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The Cardiidae of the Panglao Marine Biodiversity Project 2004 and the Panglao 2005 Deep-Sea Cruise with descriptions of four new species (Bivalvia)

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'... an island of knowledge, located in an ocean of ignorance, surrounded by a beach full of interesting questions. The more science advances, the more the island grows, and with it the beach. As a result, you can increasingly play more, take longer walks, find more beautiful shells and delight in the breathtaking view'

Robbert Dijkgraaf, 'Blikwisselingen' [translated].

ABSTRACT

Sixty-three Cardiidae species (including Tridacninae) sampled by the 2004 Panglao Marine Biodiversity Project (PMBP) to Panglao, Philippines, and the PANGLAO 2005 Deep-Sea Cruise are described. In addition, Cardiidae species lists of the Philippine Cuming Tour 2005 and AURORA 2007 expedition are provided. Four species are new to science: *Fragum grasi* spec. nov., *Frigidocardium helios* spec. nov., *F. sancticaroli* spec. nov. and *Microcardium velatum* spec. nov. For the following six species this paper includes the first published records for the Philippines: *Acrosterigma dianthinum* (Melvill & Standen, 1899), *F. torresi* (E.A. Smith, 1885), *Fulvia* (*Laevifulvia*) *subquadrata* Vidal & Kirkendale, 2007, *Microfragum erugatum* (Tate, 1889), *M. subfestivum* (Vidal & Kirkendale, 2007) and *Vasticardium sewelli* (Prashad, 1932). Indo-Pacific range extensions for several other species are given. Ecological data support assignment of *Afrocardium* to Orthocardiinae. *Cardium* (*Ctenocardia*) *victor* Angas, 1872 and *Cardium bomasense* Martin, 1917 are transferred to *Freneixicardia*, the former being the sole extant representative of the genus, and of which *Cardium* (*Trachycardium*) *hulshofi* Pannekoek, 1936 is a new synonym. Based on shell morphology, it is shown that the current variously adopted generic assignments of *Cardium lobulatum* Deshayes, 1855, *C. attenuatum* G.B. Sowerby 2nd, 1841, *C. biradiatum* Bruguière, 1789 and *C. multipunctatum* G.B. Sowerby 1st in Broderip & Sowerby 2nd, 1833 are unsatisfactory. As a consequence, the alleged Indo-Pacific presence of the genus *Laevicardium* is questionable. *Fulvia* (*Laevifulvia*) *imperfecta* Vidal & Kirkendale, 2007 is a new synonym of "*Laevicardium*" *lobulatum* Deshayes, 1855. Habitat preferences of the taxa encountered during PMBP 2004 are defined, based on four main macro-habitat categories. SEM photos, showing the early ontogenetic stages, demonstrate markedly allomorphic growth of some taxa. Description of the process of development to the terminal shell shape provides a more complete species concept and rigorous species delimitation.

CONTENTS

INTRODUCTION

Quite a few currently recognised valid Cardiidae taxa, all either introduced in the mid 19th century or late 20th-early 21st century, have a Philippine type locality or are largely based on Philippine material: *Acrosterigma hobbsae* Vidal, 1999, *A. oxygonum* (G.B. Sowerby 2nd, 1834), *A. suduirauti* Vidal & Ter Poorten, 2007, *A. suluanum* Vidal, 1999, *A. variegatum* (G.B. Sowerby 2nd, 1840), *Fragum nivale* (Reeve, 1845), *Frigidocardium iris* Huber & Ter Poorten, 2007, *Fulvia* (*Fulvia*) *boholensis* Vidal, 1994, *F.* (*F.*) *colorata* Vidal & Kirkendale, 2007, *Hippopus porcellanus* Rosewater, 1982, *"Laevicardium" lobulatum* (Deshayes, 1855), *Lyrocardium lyratum* (G.B. Sowerby 2nd, 1840), *Microcardium aequiliratum* Poutiers, 1981, *M. tenuilamellosum* Poutiers, 1981, *Nemocardium* (*Nemocardium*) *bechei* (Reeve, 1847), *Vasticardium luteomarginatum* (Voskuil & Onverwagt, 1991), *V. mindanense* (Reeve, 1844), *V. papuanum* Vidal, 1996, *Vepricardium incarnatum* (Reeve, 1844), *V. multispinosum* (G.B. Sowerby 2nd, 1839) and *V. rubrohamatum* Voskuil & Onverwagt, 1988. The majority of the species described by G.B. Sowerby 2nd, L.A. Reeve and G.P.

Deshayes had been collected by the famous H. Cuming during his 1836-1840 voyage to the Philippine Islands. Only one of the above species, *Fragum nivale*, does not actually live in Philippine waters but is limited to the western Indian Ocean. The presence of *Vasticardium luteomarginatum* in the Philippines is doubtful.

Compared to that of several neighbouring countries the malacofauna of the Philippines is understudied. Although several expeditions collected in the Philippines, reviews or faunal lists containing Philippine Cardiidae are scarce. The first expedition after Cuming's voyage (*Samarang*, 1843-1846; treated by Adams & Reeve, 1850) resulted in a new cardiid described by Reeve (1847). Another expedition (*Challenger*, 1872-1876) visited the Philippines only briefly, leading to the report of Smith (1885) who lists 3 cardiids. The *Siboga* Expedition (1899-1900) focussed on Indonesia and only briefly sampled the Philippine Sulu archipelago, resulting in few cardiids (Prashad, 1932, Stns 93-110). Of the *Albatross* Philippine Expedition (1907-1910) there is no published survey that includes Cardiidae. Poutiers (1981) treated the bivalves of the 1976 MUSORSTOM 1 expedition to the bathyal zone and lower continental shelf of Lubang area, comprising 3 cardiids. For subsequent Philippine expeditions (MUSORSTOM 2, 1980, and 3, 1985 – primarily focussing on Crustacea) there is no published review of the Cardiidae. The 2005 Cuming Tour revealed 28 Cardiidae species (table 10) and the 2007 AURORA campaign resulted in 19 Cardiidae species (table 10). Material of the 2008 LUMIWAN expedition (Bouchet *et al*., 2008) is currently being processed. Of the three main Philippine molluscan overviews, Hidalgo (1903) gave exhaustive descriptions and references, treating 37 cardiids (+ 13 tridacnines) but still relied heavily on Cuming's material. Faustino (1928) treated 42 cardiids (+ 14 tridacnines), many of which are now considered synonymous. Springsteen & Leobrera (1986), not intending to be comprehensive and restricting their book to macromolluscs, discussed and depicted 19 cardiids (+7 tridacnines). With the recent publication of the first two of three planned volumes of 'Philippine marine mollusks' (Poppe, 2008a, 2008b) an extensive review reflecting our current state of knowledge – including Cardiidae, to be treated in the third volume (Ter Poorten, in press) – will finally be available.

In contrast with this relative lack of study, the family Cardiidae is one of the most diverse and widely distributed families of Bivalvia. Cardiids constitute one of the principal heteroconch families (Crame, 2000; 2002). Richer de Forges (1991: 63) calculated that cardiids occurred in 61.33% of the 481 dredge stations in the south-west lagoon of New Caledonia, ranked second after Veneridae. Among bivalves, Bouchet *et al*. (2002) mentioned 4,328 (9.5%) cardiid specimens (tridacnines included) from the Koumac coral reefs complex, surpassed only by Veneridae (11.0%) and Mytilidae (10.0%).

Compared to many other bivalve families, cardiids have recently received relatively greater attention, in the past two decades resulting in an illustrated and annotated bibliography with depictions of type material (Hylleberg, 2004); in reviews at the subfamily level (Kafanov, 1998a, 1998b, 1999, 2000, 2001, 2002, 2003, 2004; Nevesskaja *et al*., 2001) and genus level (Kafanov, 1997; Vidal, 1994, 1999a, 2000b; Voskuil & Onverwagt, 1991a, c); in phylogenetic studies (Benzie & Williams, 1998; Kirkendale, 2009; Mohamed *et al*., 2006; Nevesskaja *et al*., 2001; Schneider, 1992, 1995, 1998a, b, 2002; Schneider & Ó Foighil, 1999) and regional faunal surveys (Vidal & Kirkendale, 2007; Ter Poorten, 2007a). Consequently, many new taxa have been described. For instance, 18 of the cardiid species treated in this paper (including the ones described herein) have been introduced in the past 20 years, representing 28.5% of PMBP 2004 and PANGLAO 2005 Cardiidae. It is evident that with such a large number of new species, Indo-Pacific Cardiidae taxonomy is still far from settled and the true diversity underestimated.

Unfortunately, due to severe undersampling of large parts of the Indo-Pacific, this situation will be similar for most other molluscan families.

MATERIALS AND METHODS

The material examined for this study originates primarily from the Panglao Marine Biodiversity Project (PMBP) 2004 and the PANGLAO 2005 Deep-Sea Cruise (see Bouchet *et al*., 2009; Richer de Forges *et al*., 2009, for expedition reports and station lists). In cases of new species and range extensions, it is supplemented with material from various other institutions and private collections. Both PMBP 2004 and PANGLAO 2005 material is deposited in MNHN. Parts of it – including type material – will be housed in NMP (for acronyms, see below).

In addition, this regional monograph includes the Cardiidae of the 'Cuming Tour' (abbreviated CT) conducted by Rudo von Cosel in the footsteps of Hugh Cuming which surveyed many 'classical' Philippines localities, such as Negros, Marinduque, Mindanao, etc. Moreover, Cuming's sampling methods (restricted to intertidal sampling, beach combing and fish markets) were also adopted (R. von Cosel, unpublished notes). The species encountered, though not treated in the systematic part herein, are listed in table 10. CT 2005 resulted in 120 cardiid samples, representing 28 species. A similar approach has been followed for the second one, the Philippine AURORA 2007 expedition (48 samples, 19 species; table 10), as the area sampled (Pacific seaboard of Luzon) is far from the Panglao region (fig. 1).

PMBP 2004 cardiids (tables 10-11) were obtained using a range of sampling techniques: from shallow water by intertidal picking (stns M1-61), dive hand picking (stns R1-78), brushing dead coral and stones for epibenthos (stns B1-42), dredging (stns D1-16) and collecting sea bottom samples by suction sampling using a 'vacuum cleaner' (stns S1-53); and from deeper water by lumun lumun nets (stns L35-75), tangle nets (stns P1-7), trawling (stns T1-44) and grabbing (stn G1). The use of baited traps (stns N1-13), for obvious reasons did not yield any Cardiidae species. The bathymetric range inves-

tigated covers the intertidal zone and the continental shelf, essentially down to 150 m, sporadically to 210 m. One additional tangle net station (P2, from local fishermen) originated from a depth of 400 m but did not include any cardiids. In total, 320 stations were sampled (fig. 1, table 4) ranging from brackish mangrove habitats of the Abatan river mouth to a wide range of coral reef environments covering Panglao, Balicasag and Pamilacan Islands. A small additional fraction was obtained from local fishermen, operating in the immediate vicinity of Panglao, and is listed at the end of the material examined. Supplementary Panglao material collected during preparations for the expedition (October 2003) is also included (stns D15-16, G1, L51-75, M60-61, P6-7 and T43). Sampling of tridacnines was much restricted due to their protected status by Philippine law and their CITES listing. Therefore, the available samples do not provide a fair representation of their Panglao occurrence.

PANGLAO 2005 Cardiidae species (tables 10-11) were either trawled (CP stns) or dredged (DW stns). No cardiids were recovered using traps (CA stns). Sampling took place in the Bohol Sea waters around Panglao Island (off Balicasag Island, Pamilacan Island and Maribojoc Bay; fig. 1) to the eastern edge of the Sulu Sea (off Aliguay Island, Dipolog Bay) in depths of 64-2323 m (deepest cardiid sample 679-740 m).

All species are treated systematically; they are grouped by morphological similarity to allow easier comparison. Data on horizontal and vertical distribution and ecology are included, derived from reliable literature data with clearly identifiable photos, augmented with personally verified collection material. As needed, additional remarks are given. For each species a map is given showing the PMBP 2004 collecting stations at which the species was found; indicating the sampling method and whether recorded live or dead (solid and open symbols respectively). PANGLAO 2005 records are also shown, if falling within the map range. A legend of the symbols used is given in fig. 1. Maps of tridacnines have been omitted, due to their limited sampling. Photographs are provided for all species, whenever possible supplemented by SEM photographs showing early ontogeny.

The PMBP 2004 and PANGLAO 2005 stations are listed in alphabetical order (prefix showing sampling technique), and within this in numerical order (station number). For samples partly or completely taken alive an 'A' is included in brackets. Material processed for DNA analysis is indicated by 'DNA' in brackets. Bathymetric ranges are given separately for live taken and dead material, based on combined data from both expeditions, except in instances for which the differences between expeditions are considerable and unlikely to reflect the natural distribution. Synonymies are not intended to be exhaustive.

The terms small, medium and large are related to congeneric species. The height is measured along an axis perpendicular to the hinge, and the length is the greatest distance between anterior and posterior ends, parallel to the hinge. Shell measurements refer to the size of average mature specimens followed by those of unusually large adults. The term 'lunular heart' (proposed by Vidal, 1994) is used here in a broad sense for the variably raised process that may appear on the antero-dorsal margin just in front of the umbo, regardless of its true structure, which is highly variable among cardiid species. The length is given for species in which it exceeds the height and vice versa. The following depth designations are used: littoral (0-20 m), sublittoral (20-200 m) and upper bathyal (200-500 m).

The difficulty of resolving the correct year of publication of the numerous taxa introduced by G.B. Sowerby 1st, 2nd and 3rd has been treated excellently by Petit (2009). His views are followed here. Accordingly, the small plate explanation sheets that accompanied the cardiids depicted in *The Conchological Illustrations* (G.B. Sowerby 2nd, 1834; 1839; 1840) are considered to constitute a published work (I.C.Z.N., 2001: Article 8.1; Petit, 2009: 20), validly proposed 'in association with an illustration of the taxon being named' (I.C.Z.N., 2001: Article 12.2.7; pers. comm. G. Kronenberg, 08.2009).

ABBREVIATIONS

Acronyms of institutions and repositories

ANSP	Academy of Natural Sciences, Philadelphia, U.S.A.;
BMNH	The Natural History Museum, London, United Kingdom;
MH	Coll. M. Huber, Winterthur, Switzerland;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
NMP	National Museum of the Philippines, Manila, Philippines;
NMR	Natuurhistorisch Museum Rotterdam, The Netherlands;
NMSA	Natal Museum, Pietermaritzburg, Republic of South Africa;
RMNH	Nationaal Natuurhistorisch Museum Naturalis, Leiden, The Netherlands;
TP	Coll. J.J. ter Poorten, Hilversum, The Netherlands;
WAM	Western Australian Museum, Welshpool, Australia;
ZMA	Zoölogisch Museum Amsterdam, The Netherlands.

PMBP 2004 stations data

B	brushing;
D	dredge;
G	grabbing;
L	lumun lumun nets;
M	intertidal picking;
P	tangle nets;
R	dive hand picking;
S	suction sampling;
T	trawl;
s/n	station number lacking.

PMBP 2005 stations data

CP	beam trawl;
DW	Warén dredge.

Other abbreviations

A	sample found (partly) alive;
DNA	sample (partly) used for DNA processing;
H	height;
L	length;
lv, rv	left valve, right valve;
pv	paired valves;
v	valve(s);
W	width;
†	fossil taxon.

RESULTS

In total, 57 Cardiidae species (5 tridacnines included) consisting of 4383 specimens from 694 samples were recorded during PMBP 2004, which is about two-thirds of the total of 85 Cardiidae species presently known from the Philippine archipelago (Ter Poorten, in press and unpubl. data). Only two of these appear to be endemic to the Philippines, which agrees with the low rate of endemism reported by Springsteen & Leobrera (1986) and Vallejo (2003). Of the 320 stations 202 yielded cardiid material, of which 111 contained live material (table 4). Table 10 provides an overview of all taxa found with numbers of specimens and stations. For the sake of completeness Table 10 includes circa 8-10 adult valves of *Tridacna* (*Tridacna*) *gigas* (Linnaeus, 1758) that were observed north-west of Pamilacan Island (pers. comm. H. Dekker, 09.2008). These were not collected and so are not treated in the systematic part.

In total, 36 species were found alive (63%, table 10) with the adjacent stations D4 and D5 yielding the most live taken species (7 and 6 respectively). Only 3 species (5.8%) were recorded from one station only, 2 of them represented by only a single valve or a single complete specimen (3.8%; in both instances tridacnines not taken into account), which indicates that the spatial heterogeneity is adequately covered for this family. Nevertheless, despite the high internal heterogeneity a few habitats are lacking, including littoral fine mineral sand bottoms (pers. comm. R. von Cosel, 03.2008) and certain shallow soft-bottom types (pers. comm. P. Bouchet, 03.2007). This probably explains the absence of certain cardiids and the paucity of live specimens of a number of taxa. For instance, only few live *Fulvia* (*Laevifulvia*) *hungerfordi* (G.B. Sowerby 3rd, 1901) were taken, this species having a preference for protected muddy bottoms and occurring locally in high densities (Shin, 1985; Ter Poorten, 2007a).

Cardiid species diversity for six expeditions to tropical Indo-Pacific islands is shown in table 1. Apart from the sampling techniques, intensity, duration and depth range covered, several other variables including geology (paleoenvironmental changes, e.g. sea level fluctuations), hydrology (e.g. water temperature, salinity), geography (e.g. geographic location, island area) and ecology (e.g. quality and quantity of habitats), all to some degree influence diversity and hamper meaningful comparisons (Bouchet *et al*., 2002; Hoeksema, 2007; Bouchet *et al*., 2009).

For several reasons PMBP 2004 yielded by far the highest cardiid diversity. Keeping in mind the aforementioned limitations, it is obvious that the major sampling effort had a large influence on the diversity recorded when compared with Ambon, Guam, Raja Ampat Islands and Raoul. The Koumac expedition was on a more comparable scale. The geographic setting of Panglao, part of the Coral Triangle centre of marine biodiversity, also must have influenced the diversity recorded, which is supported by the fact that for Koumac the number of cardiid specimens collected, although hardly different from that for Panglao, nevertheless resulted in a much lower number of species, reflecting a lower species diversity and lower spatial heterogeneity. The outcome is roughly in line with the results for all molluscs, which show that Panglao hosts approximately 40% more species than Koumac (Bouchet, 2008). New Caledonian cardiid diversity includes 59 species: 54 mentioned by Héros *et al*. (2007) and Bouchet *et al*. (2008), supplemented by an additional 5 reported by Poutiers (2006) and Vidal & Kirkendale (2007). As the Indonesian cardiid diversity (80 species: Ter Poorten, 2007a: 263; this paper and unpubl. data) is similar to that of the Philippines (Ter Poorten, in prep.; unpublished data), it appears that the Philippine-Indonesian cardiid high diversity focus mirrors the general bivalve pattern as outlined by Crame (2000).

Despite this species richness, quite a few other Cardiidae taxa are known from Panglao or neighbouring islands, or were even described (partly) based on material from this area,

Island (location)	*Area investigated*	*Depth range covered*	*Reference*	*Cardiidae species (+Tridacninae)*	*Number of specimens*
Panglao (Philippines)	ca. 150 km^2	0-210 m	This paper	52 (+5)	4383
Koumac (New Caledonia)	ca. 300 km^2	0-120 m	Bouchet *et al.* (2002)	34 (+3)	4328
Ambon (Indonesia)	ca. 1000 km^2	0-28 m	Ter Poorten (2007a)	27 (+4)	667
Guam (Micronesia)	ca. 750 km^2	0-200 m	Paulay (2003)	25 (+4)	c. 1350
Raja Ampat Islands (Indonesia)	ca. 5000 km^2	0-40 m	Wells (2002)	14 (+7)	(not given)
Raoul (Kermadec Islands)	ca. 150 km^2	0-50 m	Brook & Marshall (1998)	1 (+0)	(not given)

Table 1. Cardiid species richness of several Indo-Pacific islands based on various expeditions. The area investigated is a rough estimate of the total area covered during the sampling period. For Panglao, PANGLAO 2005 material (6 additional species, 355 specimens) is not included because of the much larger area investigated and the sublittoral - upper bathyal depth range covered.

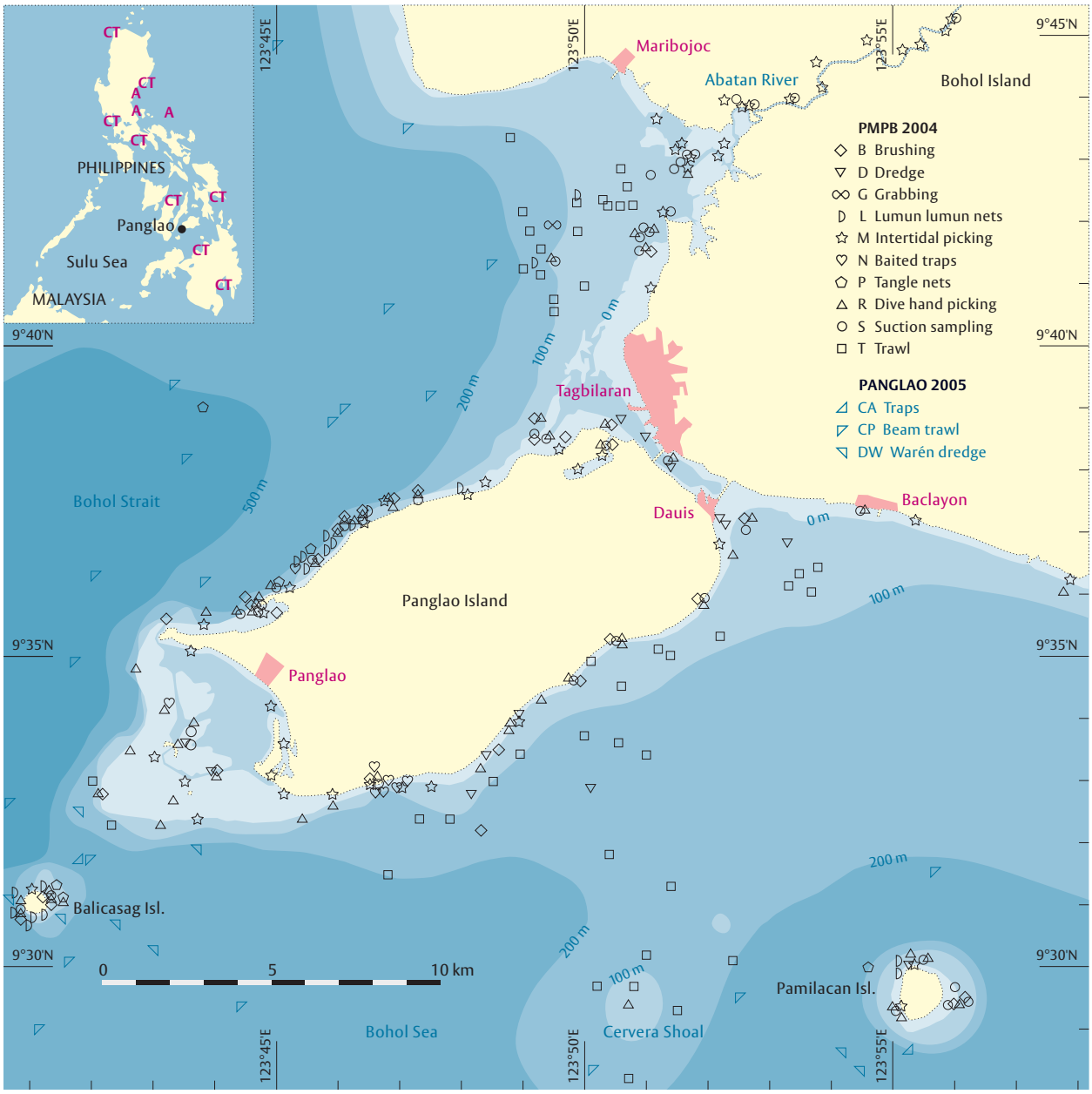


Fig. 1. Map showing the area investigated around Panglao, encompassing Balicasag and Pamilacan Islands with symbols showing all PMBP 2004 and PANGLAO 2005 stations (the latter insofar as they are covered by the geographic area of the map) and respective sampling techniques. Isobaths at 0, 100, 200 and 500 m (bathymetrics close to map edges not fully accurate due to unavailability of maps). The lightest shade of blue represents the intertidal zone (tidal amplitude approximately 1.4 m). Inset, Panglao's position in relation to the Philippines with sampling areas of Cuming Tour 2005 (CT) and AURORA 2007 (A) indicated in red.

but were not collected during the PMBP 2004 and PANGLAO 2005 expeditions. These are listed in table 2. The heterogeneous character of these species, as far as size, habitats and bathymetric range are concerned, indicates that it is not easy to point to particular deficiencies in the sampling methods used. Yet, two of these (*Acrosterigma suduirauti* Vidal & Ter Poorten, 2007; and *Vepricardium rubrohamatum* Voskuil & Onverwagt, 1988) are essentially found in tangle nets and dredged sublittorally, suggesting that if these sampling methods had been exploited more frequently, the total cardiid diversity recorded could have been even higher. The absence of *Fulvia* (*Fulvia*) *aperta* (Bruguière, 1789) may well be a result of lack of certain protected, muddy organic habitats, its preferred environment (Vidal, 1994; Ter Poorten, 2007a). Other striking PMBP 2004 and PANGLAO 2005 absentees are the common Philippine *Vasticardium elongatum elongatum* (Bruguière, 1789) and *Lyrocardium lyratum* (G.B. Sowerby 2nd, 1840). Given the general scope of both expeditions, more targeted surveys might have led to a different outcome.

The lack of certain taxa could reflect a discontinuous distribution pattern. It has been established that some extensively

Scientific name	*Source*	*Philippine localities*
Acrosterigma impolitum (G.B. Sowerby 2nd, 1834)	Coll. TP	Bohol Island
Acrosterigma suduirauti Vidal & Ter Poorten, 2007	Vidal & Ter Poorten (2007)	Balicasag Island
Acrosterigma variegatum (G.B. Sowerby 2nd, 1840)	Coll. TP	Olango Island
Fulvia (*Fulvia*) *aperta* (Bruguière, 1789)	Coll. TP	Mactan Island
Lunulicardia retusa (Linnaeus, 1767)	Coll. TP	Bohol Island
Lyrocardium aurantiacum (Adams & Reeve, 1850)	Coll. TP	Balicasag Island, Bohol Island
Lyrocardium lyratum (G.B. Sowerby 2nd, 1840)	Coll. TP	Bohol Island, south-east Negros Island
Maoricardium setosum (Redfield, 1846)	Coll. G.T. Poppe	Olango Island
Vasticardium elongatum elongatum (Bruguière, 1789)	Coll. TP	Calitoban Island, Mactan Island
Vepricardium rubrohamatum Voskuil & Onverwagt, 1988	Coll. TP	Panglao Island

Table 2. Cardiid species known from Panglao or adjacent islands that were not recorded during PMBP 2004 and PANGLAO 2005. Records only labelled 'Cebu' are considered too general and are not taken into account.

Scientific name	*Expedition*	*Philippine localities*
Acrosterigma impolitum (G.B. Sowerby 2nd, 1834)	CT	Luzon (Manila Bay)
Fulvia (*Fulvia*) *aperta* (Bruguière, 1789)	CT	Luzon (Bataan Peninsula, Manila Bay, Tayabas Bay)
Lunulicardia retusa (Linnaeus, 1767)	AURORA	East Luzon
Lyrocardium aurantiacum (Adams & Reeve, 1850)	AURORA	East Luzon
Lyrocardium lyratum (G.B. Sowerby 2nd, 1840)	AURORA	East Luzon
Maoricardium pseudolatum Voskuil & Onverwagt, 1991	CT	Marinduque Island, Luzon (Bataan Peninsula, Laoag area, Casiguran area, Manila Bay, Tayabas Bay)
Microcardium spec. nov.	AURORA	East Luzon
Vasticardium elongatum elongatum (Bruguière, 1789)	CT	Luzon (Bataan Peninsula, Casiguran area)
Vasticardium mindanense (Reeve, 1844)	CT	Luzon (Bataan Peninsula, Casiguran area); Marinduque Island
Vasticardium spec. nov.	CT	Luzon (Manila Bay)

Table 3. Cardiid species of the Philippine Cuming Tour 2005 (CT) and AURORA 2007 (material in MNHN) that were not recorded during PMBP 2004 and PANGLAO 2005. See table 10 for a complete listing of the species recorded.

collected molluscan species that have wide Indo-Pacific ranges have narrow ranges within the Philippines, showing basin localized and disjunct distributions (Springsteen & Leobrera, 1986; Vallejo, 2003). Regarding *Maoricardium pseudolatum* Voskuil & Onverwagt, 1991 and *Vasticardium mindanense* (Reeve, 1844), the numerous finds of the Cuming Tour 2005 are all confined to Luzon and Marinduque Island. However, more targeted sampling will be needed for confirmation and for a more reliable assessment of their distributions. In table 3 the CT 2005 and AURORA 2007 cardiids that were not encountered during PMBP 2004 and PANGLAO 2005 are listed.

Of the three PMBP 2004 / PANGLAO 2005 species collected in the highest numbers (all at least circa 500 specimens/valves), viz. *Fragum sueziense* (Issel, 1869) *Frigidocardium sancticaroli* spec. nov. and *Fragum grasi* spec. nov., nearly all material is from death assemblages, suggesting that their preferred habitat had not been sampled. Maybe the sampling methods employed were inappropriate for these species or possibly they occurred temporarily in low densities locally due to seasonal or long-term fluctuations in recruitment. Surprisingly, two of these apparently locally common species still proved to be undescribed.

The various sampling techniques used showed large differences in numbers of samples, species and specimens. Despite the littoral occurrence of many cardiid species, intertidal picking resulted in small numbers, sampled at relatively few stations (19 M stns in total), probably partly resulting from overexploitation by local people (pers. comm. H. Dekker, 02.2008 – PMBP 2004 participant, heading intertidal collecting group). Use of various Philippine cardiids for consumption and the local shellcraft industry is documented by Sotto & von Cosel (1982), Gomez & Alcala (1988) and Poutiers (1998). Supplementary data provided by J.-M. Poutiers (pers. comm., 06.2009) are included herein. The most productive methods in terms of both numbers of species and numbers of specimens were B, D, S and T, of which S stands out, being highly rewarding (table 4).

For the PMBP 2004 Cardiidae species four main types of distribution can be distinguished, coinciding with four macrohabitat categories:

	PMBP 2004 sampling method	*Total number of stations*	*Number of stations (%) with cardiids*	*Number of stations (%) with live cardiidspecimens*	*Number of cardiid samples*	*Number of cardiid species*
B	brushing	41	36 (**88**)	17 (41)	91	22
D	dredge	16	13 (81)	10 (**63**)	70	29
G	grabbing	1	1(100)	0 (0)	4	4
L	lumun lumun nets	21	10 (48)	7 (33)	21	9
M	intertidal picking	59	19 (32)	8 (14)	63	17
N	baited traps	13	0 (0)	0 (0)	0	0
P	tangle nets	6	3 (50)	0 (0)	8	5
R	dive hand picking	**67**	**47 (**70)	26 (39)	103	22
S	suction sampling	52	39 (75)	**28 (**54)	**195**	**36**
T	trawl	44	34 (77)	15 (34)	127	29
s/n	stn nr. lacking	–	– (–)	– (–)	12	12
	Total / mean	320	202 (63)	111 (35)	694	57

Table 4. PMBP 2004 sampling techniques related to numbers and percentages of sampled Cardiidae species. Highest number / percentages in bold type (results of the sole G station not taken into consideration). Merging of data from certain stations has been taken into account.

A Distribution restricted to perireefal environments, surrounding large parts of Panglao, Balicasag and Pamilacan Islands. Essentially oceanic habitats exposed to full wave action, mainly consisting of sand and coral rubble; littoral, occasionally extending sublittorally (e.g. *Vasticardium pectiniforme*).

B Distribution restricted to the sheltered Panglao lagoon, Tagbilaran-Panglao channel and Abatan River mouth. Lagoonal/estuarine habitats of mud and sand bottoms with extensive seagrass, sporadic mangroves and few coral heads; littoral (e.g. *Fragum unedo*).

C Distribution restricted to offshore sand, muddy sand and mud bottoms (occasionally with sponges) north and south-east of Panglao including the Cervera Shoal. Mostly trawled, dredged, taken by lumun lumun or tangle nets; sublittoral and upper bathyal (e.g. *Microcardium aequiliratum*).

D Distribution restricted to semi-sheltered muddy areas off Abatan River mouth and, to a lesser extent, east of Panglao. Transitional B-C habitat; the majority with fine-grained sediments (fine sand, silt and mud); essentially littoral though not specifically intertidal (e.g. *Fulvia* (*Laevifulvia*) *hungerfordi*).

For each PMBP 2004 species, these distribution categories are listed in table 10, provided sufficient data were available. All species appear to be roughly limited to one or two of the above habitats. Within most genera more than one macro-habitat type is used. The following related genera are typically restricted to one type: *Hippopus* and *Tridacna* (confined to type A); *Frigidocardium*, *Microcardium*, *Trifaricardium* and *Nemocardium* (confined to type C). The subgenus *Laevifulvia* seems to be roughly constrained to type D. For a number of species, type B and the littoral part of type A may be underrepresented due to the aforementioned overexploitation. Obviously, the patterns encountered for Panglao are not necessarily representative for the whole Indo-Pacific; they also appear somwehat random, probably because sampling was on only one occasion during a single season and the effort was not focused on cardiids but more generally on all molluscs and crustaceans. They therefore only provide a tentative picture, especially for those species of which only few samples were taken.

The PANGLAO 2005 campaign (focussed on type C) recovered a total of 28 sublittoral and upper bathyal cardiid species (table 10). Four of these were found alive and six were not recorded by PMBP 2004, for a combined total of 63 cardiid species.

SYSTEMATIC PART

CARDIIDAE Lamarck, 1809

Trachycardiinae Stewart, 1930

Remarks. — There is no general consensus among taxonomists about the status of Trachycardiinae. Popov (1977), Schneider (1992) and Vidal (1999a, 2000a) assigned *Vasticardium*, *Acrosterigma* and several other related genera to Cardiinae. However, Keen (1969, 1980), Schneider & Carter (2001) placed the above genera in a separate subfamily Trachycardiinae, based on shell morphology and microstructure. Subsequently, in his phylogenenetic revision of Cardiinae, Schneider (2002) excluded both genera from Cardiinae, considering Trachycardiinae a monophyletic sister group to all other living eucardiids (Cardiinae, Clinocardiinae, Fraginae, Tridacninae and Lymnocardiinae). Both genera are here incorporated in Trachycardiinae, although the validity of this placement has not been tested by phylogenetic analyses.

Acrosterigma Dall, 1900

Acrosterigma Dall, 1900: 1073, 1090 (as a section of *Trachycardium*). Type species by original designation: *Cardium dalli* Heilprin, 1887; Caloosahatchee Formation, Pliocene, Florida, U.S.A.

Diagnosis. — Shell small to medium, rarely large, commonly dorsally tapered, rather thin to medium thick shelled, elongate and pointed. Hinge plate strongly bent. Ribs close set and generally rather low, on medium part poorly ornamented, posterior ones longitudinally divided. Mean rib number medium to high (range circa 36-64). Regularly with two internal coloured rays and a radiating internal ridge (sterigma) in the middle of the umbonal cavity. Periostracum usually thin or poorly developed.

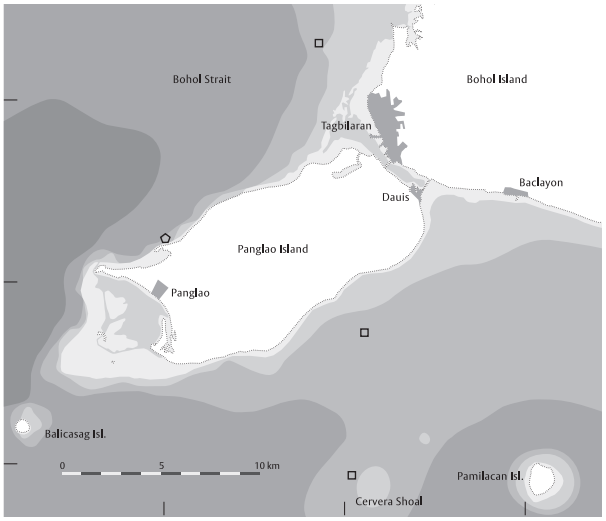
Distribution. — Miocene to Recent, Caribbean, Patagonian, Indo-Pacific, Japonic, South Australian and Panamic; littoral-sublittoral.

Remarks. — Vidal (1999a) reviewed the genus *Acrosterigma* extensively. His taxonomic views and species group subdivisions are followed here.

Acrosterigma maculosum (W. Wood, 1815)

Pl. 1 figs 1-3

Cardium maculosum W. Wood, 1815: 218-219, pl. 52 fig. 3.
Cardium multistriatum G.B. Sowerby 1st in Broderip & G.B. Sowerby 1st, 1833: 85; G.B. Sowerby 2nd, 1840a: fig. 59; 1840b: 4, sp. 47.
Cardium arenicolum Reeve, 1845: sp. 78, pl. 16 fig. 78.



Material examined. — **Philippines**: PMBP 2004, Stn P1, 90-200 m, 1 v; Stn T10, 117-124 m, 1 v; Stn T14, 101-110 m, 1 v; Stn T41, 110-112 m, 1 v.

Description. — Shell medium (H 30-50 mm), rather solid, ovoid, subequilateral, rather elongate, umbos often pointed. Rib number highly variable (43-61, present material 51-53) related to environment (Vidal, 1999a); ribs generally rounded, ornamented with weak variably disposed scales and nodules posteriorly. Interior margin deeply incised. Lunula small to indistinct, somewhat better developed on right valve. External colour white or cream, flecked with brown or purple; interior with two pink rays in umbonal cavity, occasionally completely purple.

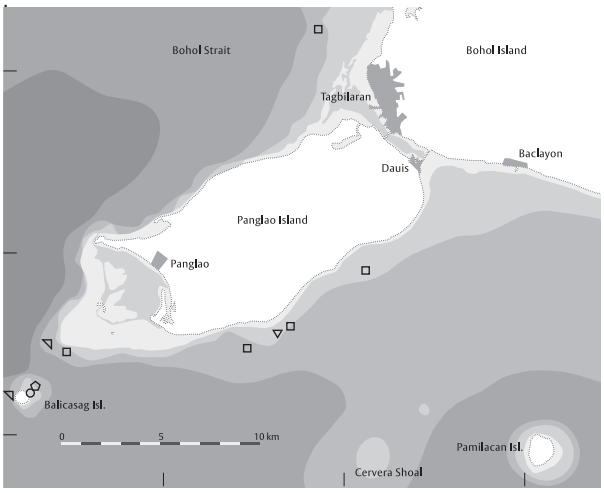
Distribution and ecology. — Tropical Indo-West Pacific, from Madagascar, Red Sea, Yemen, India, Thailand, Indonesia, Philippines, Japan (mainland) and Queensland (Vidal, 1999a). East of longitude 160° E replaced by A. maculosum howense Vidal, 1999 (its supposed subspecific status needs additional research). It lives in littoral and shallow water, but the present material – all eroded loose valves – is mainly trawled and originates from a depth of 90-200 m, possibly partly resulting from post-mortem downslope transportation.

Remarks. — *Acrosterigma maculosum* is a common species; nevertheless PMBP 2004 yielded four valves only. This might indicate a rather patchy distribution due to its preferring a particular more specific habitat and/or certain biogeographic barriers hampering dispersal. Juveniles are generally more rounded than adult specimens because of allometric growth. For differences from *A. transcendens* (Melvill & Standen, 1899) see under that species.

Acrosterigma transcendens (Melvill & Standen, 1899)

Pl. 1 figs 4-5

Cardium (*Trachycardium*) *transcendens* Melvill & Standen, 1899: 191-192, pl. 11 fig. 21.
Laevicardium pulcherrimum Sakurai & Habe, 1966: 293-296.



Material examined. — **Philippines**: PMBP 2004, Stn D15, 53-63 m, 2 v; Stn S3, 6 m, 1 pv; Stn T1, 83-102 m, 3 v; Stn T4, 82 m, 2 v; Stn T25, 160-210 m, 1 v; Stn T29, 77-84 m, 1 v; Stn T38, 80-140 m, 2 v; No stn nr., Balicasag Isl., tangle nets and lumun lumun, 'deep water', bought from fishermen, 2004, gift B. Olivera, 1 pv. PANGLAO 2005, Stn DW 2400, 111-115 m, 1 v; Stn DW 2401, 397-410 m, 1 v.

Description. — Shell small to medium (H 20-30 mm), rather thin, inflated, ovoid and equilateral, attenuated towards umbones. Numerous rounded thin radial ribs. Mean rib number (63) higher than any other congeneric species but rather

PLATE 1

Figs 1-3. *Acrosterigma maculosum* (Wood, 1815). **1.** PMBP 2004 Stn T14, lv exterior and interior, H 20.6 mm. **2-3.** Philippines, Cavite, Manila Bay, Tanza, Cuming Tour 2005 Stn CT 10. **2.** lv exterior, H 29.3 mm. **3.** rv interior, H 26.5 mm. **Figs 4-5.** *Acrosterigma transcendens* (Melvill & Standen, 1899). **4.** PMBP 2004 s/n, Balicasag Isl., tangle nets and lumun lumun 'deep water', from fishermen, gift B. Olivera, rv interior, lv exterior and dorsal, H 23.5 mm. **5.** PMBP 2004 Stn T1, rv exterior, H 25.1 mm. **Figs 6-8.** *Acrosterigma dianthinum* (Melvill & Standen, 1899). **6.** PMBP 2004 Stn S10, rv exterior and lv interior, H 10.2 mm. **7.** PMBP 2004 Stn B11, lv exterior and rv interior, H 14.0 mm. **8.** PMBP 2004 Stn S42, lv exterior, H 6.3 mm. **Figs 9-11.** *Acrosterigma hobbsae* Vidal, 1999. **9.** PMBP 2004 Stn B7, lv exterior and rv dorsal, H 9.0 mm. **10.** PMBP 2004 Stns L51-60, lv exterior, H 5.8 mm. **11.** PMBP 2004 Stn R19, lv interior, lv exterior and posterior, H 42.8 mm. **Fig. 12.** *Acrosterigma punctolineatum* Healy & Lamprell, 1992. PMBP 2004 Stn R6, posterior, rv interior and lv exterior, H 19.2 mm.

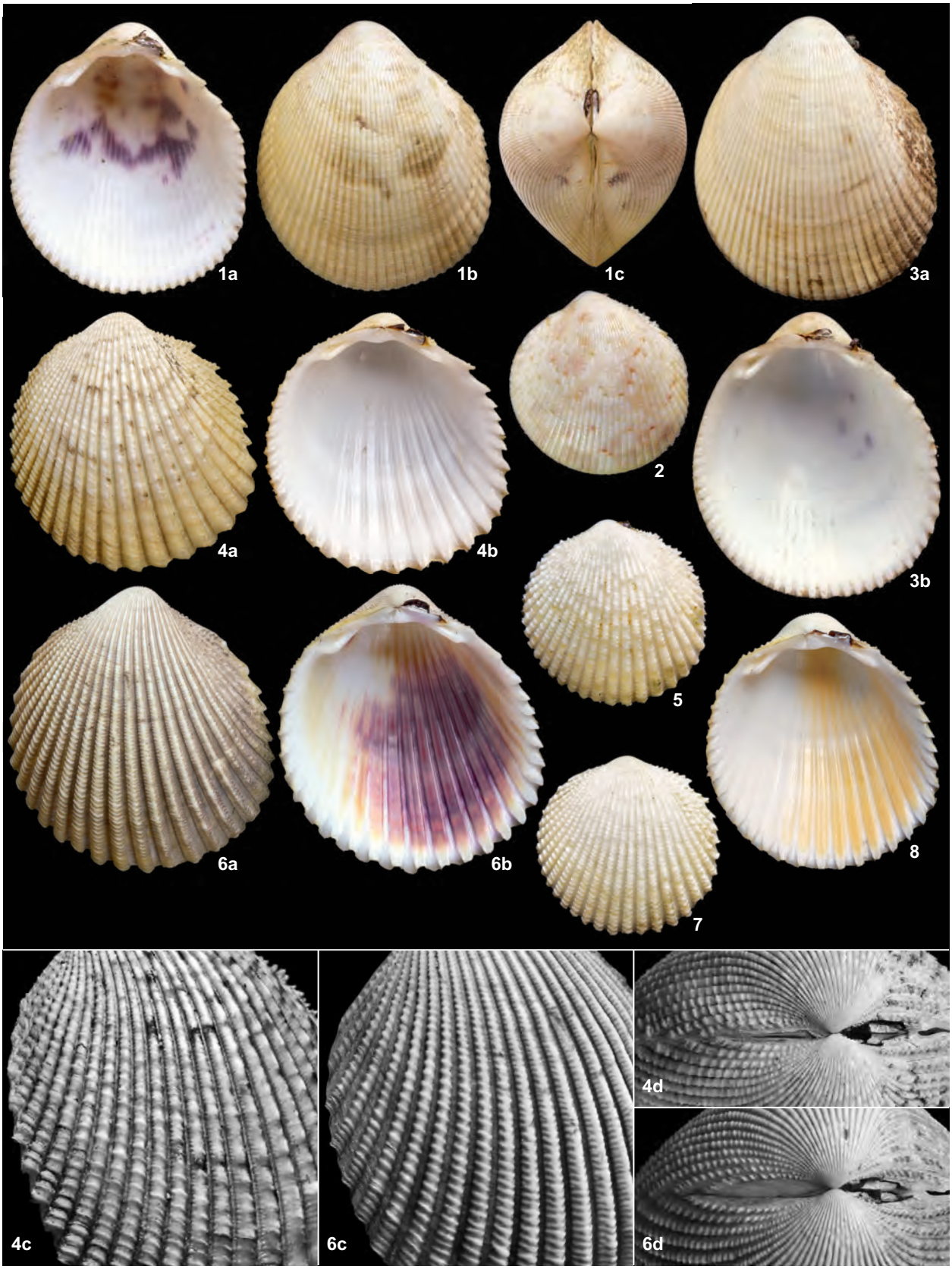


PLATE 2

Figs 1-3. *Acrosterigma simplex* (Spengler, 1799). **1.** PMBP 2004 Stn R59, rv interior, lv exterior and dorsal, H 31.3 mm. **2.** PMBP 2004 Stn S14, lv exterior, H 9.9 mm. **3.** PMBP 2004 Stn R43, lv exterior and rv interior, H 40.2 mm. **Figs 4-5.** *Vasticardium pectiniforme* (Born, 1780). **4.** PMBP 2004 Stn M23, lv exterior, rv interior, lv anterior slope and dorsal, H 36.4 mm. **5.** PMBP 2004 Stn S2, lv exterior, H 9.6 mm. **Figs 6-8.** *Vasticardium flavum subrugosum* (G.B. Sowerby 2nd, 1839). **6.** PMBP 2004 Stn M11, lv exterior, rv interior, lv anterior slope and dorsal, H 46.4 mm. **7.** PMBP 2004 Stn S23, lv exterior, L 11.4 mm. **8.** PMBP 2004 Stn M18, rv interior, H 35.9 mm.

variable, range 52-74 (55-71 for Panglao samples), posteriorly crenulated. Anterior ribs with clearly defined rugae, becoming weaker to nearly absent in the median part, most posterior ones with distantly placed drop like papillae. Rib sculpture on median part confined to posterior flanks, occasionally extending to the interstices. Colour bright but variable, exterior often cream, orange, yellow towards the margins, mottled with pink or brown. Interior white, mottled with purple and often with two darker umbonal rays. Umbonal cavity with a blush of pale orange.

Distribution and ecology. — Widely distributed in the Indo-Pacific from South Africa (Kwazulu-Natal), Sri Lanka, southern Japan (Okinawa) to northern Australia, New Caledonia to the Tuamoto archipelago. Not present in the Red Sea and north-west Indian Ocean (Vidal, 1999a). Depth range of present material 6-410 m (all dead collected), mostly from deeper than 50 m on fine sand and mud bottoms.

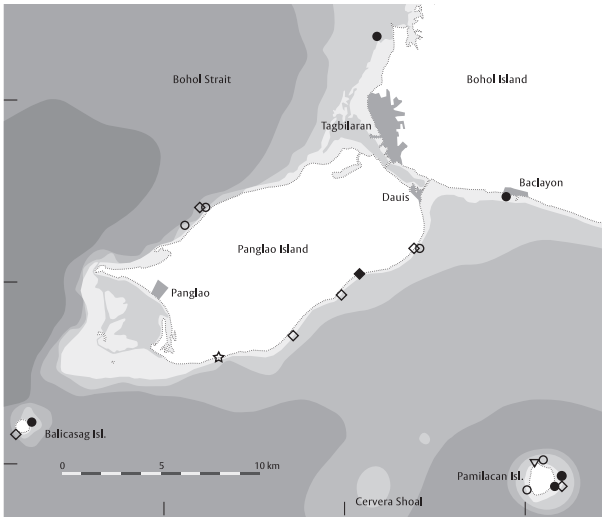
Remarks. — The vast majority of the material is rather worn and/or encrusted with various epibionts.

Its closet ally is *A. maculosum*, which is differentiated by its lower rib number (43-61), larger size and thicker shell that is less inflated and less vividly coloured. Also, the interior margin of *A. maculosum* has deeper and longer incisions and it prefers shallower habitats. Another related, similar sized species is *A. marielae* Wilson & Stevenson, 1977, which is less inflated, has a slightly lower rib number, more clearly developed rib sculpture and is less colourful. It is restricted to Western Australia. *Acrosterigma transcendens* is regularly found in tangle nets of fishermen operating around the island of Balicasag, mostly recorded from depths between 80 and 200 m (coll. TP).

Acrosterigma dianthinum (Melvill & Standen, 1899)

Pl. 1 figs 6-8, pl. 5 fig. 2

Cardium (*Trachycardium*) *dianthinum* Melvill & Standen, 1899: 190, pl. 11 figs 25, 25a.



Material examined. — **Philippines**: PMBP 2004, Stn B3, 8 m, 1 pv; Stn B5, 4 m, 1 pv (A); Stn B7, 4-30 m, 3 v; Stn B11, 2-4 m, 1 pv, 1 v; Stn B40, 22 m, 1 v; Stn B41, 17-19 m, 1 v; Stn B42, 30-33 m, 1 v; Stn D9, 2-4 m, 1 v; Stn M1, 0-1 m, 1 v; Stn S2, 4-5 m, 1 pv (A), 1 v; Stn S3, 6 m, 1 pv (A); Stn S4, 4-30 m, 1 v; Stn S5, 2-4 m, 1 pv, 1 v; Stn S8, 28-32 m, 1 v; Stn S10, 6-14 m, 1 pv (A), 4 v; Stn S14, 5-12 m, 1 pv; Stn S21, 4-12 m, 1 pv (A); Stn S22, 1 pv (A); Stn S42, 3 pv, 2 v.

