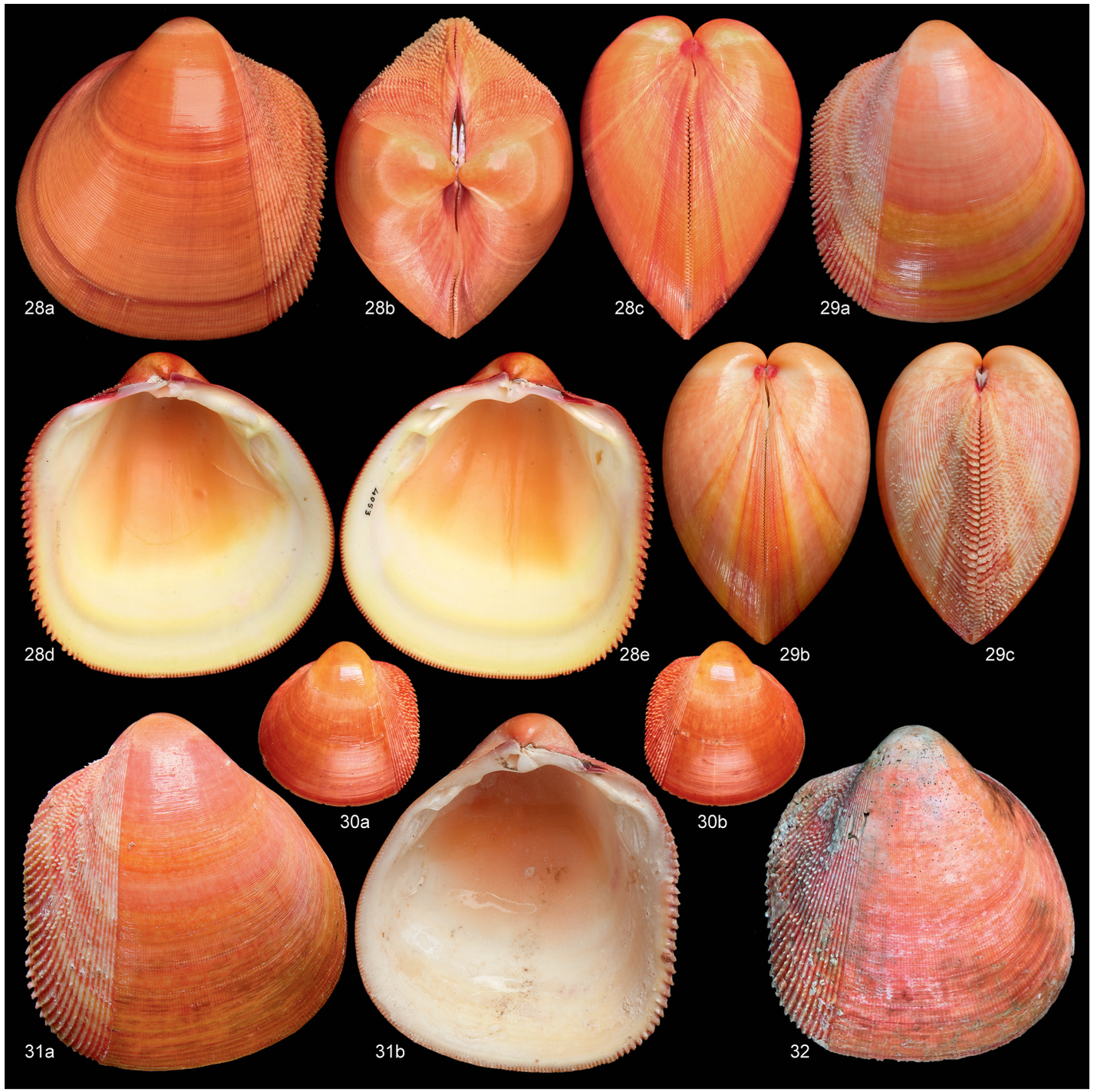
Figs 24-27. *Nemocardium australojaponicum* spec. nov. **24a-d**, Japan, Kyushu, Fukuoka Pref., Genkai Nada, off Fukuoka, Summer 1977, leg. A. Matsukuma. NSMT-Mo 58678, holotype, H 65.5 mm (a: LV exterior, b: RV interior, c: dorsal view, d: posterior view; photos courtesy Hiroshi Saito, NSMT). **25a-e**, Japan, Honshu, Aichi Pref., Mikawa Wan. JJTP 450, paratype, H 61.1 mm (a: RV interior, b: LV exterior, c: dorsal view, d: posterior view, e: anterior view). **26**, Japan, Honshu, Wakayama Pref., Minabe, from fisherman, 30-40 m, Spring 2000. JJTP 1810, paratype, H 65.1 mm, LV exterior. **27a-b**, Japan, Shikoku Isl. JJTP 2224, paratype, H 63.8 mm (a: LV exterior, b: RV interior).





by Oyama et al. (1960); repositories are found in Ichikawa (1983):

Nemocardium ezoense Takeda, 1953, Lower Oligocene of Japan. L/H ratio >1 (Oyama et al., 1960), <1 (Honda, 1989), c. 20 posterior ribs, trigonal outline.

Nemocardium iwakiense (Makiyama, 1934), Upper Oligocene of Japan. L/H ratio >1, c. 18-20 posterior ribs.

N. toriii (Nomura, 1933), Miocene-Pliocene of Taiwan. L/H ratio = 1, c. 15 posterior ribs.

Nemocardium yatsushiroense Hayami, 1965, Lower Cretaceous of Japan. L/H ratio >1, > 40 posterior ribs.

Nemocardium yokoyamai Takeda, 1953, Upper Oligocene of South Sakhalin. L/H ratio >1.

Morphometrics and geological data from Oyama et al. (1960), Hayami (1975), Honda (1989) and Terabe & Matsuoka (2009). Based on outline, posterior rib number and L/H ratio it is obvious that *Nemocardium australojaponicum* spec. nov. is not conspecific with one of these taxa. *N. ezoense* and *N. yokoyamai* were placed in subgenus *Arctopratulum* Keen, 1954 (Keen, 1954: 318) but subsequently retained in *Nemocardium* s.s. (Keen, 1973: 3). Kafanov & Amano (1996) demonstrated that *N. karaftoense* Krishtofovich, 1954 is a junior synonym of *N. yokoyamai*.