Description. — Shell small (L 10-15 mm), rather thin, transversally ovoid and often very inequilateral, elongation variable. 42-50 flat and low radial ribs, most anterior ones finely ornamented with scales, most posterior ones spined. Ribs possess characteristic, regularly disposed granules on their tops, visible under magnification and skimming light. Lunula small and elongated. External colour uniformly white to cream, often with scattered brownish blotches, posterior part often purple, ligamental nymph and umbonal cavity orange-yellow.

Distribution and ecology. — Imperfectly known, until now confined to the central Indo-West Pacific: sparse records from Queensland (Coral Sea, Torres Strait), New Caledonia (both Vidal, 1999a) and recently from Indonesia and Papua New Guinea (Ter Poorten, 2007a). In fact, this species appears to extend much farther into the Indian Ocean, as evidenced by a ZMA sample from the Seychelles (Aldabra, Grande Terre, 200 m off Anse mais, 9.416667'S, 46.36667'E, 20 m, leg. J. van Arkel; det. TP, 2008). Present material found mainly littorally in sand and coral rubble in coral reef environments from 0-33 m, alive 4-20 m.

Remarks. — This enigmatic taxon is exemplary of our still poor state of knowledge of many smaller cardiids. The PMBP 2004 samples imply a considerable northward range extension and indicate that the species is at least locally common.

Juveniles show a clear pattern of radially aligned semi-translucent blotches, corresponding with the breadth of a rib and recalling the glassy shell microstructure of several Fraginae taxa (*Corculum*, *Fragum*, *Lunulicardia*), where these blotches, termed 'windows' (Carter & Schneider, 1997) or 'shell windows' (Persselin, 1998), act as light transmitting devices for endosymbiotic algae (zooxanthellae). Whether the same is the case for juvenile *Acrosterigma* is unknown. A comparable phenomenon can also be observed in the earliest growth stages of several *Fulvia* species. The development of the posterior ribs starts much earlier than is the case for those on the remainder of the shell, which, at a very early growth stage, is smooth and covered with dense, microscopic granulations (pl. 5 fig. 2).

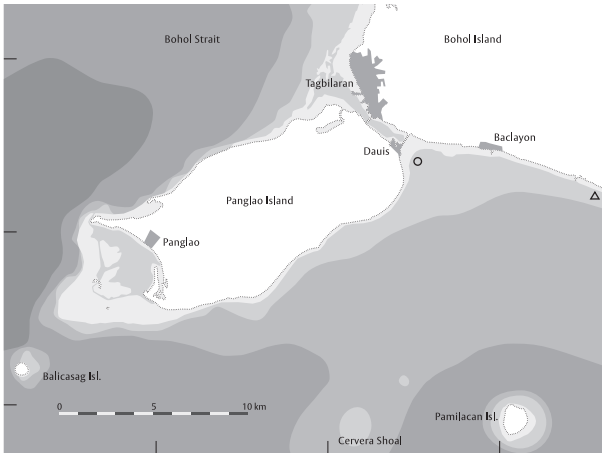
Acrosterigma punctolineatum Healy & Lamprell, 1992

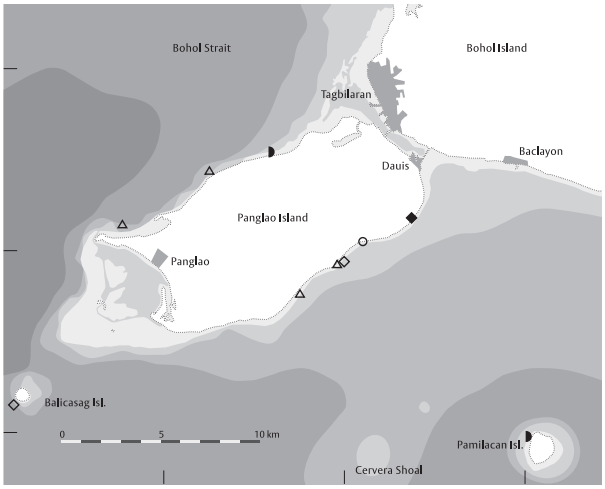
Pl. 1 fig. 12

Cardium foveolatum G.B. Sowerby 2nd – Reeve, 1845: sp. 87, pl. 18 fig. 87 (non G.B. Sowerby 2nd, 1840).

Acrosterigma punctolineata Healy & Lamprell, 1992: 87-89, pl. 3e-h.

Material examined. — **Philippines**: PMBP 2004, Stn R6, 5-12 m, 1 pv; Stn S13, 8-15 m, 2 v.





Description. — Shell small to medium (H 25-35 mm), rather thin, ovoid, equilateral to posteriorly expanded; moderately elongate. Rib number 42-55; ribs rounded with numerous transverse ridges, more prominent anteriorly and posteriorly replaced by oblique scales. Interstices small and finely striated. Lunula small and elongated. Colouration white with very characteristic broken light brown lines and subsurface green-brown spots, located on the surface and nearly black on the posterior quarter. Interior reflects exterior colouration but is more prominent.

Distribution and ecology. — Central Indo-Pacific, from Okinawa (Higo *et al*., 1999), South China Sea (coll. TP) to Queensland, New Caledonia, Solomon Islands and Vanuatu, west of longitude 170° E (Vidal, 1999a). Littoral and sublittoral water in mud, sand and coral sand with only two PMBP 2004 records between 5-15 m (dead collected).

Remarks. — *Acrosterigma punctolineatum* appears to have a slighter wider distribution than its closest congener *A. hobbsae*, which is not known from Okinawa. See under *A. hobbsae* for main differences from *A. punctolineatum*. Both taxa appear to be rather scarce throughout their ranges.

***Acrosterigma hobbsae* Vidal, 1999**

Pl. 1 figs 9-11, pl. 5 fig. 1

Acrosterigma hobbsae Vidal, 1999a: 315-318, figs 16c-h, tables 31, 32.

Material examined. — **Philippines**: PMBP 2004, Stn B7, 4-30 m, 1 pv (A), 1 v; Stn B38, 17-18 m, 2 v; Stn B40, 22 m, 1 v; Stns L51-60, 43-62 m, 1 pv (A); Stns L65-68, 55-81 m, 1 pv (A); Stn R4, 2-30 m, 1 pv; Stn R19, 2-54 m, 1 pv; Stn R49, 1-32 m, 2 pv; Stn R51, 2-52 m, 1 v; Stn S1, 5 m, 1 pv (A); Stn. S13, 8-15 m, 1 v.

Description. — Shell medium (H up to 45 mm), rather thin, ovoid, slightly inequilateral with posterior expansion and steep postero-dorsal slope. 58-66 low and rounded radial ribs, on anterior part ornamented with regularly placed scales, posteriorly with tiny tubercular pustules. Interstices very small and unsculptured. Lunula clearly developed and elongate. Exterior white or tan with various irregular patches of purple, becoming greenish-brown posteriorly. Interior reflects exterior colouration but more prominent with two umbonal rays.

The early juvenile stage shows a much more pronounced keeled appearance with a markedly attenuate umbo and the presence of minute, partly commarginally aligned granulations. Also, the development of the anterior and median radial ribs starts relatively late and gradually (pl. 5 fig. 1).

Distribution and ecology. — Recorded from the Philippines, Indonesia, Guam, Queensland and New Caledonia (Vidal, 1999a); also from the Solomon Islands and Malaysia (coll. TP). Depth range of present material 2-81 m (alive 4-81 m) on sandy bottoms in coral reef environments.

Remarks. — Its closest relative, *A. punctolineatum* Healy & Lamprell, 1992, is smaller, more equilateral, has a lower rib number with ribs that start to develop earlier during ontogeny, a less pointed umbo and distinctive dark brown blotches on the posterior slope.

***Acrosterigma simplex* (Spengler, 1799)**

Pl. 2 figs 1-3, pl. 5 fig. 3

Cardium simplex Spengler, 1799: 31.
Cardium unicolor G.B. Sowerby 2nd, 1834: fig. 29; 1840a: fig. 42; 1840b: 4, sp. 46.
Cardium nebulosum Reeve, 1845: sp. 99, pl. 19 fig. 99.
Laevicardium soyeri Fischer-Piette, 1977: 19-20, pl. 1 figs 4-7.

Material examined. — **Philippines**: PMBP 2004, Stn B11, 2-4 m, 4 pv, 1 v; Stn B13, 3-5 m, 1 pv (A), 1 v; Stn B25, 16 m, 1 v; Stn B40, 22 m, 1 v; Stn D9, 2-4 m, 1 pv (A), 1 v; Stn L43, 60 m, 1 v; Stn L46, 90-110 m, 1 v; Stn R4, 2-30 m, 1 pv; Stn R14, 6-8 m, 6 pv (A); Stn R16, 6-22 m, 2 pv; Stn R19, 2-54 m, 2 pv; Stn R20, 7-48 m, 1 pv; Stn R23, 1-5 m, 1 pv (A); Stn R31, 10-41 m, 4 pv (A); Stn R38, 6-37 m, 7 pv (A), 1 v; Stn R42, 8-22 m, 1 pv; Stn R43, 3-41 m, 2 pv (A); Stn R49, 1-32 m, 1 pv; Stn R51, 2-52 m, 2 pv (A); Stn R59, 2-20 m, 1 pv; Stn R73, 2-30 m, 1 pv (A); Stn R75, 3-35 m, 1 pv; Stn R77, 2-10 m, 1 pv; Stn S3, 6 m, 4 pv (A); Stn S5, 2-4 m, 1 v; Stn S8, 28-32 m, 1 v; Stn S10, 6-14 m, 19 pv (A), 13 v; Stn S12, 6-8 m, 4 pv (A), 1 v; Stn S14, 5-12 m, 3 pv (A), 2 v; Stn S16, 15-18 m, 2 pv (A), 1 v; Stn S17, 6 m, 9 pv (A); Stn S21, 4-12 m, 5 pv (A), 1 v; Stn S22, 15-20 m, 10 pv (A), 10 v; Stn S24, 2-4 m, 1 v; Stn S42, 15-20 m, 1 pv, 4 v; Stn T13, 90-100 m, 1 v; Stn T41, 110-112 m, 1 v; Stn s/n, Panglao Isl., 2 pv (A). PANGLAO 2005, Stn DW 2401, 397-410 m, 2 v.

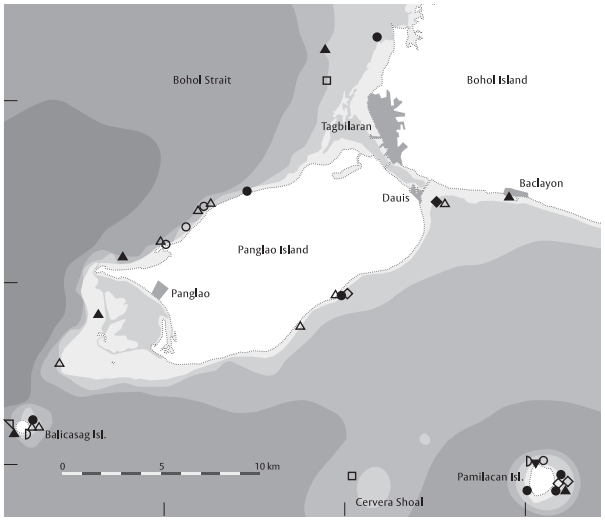
Description. — Shell medium (H 30-50 mm), rather solid, inflated, umbo tumid, subequilateral, variably elongated, pos-

PLATE 3

Figs 1-3. *Vasticardium angulatum* (Lamarck, 1819). **1.** PMBP 2004 Stn R59, dorsal, lv exterior and rv interior, H 67.1 mm. **2.** PMBP 2004 Stn R75, dorsal, lv exterior and rv interior, H 63.4 mm. **3.** PMBP 2004 Stn. B7, rv exterior and interior, H 14.8 mm. **Figs 4-5.** *Vasticardium philippinense* (Hedley, 1899). **4.** PMBP 2004 Stn. S15, rv exterior and interior, H 8.9 mm. **5.** PMBP 2004 Stn R41, rv interior, lv exterior and dorsal, H 88.8 mm.

PLATE 4

Figs 1-2. *Vasticardium kenyanum* (Cox, 1930). **1.** Philippines, Calamian Group, Culion Isl., coral sand, by diver, ix.1991, lv exterior, rv interior and posterior, H 41.5 mm (TP 722). **2.** PANGLAO 2005 Stn DW 2370, rv exterior, interior and ventral, H 15.5 mm. **Figs 3-4.** *Vasticardium sewelli* (Prashad, 1932). **3.** PMBP 2004 Stn T4, rv exterior and interior, H 6.7 mm. **4.** Philippines, Panay Isl., Buruanga Point, 11°51.855'N-121°52.701'E, iv.2007, leg. G.T. Poppe, lv exterior, rv interior, anterior and dorsal, H 17.2 mm (TP 3355). **Figs 5-7.** *Vasticardium papuanum* Vidal, 1996. **5.** PMBP 2004 Stn T33, rv exterior and interior, H 11.6 mm. **6.** PMBP 2004 Stn S21, rv exterior and interior, H 7.0 mm. **7.** Philippines, Bohol Isl., N. side, Calitoban Isl., on mud, 9 m, 2004, lv exterior and rv interior, H 63.6 mm (TP 1946).



teriorly slightly expanded and truncated. Ribs numerous (41-59), rather flattened, rib sculpture anteriorly crenate laterally, posteriorly poorly ornamented. Interstices small, showing fine growth striae. Lunula large and asymmetric, larger on right valve. Periostracum relatively well developed on posterior slope. Exterior uniform light greyish-cream or yellowish, often darkened posteriorly, interior white, sometimes with splashes of pink or purple.

The ontogenetic development is typically allomorphic with the L/H ratio changing from H ≤ L to H > L (pl. 5 fig. 3 – pl. 2 fig. 3).

Distribution and ecology. — Throughout the tropical Indo-West Pacific from Mozambique to Japan, Marshall Islands, Kiribati, northern Australia and New Caledonia (Vidal, 1999a). A single Red Sea record (Vidal, 1999a: 319) is here considered doubtful as it is not mentioned elsewhere in the literature (Oliver, 1992; Dekker & De Ceuninck van Capelle, 1994; Dekker & Orlin, 2000; Zuschin & Oliver, 2003) and it appears to be absent in the north-west Indian Ocean. Littoral and sublittoral water, in exposed coral reef environments, often on sand and rubble. Depth range of present material 2-112 m (alive 1-52 m), valves of both deeper water trawled stations worn / fragmented, probably transported downslope. Likewise, the two PANGLAO 2005 valves (397-410 m) in all probability do not reflect the true distribution of the species but may be related to the steep slopes and drop-offs west of Balicasag Island.

Remarks. — *Acrosterigma simplex* is a common species with a huge range and was by far the most frequently encountered *Acrosterigma* of PMBP 2004 (table 10).

Vasticardium Iredale, 1927

Vasticardium Iredale, 1927b: 75-76. Type species by original designation: *Cochlea nebulosa* Martyn, 1784 [= *Cardium elongatum* Bruguière, 1789]; Recent (type locality not mentioned).

Regozara Iredale, 1936: 275. Type species by original designation: *Regozara olivifer* Iredale, 1936 [= *Cardium vertebratum* Jonas, 1844]; Recent, Sydney Harbour, New South Wales, Australia.

Diagnosis. — Shell medium to very large, generally not dorsally tapered, often rather thick and elongate. Cardinal teeth in right valve separate or only touching at their bases. Ribs generally high and well ornamented, posterior ones not longitudinally divided. Mean rib number low to medium (range circa 25-44). Interstices rather deep, broad and striated. Ventral margin often coloured, usually no internal coloured rays. Internal umbonal ridge normally lacking. Periostracum often rather well developed.

Distribution. — Miocene to Recent, Indo-Pacific, South African, Japonic.

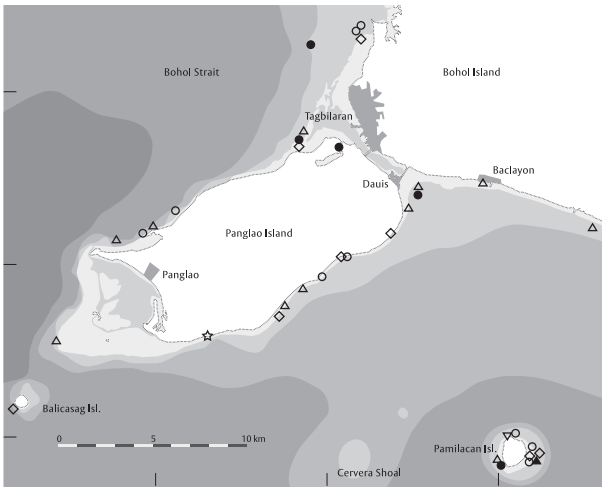
Remarks. — Vidal's (1991; 1993; 1996; 1997a, b; 1999a, b) taxonomic views in his extensive comparative diagnoses of the genera *Trachycardium*, *Vasticardium* and *Acrosterigma* are adopted here. Vidal (1997a, b) demonstrated that the elaborate rib morphology and ornamentation can be used as a primary character for identification at the species level.

Vasticardium angulatum (Lamarck, 1819)

Pl. 3 figs 1-3, pl. 5 fig. 4

Cardium angulatum Lamarck, 1819: 9.

Cardium alternatum G.B. Sowerby 2nd, 1840a: fig. 64; 1840b: 5, sp. 60; 1841: 108.



Material examined. — **Philippines**: PMBP 2004, Stn B3, 8 m, 2 v; Stn B5, 4 m, 1 pv; Stn B7, 4-30 m, 1 v; Stn B14, 2-4 m, 1 pv; Stn B20, 2-8 m, 1 pv; Stn B26, 35 m, 1 pv; Stn B28, 25 m, 1 v; Stn B41, 17-19 m, 1 pv; Stn D9, 2-4 m, 1 v; Stn M1, 0-1 m, 1 pv; Stn R4, 2-30 m, 1 pv; Stn R5, 5-16 m, 2 pv; Stn R6, 5-12 m, 3 pv; Stn R14, 6-8 m, 1 pv; Stn R31, 10-41 m, 2 pv (A); Stn R42, 8-22 m, 1 v; Stn R45, 3-7 m, 1 v; Stn R47, 4-25 m, 1 pv; Stn R51, 2-52 m, 3 pv; Stn R59, 2-20 m, 1 pv; Stn R61, 4-22 m, 1 pv; Stn R75, 3-35 m, 1 pv; Stn S1, 5 m, 1 pv, 1 v; Stn S7, 1 pv (A); Stn S8, 28-32 m, 3 v; Stn S10, 6-14 m, 1 v; Stn S13, 8-15 m, 1 pv (A); Stn S14, 5-12 m, 1 pv (A); Stn S15, 4-6 m, 1 pv (A); Stn S17, 6 m, 1 pv, 1 v; Stn S21, 4-12 m, 1 v; Stn S22, 15-20 m, 4 v; Stn S25, 21 m, 1 pv; Stn S32, 2-3 m, 2 v; Stn S34, 2 m, 1 pv (A); Stn S42, 15-20 m, 1 v; Stn s/n, Panglao Isl., 1 v.

Description. — Shell medium to large (H 60-90 mm), rather thin, obliquely ovoid, rather flattened, strongly inequilateral, gaping posteriorly and anteriorly. Rib number about 25 to 32; ribs triangular and asymmetric in cross-section, retro-ridged on posterior part of the shell, triangular and finely retro-ridged on median part, rounded and strongly rugose

on anterior part; interstices smooth, often shaped as a low rounded riblet. Lunula very small and elongate. Exterior white, variably coloured with scattered blotches of tan and occasionally yellow, purple or orange towards the margins, interior white, occasionally with purple margins. Periostracum thick and well developed.

Strongly allomorphic species: in juveniles the length clearly exceeds the height, whereas in adults the opposite is the case. Small juveniles of *V. angulatum* can be separated from congeners by their relatively high triangular ribs, wide interstices, inequilateral strongly prosogyrate shell, and keeled appearance with markedly angular postero-ventral margin. The interstices are sculptured with quite distantly placed thin lamellae and the prodissoconch is clearly separated from the rest of the shell (pl. 5 fig. 4).

Distribution and ecology. — Depth range of present material 0-52 m (alive 5-41 m). Tropical Indo-West Pacific, from Mozambique (coll. TP), Thailand, Vietnam (Hylleberg & Kilburn, 2003) to islands south of mainland Japan (Matsukuma, 2000), Indonesia, northern Australia (Lamprell & Whitehead, 1992), Solomon Islands to Gilbert Islands, Tarawa in the West Pacific (Paulay, 2001). Not present in the north-west Indian Ocean. Littoral and shallow water, mainly on sand bottoms, often in exposed coral environments.

Remarks. — Some variation exists in the degree of development of twisted scales on the rib tops of the median-postero part of the shell, in some cases leading to tuberculated forms. This ornamentation is not geographically related but occurs within populations. The species is collected for food in the Philippines (Sotto & von Cosel, 1982; Poutiers, 1998). The type locality as indicated by Lamarck (1819: 9) 'les mers d'Amérique?' (American seas?) was emended to Samar, Philippines by Voskuil & Onverwagt (1991c).

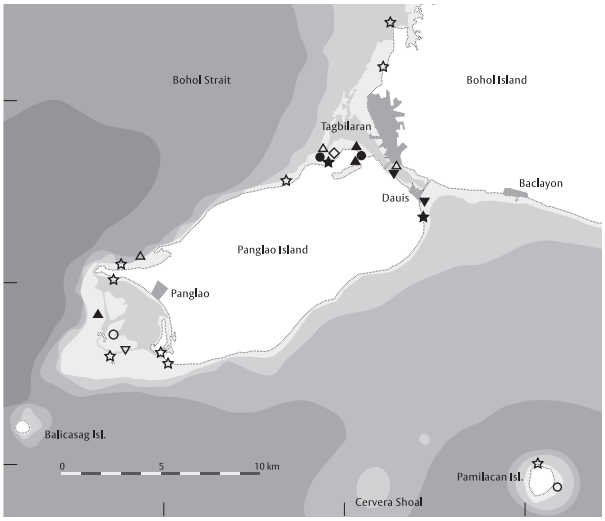
Vasticardium flavum subrugosum (G.B. Sowerby 2nd, 1839)

Pl. 2 figs 6-8

Cardium subrugosum G.B. Sowerby 2nd, 1839: fig. 34; 1840a: fig. 71; 1840b: 5, sp. 59.

Material examined. — **Philippines**: PMBP 2004, Stn B18, 3-5 m, 1 v; Stn D1, 2 m, 2 pv (A), 3 v; Stn D4, 0-2 m, 1 pv, 1 v; Stn D13, 2-3 m, 1 pv (A), 2 v; Stn M3, 0-2.5 m, 2 pv; Stn M5, 0-2 m, 3 pv; Stn M9, 0.5 m, 1 pv, 2 v; Stn M10, 0-3 m, 4 pv, 2 v; Stn M11, 0-3 m, 5 pv (A); Stn M18, 0-1 m, 8 pv, 1 v; Stn M19, 0-2 m, 2 pv; Stn M23, 0-1 m, 1 pv; Stn M24, 0-1 m, 4 pv; Stn M26, 0-2 m, 2 pv, 1 v; Stn M44, 0 m, 1 v; Stn M51, 0 m, 3 pv (A); Stn R23, 1-5 m, 5 pv (A); Stn R26, 1-5 m, 2 pv; Stn R50, 3-7 m, 2 pv, 1 v; Stn R65, 1-2 m, 5 pv (A); Stn R66, 1-3 m, 10 pv (A), 1 v; Stn R67, 3-3.5 m, 2 pv; Stn R68, 3-3.5 m, 2 pv; Stn S11, 2 m, 1 v; Stn S22, 15-20 m, 1 v; Stn S23, 2 m, 1 pv, 1 v; Stn S34, 2 m, 2 pv (A), 1 v; Stn S40, 2-4 m, 1 pv (A), 1 v.

Description. — Shell medium (H 45-60 mm), often nearly equilateral, subelongate. Circa 25-34 rounded to triangular ribs, on median-postero slope becoming flattened during ontogeny. Ribs carrying transverse ridges that are thick, close-set and very regular on the anterior part. Ribs ridged on both sides with smoothened crest on median part. Lunula well developed, hollowed and larger in right valve. Exterior white, lemon-yellow, pink or purple, with white posterior slope;



interior white with large patches of pink, purple or yellow. Philippine specimens rarely with completely white interior. Periostracum thick, normally uniform olive-green to brownish.

Distribution and ecology. — Tropical central Indo-West Pacific: eastern India, Sri Lanka, Thailand, Malaysia, Indonesia, Philippines, Vietnam, China and islands south of mainland Japan (all Vidal, 1997a, 1999b). Replaced southeastwards in the Pacific by the nominotypical subspecies. Depth range of present material 0-20 m (alive 0-5 m), mostly confined to the non-exposed Panglao Bay and Tagbilaran-Panglao channel, occurring littorally (mainly low intertidally) on sand and muddy sand, often in association with seagrass and/or fringe mangrove.

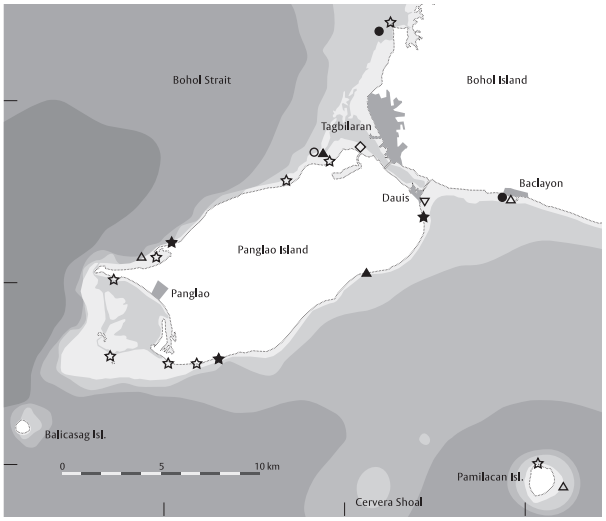
Remarks. — For differences from *V. pectiniforme* (Born, 1780) see under that species. Vidal (1999b) mentioned the presence of a transitional zone between *V. flavum subrugosum* and *V. f. flavum* (Linnaeus, 1758) in Sulawesi and Nusa Tenggara, Indonesia. This could possibly be explained by the existence in the late Quaternary of the Sunda Shelf, which would have separated two marine basins, leading to slightly different evolutionary trajectories (Vidal, 1999b: 361). The PMBP 2004 material does not show any intermediates. The species is consumed locally (Sotto & von Cosel, 1982; Poutiers, 1998).

Vasticardium pectiniforme (Born, 1780)

Pl. 2 figs 4-5

Cardium pectiniforme Born, 1780: 49, pl. 3 fig. 10.
Cardium regulare Bruguière, 1789: 227-228.
Cardium rugosum Lamarck, 1819: 10.
Trachycardium peregrinum Jousseaume, 1888: 212-213.
Vasticardium nigropunctatum Habe & Kosuge, 1966a: 154, pl. 59 fig. 9; 1966b: 324-325, pl. 29 fig. 16.

Material examined. — **Philippines**: PMBP 2004, Stn B31, 1-2 m, 1 pv, 1 v; Stn D1, 2 m, 1 v; Stn M1, 0-1 m, 7 pv (A); Stn M2, 0-2 m, 3 pv; Stn M3, 0-2.5 m, 3 pv; Stn M5, 0-2 m, 7 pv; Stn M7, 0-3 m, 9 pv (A); Stn M9, 0.5 m, 5 pv; Stn



M10, 0-3 m, 13 pv, 1 v; Stn M11, 0-3 m, 1 pv; Stn M18, 0-1 m, 1 pv; Stn M19, 0-2 m, 1 pv; Stn M23, 0-1 m, 3 pv; Stn M24, 0-1 m, 1 pv; Stn M40, 0-3 m, 1 pv; Stn M51, 0 m, 1 pv (A); Stn R10, 2-10 m, 1 pv (A); Stn R14, 6-8 m, 1 pv; Stn R26, 1-5 m, 2 pv (A); Stn R38, 6-37 m, 1 pv; Stn R50, 3-7 m, 1 v; Stn S2, 4-5 m, 1 pv (A); Stn S7, 1-4 m, 1 v. – Stn S25, 21 m, 2 pv (A), 1 v. PANGLAO 2005, Stn CP 2358, 569-583 m, 1 pv.

Description. — Shell medium (H 40-70 mm), often nearly equilateral, subelongate. Rib number 25 to 34. Ribs strong, rounded to triangular, anteriorly with well developed but rather thin, irregularly arranged ridges that are relatively widely spaced; ribs on median part less pronounced, laterally ridged, often not reaching top zone. Posterior ribs remain high and well sculptured on top and flanks during ontogeny. Lunula small to virtually absent, elongate. Colour externally and internally uniformly white to tan, sometimes yellow (eastern part of range) or with a pattern of brownish spots; umbonal cavity very occasionally pale yellow. Periostracum olive-green to brownish, very often with darker coloured blotches on median and posterior sides.

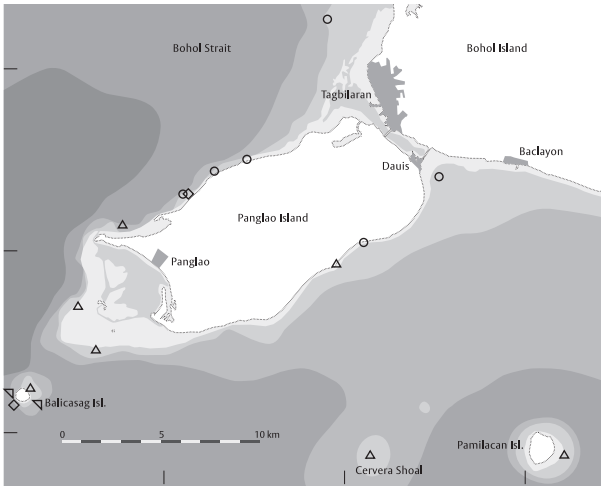
Distribution and ecology. — Throughout the tropical Indo-West Pacific, from South Africa (Kwazulu Natal) to the Red Sea, to islands south of mainland Japan and northern Australia to Fiji in the West Pacific (Vidal, 1999b). A very common littoral species. PMBP 2004 specimens appear to prefer coral reef and rocky environments; they were found alive in sand, mud and rubble in 0-21 m and dead in 0-37 m, sometimes in association with seagrass. This accords with the findings of Vidal (1997a: 246) that in New Caledonia the species was not found in any of the 1200 stations of the dredging program in the lagoon, yet occurred in abundance on all beaches around the main island. The PANGLAO 2005 record of a rather fresh dead collected specimen from 569-583 m deep is puzzling, but does not reflect its original habitat.

Remarks. — *Vasticardium pectiniforme* has very often been erroneously named *V. flavum*. These species differ in the character of the anterior and posterior rib ornamentation, the nature and sculpture of the posterior ribs, the shape of the lunula, the constitution of the periostracum and the shell colouration. Also, they appear to have somewhat different ecological preferences. Nevertheless, identification of worn, discoloured material and juveniles sometimes remains problematic, if not impossible. For this reason, apart from the material examined mentioned under *V. flavum subrugosum* and *V. pectiniforme*, the following supplementary samples could not be distinguished with certainty: Stn D1 (8 v), D5 (1 v), S6 (1 pv), S9 (1 v), S22 (2 v), S23 (1 pv, 1 v), S25 (1 pv), S34 (3 pv, 1 v), S38 (1 v), S40 (1 v). *Vasticardium pectiniforme* is used for food and appears in local markets in the central Philippines (Poutiers, 1998).

Vasticardium philippinense (Hedley, 1899)

Pl. 3 figs 4-5

Cardium angulatum Lamarck sensu Reeve, 1845: sp. 70, pl. 14 fig. 70 (not *Cardium angulatum* Lamarck, 1819).
Cardium philippinense Deshayes: Hedley, 1899: 503-504.
Cardium (*Trachycardium*) *pseudoangulatum* Bülow, 1905: 79-80, pl. 1 fig. 3.



Material examined. — **Philippines**: PMBP 2004, Stn B10, 3-14 m, 1 v; Stn B38, 17-18 m, 1 v; Stn R1, 5-7 m, 1 pv; Stn R29, 3-35 m, 1 pv; Stn R31, 10-41 m, 1 pv; Stn R38, 6-37 m, 1 v; Stn R41, 11-40 m, 1 pv; Stn R49, 1-32 m, 1 pv; Stn R51, 2-52 m, 1 pv; Stn R56, 1-10 m, 1 pv; Stn S1, 5 m, 3 v; Stn S8, 28-32 m, 1 v; Stn S13, 8-15 m, 2 v; Stn S15, 4-6 m, 1 v; Stn S16, 15-18 m, 1 v; Stn S28, 28-32 m, 1 v. PANGLAO 2005, Stn DW 2401, 397-410 m, 1 v; Stn DW 2402, 101-118 m, 1 v.

Description. — Shell medium to large (H 70-110 mm), thick and elongate, subequilateral to clearly inequilateral in the adult with slight expansion of posterior slope. Anterior and ventral margin occasionally straight in fully adult specimens. Hinge with hooked base of the anterior lateral on both valves, hinge plate broad. Lunula large and well delimited with raised margins. Rib number 36-42, ribs square to triangular, with top or posterior oblique flank ridges. External colour white or tan with brownish-purple irregular splashes, more pronounced posteriorly and with dark brown stains towards posterior margin; internally white to yellow with posterior margin bright purple and hinge plate bordering lunula orange-yellow. Pedomorphic ontogenetic development with a limited change in the L/H ratio, becoming only slightly more elongate.

Distribution and ecology. — Tropical West Pacific and south-eastern Indian Ocean, east of about longitudes 100-110°E, from Japan (restricted to Amami Islands and Okinawa), Vietnam (Hylleberg & Kilburn, 2003), Philippines, Indonesia, northern Australia, New Caledonia, Tonga and Kiribati (Vidal, 1997b; coll. TP). Also listed from the Cocos (Keeling) Islands (Wells, 1994). Littoral and sublittoral water, exposed reef environments, predominantly on sandy bottoms. The present material was all collected dead in 1-52 m (PMBP 2004) and 101-410 m (PANGLAO 2005), the latter presumed to have been transported downslope.

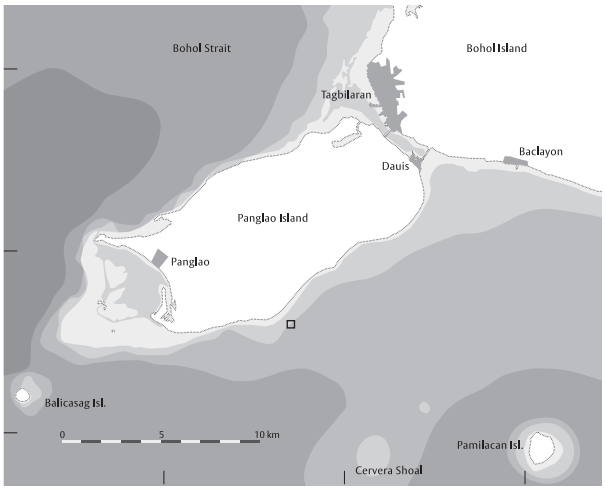
Remarks. — Vidal (1997b) considered this a polytypic species and defined four perfectly parapatric geographic subspecies: *V. orbita orbita* (Broderip & G.B. Sowerby 1st, 1833), *V. o. mendanaense* (G.B. Sowerby 3rd, 1897), *V. o. philippinense* and *V. o. hawaiensis* (Dall, Bartsch & Rehder, 1938). Although these share a related shell morphology and belong to the same species group, obvious intermediate forms are lacking (Vidal, 1999b: 357), which is an argument for assigning specific rank. Moreover, all except *V. o. philippinense* represent remote Pacific island endemics, among which gene flow seems implausible. *Vasticardium philippinense* is locally collected for consumption in the Philippines.

Vasticardium sewelli (Prashad, 1932)

Pl. 4 figs 3-4

Cardium (*Trachycardium*) *sewelli* Prashad, 1932: 268, pl. 6 figs 25-26.

Cardium (*Trachycardium*) *laddi* Abrard, 1946: 33-34, pl. 3 figs 1-2.



Material examined. — **Philippines**: PMBP 2004, Stn T4, 82 m, 1 v.

Description. — Shell medium (H 50-65 mm), solid and elongate, subquadrate, subequilateral and strongly inflated. Juveniles more rounded. Umbones weakly prosogyrate. Rib number circa 36-41. Anterior and medial ribs with pronounced, closely set imbricating scales, rounded on anterior slope, more or less chevron-shaped and slightly transverse on central part. Posterior ribs with raised, transverse imbricating scales, more distantly placed and wearing off easily. Interstices with fine growth striae. Lunula and escutcheon narrow but clearly defined. Hinge plate strong, broad and weakly arched. Exterior colouration ranging from white or yellow to pinkish, mottled with tan-orange or brownish blotches. Lunula and escutcheon may be pink or purple. Interior white with the umbonal cavity occasionally pale cream; margins sometimes reddish brown or yellowish brown.

Distribution and ecology. — Tropical central Indo-West Pacific: Indonesia, Papua New Guinea, Queensland, Solomon Islands, New Caledonia and Fiji (Ter Poorten, 1997). Also known from Thailand, Guam and Vanuatu (Vidal, 1999a; Paulay, 2003). The only known live taken specimen originates from a depth of 20-30 m (New Caledonia, MNHN). The PMBP 2004 valve, although immature and worn, represents the first published Philippine record.

Remarks. — The characteristic imbricating scales, appearing on all the ribs, are not found in any other congeneric species. *Cardium* (*Trachycardium*) *laddi* Abrard, 1946 shows all the characteristics of *V. sewelli* and was reported from the Upper Miocene of Epi Island, Vanuatu. Juvenile specimens superficially resemble *Ctenocardia translata* (Prashad, 1932), but the latter has a lower rib number, the scales are less delicate and the length equals or exceeds the height. Despite its large geographical range, *V. sewelli* appears to be scarce, known from a limited number of records. Another Philippine specimen is present in coll. TP (north-west part of Panay Island, Buruanga Point, 11°51.855'N, 121°52.701'E, iv.2007, leg. G.T. Poppe – Pl. 4 fig. 4).

Vasticardium kenyanum (Cox, 1930)

Pl. 4 figs 1-2

Cardium (*Trachycardium*) *kenyanum* Cox, 1930: 159, pl. 15 figs 13a-b.

Acrosterigma fidele Vidal, 1992: 24-26, figs 1-5.

Material examined. — **Philippines**: PANGLAO 2005, Stn DW 2370, 92-96 m, 1 v.

Description. — Shell medium to large (H 70-95 mm), solid and elongate, ovate, markedly inequilateral. Antero-dorsal margin steeply sloping, posterior margin straight or slightly concave, ventral margin regularly rounded. Sculpture consisting of about 29-34 prominent, flat-topped ribs, separated by deep interstices of about the same width. Flanks of the ribs finely and obliquely striated, rib top enlarged, partly overhanging the interstices. Circa 6-7 posterior ribs bearing twisted scales. Ventrally, small apertures are visible below each rib. Posterior cardinal tooth of left valve relatively strong. Exterior colour orange-yellow to pinkish-brown, darker posteriorly. Interior white with pale orange margins and umbonal cavity. Periostracum rather thin.

Distribution and ecology. — Tropical Indo-West Pacific from South Africa (Kwazulu-Natal), Mozambique,

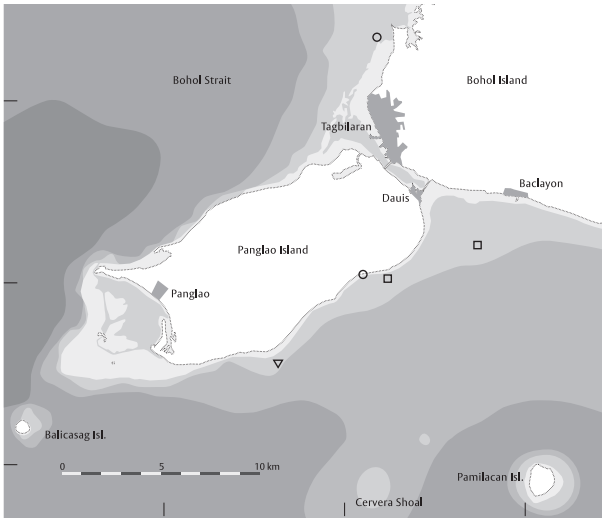
Madagascar, Kenya, India, Sri Lanka, Myanmar, Thailand, Malaysia, Singapore, Vietnam, Philippines, islands south of mainland Japan and Wallis and Futuna (Ter Poorten, 2005 and references therein). It occurs sublittorally and is mostly found trawled or dredged by fishermen.

Remarks. — *Vasticardium kenyanum* was described from Pleistocene deposits of Kenya and should be regarded as a senior synonym of *V. fidele* (Vidal, 1992), as demonstrated by Ter Poorten (2005). *Cardium* (*Acanthocardia*) *denticostulatum* Beets, 1941 (Upper Miocene of Borneo) has a similar rib cross-section, but clearly differs in outline and rib sculpture. The sole PANGLAO 2005 valve is juvenile and rather worn but readily identified by the unique cross-section of the ribs.

Vasticardium papuanum Vidal, 1996

Pl. 4 figs 5-7

Vasticardium papuanum Vidal, 1996: 78, figs 1-7, teble 1.



Material examined. — **Philippines**: PMBP 2004, Stn D15, 53-63 m, 1 v; Stn S1, 5 m, 1 pv, 1v; S21, 4-12 m, 2 v; Stn T6, 34-82 m, 1 v; Stn T33, 67-74 m, 1 v.

Description. — Shell medium to large (H 75-95 mm), solid and elongate, ovoid to subquadrate, adults subequilateral with minor posterior expansion. Umbones clearly prosogyrate. Rib number circa 34-41, posteriorly elaborately sculptured with oblique scales, intercalated with small crenulations on the flanks, sometimes forming small pseudo-ribs and becoming less well developed in adults. Anterior ribs with regular placed curved rugae. Juveniles with median part having more pronounced sculptured rib flanks, forming a herringbone structure. Partially tuberculate forms exist, with the tuberculations situated on the median-posterior rib crests, sometimes disappearing towards the later parts of the shell (Pl. 4 fig. 7). Interstices finely striated. Lunula elongate and well delimitated. Exterior yellow to red-brown, darker towards the margins, with brownish maculations in juveniles. Interior white with yellow and brown-purple margin.

Distribution and ecology. — Tropical central Indo-West Pacific: Philippines, Indonesia (Moluccas), Palau, Papua New Guinea and Solomon Islands (Vidal, 1996; 1999a). Present material all collected dead in 4-82 m. It appears to prefer sand, silt and mud bottoms in coral reef environments and has been found littorally and sublittorally.

Remarks. — All material encountered is juvenile. Although compared by Vidal (1996) with *V. orbita* s.l., shell shape and colouration are in fact more related to *Vasticardium elongatum elongatum* (Bruguière, 1789), which has been found sympatric with *V. papuanum*, for instance in nearby Calitoban Island (coll. TP). It proved to be one of the most frequently sampled cardiids during the 2005 Indonesian Pulau Seribu Expedition, found in 5-35 m (ZMA, TP unpubl. data). This locality implies a westward range extension. As a fossil it is known from the Late Pliocene of Niue and the Cook Islands (Vidal, 1996; Paulay, 1996 – as *Vasticardium* n.sp.). The species is thought to have experienced a range contraction since the Plio-Pleistocene caused by habitat loss associated with tectonic uplift (Paulay, 1996).

Cardiinae Lamarck, 1809

Remarks. — The dismantling and modifying of Cardiinae, the type subfamily of the Cardiidae, has been an ongoing process for two centuries. The latest major amendments were by Schneider (2002), who demonstrated that Cardiinae, as usually construed, is paraphyletic (see also Trachycardiinae remarks). The results of his cladistic analysis led him to restrict the following (sub)genera to Cardiinae: *Cardium*, *Bucardium*, *Vepricardium*, *Dinocardium* (extant, together forming one subclade), *Planicardium*, *Chesacardium* (both extinct, forming a second subclade), *Acanthocardia* s.s. and *A.* (*Rudicardium*) (extant, forming a third subclade). The identity of the type species of the type genus, *Cardium costatum* Linnaeus, 1758, has recently been elucidated (Ter Poorten, 2007b).

Vepricardium Iredale, 1927

Pectunculus Mörch, 1853: 33 (non Da Costa, 1778). Type species by subsequent designation (von Martens, 1870: 586): *Cardium asiaticum* Bruguière, 1789; Recent, 'Indiae orientalis' (Central Indo-West Pacific).

Vepricardium Iredale, 1929b: 338, pl. 37 fig. 5. Type species by original designation: *Vepricardium pulchricostatum* Iredale, 1929b [= *Cardium multispinosum* G.B. Sowerby 2nd, 1839]; Recent, Caloundra, Queensland, Australia.

Diagnosis. — Shell medium to large, inflated, rounded and equilateral. Strong radial ribs, carrying variously shaped spines, tubercles or radial lamellae along their crests. Cardinal teeth in right valve connected by a high saddle, separate in left valve. Lunula large and broad, often with prominent lunular heart; escutcheon well developed. Shell resorption in umbonal cavity. Shell surface often partly covered with a microsculpture of minute pustules. Colour usually white or

cream, becoming pink towards margins, lunula and escutcheon. Guard tentacles on incurrent and excurrent aperture carrying ocular organs on their tip.

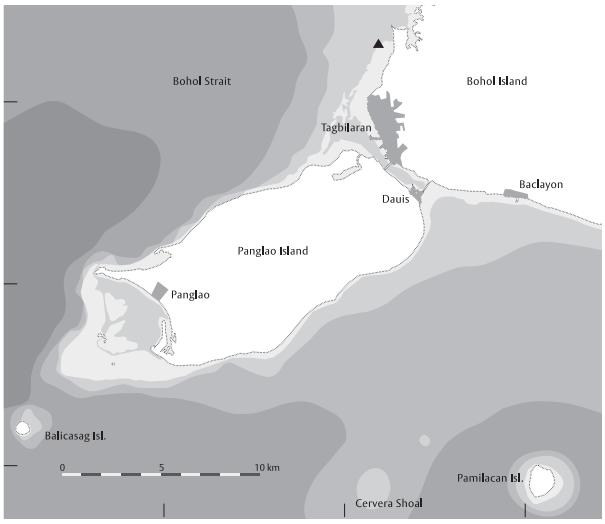
Distribution. — Eocene to Recent, South-African, Indo-Pacific; littoral-sublittoral.

Remarks. — The peculiar process of shell resorption, uniting *Cardium* and *Vepricardium*, was discussed by Savazzi (1985). The genus was revised by Voskuil & Onverwagt (1988) and Vidal (2000b). Whereas Lambiotte (1979) recognised only four species, this number has currently risen to nine (Ter Poorten & Dekker, 2002).

Vepricardium incarnatum (Reeve, 1844)

Pl. 6 figs 1-2

Cardium incarnatum Reeve, 1844: sp. 2, pl. 1 fig. 2.
Cardium mirabile Deshayes, 1855: 332.



Material examined. — **Philippines**: PMBP 2004, Stn R62, 2-15 m, 1 pv (A).

Description. — Shell large (H 50-64 mm), solid, inflated, nearly circular and equilateral, Circa 21-30 strong radial ribs, rounded triangular shaped, carrying close-set twisted rugae, posteriorly interconnected, forming an irregular calcareous palisade. Rib sculpture highly allomorphic: in early ontogeny consisting of distantly placed, rounded tubercles on the entire shell. Interstices rather narrow, rib impressions readily visible internally. Shell surface partly covered with microscopic pustules. Lunula large, but rather small lunular heart barely defined, escutcheon overlapping in right valve. Exterior colour yellowish-cream, pink towards the margins. Middle part of the shell often with ferruginous deposit on interstices, reflecting interior shell resorption. Interior white with pinkish margin, mainly posteriorly and below the ligament.

Distribution and ecology. — Imperfectly known, so far confined to the central Indo-West Pacific with records from Taiwan (Lee, 1989), Vietnam (Hylleberg & Kilburn, 2003), the Philippines (Vidal, 2000b) and Indonesia (Dharma, 2005: pl. 105 fig. 4, as *Bucardium asiaticum*). Due to confusion with other taxa, literature data are doubtful and need confirmation. The sole PMBP 2004 specimen is immature and was taken alive in 2-15 m on a hard bottom with patches of sediment.

Remarks. — This species was described from Manila Bay, Philippines, from which country the vast majority of the known records originate. It most closely resembles *V. multispinosum* (G.B. Sowerby 2nd, 1839), which was also described from the Philippines ('Mindanao and Cebu') but was not collected by PMBP 2004. The same applies to a third congener of Philippine (Bantayan Island) origin: *V. rubrohamatum* Voskuil & Onverwagt, 1988, which is known from Panglao as well (table 2). Both species are easily differentiated by their higher rib number: 31-41 for *V. multispinosum* and 45-51 for *V. rubrohamatum*. Smith (1885) reported *V. incarnatum* (as *Cardium* (*Bucardium*) *mirabile*) from the Philippines, Visayan Sea, in mud at a depth of 12-20 fathoms and gave a detailed illustration.

Orthocardiinae Schneider, 2002

Remarks. — Schneider (2002) included two extant genera in his recently erected subfamily, viz. *Afrocardium* Tomlin, 1931 and *Europicardium* Popov, 1977. Schneider (2002) showed that *Afrocardium* shares no derived characters, either conchological or anatomical, with any member of the Fraginae. Furthermore he demonstrated a close affinity with the extinct genus *Agnocardia* Stewart, 1930, for instance because of the shared slightly concave nature of the ribs, rib ornamentation that is entirely microstructurally discontinuous with the outer shell layer and a ribbing pattern of alternating strength in early juveniles. Together, *Afrocardium* and *Agnocardi*a form a tropical Tethyan clade. *Freneixicardia* Schneider, 2002 is a third included genus (hitherto known from the Eocene and Lower Oligocene of Europe and Egypt), where this specific ribbing pattern is present throughout ontogeny, and which in this paper is considered extant as well.

Afrocardium Tomlin, 1931

Afrocardium Tomlin, 1931: 449-450 (as a subgenus of *Fragum).* Type species by original designation: *Fragum* (*Afrocardium*) *shepstonense* Tomlin, 1931; Recent, Port Shepstone, Kwazulu-Natal, South Africa.