Additionally, the following Japanese and South-East Russian taxa have been assigned to *Nemocardium*, all of which differ from *N. australojaponicum* spec. nov.

Nemocardium khomenkoi Kafanov & Ogasawara in Kafanov et al., 1999, Upper Miocene of Sakhalin, Russia. L/H ratio <1 but the holotype is strongly inequilateral and only 10-12 posterior ribs are present.

Protocardia koshikijimensis Amano, 1957, Upper Cretaceous (Santonian (?)-Campanian) of Japan. Original generic assignment followed by Keen (1973), but transferred to *Nemocardium* by Hayami (1975). Placed by Tashiro (1976: 66-67, pl. 11 figs 1-3) in *Protocardia* (s.l.); his figures do not allow for a definite generic assignment.

Nemocardium nodaense Scheremetjeva, 1977 (ex Krishtofovich, MS), Takaradayskaya Suite (= Lower Oligocene – Kafanov & Amano, 1996: table 1) of South Sakhalin, Russia. L/H ratio >1, 20 posterior ribs. Lectotype (Scheremetjeva, 1977: pl. 19 figs 1-1a; selected by Kafanov et al., 2001) represents *N.* cf. *kovatschense* Krishtofovich, 1947 (Kafanov et al., 2001).

Nemocardium takaradaiense Scheremetjeva, 1977, Takaradayskaya Suite (Lower) of South Sakhalin, Russia. L/H ratio >1, 20 posterior ribs.

Type series and other material examined. – **Japan** (FMNH 82321, 1 p.v., **paratype**; FMNH 169014, 1 p.v., **paratype**; RMNH.MOL.119657, ex coll. J. Mulder, 1 p.v., **paratype**); 1963 (ZMA.MOLL.185845, ex coll. H.H. Kool, 1 p.v., **paratype**); E. side, ex coll. Van der Peijl (RMNH.MOL.119655, 1 p.v., **paratype**); Kyushu, Fukuoka Pref., Genkai Nada, off Fukuoka, Summer 1977, leg. A. Matsukuma (NSMT-Mo 58678, **holotype**); Honshu, Aichi Pref., Mikawa Wan, before 1977 (JJTP 450, 1 p.v., **paratype**); Wakayama Pref., from fishing net for lobsters, 1991 (JJTP 214, 1 p.v.); Minabe, from fishermen, in net, 30-40 m, Spring 2000 (JJTP 1810, 1 p.v., **paratype**); Minabe, 20-30 fm [36-54 m], alive, 1988 (JJTP 2227, 1 p.v.); Kii Suido (EK 157.3, 3 p.v.); off Nada, trawled 20-40 fm [36-72 m] (EK 681.1, 1 p.v.; EK 681.2, 3 p.v.); Nada, trawled, 42-80 m (MH QQ11, 1 p.v.); Nada, 20-40 fm [36-72 m] (MH QQ11.1, 2 p.v.); Nada, trawled, 20-40 fm [36-72 m], sandy bottom, 04.1985 (ZMA.MOLL.10020, ex coll. N. Koekkoek 1275, 1 p.v., **paratype**); Nada, trawled, 20-40 fm [36-72 m], leg. S. Akita, 1980 (JJTP 2225, 1 p.v.); W. Hondo, fished offshore, 1902 (RMNH.MOL.119656, ex coll. D. Smits, 1 p.v., **paratype**); Minabe-cho, gill nets, 40-60 m, alive, 04.1998 (JJTP 3074, 1 p.v.); Shikoku Isl., alive (JJTP 2224, 1 p.v., **paratype**); Kochi Pref., Tosa Bay (EK 2432.2, 2 p.v.); Tosa (ANSP 252661, ex coll. A.R. Cahn, 4 p.v., **paratypes**); unknown Pref., Nada Iohan, dredged, 30-60 m (JJTP 3440, 1 p.v.).

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Figs 28-32. *Nemocardium fulvum* spec. nov. **28a-e**, India, S.E. part, Tamil Nadu, off Colachel, trawled by fishermen, 70-125 m, 08.2011. MNHN 26377, holotype, H 69.2 mm (a: LV exterior, b: dorsal view, c: anterior view, d: LV interior, e: RV interior). **29a-c**, Philippines, Mactan Island, on reef by local divers. EK 1406.1, paratype, H 67.9 mm (a: RV exterior, b: anterior view, c: posterior view). **30a-b**, Same locality as 28. JJTP 4053, paratype, H 31.4 mm (a: LV exterior, b: RV exterior). **31a-b**, Philippines, Balicasag Island, tangle nets and lumun lumun 'deep water', from fishermen, gift B. Oliveira, PMPB 2004 s/n, ex Ter Poorten, 2009: pl. 22 fig. 4. MNHN 26378, paratype, H 71.4 mm (a: RV exterior, b: RV interior). **32**, Seychelles, S.E. of Mahé, 4°46'S, 55°33'E, 45-50 m, 24.12.1992, NIOP-E, 'Tyro' Seychelles Expedition 1992/93, st. 742. RMNH.MOL.41402, paratype, H 59.3 mm, RV exterior.

Nemocardium fulvum spec. nov. (Figs 1-2, 28-32, 42)

? *Nemocardium bechei* (Reeve, 1847) – Tantanasiriwong, 1979: 9.

Nemocardium (*Nemocardium*) cf. *bechei* (Reeve, 1847) – Ter Poorten, 2009: 80-81, tables 9-11, pl. 22 fig. 4.

Description. – Shell large (H 60-72 mm), L smaller than H (mean L/H ratio 0.94, range 0.90-0.98, n= 15); inflated (mean W ratio 1.34, range 1.29-1.42, n = 15), almost equilateral (AL slightly larger than PL), quadrate with antero-dorsal margin steeply sloping, postero-dorsal margin distinctly quadrangular and posterior margin straight or very slightly concave. In RV, angle formed by tip of ventral laterals and posterior margin less than 90°. Anterior and median zone covering c. 75% of the shell, weakly anastomosing, regular placed commarginal cords on anterior slope (Fig. 42b), otherwise nearly smooth with numerous subsurface radial ribs; posterior zone with c. 30 rounded, rather well developed radial ribs (mean 29.76, range 26-37, n = 25), carrying relatively small, ventral-dorsally elongate spines (Fig. 42a); interstices smooth and shallow. Margins with c. 160-185 marginal crenulations, posteriorly much more pronounced and digitate. Hinge typical for the genus, ventral anterior lateral tooth robust and pointed downwards (Fig. 42c, arrow). In RV, ventral anterior lateral and posterior lateral approximately equidistant from posterior cardinal tooth. Anterior adductor muscle scar slightly sunken, bordered by a radial depression. Exterior colour, including umbo, deep orange-brown, generally a few yellow-orange collars present. Interior white to lemon-yellow, umbonal cavity orange and margins orange-brown. Periostracum well developed, dark olive-green.

Distribution (Fig. 1). – So far known from Mozambique, Madagascar, Seychelles, India, Philippines and Vanuatu. Bathymetric range: 70-125 m (alive); 10-102 m (dead). Tantanasiriwong (1979: 9) reported *Nemocardium bechei,* 'dredged from sandy mud bottom at a depth of 80 metres' off Phuket and surrounding offshore islands, W. Thailand. This record may refer to *N. fulvum* spec. nov.

Etymology. – The specific epithet refers to the colour: the Latin word *fulvus* meaning reddish yellow, gold colored; referring to the yellow-orange collars and the yellow-orange interior of the shell.

Remarks. – Interestingly, *Nemocardium fulvum* spec. nov. has a much wider longitudinal range than all other *Nemocardium* species under discussion, occurring sympatrically with *N. bechei* in the Philippines and Indonesia. Nevertheless, over its range it is quite uniform as far as shell shape and coloration are concerned. Contrary to its congeners, the characteristic outline remains about the same during ontogeny, rendering it the most easily recognizable species.

Cardium (*Nemocardium*) *bhagothorense* Vredenburg, 1928, from the post-Eocene (= Lower to Upper Oligocene; Kachhara et al., 2012) of NW India (currently SE Pakistan), can be easily differentiated by having a L/H ratio of c. 1 and by the presence of rather well-developed commarginal ribbing on the anterior and median part of the shell, in particular close to the margins.

Laevicardium bechei Reeve sensu Pannekoek (1936: 68-69, pl. 4 figs 50, 50a) from the Lower Miocene of Java, Indonesia, much more closely agrees with *N. fulvum* spec. nov. than with *N. bechei*. The cited material (RGM 5492, RGM 794164; Figs 9-11) was studied by the author and can be differentiated by the following characters: 39-40 posterior ribs separated by very narrow interstices; very tiny rib sculpture, tending to arise from rib flanks or interstices; postero-dorsal margin less markedly shouldered and posterior margin very strongly digitate. It probably represents an undescribed species and may well represent the most direct ancestor of *N. fulvum* spec. nov. Another cardiid from the Lower Miocene of Java, Indonesia, *Cardium* (*Nemocardium*) *jogjacartense* Martin, 1917, does not belong in *Nemocardium*. It may possibly be a *Fulvia*, although the poor preservation hampers identification severely.

Cardium (*Laevicardium*) *auberti* Abrard, 1946, from the Upper Miocene of Vanuatu, has a roughly similar outline. However, the holotype (MNHN.F.A26990, Figs 6a-c) has a much more weakly shouldered postero-dorsal margin, a much more strongly demarcated escutcheon and more pronounced, round tubercles on the posterior ribs. Also the morphometrics are somewhat different, being more elongate and inflated: H 52.0; L 46.4; W 40.5 mm; L/H 0.89; W ratio 1.21.

Type series and other material examined. – **Mozambique**, ca. 50 mi SE. of Beira, 20°30'S, 35°43'E, 62 m. A. Bruun st. 400c, shrimp tr., 03.10.1964

(USNM 718598, 2 s.v., **paratypes**).

Madagascar, S. part, secteur de Fort-Dauphin, 25°14.6'S, 47°09.1'E, 79-80 m, 29.04.2010. 'Nosy Be 11' ATIMO VATAE, st. CP3510 (MNHN 26372, 3 s.v., **paratypes**); 25°08.3'S, 47°09.1'E, 77 m, 08.05.2010. 'Nosy Be 11' ATIMO VATAE, st. CP3571 (MNHN 26373, 1 s.v., **paratype**); 25°11.7'S, 47°12.5'E, 75-77 m, 08.05.2010. 'Nosy Be 11' ATIMO VATAE, st. CP3572 (MNHN 26374, 1 s.v., **paratype**); 25°13.5'S, 47°13.8'E, 87-88 m, 08.05.2010. 'Nosy Be 11' ATIMO VATAE, st. CP3573 (MNHN 26375, 1 s.v., **paratype**); NW. part, Sud Cap Saint-Sébastien, 12°37.6'S, 48°26.0'E, MIRIKY St. CP 3205, 60-63 m. Leg. Bouchet, Richer & Puillandre, 29.06.2009 (MNHN 26376, 2 s.v., **paratypes**); Baie Mahajamba, 14°54.6'S, 46°55.5'E, MIRIKY St. CP 3280, 57-87 m. Leg. Bouchet, Rosado & Kantor, 13.07.2009 (MNHN 26657, 1 s.v., **paratype).**

Seychelles, W of Poivre atoll, soft bottom, 5°46'S 53°11'E, 57 m, 3.5 m Agassiz trawl, 01.01.1993, NIOP-E, 'Tyro' Seychelles Expedition 1992/93, SEY.778, st. 778 (RMNH.MOL. 41403, 1 s.v., **paratype**); SE. of Mahé, 4°46'S 55°33'E, 45-50 m, rectangular dredge (2x), 24.12.1992, NIOP-E, 'Tyro' Seychelles Expedition 1992/93, SEY.742, st. 742 (RMNH.MOL. 41402, 1 s.v., **paratype**).