Diagnosis. — Shell small, rather fragile, submodioliform to circular, inflated and strongly inequilateral. Posterior margin digitate. Circa 36-43 low radial ribs, slightly concave with a central groove; in juveniles of alternating strength. Ribs elaborately ornamented with often irregular squamose or spinose scales. Interstices with commarginal striae. Colour highly variable.

Distribution. — Middle Eocene to Recent, Mediterranean, South African, Indo-Pacific, Japonic; littoral-sublittoral.

Remarks. — A poorly understood genus represented by

relatively few species, often misidentified in the literature. It used to be placed in the subfamily Fraginae, as a separate genus (Vidal, 2000a), as a subgenus of *Ctenocardia* H. & A. Adams, 1858 (Keen, 1951, 1969, 1980) or as a synonym of *Plagiocardium* Cossmann, 1886 (Popov, 1977).

Afrocardium exochum (Melvill in Melvill & Standen, 1907)

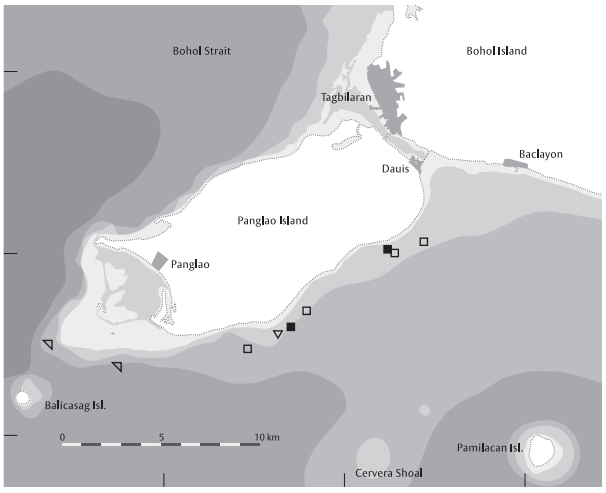
Pl. 5 fig. 5, pl. 6 fig. 3-5

Cardium (*Acanthocardia*) *exochum* Melvill in Melvill & Standen, 1907: 838, pl. 53 fig. 6.

Cardium radula Thiele & Jaeckel, 1931: 227, pl. 4 [9] fig. 99 (non Deshayes 1832, nec Broderip & G.B. Sowerby 1st, 1829).

Cardium (*Trachycardium*) *infantule* Nomura & Zinbô, 1934: 156, pl. 5, figs 17a-b.

Laevicardium (*Trachycardium*) *thielei* Fischer-Piette, 1977: 55 (nom. nov. for *Cardium radula* Thiele & Jaeckel, 1931 non Deshayes 1832, nec Broderip & G.B. Sowerby 1st, 1829).



Material examined. — **Philippines**: PMBP 2004, Stn D15, 53-63 m, 3 v; Stn T1, 83-102 m, 6 v; Stn T4, 82 m, 7 pv (A), 23 v; Stn T5, 84-87 m, 2 v; Stn T6, 34-82 m, 1 pv (A), 19 v; Stn T28, 80 m, 4 v; Stn T44, 83-86 m, 4 v.PANGLAO 2005, Stn DW 2339, 164-176 m, 1 v; Stn DW 2370, 92-96 m, 2 v; Stn CP 2380, 150-163 m, 4 v; Stn DW 2400, 111-115 m, 1 v.

Description. — Shell small (L 5-9 mm), rather thin shelled, nearly circular, inequilateral with umbo noticeably curved towards anterior and well inflated. Posterior margin markedly digitate. Hinge heavily compressed anteriorly, extended and curved posteriorly. Circa 35-45 low radial ribs, slightly concave with a central groove. In early juveniles ribs of alternating width (Pl. 5 fig. 5; Schneider, 2002: fig. 8a). Ribs delicately sculptured with dense imbricated scales. Interstices small with fine commarginal striae. Exterior colouration whitish, posterior often orange-brown or pink; interior white or with pink posterior half.

Distribution and ecology. — Tropical Indo-West Pacific from South Africa (coll. TP), Tanzania (Thiele & Jaeckel, 1931), Persian Gulf (Melvill & Standen, 1907), Myanmar (ANSP, det. TP), Japan (Matsukuma, 2000), Indonesia (Ter Poorten, 2007a), Guam (Paulay, 2003) and Vanuatu (MNHN, det. TP). Depth range of present material: 34-176 m (dead), 34-82 m (alive). Occurs rather locally south of Panglao. Both live taken samples (stns T4, T6) were associated with sponges.

Remarks. — The poorly recognized status of the species probably results from the relatively small size and scarcity. Hence, the available distributional data are rather scattered and incomplete. It probably ranges throughout the Indo-West Pacific. In contrast to its sole congener, *A. richardi* (Audouin, 1826), during PMBP 2004 it was found exclusively in a narrow sublittoral zone by trawling/dredging off southern Panglao, suggesting more specific ecological preferences and rather limited intraspecific variability.

Afrocardium richardi (Audouin, 1826)

Pl. 5 fig. 6, pl. 6 fig. 6-10

Cardium richardi Audouin, 1826: 51 [refers to Savigny, 1817: pl. 9 fig. 14].

Cardium carditaeforme Reeve, 1845: sp. 127, pl. 22 fig. 127.

Cardium arabicus Issel, 1869: 77.

Cardium skeeti Hedley, 1906: 476, pl. 38 fig. 25.

Cardium (*Fragum*) *crenelloides* Melvill, 1909: 75, 134, pl. 5 fig. 13.

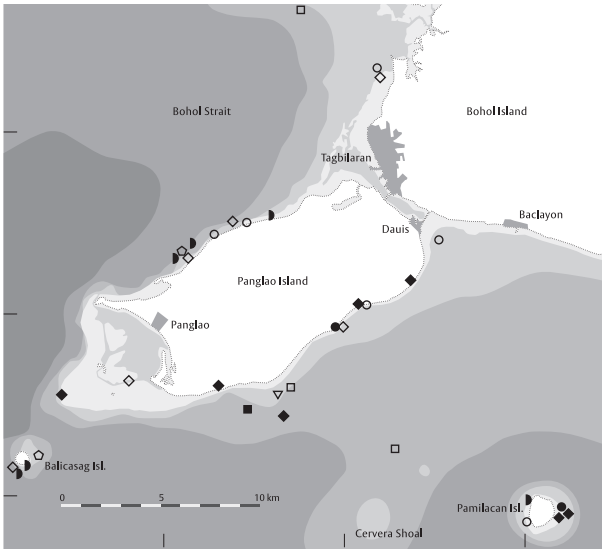
Cardium (*Fragum*) *roseolum* Melvill, 1909: 134, pl. 5 fig. 14.

Cardium (*Fragum*) *rubescens* E.A. Smith, 1911: 317-318, fig.

Cardium euglyptum G.B. Sowerby 3rd, 1914: 480, pl. 19 fig. 14.

Cardium ebaranum Yokoyama, 1927: 430-431, pl. 48 fig. 15.

? *Fragum* (*Afrocardium*) *shepstonense* Tomlin, 1931: 449-450, pl. 33 fig. 8.



Material examined. — **Philippines**: PMBP 2004, Stn B1, 1 v; Stn B2, 5 m, 1 pv (A); Stn B4, 24 m, 3 pv (A), 1 v; Stn B5, 4 m, 1 pv (A); Stn B7, 4-30 m, 2 pv (A), 6 v; Stn B9, 8-10 m, 1 v; Stn B10, 3-14 m, 2 v; Stn B11, 2-4 m, 2 pv (A), 1 v; Stn B12, 24-27 m, 1 v; Stn B17, 3-21 m, 2 v; Stn B19, 17 m, 1 pv (A); Stn B20, 2-8 m, 2 pv (A); Stn B24, 38 m, 1 pv (A); Stn B25, 16 m, 1 pv (A); Stn B39, 17-25 m, 2 pv (A); Stn B40, 22 m, 2 v; Stn B41, 17-19 m, 1 v; Stn D15, 53-63 m, 4 v; Stn L46, 90-110 m, 8 pv (A); Stn L50, 120 m, 2 pv (A); Stns

L51-60, 43-62 m, 11 pv, 2 v (A); Stns L65-68, 55-81 m, 36 pv (A), 9 v; Stns L69-73, 90-98 m, 6 pv (A), 6 v; Stns L74-75, 120-139 m, 10 pv (A), 2 v; Stn L76, ca. 80 m, 37 pv (A), 5 v; Stn P3, ca. 100 m, 1 v; Stn P4, 80-120 m, 5 pv, 6 v; Stn S1, 5 m, 1 pv, 5 v; Stn S10, 6-14 m, 1 pv (A); Stn S13, 8-15 m, 7 v; Stn S14, 5-12 m, 4 v; Stn S16, 15-18 m, 1 v; Stn S17, 6 m, 1 pv (A); Stn S21, 4-12 m, 2 pv, 44v; Stn S22, 15-20 m, 1 pv, 8 v ; Stn S28, 28-32 m, 2 v; Stn T1, 83-102 m, 1 pv (A), 5 v; Stn T4, 82 m, 8 v; Stn T26, 123-135 m, 1 v; Stn T34, 145-163 m, 2 v.

Description. — Shell small to medium (L 10-15 mm), thin shelled, outline highly variable, from submodioliform to oblique quadrangular, strongly inequilateral with beaks towards the anterior and occasionally a slight concave ventral margin. Posterior margin markedly digitate. Hinge line long and bent with posterior laterals far from cardinal teeth. Circa 36-43 low radial ribs, slightly concave with a central groove; in early juveniles of alternating width (Schneider, 2002, fig. 20). Ribs heavily ornamented with often irregular, close-set squamose scales, posteriorly short spinose. Interstices with commarginal striae. Colour extremely variable: often various shades of red-brown, orange, pink, lemon, purple, in the majority with darker streaks posteriorly. Interior colours similarly variable.

Distribution and ecology. —Eastern Mediterranean (Bogi & Galil, 1999), Red Sea (Audouin, 1826), Indo-West Pacific to Vanuatu (MNHN, det. TP), New Caledonia (G.B. Sowerby 3rd, 1914), northern Australia (Hedley, 1906 and WAM, det. TP) and mainland Japan (Matsukuma, 2000). Depth range of present material: 2-163 m (dead), 2-139 m (alive). The PMBP 2004 data indicate that the species occupies a wide ecological and bathymetrical range, essentially in exposed environments. See remarks for further ecological data.

Remarks. — The great variability in shell shape and colour has led to a large number of synonyms, mainly based on differences in outline, colouration and geographic origin, but among which the rib number (35-40), nature of the rib sculpture and constitution of the interstices is invariably very similar. The rich PMBP 2004 material, however, exhibits various intermediate forms.

The unusual shell shape of *A. richardi* is unlike that of most burrowing species (Zuschin & Oliver, 2003) and could be related to an epifaunal habit. *Afrocardium richardi* has a strongly developed byssus (Pelseneer, 1911: pl. 21 fig. 6, as *Papyridea rugata*?), the functionality of which is probably not restricted to early juveniles, as Delongueville & Scaillet (2006) reported a live specimen (5.6 mm) among the lamellae of a *Spondylus*. This could explain its presence in a large portion of dead coral and stone brushing samples (B stns) and the fact that all seven lumun lumun net samples contained live specimens (L stns). An epifaunal nestling habit might account for the extreme variability in shell shape. Also, this is unlike the fragine life habit (no fragines were recovered live from L or T stns) and thus supportive of placement in a different subfamily. Whereas Fraginae have one closed and one ventrally open siphonal aperture, in *Afrocardium* both are closed, as noted by Vidal (2000a: 642). The supposed rarity of the species (Schneider, 1998b: 324) is contradicted by the numerous finds of the 2005 Indonesian Pulau Seribu Expedition (ZMA), being found at the largest number of stations (unpubl. data TP), and those of the PMBP 2004 expedition, being found at 40 stations of which live specimens were taken at 20, representing the highest number of stations for all Cardiidae recorded (table 10). It probably simply reflects an as yet inadequate sampling of its preferred habitat, in combination with a rather small size.

Freneixicardia Schneider, 2002

Freneixicardia Schneider, 2002: 367. Type species by original designation: *Cardium verrucosum* Deshayes, 1829; Middle Eocene, Lutetian, France; Eocene, Egypt; Lower Oligocene, Rupelian, Germany.

Diagnosis. — Shell medium to large, inflated, rounded to obliquely quadrate. Umbos strongly prosogyrous. Ribs of alternating strength throughout ontogeny, except for posterior slope where the ribbing is of similar strength; rip tops flattened. Main ribs strongly ornamented variously with knoblike or pointed spines, smaller ribs showing minute imbricated scales. Cardinal teeth of unequal size.

Distribution. — Middle Eocene to Recent, Indo-Pacific; sublittoral.

Remarks. — Hitherto considered an extinct European genus.

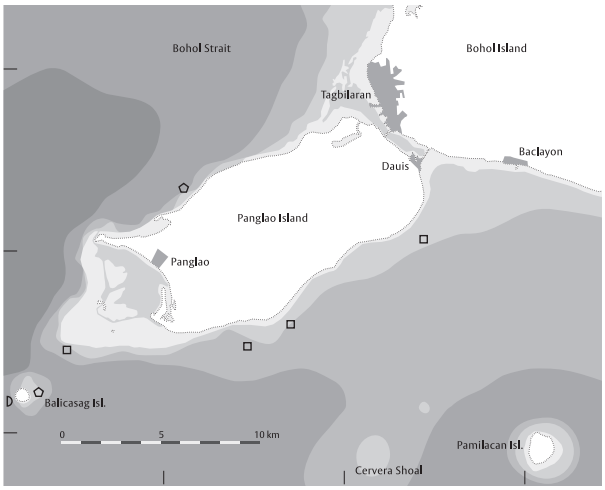
Freneixicardia victor (Angas, 1872) comb. nov.

Pl. 5 fig. 7, pl. 6 figs 11-13

Cardium (*Ctenocardia*) *victor* Angas, 1872: 612, pl. 42, fig. 9.

Cardium (*Trachycardium*) *hulshofi* Pannekoek, 1936: 69-71, pl. 4 figs 48-49, 49a-b, text fig. 10 [†; **syn. nov**.].

Ctenocardia kinai Habe & Murakami, 1970: 8, 2 fig.



Material examined. — **Philippines**: PMBP 2004, Stns L61-64, 87-111 m, 1 v; Stn P3, ca. 100 m, 1 pv; Stn P4, 80-120 m, 1 v; Stn T1, 83-102 m, 6 v; Stn T4, 82 m, 1 v; Stn T5, 84-87 m, 1 v; Stn T38, 80-140 m, 1 v; No Stn nr., Balicasag Isl., tangle nets and lumun lumun, 'deep water', bought from fishermen, 2 v.

Description. — Shell large (H 40-60 mm), solid, inequilateral, obliquely quadrate, elongate and inflated with posterior margin nearly straight. Circa 49-53 flat-topped ribs that are of alternating strength (much more easily observed in worn specimens) except on the posterior slope. Main ribbing strongly spined, broad and irregularly covered by fine scales anteriorly, becoming extremely pointed towards crest of umbonal keel and to a lesser extent on the posterior slope. Intermediate ribs somewhat smaller, these and interstices minutely scaled. Lunula with several spinose ribs. Cardinals unequal, largest very strong and curved upwards, joined by dorsal saddle in right valve. Ventral anterior lateral pointed downwards and truncated, single posterior lateral tooth. Exterior white or cream with orange-red blotches and splashes. Lunula reddish. Interior white with yellow or orange umbonal cavity, sometimes extending up to the margins; exterior colouration vaguely visible from interior.

Distribution and ecology. — Tropical Indo-West Pacific from Mauritius (Angas, 1872), Réunion (coll. TP), Maldives (ZMA), islands south of mainland Japan (Matsukuma, 2000), northern Australia (Lamprell & Whitehead, 1992), New Caledonia (Héros *et al*., 2007) and Vanuatu (MNHN, det. TP). Present material all sublittoral, recovered dead from 80-140 m, often associated with sponges, either trawled or by lumun lumun/tangle nets. Surprisingly, PANGLAO 2005 did not collect this relatively deep water species.

Remarks. — This species has been tentatively referred to *Ctenocardia* by several authors but is atypical in several aspects. The right valve has a single posterior lateral tooth and the alternating broad and small ribs throughout ontogeny do not agree with this genus, nor with any other extant genus. Besides, it would represent the only fragine cardiid that is restricted to deep water and by far the largest Indo-Pacific *Ctenocardi*a. Wilson & Stevenson (1977) and Voskuil (1998), feeling uncomfortable with the commonly used generic allocation, left the generic status in doubt. Molecular analyses by Kirkendale (2009) demonstrated that it consistently fell with distantly related outgroup species instead of with *Ctenocardia*.

In fact, only the extinct *Freneixicardia* has an identical ribbing pattern, with only the ribs posterior to the keel of the same width. Close examination of the type species, *Cardium verrucosum* Deshayes, 1829, shows additional similarities in rib sculpture (the broad ribs being exclusively coarsely sculptured – though easily worn off), hinge (cardinals of unequal size, largest strongly curved; ventral anterior lateral pointed downwards) and outline (subquadrate). A case of convergence cannot be excluded but the similarity of the combination of shell characteristics justifies inclusion in this genus. It implies that *F. victor* should be considered the sole living representative of a genus that originated in the European Eocene. Presumably it represents an Indo-Pacific Tethyan element: an evolutionary pathway that is well-known for *Nemocardium* (Keen, 1950) and has recently been established for *Tridacna* (Harzhauser *et al*., 2007; 2008).

The rib morphology of the Eocene *Cardium asperulum* Lamarck, 1805 also shows similarities (e.g. Tremlett, 1950: pl. 18 figs 18a-b), as indicated by Voskuil (1998), although the rib sculpture is different and more evenly developed; also, the intermediate ribs are unsculptured. The description and figures of *Cardium* (*Trachycardium*) *hulshofi* Pannekoek, 1936 (Lower Miocene of Jawa, Indonesia) agree in all respects with a juvenile *F. victor* and the two are here considered synonymous. Unfortunately, the type material of *C. hulshofi* is not present in ZMA (pers. comm. R.G. Moolenbeek, 02.2008); the geological collection has been partly deposited in Artis (Amsterdam) before being moved to RMNH, where at present it is not yet ready for consultation (pers. comm. F.P. Wesselingh, 09.2008).

Examination of the type material of *Cardium bomasense* Martin, 1917 (Lower Miocene of Jawa, Indonesia; pl. 7 fig. 14) made it clear that this species is also congeneric but differs specifically in its more rounded postero-ventral margin, less pronounced keel and smaller width of the interstices. *Freneixicardia victor* has been recorded from the Upper Miocene of Epi Island, Vanuatu (Abrard, 1946).

Fraginae Keen, 1951

Remarks. — Regarding the taxa treated herein, there is general consensus that they belong in the Fraginae (e.g. Popov, 1977; Keen, 1980; Vidal, 2000a). An exception is *Afrocardium*, which is also usually considered as a fragine cardiid (see remarks under Orthocardiinae). Schneider (1998b) demonstrated that the representatives of the subfamilies Clinocardiinae, Fraginae, Tridacninae and Lymnocardiinae form a monophyletic group. His results further indicate that photosymbiosis with dinoflagellate algae evolved separately in Tridacninae and Fraginae. Within Fraginae, photosymbiosis appears to be restricted to *Corculum*, *Fragum* and *Lunulicardia* (Persselin, 1998; Kirkendale, 2009). Molecular phylogenetic research including all genera did not support a monophyletic Fraginae (Kirkendale, 2009).

Corculum Röding, 1798

Corculum Röding, 1798: 188. Type species by subsequent designation (von Martens, 1870: 586): *Cardium cardissa* Linnaeus, 1758; Recent, 'O. Asiatico' (Indo-West Pacific).

Cardissa Megerle von Mühlfeld, 1811: 52. Type species by monotypy: *Cardissa alba* Megerle von Mühlfeld, 1811; Recent (type locality not mentioned).

Cardissa Swainson, 1840: 373. Type species by monotypy: *Cardissa spinosa* Swainson, 1840; Recent (type locality not mentioned).

Diagnosis. — Shell medium to large, thin, laterally heart-shaped, anterior and posterior slope of variable convexity but always highly compressed, bordered by a smooth to strongly ridged or spinose radial keel. Margins curved, leading to a 'dished' appearance. Offset umbones: one positioned anteriorly, the other posteriorly. Sculpture of faint radial ribs.

Posterior area of a glassy texture.

Distribution. — Late Pliocene to Recent, Indo-Pacific.

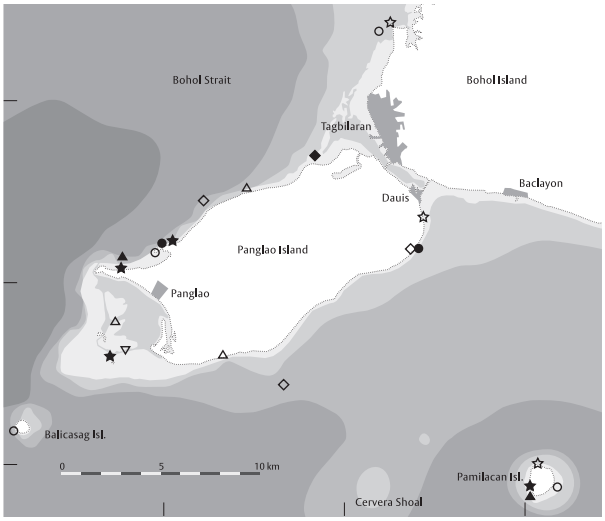
Remarks. — As in Tridacninae and some other genera of Fraginae, *Corculum* exhibits a photosymbiosis with dinoflagellate algae (zooxanthellae), which are present in the gills and mantle tissues under the shell. This photosymbiosis is not only enhanced by major adaptations in the gross shell morphology but also by a very specialised shell microstructure, posteriorly consisting of more or less triangular light-condensing lenses ('windows'), focussing toward the deeper tissues (Carter & Schneider, 1997; Schneider & Carter, 2001) that are of a more highly evolved nature (lenses rather than just non-focussing windows) than in the *Fragum* and *Lunulicardia* taxa studied (Persselin, 1998). Also, the adoption of the photosymbiosis is correlated with a reduction of the digestive structures (Schneider, 1998b).

The distinct shell morphology is an adaptation to an epifaunal shallow water life habit: anteriorly byssally attached (Pelseneer, 1911: pl. 21 fig. 2) to the sandy sediment, offering the best opportunities for maximal exposure to sunlight. Feeding mode and life habit probably also form a depth-limiting factor.

Corculum cardissa (Linnaeus, 1758)

Pl. 10 figs 1-3

Cardium cardissa Linnaeus, 1758: 678.
Cardium humanum, maculis […] Chemnitz, 1782: pl. 14 figs 145-146 (not binominal).
Cardium roseum, testa […] Chemnitz, 1782: pl. 14 figs 147-148 (not binominal).
Cardium monstrosum, testa […] Chemnitz, 1782: pl. 14 figs 149-150 (not binominal).
Cardium impressum Lightfoot, 1786: 155.
Cardium protrusum Lightfoot, 1786: 178.
Cardium roseum Gmelin, 1791: 3245.
Cardium monstrosum Chemnitz: Gmelin, 1791: 3253.
Corculum humanum Röding, 1798: 189, no. 385.
Corculum inflatum Röding, 1798: 189, no. 386.
Corculum dolorosum Röding, 1798: 189, no. 387.
Cardium replicatum Spengler, 1799: 52.
Cardissa alba Megerle von Mühlfeld, 1811: 52-53.
Cardium inversum Lamarck, 1819: 16.
Cardium junoniae Lamarck, 1819: 17.
Cardium dionaeum Broderip & G.B. Sowerby 1st, 1829: 367.
Cardium unimaculatum G.B. Sowerby 1st in Broderip & G.B. Sowerby 1st, 1833: 84-85.
Cardissa spinosa Swainson, 1840: 373.
Cardium aequale Deshayes, 1855: 332.
Cardium productum Deshayes, 1855: 333 (non J. Sowerby, 1832).
Corculum obesum Bartsch, 1947: 224-225, pl. 1 fig. 2.
Corculum levigatum Bartsch, 1947: 226, pl. 1 fig. 1.
Corculum aselae Bartsch, 1947: 226, pl. 2 fig. 1.
Corculum kirai Shikama, 1964: 75, figs 137 (15, 16), 138 (8).



Material examined. — **Philippines**: PMBP 2004, Stn B4, 24 m, 1 v; Stn B7, 4-30 m, 1 v; Stn B8, 3 m, 1 pv (A); Stn B14, 2-4 m, 2 pv (A); Stn D4, 0-2 m, 2 v; Stn M5, 0-2 m, 5 pv (A); Stn M7, 0-3 m, 1 pv (A); Stn M18, 0-1 m, 2 pv (A); Stn M19, 0-2 m, 1 v; Stn M20, 0-2 m, 1 pv (A); Stn M24, 0-1 m, 1 pv; Stn M51, 0 m, 1 pv; Stn R3, 5-24 m, 1 pv (A); Stn R40, 8-33 m, 1 pv (A); Stn R44, 2 m, 1 pv; Stn R48, 4-20 m, 1 pv; Stn R51, 2-52 m, 2 pv (A); Stn S4, 4-30 m, 1 pv (A); Stn S22, 15-20 m, 3 v; Stn S24, 2-4 m, 1 pv (A); Stn S25, 21 m, 1 v; Stn S32, 2-3 m, 1 v; Stn S46, 14 m, 1 v; No Stn nr., Panglao Isl., Momo Beach and vicinity, 'shallow water', bought from fishermen, 2004, gift of B. Olivera, 1 pv.

Description. — Shell medium to large (H 35-70 mm), rather thin and glassy, inequilateral with anterior slope more expanded than posterior, which becomes ventrally concave; shell tumid and excessively flattened, extremely reduced in length; presence of an acute, ridged to spinose radial keel; in lateral view, the shell looks like a stylized heart. Circa 12-18 flattened ribs on each slope, bearing tubercles, sometimes slightly ridged; interstices smooth. Antero-dorsal margin not touching umbo, slightly depressed in front of it; posterior part of hinge with an extremely short nymphal plate and ligament, but a long escutcheon zone. Colour extremely variable: white, lemon-yellow, pink, orange, brown, sometimes with radially aligned purple stripes on the lighter background.

Distribution and ecology. — Tropical Indo-Pacific, excluding Red Sea (Mienis, 2000) and East Africa, from India (Bartsch, 1947), Thailand (coll. TP), Vietnam (Hylleberg & Kilburn, 2003), China (Zhongyan, 2004), islands south of mainland Japan (Matsukuma, 2000), Indonesia (Ter Poorten, 2007a), Queensland (Lamprell & Whitehead, 1992), New Caledonia (Héros *et al*., 2007), Cook Islands (Paulay, 1987) and Pitcairn Islands (Paulay, 1989). Littoral and sublittoral, on sand and coral rubble, at times in association with seagrass, predominantly in exposed but sometimes more protected environments. Depth range of present material 0-52 m (dead and alive).

Remarks. — Due to the unique and attractive shell shape the species has received a lot of attention in the literature. This has led to a large number of synonyms that appear to reflect merely ecophenotypic forms of infrasubspecific status, resulting in a genus that is herein provisionally considered monotypic. Several of these forms, like *Cardium roseum*

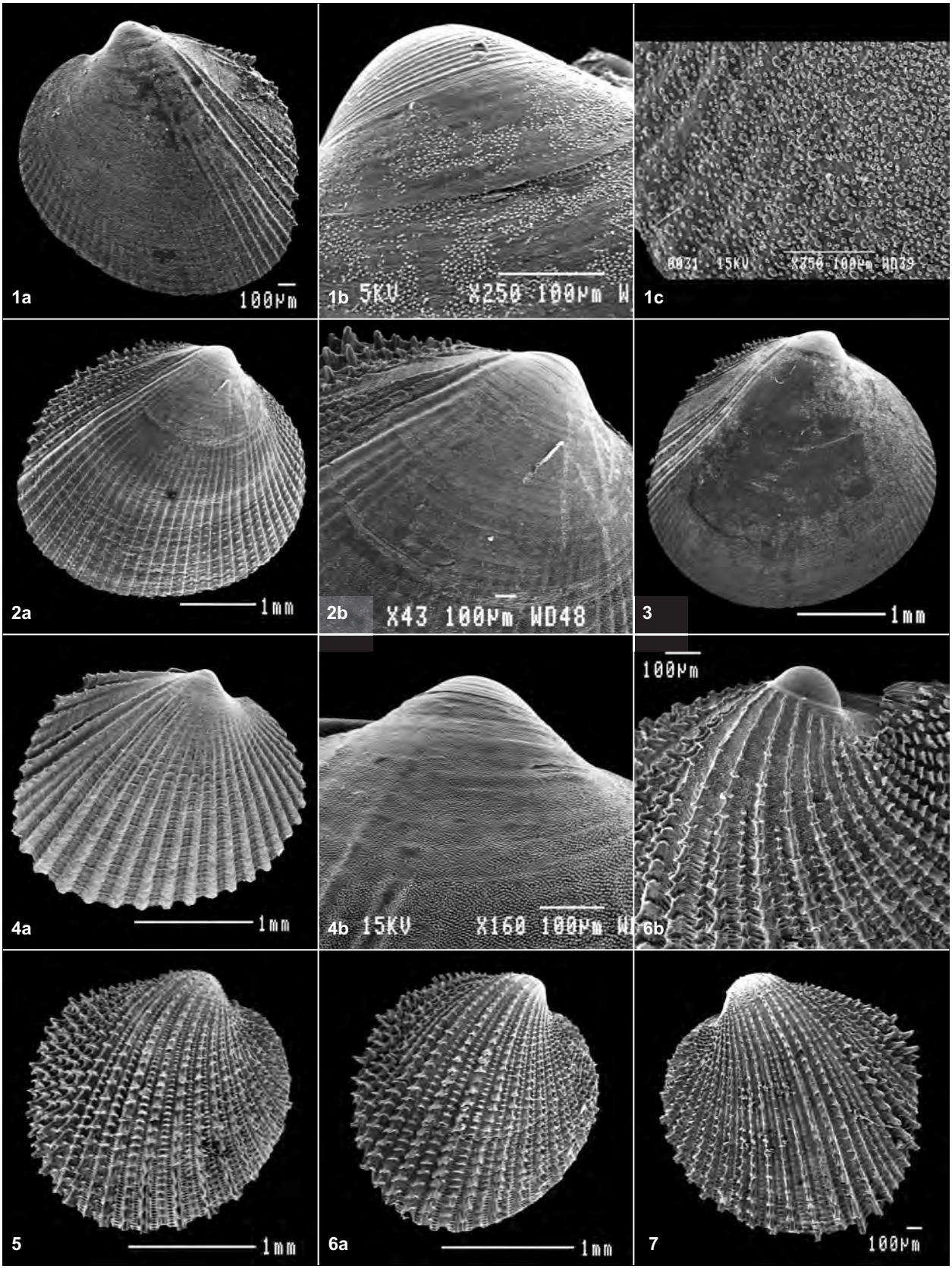


PLATE 5

Figs 1-7. Early ontogenetic stages of various juvenile PMBP 2004 cardiid taxa. Scale bars: 1 mm and 100 µm. **Fig. 1.** *Acrosterigma hobbsae* Vidal, 1999, PMBP 2004 Stns L65-68, lv exterior, umbonal area and antero-ventral slope. **Fig. 2.** *Acrosterigma dianthinum* (Melvill & Standen, 1899), PMBP 2004 Stn B7, rv exterior and umbonal area. **Fig. 3.** *Acrosterigma simplex* (Spengler, 1799), PMBP 2004 Stn B11, rv exterior. **Fig. 4.** *Vasticardium angulatum* (Lamarck, 1819), PMBP 2004 Stn S7, rv exterior and umbonal area. **Fig. 5.** *Afrocardium exochum* (Melvill in Melvill & Standen, 1907), PANGLAO 2004 Stn T4, rv exterior. **Fig. 6.** *Afrocardium richardi* (Audouin, 1826), PANGLAO 2004 Stns L69-73, rv exterior and umbonal area with prodissoconch. **Fig. 7.** *Freneixicardia victor* (Angas, 1872) comb. nov., PANGLAO 2004 Stns L61-64, lv exterior.

PLATE 6

Figs 1-2. *Vepricardium incarnatum* (Reeve, 1844). **1.** PMBP 2004 Stn R62, lv exterior and dorsal, L 29.0 mm. **2.** Philippines, Cavite, Manila Bay, Tanza, Cuming Tour 2005 Stn CT 10 (topotype), lv exterior and interior, H 45.9 mm. **Figs 3-5.** *Afrocardium exochum* (Melvill in Melvill & Standen, 1907). **3.** PMBP 2004 Stn T44, rv exterior and interior, H 7.9 mm. **4.** PMBP 2004 Stn D15, rv exterior, L 5.3 mm. **5.** PMBP 2004 Stn T4, lv exterior and rv hinge, H 7.4 mm. **Figs 6-10.** *Afrocardium richardi* (Audouin, 1826). **6.** PMBP 2004 Stn L76, lv exterior, H 5.8 mm. **7.** PMBP 2004 Stn S22, lv exterior, H 12.0 mm. **8.** PMBP 2004 Stn B20, lv exterior and rv interior, H 11.5 mm. **9.** PMBP 2004 Stn L76, rv hinge, H 8.6 mm. **10.** PMBP 2004 Stn L76, lv exterior, H 8.1 mm. **Figs 11-13.** *Freneixicardia victor* (Angas, 1872) comb. nov. **11.** Philippines, Bohol, lv exterior, rv interior, dorsal and anterior, H 42.7 mm (TP 161). **12.** PMBP 2004 Stn P3, rv interior and lv exterior, H 19.8 mm. **13.** PMBP 2004, s/n, Balicasag Isl., tangle nets and lumun lumun 'deep water', from fishermen, gift B. Olivera, rv exterior, H 31.0 mm. **Fig. 14.** *Freneixicardia bomasense* (Martin, 1917) comb. nov. Indonesia, Jawa, West Progo Beds near Kembang Sokkoh. Lower Miocene, lv exterior, H 18 mm (Syntype RGM 5482a).

Gmelin, 1791 and *Cardium aequale* Deshayes, 1855 invariably are lacking almost any shell windows and have slightly different shell characters. Whether these taxa originate from moderately deep water – therefore to a lesser extent depending on symbiotic algae, if at all – is still unresolved. More comprehensive and targeted sampling at various depth intervals and rigorous analysis that should include DNA data is needed to elucidate this problem.

Remarkably, practically all PMBP 2004 samples clearly represent the typical large and rather pale coloured cardissa form with a prominent sculptured keel and regularly arranged shell windows on the posterior shell half, except for one of the stn R51 specimens (pl. 10 fig. 3) that completely lacks the posterior windows and has a nearly smooth umbonal keel. It derives from the deepest *Corculum* station.

Fragum Röding, 1798

Fragum Röding, 1798: 189. Type species by absolute tautonomy *Fragum flavum* Röding, 1798 [= *Cardium fragum* Linnaeus, 1758]; Recent, 'O. Asiatico, Americano' (Indo-West Pacific, restricted to Ambon, Indonesia by Wilson & Stevenson, 1977).

Hemicardium Swainson, 1840: 373 (non Spengler, 1799). Type species by subsequent designation (J.E. Gray, 1847: 185): *Cardium unedo* Linnaeus, 1758; Recent (type locality not mentioned).

Diagnosis. — Shell small to large, triangular or trapezoidal, inflated, with longitudinal medio-posterior angulation of variable strength. Posterior margins strongly serrated. Ribs ornamented with scales or tubercles. Lunula and escutcheon poorly defined. Hinge not parallel to the ventral margin, often short and rather angled. Cardinal teeth about equal in both valves, joined dorsally in right valve.

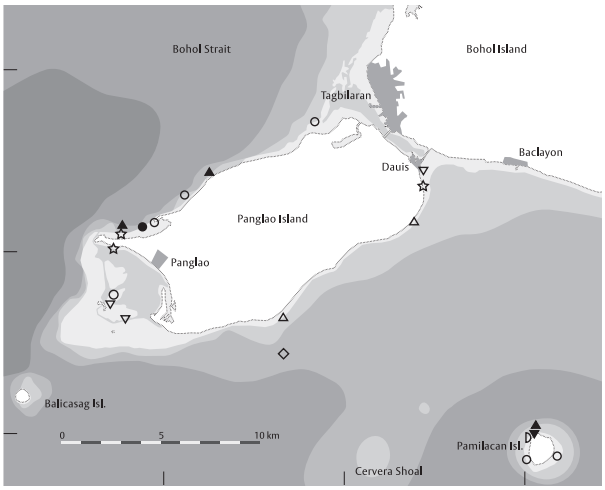
Distribution. — Miocene to Recent, Indo-Pacific, South African, Japonic.

Remarks. — Most species exhibit large intraspecific variation that may complicate identification, particularly of worn juvenile material. See remarks under the respective species. Persselin (1998) argued that several taxa, e.g. *Fragum mundum* (Reeve, 1845) and *F. nivale* (Reeve, 1845), have shell windows and a posterior shell pigmentation and microstructure that is almost as complex and only slightly different from that of *Corculum cardissa* (Linnaeus, 1758), representing an adaptation for harbouring endosymbiotic zooxanthellae (Schneider, 1998b). The presence of zooxanthellae was initially reported in two other congeners: *F. fragum* (Linnaeus, 1758) and *F. unedo* (Linnaeus, 1758) (Kawaguti, 1983) but it turns out that all *Fragum* taxa are photosymbiotic. Nevertheless, molecular research has shown clearly that the genus is paraphyletic (Kirkendale, 2009).

Fragum fragum (Linnaeus, 1758)

Pl. 7 figs 1-2

Cardium fragum Linnaeus, 1758: 679.
Cardium imbricatum Born, 1778: 29-30.
Fragum flavum Röding, 1798: 189, no. 389.



Material examined. — **Philippines**: PMBP 2004, Stn B4, 24 m, 1 v; Stn D1, 2 m, 3 v; Stn D4, 0-2 m, 2 v; Stn D5, 0-2 m, 2 v; Stn D9, 2-4 m, 3 pv (A); Stns L65-68, 55-81 m, 1 v; Stn M5, 0-2 m, 2 v; Stn M9, 0.5 m, 1 v; Stn M51, 0 m, 1 v; Stn R7, 5-22 m, 1 pv; Stn R18, 2-46 m, 1 pv; Stn R19, 2-54 m, 4 pv (A); Stn R36, 3-32 m, 5 pv (A); Stn R51, 2-52 m, 2 pv (A); Stn S6, 1-4 m, 15 v; Stn S8, 28-32 m, 2 v; Stn S9, 3 m, 1 v; Stn S14, 5-12 m, 1 pv, 7 v; Stn S18, 0-2 m, 1 pv (A); Stn S22, 15-20 m, 4 v; Stn S23, 2 m, 9 v.

Description. — Shell medium (H 25-45 mm), solid, inequilateral, trapezoidal in outline; posterior slope demarcated from the rest of the shell by a sharp radial angulation, steeply sloping, forming a postero-ventral angle of circa 75°-90°. Posterior margin nearly straight, anterior margin convex and dilated. Circa 32 (20 anteriorly, 12 posteriorly) flattened ribs with close set transverse curved scales, becoming coarser anteriorly. Interstices narrow, smooth; antero-dorsal margin erect and touching umbo. Colour uniform white to cream-yellow; interior white, commonly with two yellow-orange stripes.

Distribution and ecology. — Throughout the tropical Indo-Pacific (except the Red Sea) from south-east Africa (coll. TP), to southern Japan (Matsukuma, 2000), northern Australia (Lamprell & Whitehead, 1992), and eastwards to the Tuamotu Islands (Richard, 1982). Littoral and sublittoral. Depth range of present material 0-81 m (dead), 0-54 m (alive) in open coral reef with sand and mixed bottoms; in addition found dead in seagrass bottoms.

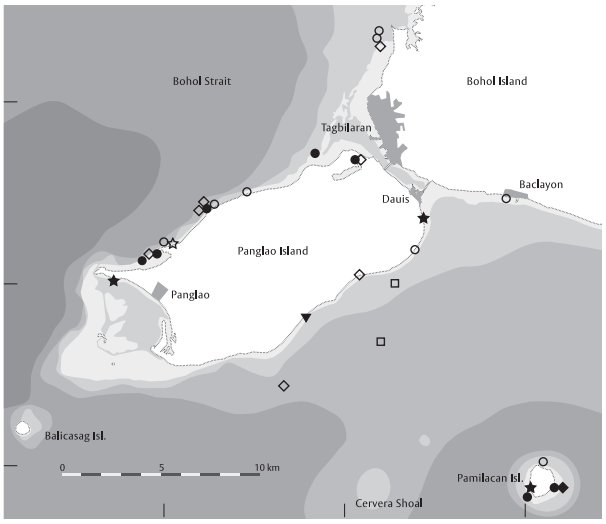
Remarks. — Like many Fraginae species *F. fragum* hosts symbiotic zooxanthellae, which may partly explain its restriction to mostly shallow water communities like inner reef habitats, consisting of moats and lagoons (Paulay, 1987). According to Schneider (1992, 1998b: fig. 13), it has a byssus that is functional in the adult. The closely related congener *F. nivale* (Reeve, 1845) has a semi-infaunal life habit, living with the flattened postero-dorsal area orientated to the surface of sand flats in lagoons and other sheltered sites (Zuschin &

Oliver, 2003). It replaces *F. fragum* in the Red Sea, with which it is sympatric in western Indian Ocean localities. Although the type material supposedly originates from the Philippines ('Island of Corrigidor'), its true range is probably confined to the western Indian Ocean. *Fragum fragum* is extremely abundant in the shallow sandy borders of the lagoon of Anaa (Tuamotu Islands), a closed 25 x 5 km atoll with an estimated population of 600 million individuals and densities of up to 560 per m^2 (Richard, 1982). *Fragum fragum* is occasionally collected for consumption and shellcraft purposes in the Philippines.

***Fragum mundum* (Reeve, 1845)**

Pl. 7 figs 3-4, pl. 8 fig. 3

Cardium mundum Reeve, 1845: sp. 125, pl. 22 fig. 125.
Cardium arcuatulum G.B. Sowerby 3rd, 1874: 721, pl. 59 fig. 10.
Fragum thurstoni Dall, Bartsch & Rehder, 1938: 154-155, pl. 41 figs 9-10.



Material examined. — **Philippines**: PMBP 2004, Stn B4, 24 m, 2 v; Stn B5, 4 m, 1 v; Stn B8, 3 m, 2 v; Stn B11, 2-4 m, 1 pv (A), 3 v; Stn B20, 2-8 m, 8 v; Stn B32, 20 m, 1 v; Stn B34, 1-2 m, 2 v; Stn B42, 30-33 m, 1 v; Stn D8, 1-4 m, 1 pv (A); Stn M7, 0-3 m, 3 v; Stn M9, 0.5 m, 3 pv (A); Stn M20, 0-2 m, 1 pv (A); Stn M51, 0 m, 1 pv (A), 1 v; Stn S2, 4-5 m, 3 v; Stn S4, 4-30 m, 3 v; Stn S5, 2-4 m, 3 pv (A), 8 v; Stns S6-S7, 1-4 m, 1 pv (A), 9 v; Stn S12, 6-8 m, 1 pv (A); Stn S14, 5-12 m, 1 pv (A); Stn S16, 15-18 m, 4 v; Stn S18, 0-2 m, 2 pv (A), 3 v; Stn S21, 4-12 m, 1 v; Stn S22, 15-20 m, 2 pv (A), 44 v; Stn S24, 2-4 m, 3 v; Stn S25, 21 m, 35 v; Stn S28, 28-32 m, 4 v; Stn S32, 2-3 m, 1 pv (A), 7 v; Stn S34, 2 m, 1 pv (A), 2 v; Stn S43, 2-3 m, 3 v; Stn T27, 106-137 m, 1 v; Stn T28, 80 m, 1 v.

Description. — Shell very small to small (H 5-12 mm), very inequilateral, rather solid, trapezoidal with rounded anterior margin and straight to slightly concave posterior margin and a sharp longitudinal angulation, forming a postero-ventral angle of circa 65-80°. Circa 26-30 radial ribs (of which 9-10 on posterior slope); ribs flat with more or less imbricate rather crowded scales on top, becoming spiny on the posterior slope; interstices narrow, finely striated; antero-dorsal margin not touching umbo, slightly depressed near it. Hinge plate broad, hooked basement of the anterior lateral. Exterior and interior cream to yellow (seldom with pinkish streaks posteriorly) with semi-translucent green-greyish or tan spots, of the same width as the ribs, acting as shell windows. The windows are associated with well-defined interior convexities in the umbonal keel region. Juveniles of 2-3 mm are generally more subquadrate and less angular.

Distribution and ecology. — Tropical West Pacific, from Amami Islands and southward (Higo *et al*., 1999) to Guam (Paulay, 2003), Indonesia (Ter Poorten, 2007a), New Caledonia (Héros *et al*., 2007), Cook Islands (Paulay, 1987), Hawaii (Kay, 1979), the Tuamotu archipelago (coll. TP) and Pitcairn Islands (Paulay, 1989). Littoral and sublittoral, mainly on sand and mud bottoms in exposed coral reefs and occasionally seagrass environments. Depth range of present material 0-137 m (dead), 0-20 m (alive).

Remarks. — Probably due to its small size and relative scarcity, distribution reords are patchy. Sometimes confused with juveniles of congeneric species, like *F. fragum* and *F. scruposum* (Deshayes, 1855), in part because of the great variability of the postero-dorsal angle. The generally stronger inequilateral shape of the present species permits taxonomic separation. According to Kay (1979: 555) this species is 'common in shallow water, occurring singly nestling in the algal-sand mat of tide pools and shoreward on fringing reefs'. Paulay (1996: 47) reported it from Niue and considered it an 'inner-reef-specialist', a micro-habitat which in Niue consists of an intertidal to shallow subtidal reef pavement with pockets of coarse sediments (not to be confused with habitat category B, described above, which is not dominated by hard substrata).

***Fragum scruposum* (Deshayes, 1855)**

Pl. 7 figs 5-8, pl. 8 fig. 2

Cardium scruposum Deshayes, 1855: 333.
Hemicardium (*Fragum*) *fragum* var. *carinata* Lynge, 1909: 261, pl. 5 fig. 20 (non *Cardium carinatum* Bronn, 1831).
Fragum whitleyi Iredale, 1929a: 264, pl. 30 fig. 14.
Corculum (*Fragum*) *bannoi* Otuka, 1937: 138-139, figs 54a-b.
Fragum loochooanum Kira, 1959: 137, pl. 54 fig. 13.

Material examined. — **Philippines**: PMBP 2004, Stn B4, 24 m, 2 v; Stn B5, 4 m, 1 v; Stn B8, 3 m, 2 v; Stn B11, 2-4 m, 1 pv (A), 3 v; Stn B20, 2-8 m, 8 v; Stn B32, 20 m, 1 v; Stn B34, 1-2 m, 2 v; Stn B42, 30-33 m, 1 v; Stn D8, 1-4 m, 1 pv (A); Stn M7, 0-3 m, 3 v; Stn M9, 0.5 m, 3 pv (A); Stn M20, 0-2 m, 1 pv (A); Stn M51, 0 m, 1 pv (A), 1 v; Stn S2, 4-5 m, 3 v; Stn S4, 4-30 m, 3 v; Stn S5, 2-4 m, 3 pv (A), 8 v; Stns S6-S7, 1-4 m, 1 pv (A), 9 v; Stn S12, 6-8 m, 1 pv (A); Stn S14, 5-12 m, 1 pv (A); Stn S16, 15-18 m, 4 v; Stn S18, 0-2 m, 2 pv (A), 3 v; Stn S21, 4-12 m, 1 v; Stn S22, 15-20 m, 2 pv (A), 44 v; Stn S24, 2-4 m, 3 v; Stn S25, 21 m, 35 v; Stn S28, 28-32 m, 4 v; Stn S32, 2-3 m, 1 pv (A), 7 v; Stn S34, 2 m, 1 pv (A), 2 v; Stn S43, 2-3 m, 3 v; Stn T27, 106-137 m, 1 v; Stn T28, 80 m, 1 v.

Description. — Shell small (H 10-15 mm), inequilateral, solid, fairly inflated, subquadrate, with rather sharp (keeled) medio-posterior angulation forming a postero-ventral angle of circa 80-90° and with a rounded anterior margin. Postero-dor-

PLATE 7

Figs 1-2. *Fragum fragum* (Linnaeus, 1758). **1.** PMBP 2004 Stn R36, lv exterior, rv interior and posterior, H 37.2 mm. **2.** PMBP 2004 Stn S23, rv exterior and interior, H 28.1 mm. **Figs 3-4.** *Fragum mundum* (Reeve, 1845). **3.** PMBP 2004 Stn S18, lv and rv exterior, H 7.5 mm. **4.** PMBP 2004 Stn M20, lv exterior and rv interior (with dried animal), H 8.1 mm. **Figs 5-8.** *Fragum scruposum* (Deshayes, 1855). **5.** SANTO 2006 Stn LD34, rv exterior with life animal, size unknown. **6.** PMBP 2004 Stn D5, lv and rv exterior, H 9.4 mm. **7.** PMBP 2004 Stn M18, lv exterior and interior, H 11.2 mm. **8.** PMBP 2004 Stn D1, lv exterior, H 6.0 mm. **Figs 9-11.** *Fragum sueziense* (Issel, 1869). **9.** PMBP 2004 Stn S9, lv exterior and interior, L 8.0 mm. **10.** PMBP 2004 Stn R38, rv interior and lv exterior, L 5.1 mm. **11.** PMBP 2004 Stn S42, rv exterior, L 4.8 mm. **Figs 12-16.** *Fragum grasi* spec. nov. **12.** PMBP 2004 Stn D5, rv and lv exterior, dorsal and anterior, H 5.2 mm (Holotype NMP). **13-15.** PMBP 2004 Stn S9. **13.** rv exterior, H 7.9 mm (MNHN). **14.** rv exterior and interior, L 6.7 mm (MNHN). **15.** lv exterior and interior, L 6.3 mm (MNHN). **16.** Indonesia, West Papua, Waigeo Isl., Dusum Mumes, 29.i.2004, leg. & coll. B. Gras, rv exterior, H 5.5 mm.