India, SE. part, Tamil Nadu, off Colachel, trawled by fishermen, 70-125 m, 08.2011, alive (MNHN 26377, 1 p.v., **holotype**; JJTP 4053, 2 p.v., **paratypes**; JJTP 4167, 2 p.v., **paratypes**).

Philippines, Balicasag Isl., tangle nets and lumun lumun 'deep water', from fishermen, gift B. Olivera, 07.2004. PMBP 2004 s/n. (MNHN 26378, 2 s.v., **paratypes**); Panglao Isl., Bolod, mud and many sponges, 9°32.4'N, 123°47.3'E, 83-102 m, 30.05.2004. PMBP 2004, st. T1 (MNHN 26379, 1 s.v., **paratype**); Mactan Isl., on reef by local divers (EK 1406.1, 1 p.v., **paratype**); Mindanao, Zamboanga, 10-25 m, 2012 (JJTP 4306, 1 p.v., **paratype**).

Indonesia, Moluccas, off Tg. Tutuhuhur, Piru Bay, Ceram, 3°15'S, 128°8'E, 23-35 fm [42-64 m], 01.06.1970 WAM Mariel King Memorial Exp. 1970 (USNM 746591, 1 s.v., **paratype**).

Vanuatu, N.N.W. Mavéa Isl., 15°22.4'S, 167°12.6'E, 57-81 m, 27.09.2006. SANTO 2006 st. AT39 (MNHN 26380, 2 s.v., **paratypes**).

Nemocardium enigmaticum spec. nov.
(Figs 1-2, 33-38, 43)

Laevicardium beechei [sic!] (Adams & Reeve, 1850) – Brazier, 1877: 306-307 [pars, New Caledonian record].

Nemocardium (*Pratulum*) *probatum* Iredale, 1927 – Powell, 1958: 77.

Nemocardium bechei (Reeve, 1840) – Poutiers, 1992: fig. 2b (MNHN 26368).

? *Nemocardium bechei* (Reeve) – Brook, 1998: 198, table 5.

? *Nemocardium bechei* – Virly et al., 1998: 17, table 3.

Nemocardium bechei (Adams & Reeve, 1850) – Bouchet, 2002: 13, unnumbered fig. (MNHN 26371); Héros et al., 2007: 251.

Nemocardium bechei (Reeve, 1852) – Spencer et al., 2009: 198.

Description. – Shell large (H 55-68 mm), L smaller than H (mean L/H ratio 0.91, range 0.87-0.97, n= 21); strongly inflated (W ratio 1.23, range 1.16-1.31, n = 21), ovately rounded, very solid and slightly inequilateral (AL larger than PL). In RV, angle formed by tip of ventral laterals and posterior margin circa 90°. Beaks prominent, anterior and ventral margins rounded, posterior margin straight. Anterior and median zone covering c. 75% of the shell, anterior slope in adult stage commonly with relatively well developed, irregular commarginal ridges (Fig. 43b), otherwise smooth with numerous subsurface radial ribs; posterior zone with c. 28 posterior radial ribs (mean 27.64, range 24-31, n = 27), carrying relatively pronounced, blunt tubercles (Fig. 43a); interstices smooth and rather shallow. Margins with c. 138-150 marginal crenulations, posteriorly wider and stronger. Hinge typical for the genus, solid, with cardinal teeth separated by a deep and wide anterior cardinal socket (Fig. 43c, arrow a); hinge plate relatively broad, ventral anterior lateral tooth robust and markedly pointed downwards (Fig. 43c, arrow b). In RV, posterior lateral closer to posterior cardinal than ventral anterior lateral tooth. Anterior adductor muscle scar slightly sunken and ventrally somewhat elevated in adult shells (Fig. 43c, arrow c). Exterior colour reddish-brown, early juvenile stage white, sharply demarcated. Interior white, except for reddish-brown posterior marginal area and deep pink marking below nymph plate. Periostracum well developed, dark olive-green.

Distribution (Fig. 1). – So far known from islands east of Australia: Lord Howe Island, Norfolk Ridge, Chesterfield-Bellona Plateau, New Caledonia, the Loyalty Islands and the Kermadec Islands. Bathymetric range: 30-121 m (alive); 11-960 m (dead).

Etymology. – The specific epithet refers to the enigmatic nature of the species: only known from localities in the Southwest Pacific, in combination with the limited availability of well preserved, adult material.

Remarks. – The species occupies a niche at the southern edge of the Indo-Pacific faunal province, adjacent to the intermediate zone with the temperate Southern Australia faunal province. The location of this border being somewhat arbitrary, part of this region between latitudes 24°S and 33°S may be considered subtropical (Brook, 1998). Exemplary is Lord Howe Island, located circa 31°33'S, which has the most southerly coral reef in the world (Ponder et al., 2002). *Nemocardium fulvum* spec. nov. is known from relatively nearby Vanuatu which, however, is biogeographically separated from New Caledonia by the New Hebrides Trench. A similar deep barrier, the Tasman Sea Basin, exists between Lord Howe Island and mainland New South Wales, where *N. probatum* occurs.

Powell (1958) recorded juvenile specimens of *N. probatum* from the Kermadec Islands (Raoul Island) and Norfolk Island with a maximum H of only 14.7 mm. Given the localities and the examined NMNZ material from the Kermadecs, these records can only refer to juveniles of *N. enigmaticum* spec. nov. It seems likely that Early Pleistocene records of *N. bechei* from the northern Kermadec Islands (Brook, 1998: table 5) refer to *N. enigmaticum* spec. nov. The Kermadec Islands record of "*Nemocardium* sp. (NZOI T256)" in Spencer et al. (2009) has been identified as *Microcardium trapezoidale* Poutiers, 2006 (B. Marshall, in lit. 04.2013).

Brazier (1877) reported a specimen from Bulari Passage [Passe de Boulari], southern New Caledonia in the stomach of a snapper, *Pagrus unicolor* (Quoy & Gaimard, 1824), currently known as *Chrysophrys auratus* (Forster, 1801).