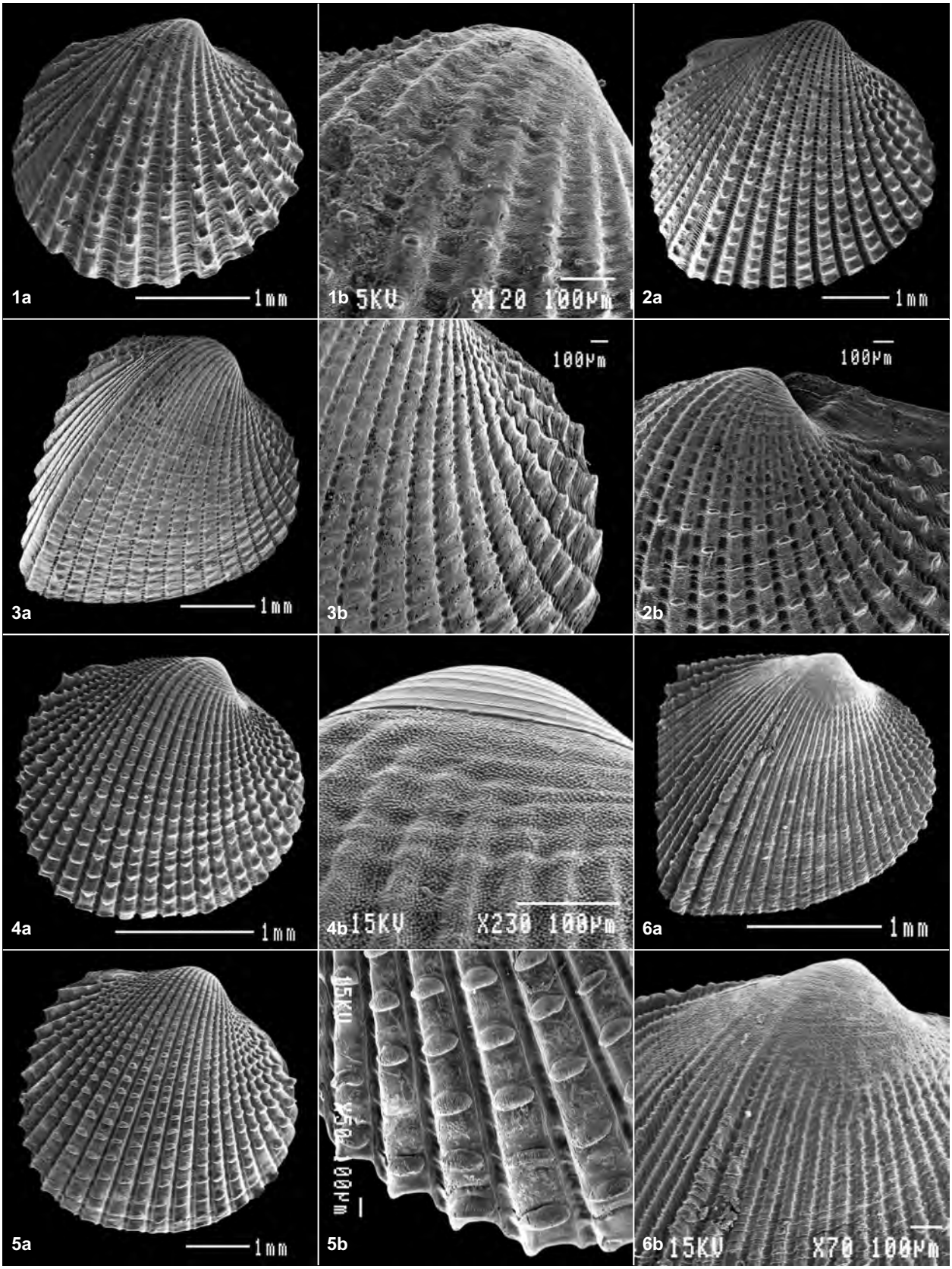
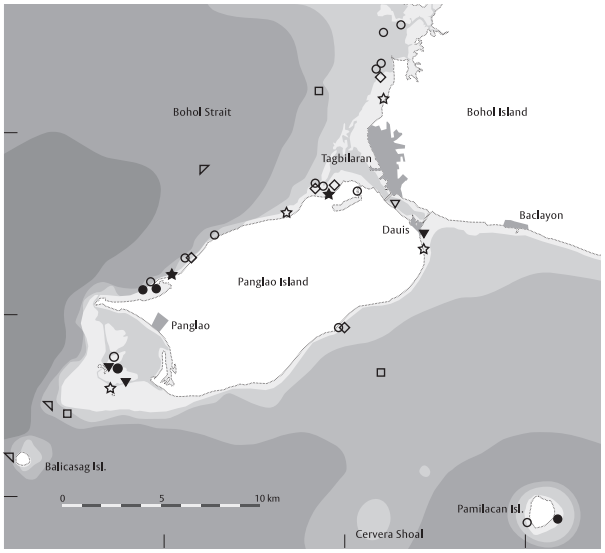


PLATE 8

Figs 1-6. Early ontogenetic stages of juvenile PMBP 2004 *Fragum* and *Ctenocardia* taxa. Scale bars: 1 mm and 100 µm. **Fig. 1.** *Fragum grasi* spec. nov., PMBP 2004 Stn D5, rv exterior and umbonal area. **Fig. 2.** *Fragum scruposum* (Deshayes, 1855), PMBP 2004 Stn D1, rv exterior and umbonal area. **Fig. 3.** *Fragum mundum* (Reeve, 1845), PMBP 2004 Stn B11, rv exterior and anterior slope. **Fig. 4.** *Fragum sueziense* (Issel, 1869), PMBP 2004 Stn D5, rv exterior and umbonal area. **Fig. 5.** *Fragum unedo* (Linnaeus, 1758), PMBP 2004 Stn D5, rv exterior and postero-ventral slope. **Fig. 6.** *Ctenocardia gustavi* Vidal & Kirkendale, 2007, PMBP 2004 Stn B32, rv exterior and umbonal area.



sal margin located at the same line or even extending above the umbo. Circa 18-27 rather well developed radial ribs, usually with straight, coarse scales, becoming coarsely tubercular anteriorly and finely tubercular posteriorly; interstices rather broad and coarsely striated. One or two ribs on keeled angulation occasionally more prominent. Antero-dorsal hinge margin not touching umbo. Normally white, sometimes with patches of cream; juveniles occasionally pink or yellow with pinkish blotches.

Distribution and ecology. — Tropical Indo-West Pacific, excluding the Red Sea, from South Africa (coll. TP) to Japan (Higo *et al*., 1999), Vietnam (Hylleberg & Kilburn, 2003), Guam, (Paulay, 2003), Indonesia (Ter Poorten, 2007a), northern Australia (Lamprell & Whitehead, 1992), New Caledonia (Héros *et al*., 2007) and Vanuatu (MNHN, det. TP). Probably not extending farther into the Pacific. Littoral and sublittoral on sand and mud bottoms, often sheltered habitats in association with seagrass. Depth range of present material 0-210 m (dead), 0-20 m (alive); PANGLAO 2005 111-453 m (dead).

Remarks. — The rib sculpture is highly variable intraspecifically, ranging from rounded tubercles to elongated commarginal scales. *Fragum scruposum* resembles *F. fragum*, but the latter attains much larger sizes and has a higher rib number. Another related species is *F. mundum*, which however is smaller, more sharply angulate with an approximately straight posterior margin and has more flattened ribs with narrow interstices. *Fragum sueziense* (Issel, 1869) is less inequilateral, smaller and has a more rounded postero-ventral margin. *Fragum unedo* (Linnaeus, 1758), when juvenile, is less sharply keeled, has a blunter umbo and has unsculptured interstices.

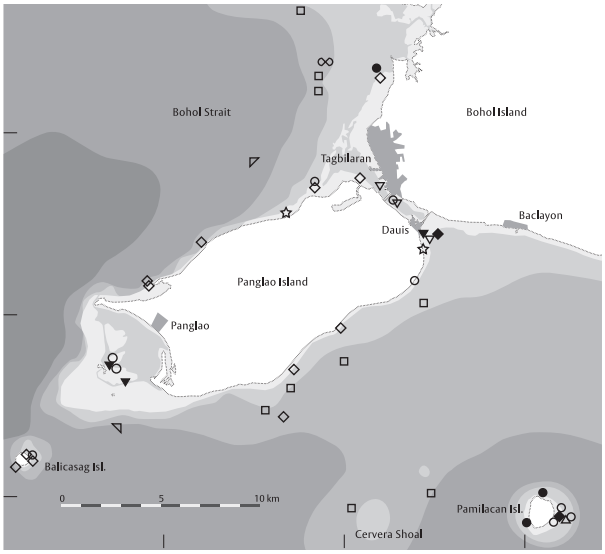
The mostly rather fresh valves from stns S51-53 originate from the brackish Abatan River estuary, representing the only cardiid species from this area. Although no live specimens were collected, this suggests that the species can tolerate lowered salinities. The three valves of the T-stations are much worn and presumably were transported downslope; likewise for the PANGLAO 2005 valves.

Live specimens of *F. scruposum* were found sympatrically with *F. grasi* spec. nov., *F. sueziense* and *F. unedo* at stns D4-5 in a non-exposed littoral environment (0-2 m, habitat type B) consisting of a soft bottom with seagrass.

***Fragum sueziense* (Issel, 1869)**

Pl. 7 figs 9-11, pl. 8 fig. 4

Cardium sueziensis Issel, 1869: 76, 252, pl. 3 fig. 4.
Cardium (*Acanthocardia*) *omanense* Melvill in Melvill & Standen, 1907: 838-839, pl. 53 fig. 5.
Cardium transclathratum Viader, 1951: 143, pl. 3 fig. 7.



Material examined. — **Philippines**: PMBP 2004, Stn B3, 8 m, 1 v; Stn B4, 24 m, 2 v; Stn B6, 12-14 m, 1 v; Stn B11, 2-4 m, 1 pv (A), 1 v; Stn B13, 3-5 m, 2 pv (A); Stn B14, 2-4 m, 9 v; Stn B20, 2-8 m, 1 v; Stn B23, 20-25 m, 158 v; Stn B31, 1-2 m, 1 v; Stn B32, 20 m, 1 v; Stn B35, 31 m, 1 v; Stn B38, 17-18 m, 1 v; Stn B40, 22 m, 2 v; Stn B42, 30-33 m, 1 v; Stn D1, 2 m, 1 pv (A), 12 v; Stn D3, 4-5 m, 1 v; Stn D4, 0-2 m, 1 pv (A), 6 v; Stn D5, 0-2 m, 9 pv (A), 17 v; Stn D12, 2-4 m, 2 pv, 91 v; Stn D13, 2-3 m, 20 v; Stn G1, 100 m, 7 v; Stn M10, 0-3 m, 1 v; Stn M51, 0 m, 1 v; Stn R38, 6-37 m, 1 pv; Stn R68, 3-3.5 m, 1 v; Stn S3, 6 m, 2 pv, 5 v; Stn S4, 4-30 m, 1 pv; Stns S6-S7, 1-4 m, 91 v; Stn S9, 3 m, 2 v; Stn S10, 6-14 m, 4 v; Stn S11, 2 m, 2 pv, 9 v; Stn S12, 6-8 m, 1 v; Stn S14, 5-12 m, 7 pv (A), 85 v; Stn S21, 4-12 m, 1 pv (A), 2 v; Stn S22, 15-20 m, 1 v; Stn S38, 3-4 m, 3 v; Stn S39, 3-4 m, 6 pv, 132 v; Stn S42, 15-20 m, 1 pv (A), 32 v; Stn T2, 152 m, 3 v; Stn T4, 82 m, 2 v; Stn T5, 84-87 m, 1 v; Stn T9, 97-120 m, 2 v; Stn T14, 101-110 m, 6 v; Stn T25, 160-210 m, 1 v; Stn T26, 123-135 m, 36 v; Stn T39, 100-138 m, 1 v; Stn T41, 110-112 m, 2 v. PANGLAO 2005, Stn CP 2331, 255-268 m, 1 v; Stn DW 2339, 164-176 m, 1 v.

Description. — Shell very small to small (H 5-10 mm), rather solid, moderately inflated, outline subquadrate or rounded, generally slightly inequilateral with posterior margin somewhat straightened, but at times equilateral. Circa 22-28 rather low and broad square ribs, topped with tubercles or slightly curved scales, sometimes partly commarginally aligned. Interstices often with concentric striae, varying from close set to quite widely spaced; antero-dorsal margin not touching umbo, with most antero-dorsal part of the shell depressed beside umbo. Shell completely white to cream occasionally with brown-pink spots or 2 purple-brown rays, visible inside and outside, or rarely completely pure lemon-yellow.

Distribution and ecology. — Widely distributed throughout the tropical Indo-West Pacific, including the Red Sea (Oliver, 1992) and South Africa (Kwazulu Natal) to Vietnam (Hylleberg & Kilburn, 2003), north-western Australia (WAM, det. TP), New Caledonia (Héros *et al*., 2007) and the Gilbert Islands (Tarawa) in the West Pacific (Paulay, 2001). Littoral and sublittoral on sandy and muddy bottoms with coral rubble and seagrass. Depth range of present material 0-210 m (dead), 0-20 m (alive); PANGLAO 2005 164-268 m (dead).

Remarks. — This taxon has been placed by several authors in the amphi-Atlantic genus *Parvicardium* (Oliver, 1992, 1995; Hoenselaar & Dekker, 1998; Dekker & Orlin, 2000; Zuschin & Oliver, 2003). Placement in *Fragum* is more appropriate because of the broad and solid hinge plate, the strong hinge, and the depressed area just anterior of the umbo. Juveniles of *F. unedo* (Linnaeus, 1758) can look very similar because of a much less developed medio-posterior angulation in early ontogeny. These can be separated from *F. sueziense* by their postero-dorsal margin located at the same position or even extending well above the umbo, with a stronger incurved area between; by their rib impressions, which are often deeper incised and visible over a longer distance from the interior margin; and by the somewhat stronger, more pointed digitate posterior margin.

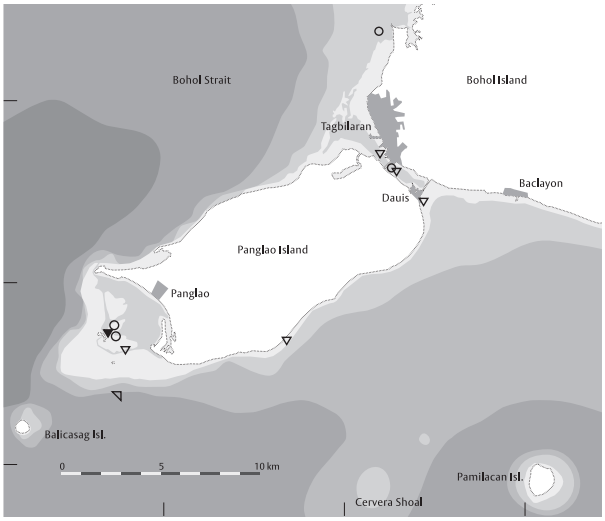
Fragum sueziense proved to be one of the dominant bivalve taxa in the quantitative bulk samples of the northern bay of Safaga, Red Sea, with bottom facies consisting of sand with coral patches, with seagrass and a mangrove channel (Zuschin & Oliver, 2003). Likewise, it outnumbers all PMBP 2004 cardiids in terms of the numbers of specimens and samples (table 10), yet resulting in limited live taken material. The rather uniform distribution over the studied area suggests that it occupies a mosaic of reef and perireef habitats, not 'entirely restricted to relatively turbid, subtidal environments typical of lagoons and large bays', as stated by Kirkendale (2009: 460). The samples of all T-stations consist of rather worn loose valves, which probably had been transported downslope. PANGLAO 2005 resulted in very few valves, demonstrating that the true bathymetric range is more confined to the littoral zone.

Fragum grasi **spec. nov.**

Pl. 7 figs 12-16, pl. 8 fig. 1

Holotype. — PMBP 2004, Stn D5, Panglao Isl., Pontod Islet, 9°33.6'N, 123°43.5'E, soft bottom with seagrass, 0-2 m, alive (with dried animal), 06.vi.2004. 1 pv (A, NMP). Paratypes as listed below.

Other material examined. — **Philippines**: PMBP 2004, Stn B14, 2-4 m, 1 v; Stn D1, 2 m, 5 v; Stn D4, 0-2 m, 57 v; Stn D5, 0-2 m, 1 pv (paratype 1, MNHN 22271), 158 v (paratypes 2-10, MNHN 22276); Stn D6, 3 m, 1 v; Stn D7, 2-3 m, 2 v; Stn D12, 2-4 m, 13 v; Stn D13, 2-3 m, 33 v; Stn S9, 3 m, 88 v; Stn S11, 2 m, 2 pv, 143 v; Stn S25, 21 m, 1 pv, 1 v; Stn S39, 3-4 m, 4 v. PANGLAO 2005, Stn DW 2339, 164-176 m, 2 v. **Indonesia**, West Papua, Waigeo Isl., Dusum Mumes, beached, Stn 22, 29.i.2004, leg. B. Gras, 1 v. (coll. B. Gras, The Netherlands, no catalog number).



Description. — Shell very small to small (H 5-8 mm), rather solid, moderately inflated, outline rounded and slightly inequilateral with umbo just in front of the midline. L/H ratio 0.96-1.03 (mean 1.00, n = 11). Circa 15-21 strong, rounded ribs, regularly sculptured with tubercles or coarse scales, becoming more prominent anteriorly and much weaker posteriorly. Ribbing less pronounced on the posterior slope, of a more irregular strength and occasionally with a secondary riblet. Rib impressions clearly visible throughout shell interior, margins crenulated. Interstices wide, about the same width as ribs, with clearly developed concentric striae. Lunula small, escutcheon almost indiscernible, dorsal margin indented immediately anterior to umbones. Hinge typical for the genus with lateral teeth inequidistant from cardinals, anterior laterals closer than posterior laterals. Hinge plate rather narrow and gently curved. Shell exterior and interior completely dull white or cream.

Distribution and ecology. — Known so far from the Philippines and eastern Indonesia. Found in the littoral zone (mainly low intertidal) on sandy and muddy bottoms, often with seagrass or coral rubble. Depth range of present material 0-21 m (dead), 0-2 m (alive), clearly confined to sheltered, low wave energy environments. These ecological preferences appear to be roughly similar to those of *F. unedo*. However, the holotype (the only live taken specimen, stn D5) was found sympatric with two other congeneric species: *F. scruposum* and *F. sueziense*. The PANGLAO 2005 sample originates from 164-176 m (dead), in all probability not reflecting the natural habitat.

Etymology. — Named after Bavius Gras, who collected the first specimen in Indonesia and subsequently brought it to my attention. It also relates to its preferred seagrass environment.

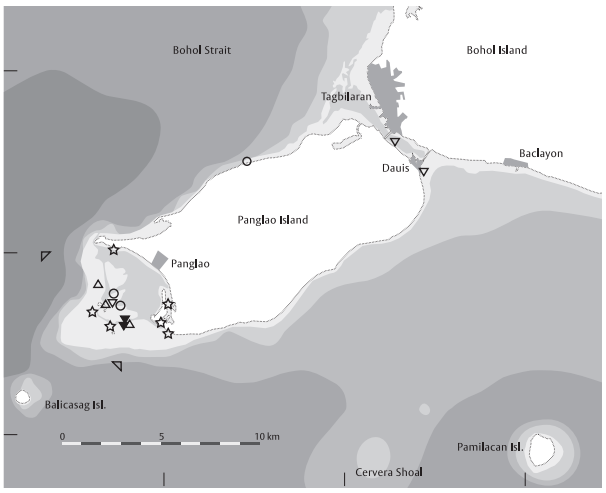
Remarks. — The combination of small size, rounded outline, absence of an umbonal keel, strong visibility of the rib impressions and relatively low rib number readily distinguish this species from its congeners. There is some variation in the nature of the rib sculpture: on some specimens the tubercles become transversely elongate, particularly anteriorly. The

supposed abundance (PMBP 2004 resulted in 5 pv and 506 v, predominantly found in Panglao Bay) might be partly the result of a sampling artefact, the suction sampling technique being a highly effective and quantitatively rewarding method. It could also reflect previous undersampling of seagrass related habitats and small-sized taxa.

Fragum unedo (Linnaeus, 1758)

Pl. 8 fig. 5, pl. 9 figs 1-3

Cardium unedo Linnaeus, 1758: 680.
Cardium cruentum Perry, 1811: pl. 57 fig. 1.
Hemicardium tegulatum Dautzenberg, 1900: 5-8, pl. 1 figs 3-6.



Material examined. — **Philippines**: PMBP 2004, Stn D1, 2 m, 1 v; Stn D4, 0-2 m, 6 pv (A), 18 v; Stn D5, 0-2 m, 17 v; Stn D7, 2-3 m, 2 pv (A), 8 v; Stn D13, 2-3 m, 1 v; Stn M3, 0-2.5 m, 1 v; Stn M9, 0.5 m, 3 v; Stn M17, 0-1 m, 1 pv; Stn M18, 0-1 m, 2 pv; Stn M44, 0 m, 1 v; Stn M47, 0-0.5 m, 3 v; Stn R23, 1-5 m, 4 pv; Stn R32, 4 m, 2 pv; Stn R39, 3 m, 3 pv; Stn S9, 3 m, 24 v; Stn S11, 2 m, 15 v; Stn S16, 15-18 m, 1 v; Stn s/n, Panglao Isl., 2 pv (A), 1 v. PANGLAO 2005, Stn DW 2339, 164-176 m, 1 v; Stn CP 2397, 642-669 m, 1 v.

Description. — Shell medium to large (H 40-65 mm), very solid, inequilateral, subquadrate to trapezoidal, with rounded anterior margin and almost straight strongly digitate posterior margin; posterior slope separated by a non acute angulation (completely lacking or only weakly developed in juveniles). Circa 23-30 ribs, flatly rounded with distantly spaced transverse scales, not covering full rib width; interstices narrow and smooth; antero-dorsal margin erect, touching umbo. Rib impressions deeply incised, particularly posteriorly, visible over a long distance from the interior margin. Exterior white to yellow-cream, scales usually pink to dark red with similar coloured blotches on posterior slope, occasionally whitish. Interior white, exceptionally with a yellowish radial streak posteriorly.

Distribution and ecology. — Central Indo-West Pacific, from Thailand (Lynge, 1909) to mainland Japan (Matsukuma, 2000), northern Australia (Lamprell & Whitehead, 1992) up to Tonga (Poutiers, 1998). Littoral on sandy bottoms, generally with seagrass. Depth range of present material 0-18 m (dead), 0-3 m (alive), almost exclusively in lagoon and other non-exposed environments, generally in the lower part of the intertidal zone and often sympatric with *Fulvia laevigata* (Linnaeus, 1758). Both PANGLAO 2005 valves (164-669 m) are worn and discoloured, and do not represent the true bathymetric range.

Remarks. — Live specimens are found in abundance on intertidal sand flats in sheltered bays in north-western Australia (Wilson & Stevenson, 1977). The habitat preference is similar to that of *Fragum grasi* spec. nov. and *Lunulicardia hemicardium* (Linnaeus, 1758), but contrasts with the predominantly perireef occurrence of *F. fragum*. Despite their gross morphological similarities, Kawaguti (1983) noted striking differences in life habit between *F. unedo* and *F. fragum*: *F. unedo* opens its valves widely and protrudes the siphonal mantle edges, where most zooxanthellae are found, extensively over the sediment. *Fragum fragum* opens its valves only slightly, does not expand its mantle and has an almost even distribution of zooxanthellae in the mantle. Apparently, this behaviour allows *F. unedo* to benefit from zooxanthellae without the need for a specialised, semi-translucent posterior shell microstructure but requires environments with low energy wave action. The expansion of the siphonal mantle edges of *F. scruposum* (live specimen: pl. 7 fig. 5) suggests that this species at times may display a similar life habit. The present species is locally used for consumption and for the shellcraft industry (Sotto & von Cosel, 1982; Poutiers, 1998). For differences with *F. sueziense* see that species.

Lunulicardia J.E. Gray, 1853

Hemicardia Spengler, 1799: 4. Type species by subsequent designation (Stewart, 1930: 270): *Cardium hemicardium* Linnaeus, 1758; Recent, 'O. Asiatico' (Central Indo-West Pacific, probably Ambon, Moluccas) [invalidly proposed].
Lunulicardia J.E. Gray, 1853: 41. Type species by monotypy: *Cardium retusum* Linnaeus, 1767; Recent, 'India' (Indo-West Pacific).
Hemicardium Dall, 1900: 1075 (as a section of *Fragum*). Type species by absolute tautonomy: *Cardium hemicardium* Linnaeus, 1758.

Diagnosis. — Shell small to large, trapezoidal to triangular, with acute medio-posterior angulation and relatively glossy surface. Hinge strongly bent, sometimes distorted due to deeply impressed lunula. Ribs rather flattened and smooth, bearing small nodules or transverse scales; interstices finely striated.

Distribution. — Pleistocene to Recent, Indo-Pacific, Japonic; littoral-sublittoral.

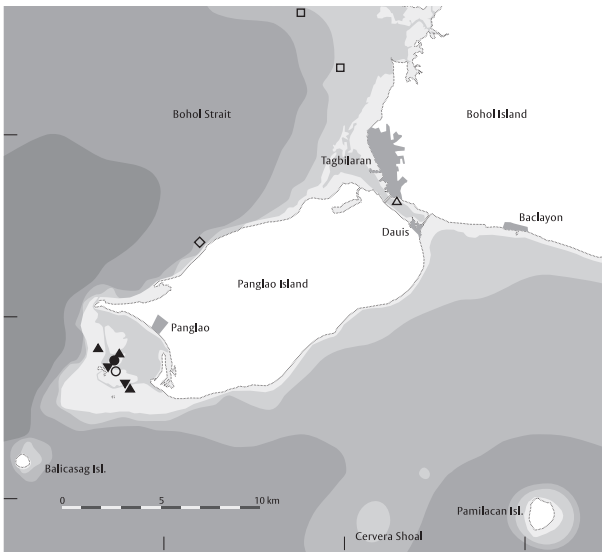
Remarks. — Stewart (1930: 270-271) and Dodge (1952: 56) discussed the nomenclatural difficulties regarding *Hemicardi*a Spengler, 1799 (see Knudsen & Hylleberg, 1999, for an English translation of Spengler). Here the views of Wilson & Stevenson (1977: 41) and Keen (1980: 7) are

adopted by considering Spengler's usage an informal plural group name for several species. Wilson & Stevenson (1977) pointed out close affinities between *Hemicardia* and *Lunulicardia*. The latter is herein given generic rank rather than considered a subgenus of *Fragum* (Wilson & Stevenson, 1977; Keen, 1980) or *Corculum* (Popov, 1977). Like all Fraginae genera, *Lunulicardia* is in need of revision.

Lunulicardia hemicardium (Linnaeus, 1758)

Pl. 9 figs 4-5

Cardium hemicardium Linnaeus, 1758: 678.
Cardium tumoriferum Lamarck, 1819: 15.
Cardium guichardi Bernardi, 1857: 53-54, pl. 2 fig. 4.



Material examined. — **Philippines**: PMBP 2004, Stn B42, 30-33 m, 1 v; Stn D4, 0-2 m, 2 pv (A), 3 v; Stn D5, 0-2 m, 7 pv (A), 3 v; Stn D7, 2-3 m, 6 pv (A), 3 v; Stn R23, 1-5 m, 8 pv (A), 1 v; Stn R32, 4 m, 6 pv (A); Stn R44, 2 m, 3 pv (A); Stn R67, 3-3.5 m, 1 pv; Stn S9, 3 m, 3 pv (A), 5 v; Stn S11, 2 m, 2 pv, 8 v; Stn T18, 80-100 m, 1 v; Stn T26, 123-135 m, 7 v; Stn s/n, Panglao Isl., 4 pv (A), 1 v.

Description. — Shell medium to large (H 35-65 mm), inequilateral, trapezoidal in outline, ventrally pointed; posterior margin less expanded than anterior, sometimes straight or slightly concave. Sharp and prominent radial keel separating posterior slope. Circa 18-27 radial ribs, flattened, bearing sessile rounded tubercles or scales. Interstices narrow, regularly notched; anterior margin not touching umbo, slightly depressed in front of it; posterior part of hinge very short. Lunula broad and flat, nymphal plate and ligament very short. Colour white to cream, or pinkish, mainly on posterior slope, sometimes with reddish-brown spots. Periostracum thin but conspicuous. Pedomorphic development, although in early ontogeny the umbo is relatively blunt.

Distribution and ecology. — Tropical Central Indo-West Pacific, from islands south of mainland Japan (Matsukuma, 2000) to northern Australia (Lamprell & Whitehead, 1992), New Caledonia (Bernardi, 1857) to Polynesia (Poutiers, 1998). Littoral and sublittoral waters. Probably not in the Western Indian Ocean and Red Sea (Ter Poorten, 2007a: 291-292). All live taken specimens originate from Panglao Bay, indicating a noticeable preference for sheltered habitats. Depth range of present material 0-135 m (dead), 0-5 m (alive).

Remarks. — The degree of development of the rib strength and sculpture shows some geographic variation that merits additional investigation. Material from Luzon Island and Marinduque Island (Philippines) often has a shallow excavated lunula (CT material, MNHN; coll. TP), becoming morphologically close to *L. retusa* (Linnaeus, 1767). Western Australian specimens, at times having extreme dimensions (H 73 mm, Shark Bay, leg. P.L. van Pel, ZMA), are found alive in abundance on intertidal sand flats in sheltered bays (Wilson & Stevenson, 1977), a similar environment to that of the PMBP live taken specimens. A similar preference is exhibited by *Fragum unedo* (Linnaeus, 1758) and *F. grasi* spec. nov. *Lunulicardia hemicardium* is locally collected for consumption in the Philippines.

Ctenocardia H. & A. Adams, 1858

Ctenocardia H. & A. Adams, 1858: 459 (as a subgenus of Hemicardia). Type species by subsequent designation (Dall, 1900: 1075): *Cardium hystrix* Reeve, 1844 (non Lightfoot, 1786) [= *Fragum* (*Ctenocardia*) *symbolicum* Iredale, 1929a; nom. nov. for *Cardium hystrix* Reeve, 1844]; Recent, Corrigidor Isl., Philippines, c. 7 fms.
Americardia Stewart, 1930: 37, 267. Type species by original designation: *Cardium medium* Linnaeus, 1758; Recent, 'O. Indico' (Caribbean, restricted to Havana, Cuba by McLean, 1939).

Diagnosis. — Shell small to medium, subquadrate to obliquely trigonal with clear medio-posterior angulation and truncate posterior margin. Radial ribs with imbricating, tubular spines or lamellae. Interstices with imbricating scales. Lunula present. Right valve with unequal cardinal teeth, joined by a dorsal saddle and second posterior lateral tooth, which is sometimes poorly developed.

Distribution. — Miocene to Recent, Californian, Panamic, Peruvian, Caribbean, Patagonian, South African, Indo-Pacific, Japonic; littoral-sublittoral.

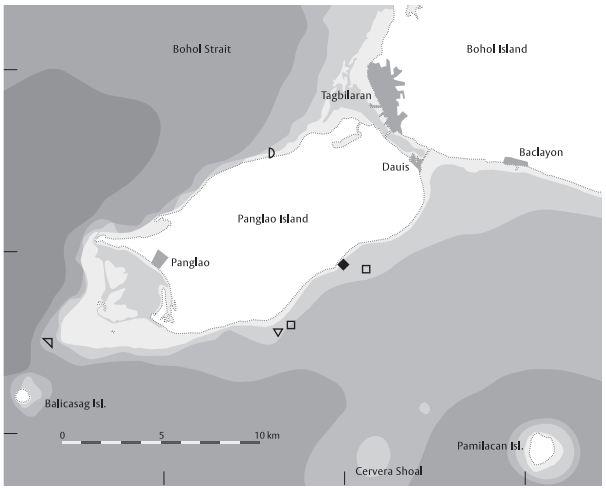
Remarks. — See Voskuil (1998), Vidal & Kirkendale (2007) and Kirkendale (2009) for further generic comments.

Ctenocardia fornicata (G.B. Sowerby 2nd, 1840)

Pl. 10 figs 7-10

Cardium fornicatum G.B. Sowerby 2nd, 1840a: figs 50, 50a; 1840b: 7, sp. 84; 1841: 110.
Cardium adamsii Reeve in Adams & Reeve, 1850: 77, pl. 22 fig. 2.

Material examined. — **Philippines**: PMBP 2004, Stn B40, 22 m, 1 pv (A); Stn D15, 53-63 m, 1 pv, 4 v; Stns L51-60, 43-62 m, 1 v; Stn T4, 82 m, 2 v; Stn T29, 77-84 m, 1 v. PANGLAO 2005, Stn DW 2400, 111-115 m, 1 v.



Description. — Shell medium (L 20-39 mm), rather solid, well-inflated, inequilateral and quadrate, height about equal to length. Umbonal keel strongly angled, posterior margin straight or slightly concave. Circa 38-44 squarish ribs with elaborate ornamentation on shell anterior, i.e. erect top spines or spinose scales and small bilateral spines; posteriorly likewise but often less well developed, occasionally ribs bearing only imbricated lamellae. Interstices narrow, finely striated. Colour cream, mottled with brown-red, lunula purple; interior reflects exterior by translucency, white often suffused with yellow, orange or pink.

Distribution and ecology. — Indo-West Pacific from South Africa (coll. TP), the Red Sea (Oliver, 1992), mainland Japan (Matsukuma, 2000), Guam (Paulay, 2003) and northern Australia (Lamprell & Whitehead, 1992) to Vanuatu (MNHN, det. TP). Depth range of present material 22-84 m (dead), 22 m (alive); PANGLAO 2005 111-115 m (dead).

Remarks. — This species is scarce and rather enigmatic. It displays significant intraspecific variability in the nature of the lunula, rib sculpture, colour and rib number, especially when material of various extremes of the distribution is involved. Additional research is needed to investigate the conspecificity of these forms.

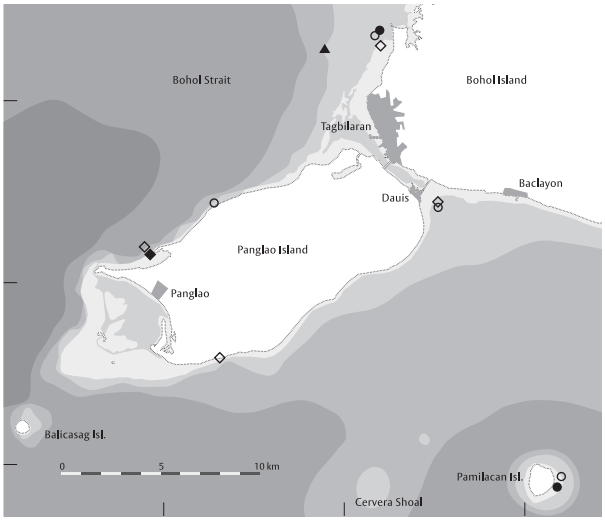
Ctenocardia gustavi Vidal & Kirkendale, 2007

Pl. 8 fig. 6, pl. 10 figs 4-6

Ctenocardia gustavi Vidal & Kirkendale, 2007: 98-100, figs 5e-g, table 7.

Material examined. — **Philippines**: PMBP 2004, Stn B2, 5 m, 3 v; Stn B13, 3-5 m, 1 v; Stn B20, 2-8 m, 1 v; Stn B32, 20 m, 1 pv (A); Stn B36, 24 m, 1 v; Stn R43, 3-41 m, 1 pv (A); Stn S10, 6-14 m, 1 pv, 1 v — Stn S12, 6-8 m, 1 pv (A); Stn S13, 8-15 m, 1 pv [fide Vidal & Kirkendale, 2007: 99] — Stn S21, 4-12 m, 3 v; Stn S22, 15-20 m, 2 v; Stn S25, 21 m, 1 pv (A), 2 v; Stn S28, 28-32 m, 7 v.

Description. — Shell small to medium (L 15-25 mm), rather solid, well-inflated, inequilateral and quadrate.



Umbonal keel strongly angled with concave posterior slope. Circa 39-45 low flattened radial ribs carrying minute, densely placed and strongly arched lamellae of irregular strength, becoming more pronounced near anterior and posterior margins. Interstices narrow. Exterior cream with irregularly placed pale purple and yellowish spots. Small orange blotches on lunula and posteriormost rib(s). Interior variable, often white or with purple to orange umbonal ray on posterior quarter, sometimes with two reddish-brown rays.

Distribution and ecology. — Tropical West Pacific from Indonesia, Philippines, Papua New Guinea, Mariana Islands, Caroline Islands, Solomon Islands, New Caledonia and Niue (Vidal & Kirkendale, 2007). Depth range of present material 2-41 m (dead), 3-41 m (alive), exclusively in coral reef environments on sand, coral rubble and mud.

Remarks. — The minute bright orange blotches on the lunula and posteriormost rib(s) are typical. *Cardium nodulosum* Spengler, 1799 has a similar shell morphology (type material figured by Hylleberg, 2004: 906); it is here considered synonymous with *Ctenocardia media* (Linnaeus, 1758). Unpublished molecular phylogenetic analyses by L. Kirkendale have confirmed the distinctiveness of *C. gustavi* from congeneric species, providing further support for its specific status (Vidal & Kirkendale, 2007: 104).

Ctenocardia translata (Prashad, 1932)

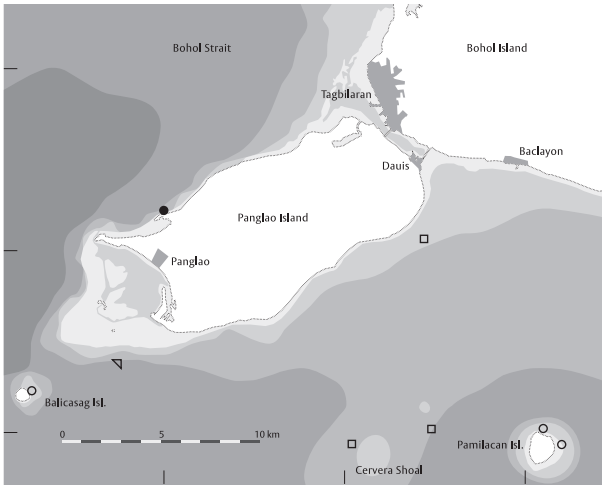
Pl. 10 figs 11-12

Cardium rigidum Reeve, 1845: sp. 105, pl. 20 fig. 105 (non W. Wood, 1815)

? *Cardium robillardi* G.B. Sowerby 3rd, 1894: 47, pl. 4 fig. 20.

Cardium (*Ctenocardia*) *translatum* Prashad, 1932: 277 (nom. nov. for *Cardium rigidum* Reeve, 1845)

Material examined. — **Philippines**: PMBP 2004, Stn S3, 6 m, 1 pv; Stn S10, 6-14 m, 1 v; Stn S24, 2-4 m, 1 pv (A); Stn S42, 15-20 m, 2 v; Stn T5, 84-87 m, 1 v; Stn T39, 100-138 m, 1 v; Stn T41, 110-112 m, 2 v. PANGLAO 2005, Stn DW 2339, 164-176 m, 1 v.



Description. — Shell small (L 10-16 mm), nearly equilateral, moderately inflated, rounded, umbonal keel weekly marked. Circa 29-38 radial rounded ribs. Rib sculpture highly allomorphic: in earliest growth stages valves usually with extremely dense scales, gradually developing into much more widely spaced spatuliform blunt scales, becoming more tubercular near anterior margin. Width of the interstices variable among specimens, ranging from as large as ribs to less than half the width of the ribs, thinly laminated. Exterior colour whitish with red-brown stains, sometimes predominantly red-brown; interior variable, pink in the umbonal cavity.

Distribution and ecology. — Tropical Indo-West Pacific from Seychelles (ZMA), Maldives (ANSP), Vietnam (Hylleberg & Kilburn, 2003), Indonesia (Prashad, 1932), New Caledonia (Héros *et al*., 2007) and Vanuatu (MNHN, det. TP). Depth range of present material 2-138 m (dead), 2-4 m (alive), essentially in coral reef environments on sand; PANGLAO 2005 164-176 m (downslope transportation).

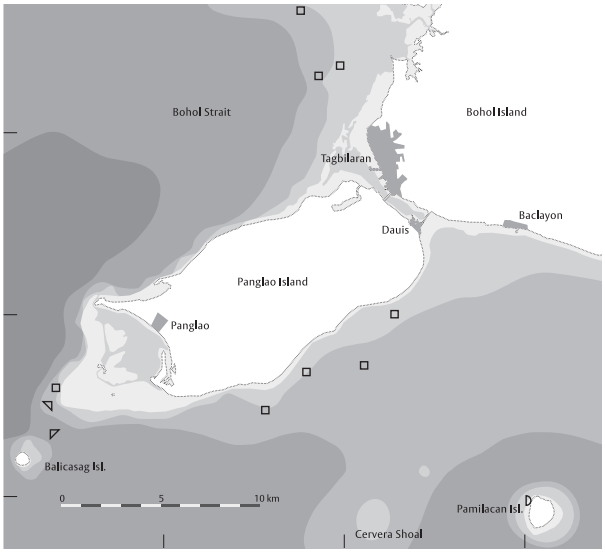
Remarks. — For taxonomic notes regarding *Cardium robillardi* G.B. Sowerby 3rd, 1894 see Ter Poorten (2007a). The present species is superficially close to juveniles of *Vasticardium sewelli* (Prashad, 1932). The latter can be separated by the pedomorphic nature and shape of its rib sculpture, as well as by its higher rib number and its elongate shape. *Fragum sueziense* (Issel, 1869) differs in having a lower rib number, smaller size and pedomorphic rib sculpture.

***Ctenocardia virgo* (Reeve, 1845)**

Pl. 10 figs 13-15

Cardium imbricatum G.B. Sowerby 2nd, 1840a: fig. 48; 1840b: 7, sp. 85; 1841: 110 (non Born, 1778).
Cardium hystrix Reeve, 1844: sp. 40, pl. 8 figs 40a-b (non Lightfoot, 1786).
Cardium virgo Reeve, 1845: sp. 120, pl. 21, fig. 120.
Fragum (*Ctenocardia*) *perornatum* Iredale, 1929a: 264 (nom. nov. for *Cardium imbricatum* G.B. Sowerby 2nd, 1840).
Fragum (*Ctenocardia*) *symbolicum* Iredale, 1929a: 264 (nom. nov. for *Cardium hystrix* Reeve, 1844).

Material examined. — **Philippines**: PMBP 2004, Stns L65-68, 55-81 m, 1 v; Stn T2, 152 m, 1 v; Stn T10, 117-124 m, 2 v; Stn T14, 101-110 m, 5 v; Stn T18, 80-100 m, 2 v; Stn T26, 123-135 m, 2 v; Stn T28, 80 m, 1 v; Stn T31, 100-140 m, 3 v; Stn T44, 83-86 m, 1 v. PANGLAO 2005, Stn CP 2399, 309-342 m, 1 v; Stn DW 2400, 111-115 m, 1 v.



Description. — Shell small to medium (H 20-30 mm), solid, inflated, inequilateral to subequilateral and quadrate, height slightly exceeds length. Angulation between posterior slope and anterior zone variable, acute to very weak. Circa 28-36 radial ribs, squarish except for the flattened and rounded ribs on the posterior slope. Ribs with erect tubular spines, hollow ventrally; much more weakly sculptured posteriorly, some ribs bearing only imbricated lamellae. Interstices broad, usually finely striated. White colouration throughout, occasionally yellowish and brownish posteriorly; interior variable, frequently with bright pink and orange zones in umbonal cavity and posteriorly.

Distribution and ecology. — Central Indo-West Pacific from Thailand (Swennen *et al*., 2001), Vietnam (Hylleberg & Kilburn, 2003), islands south of mainland Japan (coll. TP), Indonesia (Ter Poorten, 2007a), northern Australia (Lamprell & Whitehead, 1992) to areas west of New Caledonia (Virly *et al*., 1998). Depth range of present material, mainly trawled and exclusively consisting of loose valves, 55-152 m (dead); PANGLAO 2005 111-342 m (dead). Presumably, most of the material, often worn, was not derived from its preferred habitat, which appears to be essentially littoral and sublittoral up to 40-50 m. The fact that, given the massive sampling efforts, only loose valves of this rather common species were recovered suggests a highly localised occurrence and/or inappropriate sampling methods. Prolonged sampling and monitoring are needed to assess whether this reflects a decline or local extinction.

Remarks. — Fresh Philippine specimens tend to be much more strongly coloured than those from other parts of its range, the exterior having a yellow-orange appearance (pl. 10 fig. 15). See Ter Poorten (2007a: 285-286) for further taxonomic remarks.

Microfragum Habe, 1951

Microfragum Habe, 1951: 148. Type species by original designation: *Cardium festivum* Deshayes, 1855; Recent, 'New Ireland' (Bismarck archipelago, Papua New Guinea).

Diagnosis. — Shell small, rather solid, subquadrate or flabelliform, weakly truncated posterior margin. Medio-posterior angulation rather more rounded than carinate. Ribs ornamented with thin concentric scales, often crowded. Interstices small.

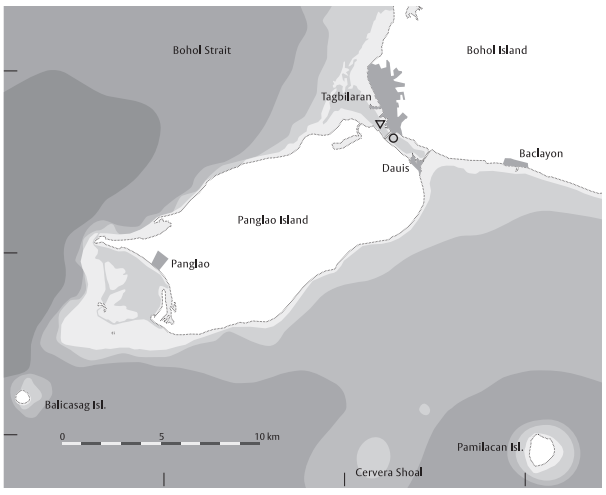
Distribution. — Pleistocene (postulated to have originated in the Miocene) to Recent, Indo-Pacific, Japonic; littoral.

Remarks. — Relegated by Vidal & Kirkendale (2007: 97) to a subgenus of *Ctenocardia* but here assigned generic rank, following Schneider (1998b: 324).

Microfragum erugatum (Tate, 1889)

Pl. 9 figs 10-12

Cardium erugatum Tate, 1889: 62, pl. 11 fig. 6.
Cardium levisulcatum E.A. Smith, 1903: 624-625, pl. 36 figs 25-26.
Fragum hamelini Iredale, 1949: 18-19.
Cardium (*Cerastoderma*) *iranjanense* Fischer-Piette, 1977: 91-92, fig. 9.



Material examined. — **Philippines**: PMBP 2004, Stn D12, 2-4 m, 2 v; Stn S38, 3-4 m, 1 v; Stn S39, 3-4 m, 1 v.

Description. — Shell small to medium (L 10-15 mm), rather solid, sub-trapezoidal to obliquely quadrate, clearly inequilateral. Circa 25 ribs, anterior ones with rather strongly developed scales (occasionally even more rugae or papillae like), gradually disappearing towards the posterior part; ribs themselves also becoming weaker. Majority white, both exterior and interior, but yellowish, partly orange-pink and white specimens mottled with brown also occur. Shell opaque or slightly translucent. Juveniles much more rounded with rib sculpture sometimes extending all over the shell.

Distribution and ecology. — A littoral species, known from Mozambique (coll. TP), Madagascar (Fischer-Piette, 1977), Maldives (Smith, 1903) and Western Australia (Wilson & Stevenson, 1977). Depth range of present material 2-4 m, based solely on loose valves. The three PMBP 2004 samples represent the first records from the Philippines and were found close to each other in a sheltered environment with mud and grey sand. All valves are immature with a maximum length of 7 mm. In coll. MH there is an additional Philippine specimen (pl. 9 fig. 12).

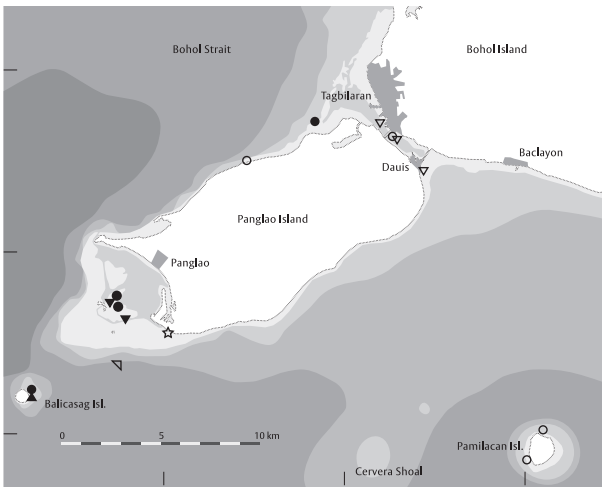
Remarks. — Voskuil & Onverwagt (1991b) elucidated the confusion regarding the taxonomic status of *Cardium levisulcatum* Smith, 1903 and *Cardium* (*Cerastoderma*) *iranjanense* Fischer-Piette, 1977 and illustrated type material of both taxa.

In Western Australia the species lives locally in dense populations (Wilson & Stevenson, 1977). Here, its preferred hypersaline protected shallow water habitat constitutes a highly specialised niche. This may well be reflected in its discontinuous distribution and possibly adds to the large intraspecific variation. The animal possesses symbiotic zooxanthellae and can attach itself to a substrate with a single byssus thread (Morton, 2000). Like many other fragines, juvenile *M. erugatum* may exhibit a window shell structure. However, the possession of a separate incurrent and excurrent aperture is atypical (Morton, 2000, fig. 4).

Microfragum festivum (Deshayes, 1855)

Pl. 9 figs 6-7

Cardium parvum G.B. Sowerby 2nd, 1839: fig. 33; 1840b: 6, sp. 80; 1841: 110 (non Da Costa, 1778; nec Philippi, 1844).
Cardium festivum Deshayes, 1855: 332.



Material examined. — **Philippines**: PMBP 2004, Stn D1, 2 m, 1 v; Stn D4, 0-2 m, 5 pv (A), 20 v; Stn D5, 0-2 m, 5 pv (A), 17 v; Stn D7, 2-3 m, 1 pv (A), 8 v; Stn D12, 2-4 m, 2 v; Stn D13, 2-3 m, 1 pv; Stn M3, 0-2.5 m, 1 v; Stn R17, 3-15 m, 1 pv (A); Stn S3, 6 m, 1 pv (A), 2 v; Stn S6, 1-4 m, 5 pv (A), 15 v; Stn S9, 3 m, 1 pv (A), 23 v; Stn S11, 2 m, 2 pv (A), 23 v; Stn S14, 5-12 m, 2 v; Stn S16, 15-18 m, 1 v; Stn S39, 3-4 m, 1 v; Stn S42, 15-20 m, 1 pv. PANGLAO 2005, Stn DW 2339, 164-176 m, 1 v.

Description. — Shell small to medium (H 10-15 mm), solid, subequilateral, rounded quadrate, longer than high, posterior margin slightly truncated. Exterior colour whitish to cream with brown-pinkish splashes; interior variable, ranging from white to orange in umbonal cavity or with brownish rays. Rib number ranging from 33 to 45; ribs flattened, rounded and densely covered with arched, thin imbricated lamellae that easily wear off, even in fresh material. The lamellae are of a homogeneous size and strength. Interstices very narrow and finely punctuated.

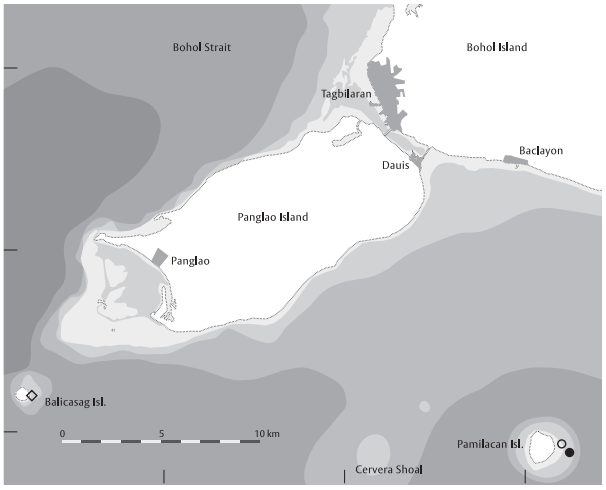
Distribution and ecology. — Tropical West Pacific, from mainland Japan (Matsukuma, 2000), Vietnam (Hylleberg & Kilburn, 2003), Indonesia (Ter Poorten, 2007a), Guam (Paulay, 2003), Queensland (Lamprell & Whitehead, 1992), New Caledonia (Héros *et al*., 2007) and Vanuatu (MNHN, det. TP). Depth range of present material 0-20 m (dead), 0-15 m (alive), predominantly in lagoon and other non-exposed environments on soft bottoms and sand. In addition, one worn PANGLAO 2005 valve was found at a depth of 164-176 m, which clearly had been washed down.

Remarks. — The closely related *M. subfestivum* (Vidal & Kirkendale, 2007) is differentiated by its somewhat smaller size, by being more asymmetrical and oblique, by having wider interstices and by the less numerous but more irregular lamellae. Judging from the available PMBP 2004 data, it also appears to have slightly different ecological preferences, being mainly restricted to exposed coral reef environments. Moreover, *M. subfestivum* has a deeper bathymetrical range with records of complete specimens down to 400 m (Vidal & Kirkendale, 2007) and has penetrated the Pacific more deeply.

***Microfragum subfestivum* (Vidal & Kirkendale, 2007) comb. nov.**

Pl. 9 figs 8-9

Ctenocardia (*Microfragum*) *subfestivum* Vidal & Kirkendale, 2007: 100-104, figs 5h-j, table 8.



Material examined. — **Philippines**: PMBP 2004, Stn B6, 12-14 m, 1 v; Stn S10, 6-14 m, 10 v; Stn S22, 15-20 m, 2 pv (A), 4 v.

Description. — Shell small to medium (H 8-13 mm), solid, inequilateral, rounded quadrate, longer than high, posterior keel rounded but clearly marked, posterior margin clearly truncated. Exterior cream to pink with brown-pinkish splashes; interior variable, ranging from white to orange with brownish rays or pink in umbonal cavity. Rib number 36 to 45; ribs rounded and covered with numerous imbricate lamellae of variable strength and size. Interstices rather narrow and finely punctuated.

Distribution and ecology. — Tropical West Pacific, so far reported from mainland Japan, New Caledonia, Wallis and Futuna, Tonga, Society Islands and Austral Islands (Vidal & Kirkendale, 2007). Also known from Indonesia (Ter Poorten, 2007a) and Queensland (coll. TP). Depth range of present material 6-20 m (dead), 15-20 m (alive); sparsely found in open coral reef environments.

Remarks. — Not reported before from the Philippines, so the present records constitute a westward range extension. As yet unpublished molecular phylogenetic analyses by L. Kirkendale have confirmed its distinctiveness from *M. festivum*, providing further support for its full species status (Vidal & Kirkendale, 2007: 104). For further differences from *M. festivum* see that species.

Tridacninae Lamarck, 1819

Remarks. — Recent phylogenetic, morphological, biological and molecular research (Schneider, 1998b; Keys & Healy, 1999; Schneider & Ó Foighil, 1999) has shown that tridacnines should be considered a highly specialised subfamily of the Cardiidae rather than a separate family.

The Tridacninae appeared in the Palaeogene, with several genera found in the Western Tethys, and underwent a marked decline during the break-up of Tethys (Newman & Gomez, 2000). Modern tridacnine lineages are rooted in the Palaeogene and early Neogene of the East African-Arabian Province; during the Neogene these successfully settled in the Indo-West Pacific region (Harzhauser *et al*., 2008). All extant species host photosymbiotic zooxanthellae in their tissues and also filterfeed. The photosymbionts augment a fully functional digestive system; which may be the cause of the spectacular growth rates and sizes of giant clams (Schneider, 1998b). This symbiosis with dinoflagellate algae apparently evolved separately in Tridacninae and Fraginae (Schneider, 1998b). Despite their CITES status from 1985 onwards, severe depletion of natural stocks due to commercial exploitation is still common practice, with the resulting local extinction (Gomez & Alcala, 1988; Mingoa-Licuanan & Gomez, 2002; Richter *et al*., 2008). Other severe threats are habitat loss due to degradation of coral habitats, and mantle bleaching caused by extreme summer seawater temperatures, resulting in increased mortalities. In several countries, including the Philippines (Gomez & Mingoa-Licuanan, 2006), this has led to extensive mariculture and restocking programmes, concentrating on marine protected areas, such as sanctuaries and national parks.

Hippopus Lamarck, 1799

Hippopus Lamarck, 1799: 86. Type species by absolute tautonomy: *Chama hippopus* Linnaeus, 1758; Recent, 'M. Asiatico' (Central Indo-West Pacific).

Pelvis Megerle von Mühlfeld, 1811: 67. Type species by monotypy: *Pelvis hippopus* Megerle von Mühlfeld, 1811 [= *Chama hippopus* Linnaeus, 1758].

Diagnosis. — Shell very large, solid, elongate ovate-triangular. The presence of a small byssal gape bordered by interlocking teeth is restricted to the juvenile stage. Circa 13-14 convex primary radial rib-like folds, bearing semi-tubular spines (i.e. open on one side along their entire length). Numerous riblets on primary ribs and interstices. Monomyarian with posterior adductor muscle centralised. Mantle not projecting laterally beyond shell margins.

Distribution. — Early Miocene to Recent, Indo-Pacific; littoral.

Remarks. — The genus is represented by two extant species, both recorded from the Philippines.

Hippopus hippopus (Linnaeus, 1758)

Pl. 11 fig. 2

Chama hippopus Linnaeus, 1758: 691.
*Tridachnes ungul*a Röding, 1798: 172, no. 97.
Hippopus maculatus Lamarck, 1801: 117.
Hippopus equinus Mörch, 1853: 56.

Material examined. — **Philippines**: PMBP 2004, Stn M5, 0-2 m, 1 v.

Description. — Shell very large (L 250-400 mm), very solid, strongly inflated, elongate triangular, inequilateral with a sharp carina separating the byssal area. The presence of a small byssal gape, bearing a row of tightly fitting teeth, is limited to juveniles. Circa 12-14 convex primary radial rib-like folds, usually elaborately sculptured with differently directed semi-tubular spines and numerous riblets that extend into the interstices. Umbonal cavity often considerably thickened. Exterior white or yellowish, spotted with purple blotches, mainly on primary folds; interior white with orange ligamental nymph. The mantle is yellow-brown, dull green or grey (dull in comparison to the Tridacna species), not projecting beyond the margins of the shells. The incurrent aperture lacks guard tentacles (Lucas, 1988).

Distribution and ecology. — Limited to the tropical West Pacific from western Indonesia, Philippines, islands south of mainland Japan, northern Australia, New Caledonia, Gilbert Islands and Marshall Islands (Rosewater, 1965; Paulay, 1996). Adults can be found unattached on very shallow reef flats and moats. Present material found dead (0-2 m).

Remarks. — The species presumably has suffered range contraction since the Plio-Pleistocene caused by sea-level fluctuations and human predation, resulting in local extinction in the Fiji-Tonga-Niue area, Mariana Islands and Aldabra Island (Paulay, 1996). The restricted and disjunct geographic range of its sole congener (*H. porcellanus* Rosewater, 1982) may be regarded as relict populations of a once more wide-ranging species that has been replaced over almost all of its former range by *H. hippopus* (Schneider & Ó Foighil, 1999). Several Philippine specimens (coll. TP and MH) differ in the following characters: they are less inflated; rather thin shelled, especially towards the margins; rib sculpture confined to the top of the primary folds, which lack secondary riblets; and a more colourful exterior and interior. More material is needed for an evaluation of the taxonomic status.

Tridacna Bruguière, 1797

Tridacna Bruguière, 1797: pl. 235 (heading). Type species by subsequent monotypy (Lamarck, 1799: 86): *Chama gigas* Linnaeus, 1758; Recent, 'M. Asiatico' (Central Indo-West Pacific, restricted to Ambon, Indonesia, by Rosewater, 1965).

Tridachnes Röding, 1798: 171. Type species by subsequent designation (Iredale, 1937: 236): *Chama gigas* Linnaeus, 1758.

Diagnosis. — Shell large to extremely large, solid, elongate triangular, inequilateral to nearly equilateral. Shell bearing prominent rib-like folds, unsculptured or ornamented with concentric ridges, scales or flutes. Well developed byssal gape that does not have interlocking teeth. Mantle colourful, projecting laterally beyond the shell margins when fully extended.

Distribution. — Early Miocene to Recent, Indo-Pacific; littoral.

Remarks. — Two subgenera are distinguished: *Tridacna* s.s. and *Chametrachea* Herrmannsen, 1846. During PMBP 2004, only one representative of the former, *Tridacna* (*Tridacna*) *gigas* (Linnaeus, 1758), was observed (northwest of Pamilacan Island – see 'Results'), but it was not collected, so the subgenus is not treated further here. Following Schneider & Ó Foighil (1999), the subgenus *Persikima* Iredale, 1937 is considered a subjective junior synonym of *Tridacna* s.s.

Subgenus *Chametrachea* Herrmannsen, 1846

Chametrachea Herrmannsen, 1846: 220 (emendation of *Chamaetrachaea* Klein, 1753; refers to Rumphius, 1705: pl. 42 [43] fig. B). Type species by monotypy *Chama aspera* Rumphius, 1705 [= *Tridacna crocea* Lamarck, 1819]; Recent, Ambon, Indonesia.

Chametrachea Mörch, 1853: 56. Type species by subsequent designation (Iredale, 1937: 236): *Tridacna crocea* Lamarck, 1819; Recent, 'l'Océan indien' (Central Indo-West Pacific, restricted to the Philippines by Rosewater, 1965).

Flodacna Iredale, 1937: 238. Type species by original designation: *Tridacna squamosa* auct. [= *Tridacna squamosa*

Lamarck, 1819]; Recent, 'l'Océan indien' (Indo-West Pacific, restricted to Ambon, Indonesia, by Rosewater, 1965).

Sepidacna Iredale, 1937: 239. Type species by original designation: *Tridacna troughtoni* Iredale, 1927b. [= *Tridachnes maxima* Röding, 1798]; Recent, Vanikoro, Solomon Islands.

Vulgodacna Iredale, 1937: 239. Type species by original designation: *Tridacna maxima* var. *fossor* Hedley, 1921 [= *Tridachnes maxima* Röding, 1798]; Recent, Mast Head Island, Capricorn Group, Australia.

Diagnosis. — Shell large to very large, solid, elongate triangular, strongly inequilateral to subequilateral with the umbos placed anteriorly. Rib-like folds ornamented with concentric ridges, scales or flutes. Incurrent aperture ringed with small to rather large guard tentacles. Often living byssally attached to coral rubble or embedded in coral.

Distribution. — Miocene to Recent, Indo-Pacific, Japonic; littoral.

Tridacna (*Chametrachea*) *maxima* (Röding, 1798)

Pl. 11 figs 3-4

Tridachnes maxima Röding, 1798: 171, no. 184.
Tridachnes noae Röding, 1798: 171, no. 186.
Tridachnes imbricata Röding, 1798: 172, no. 190.
Tridacna elongata Lamarck, 1819: 106.
Tridacna mutica Lamarck, 1819: 106-107 (part).
Tridacna rudis Reeve, 1862: sp. 4, pl. 5 figs 4a-c.
Tridacna compressa Reeve, 1862: sp. 5, pl. 6, fig. 5; pl. 7 figs 5b-c.
Tridacna cumingii Reeve, 1862: sp.7, pl. 7 fig. 7b (part).
Tridacna lanceolata G.B. Sowerby 2nd, 1884: 181-182, pl. 489* fig. 19 [18].
Tridacna lamarcki Hidalgo, 1903: 385-386 (part) (nom. nov. for *Tridacna gigas* Lamarck, 1819).
Tridacna reevei Hidalgo, 1903: 389-390 (nom. nov. for *Tridacna elongata* Reeve, 1862).
Tridacna acuticostata G.B. Sowerby 3rd, 1912: 30-31, fig.
Tridacna maxima var. *fossor* Hedley, 1921: 171, pl. 29 fig. 6; pl. 30 fig. 7; pl. 33 fig. 11.
Tridacna troughtoni Iredale, 1927b: 75, pl. 5 figs 9-10.

Material examined. — **Philippines**: PMBP 2004, Stn M1, 0-1 m, 1 pv; Stn R37, 28-32 m, 1 pv (A); Stn S13, 8-15 m, 2 v.

Description. — Shell very large (L 250-350 mm), solid, inflated, elongate, strongly inequilateral. Pronounced and elongate byssal gape. Shell bearing circa 5-7 broad, low radial rib-like folds; anteriorly 5-6 flattened folds, becoming obsolete near postero-ventral margin. Main folds bearing close-set scales or flutes and numerous unsculptured riblets on the folds and interstices. Exterior white or yellowish, sometimes orange or pink near margins, interior white, and often yellow, orange or pink near margins. Incurrent aperture with indistinct guard tentacles.

Distribution and ecology. — The most widely distributed tridacnine, ranging in the Indo-Pacific from South Africa (Kwazulu Natal), the Red Sea, mainland Japan, northern Australia, New Caledonia, deep into the West Pacific to the Tuamotu archipelago and Pitcairn Islands (Rosewater, 1965; Paulay, 1989). Littoral and (occasionally) sublittoral waters. Depth range of present material 0-15 m (dead), 28-32 m (alive). The depth of the live taken specimen is remarkable as it is supposed to live littorally. Newman & Gomez (2007) stated that only *T.* (*C.*) *mbalavuana* Ladd, 1934 has been recorded deeper than 25.5 m.

Remarks. — Occurs on hard substrates in a variety of reef environments, usually byssally attached. It tends to bore into the reef, partially embedding itself in the substrate (Lucas, 1988), adding to the high intraspecific variability and consequential difficulties in species delimitation. The identity of two very small live taken *Tridacna* (*Chametrachea*) specimens remains uncertain due to the unavailability of adequate growth series (pl. 11 figs 5-6). They show a markedly high triangular outline, present during the earliest ontogenetic stages (see also Rosewater, 1965: pl. 268 figs 1-2). Another specimen (pl. 11 fig. 4) shows similarities in gross morphology to *T. lanceolata* G.B. Sowerby 2nd, 1884 and *T. acuticostata* G.B. Sowerby 3rd, 1912, both described from the Philippines and generally considered synonymous with *T.* (*C.*) *maxima*.

Tridacna (*Chametrachea*) *crocea* Lamarck, 1819

Pl. 11 fig. 7

Tridacna crocea Lamarck, 1819: 106.
Tridacna cumingii Reeve, 1862: sp.7, pl. 7 fig. 7a (part).
Tridacna ferruginea Reeve, 1862: sp. 8, pl. 8 fig. 8a-b.

Material examined. — **Philippines**: PMBP 2004, Stn M7, 0-3 m, 1 pv.

Description. — Shell large (L 125-150 mm), solid, inflated, triangular ovate, inequilateral. Very large broad byssal gape. Circa 6-10 broad, very low radial rib-like folds, largest on median part of the shell, bearing close-set undulating low scales (best preserved close to the margins) and numerous riblets on the folds and interstices, resulting in a comparatively smooth surface. Exterior dull greyish-white, sometimes tinted with yellow, orange or pink; interior same colour, stronger towards the margins. Incurrent aperture with indistinct guard tentacles.

Distribution and ecology. — Limited to the central Indo-West Pacific from Indonesia (Sumatra), islands south of mainland Japan, northern Australia, to the Solomon Islands (Newman & Gomez, 2000) and Vanuatu (MNHN, det. TP). Its presence in Fiji (Rosewater, 1965) was not confirmed by Lewis *et al*. (1988). Littoral water, often deeply burrowing into hard substrates like coral heads and limestone, which regularly leads to various kinds of abrasions and malformations.

Remarks. — The sole collected specimen is juvenile but readily identified by its shape and large byssal gape. The species is known from the Late Pleistocene of Kenya but

PLATE 9

Figs 1-3. *Fragum unedo* (Linnaeus, 1758). **1.** PMBP 2004 Stn M18, lv exterior, rv interior, anterior and dorsal, H 49.1 mm. **2-3.** PMBP 2004 Stn R32. **2.** lv exterior, H 35.0 mm. **3.** lv exterior, H 39.0 mm. **Figs 4-5.** *Lunulicardia hemicardium* (Linnaeus, 1758). **4.** PMBP 2004 Stn D5, lv exterior and rv interior (with dried animal), H 48.6 mm. **5.** PMBP 2004 Stn R23, rv interior, lv exterior, dorsal, anterior and posterior, H 42.5 mm. **Figs 6-7.** *Microfragum festivum* (Deshayes, 1855). **6-7.** PMBP 2004 Stn D5. **6.** rv exterior and interior, L 13.3 mm. **7.** rv exterior, L 12.6 mm. **Figs 8-9.** *Microfragum subfestivum* (Vidal & Kirkendale, 2007). **8-9.** PMBP 2004 Stn S10. **8.** lv interior and exterior, L 10.5 mm. **9.** rv exterior, L 8.9 mm. **Figs 10-12.** *Microfragum erugatum* (Tate, 1889). **10-11.** PMBP 2004 Stn D12. **10.** rv exterior, L 5.9 mm. **11.** lv exterior, L 6.9 mm. **12.** Philippines, Mactan, Punta Engaño, by local fishermen. 2006, rv interior and lv exterior, L 9.6 mm (MH 248).

PLATE 10

Figs 1-3. *Corculum cardissa* (Linnaeus, 1758). **1.** PMBP 2004 Stn R48, anterior, lv and rv interior, H 47.7 mm. **2.** PMBP 2004 Stn M18, posterior, lv exterior and dorsal, H 61.4 mm. **3.** PMBP 2004 Stn R51, anterior, lv exterior and posterior, H 18.9 mm. **Figs 4-6.** *Ctenocardia gustavi* Vidal & Kirkendale, 2007. **4.** Philippines, Panay, Anajawan Point, 6 m, leg. G.T. Poppe, lv exterior and rv interior, L 16.8 mm (TP 3345). **5.** PMBP 2004 Stn S25, lv interior (with flesh remainder) and rv exterior, L 7.6 mm. **6.** PMBP 2004 Stn R43, lv exterior, rv interior and dorsal, H 13.8 mm. **Figs 7-10.** *Ctenocardia fornicata* (G.B. Sowerby 2nd, 1840). **7.** PMBP 2004 Stn T29, lv exterior, H 16.9 mm. **8.** PMBP 2004 Stn D15, rv exterior and interior, L 14.7 mm. **9.** PMBP 2004 Stn B40, lv exterior, L 9.3 mm. **10.** Philippines, Mindanao, Aliguay Isl., 60-120 m, L 19.6 mm (TP 3545). **Figs 11-12.** *Ctenocardia translata* (Prashad, 1932). **11.** PMBP 2004 Stn T5, rv exterior and interior, H 13.2 mm. **12.** PMBP 2004 Stn S3, lv exterior and rv interior, H 4.2 mm. **Figs 13-15.** *Ctenocardia virgo* (Reeve, 1845). **13.** PMBP 2004 Stn T14, lv exterior and interior, L 20.3 mm. **14.** PMBP 2004 Stn T18, rv exterior, L 7.4 mm. **15.** Philippines, Masbate Isl., trawled, 20-40 m, lv exterior, H 28.9 mm (TP 1748).

became extinct in the western Indian Ocean, possibly as a result of habitat loss (Crame, 1986).

Tridacna (*Chametrachea*) *squamosa* Lamarck, 1819

Pl. 11 fig. 1

Tridacna squamosa Lamarck, 1819: 106.
? *Tridacna aegyptiaca* Chenu, 1845: 2, pl. 7 figs 1-2.
Tridacna lamarcki Hidalgo, 1903: 385-386 (part) (nom. nov. for *Tridacna gigas* Lamarck, 1819).

Material examined. — **Philippines**: PMBP 2004, Stn M18, 0-1 m, 1 pv; Stn S21, 4-12 m, 1 v; Stn R33, 1-4 m, 1 pv (A).

Description. — Shell very large (length 300-400 mm), solid, inflated, semicircular and subequilateral. Comparatively moderate to small byssal gape. Circa 5-6 broad, well developed radial rib-like folds, 5-6 small ribs near postero-ventral margin. Strong, distantly placed scales or flutes on the folds, riblets in the interstices and even finer ones on the folds. Exterior white, yellow, orange or pink; rib ornamentation lighter coloured; interior white, margins often coloured similarly to the exterior. Incurrent aperture with distinct guard tentacles.

Distribution and ecology. — Widely distributed in the Indo-West Pacific from South Africa (Kwazulu Natal), the Red Sea (?), islands south of mainland Japan, northern Australia and the West Pacific to the Pitcairn Islands (Rosewater, 1965; Paulay, 1989). According to Newman & Gomez (2000) it is apparently not known from French Polynesia, suggesting a disjunct range. Recently it has been reported from Tubuai, Austral Islands (Gilbert *et al*., 2007). In addition, J. Letourneux (pers. comm. 10.2008) informed me of its presence in the Tuamotu archipelago (Tikehau Island). Both records bridge the supposed distribution gap. Found in littoral water. Depth range of present material 0-12 m (alive 1-4 m).

Remarks. — *Tridacna* (*Chametrachea*) *squamosa* occurs unattached or weakly attached by the byssus as an adult and nestles in rubble or in reef pockets (Paulay, 1987), not embedded in the substrate. Juveniles sometimes tend to be relatively elongate, closely resembling *T.* (*C.*) *maxima*. However, the rather small byssal gape and the distantly placed rib sculpture allow taxonomic separation.

Laevicardiinae Keen, 1951

Remarks. — Laevicardiinae as erected by Keen (1936: 367) does not comply with I.C.Z.N. (1999) Article 13.1. It was rejected by Vidal (1994: 95), expressly applying Article 13 of I.C.Z.N. (1985) and is thus nomenclaturally unavailable from its original publication, according to I.C.Z.N. (1999: Article 13.2.1). However, it was validated by Keen (1951).

Following Schneider (1995), *Nemocardium* and the related genera *Frigidocardium*, *Microcardium* and *Trifaricardium* are placed in Laevicardiinae. Constructing the cardiid phylogeny based on cladistic analyses, Schneider (1995) restricted Protocardiinae to the extinct genus *Protocardia* and placed *Nemocardium* with several subgenera in Laevicardiinae Keen, 1951. The inclusion of *Nemocardium* in Protocardiinae would make the latter a polyphyletic group. He considered the resemblance between *Nemocardium* and *Protocardia* as being based upon a shared primitive character (the presence of strong radial ribs on the posterior slope only) rather than a shared derived character.

The systematic arrangement of Schneider (1995) is followed at the subfamily level. At the generic level the arrangements of Poutiers (1992; 2006) and Vidal (2000a) are adopted, assigning *Frigidocardium*, *Microcardium* and *Trifaricardium* full generic rank.

Fulvia J.E. Gray, 1853; subgenus *Fulvia*

Fulvia J.E. Gray, 1853: 40. Type species by monotypy: *Cardium apertum* Bruguière, 1789; Recent, 'l'océan Asiatique' & 'Jamaïque' (Indo-West Pacific; Jamaica in the original publication was in error).

Diagnosis. — Shell small to very large, generally rather thin shelled, occasionally slightly translucent, rounded to obliquely ovate, posterior part often expanded. Ribs generally rather low to poorly defined on median part. Ribs unsculptured, only bearing periostracal insertions. Posterior radial groove often present. Shell surface often partly covered with minute granulations. Guard tentacles on incurrent and excurrent aperture carrying ocular organs on their tips.

Distribution. — Oligocene to Recent, west African, south African, Mediterranean, Indo-Pacific, Japonic, south Australian; littoral-sublittoral.

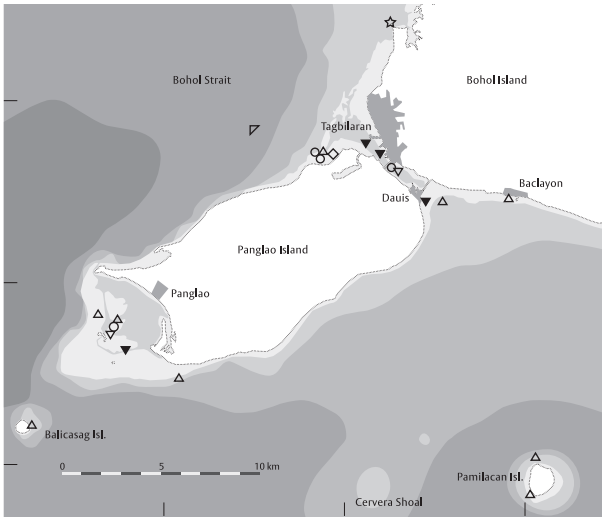
Remarks. — Following Schneider (1995) *Fulvia* is placed in Laevicardiinae. The genus was reviewed by Vidal (1994), followed by the introduction of four new taxa (Vidal & Kirkendale, 2007); two of these are present in the PMBP 2004 material and one is considered a new synonym. The morphological terminology of Vidal (1994) is adopted here.

Fulvia (*Fulvia*) *australis* (G.B. Sowerby 2nd, 1834)

Pl. 12 figs 6-10

Cardium striatum Spengler, 1799: 45. [Never used].
Cardium australe G.B. Sowerby 2nd, 1834: figs 12, 12*; 1840b: [1], sp. 10; 1841: 105.
Cardium varium G.B. Sowerby 2nd, 1834: fig. 19.
Cardium pulchrum Reeve, 1845: sp. 98, pl. 19 fig. 98.

Material examined. — **Philippines**: PMBP 2004, Stn B18, 3-5 m, 1 pv, 4 v; Stn D1, 2 m, 2 pv, 1 v (A); Stn D4, 0-2 m, 1 pv, 1 v (A); Stn D5, 0-2 m, 1 pv, 2 v; Stn D7, 2-3 m, 2 pv; Stn D12, 2-4 m, 22 pv, 9 v (A); Stn D13, 2-3 m, 2 pv, 34 v; Stn D14, 2-4 m, 9 pv, 6 v (A); Stn M24, 0-1 m, 1 pv; Stn R12, 2-20 m, 1 pv; Stn R14, 6-8 m, 1 pv; Stn R16, 6-22 m, 1 pv; Stn R23, 1-5 m, 1 pv; Stn R26, 1-5 m, 1 v; Stn R36, 3-32 m, 1 pv; Stn R40, 8-33 m, 1 pv; Stn R42, 8-22 m, 1 pv; Stn R44, 2m, 1 pv; Stn S6, 1-4 m, 5 v; Stn S9, 3 m, 1 v; Stn S38, 3-4 m, 1 v; Stn S41, 2-4 m, 2 pv; Stn s/n, Panglao Isl., 1 pv. PANGLAO 2005, Stn CP 2331, 255-268 m, 1 v.



Description. — Shell medium (H 30-40 mm), slightly obliquely ovate, H/L ratio highly variable, normally height approximately equals length, rather thin. Number of ribs extremely variable (range 34-68), pronounced and irregular on posterior third of the shell and nearly smooth on median part. Periostracal insertions present on posterior part of the ribs. Minute, evenly disposed granulations often observed on anterior half of the shell. Lunular heart small, raised and elongate. Colour variable, often whitish blotched with pink, purple or brown. Juveniles more vividly coloured. Interior white, yellowish, orange or purple; sometimes with a purple umbonal ray.

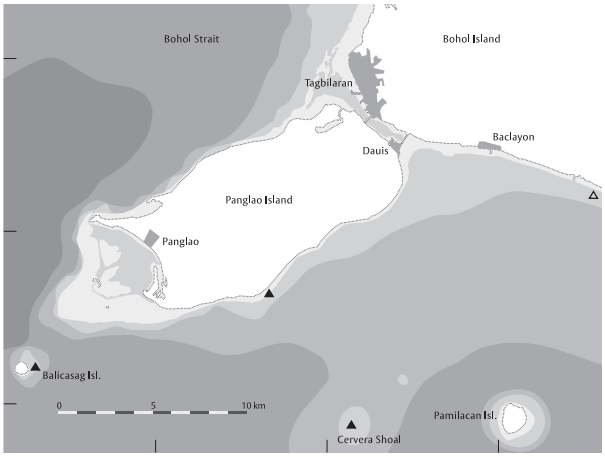
Distribution and ecology. — Throughout the tropical Indo-West Pacific, ranging from the Red Sea and Mozambique to mainland Japan, Australia, Vanuatu, Fiji and New Caledonia (Vidal, 1994). Recently penetrated into the eastern Mediterranean (Zenetos *et al*., 2003). Littoral water, on mud and sand, often with seagrass. At least around Panglao, it appears to prefer non-exposed littoral habitats as most records relate to Panglao Bay or Tagbilaran Channel. Depth range of present material 0-33 m (dead), 0-4 m (alive); PANGLAO 2005 255-268 m (dead), undoubtedly resulting from downslope transportation.

Remarks. — A very common species of *Fulvia*, highly variable in shape and colour. For differences from *F. laevigata* see that species. Juveniles sometimes difficult to separate from congeners. A related, inflated, elongate-quadrangular form with a big, sharply bordered lunula with an elevated area in the right valve is known from the Philippines-Vanuatu region (MNHN; TP) and is currently under study. Although not encountered during the present expeditions, such a specimen, from Balicasag Island, is figured for comparison (pl. 12 fig. 10).

***Fulvia* (*Fulvia*) *boholensis* Vidal, 1994**

Pl. 13 figs 1-4

Fulvia (*Fulvia*) *boholensis* Vidal, 1994: 107, pl. 3 figs 6a-b.



Material examined. — **Philippines**: PMBP 2004, Stn R6, 5-12 m, 1 pv; Stn R9, 5-22 m, 1 pv (A); Stn R20, 7-48 m, 1 pv (A); Stn R41, 11-40 m, 1 pv (A).

Description. — Shell medium (L 30-35 mm), obliquely ovate, usually longer than high, rather thin, quite often very slightly gaping posteriorly. Circa 50 flattened but readily visible ribs, more pronounced on posterior third of the shell. Internal marginal ribbing relatively smooth. Periostracal insertions present on rib crests or posteriorly, developing into tiny calcified rugae on posterior slope. Anterior half of the shell densely granulated. Lunular heart very small. Exterior and interior generally bright orange, but not uncommonly whitish with cream triangles with extensive reddish-brown maculations, becoming darker towards the umbo. In the whitish shells with cream triangles, a patch of orange is still visible near the inner posterior margin and in rib interstices of posterior slope.

Distribution and ecology. — Known from the Philippines, Western Australia (Vidal, 1994), Indonesia (Ter Poorten, 2007a), Thailand (Bight of Bangkok, leg. R.G. Moolenbeek, 15.viii.2006; det. TP, ZMA) and Vietnam (coll. TP), the latter two records representing westward range extensions. Littoral and perhaps also sublittoral water, sand and mud bottoms. Depth range of present material 5-12 m (dead), 5-48 m (alive); exclusively found by hand picking while diving (R stns).

Remarks. — The present species was described from Panglao and 'said to have been recovered at 80 fms' (= 146 m), which is improbable as all available records known to me indicate a much shallower bathymetric range. It is morphologically close to *F. australis*; nevertheless, its ecological preferences appear to be quite distinct, as it lives in slightly deeper, more exposed coral reef environments. This could suggest the possibility of an ecophenotypical variation of *F. australis*, but shell outline, dense granulations, small lunular heart, constitution of periostracal insertions and colouration enable clear differentiation. Several related taxa, like *F. aperta* (Bruguière, 1789) and *F. laevigata* (Linnaeus, 1758), only rarely have a similar pure orange colouration.

PLATE 11

Fig. 1. *Tridacna* (*Chametrachea*) *squamosa* Lamarck, 1819. PMBP 2004 Stn M18, rv exterior, lv interior and ventral, L 109.2 mm. **Fig. 2.** *Hippopus hippopus* (Linnaeus, 1758). PMBP 2004 Stn M5, rv exterior and interior, L 81.8 mm. **Figs 3-4.** *Tridacna* (*Chametrachea*) *maxima* (Röding, 1798). **3.** PMBP 2004 Stn R37, lv interior (with dried animal and byssus), rv exterior, ventral and dorsal, L 124.5 mm. **4.** PMBP 2004 Stn M1, rv exterior and lv interior, L 118.9 mm. **Fig. 5-6.** *Tridacna* (*Chametrachea*) *spec.* **5.** PMBP 2004 Stn B8, rv exterior, L 2.0 mm. **6.** PMBP 2004 Stn B8, lv exterior, L 2.4 mm. **Fig. 7.** *Tridacna* (*Chametrachea*) *crocea* Lamarck, 1819. PMBP 2004 Stn M7, lv interior and rv exterior, L 15.6 mm.

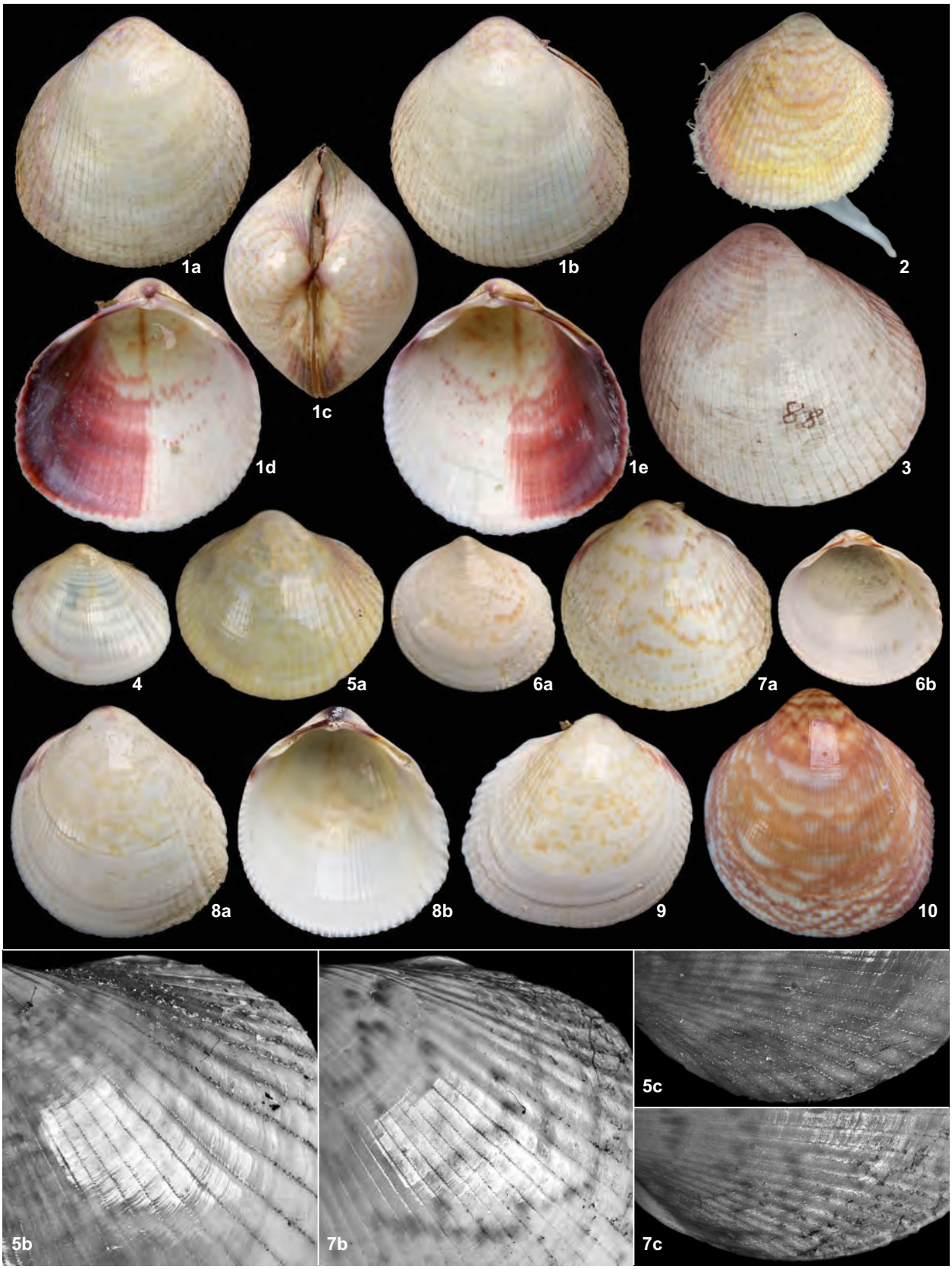


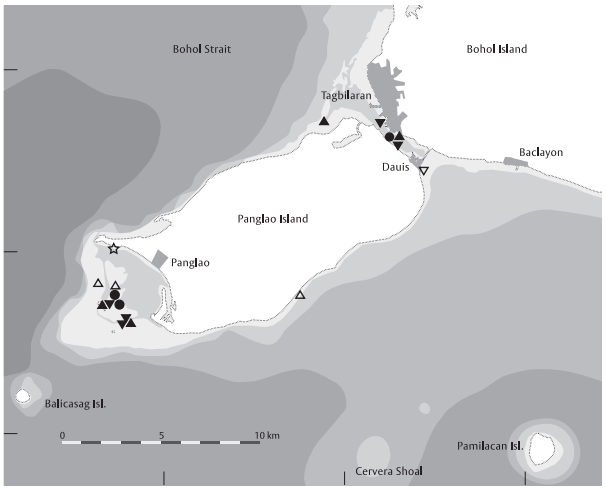
PLATE 12

Figs 1-5. *Fulvia* (*Fulvia*) *laevigata* (Linnaeus, 1758). **1.** PMBP 2004 Stn D13, rv and lv exterior, dorsal, lv and rv interior, H 42.8 mm. **2.** PMBP 2004 Stn R32, rv exterior with life animal, size unknown. **3.** Unknown provenance, lectotype of *Cardium laevigatum* Linnaeus, 1758, marked '88', lv exterior, L 46.5 mm (Linnaean Society). **4.** PMBP 2004 Stn D12, lv exterior, L 7.0 mm. **5.** PMBP 2004 Stn D12, lv exterior, lv posterior slope and lv anterior slope, L 16.9 mm. **Figs 6-9.** *Fulvia* (*Fulvia*) *australis* (G.B. Sowerby 2nd, 1834). **6.** PMBP 2004 Stn S41, lv exterior and rv interior, L 11.4 mm. **7.** PMBP 2004 Stn D12, lv exterior, lv posterior slope and lv anterior slope, L 20.6 mm. **8.** PMBP 2004 Stn R44, lv exterior and rv interior, H 24.1 mm. **9.** PMBP 2004 Stn R12, rv exterior, L 23.4 mm. **Fig. 10.** *Fulvia* (*Fulvia*) *spec. aff. australis*. Philippines, Balicasag Isl., 2004, lv exterior, H 31.4 mm (TP 3204).

Fulvia (*Fulvia*) *laevigata* (Linnaeus, 1758)

Pl. 12 figs 1-5, pl. 15 fig. 1

Cardium laevigatum Linnaeus, 1758: 680.
Cardium papyracea, testa cordata, […] Chemnitz, 1782: 190, pl. 18 fig. 184 (not binominal).
Cardium papyracea Schröter, 1788: 82 (not binominal).
Cardium papyraceum Chemnitz: Bruguière, 1789: 231.
? *Cardium pallidum* Reeve, 1845: sp. 92, pl. 18 fig. 92.
Fulvia voskuili Healy & Lamprell, 1992: 89-91, pl. 4 figs a-d.



Material examined. — **Philippines**: PMBP 2004, Stn D1, 2 m, 1 v; Stn D4, 0-2 m, 1 pv (A), 8 v; Stn D5, 0-2 m, 5 pv (A), 8 v; Stn D7, 2-3 m, 9 pv (A), 8 v; Stn D12, 2-4 m, 29 pv (A), 12 v; Stn D13, 2-3 m, 9 pv (A), 15 v; Stn M9, 0.5 m, 1 v; Stn R23, 1-5 m, 9 pv, 1 v; Stn R26, 1-5 m, 1 pv (A), 1 v; Stn R32, 4 m, 3 pv (A); Stn R39, 3 m, 4 pv (A), 1 v; Stn R44, 2 m, 3 pv, 1 v; Stn R67, 3-3.5 m, 5 pv (A), 4 v; Stn R68, 3-3.5 m, 3 pv; Stn S9, 3 m, 3 pv (A), 13 v; Stn S11, 2 m, 3 pv (A), 20 v; Stn S38, 3-4 m, 4 pv, 4 v; Stn S39, 3-4 m, 3 pv (A); Stn s/n, Panglao Isl., 1 pv, 1 v.

Description. — Shell relatively large (L 40-55 mm), rather thin and fragile, equilateral and almost circular. Some specimens with slight posterior elongation. Circa 33-48 small and weakly developed radial ribs. Interstices wide and flat. Lunula large with small lunular heart. Exterior tan, lilac posteriorly and a deep purple umbonal tip, occasionally yellow with brown zigzag lines. Interior generally much deeper coloured than exterior, often with purple posterior half and regularly concentric purple stripes with a white or yellowish umbonal cavity and a radial purple stripe. Periostracum thick, along posterior sides of the ribs, absent on anterior sides.

Distribution and ecology. — Limited to the central Indo-West Pacific from India, Singapore, Philippines, Indonesia, Queensland (all Vidal, 1994) and northwestern Australia (coll. TP). The PMBP 2004 data indicate a strong preference for protected littoral habitats like bays, lagoons and estuaries, with soft bottoms (mainly fine sand and mud), frequently in association with seagrass. Depth range of present material 0.5-30 m (dead), 0-4 m (alive).

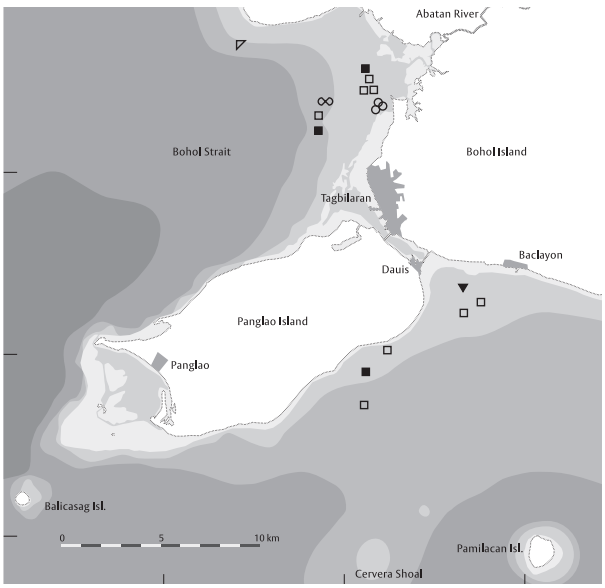
Remarks. — Hylleberg (2004: 890, first row) illustrated the lectotype of *Cardium laevigatum* Linnaeus, 1758, which was selected among the three syntypes by Vidal (1999a: 327). *C. laevigatum* is clearly a senior synonym of *F. papyracea*. Application of the Principle of Priority depends on whether both I.C.Z.N. (1999) articles 23.9.1.1 and 23.9.1.2 are met. This matter appears to be complicated by the fact that both *C. laevigatum* and *C. papyraceum* have almost invariably been wrongly interpreted in the literature, the first incorrectly as a Caribbean *Laevicardium* species, the second as *Fulvia fragilis* (Forsskål in Niebuhr, 1775). However, I.C.Z.N. (1999) only mentions the usage, not the interpretation, in which case it is clear that the senior synonym indeed has been used as a valid name after 1899 (condition 23.9.1.1). Stability in nomenclature is best served by strictly applying the Principle of Priority for which reason the name of Linnaeus should be used. The lectotype of *C. laevigatum* is here refigured (pl. 12 fig. 3).

The shell morphology of juveniles is often close to that of *F. australis*. One of the clear distinguishing features is the transition between the median and posterior zones: in *F. laevigata* this is formed by thin, very broadly spaced radial cords, whereas in juvenile *F. australis* small but elevated ribs begin to develop with relatively small interstices. The same applies to the anterior – median zones. *Fulvia laevigata* is slightly thinner, generally more rounded and has a lower mean rib number. Juveniles are often more broadly elliptical and not uncommonly densely granulated over large parts of the shell surface (Pl. 15, fig. 1). Also, *F. laevigata* attains larger dimensions, occupies a more specific ecological niche and has a more restricted range. The Chinese-Japanese *F. mutica* (Reeve, 1844) is also closely related but has a more northern range and a larger maximum length of 100 mm.

Fulvia (*Fulvia*) *scalata* Vidal, 1994

Pl. 13 figs 8-10, pl. 15 fig. 2

Fulvia (*Fulvia*) *scalata* Vidal, 1994: 108-109, pl. 1 figs 3-4, pl. 3 figs 5a-b, 7.



Material examined. — **Philippines**: PMBP 2004, Stn D2, 41-46 m, 1 pv, 1 v (A); Stn G1, 100 m, 1 v; Stn S20, 10 m, 1 v; Stn S21, 4-12 m, Stn S25, 21 m, 1

pv, 10 v; 1 pv; Stn T6, 34-82 m, 1 v; Stn T7, 61-62 m, 2 v; Stn T10, 117-124 m, 1 v; Stn T14, 101-110 m, 1 v; Stn T19, 10-26 m, 1 pv, 14 v; Stn T21, 1 pv, 12 m (A); T22, 11-20 m, 1 v; Stn T23, 35-45 m, 1 pv, 3 v; T25 160-210 m, 1 pv (A); Stn T29, 77-84 m, 1 pv (A); Stn T32, 60-72 m, 1 pv. PANGLAO 2005, Stn CP 2408, 121-137 m, 1 v.

Description. — Shell small (L 15-20 mm), rounded to subquadrangular, inflated, roughly equilateral and rather thin. Circa 40-45 well delimited ribs, particularly on posterior third of the shell. Commarginally aligned granules present in the interstices of the anterior and posterior slopes, close-set and placed like steps of a ladder – hence the species' name. Periostracal insertions rather weak, mainly on the posterior limit of the ribs. Very large and broad lunular heart. Exterior and interior generally uniform pale brown to pinkish, often evenly covered with slightly darker maculations. Juveniles show a pattern of irregular undulating lines with granulations over the whole shell (pl. 15 fig. 2).

Distribution and ecology. — Recorded from Oman, Madagascar, Philippines, Indonesia, northern Australia and New Caledonia (Vidal, 1994; Lamprell & Healy, 1998), and from Vietnam (Hylleberg & Kilburn, 2003) and China (Xu & Zhang, 2008: fig. 457, as *F. undatopicta*). Depth range of present material 4-210 m (dead), 12-210 m (alive) based on combined PMBP 2004 and PANGLAO 2005 records. It was strongly clustered off Abatan River mouth and east of Panglao, found sublittorally and occasionally littorally in mud or fine sand bottoms. In New Caledonia it has been found in depths of 20-50 m and in the terrigenous sandy facies of the eastern coast, rarely in clean perireef facies (Vidal, 1994). The coordinates given for the holotype in fact refer to paratype 2. The correct locality data for the holotype are: New Caledonia, LAGON, Stn 833, off Tiwaka River mouth, 20°49'8S-165°17'7E, grey mud, 52-70 m (V. Héros, pers. comm., 11.2008).

Remarks. — The typical ladder-like sculpture permits separation from its congeners.

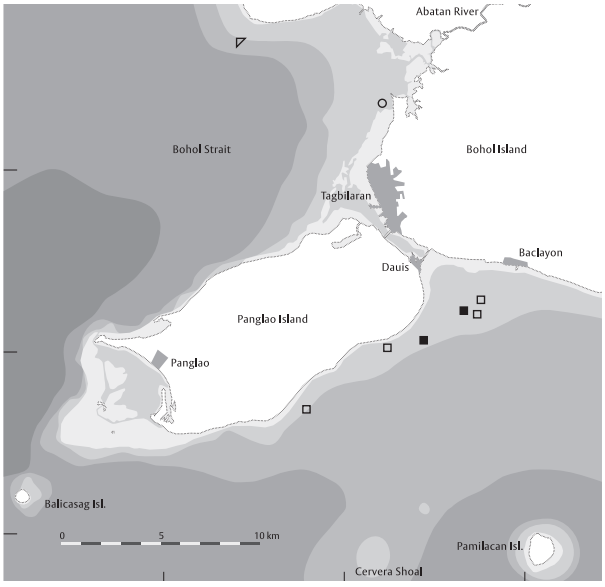
Fulvia (*Fulvia*) *colorata* Vidal & Kirkendale, 2007

Pl. 13 figs 5-7

Fulvia (*Fulvia*) *colorata* Vidal & Kirkendale, 2007: 89, figs 3a-c, table 2.

Material examined. — **Philippines**: PMBP 2004, Stn S20, 10 m, 1 pv; Stn T5, 84-87 m, 2 pv, 3 v (A); Stn T6, 34-82 m, 2 pv (paratype 1+2), 1 v (fide Vidal & Kirkendale, 2007); Stn T7, 61-62 m, 5 pv, 4 v (A); Stn T32, 60-62 m, 1 v; Stn T33, 67-74 m, 1 pv, 8 v; Stn T44, 83-86 m, 2 v. PANGLAO 2005, Stn CP 2408, 121-137 m, 1 v.