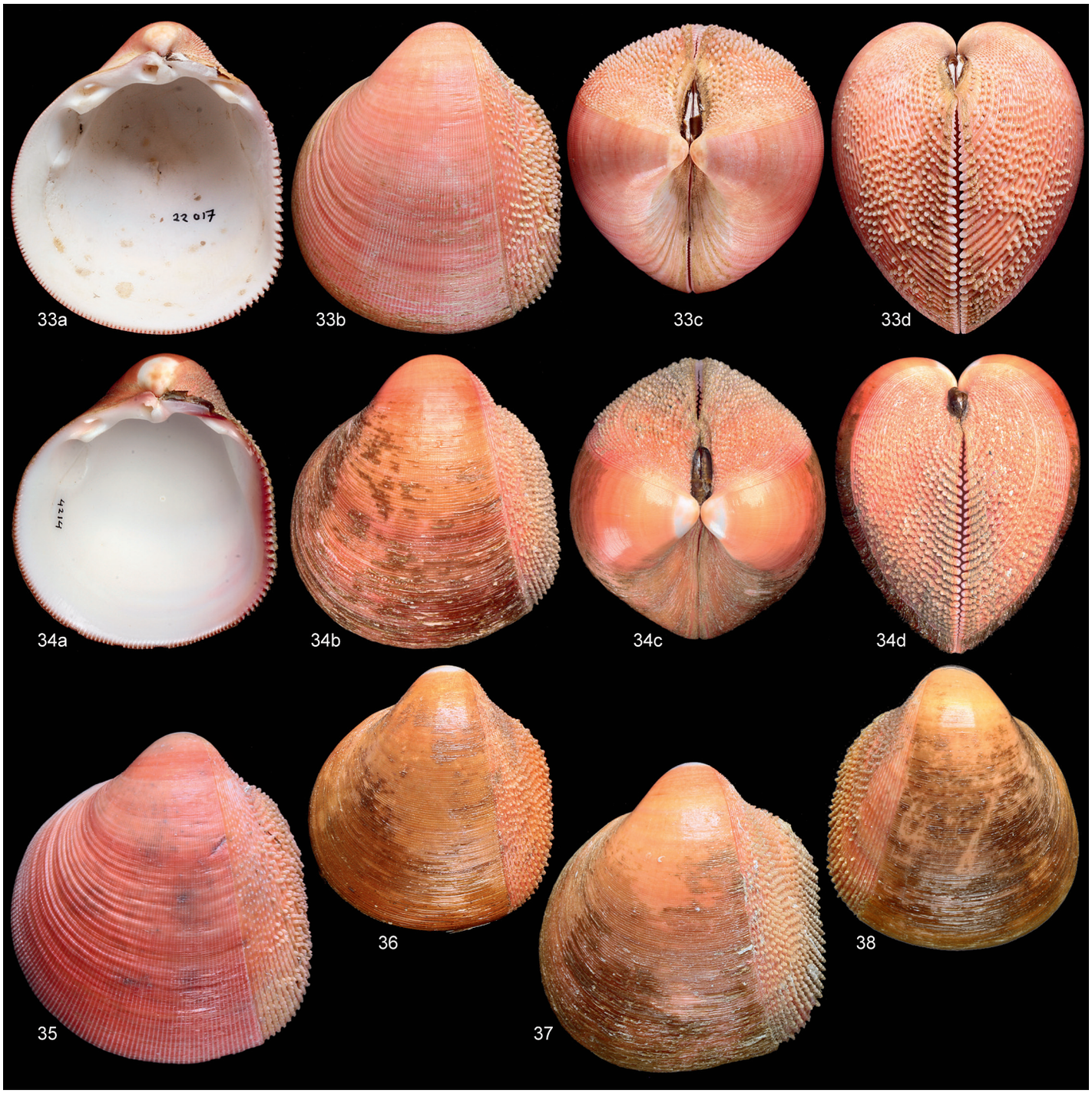
Nemocardium patulum (Hutton, 1873) (Figs 5a-d), from the Upper Oligocene - Middle Miocene of New Zealand, is very close to *N. enigmaticum spec*. nov. but can be differentiated by a larger size (L up to c. 120 mm – Boreham, 1965), the rib sculpture consisting of minute tubercles present on the anterior edges of the juvenile stage, the extremely thick shell, and the more prominent nature of the commarginal ridges on the anterior slope. It could well represent the most direct ancestor of *N. enigmaticum* spec. nov. The poorly known species *Nemocardium serum* (Hutton, 1873), from the Upper Oligocene of New Zealand, is very similar to *N. patulum*; it apparently differs only in its smaller size (H < 65 mm) and its slightly less rounded shell. It may not be distinct (Beu & Raine, 2009).