Description. — Shell small (H 15-18 mm), subquadrangular, elongate, rather inflated, roughly equilateral and rather thin. Posterior margin nearly straight. Circa 45-55 ribs, posteriorly well developed with clearly delimited interstices. Granulations virtually completely lacking, if present confined to anterodorsal margin. Periostracal insertions rather well developed, situated just posteriorly of rib tops. Large and broad lunular heart. Exterior colour cream with a brownish



broad lunular heart. Exterior colour cream with a brownish commarginally arranged zigzag pattern or dense spots. Interior similar with pinkish posterior slope.

Distribution and ecology. — Known from the Solomon Islands and the Philippines (Vidal & Kirkendale, 2007), Indonesia (Ter Poorten, 2007a) and Vanuatu (MNHN, det. TP), this last representing an eastward range extension. Depth range of present material 10-87 m (dead), 61-87 m (alive); PANGLAO 2005 121-137 m (dead). Mainly found sublittorally in mud, muddy sand and sand; occupying a somewhat similar ecological niche to that of *F. scalata*.

Remarks. — The elongate outline readily differentiates this species from its congeners. In addition, it completely lacks granulations and has a more vivid colouration, hence its name. Juveniles have a more rounded outline.

Subgenus *Laevifulvia* Vidal, 1994

Laevifulvia Vidal, 1994: 97. Type species by original designation: *Cardium hungerfordi undatopictum* Pilsbry, 1904: Recent, 'Hirado, Hizen' (Hirado Isl., western Kyūshū, Japan).

Diagnosis. — Same as genus *Fulvia*; periostracal insertions absent and shells relatively small.

Distribution. —Recent (thus far no fossil record), Indo-Pacific, Japonic; littoral-sublittoral.

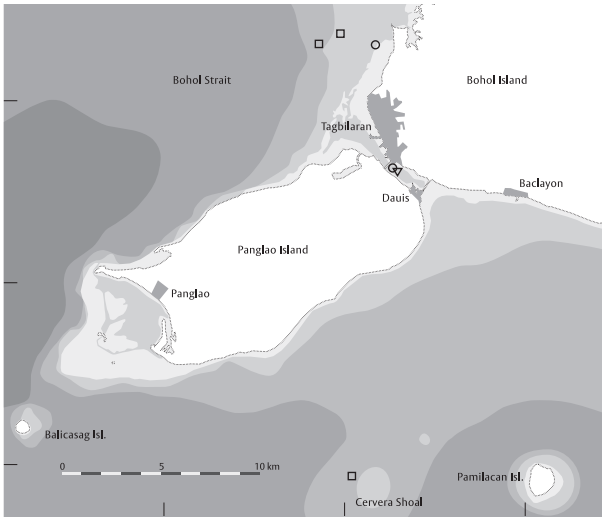
Remarks. — Remarkably, all PMBP 2004 *Laevifulvia* taxa were roughly confined to two locations: the semi-sheltered muddy estuarine environment off Abatan River mouth and, to a lesser extent, east of Panglao. No specimen was taken around the exposed waters off Balicasag Island and Pamilacan Island. The similar sized *F. colorata* and *F. scalata* share a similar distribution, whereas other larger sized *Fulvia* s.s. species occupy completely different ecological niches.

Fulvia (*Laevifulvia*) *undatopicta* (Pilsbry, 1904)

Pl. 14 figs 1-4

Cardium hungerfordi undatopictum Pilsbry, 1904: 556, pl. 40 figs 14-15.

Cardium hungerfordi stigmaticum Pilsbry, 1904: 556-557, pl. 41 figs 13-14.



Material examined. — **Philippines**: PMBP 2004, Stn D13, 2-3 m, 8 v; Stn S27, 12 m, 2 v; Stn S39, 3-4 m, 1 v; Stn T14, 101-110 m, 1 v; Stn T18, 80-100 m, 2 v; Stn T41, 110-112 m, 1 v.

Description. — Shell small (H 10-18 mm), roughly equilateral and rounded, a little truncated posteriorly; height often slightly exceeds length. Circa 46-53 ribs; a few strong ribs on posterior part of the shell, weak anteriorly, almost smooth elsewhere. Scattered granulations present, often more or less commarginally aligned, especially on anteroventral part of the shell. Internal marginal crenulations usually clearly defined. Lunular heart rather small, elongated. Colour extremely variable, often whitish with irregular reddish brown streaks or spots, at times with four reddish spots or streaks forming a cross.

Distribution and ecology. — Throughout the tropical Indo-West Pacific, recorded from Madagascar (Vidal, 1994) and the Red Sea (coll. TP) to mainland Japan (Matsukuma, 2000), Guam (Paulay, 2003), northeastern Australia (Lamprell & Healy, 1998) and New Caledonia (Vidal, 1994). Littoral and sublittoral in mud and sand. The limited present material was all collected dead in 2-112 m, and consists solely of loose valves, which hampers determining its macro-habitat category. Moreover, the material of the T-stations is invariably worn and discoloured. In New Caledonia it 'lives in reefal or perireefal calcareous facies, between 10 and 35 m' (Vidal, 1994), which is in agreement with type A.

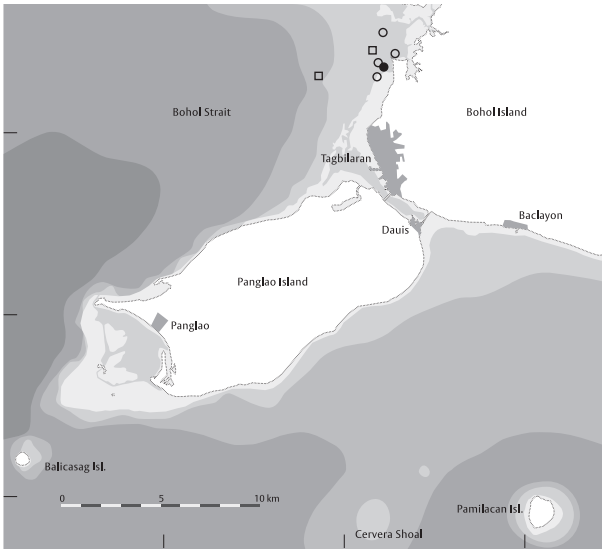
Remarks. — Often confused with juveniles of *F. australis* but clearly differentiated by its shell shape, nature of the granulations and colouration. Photos of live specimens (Matsukuma, 2000: 954-955) clearly show the large guard tentacles carrying ocular organs on their tips.

Fulvia (*Laevifulvia*) *hungerfordi* (G.B. Sowerby 3rd, 1901)

Pl. 14 figs 5-8, pl. 15 figs 3-4

Cardium (*Papyridia*) [sic! err. pro *Papyridea*] *hungerfordi* G.B. Sowerby 3rd, 1901: 103, pl. 9 fig. 5.

Fulvia (*Laevifulvia*) *prashadi* Vidal, 1994: 111-112, pl. 3 figs 8a-b.



Material examined. — **Philippines**: PMBP 2004, Stn S19, 3-4 m, 3 v; Stn S20, 10 m, 4 pv, 29 v (A); Stn S25, 21 m, 1 v; Stn S27, 12 m, 24 v; Stn S52, 2 m, 2 v; Stn T14, 101-110 m, 1 v; Stn T19 10-26 m, 1 v.

Description. — Shell small (L 10-15 mm), well inflated, generally inequilateral with posterior third expanded and posterior margin truncated. Ribs strongly developed on posterior third, anteriorly less accentuated, obsolete on median part, which has a glossy and smooth appearance. Dense granulations can be present, often limited to posterior quarter of the shell and near the ventral margin. Internal marginal crenulations usually weakly defined in the mid ventral margin edge, well developed towards anterior and posterior margin and visible over a long distance from the margins. Lunular heart small. Colour uniform whitish to reddish brown, adults sometimes with concentric growth lines visible as a change in shell colour and opacity.

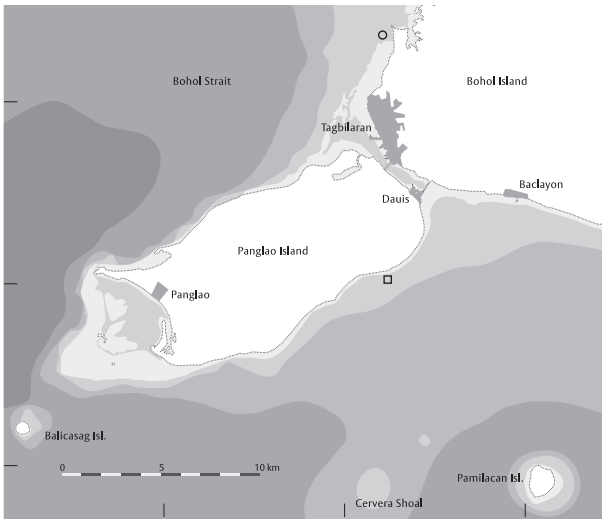
Distribution and ecology. — Central Indo-Pacific, ranging from mainland Japan to the Philippines, Indonesia and New Caledonia (Vidal, 1994), as well as Thailand (Lynge, 1909; Hylleberg, 2004), Vietnam (Hylleberg & Kilburn 2003) and Vanuatu (MNHN, det. TP). Depth range of present material 2-110 m (dead), 10 m (alive), all originating from muddy sediments in the immediate vicinity of Abatan River mouth; essentially found littorally.

Remarks. — See Ter Poorten (2007a) for remarks regarding the taxonomic status of *F. prashadi* Vidal, 1994. The marked preference for non-exposed muddy habitats is confirmed by its occurrence in the sheltered Ambon Bay, Indonesia (Ter Poorten, 2007a), the inshore embayment of Tolo Harbour, Hong Kong, where it is the dominant mollusc

(Shin, 1985), and the Jintololo Channel, north of Panay Island, Philippines (MUSORSTOM 3, Stn DR 140, fide Vidal, 1994: 111). Reid & Shin (1985) suspected the absence of significant predators, two species of the starfish *Luidia*, in the turbid and polluted Tolo Harbour to be the cause of the flourishing population of *F. hungerfordi*.

***Fulvia* (*Laevifulvia*) *subquadrata* Vidal & Kirkendale, 2007**
Pl. 14 figs 9-10

Fulvia (*Laevifulvia*) *subquadrata* Vidal & Kirkendale, 2007: 90-92, figs 3g-i, table 3.



Material examined. — **Philippines**: PMBP 2004, Stn S20, 10 m, 1 v; Stn T6, 34-82 m, 1 v.

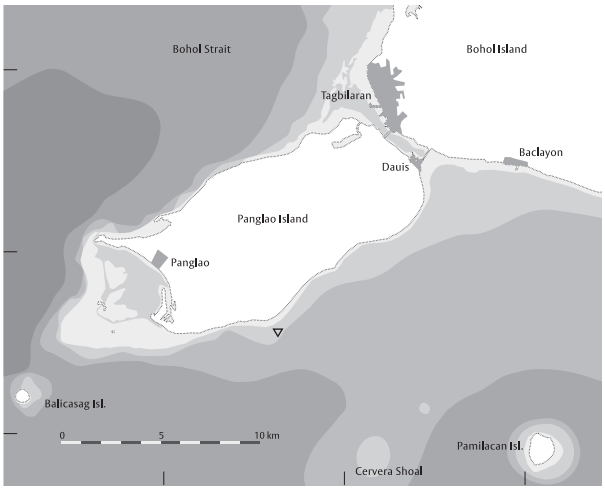
Description. — Shell very small (L 5-9 mm), well inflated, subquadrangular and subequilateral with rather straight posterior margin. L/H ratio about 1. Circa 36-42 ribs, best developed on posterior slope, indistinct on median part. On fresh material, dense granulations are present towards all of the margins, extending over nearly all the shell in fresh valves. Internal marginal crenulations usually quite well developed, even in the middle of the ventral margin edge. Lunular heart small but well defined. External and internal colour uniform brown or pink; lunular area whitish, occasionally very white.

Distribution and ecology. — Known from the Solomon Islands, New Caledonia (Vidal & Kirkendale, 2007) and Vanuatu (MNHN, det. TP). The present Philippine records represent a considerable westward range extension and originate from a depth of 10-82 m (dead), in mud, silt and muddy sand bottoms. The Cuming Tour 2005 yielded an additional valve (Philippines, Luzon, Quezon, Tayabas Bay, Sariaya, beached, Stn CT 35 – Pl. 14 fig. 18); another Philippine specimen is also known (Leyte Isl., Albuera, 10°51.83'N-124°38.245'E, 80-100 m, 2007, leg. G.T. Poppe, coll. TP).

Remarks. — The outline and the extensive granulations are unique and readily separate this species from related taxa. The bathymetrical range appears to be mainly littoral as the species has been live taken from 0-6 m in New Caledonia (Vidal & Kirkendale, 2007) and from 4-7 m in Vanuatu (MNHN), in both instances from non-exposed habitats.

***Fulvia* (*Laevifulvia*) *lineonotata* Vidal, 1994**
Pl. 14 figs 11-14

Fulvia (*Laevifulvia*) *lineonotata* Vidal, 1994: 110-111, pl. 3 figs 4a-b.



Material examined. — **Philippines**: PMBP 2004, Stn D15, 53-63 m, 4 v.

Description. — Shell small (H 10-15 mm) rather elongate (juveniles more rounded) and inequilateral with rounded anterior margin and angular postero-ventral margin. Posterior zone with well developed ribs; anterior and median part smooth and glossy. Based on the marginal crenulations, circa 50-55 ribs. Minute, scattered granulations may be present, mainly on the anterior half of the shell exterior. Lunular heart long and narrow, barely defined. Interior and exterior whitish, variably but vividly coloured with imbricated whitish triangles that have purple or reddish brown edges and similarly-coloured spots, radially aligned, especially along the medio-posterior line.

Distribution and ecology. — Tropical Indo-West Pacific, recorded from Mauritius, India and New Caledonia (Vidal, 1994), and from the Philippines (Ter Poorten, 2007a), Malaysia (coll. MH; TP) Vanuatu and Fiji (MNHN, det. TP). The sole sample from the present expedition comes from 53-63 m depth, of an unspecified bottom type.

Remarks. — In New Caledonia recorded from clean calcareous facies in 25-60 m (Vidal, 1994). The Rumphius Expedition to Ambon, Indonesia, yielded live specimens in 4-20 m, originating from a muddy sand bottom (Ter Poorten, 2007a). The elongate, inequilateral shape and complex, vivid colouration readily distinguishes this species from its congeners.

Pseudofulvia Vidal & Kirkendale, 2007

Pseudofulvia Vidal & Kirkendale, 2007: 93. Type species by original designation: *Pseudofulvia caledonica* Vidal & Kirkendale, 2007; Recent, 20°40.4'S, 164°14.9'E, Passe de Koumac, New Caledonia, 10-60 m.

Diagnosis. — Shell small, thin, inequilateral, elongate. Relatively pronounced keel present. Posterior ribbing strong and triangular in cross-section; remainder of the shell almost smooth. Periostracal insertions present or absent, depending on species.

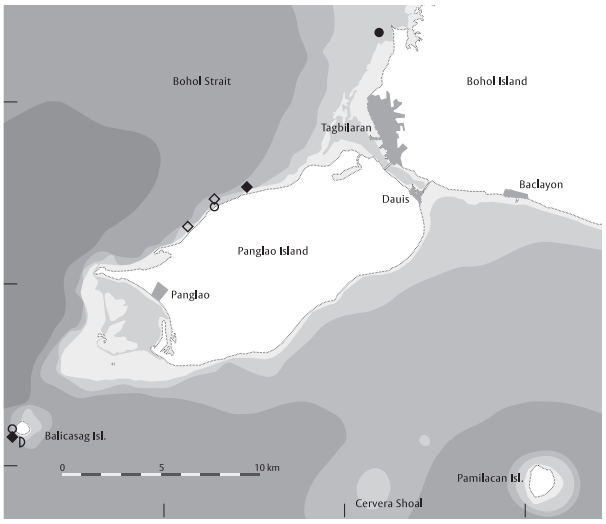
Distribution. — Recent (thus far no fossil records), Indo-Pacific; littoral-sublittoral.

Remarks. — Morphologically close to *Fulvia* (*Fulvia*) and *Fulvia* (*Laevifulvia*) but differentiated by its 'fragiform' outline, with a rather well developed keel and a highly contrasting rib pattern: almost smooth anterior and median zones, combined with strong ribbing on the posterior zone.

Pseudofulvia caledonica Vidal & Kirkendale, 2007

Pl. 14 figs 19-20, pl. 15 figs 7-8

Pseudofulvia caledonica Vidal & Kirkendale, 2007: 93-94, figs 4a-c, table 4.



Material examined. — **Philippines**: PMBP 2004, Stn B10, 3-14 m, 1 pv; Stn B16, 20 m, 1 pv (A); Stn B21, 20-21 m, 1 pv; Stn B37, 19-20 m, 1 pv (A) [*fide* Vidal & Kirkendale, 2007: 93]; Stns L74-75, 120-139 m, 1 v; Stn S25, 21 m, 1 pv (A) [*fide* Vidal & Kirkendale, 2007: 93]; stn S28, 28-32 m, 1 v; stn S46, 14 m, 1 pv.

Description. — Shell small (H 10-13 mm), thin, inequilateral, elongate, inflated with a moderately developed umbonal-ventral keel. Margins rounded except for rather angular postero-ventral margin and nearly straight posterior margin. Posterior slope having 12-13 large, roundly triangular ribs bearing thin periostracal insertions on top that often become finely spinose. Remainder of shell having circa 30 very weakly developed ribs, lacking periostracal insertions. Minute, dense granulations readily perceptible, particularly in the interstices and towards the margins. Exterior white, becoming cream towards umbonal area, umbonal tip reddish-brown and lunular area yellow. Posterior slope with brown zigzag patterns. Interior white, with exterior colours visible through translucent shell.

Distribution and ecology. — Known from the Philippines, New Caledonia, Loyalty Islands and Fiji (Vidal & Kirkendale, 2007). The recent find of a valve from Flic en Flac, Mauritius, in 30 m (ZMA; leg. R.G. Moolenbeek, 12.vii.2008; det. TP) expands tremendously the known range to the western Indian Ocean. Depth range of present material 14-139 m (dead), 19-21 m (alive). The species has a preference for exposed littoral and sublittoral coral reef environments, often in muddy sediments.

Remarks. — The live taken specimens of Stns B37, S25 were subsampled for molecular analysis (Vidal & Kirkendale, 2007: 104). As in *Fulvia* s.l., the opacity of the shell is variable, containing opaque white parts and more or less translucent coloured parts. Contrary to *Fulvia* s.l. the animal lacks ocular organs on the guard tentacles, and it appears to occupy a quite different habitat category (table 10).

Laevicardium Swainson, 1840

Laevicardium Swainson, 1840: 373 (as a subgenus of *Cardium*). Type species by subsequent designation (Stoliczka, 1871: 209): *Cardium oblongum* Gmelin, 1791; Recent, 'mari mediterraneo' ('Mediterranean').

Liocardium Agassiz, 1846: 199, 212 (unnecessary emendation of *Laevicardium*).

Diagnosis. — Shell small to very large, elongately ovate or rounded triangular and rather inflated, radial ribs very low to indistinct, resulting in a smooth, often glossy appearance. Posterior margin relatively weakly crenulated. Hinge line long and arched, lateral teeth relatively large.

Distribution. — Eocene to Recent, North Atlantic, Mediterranean, West African, Transatlantic, Caribbean, Patagonian, Californian, Panamic, Indo-Pacific (?), Japonic (?); littoral-sublittoral.

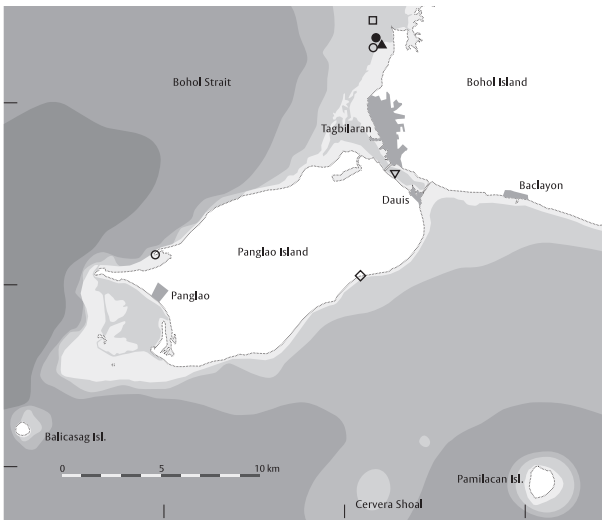
Remarks. — See Wilson & Stevenson (1977: 57) and Vokes (1989: 126-127) for taxonomic comments regarding the shell morphology of *Laevicardium* taxa related to that of the type species and the original description of Swainson, demonstrating the present lack of homogeneity in *Leavicardium*. All four Indo-Pacific taxa traditionally assigned to *Laevicardium* were encountered by the present expeditions. Based on gross morphology, these at first sight smooth cardiids share a superficial resemblance with *Laevicardium*. However, their microsculptural characters rarely fit the *Laevicardium* concept (see below); allocation by some authors to *Acrosterigma* or *Lyrocardium* is also unsatisfying. Consequently, the alleged Indo-Pacific presence of *Laevicardium*, classically encompassing medium to large sized elongate shells with a virtually smooth shell surface, is here considered doubtful. It appears that the morphology of

Indo-Pacific species hitherto considered as belonging to *Laevicardium* may well be a case of convergence rather than resulting from phylogenetic relationship. Moreover, these four species display considerable mutual differences. Additional research and molecular-phylogenetic analysis is needed for a better understanding of this heterogeneity, leading to a more appropriate generic placement.

"*Laevicardium*" *lobulatum* (Deshayes, 1855)

Pl. 14 figs 15-18, pl. 15 figs 5-6, pl. 16 figs 13-15

Cardium lobulatum Deshayes, 1855: 332.
Fulvia (*Laevifulvia*) *imperfecta* Vidal & Kirkendale, 2007: 92-93, figs 3j-l [**syn. nov.**].



Material examined. — **Philippines**: PMBP 2004, Stn B5, 4 m, 1 v; Stn D13, 2-3 m, 3 v; Stn R62, 2-15 m, 2 pv (A); Stn S21, 4-12 m, 6 pv, 11 v (A); Stn S27, 12 m, 2 pv, 4 v; Stn S32, 2-3 m, 1 v; Stn T19, 10-26 m, 1 v.

Description. — Shell small to medium (H 25-35 mm), rather solid, inequilateral, elongately oblique. Allomorphic growth pattern: juveniles more rounded-quadrangular, less inflated and relatively thin. Shell surface glossy and smooth with minute growth lines. On the medio-posterior part these lines are crossed by circa six weakly developed ribs, creating a finely undulating pattern. Margins rounded, except for a short posterior straightening or indentation, better developed in adults. Internal margin carrying about 70-95 crenulations. Lunula elongate, slightly protruding. Hinge long and arched. Exterior cream with brown radial or inverted v-shaped markings, occasionally with a zigzag pattern and with margins usually lighter coloured. Interior often darker reddish-brown. Hinge plate chocolate brown to purple.

Young juveniles exhibit a sharp carina (of variable strength), separating the median-posterior area, resulting in a straight or slightly concave ventral margin, and well developed radial and concentric riblets (pl. 15 fig. 5) forming a reticulate pattern.

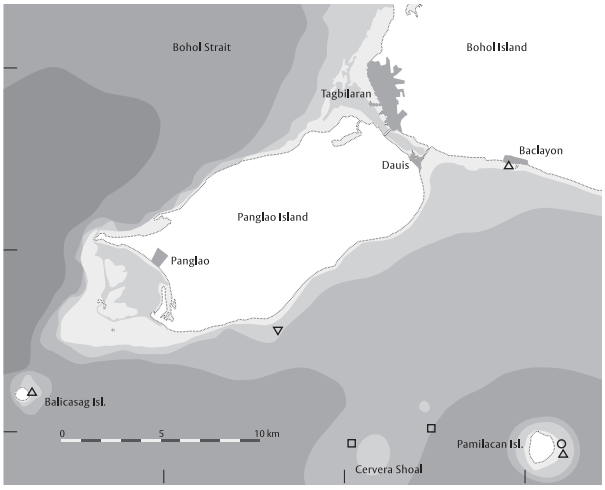
Distribution and ecology. — Central Indo-West Pacific from Thailand (Lynge, 1909), Indonesia (Ter Poorten, 2007a), Philippines (Deshayes, 1855), islands south of mainland Japan (Higo *et al*., 1999), Queensland (coll. TP), New Caledonia (Héros *et al*., 2007) and Vanuatu (MNHN, det. TP). It is uncommon and appears to prefer bottoms of sand, mud and silt in semi-protected littoral habitats. Depth range of present material 2-26 m (dead), 4-12 m (alive).

Remarks. — Stations R62, S21 and S27 consist of a hard bottom with sediment patches, supplemented with mud, sand and corals, located at a reef edge in a channel (Bouchet *et al*., 2009; information from Google Earth). G.T. Poppe (e-mail, 2006) has found this species near Palompon (Philippines, Leyte Island; pl. 16 fig. 15) in a similar semi-exposed habitat: a channel with mangroves, seagrass and a mud bottom, obtained via scuba, suggesting rather specific ecological preferences. Vidal (1994: 111) pointed out the similarities with *Fulvia* (*Laevifulvia*) *lineonotata*. With adequate growth series at hand it becomes apparent that *F.* (*L.*) *imperfecta* Vidal & Kirkendale, 2007 is based on juvenile material of the present species. The reticulated nature of the protoconch combined with the sharp carina, both quickly disappearing during ontogeny, are unique characters never observed in any other *Laevicardium* species. The same is the case for the finely undulating appearance of the posterior slope.

"*Laevicardium*" *biradiatum* (Bruguière, 1789)

Pl. 16 figs 1-5

Cardium biradiatum Bruguière, 1789: 231.
Laevicardium rubropictum Habe & Kosuge, 1966a: 153, pl. 59 fig. 2; 1966b: 324, pl. 29 fig. 20.



Material examined. — **Philippines**: PMBP 2004, Stn D15, 53-63 m, 1 v; Stn R14, 6-8 m, 1 pv; Stn R16, 6-22 m, 1 pv; Stn R31, 10-41 m, 1 pv; Stn R38, 6-37 m, 1 pv; Stn S10, 6-14 m, 1 v; Stn T39, 100-138 m, 1 v; Stn T41, 110-112 m, 1 v.

Description. — Shell medium (H 30-50 mm), solid, subequilateral, elongate and pear-shaped, umbos pointed, anterior margin rounded, posterior margin almost straight for a short distance. Circa 40-60 very weakly developed to obsolete radial ribs, strongest on the median area and usually lacking orna-

mentation except for posteriormost ones that may carry small knobs when juvenile. Hinge plate strongly arched. Lunula raised in right valve, slightly protruding. Colour variable, mottled brown and cream with splashes of purple brown, stronger near dorsal margins; interior white and yellowish with two variably developed radial rays of purple or pink. Periostracum olive-green.

Distribution and ecology. — Throughout the tropical Indo-West Pacific from South Africa (Kwazulu-Natal) and the Red Sea (Oliver, 1992) to mainland Japan (Matsukuma, 2000), northern Australia (Lamprell & Whitehead, 1992) and Wallis and Futuna (Vidal, 1999a). Littoral and sublittoral waters in coral reef environments. Depth range of present material 6-138 m, dead only. Both T-station samples are worn, presumably not reflecting the original habitat, which is confined to shallower waters.

Remarks. — Vidal (1999a) placed this taxon together with *L. attenuatum* in *Acrosterigma*. Ter Poorten (2007a) argued for placing it in *Laevicardium* (see also remarks under *L. attenuatum*). An atypical feature of both *Laevicardium* and *Acrosterigma* is the occasional presence of commarginal rib sculpture near the anterior margin consisting of undulating anastomosing cords (pl. 16 fig. 5). This makes clear that, although to a certain extent both *L. biradiatum* and *L. attenuatum* display an intermediate position between the two genera, the correct assignment is far from settled. Additional anatomical and DNA research will provide more insight into their phylogenetic positions and might lead to further subdivision. *Laevicardium biradiatum* is collected locally for consumption in the Philippines.

"*Laevicardium*" *attenuatum* (G.B. Sowerby 2nd, 1841)

Pl. 16 figs 6-8

Cardium attenuatum G.B. Sowerby 2nd, 1841: 109.

Material examined. — **Philippines**: PANGLAO 2005, Stn DW 2370, 92-96 m, 1 v.

Description. — Shell large (H 70-85 mm), solid, inequilateral, extremely elongate and attenuated, umbos markedly pointed, anterior margin rounded, posterior margin almost straight for a long distance and strongly crenulated. H/L ratio generally increases considerably during ontogeny. Circa 50-65 very weakly developed to obsolete radial ribs, strongest on the median area and lacking ornamentation. Hinge plate very strongly arched. Lunula raised in right valve, slightly protruding. Colour variable, exterior cream with yellowish or brownish spots posteriorly. Interior white or with two orange-pink radial rays. All white and all yellow specimens occur. Periostracum olive-green and rather thick.

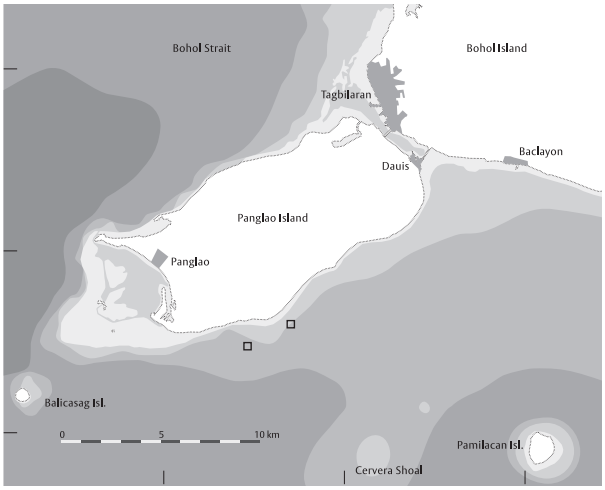
Distribution and ecology. — Throughout the tropical Indo-West Pacific from South Africa (Kwazulu-Natal) and the Red Sea (Mienis, 2002), to isalnds south of mainland Japan (Matsukuma, 2000), northern Australia (Lamprell & Whitehead, 1992), New Caledonia (Vidal, 1999a) and Vanuatu (MNHN, det. TP). The sole PANGLAO 2005 valve (92-96 m) is immature and heavily worn. Nevertheless, the species is well-known from the Philippines and neighbouring islands (coll. TP). Apart from being relatively less elongate, juveniles are often more flattened and thus easily confused with L. biradiatum.

Remarks. — There are 1-2 radial grooves or cords near the postero-dorsal margin (pl. 16 fig. 7c), especially easily discernable on well preserved juvenile valves. The anterior quarter is demarcated by a weakly developed line, consisting of a series of discontinuous shallow radial notches. Both characters represent features never observed in *Acrosterigma*. The occasional presence of commarginal rib sculpture near the anterior margin, consisting of undulating cords (pl. 16 fig. 8), is not seen in *Laevicardium* or *Acrosterigma* and only occurs in *Lyrocardium*.

"*Laevicardium*" *multipunctatum* (G.B. Sowerby 1st in Broderip & G.B. Sowerby 1st, 1833)

Pl. 16 figs 9-12

Cardium multipunctatum G.B. Sowerby 1st in Broderip & G.B. Sowerby 1st, 1833: 84; G.B. Sowerby 2nd, 1834: sp. 70, fig. 14; 1840b: 6, sp. 70.



Material examined. — **Philippines**: PMBP 2004, Stn T1, 83-102 m, 1 v; Stn T4, 82 m, 1 v.

Description. — Shell relatively large (H 40-55 mm), rather solid, inequilateral, elongately oblique. Shell surface glossy and partly smooth; anterior third sculptured with circa 25-40 scissulate cords (counted in adult specimens), radial ribbing obsolete on median part, weakly developed on posterior slope. Lunular heart lanceolate and raised. Exterior colour consisting of commarginal pink to purple bands, darker towards the margins, on a cream background with brownish splashes. Interior orange or brown to deep pink. Umbonal cavity lighter.

Distribution and ecology. — Imperfectly known, in all probability restricted to the tropical West Pacific from islands south of mainland Japan (Higo *et al*., 1999), China (G.B. Sowerby 1st, 1833; coll. TP), Vietnam (Hylleberg & Kilburn,

2003), Philippines (Hidalgo, 1903; Faustino, 1928), Indonesia (Dharma, 2005) and Vanuatu (MNHN, det. TP). Present material juvenile, found dead sublittorally at a depth range of 82-102 m.

Remarks. — This species has often been referred to *Laevicardium* and occasionally to *Discors* (Abbott & Dance, 1982; Higo *et al*., 1999) and *Lyrocardium* (Ter Poorten, 2007). The outline, the long and curved hinge plate and the inconspicuous radial ribbing are in agreement with *Laevicardium* but the well developed transverse oblique cords strongly agree with *Discors* and *Lyrocardium*. This character connects the present species with *Laevicardium biradiatum* and *L. attenuatum* in which it can also be observed occasionally, though only rudimentarily. Although quite distinctive, it was not considered by G.B. Sowerby 1st (1833) nor by nearly all subsequent workers. Pending possible future combined morphological, anatomical and DNA research, I prefer to leave the question of generic assignment open and provisionally retain the unsatisfactory placement in *Laevicardium*.

The majority of the Chinese specimens tend to have a more regular rounded outline and more prominent brownish spots – hence the species' name – which thus reflects the fact that the species was originally described from 'ad littora Chinae'.

Frigidocardium Habe, 1951

Erigidocardium [sic! err. pro *Frigidocardium*] Habe, 1951: 152 (as a subgenus of *Nemocardium*). Type species by original designation: *Cardium* (*Fragum*?) *eos* Kuroda, 1929; Recent, Kii peninsula, Honshū, Japan.

Diagnosis. — Shell small to medium sized, rather thin to medium thick, often well inflated. Ribbing structure homogeneous, often with numerous radial ribs, covering the whole surface and with rows of tubular to spatuliform spines of variously alternating strength (Poutiers, 1992). Sculpture may arise from rib tops, rib flanks or interstices. Ribs either all sculptured or alternating with 2-5 unsculptured ribs and/or interstices. Transverse sculpture of interstices variably developed to absent.

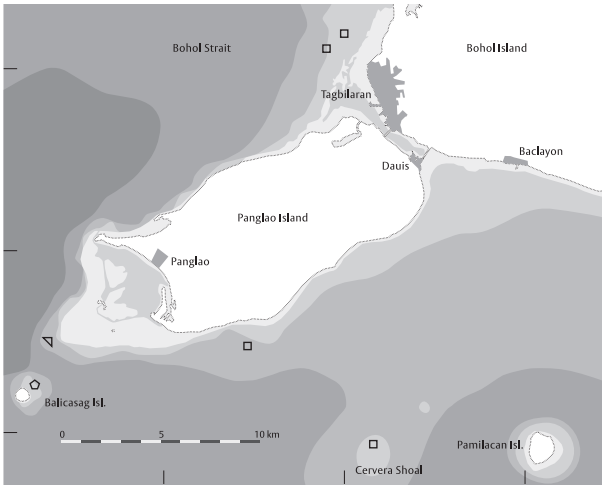
Distribution. — Miocene to Recent, Indo-Pacific, Japonic; sublittoral to upper bathyal.

Remarks. — *Frigidocardium* is a rather poorly known genus, probably due to its relatively deep water occurrence and fairly small size. Confusion has often arisen with other related genera like *Microcardium* Thiele, 1934 and, to a lesser extent, *Nemocardium* Meek, 1876. For reasons given in the introduction to Laevicardiinae, these three genera and the closely related genus *Trifaricardium* are placed in this subfamily rather than Protocardiinae. In the *Frigidocardium* species descriptions, primary and secondary radial sculpture refers respectively to rows of relatively larger and smaller spines; when all spine rows are of equivalent strength, they are considered primary.

Frigidocardium eos (Kuroda, 1929)

Pl. 17 figs 1-4, pl. 20 fig. 3, table 7

Cardium (*Fragum*?) *eos* Kuroda, 1929: 93, pl. 3 fig. 5.



Material examined. — **Philippines**: PMBP 2004, Stn T1, 83-102 m, 1 v; Stn T11, 78-95 m, 1 v; Stn T13, 90-100 m, 1 v; Stn T40, 80-98 m, 1 v; No stn nr., Balicasag Isl., tangle nets and lumun lumun, 'deep water', bought from fishermen, 2004, gift of B. Olivera, 3 pv. PANGLAO 2005, Stn DW 2400, 111-115 m, 9 v.

Description. — Shell relatively large (H up to 25-30 mm), inflated, ovate-quadrangular and slightly inequilateral. Length generally slightly exceeds height, although in Chinese/Taiwanese/Japanese material the opposite is the case. Circa 130-145 radial ribs, all sculptured on anterior flank with a row of erect but delicate spines of distinctly alternating strength, becoming slightly spatulate anteriorly and coarser posteriorly; commarginal sculpture of rib interstices usually inconspicuous. Lunular heart well defined, elevated, orange coloured and rather broad. Lunular area more finely sculptured but with no clear border; lunular margin straight. Shell white and orange, radially and commarginally streaked (coinciding with growth interruptions), lunula orange, umbo mostly yellowish. Occasionally the entire shell is pure lemon yellow.

Distribution and ecology. — Known from mainland Japan (Higo *et al*., 1999; Matsukuma, 2000), China, Philippines and Indonesia (Huber & Ter Poorten, 2007) and Western Australia (WAM, det. TP). Apparently not extending farther into the West Pacific. Mostly collected from mud or sand bottoms by tangle nets. Depth range of present material 78-115 m, based solely on loose valves.

Remarks. — Well known from Balicasag Island where it is regularly found in tangle nets of local fishermen. In the literature often confused with *F. torresi* (E.A. Smith, 1885), which is much smaller, less colourful and which has well-developed crossbars in the rib interstices. See table 7 for further comparisons. The overall shape, size and colouration are very similar to those of *F. valdentatum* Poutiers, 2006 but the latter has a West Pacific range from Vanuatu, New Caledonia, Fiji and Tonga. *Frigidocardium valdentatum* also differs in having more radial ribs (about 150-180), a stronger serrated posterior margin (in part) and secondary sculpture consisting of minute granules.

Frigidocardium iris Huber & Ter Poorten, 2007

Pl. 17 figs 5-7, pl. 20 fig. 5, table 7

Frigidocardium iris Huber & Ter Poorten, 2007: 105-107, pl. 1 figs 1-10, pl. 2 figs 7-10, tables 1-2.

Material examined. — **Philippines**: PANGLAO 2005, Stn DW 2370, 92-96 m, 8 v; Stn DW 2371, 172-175 m, 1 v.

Description. — Shell relatively large (H 25-28 mm), inflated, ovate-quadrangular and subequilateral. Postero-ventral margin quadrangular. L/H ratio about 1. Shell rather thin. Over 100 radial ribs, of which circa 30-40 bear finely upright spines, positioned on the flanks and becoming slightly larger and more crowded posteriorly and spatulate to almost knobby anteriorly. Primary rib sculpture regularly alternating with row of tiny secondary spines, also positioned on the rib flanks. Larger spines arising from anterior flanks over the entire surface, but smaller spines arise from posterior flanks of ribs on the anterior 3/5 and from anterior flanks on the posterior 2/5. Interstices with poorly developed cross-striae, sometimes lacking. Lunular area readily distinguishable because of its very weak sculpture, contrasting with the adjacent radial rows of strong tubercles. Lunular heart well defined, forming a rounded ovate bulge of the dorsal margin and only flattened on a very narrow lanceolate area along the antero-dorsal margin of each valve. Exterior white, usually with red collars, commarginally arranged and more prominent towards the margins. Specimens that are almost all pinkish-red or white occur. Inside white, umbonal cavity usually deep yellow. Lunular area generally deep orange-red.

Distribution and ecology. — At present recorded from Philippines, Indonesia and northern and north-western Australia from 40-200 m on fine sandy bottoms (Huber & Ter Poorten, 2007). PANGLAO 2005 material found dead in 92-175 m.

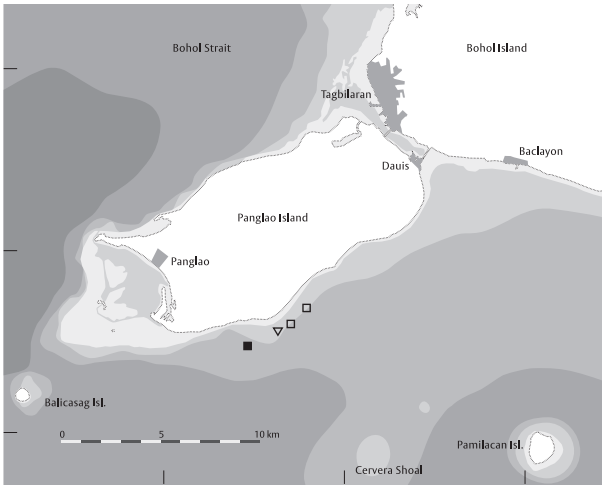
Remarks. — Known from Balicasag Island where it is occasionally found in tangle nets of local fishermen (ZMA; TP). Nevertheless not recorded by PMBP 2004. Its most closely related species, *F. exasperatum* (G.B. Sowerby 2nd, 1839), differs mainly in its very asymmetric sinuous lunula, which is much larger in the left valve than in the right one. Also, it is more coarsely sculptured, is white and has a more northern distribution from Japan to Vietnam (see table 7). *Frigidocardium sancticaroli* spec. nov. is much smaller, has a poorly demarcated lunular area and is completely white.

Frigidocardium helios Ter Poorten & Poutiers spec. nov.

Pl. 18 figs 1-6, pl. 19 fig. 2, pl. 20 fig. 1, tables 5, 7

Frigidocardium spec. nov. Ter Poorten & Poutiers, MS – Van der Meij *et al*., 2009: 104, table 2.

Holotype. — Vanuatu, SANTO 2006, Stn 'FB94', S.E. corner of Santo (exact locality data not recorded), ix-x.2006, 1 pv (A/DNA, MNHN 30161). Paratypes as listed below.



Other material examined. — **Philippines**: PMBP 2004, Stn D15, 53-63 m, 1 pv (paratype 1, NMP); Stn T1, 83-102 m, 1 pv (A), 2 v (paratypes 2-4, MNHN 22273); Stn T4, 82 m, 1 v (paratype 5, MNHN 22272); Stn T44, 83-86 m, 1 v (paratype 6, MNHN 22044); Siquijor Isl., offshore Tubod, dredged 69 m, Guphil I. 01.v.2004, leg. G.T. Poppe, 1 pv (paratype 14, coll. Poppe 169352); **Malaysia**, Borneo, off Sabah, W of Brunei, Central Luconia Shoals, 5°37.139'N, 112°30.589'E, on rubble slope and reef flat in sand pockets, 10-50 m. x.2006, leg. F. Lorenz & H. Morrison, 2 pv (A) (paratypes 16-17, TP 3700); **Indonesia**, Banda Sea, Wakatobi Isl. group, N side of Koka reef, 6°02'089"S, 124°22'840"E, on wall, in sand + grit samples, dived, 40-50 m. 19.x.2005, leg. F. Lorenz & H. Morrison, 1 v (paratype 15, TP 2932); Sulawesi, Salibabu Island, anchorage off Lirung, mud, hard sand, trawl, dredge, reef-exploration, townet, up to 36 m. 27.vii.1899, SIBOGA, Stn 133.2, 1 pv (paratype 9, ZMA Moll.4.09.039); Jawa, Hantu Besar, 5°31'47"S, 106°32'20"E, scuba 5-35 m, Kepulauan Seribu Exp., 2005, Stn SER05/21, 14.ix.2005, leg. R.G. Moolenbeek & S. van der Meij, 2 v (paratype 10, ZMA Moll.4.09.040; paratype 11, ZMA Moll.4.09.041); Jawa, Pari off S shore, 5°52'51"S, 106°38'07"E, on plateaux, 10-25 m, Kepulauan Seribu Exp., 2005, Stn SER05/46, 27.ix.2005, leg. R.G. Moolenbeek & S. van der Meij, 2 v (paratype 12, ZMA Moll.4.09.042; paratype 13, ZMA Moll.4.09.043); **Vanuatu**, SANTO 2006, Stn AT75, Bruat Channel, 15°37.0/37.3'S 167°9.2/9.6'E, 52-66 m, 10.x.2006, 1 pv (A) (paratype 7, MNHN 22335); Stn EP21, NW coast of Malo Isl., 15°37.7'S 167°5.2'E, 99 m, 20.ix.2006, 1 v (paratype 8, MNHN 22336); **New Caledonia**, MONTROUZIER, 1993, Stn 1314, Passe de Koumac, 20°39.8'S-164°14.7'E, muddy sand with shells, 30-63 m, 1 pv, 1 v (MNHN); Stn 1315, Passe de Koumac, 20°40.7'S-164°15.3'E, muddy sand with shells, 66-87 m, 1 pv, 3 v (MNHN); Stn 1321, Koumac area, Passe Deverd, 20°44.7'S-164°14.9'E, muddy sand, 90-115 m, 2 pv (A) (paratypes 18-19 MNHN 22337), 6 v (MNHN); Stn 1322, Koumac area, Passe Deverd, 20°45.2'S-164°15.2'E, muddy sand, 53-71 m, 4 v (MNHN); Stn 1323, Koumac area, Chenal de la Passe de Koumac, 20°40.9'S-164°14.18'E, muddy shelly sand, 82-120 m, 4 pv, 8 v (MNHN).

Description. — 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 45-65 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 yellowish hue; interior same colouration because of the translucency of the shell.

Distribution and ecology. — Known from the Philippines, Malaysia, Indonesia, New Caledonia and Vanuatu. Remarkably, all PMBP 2004 records originate from four localities, consisting of sublittoral muddy bottoms with sponges at depths of 53-102 m (dead) and 83-102 m (alive). The available data and absence of PANGLAO 2005 records suggest that the species is more confined to shallower sublittoral waters.

Etymology. — Named after Helios, the Greek god of the sun, referring to the colouration, and reflecting its relationship to two congeneric species *F. eos* and *F. iris*, named respectively after the Greek goddesses of the dawn and the rainbow.

Remarks. — Its closest congener *F. eos* differs in its larger size, more vivid colouration, lower rib number, presence of secondary radial sculpture, absence of developed crossbars in rib interstices and structure of the lunular area. *Frigidocardium torresi* has a much lower rib number, a lower number of sculptured radial rows, a more solid and more strongly inflated, quadrangular appearance and is less colourful. Its interstices are coarsely sculptured with crossbars. *Frigidocardium kirana* can be easily differentiated by its angular outline and umbonal keel. See table 7 for comparisons with these and other taxa.

Frigidocardium kirana Sakurai & Habe, 1966

Pl. 17 figs 8-10, pl. 19 fig. 4, pl. 20 fig. 4, table 7

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

Material examined. — **Philippines**: PMBP 2004, Stn L42, 80-90 m, 1 v; Stn L46, 90-110 m, 2 v; L50, 120 m, 1 v; Stns L51-60, 43-62 m, 2 pv (A); Stns L74-75, 120-139 m, 1 pv, 1 v; Stn P4, 80-120 m, 1 v; Stn S8, 28-32 m, 1 pv, 1 v; Stn T38, 80-140 m, 1 v; No stn nr., Panglao Isl., Momo Beach zone, 9°36'N, 123°45'E, tangle nets from Jo Arbasto, 1 v. PANGLAO 2005, Stn DW 2400, 111-115 m, 1 pv, 1 v.

Description. — Shell medium sized (H up to 16 mm) and rather thin, inequilateral with strong umbono-ventral flexure, angled postero-ventral margin and straight or slightly concave posterior margin. Length usually equal to height. Numerous (circa 120-130) radial ribs, all finely sculptured. Spines tiny,

	L	*H*	*W*	*L/H*	*W/L*	*Ribs*	*Sculptured Rows*
SANTO 'FB94' MNHN 30161 Holotype (pv)	7.3 mm	7.0 mm	5.3 mm	1.04	0.73	c. 145	c. 55
PMBP D15 NMP Paratype 1 (pv)	6.7 mm	6.6 mm	5.0 mm	1.02	0.75	c. 155	c. 56
PMBP T1 MNHN 22273 Paratype 2 (pv)	5.1 mm	5.0 mm	3.6 mm	1.02	0.71	c. 150	c. 50
PMBP T1 MNHN 22273 Paratype 3 (lv)	8.7 mm	8.8 mm	(6.8 mm)	0.99	0.78	c. 165	c. 66
PMBP T1 MNHN 22273 Paratype 4 (rv)	6.1 mm	6.0 mm	(4.3 mm)	1.02	0.70	c. 155	c. 49
PMBP T4 MNHN 22272 Paratype 5 (rv)	5.4 mm	5.3 mm	(4.0 mm)	1.02	0.74	c. 175	c. 46
PMBP T44 MNHN 22044 Paratype 6 (rv)	9.5 mm	9.7 mm	(7.6 mm)	0.98	0.80	c. 160	c. 49
SANTO AT75 MNHN 22335 Paratype 7 (pv)	6.4 mm	6.5 mm	[1]	0.98	[1]	c. 160	c. 52
SANTO EP21 MNHN 22336 Paratype 8 (rv)	4.6 mm	4.4 mm	(3.2 mm)	1.05	0.70	c. 155	[2]
Siboga 133.2 ZMA Moll.4.09.039 Paratype 9 (pv)	9.4 mm	9.0 mm	6.8 mm	1.04	0.72	c. 145	c. 55
SER05/21 ZMA Moll.4.09.040 Paratype 10 (lv)	3.0 mm	2.9 mm	–	1.03	–	–	–
SER05/21 ZMA Moll.4.09.041 Paratype 11 (lv)	2.7 mm	2.5 mm	–	1.08	–	–	–
SER05/46 ZMA Moll.4.09.042 Paratype 12 (lv)	2.0 mm	1.9 mm	–	1.05	–	–	–
SER05/46 ZMA Moll.4.09.043 Paratype 13 (rv)	(fragment, c. 3 mm)		–	–	–	–	–
Poppe 169352 Paratype 14 (pv)	5.7 mm	5.3 mm	4.0 mm	1.08	0.71	c. 155	c. 51
TP 2932 Paratype 15 (lv)	5.3 mm	5.2 mm	(4.0 mm)	1.02	0.75	c. 135	c. 47
TP 3700 Paratype 16 (pv)	5.8 mm	5.5 mm	4.4 mm	1.05	0.76	c. 130	c. 50
TP 3700 Paratype 17 (pv)	5.9 mm	5.5 mm	4.3 mm	1.07	0.73	c. 145	c. 46
MONTROUZIER 1321 MNHN 22337 Paratype 18 (pv)	9.5 mm	9.3 mm	7.2 mm	1.02	0.76	c. 150	c. 55
MONTROUZIER 1321 MNHN 22337 Paratype 19 (pv)	8.1 mm	7.9 mm	6.3 mm	1.03	0.78	c. 145	c. 53
Mean values				1.03	0.74	152	52

Table 5. Shell measurements and rib count of *Frigidocardium helios* spec. nov. Extrapolated sizes in brackets. Rib number based on counting actual ribs rather than marginal crenulations, lunular area excluded.
[1] Not measurable due to the fact that rv is partly missing.
[2] Not countable due to poor state of preservation.

PLATE 13

Figs 1-4. *Fulvia* (*Fulvia*) *boholensis* Vidal, 1994. **1.** PMBP 2004 Stn R9, lv exterior, dorsal and posterior, L 31.7 mm. **2.** PMBP 2004 Stn R20, lv exterior, L 25.5 mm. **3.** PMBP 2004 Stn R6, lv exterior and rv interior, L 15.4 mm. **4.** Philippines, Panglao, 25 m, lv exterior, dorsal and rv interior, L 27.9 mm (TP 2258). **Figs 5-7.** *Fulvia* (*Fulvia*) *colorata* Vidal & Kirkendale, 2007. **5.** PMBP 2004 Stn T33, lv exterior, rv interior and dorsal, H 12.3 mm. **6-7.** PMBP 2004 Stn T7. **6.** lv exterior, H 14.4 mm. **7.** lv exterior, H 7.9 mm. **Figs 8-10.** *Fulvia* (*Fulvia*) *scalata* Vidal, 1994. **8.** PMBP 2004 Stn T19, rv exterior and interior, H 16.1 mm. **9.** PMBP 2004 Stn S25, lv exterior, rv interior and anterior, L 14.8 mm. **10.** PMBP 2004 Stn T19, lv exterior, rv interior, dorsal and posterior, H 14.0 mm.

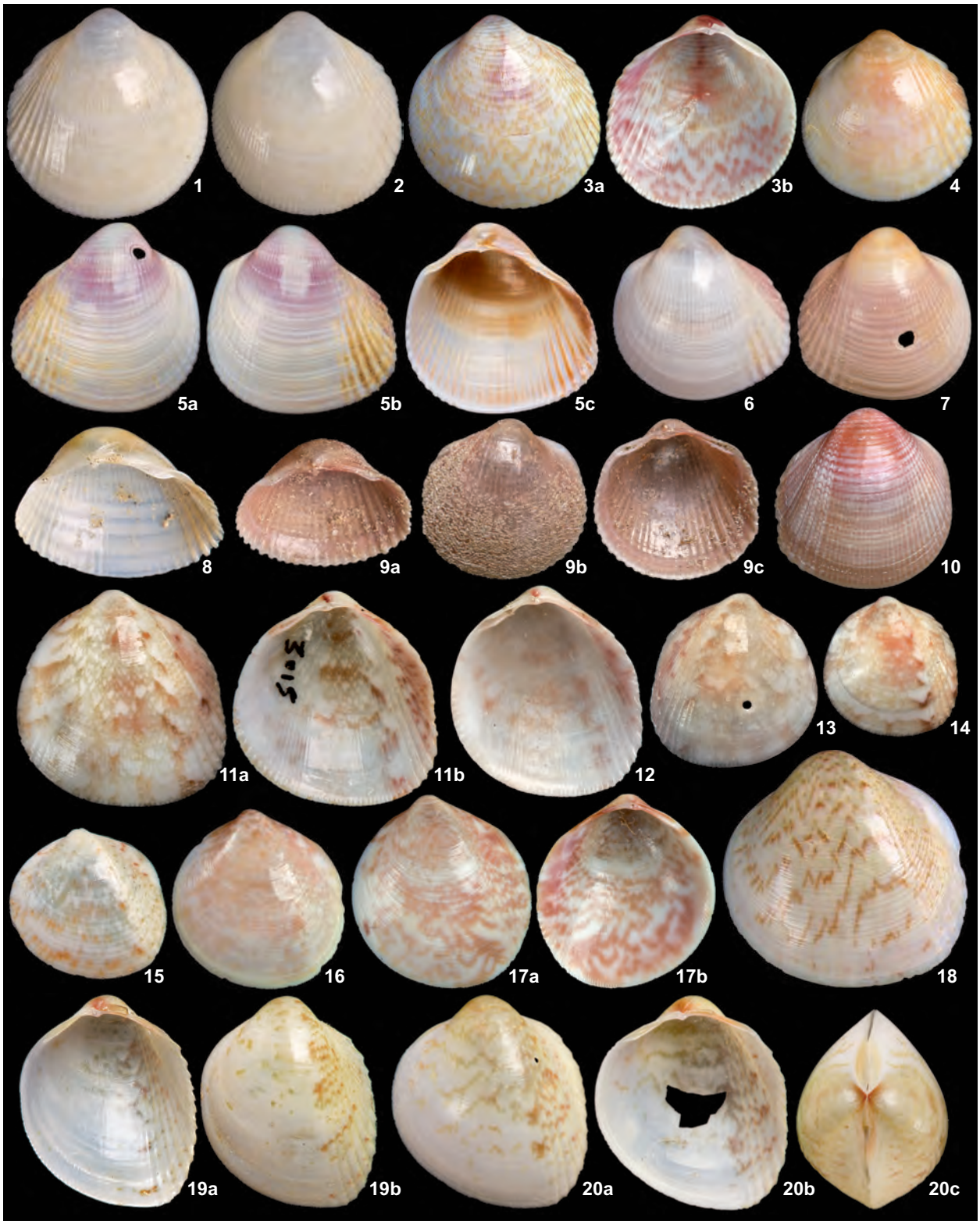
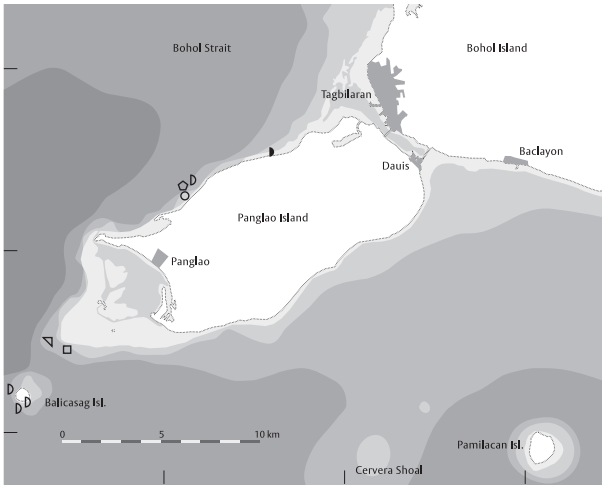


PLATE 14

Figs 1-4. *Fulvia* (*Laevifulvia*) *undatopicta* (Pilsbry, 1904). **1-2.** PMBP 2004 Stn D13. **1.** rv exterior, H 13.3 mm. **2.** lv exterior, H 12.8 mm. **3.** PMBP 2004 Stn S27, lv exterior and interior, H 12.0 mm. **4.** Philippines, Bohol, Pipe Point, 12.iii.2005, leg. G.T. Poppe, lv exterior, H 9.6 mm (TP 2496). **Figs 5-8.** *Fulvia* (*Laevifulvia*) *hungerfordi* (G.B. Sowerby 3rd, 1901). **5.** PMBP 2004 Stn S20, rv and lv exterior, rv interior, L 9.6 mm. **6-7.** PMBP 2004 Stn S27. **6.** lv exterior, L 7.8 mm. **7.** rv exterior, H 7.7 mm. **8.** PMBP 2004 Stn S20, rv marginal crenulations, L 4.4 mm. **Figs 9-10.** *Fulvia* (*Laevifulvia*) *subquadrata* Vidal & Kirkendale, 2007. **9.** PMBP 2004 Stn S20, rv marginal crenulations, exterior and interior, L 3.6 mm. **10.** Philippines, Luzon, Quezon, Tayabas Bay, Cuming Tour 2005 Stn CT 35, rv exterior, H 6.2 mm. **Figs 11-14.** *Fulvia* (*Laevifulvia*) *lineonotata* Vidal, 1994. **11.** Philippines, Sulu Sea, vi.1996, lv exterior and rv interior, H 11.8 mm (TP 3015). **12-14.** PMBP 2004 Stn D15. **12.** rv interior, H 11.1 mm. **13.** rv exterior, H 8.3 mm. **14.** lv exterior, H 5.8 mm. **Figs 15-18.** "*Laevicardium*" *lobulatum* (Deshayes, 1855). **15.** PMBP 2004 Stn S21, lv exterior, L 6.8 mm. **16.** PMBP 2004 Stn S27, lv exterior, H 10.2 mm. **17.** PMBP Stn T19, lv exterior and interior, H 11.8 mm. **18.** Philippines, Dinagat Isl., Pelotes Point, 10 m, 04/05.xii.2005, leg. G.T. Poppe, lv exterior, H 15.0 mm (TP 2897). **Figs 19-20.** *Pseudofulvia caledonica* Vidal & Kirkendale, 2007. **19.** PMBP 2004 Stn B10, rv interior and lv exterior, H 10.1 mm. **20.** PMBP 2004 Stn S46, lv exterior, rv interior and dorsal, H 10.3 mm.

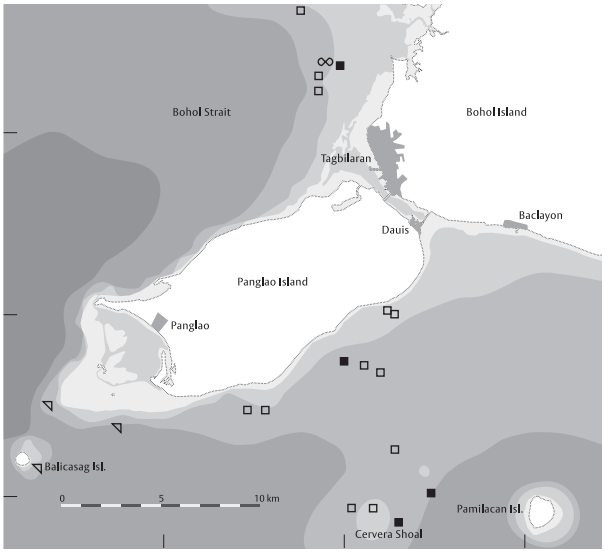


of highly variable thickness, mainly arising from rib interstices though they may encroach on anterior flank of ribs on posterior half of valves, on posterior flank on anterior half of valves and even extend to top of ribs on anterior slope. The change from spines that arise on anterior as opposed to 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.

Distribution and ecology. — Widely distributed in the tropical West Pacific, ranging from southern Japan and southern China to the Coral Sea, New Caledonia, Wallis, Fiji, Tonga and the Mascarene Islands (Poutiers, 2006 and references therein). Also known from Indonesia (Ter Poorten, 2007a), Malaysia (coll. TP; MH), Philippines (Huber & Ter Poorten, 2007) and Guam (Paulay, 2003). Known from fine sublittoral sandy bottoms in coral reef environments and reef slopes. Depth range of present material 28-140 m (alive 43-62 m), mostly found in lumun lumun and tangle nets.

Remarks. — Distinguished from *F. eos* by its smaller size, clear posterior flexure, strong angulation on postero-dorsal slope, darker red/orange umbo and different, slightly finer, sculptured ribbing. In contrast to its congeners, most of the samples originated from lumun lumun nets set out on reef slopes, whereas only one sample was trawled. Therefore, a preference for perireef facies seems probable. The name of this species is based on T. Kira (a famous malacologist), used as an adjective through the addition of the invariable Japanese suffix -na; it has occasionally been changed to *kiranum* (Keen, 1973; Habe, 1977) but, according to the Code (I.C.Z.N., 1999: Art. 32.5), the original spelling of *kirana* must be retained and *kiranum* is an unjustified emendation (Art. 33.2.3.1).

Frigidocardium sancticaroli
Ter Poorten & Poutiers spec. nov.
Pl. 18 figs 7-10, pl. 19 fig. 1, pl. 20 fig. 2, tables 6-7



Holotype. — Philippines, Aliguay Isl., from fishermen, 2006, 1 pv (MNHN 22391, ex coll. TP 3197). Paratypes as listed below.

Other material examined. — **Philippines**: PMBP 2004, Stn G1, 100 m, 19 v; Stn T1, 83-102 m, 2 v; Stn T2, 152 m, 21 v; Stn T6, 34-82 m, 1 v; Stn T9, 97-120 m, 2 pv (A), 61 v; Stn T10, 117-124 m, 4 v; Stn T14, 101-110 m, 3 v; Stn T18, 80-100 m, 1 pv (A), 13 v; Stn T25, 160-210 m, 1 v; Stn T26, 123-135 m, 24 v; Stn T27, 106-137 m, 8 v; Stn T28, 80 m, 2 v; Stn T34, 145-163 m, 7 v; Stn T36, 95-128 m, 11 pv (A, paratype 1 NMP, paratypes 2-5, MNHN 22274), 296 v; Stn T39, 100-138 m, 1 pv (A), 13 v; Stn T40, 80-98 m, 1 v; Stn T41, 110-112 m, 7 v. PANGLAO 2005, Stn DW 2339, 164-176 m, 1 v; Stn DW 2370, 92-96 m, 23 v; Stn DW 2371, 172-175 m, 1 v; Stn CP 2380, 150-163 m, 24 v (paratype 6, MNHN 22275); Stn DW 2400, 111-115 m, 2 v; Stn DW 2402, 101-118 m, 1 v. MUSORSTOM 2, 1980, Stn CP 2, N of Lubang Isl., 14°00,5'N-120°17,3'E, 184-186 m, 1 v (MNHN); Stn CP 51, N of Lubang Isl., 14°00'N-120°17'E, 170-187 m, 1 v; Stn CP 72, N of Lubang Isl., 14°00'N-120°18'E, 178-205 m, 1 v; Stn CP 80, Balayan Bay, off Santiago Cape, Luzon Isl. 13°45'N-120°37'E, 178-205 m, 1 v. MUSORSTOM 3, 1985, Stn DR 102, N of Lubang Isl., 14°01'N-120°18'E, 192 m, 9 v. AURORA 2007, Stn CP 2666, 15°57.6'N-121°45.3'E, 199-307 m, 1 v (MNHN); Stn DW 2706, 15°4.2'N-121°42.9'E, 478-480 m, 1 v (MNHN); Stn CP 2711, 15°19.7'N-121°31.6'E, 184-200 m, 1 v (MNHN); Stn DW 2738, 16°3.6'N-121°55.8'E, 111-113 m, 45 v (MNHN); Stn DW 2739, 16°5.2'N-121°57.8'E, 96 m, 1 v (MNHN); Stn DW 2749, 15°56.6'N-121°50.2'E, 473 m, 5 v (MNHN). Balicasag Isl. 2004, leg G.T. Poppe, 2 v (ZMA); Bantayan Isl., tangle nets, 80-100 m, 1 pv (paratype 7, TP 1175); Siquijor Isl., Tubod, 1 pv (TP 1848); Mindanao, Aliguay Isl., trawled, 100-150 m. 2004, 1 pv (paratype 8, TP 3011); Aliguay Isl., trawled, 100 m. 2000, 1 pv (MH QQ214); Aliguay Isl., trawled, 60-120 m. 2004, 1 pv (TP 3196); Aliguay Isl., trawled, 100-150 m. 2008, 1 pv (TP 3660); Mactan Isl., off Hadsan, 200 m. v.2004, 1 pv (paratype 9, TP 3012). **Indonesia**, NE coast of Sumba, E of Melolo, 09°53.2'S-120°43.2'E, 100 m, muddy sand with calcareous nodules. 13.ix.1984. SNELLIUS-II Exp. stn 4.047, 4 v (RMNH); Sulawesi, Spermonde Arch., 04°57.5'S, 119°2.8'E, 18 m, Hensen vertical net, from 11 m to surface, electric light in net. 08.vi.1899. SIBOGA Exp., Stn 75, 1 v (paratype 10, ZMA Moll.4.09.044). **Papua New Guinea**, New Ireland, Steffen Strait, dredged offshore, 2°33,683'S-150°36.275'E, 108-110 m. Leg. F. Lorenz, 1 pv (MH QQ2141). **Solomon Islands**, SALOMON 1, 2001, Stn DW 1745, N of Honiara, Guadalcanal, 09°23.4'S-159°58.5'E, 253-356 m, 1 v (MNHN); Stn DW 1762, SE of Santa Isabel, 08°39.9'S-160°03.9'E, 396-411 m, 15 v (MNHN); Stn DW 1765, SE of Santa Isabel, 08°43.1'S-160°06.5'E, 325-380 m, 1 v (MNHN); Stn DW 1767, off NW Malaita, 08°19.4'S-160°39.9'E, 98-200 m, 2 v (MNHN); Stn DW 1823, E of Guadalcanal, 09°50.4'S-160°53.2'E, 82-83 m, 11 v (MNHN); Stn DW 1840, N of San Cristobal, 10°17.0'S-161°43.0'E, 97-223 m, 3 v (MNHN); Stn DW 1848, 10°27.2'S-161°58.5'E, 159-169 m, 3 v. SALOMON 2, 2004, Stn DW 2169, Russel Isl., W bay, 09°01.1'S-159°05.7'E,

100-200 m, 1 v (MNHN); Stn DW 2183, SE of Santa Isabel, 489-491 m, 4 v (MNHN); Stn DW 2229, Choiseul Isl., Bougainville Strait, 06°35.5'S-156°20.0'E, 315-418 m, 1 v (MNHN); Stn DW 2294, South Tetepare Isl., 08°46.5'S-157°30.3'E, 105-128 m, 3 v (MNHN). SALOMONBOA 3, 2007, Stn DW 2775, Guadalcanal, 09°23'S-160°57'E, 282-427 m, 3 v (MNHN); Stn DW 2811, S Malaita, 09°42'S-161°30'E, 228-238 m, 1 v (MNHN); Stn DW 2827, N San Cristobal, 10°26'S-161°51'E, 134-272 m, 1 v (MNHN); Stn DW 2840, W San Cristobal, 10°25'S-161°22'E, 121-180 m, 1 v (MNHN); Stn DW 2843, W San Cristobal, 10°26'S-161°28'E, 90-112 m, 1 v (MNHN); Stn DW 2853, Marau Sound, 9°47'S-160°54'E, 264-285 m, 1 v (MNHN).

Description. — Shell relatively small and thin-shelled (largest specimen H 11.3 mm, holotype), rather quadrate to ovate, almost equilateral and inflated. Posterior margin truncate, a little convex to slightly concave. L/H ratio 0.93-1.00, (mean 0.96, n = 13). Inner margins finely crenulated. Exterior covered with circa 82-105 densely and finely spinose radial ribs, of which about 35-42 can be regarded as possessing primary sculpture. Spines small and erect, arising from posterior side of ribs on the anterior 3/5 of the surface and from anterior side on the posterior 2/5. Central and anterior part of shell with a regular pattern of spine rows of alternating thickness, main spines blunt and tubular, becoming spatulate anteriorly. Posterior quarter more weakly ribbed, with sculpture of a more irregular strength. The extent of development of the secondary row of spines is rather variable among the available samples and increases during ontogeny. Rib interstices generally rather weakly developed with small crossbars, largely hidden under dense overhanging spine pattern. Lunular area symmetrical, radially sculptured with small spines, not clearly demarcated from the rest of the shell. Lunular heart raised, rather broad, flat-topped and finely wrinkled; escutcheon clearly defined and, contrary to lunular area, sharply delimited. Hinge relatively strong with two unequal cardinals, the more ventral cardinal being large and thick and the more dorsal one small. Cardinals in right valve joined by a saddle. Anterior lateral teeth distinctly closer to cardinals than posterior lateral teeth. Exterior and interior entirely white.

Distribution and ecology. — Known from the Philippines, Indonesia, Papua New Guinea and the Solomon Islands. The available combined bathymetric data of PMBP 2004 and PANGLAO 2005 indicate a sublittoral and upper bathyal occurrence in 34-210 m (alive 80-138 m) on sand and mud bottoms, almost exclusively trawled or found in tangle nets.

Etymology. — Named after the University of San Carlos, Cebu City, the Panglao project leading institution in the Philippines

Remarks. — Compared to its most similar congener, *F. iris* Huber & Ter Poorten, 2007, this species is much smaller and lacks any colouration. Moreover, the pattern on the median part of the shell, consisting of one primary sculptured radial row alternating with one secondary sculptured row, is different and the spines are clearly less projecting than in *F. iris*. The lunular area of *F. sancticaroli* spec. nov. is well sculptured and poorly differentiated from the surrounding shell surface, contrasting with the condition in *F. iris*. Mean number of primary sculptured ribs is slightly higher: 38, whereas *F. iris* on average has 35.

***Frigidocardium torresi* (E.A. Smith, 1885)**

Pl. 17 figs 11-15, pl. 19 fig. 3, pl. 20 fig. 6, table 7

Cardium (*Fragum*) *torresi* E.A. Smith, 1855: 164-165, pl. 8 figs 4, 4a-b.

Material examined. — **Philippines**: PMBP 2004, Stn B38, 17-18 m, 1 v; Stn D15, 53-63 m, 1 v; Stn G1, 100 m, 9 v; Stn T1, 83-102 m, 1 v; Stn T4, 82 m, 2 pv (A), 6 v; Stn T5, 84-87 m, 1 v; Stn T6, 34-82 m, 1 pv (A), 23 v; Stn T9, 97-120 m, 1 pv (A), 10 v; Stn T11, 78-95 m, 17 v; Stn T14, 101-110 m, 1 v; Stn T18, 80-100 m, 4 v; Stn T19, 10-26 m, 1 v; Stn T25, 160-210 m, 1 v; Stn T26, 123-135 m, 1 pv (A), 8 v; Stn T27, 106-137 m, 2 v; Stn T28, 80 m, 1 pv (A), 47v; Stn T30, 59-65 m, 1 v; Stn T32, 60-62 m, 4 v; Stn T34, 145-163 m, 1 v;

	L	*H*	*W*	*L/H*	*W/L*	*Sculpt. rows*	*Sculpt. rows (main)*
MNHN 22391 Holotype (ex TP 3197) (pv)	10.6 mm	11.3 mm	9.3 mm	0.94	0.88	c. 102	c. 42
PMBP T36 NMP Paratype 1 (pv)	8.6 mm	9.0 mm	7.6 mm	0.96	0.88	c. 90	c. 35
PMBP T36 MNHN 22274 Paratype 2 (pv)	7.7 mm	8.0 mm	6.9 mm	0.96	0.90	c. 88	c. 38
PMBP T36 MNHN 22274 Paratype 3 (pv)	6.4 mm	6.7 mm	5.6 mm	0.96	0.88	c. 82	c. 37
PMBP T36 MNHN 22274 Paratype 4 (pv)	5.5 mm	5.7 mm	4.7 mm	0.96	0.86	[1]	[1]
PMBP T36 MNHN 22274 Paratype 5 (pv)	4.3 mm	4.5 mm	3.6 mm	0.96	0.84	[1]	[1]
PMBP CP2380 MNHN 22275 Paratype 6 (rv)	10.3 mm	10.6 mm	(8.5 mm)	0.97	0.83	c. 87	c. 38
Siboga 75 ZMA Moll.4.09.044 Paratype 10 (rv)	6.5 mm	6.8 mm	(5.6 mm)	0.96	0.86	c. 90	c. 39
TP 1175 Paratype 7 (pv)	9.5 mm	9.5 mm	8.5 mm	1.00	0.89	c. 82	c. 35
TP 3011 Paratype 8 (pv)	10.5 mm	10.7 mm	9.1 mm	0.98	0.87	c. 105	c. 42
TP 3012 Paratype 9 (pv)	9.5 mm	9.8 mm	8.3 mm	0.97	0.87	c. 90	c. 39
TP 3660 (pv)	8.7 mm	9.4 mm	7.8 mm	0.93	0.90	c. 98	c. 38
TP 3196 (pv)	9.4 mm	10.0 mm	8.6 mm	0.94	0.91	c. 107	c. 39
Mean values				0.96	0.87	92.8	38.4

Table 6. Shell measurements and rib count of *Frigidocardium sancticaroli* spec. nov. Extrapolated sizes in brackets. Rib number based on counting actual ribs rather than marginal crenulations, lunular area excluded.
[1]) Not counted because at this size some rows of radial sculpture are not adequately developed.

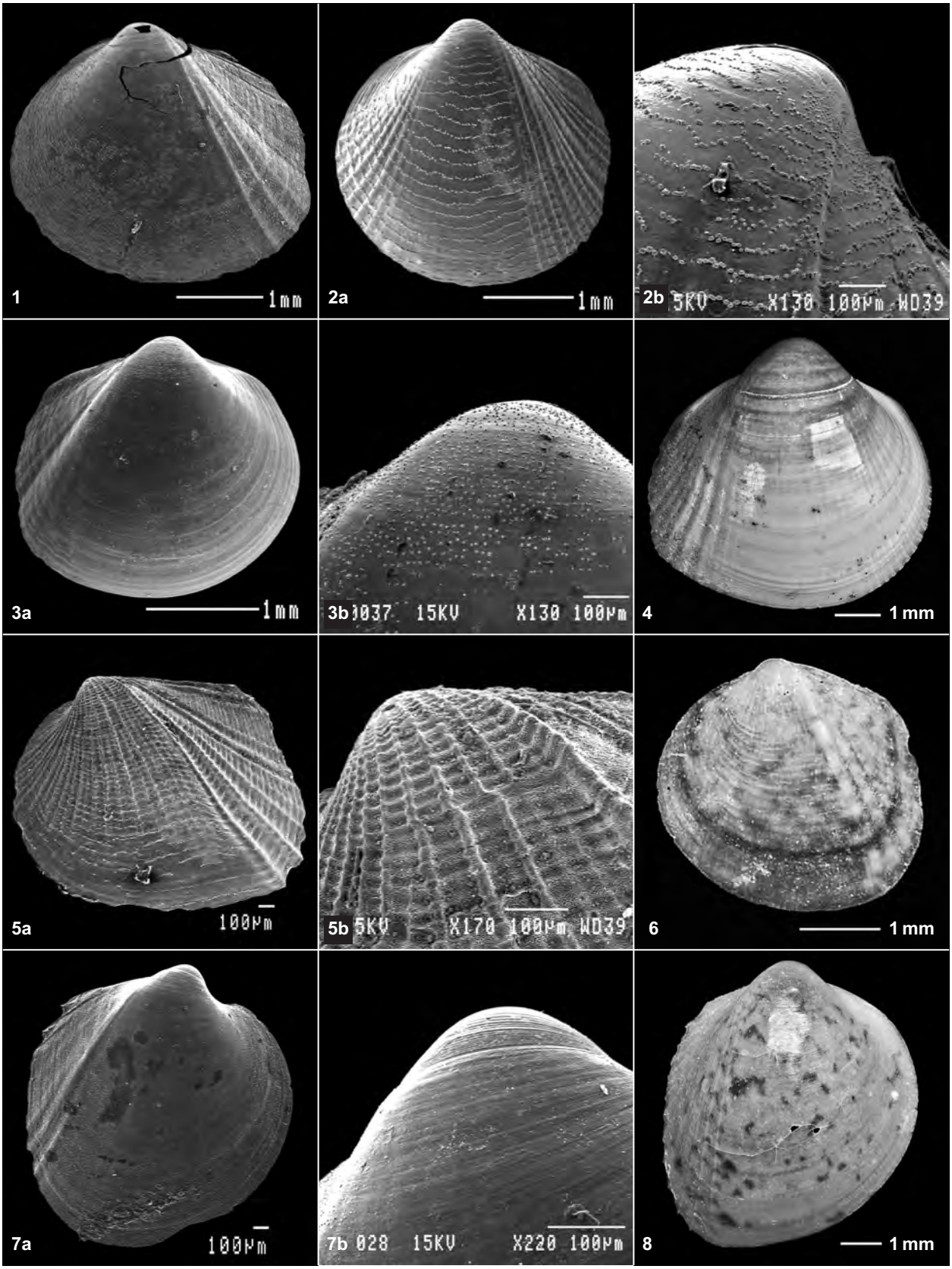


PLATE 15

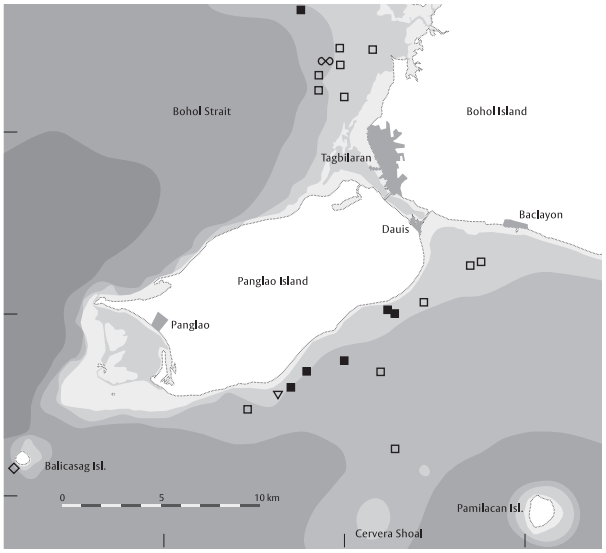
Figs 1-5. Early ontogenetic stages of juvenile PMBP 2004 *Fulvia* and *Pseudofulvia* taxa. Scale bars: 1 mm and 100 µm. **Fig. 1.** *Fulvia* (*Fulvia*) *laevigata* (Linnaeus, 1758), PMBP 2004 Stn D5, lv exterior. **Fig. 2.** *Fulvia* (*Fulvia*) *scalata* Vidal, 1994, PMBP 2004 Stn T19, lv exterior and umbonal area. **Figs 3-4.** *Fulvia* (*Laevifulvia*) *hungerfordi* (G.B. Sowerby 3rd, 1901). **3.** PMBP 2004 Stn T19, rv exterior and umbonal area. **4.** PMBP 2004 Stn S20, rv exterior. **Figs 5-6.** "*Laevicardium*" *lobulatum* (Deshayes, 1855). **5.** PMBP 2004 Stn S21, lv exterior and umbonal area. **6.** PMBP 2004 Stn S21, lv exterior. **Figs 7-8.** *Pseudofulvia caledonica* Vidal & Kirkendale, 2007. **7.** PMBP 2004 Stns L74-75, rv exterior and umbonal area. **8.** PMBP 2004 Stn S28, rv exterior.

PLATE 16

Figs 1-5. "*Laevicardium*" *biradiatum* (Bruguière, 1789). **1.** PMBP 2004 Stn R31, rv interior, lv exterior, and posterior, H 34.9 mm. **2.** PMBP 2004 Stn R16, lv exterior, H 18.8 mm. **3.** Philippines, Mindanao, Aliguay Isl., 40 m, lv exterior, H 24.5 mm (TP 2015). **4.** PMBP 2004 Stn R14, lv exterior, H 31.8 mm. **5.** Philippines, Bantayan, N. coast, dredged, lv anterior slope, H 39.2 mm (TP 2402). **Figs 6-8.** "*Laevicardium*" *attenuatum* (G.B. Sowerby, 2nd, 1841). **6.** PANGLAO 2005 Stn DW 2370, rv exterior and interior, H 17.0 mm. **7.** Philippines, Talikud Isl., lv exterior, rv interior and postero-dorsal slope, H 56.0 mm (TP 2231). **8.** Thailand, Gulf of Thailand, Ban Pak Nam Sakom, local fishery, 22.i.2000, leg. B. Gras, anterior slope, H 46.9 mm (TP 1043). **Figs 9-12.** "*Laevicardium*" *multipunctatum* (G.B. Sowerby 1st in Broderip & Sowerby, 1833). **9.** Philippines, Balicasag Isl., 140 m, lv exterior and anterior slope, H 34.3 mm (TP 3279). **10.** Philippines, Mactan Isl., Punta Engaño, lv exterior and rv interior, H 43.0 mm (TP 3504). **11.** PMBP 2004 Stn T4, lv exterior, H 15.8 mm. **12.** PMBP 2004 Stn T1, rv exterior, H 14.0 mm (def.). **Figs 13-15.** "*Laevicardium*" *lobulatum* (Deshayes, 1855). **13.** Philippines, Mindanao, Aliguay Isl., 2008, lv exterior, H 14.2 mm (TP 3663). **14.** PMBP 2004 Stn R62, rv interior and lv exterior, H 25.5 mm. **15.** Philippines, Leyte, Palompon, 29.vii.2006, leg. G.T. Poppe, rv interior and lv exterior, H 28.5 mm (TP 3180).

Species	*Max. size L(ength) or H(eight)*	*Rib number*	*Number of primary sculptured rows*	*Secondary sculptured rows present*	*Lunular heart (LH) Lunular area (LA)*	*Exterior colouration*	*Distribution*
F. eos	H 25-30 mm	130-145	130-145 all of distinctly alternating strength	All rows of distinctly alternating, strength	LH well defined, elevated, orange LA fine sculptured, vaguely demarcated	White with orange streaks radially and commarginally	Japan to Western Australia
F. iris	H 25-28 mm	> 100	30-45	Yes, on entire shell	LH well defined, elevated LA well demarcated, with very low sculpture	White with reddish commarginal bands, more towards margins	Philippines to Western Australia
F. exasperatum	L 25-30 mm	80-90	25-32	At most weakly developed	LH hardly visible LA sinuous, asymmetric	Completely white, LA orange	Japan, China, Taiwan, Vietnam
F. helios spec. nov.	L 5-9.5 mm	130-175	46-66	Limited to antero-dorsal part	LH small but broad and elevated LA vaguely demarcated yellowish	White, often vaguely streaked orange, reddish umbonal tip	Philippines, Indonesia, Malaysia, N. Caledonia, Vanuatu
F. kirana	H 10-16 mm	120-130	Highly variable	Yes, on entire shell	LH + LA barely defined	White, often with orange-red rays Posterior slope + umbo red	S. Japan to Indonesia Mascarene Islands
F. sancticaroli spec. nov.	H 8-11 mm	82-105	35-42	Yes, on entire shell	LH elevated LA vaguely defined, distinctly sculptured	Completely white	Philippines, Indonesia, Papua N G, Solomons
F. torresi	L 5-9 mm	75-90	22-28	No, only rarely a few present	LH narrow, smooth LA unsculptured, not sharply demarcated	White with reddish umbonal tip	E. Africa to northern Australia, Vanuatu

Table 7. Comparative morphological data for Philippine *Frigidocardium* taxa and the related *F. exasperatum*.



Stn T43, 70-96 m, 3 v; Stn T44, 83-86 m, 1 pv (A). PANGLAO 2005, Stn DW 2370, 92-96 m, 1 v; Stn CP 2378, 65 m, 1 v.

Description. — Shell relatively small (L up to 9 mm, often about 5 mm), thickness rather variable, well inflated, quadrangular, with truncated posterior margin, sometimes slightly concave. Length usually slightly exceeds height. Radial rib number quite variable (range 75-90), ribs rather square-shaped in cross section and as wide as the interstices in median area, gradually becoming lower and rounder towards dorsal margin. Circa 22-28 radial rows of close-set blunt spines or spoon-shaped projections, approximately of equal strength and arising from the interstices, often appearing as more chevron-shaped scales in juveniles. Secondary radial sculpture generally absent and if present confined to very few interstices. Radial spiny sculpture regularly alternating with interstices that carry well-developed crossbars, somewhat differing in strength among specimens. Lunular heart smooth, rather long and narrow; lunular area unsculptured, not sharply bordered. Colour entirely white with reddish-orange umbonal tip. Occasionally with similarly coloured umbonal cavity.

Distribution and ecology. — Tropical Indo-West Pacific, at present known from Tanzania (Thiele & Jaeckel, 1931), Philippines and Indonesia (ZMA, det. TP), Guam (Paulay, 2003), Western Australia (WAM, det. TP/MH), northern Queensland (Smith, 1885) and Vanuatu (MNHN, det. TP). Depth range of present material 17-210 m (alive 34-135 m), very often sublittorally trawled on fine sand and muddy bottoms. Hitherto not recorded from the Philippines. Geographic distribution imperfectly known due to confusion with other taxa.

Remarks. — Although the description of Smith (1885) is very detailed, this taxon has often been variously interpreted in the literature, for instance because of the erroneous assumption that the type material (figured by Hylleberg, 2004: 900, fig.) is juvenile (e.g. Smith, 1885: 165; Prashad, 1932: 275; Wilson & Stevenson, 1977: 66). See table 7 for comparisons with congeneric taxa.

Microcardium Thiele, 1934

Microcardium Thiele, 1934: 878. Type species by subsequent designation (Keen, 1937: 14-15): *Cardium* (*Fulvia*) *perambilis* Dall, 1881; Recent, 23°13'N, 89°16'W, off Yucatan, Mexico, 154 m.

Decussicardium Fischer-Piette, 1977: 94. Type species by original designation: *Cardium gilchristi* G.B. Sowerby 3rd, 1904; Recent, Algoa Bay, South Africa, 15 fms.

Tobarum Noda, 1988: 74. Type species by original designation: *Frigidcardium* [sic! err. pro *Frigidocardium*] (*Tobarum*) *tobaruensis* Noda, 1988; Pliocene, Shinzato Formation, Okinawa, Japan.

Diagnosis. — Shell relatively small, usually rather thin, rounded to quadrate and inflated. Ribbing structure heterogeneous, surface divided into two very differently sculptured zones. Both zones finely radially ribbed, crossed by fine, approximately concentric ridges on anterior zone. Interstices of posterior zone sculptured with alternating nodular spines and transverse bars or fine lamellae. Posterior ribs themselves not spinose.

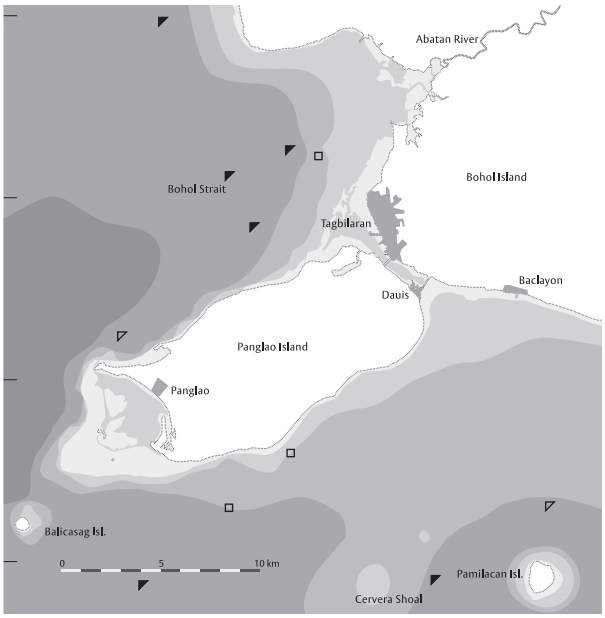
Distribution. — Miocene to Recent, Panamic, Caribbean, Patagonian, Indo-Pacific, South African, Japonic; sublittoral-upper bathyal.

Remarks. — According to Schneider (1995: 326, fig. 6b) *Microcardium* taxa change their ribbing pattern through ontogeny from the *Nemocardium* pattern (strong radial ribs on the posterior slope and weak radial ribs on the central and anterior slopes) to a pattern of entirely radial ribs of roughly equal strength and width. The posterior zone of sculpture increases in size anteriorwards during ontogeny resulting in a slightly oblique running demarcation line, related to the radial ribbing. This is either restricted to juveniles (e.g. *M. velatum* spec. nov., pl. 19 fig. 5a) or continues to develop through to maturity (e.g. *M. gilchristi* G.B. Sowerby 3rd, 1904).

Microcardium aequiliratum Poutiers, 1981

Pl. 20 fig. 10, pl. 22 figs 1-3

Microcardium aequiliratum Poutiers, 1981: 339-340, pl. 1 figs 10-11, text figs 3a-b.



Material examined. — **Philippines**: PMBP 2004, Stn T3, ca. 150 m, 1 v; Stn T4, 82 m, 1 v; Stn T25, 160-210 m, 5 v. PANGLAO 2005, Stn CP 2331, 255-268 m, 13 pv (A/DNA), 21 v; Stn CP 2340, 271-318 m, 12 pv (A), 13 v; Stn CP 2343, 273-356 m, 1 v; Stn CP 2344, 128-142 m, 1 pv (A), 1 v; Stn CP 2348, 196-216 m, 5 pv (A), 17 v; Stn CP 2349, 219-240 m, 4 v; Stn DW 2371, 172-175 m, 5 v; Stn CP 2380, 150-163 m, 12 pv, 15 v; Stn CP 2381, 259-280 m, 1 pv, 2 v; Stn CP 2395, 382-434 m, 1 pv, 2 v; Stn CP 2406, 334-387 m, 1 pv (A); Stn CP 2407, 256-268 m, 1 pv (A), 8 v; Stn CP 2409, 220-257 m, 12 pv (A), 44 v.

Description. — Shell medium sized (L 15-26.5 mm), rounded quadrate, nearly equilateral, slightly longer than high. Umbos clear, blunt, prosogyrate, positioned just anterior of the midline. Inner margins very finely crenulated. Shell surface divided into two distinct sculptured zones. Total rib number about 85-90 (anterior zone 35; posterior zone 50). Anterior zone, covering 35-45% of the shell, with low rounded ribs and blunt reticulate sculpture, vanishing towards dorsal margin. Posterior zone, covering 55-65% of the shell, with well developed square ribs and prominent homogeneous cross-bars in interstices, nearly as high as adjacent ribs; every second to fifth interstice sculptured with erect, blunt spines, distantly placed and notched dorsally. Demarcation line dividing the zones running parallel with the radial ribs, except in early juveniles. Lunular heart elevated, on each valve forming a roughly semi-circular, flat-topped and minutely ridged process over the thickened antero-dorsal margin. Exterior and interior entirely white, occasionally with traces of lemon yellow.

Distribution and ecology. — Until now *M. aequiliratum* was considered an endemic Philippine species (Poutiers, 2006), mainly living on the lower continental shelf with 350 m being the deepest record (Poutiers, 1992: 139). However, an ANSP sample from Myanmar/Burma (coll. nr. 291960,

PLATE 17

Figs 1-4. *Frigidocardium eos* (Kuroda, 1929). **1.** PMBP 2004 s/n, Balicasag Isl., tangle nets and lumun lumun 'deep water', from fishermen, gift B. Olivera, lv exterior, rv interior, dorsal and anterior, H 25.4 mm. **2-3.** PANGLAO 2005 Stn DW 2400. **2.** lv exterior, H 16.9 mm. **3.** lv exterior, H 15.8 mm. **4.** Philippines, Mindanao, Aliguay Isl., trawled, 100-150 m, lv exterior, H 12.2 mm (TP 3542). **Figs 5-7.** *Frigidocardium iris* Huber & Ter Poorten, 2007. **5.** PANGLAO 2005 Stn DW 2370, lv exterior and dorsal, H 11.6 mm. **6.** PANGLAO 2005 Stn DW 2370, lv exterior, H 10.9 mm. **7.** Philippines, Bohol, Balicasag Isl., tangle nets, 150 m. H 24.8 mm (Paratype ZMA Moll. 4.07.011). **Figs 8-10.** *Frigidocardium kirana* Sakurai & Habe, 1966. **8.** PMBP 2004 Stn S8, rv interior and lv exterior, H 6.0 mm. **9.** PMBP 2004 Stn S8, lv exterior and lv interior, H 11.0 mm. **10.** PANGLAO 2005 Stn DW 2400, rv and lv exterior, rv interior, dorsal and posterior, H 11.7 mm. **Figs 11-15.** *Frigidocardium torresi* (Smith, 1885). **11.** PMBP 2004 Stn T6, lv exterior, L 4.8 mm. **12.** PMBP 2004 Stn T4, rv exterior and hinge, L 5.3 mm. **13.** PMBP 2004 Stn T4, rv exterior and hinge, L 5.2 mm. **14.** PMBP 2004 Stn T4, lv exterior and dorsal, L 6.1 mm. **15.** PMBP 2004 Stn T9, lv exterior, L 2.3 mm.

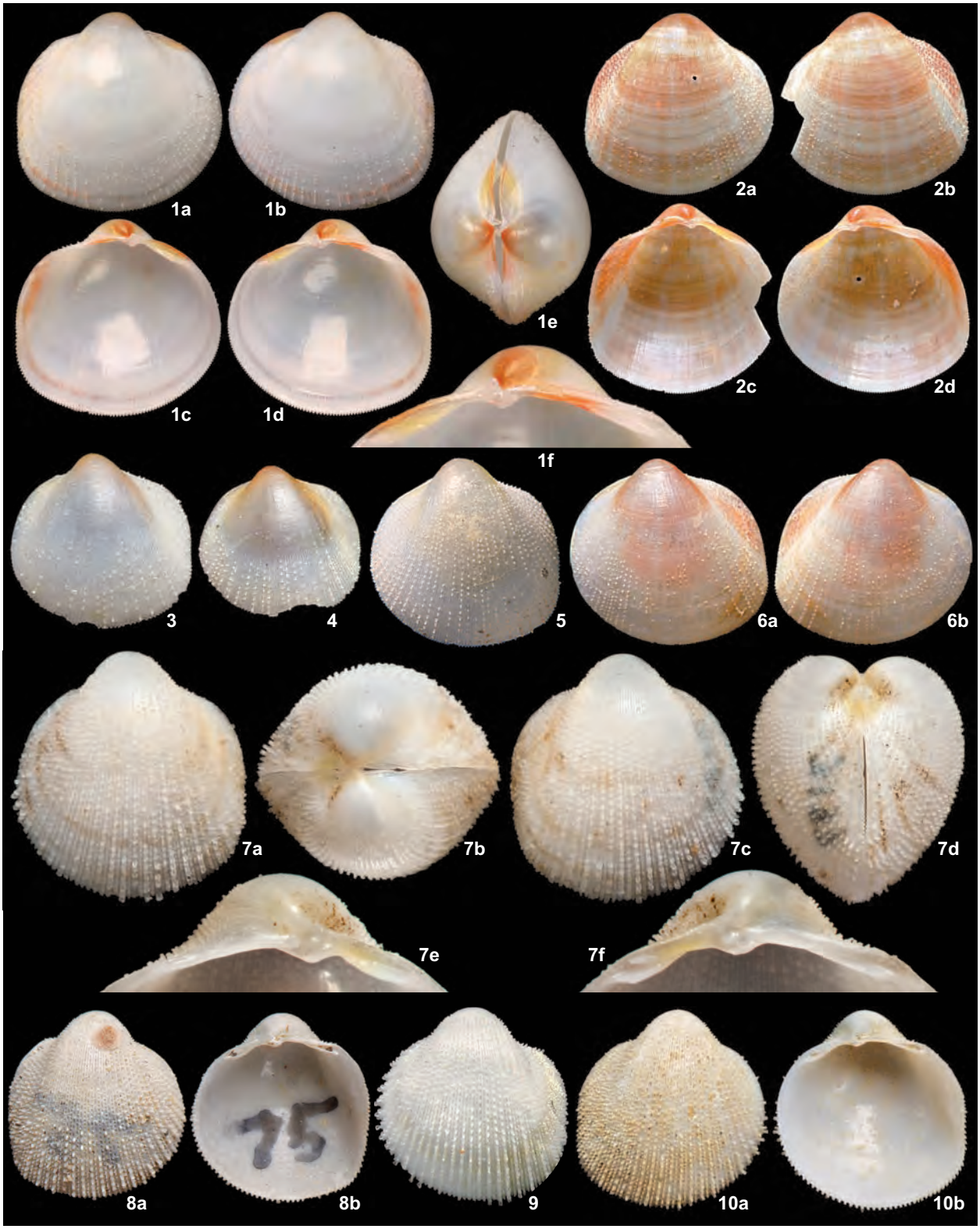


PLATE 18

Figs 1-6. *Frigidocardium helios* spec. nov. **1.** SANTO 2006, S.E. corner of Santo, ix-x.2006, rv and lv exterior, lv and rv interior, dorsal and rv hinge, L 7.3 mm (Holotype MNHN 30161). **2.** PMBP 2004 Stn D15, rv and lv exterior, lv and rv interior, L 6.7 mm (Paratype 1 NMP). **3.** Indonesia, Jawa, Stn SER 05/21, 27.ix.2005, leg. R.G. Moolenbeek & S. van der Meij, lv exterior, L 3.0 mm (Paratype 10 ZMA Moll. 4.09.040). **4.** Indonesia, Jawa, Stn SER 05/21, 27.ix.2005, leg. R.G. Moolenbeek & S. van der Meij, lv exterior, L 2.7 mm (Paratype 11 ZMA Moll. 4.09.041). **5.** Indonesia, Banda Sea, Koka Reef, 40-50 m, 19.x.2005, leg. F. Lorenz & H. Morrison, lv exterior, L 5.3 mm (Paratype 15 TP 2932). **6.** Philippines, Siquijor Isl., Tubod, dredged 69 m, 01.v.2004, leg. G.T. Poppe, lv and rv exterior, L 5.7 mm (Paratype 14 Poppe 169352). **Figs 7-10.** *Frigidocardium sancticaroli* spec. nov. **7.** Philippines, Mindanao, Aliguay Isl, from fishermen, 2006, lv exterior, dorsal, rv exterior, posterior, lv and rv hinge, H 11.3 mm (Holotype MNHN 22391). **8.** Indonesia, Sulawesi, Spermonde Arch., SIBOGA Stn 75, 08.vi.1899, rv exterior and interior, H 6.8 mm, (Paratype 14 ZMA Moll. 4.09.044). **9.** Philippines, Bantayan Isl., tangle nets, 80-100 m, lv exterior, H 9.5 mm (Paratype 7 TP 1175). **10.** PANGLAO 2005 Stn CP 2380, lv exterior and interior, H 10.6 mm (Paratype 6 MNHN 22275).

Andaman Sea, 30 miles west of Twin Island, 10°39'N-97°06'E, dredge, 274-293 m, sand-mud, 24.iii.1963. Anton Bruun Sta. 22B. International Indian Ocean Expedition) considerably extends the known distribution (det. J. Vidal, 1997, and TP, 2005). It is also now known from Vanuatu (MNHN, det. TP). Present material nearly exclusively trawled, depth range 82-434 m (dead) and 128-387 m (alive), on fine sand and mud bottoms. *Microcardium aequiliratum* was by far the most abundant cardiid of PANGLAO 2005 (table 10) and was recovered alive in a relatively large percentage of the samples, at many of the stations being the sole cardiid species.

Remarks. — *Microcardium aequiliratum* is well characterised by the wide posterior sculptural zone with prominent homogeneous crossbars in rib interstices throughout. The Pliocene *Frigidocardium* (*Tobarum*) *tobaruensis* Noda, 1988 is a closely similar species. Described from Okinawa, Japan, with 100 ribs (Noda, 1988) and exhibiting a similarly positioned demarcation and similar sculpture, it could represent an ancestor or junior synonym of *M. aequiliratum*.