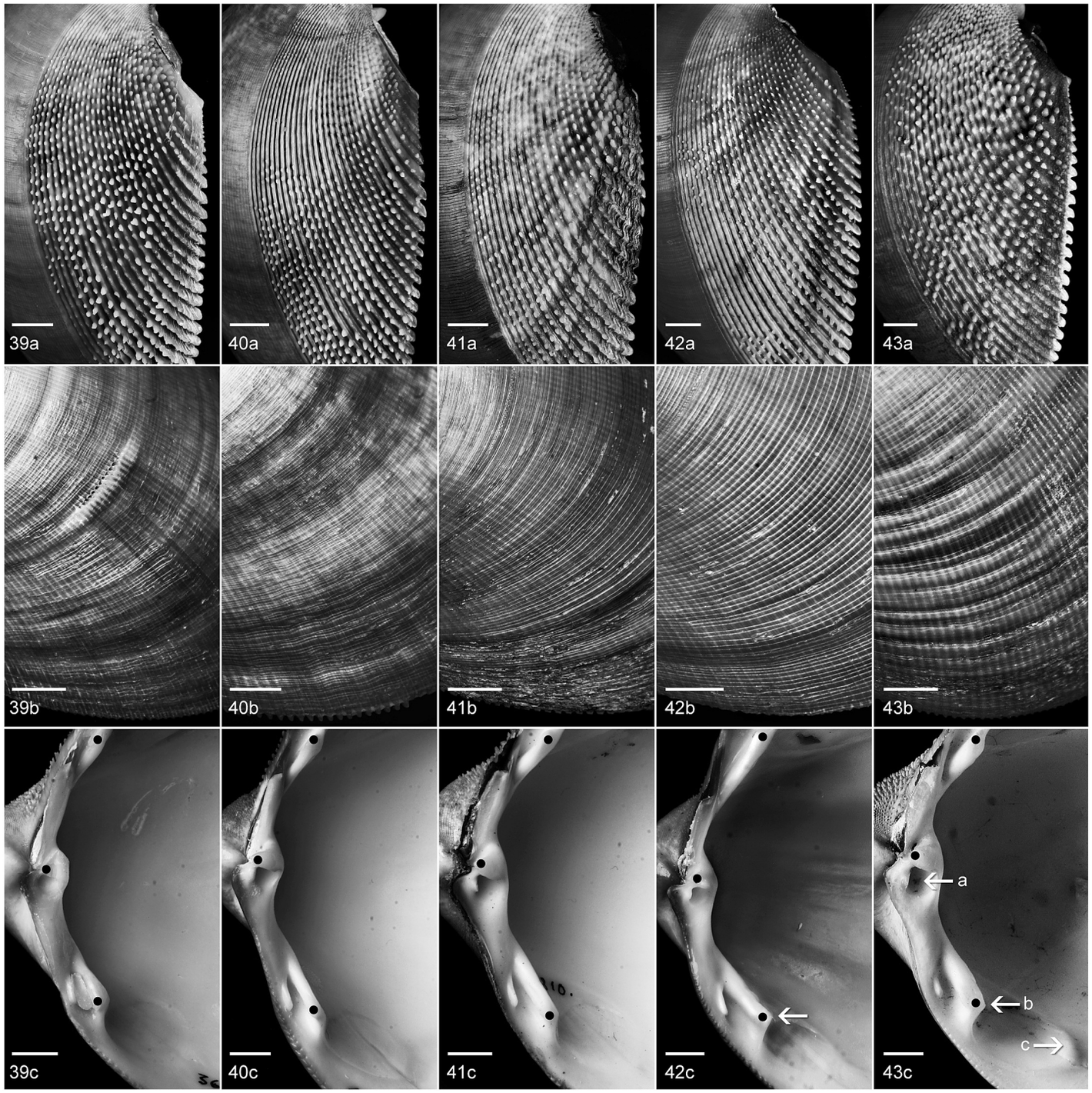
Type series and other material examined. – **Australia**, New South Wales, N. side of Lord Howe Isl., Admirality Group of Isls., 31°30'S, 159°04'E, on sand, 30 m. Leg. H. Morrison, 07.2012 (TP 4214, 1 p.v., **paratype**); off Lord Howe Isl., 31°45.73'S, 159°20.93'E, 565-960 m, RV *Tangaroa*, st. 2003066, 23.05.2003 (NMNZ M.171156, 7 s.v., **paratypes**); West Norfolk Ridge, Wanganella Bank, summit, 32°32.20'S, 167°30.70'E, 113 m, 29.01.1981, RV *Tangaroa*, st. 1981883 (NMNZ M.242735, 3 s.v., **paratypes**).

New Caledonia, Chesterfield-Bellona Plateau, 19°18'S, 158°34'E, 50 m, 23.07.1988, CORAIL 2, RV *Coriolis* st. DW50 (MNHN 26364, 1 p.v., **paratype**); 20°46'25S, 158°41'64E, 70 m, 12-31.07.1984, CHALCAL 1, RV *Coriolis* st. D48 (MNHN, 1 s.v.); 12-31.07.1984, CHALCAL 1, RV *Coriolis*, no st. number (MNHN, 1 s.v.); 21°03'S, 158°36'E, 352-370 m, 12.10.2005, EBISCO, RV *Alis* st. DW2553 (MNHN, 1 s.v.); Lansdowne-Fairway, 20°36'09S, 161°05'82E, 87 m, 12-31.07.1984, CHALCAL 1, RV *Coriolis* st. D10 (MNHN, 1 s.v.); 20°56'S, 161°41'E, 59 m, 20.07.1988, CORAIL 2, RV *Coriolis* st. DW01 (MNHN, 1 s.v.); 20°50'S, 161°37'E, 62 m, 20.07.1988, CORAIL 2, RV *Coriolis* st. DW02 (MNHN, 2 s.v.); 20°52'S, 161°37'E, 64 m, 20.07.1988, CORAIL 2, RV *Coriolis* st. DW04 (MNHN, 5 s.v.); 20°53'S, 161°35'E, 62 m, 20.07.1988, CORAIL 2, RV *Coriolis* st. DW09 (MNHN, 2 s.v.); 20°52'S, 161°41'E, 60 m, 20.07.1988, CORAIL 2, RV *Coriolis* st.

(next page)

Figs 33-38. *Nemocardium enigmaticum* spec. nov. **33a-d**, New Zealand, Kermadec Islands, off Hutchison Bluff, Raoul Island, 29°13'S, 177°59'W, 84-113 m, 24.08.1972, RV *Acheron* st. 1972296. NMNZ M.222017, holotype, H 68.0 mm (a: RV interior, b: LV exterior, c: dorsal view, d: posterior view). **34a-d**, Australia, N. side of Lord Howe Island, Admirality Group of Islands, 31°30'S, 159°04'E, on sand, 30 m. Leg. H. Morisson, 07.2012. JJTP 4214, paratype, H 56.2 mm (a: RV interior, b: LV exterior, c: dorsal view, d: posterior view). **35**, Australia, off Lord Howe Island, 31°45.73'S, 159°20.93'E, 565-960 m, 23.05.2003, RV *Tangaroa* st. 2003066. NMNZ M.2220, paratype, H 61.9 mm, LV exterior. **36**, New Caledonia, Grand Récif Sud, 22°52'S, 167°00'E, 65 m, 17.07.1985, LAGON, RV *Vauban* st. 572. MNHN 26370, paratype, H 41.5 mm, LV exterior. **37**, New Caledonia, Lansdowne-Fairway Bank, 20°36'S, 161°02'E, 86 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. DW21. MNHN 26365, paratype, H 50.4 mm, LV exterior. **38**. New Caledonia, Lagon Nord, 19°09'S, 163°23'E, 61 m, 06.03.1985, LAGON, RV *Vauban* st. 536. MNHN 26367, paratype, H 49.3 mm, RV exterior.





DW10 (MNHN, 2 s.v.); 20°44'S, 161°00'E, 69 m, 21.07.1988, CORAIL 2, RV *Coriolis* st. DW18 (MNHN, 1 s.v.); 20°39'S, 161°01'E, 88 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. DW20 (MNHN, 1 s.v.); 20°36'S, 161°02'E, 86 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. DW21 (MNHN 26365, 1 p.v., **paratype**); 20°33'S, 161°01'E, 85-88 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. CP22 (MNHN 26366, 1 p.v., **paratype**); 20°31'S, 161°04'E, 80-83 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. CP23 (MNHN, 1 s.v.); 20°21'S, 160°59'E, 74-75 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. CP27 (MNHN, 2 s.v.); 20°31'S, 160°53'E, 79-84 m, 22.07.1988, CORAIL 2, RV *Coriolis* st. CP29 (MNHN, 1 s.v.); Lagon Nord, 19°08'S, 163°29'E, 65-120 m, 19.09.1985, LAGON, RV *Vauban* st. DW187 (MNHN 2 s.v.); 19°09'S, 163°23'E, 61 m, 06.03.1985, LAGON, RV *Vauban* st. DW536 (MNHN 26367, 1 p.v., alive, 1 s.v., **paratypes**); 19°06'4E, 163°10'0S, 50 m, 06.03.1985, LAGON, RV *Vauban* st. DW542 (MNHN 26368, 1 p.v., alive; figured by Poutiers, 1992: fig. 2b, **paratype**); Secteur des Belep, 19°10'S, 163°13'E, 55 m, 30.10.1989, LAGON, RV *Alis* st. DW1156 (MNHN, 2 s.v.); 19°10'S, 163°10'E, 48 m, 30.10.1989, LAGON, RV *Alis* st. DW1157 (MNHN, 2 s.v.); Secteur de Poum, 20°05'E, 163°48'E, 29 m, 03.05.1988, LAGON, RV *Alis* st. 1026 (MNHN, 1 s.v.); Secteur de Touho, 20°46'-20°47'S, 165°15'-165°16.5'E, 45-56 m, 09.1993, MONTROUZIER, st. 1261 (MNHN, 2 s.v.); Secteur de Poindimié, 21°12'S, 165°44'E, 37 m, 08.01.1987, LAGON, RV *Vauban* st. DW764 (MNHN, 1 s.v.); 20°57'S, 165°30'E, 30 m, 10.01.1987, LAGON, RV *Vauban* st. DW808 (MNHN 26369, 1 p.v., alive, **paratype**); 20°56'S, 165°28'E, 34 m, 10.01.1987, LAGON, RV *Vauban* st. DW809 (MNHN, 1 s.v.); Secteur de Canala, 21°29'S, 166°12'E, 57-41 m, 10.08.1986, LAGON, RV *Vauban* st. DW696 (MNHN, 2 s.v.); 21°22'S, 166°04'E, 39-40 m, 10.08.1986, LAGON, RV *Vauban* st. DW709 (MNHN, 2 s.v.); 21°19'S, 165°56'E, 41-43 m, 12.08.1986, LAGON, RV *Vauban* st. DW725 (MNHN, 2 p.v.); Secteur de Nouméa, 22°16'S, 166°32'E, 11 m, 09.11.1984, LAGON, RV *Vauban* st. DW290 (MNHN, 2 s.v.); Secteur de Yaté, 22°19'S, 167°06'E, 73-75 m, 05.08.1986, LAGON, RV *Vauban* st. DW598 (MNHN, 1 s.v.); 22°16'S, 167°05'E, 78-80 m, 05.08.1986, LAGON, RV *Vauban* st. DW603 (MNHN, 1 p.v.); 22°04'S, 166°58'E, 49 m, 05.08.1986, LAGON, RV *Vauban* st. DW617 (MNHN, 1 s.v.); 22°02'S, 166°56'E, 50-52 m, 06.08.1986, LAGON, RV *Vauban* st. DW620 (MNHN, 1 s.v.); 22°01'S, 166°53'E, 55-56 m, 06.08.1986, LAGON, RV *Vauban* st. DW621 (MNHN, 1 s.v.); 21°60'S, 166°52'E, 46-44 m, 06.08.1986, LAGON, RV *Vauban* st. DW624 (MNHN, 1 s.v.); 21°58'S, 166°53'E, 47-48 m, 06.08.1986, LAGON, RV *Vauban* st. DW626 (MNHN, 2 s.v.); 21°58'S, 166°48'E, 43 m, 06.08.1986, LAGON, RV *Vauban* st. DW631 (MNHN, 1 p.v.); 21°57'S, 166°50'E, 44-45 m, 06.08.1986, LAGON, RV *Vauban* st. DW632 (MNHN, 1 p.v.); Ile Ouen-Baie du Prony, 22°31'S, 166°28'E, 33 m, 21.08.1984, LAGON, RV *Vauban* st. DW80 (MNHN, 1 p.v., 1 s.v.); 22°31'S, 166°47'E, 44-55 m, 23.08.1984, LAGON, RV *Vauban* st. DW129 (MNHN, 1 s.v.); 22°32'S, 166°51'E, 60 m, 23.10.1984, RV *Vauban* st. DW234bis (MNHN, 1 p.v.); 22°24'S, 166°58'E, 43 m, 23.10.1984, LAGON, RV *Vauban* st. DW239 (MNHN, 1 p.v.); 22°21'S, 167°00'E, 35 m, 23.10.1984, LAGON, RV *Vauban* st. DW241 (MNHN, 1 p.v., alive); Grand Récif Sud, 22°43'S, 166°45'E, 38 m, 27.11.1984, LAGON, RV *Vauban* st. DW306 (MNHN, 1 s.v.); 22°44'S, 166°47'E, 36 m, 27.11.1984, LAGON, RV *Vauban* st. DW311 (MNHN, 1 s.v.); 22°24'S, 167°03'E, 39 m, 28.11.1984, LAGON, RV *Vauban* st. DW324 (MNHN, 1 p.v.; 2 s.v.); 22°38'S, 166°54'E, 47 m, 28.11.1984, LAGON, RV *Vauban* st. DW334 (MNHN, 1 p.v.); 22°42'S, 166°55'E, 45 m, 29.11.1984, LAGON, RV *Vauban* st. DW348 (MNHN, 1 s.v.); 22°40'S, 166°55'E, 55 m, 29.11.1984, LAGON, RV *Vauban* st. DW349 (MNHN, 2 s.v.); 22°34'S, 167°01'E, 70 m, 29.11.1984, LAGON, RV *Vauban* st. DW353 (MNHN, 1 s.v.); 22°31'S, 167°05'E, 50 m, 29.11.1984, LAGON, RV *Vauban* st. DW358 (MNHN, 1 p.v., alive); 22°33'S, 167°04'E, 74 m, 29.11.1984, LAGON, RV *Vauban* st. DW359 (MNHN, 1 s.v.); 22°39'S, 166°59'E, 67 m, 29.11.1984, LAGON, RV *Vauban* st. DW363 (MNHN, 1 s.v.); 22°35'S, 167°05'E, 70 m, 30.11.1984, LAGON, RV *Vauban* st. DW368 (MNHN, 1 p.v.); 22°28'S, 167°11'E, 52-57 m, 21.01.1985, LAGON, RV *Vauban* st. DW373 (MNHN, 3 s.v.); 22°36'S, 167°10'E, 75 m, 22.01.1985, LAGON, RV *Vauban* st. DW385 (MNHN, 1 s.v.); 22°35'S, 167°18'E, 45 m, 23.01.1985, LAGON, RV *Vauban* st. DW403 (MNHN, 2 s.v.); 22°37'S, 167°16'E, 60 m,

(previous page)

Figs 39-43. LV posterior slope, LV antero-ventral slope and RV hinge region of living *Nemocardium* species. **39a-c.** *Nemocardium bechei* (Reeve, 1847). Philippines, Balicasag Isl., tangle nets, 80 m, 04.2008 (ventral cardinal broken off). JJTP 3602. **40a-c.** *Nemocardium probatum* (Iredale, 1927). Australia, Queensland, Keppel Bay. JJTP 451. **41a-c.** *Nemocardium australojaponicum* spec. nov. Japan, Honshu, Wakayama Pref., Minabe, from fisherman, 30-40 m, Spring 2000. JJTP 1810, paratype. **42a-c.** *Nemocardium fulvum* spec. nov. India, S.E. part, Tamil Nadu, off Colachel, trawled by fishermen, 70-125 m, 08.2011. MNHN 26377, holotype. **43a-c.** *Nemocardium enigmaticum* spec. nov. New Zealand, Kermadec Islands, off Hutchison Bluff, Raoul Island, 29°13'S, 177°59'W, 84-113 m, 24.08.1972, RV *Acheron* st. 1972296. NMNZ M.222017, holotype. Scale bars: 5 mm. Black circles indicate position of ventral lateral and cardinal teeth; see text for explanation of arrows.

24.01.1985, LAGON, RV *Vauban* st. DW414 (MNHN, 1 p.v.); 22°43'S, 166°57'E, 48 m, 16.07.1985, LAGON, RV *Vauban* st. DW560 (MNHN, 1 p.v.); 22°44'S, 166°59'E, 48 m, 16.07.1985, LAGON, RV *Vauban* st. DW562 (MNHN, 1 p.v.); 22°50'S, 167°01'E, 53 m, 17.07.1985, LAGON, RV *Vauban* st. DW570 (MNHN, 1 s.v.); 22°52'S, 167°00'E, 65 m, 17.07.1985, LAGON, RV *Vauban* st. DW572 (MNHN 26370, 1 p.v., **paratype**); 23°00'S, 167°02'E, 50 m, 17.07.1985, LAGON, RV *Vauban* st. DW578 (MNHN, 1 p.v., alive).

Loyalty Islands, Santal Bay, Récif Shelter, 20°54.0'S, 167°02.1'E, dredged 100-120 m, 07/19/23.11.2000, LIFOU st. 1461 (MNHN 26371, 1 p.v.; figured by Bouchet, 2002: 13, **paratype**).

New Zealand, Kermadec Isls, N.W. of Fleetwood Bluff, Raoul Isl., 29°12.70'S, 177°56.10'W, 135 m, 25.10.1975, RV *Acheron*, st. 1975434 (NMNZ M.225420, 1 s.v., **paratype**); off Hutchison Bluff, Raoul Isl., 29°13.00'S, 177°59.00'W, 84-113 m, 24.08.1972, RV *Acheron*, st. 1972296 (NMNZ M.222017, 1 p.v., **holotype**, NMNZ M.310090, 1 s.v., **paratype**); S.E. of Nugent Isl., Raoul Isl., 29°14.70'S, 177°49.40'W, 146-165 m, 28.10.1975, RV *Acheron*, st. 1975438 (NMNZ M.225652, 2 p.v., **paratypes**); between Met. Station and Hutchison Bluff, Raoul Isl., 29°13.00'S, 177°55.80'W, 110-121 m, 04.04.1973, RV *Acheron*, st. 1973308 (NMNZ M.222139, 1 p.v., alive, with dried animal, **paratype**); S.E. of Smith Bluff, Raoul Isl., 29°18.90'S, 177°56.40'W, 82-100 m, 10.09.1976, RV *Acheron*, st. 1976572 (NMNZ M.226583, 1 s.v., **paratype**).

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