Microcardium tenuilamellosum Poutiers, 1981

Pl. 20 fig. 9, pl. 21 fig. 8

Microcardium tenuilamellosum Poutiers, 1981: 338-339, pl. 1 figs 8-9, text figs 2a-b.

Material examined. — **Philippines**: PANGLAO 2005, Stn CP 2380, 150-163 m, 2 v.

Description. — Shell small (L 9-12 mm), rounded quadrate, nearly equilateral, mostly slightly longer than high. Umbos clear, blunt, prosogyrate, positioned just anterior of the midline. Inner margins finely crenulated. Shell surface divided into two distinct sculptured zones. Total rib number about 100-105 (anterior zone 40-45; posterior zone 60). Anterior zone covering 35-40% of the shell, with low rounded ribs with blunt reticulate sculpture, vanishing towards dorsal margin. Posterior zone covering 60-65% of the shell, with well developed squarish ribs, every second (median part) to fifth (postero-dorsal part) interstice sculptured with erect, blunt spines, notched dorsally. Other interstices carrying well developed cross-bars, abruptly becoming dense and lamellate on the posterior slope. Lunular heart small and poorly demarcated, mainly reduced to a small thickening of the antero-dorsal margin. Exterior and interior entirely white.

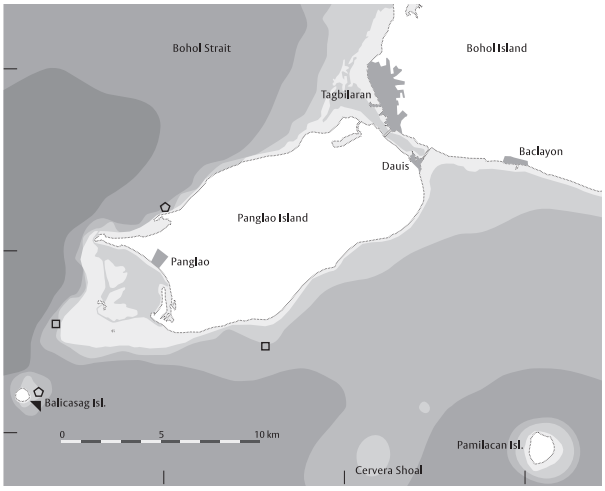
Distribution and ecology. — Known from the Philippines, Solomon Islands (Poutiers, 2006) and Vanuatu (MNHN, det. TP); not recorded by PMBP 2004 and only once by PANGLAO 2005 (2 valves, 150-163 m).

Remarks. — This species was described on the basis of one individual from MUSORSTOM 1, originating from the lower continental shelf of the Philippine Lubang area, at a depth of 184-193 m. It is considered rare (Poutiers, 1982) and was only encountered once by the subsequent MUSORSTOM 2 and MUSORSTOM 3 expeditions visiting the same area. However, it was sampled abundantly in 1908/1909 by the U.S. Fisheries Steamer 'Albatross' during its Philippine Expedition in the western Luzon and Mindoro areas in 187-402 m (12 stations, with a total of 441 v + 1 pv, J.-M. Poutiers, pers. comm. 06.2009), suggesting a patchy Philippine distribution. The demarcation line dividing the shell sculpture zones does not run parallel (i.e. not confluent) to the radial ribs but at a slightly oblique diagonal. It originates posteriorly of the umbo and during ontogeny gradually develops a little towards the anterior half of the shell. An even more obvious example of such an oblique demarcation line is provided by *M. gilchristi* (G.B. Sowerby 3rd, 1904), which differs in its uniform sculpture on the interstices of the posterior zone and its endemic South African distribution.

Microcardium sakuraii (Habe, 1961)

Pl. 20 fig. 7, pl. 21 figs 1-2

Nemocardium (*Microcardium*) *sakuraii* Habe, 1961: 152, 155-156, fig. 9.



Material examined. — **Philippines**: PMBP 2004, Stn P1, 90-200 m, 1 pv; Stn P3, ca. 100 m, 1 v; Stn T2, 152 m, 1 v; Stn T31, 100-140 m, 1 v. PANGLAO 2005, Stn CP 2362, 679-740 m, 1 v; Stn CP 2380, 150-163 m, 2 v; Stn DW 2402, 101-118 m, 1 pv (A/DNA).

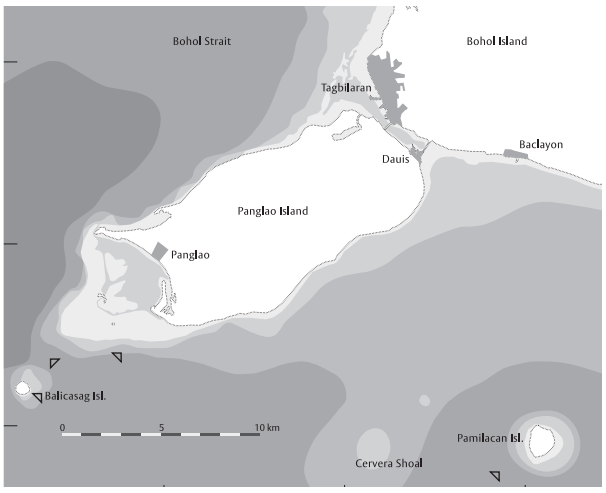
Description. — Shell rather small (L up to 18 mm), H/L ratio about 1, rounded and inflated, nearly equilateral and rather thin-shelled. Umbos clear, prosogyrate, positioned just anterior of the middle of the shell. Posterior margin straight or slightly concave. Inner margins finely crenulated. Anterior zone covering 60-65% of the shell, with tiny reticulate sculpture forming a pattern of undulating concentric ridges, stronger towards anterior margin. Posterior zone covering 35-40% of the shell, with barred sculpture, bearing well defined cross-bars in the interstices, each third to fifth interstice carrying small but erect, blunt spines; remainder unsculptured or occasionally carrying minute spinelets. Sculpture often becoming more laminate towards postero-dorsal margin. Total rib number: 125-145. The demarcation line dividing the two zones is directed obliquely in juveniles; during subsequent ontogeny it runs parallel with the ribs. Lunular heart somewhat variable; mostly rather poorly developed and ele-

vated, vaguely delimitated. Exterior and interior entirely white.

Distribution and ecology. — Known from mainland Japan (Habe, 1961; Higo *et al*., 1999), eastern China Sea (coll. TP), Philippines (Poutiers, 2006), Indonesia (Ter Poorten, 2007a: 263), Solomon Islands and Vanuatu (both MNHN, det. TP). Although not recorded by Wilson & Stevenson (1977), in coll. TP three samples from Western Australia (North West Cape, trawled offshore on sand and mud, 400-500 m, and Rowley shoals, off Mermaid Reef, in sand and mud, by scampi trawler, 400-450 m) further extend the known distribution to the south. The present material has a depth range of 90-200 m (dead) and 101-118 m (alive), except for the PANGLAO 2005 stn CP 2362 valve (679-740 m) which is worn and may have been transported downslope.

Remarks. — The posterior zone of the present species is never subdivided into two zones and lacks any abrupt changes in the rib sculpture, which readily separates it from its closest congener, *M. velatum* spec. nov. Some of the Philippine specimens examined are only tentatively referred to *M. sakuraii*, for they exhibit rather wide variation in shell features when compared with typical Japanese specimens. A re-evaluation with additional material is needed, to determine if these specimens indeed fall within the intraspecific variability of the species.

Microcardium velatum **Ter Poorten & Poutiers spec. nov.**
Pl. 19 fig. 5, pl. 20 fig. 8, pl. 21 figs 3-7, table 8



Holotype. — PANGLAO 2005, Stn CP 2343, Bohol Sea, off Pamilacan Isl., 9°27.4'N, 123°49.4'E, 273-356 m, 23.v.2005, 1 pv (A, NMP). Paratypes as listed below.

Other material examined. — **Philippines**: PANGLAO 2005, Stn DW 2339, 164-176 m, 10 v; Stn CP 2343, 273-356 m, 6 pv (A, paratypes 1-4, MNHN 22390; A/DNA, paratypes 6-7 MNHN 32277-32278), 1 v; Stn DW 2347, 198-233 m, 2 v; Stn DW 2368, 318-322 m, 1 pv (A, paratype 5, MNHN 22338); Stn DW 2371, 172-175 m, 4 v; Stn CP 2380, 150-163 m, 3 pv (A), 10 v; Stn CP 2381, 259-280 m, 1 v; Stn CP 2399, 309-342 m, 1 v; Stn DW 2402, 101-118 m, 1 v. AURORA 2007, Stn CP 2671, 14°53'N-121°45.3'E, 269-277 m, 6 v (MNHN); Stn CP 2716, 14°30.4'N-121°41.2'E, 335-356 m, 2 v (MNHN). MUSORSTOM 3, 1985, Stn CP 88, 14°01'N-120°17'E, 183-187 m, 1 v (MNHN); Stn CP 91, 14°00'N-120°18'E, 190-203 m, 1 v (MNHN); Stn DR 93, 13°49'N-120°02'E, 540 m, 1 v (MNHN). Panglao Isl., tangle nets, 73-110 m, 2 pv (TP 1571; coll. S. Hobbs, U.S.A.); Balicasag Isl., tangle nets, 200 m, 2000, 1 pv (MH QQ163); N of Dipolog, Aliguay Isl., trawled, 150-240 m, 1 pv (TP 1811); Aliguay Isl., trawled, 50-150 m, 2008, 2 pv (paratypes 8-9, TP 3659); Aliguay Isl., local fishermen, 2006, 1 pv (paratype 10, MH QQ163.1); Aliguay Isl., dredged by local fishermen, 50-150 m, 2009, 1 pv (TP 3806); Balicasag Isl., tangle nets, 150-200 m, 1 pv (coll. G.T. Poppe, 151120); Cebu, Bohol area, dredged, 150 m, leg. R. Martin, 1989, 1 pv (paratype 11 NMSA K5207).

Description. — Shell rather small (H up to 16 mm), H/L ratio about 1, subquadrate to rounded, inflated, nearly equilateral and rather thin-shelled. Umbos clear, prosogyrate, positioned just anterior of the middle of the shell. Anterior and ventral margins rounded, postero-ventral corner angular, posterior margin straight with a clear indention. Inner margins finely crenulated. Anterior zone covering 55-60% of the shell, with small interstices and broad, low and rounded ribs sculptured with tiny reticulations, forming an interlaced pattern of weakly undulating concentric ridges, anastomosing anteriorly and stronger towards anterior margin whereas radial ribs are fading out. Posterior zone covering 40-45% of the shell divided into two distinct areas: one immediately following the anterior part (10-15%) finely ribbed with coarse, pronounced concentric cross-bars in the rather broad interstices, each second to fourth one carrying a row of small, blunt spines; followed on the posterior slope by a zone (25-30%) that carries even finer ribs, alternating with interstices that consist of much more crowded and extremely fine, microscopic laminae and, except close to postero-dorsal margin, generally almost entirely devoid of spines. A very few radial rows of small spines sometimes occur in early juveniles on posterior slope. In fresh specimens, an additional thin calcified layer, which is microscopically commarginally striated, largely covers this zone, sometimes extending over a small part of the second zone. Demarcation line between anterior and posterior zones becoming almost parallel to radial sculpture at maturity, whereas the limit between laminated and barred areas of posterior zone gradually moves anteriorward during ontogeny, causing a progressive reduction of rib number in the barred area on the disc. Total rib number circa 100-130 (anterior zone 55-70; posterior zone 45-60). Lunular heart small, broad and elevated, clearly delimitated; lunular area large and smoothish, not clearly separated from the rest of the shell. Hinge plate arched; hinge rather finely built with two unequal cardinals, the more ventral cardinal being large and thick and the more dorsal one small, partially joined in right valve by a saddle. Anterior lateral teeth closer to cardinals than posterior laterals. Exterior and interior entirely white.

Distribution and ecology. — At present considered a range-restricted species, known from central and northern Philippines, exclusively in sublittoral and upper bathyal waters. Sampled by PANGLAO 2005 in depths of 150-356 m (alive) and 101-342 m (dead).

Etymology. — Latin adjective: veiled, covered with a veil. Referring to the additional layer covering the posterior slope of fresh specimens, appearing like a delicate veil.

Remarks. — The unique subdivision into three zones is highly distinctive, as is the peculiar deposition of an additional shell layer exhibiting striations perpendicular to the radial

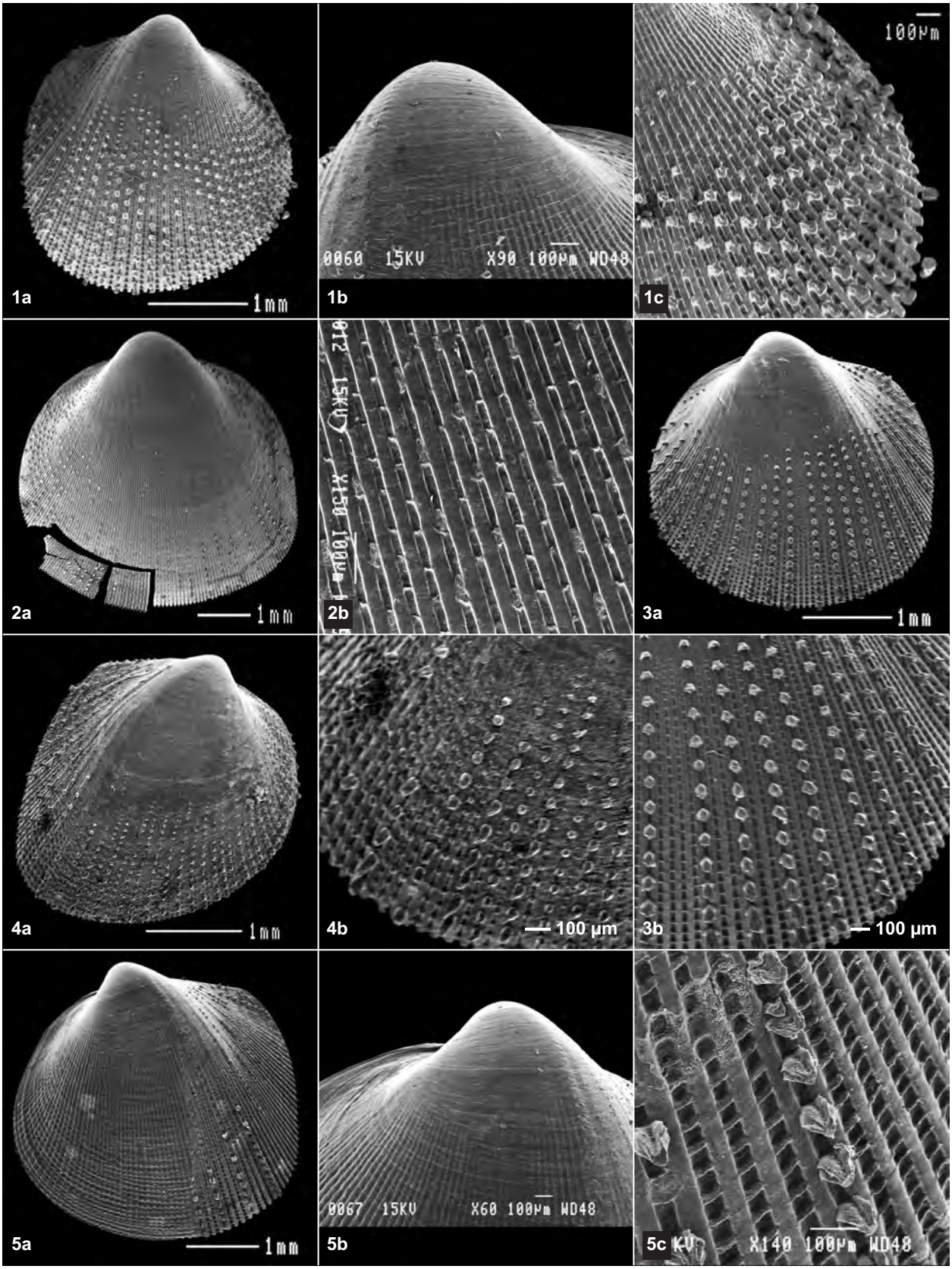


PLATE 19

Figs 1-6. Early ontogenetic stages of juvenile PMBP 2004 and PANGLAO 2005 *Frigidocardium* and *Microcardium* taxa. Scale bars: 1 mm and 100 µm. **Fig. 1.** *Frigidocardium sancticaroli* spec. nov., PMBP 2004 Stn T36, rv exterior, umbonal area and anterior slope. **Fig. 2.** *Frigidocardium helios* spec. nov., PMBP 2004 Stn T1 (Paratype 2 MNHN 22273), lv exterior and detail of median part. **Fig. 3.** *Frigidocardium torresi* (Smith, 1885), PMBP 2004 Stn T28, lv exterior and postero-ventral slope. **Fig. 4.** *Frigidocardium kirana* Sakurai & Habe, 1966, PMBP 2004 Stns L51-60, rv exterior and postero-ventral slope. **Fig. 5.** *Microcardium velatum* spec. nov., PANGLAO 2005 Stn DW 2339, lv exterior, umbonal area and transition in interstices sculpture of both posterior zones.

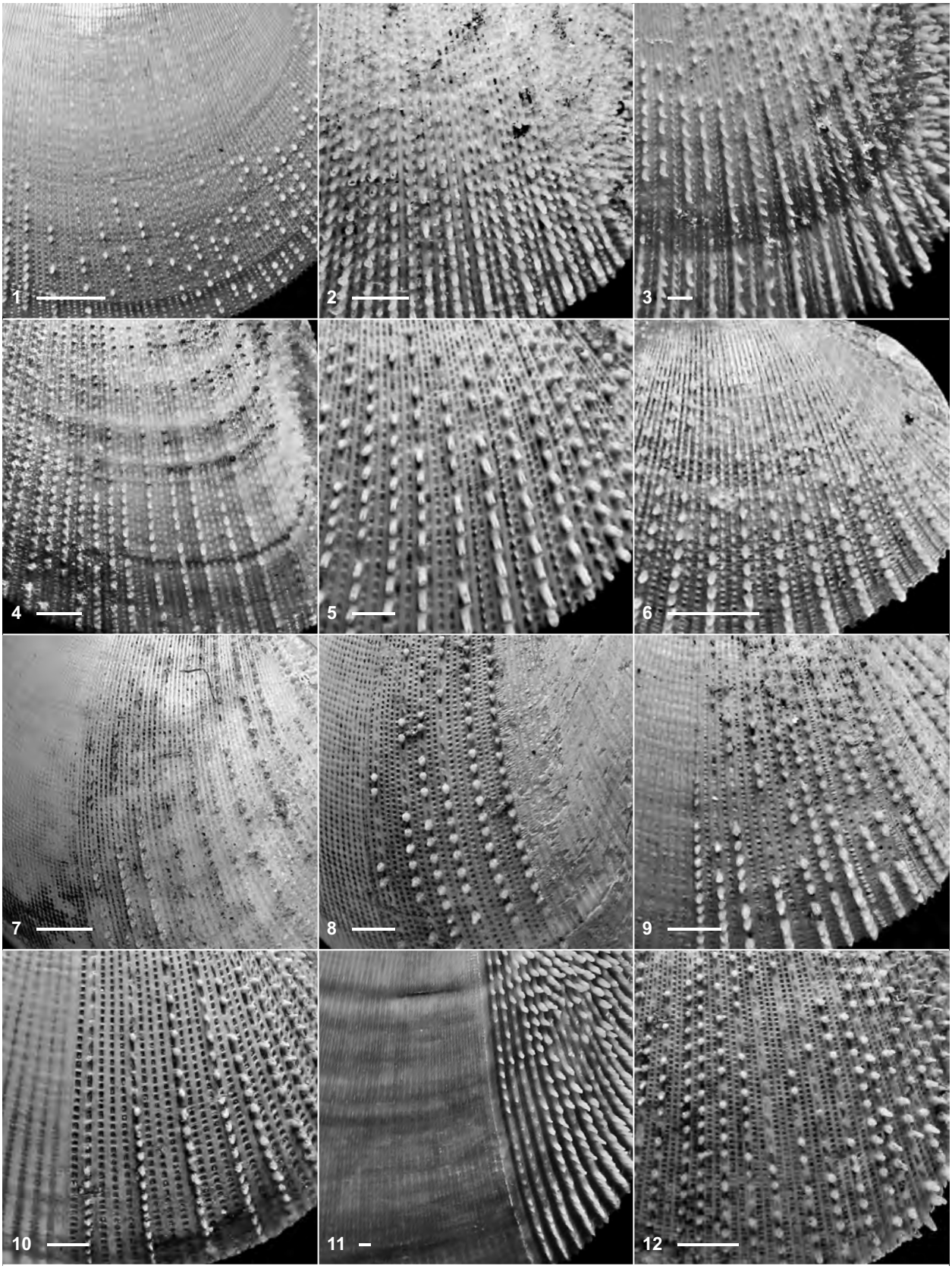


PLATE 20

Figs 1-12. Postero-ventral slope structures on left valves of PMBP 2004 and PANGLAO 2005 cardiid taxa. Scale bars: 1 mm. **1.** *Frigidocardium helios* spec. nov., SANTO 2006 Stn FB94 (Holotype MNHN 30161). **2.** *Frigidocardium sancticaroli* spec. nov., PMBP 2004 Stn T36 (Paratype 1, NMP). **3.** *Frigidocardium eos* (Kuroda, 1929), PMBP 2004 s/n. **4.** *Frigidocardium kirana* Sakurai & Habe, 1966, PMBP 2004 Stn S8. **5.** *Frigidocardium iris* Huber & Ter Poorten, 2007, PANGLAO 2005 Stn DW 2370. **6.** *Frigidocardium torresi* (Smith, 1885), PMBP 2004 Stn T6. **7.** *Microcardium sakuraii* (Habe, 1961), PMBP 2004 Stn P1. **8.** *Microcardium velatum* spec. nov., PANGLAO 2005 Stn CP 2343 (Holotype NMP). **9.** *Microcardium tenuilamellosum* Poutiers, 1981, PANGLAO 2005 Stn CP 2380. **10.** *Microcardium aequiliratum* Poutiers, 1981, PANGLAO 2005 Stn CP 2348. **11.** *Nemocardium* (*Nemocardium*) *bechei* (Reeve, 1847), Philippines, Balicasag (TP 3602). **12.** *Trifaricardium nomurai* Kuroda & Habe, 1951, PANGLAO 2005 Stn CP 2343.

	L	*H*	*W*	*L/H*	*W/L*
CP 2343 NMP Holotype (pv)	12.2 mm	12.7 mm	10.3 mm	0.96	0.84
CP 2343 MNHN 22390 Paratype 1 (pv)	11.3 mm	11.7 mm	9.1 mm	0.97	0.81
CP 2343 MNHN 22390 Paratype 2 (pv)	11.7 mm	11.5 mm	9.0 mm	1.02	0.77
CP 2343 MNHN 22390 Paratype 3 (pv)	11.5 mm	11.3 mm	8.6 mm	1.02	0.75
CP 2343 MNHN 22390 Paratype 4 (pv)	10.1 mm	10.2 mm	8.0 mm	0.99	0.74
DW 2368 MNHN 22338 Paratype 5 (pv)	9.0 mm	8.7 mm	6.7 mm	1.03	0.79
CP 2343 MNHN 32277 Paratype 6 (pv)	10.2 mm	10.4 mm	7.9 mm	0.98	0.77
CP 2343 MNHN 32278 Paratype 7 (pv)	10.5 mm	10.3 mm	7.6 mm	1.02	0.72
CP 2380 MNHN (pv)	11.4 mm	11.5 mm	9.0 mm	0.99	0.79
CP 2380 MNHN (pv)	11.5 mm	11.7 mm	9.3 mm	0.99	0.79
TP 1571 (pv)	12.0 mm	12.2 mm	9.2 mm	0.98	0.77
TP 1811 (pv)	9.4 mm	9.6 mm	7.3 mm	0.98	0.78
TP 3659/1 Paratype 8 (pv)	12.0 mm	12.3 mm	10.2 mm	0.98	0.85
TP 3659/2 Paratype 9 (pv)	11.0 mm	11.5 mm	9.6 mm	0.96	0.87
MH QQ163.1 Paratype 10 (pv)	14.0 mm	14.5 mm	11.6 mm	0.97	0.83
NMSA K5207 Paratype 11 (pv)	10.9 mm	10.7 mm	8.3 mm	1.02	0.76
Hobbs (pv)	15.7 mm	16.2 mm	12.7 mm	0.97	0.81
Mean values				0.99	0.79

Table 8. Shell measurements of *Frigidocardium velatum* spec. nov.

ribbing pattern of the third zone. Both features are lacking in *M. sakuraii*, which can be considered the most closely related species. Given the ranges of congeneric species, it seems improbable that the present species is restricted to the Philippines.

Nemocardium Meek, 1876; subgenus *Nemocardium*

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.

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. Interstices of ribs devoid of spines and transverse elements. Marginal crenulations, in accordance with ribs, much more strongly serrated on posterior zone. Hinge with very unequal cardinal teeth, the larger strongly curved.

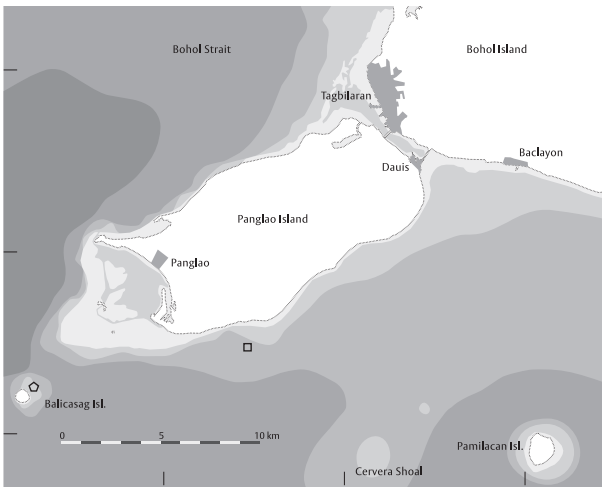
Distribution. — Early Cretaceous to Recent, Indo-Pacific, Japonic; sublittoral-upper bathyal.

Remarks. — *Nemocardium bechei* (Reeve, 1847) is the only extant species of the genus, which is known from the Early Cretaceous onwards, flourishing particularly in Europe during the Eocene. It is a typical Tethyan representative (Keen, 1950).

Nemocardium (*Nemocardium*) cf. *bechei* (Reeve, 1847)

Pl. 20 fig. 11, pl. 22 figs 4-5, table 9

Cardium bechei Reeve, 1847: 25-26.
? *Pratulum probatum* Iredale, 1927a: 333, pl. 46 fig. 8.



Material examined. — **Philippines**: PMBP 2004, Stn T1, 83-102 m, 1 v; No stn nr., Balicasag Isl., tangle nets and lumun lumun, 'deep water', bought from fishermen, 2004, gift of B. Olivera, 2 v.

Description. — Shell large (L 50-80 mm), solid, ovately quadrate, and nearly equilateral. Anterior and median zone covering 70-75% of the shell, nearly smooth with numerous, crowded, subsurface radial ribs; remaining posterior zone with strong spinose radial ribs. In total circa 115-125 ribs. Margins finely crenulated, changing abruptly in size at postero-ventral junction. Lunula large and broad, lunular heart

small, elevated and flattened on top, having transverse furrows in juveniles; escutcheon long and narrow. Exterior orange or pink, darker towards the margins and on lunular heart. Interior white, umbonal cavity pale orange, posterior margin pink. Periostracum prominent and silky, consisting of commarginal lamellae, restricted to anterior zone and along postero-dorsal margin.

Distribution and ecology. — Tropical West Pacific, from mainland Japan (Matsukuma, 2000), Taiwan (coll. TP), Philippines (coll. TP), northern Australia (Lamprell & Whitehead, 1992), New Caledonia (Poutiers, 1992; Virly *et al*., 1998) and the Norfolk and Kermadec Islands (Powell, 1958). Surprisingly, it appears to be absent in Indonesia (Ter Poorten, 2007a; not present in ZMA), suggesting a division of the distribution into two disjunct areas. Found in sublittoral and upper bathyal waters on sand and mud bottoms. Present material in 83-102 m (dead).

Remarks. — Although the Sulu Sea, Philippines, was given as one of two localities in the original description (Reeve, 1847: 25) and it is well-known from this area, it was not mentioned by Springsteen & Leobrera (1986), and in fact was encountered only once during PMBP 2004.

There is considerable geographic variation in shape (H/L and L/W ratio), ribbing and colour: Japanese specimens generally are relatively higher than Philippine ones and have a shorter, steeper posterior zone that has less pronounced ribbing with shallower interstices. Australian material is more equilateral, ovate, somewhat less inflated, attains very large sizes (L up to 81 mm) and is frequently pure pink with whitish patches in juveniles (table 9). *Pratulum probatum* Iredale, 1927 (described from Trial Bay, New South Wales) matches this form. Additional research based on supplementary material is needed in order to re-evaluate whether *P. probatum* indeed falls within the intraspecific variation and to what extent ontogenetic changes play a role in the variation in H/L ratios. The lectotype, selected by Wilson & Stevenson (1977: 15, pl. 1 figs 18-19, from Ticao, Philippines), agrees with the typical common Philippine form (pl. 22 fig. 5).

Surprisingly, the limited PMBP 2004 material (pl. 22 fig. 4) is of an altogether deviant form with a distinctly quadrangular postero-dorsal margin and a steeply sloping antero-dorsal margin. It is relatively high (L/H ratio circa 0.92), attains comparatively large dimensions, is ornamented with golden-yellow collars and has a lighter coloured posterior zone. The spines on the posterior zone are fairly thin. Pannekoek (1936: pl. 4 fig. 50) depicted a very similar valve from the Lower Miocene of Jawa, Indonesia. Lacking additional material apart from one well preserved specimen in NMR (Mactan Island, ex coll. Kaptein), the status of these specimens remains unresolved (Ter Poorten, in prep.).

Trifaricardium Kuroda & Habe, 1951

Trifaricardium Kuroda & Habe, 1951: 86. Type species by monotypy: *Trifaricardium nomurai* Kuroda & Habe, 1951; Recent, Japan.

Diagnosis. — Shell small to medium, thin to medium thick shelled, inflated, quadrangular to rounded. Rib structure heterogeneous, surface divided into two very differently sculptured and noticeably unequally sized zones. Both zones with numerous minute radial ribs, interstices of posterior zone with transverse bars or laminae, every second to fifth bearing small, blunt spinelets. Anterior zone limited to anterior quarter, interstices unsculptured and crossed by undulating commarginal threads.

Distribution. — Pliocene to Recent, Indo-Pacific, Japonic; sublittoral-upper bathyal.

Remarks. — Until recently considered a monotypical genus. However, Ter Poorten & Huber (2007) introduced *T. morrisoni* from north-western Australia. Also, Poutiers (1992: fig. 2m) illustrated an as yet undescribed *Trifaricardium* species from north-eastern Australia. *Trifaricardium nomurai* as depicted by Zhongyan (2004: pl. 145 fig. b) and Fengshan & Suping (2008: fig. 448) could well refer to another possibly undescribed congener.

Trifaricardium nomurai Kuroda & Habe, 1951

Pl. 20 fig. 12, pl. 22 figs 6-9

Cardium (*Acanthocardia*) *cancellatum* Nomura, 1933: 81-82, pl. 3 figs 9a-b (non Gmelin, 1791).

Trifaricardium nomurai Kuroda & Habe, 1951: 86 (nom. nov. for *Cardium cancellatum* Nomura, 1933).

Nemocardium bechei	*Mean L/H ratio (n)*	*Range L/H ratio*	*Maximum height*	*Posterior ribbing*
Australia	1.03 (12)	0.99-1.06	H 70-78 mm	ribs quadrangular, prominent, interstices broad and deep
Philippines (typical form)	0.98 (14)	0.94-1.02	H 60-65 mm	ribs rounded, well developed, interstices shallow
Philippines (deviant form)	0.92 (4)	0.91-0.93	H > 72 mm	ribs rounded, rather well developed, interstices shallow
Japan	0.93 (13)	0.88-0.98	H 70-76 mm	ribs low rounded, rather well developed, interstices shallow

Table 9. Morphometrics of *Nemocardium bechei* (Reeve, 1847) from various countries. Only (sub)adult specimens were included. Source for Australian material: Wilson & Stevenson (1977: 63), Powell (1958: 77), NMR, TP, MH; for Philippine material: PMBP 2004, NMR, TP, MH; for Japanese material: Hirase (1938: 17), NMR, TP, MH.

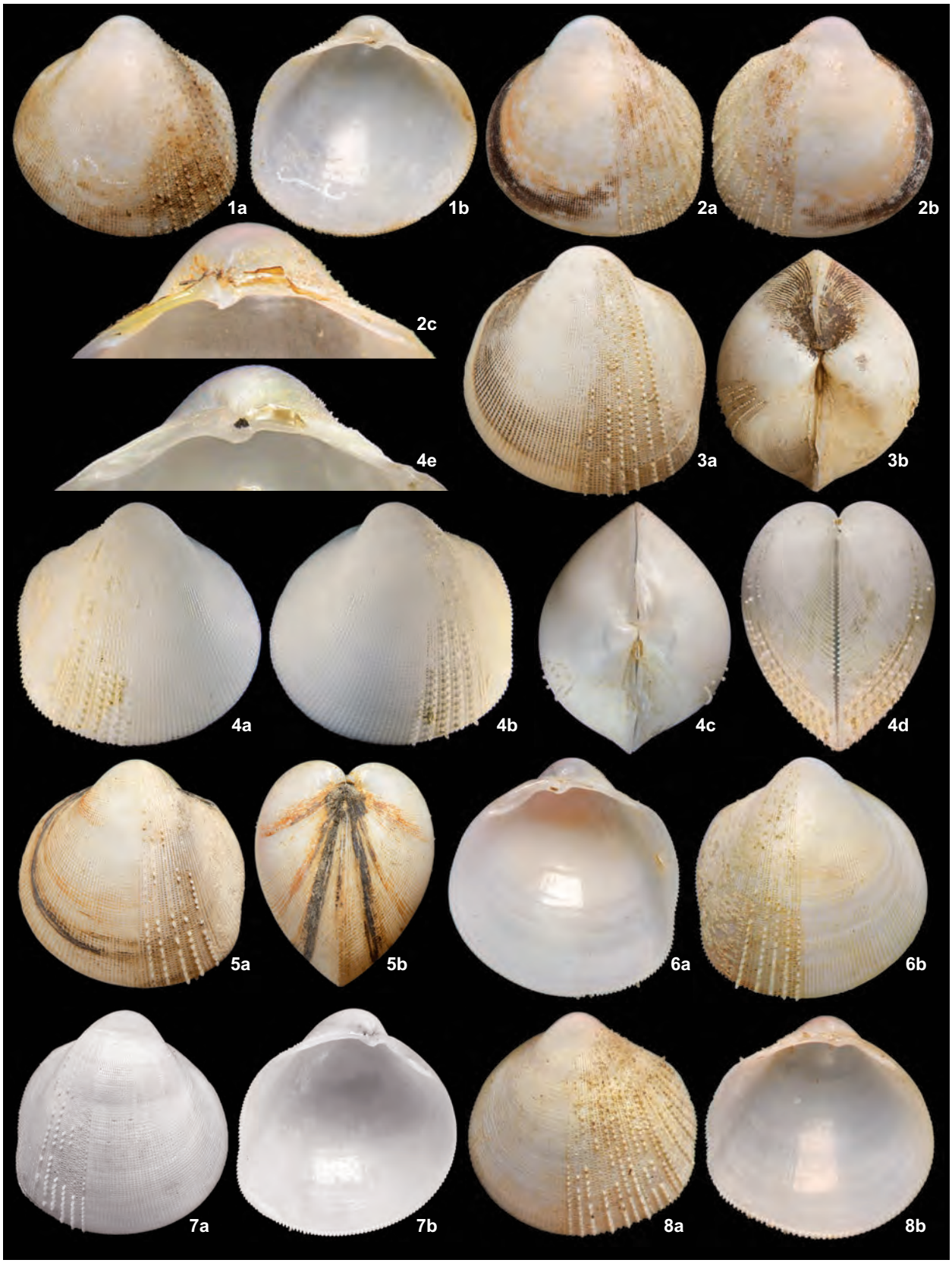


PLATE 21

Figs 1-2. *Microcardium sakuraii* (Habe, 1961). **1.** PANGLAO 2005 Stn CP 2380, lv exterior and interior, L 11.3 mm. **2.** PMBP 2004 Stn P1, lv and rv hinge, L 9.4 mm. **Figs 3-7.** *Microcardium velatum* spec. nov. **3.** PANGLAO 2005 Stn CP 2343, lv exterior and dorsal, H 12.7 mm (Holotype NMP). **4.** PANGLAO 2005 Stn CP 2343, rv exterior, lv exterior, dorsal, posterior and rv hinge, H 10.4 mm (Paratype 6 MNHN 32277) **5.** PANGLAO 2005 Stn CP 2380, lv exterior and anterior, H 11.5 mm. **6.** PANGLAO 2005 Stn DW 2339, rv interior and exterior, H 12.6 mm. **7.** Philippines, Panglao, tangle nets, 73-110 m, H 16.2 mm (coll. Hobbs). **Fig. 8.** *Microcardium tenuilamellosum* Poutiers, 1981, PANGLAO 2005 Stn CP 2380, lv exterior and interior, L 9.2 mm.

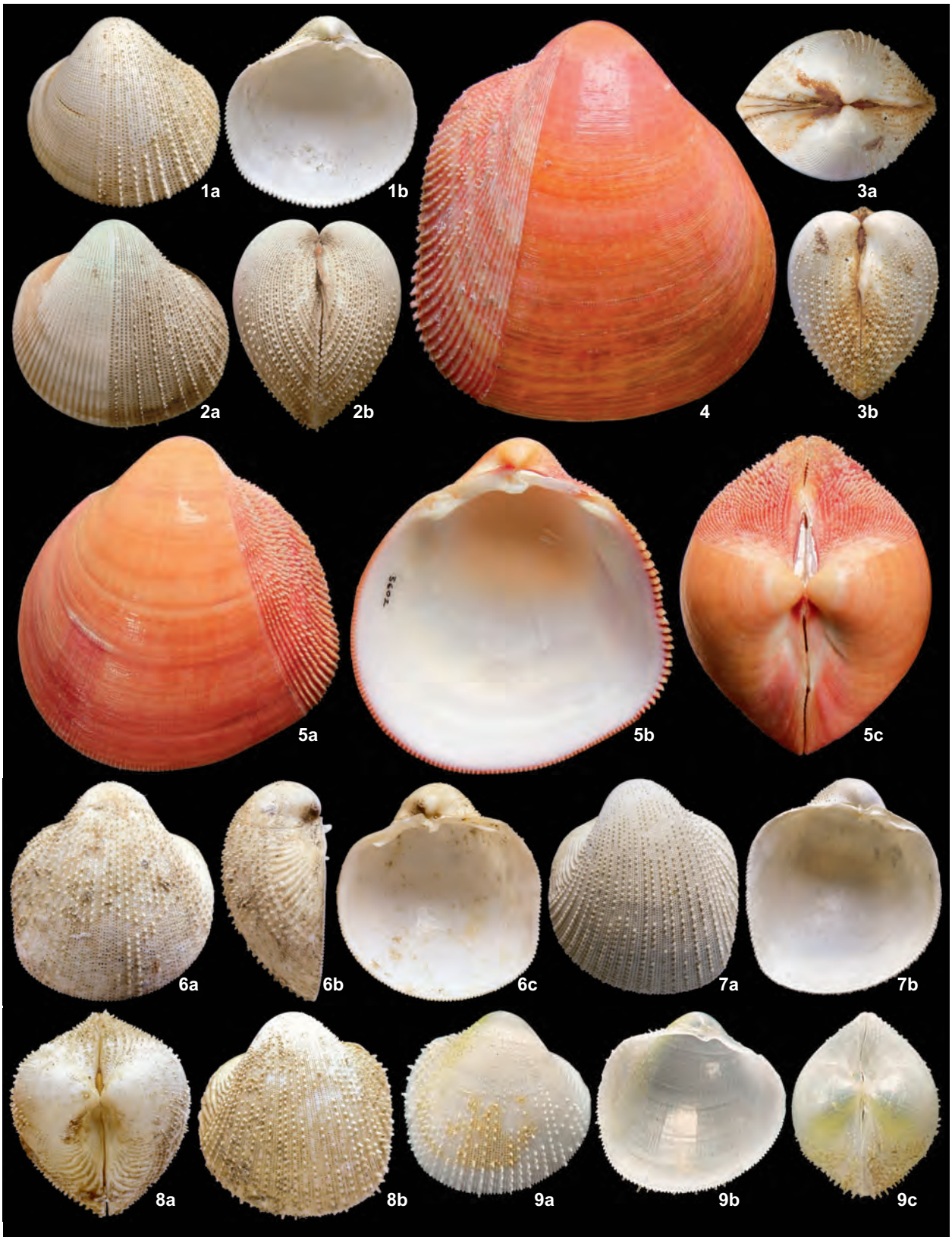


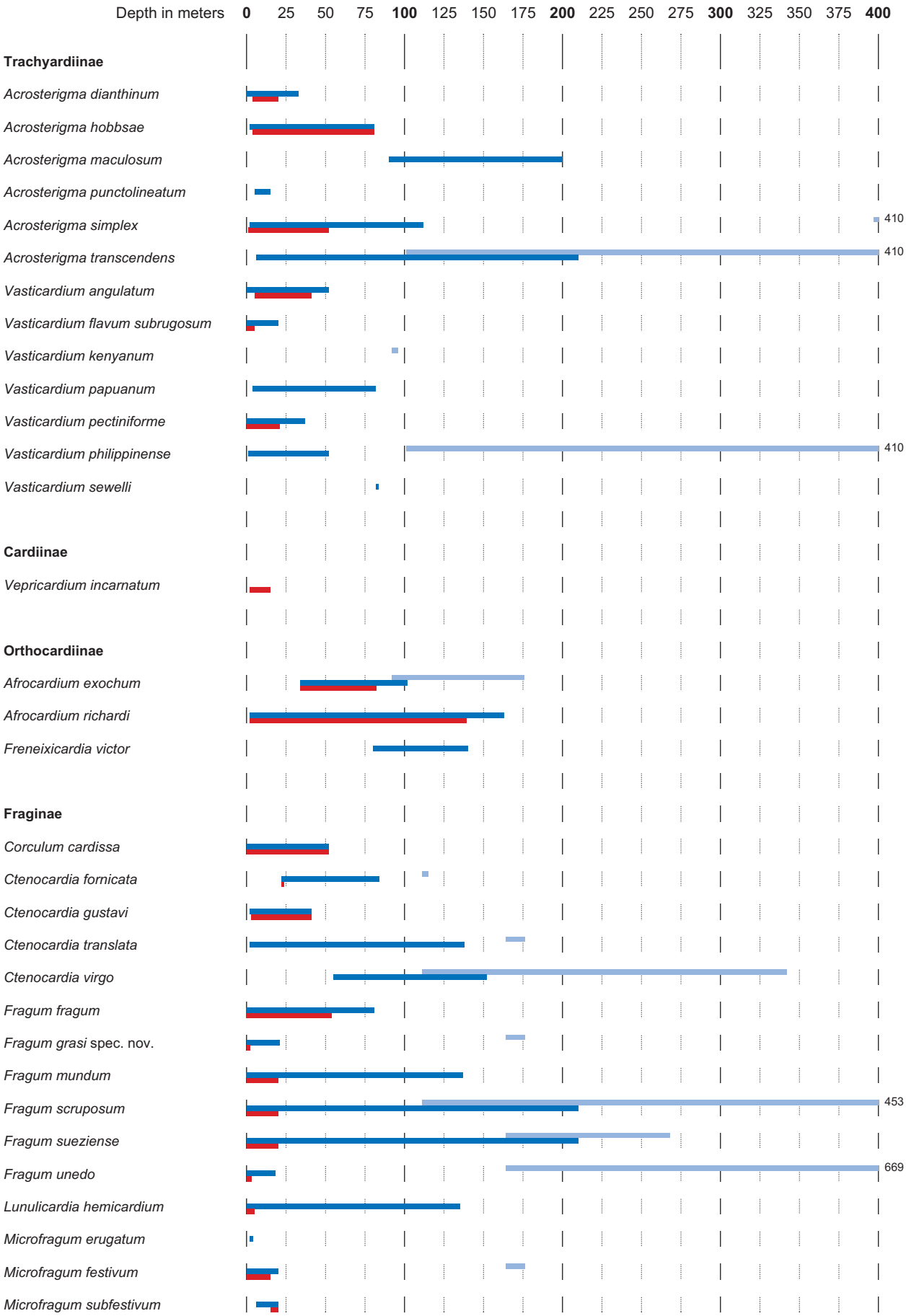
PLATE 22

Figs 1-3. *Microcardium aequiliratum* Poutiers, 1981. **1.** PANGLAO 2005 Stn CP 2344, lv exterior and interior, L 16.9 mm. **2.** PANGLAO 2005 Stn CP 2348, lv exterior and posterior, L 19.6 mm. **3.** PANGLAO 2005 Stn CP 2344, dorsal and posterior, L 15.7 mm. **Fig. 4.** *Nemocardium* (*Nemocardium*) *cf. bechei* (Reeve, 1847). PMBP 2004 s/n, Balicasag Isl., tangle nets and lumun lumun 'deep water', from fishermen, gift B. Olivera, rv exterior, H 71.4 mm (deviant form). **Fig. 5.** *Nemocardium* (*Nemocardium*) *bechei* (Reeve, 1847). Philippines, Balicasag Isl., tangle nets, 80 m, iv.2008, lv exterior, rv interior and dorsal, H 62.0 mm (TP 3602, typical form). **Figs 6-9.** *Trifaricardium nomurai* Kuroda & Habe, 1951. **6.** PANGLAO 2005 Stn CP 2343, rv exterior, anterior and interior, H 23.4 mm. **7.** PANGLAO 2005 Stn CP 2365, lv exterior and interior, H 20.7 mm. **8.** PANGLAO 2005 Stn CP 2343, dorsal and lv exterior, H 16.7 mm. **9.** PANGLAO 2005 Stn CP 2343, rv exterior, lv interior and dorsal, L 8.8 mm (MNHN 32271).

		PMBP 2004					PANGLAO 2005					
		Alive or dead	*number of samples*	*number of specimens*		*Habitat category*	*Alive or dead*	*number of samples*	*number of specimens*		***CT 2005***	***AURORA 2007***
	Trachycardiinae											
1	*Acrosterigma dianthinum*	1	19	13 pv	19 v	A	—	—	—	—	—	—
2	*Acrosterigma hobbsae*	1	11	8 pv	6 v	A	—	—	—	—	—	—
	Acrosterigma impolitum	—	—	—	—	—	—	—	—	—	+	—
3	*Acrosterigma maculosum*	0	4	—	4 v	?	—	—	—	—	+	—
4	*Acrosterigma punctolineatum*	0	2	1 pv	1 v	A	—	—	—	—	+	—
5	*Acrosterigma simplex*	1	38	100 pv	45 v	A	0	1	—	2 v	+	—
6	*Acrosterigma transcendens*	0	8	2 pv	11 v	A, C	0	2	—	2 v	—	+
7	*Vasticardium angulatum*	1	37	30 pv	22 v	A	—	—	—	—	+	—
	Vasticardium elongatum elongatum	—	—	—	—	—	—	—	—	—	+	—
8	*Vasticardium flavum subrugosum*	1	28	71 pv	24 v	B	—	—	—	—	+	—
9	*Vasticardium kenyanum*	—	—	—	—	—	0	1	—	1 v	—	—
	Vasticardium mindanense	—	—	—	—	—	—	—	—	—	+	—
10	*Vasticardium papuanum*	0	5	1 pv	6 v	?	—	—	—	—	—	—
11	*Vasticardium pectiniforme*	1	24	65 pv	6 v	A	0	1	1 pv	—	+	—
12	*Vasticardium philippinense*	0	15	7 pv	12 v	A	0	2	—	2 v	+	—
13	*Vasticardium sewelli*	0	1	—	1 v	?	—	—	—	—	—	—
	Vasticardium spec. nov.	—	—	—	—	—	—	—	—	—	+	—
	Cardiinae											
14	*Vepricardium incarnatum*	1	1	1 pv	—	?	—	—	—	—	+	—
	Orthocardiinae											
15	*Afrocardium exochum*	1	7	8 pv	61 v	C	0	4	—	8 v	—	—
16	*Afrocardium richardi*	1	40	137 pv	140 v	A, C	—	—	—	—	—	+
17	*Freneixicardia victor*	0	8	1 pv	11 v	C	—	—	—	—	—	—
	Fraginae											
18	*Corculum cardissa*	1	24	23 pv	11 v	A, B	—	—	—	—	+	—
19	*Ctenocardia fornicata*	1	5	2 pv	8 v	A, C	0	1	—	1 v	—	+
20	*Ctenocardia gustavi*	1	13	6 pv	21 v	A, C	—	—	—	—	—	—
21	*Ctenocardia translata*	1	7	2 pv	7 v	A, C	—	1	—	1 v	+	—
22	*Ctenocardia virgo*	0	9	—	18 v	?	0	2	—	2 v	+	+
23	*Fragum fragum*	1	21	18 pv	51 v	A	—	—	—	—	—	—
24	*Fragum grasi* spec. nov.	1	12	5 pv	506 v	B	0	1	—	2 v	—	—
25	*Fragum mundum*	1	32	19 pv	155 v	A	—	—	—	—	—	—
26	*Fragum scruposum*	1	36	20 pv	335 v	A, B	0	3	—	3 v	+	—
27	*Fragum sueziense*	1	47	37 pv	758 v	A, B	0	2	—	2 v	—	—
28	*Fragum unedo*	1	18	22 pv	93 v	B	0	2	—	2 v	+	+
29	*Lunulicardia hemicardium*	1	13	42 pv	32 v	B	—	—	—	—	+	—
	Lunulicardia retusa	—	—	—	—	—	—	—	—	—	—	+
30	*Microfragum erugatum*	0	3	—	4 v	B	—	—	—	—	—	—
31	*Microfragum festivum*	1	16	23 pv	116 v	A, B	0	1	—	1 v	—	—
32	*Microfragum subfestivum*	1	3	2 pv	15 v	A	—	—	—	—	—	—
	Laevicardiinae											
33	*Frigidocardium eos*	0	5	3 pv	4 v	C	0	1	—	9 v	—	+
34	*Frigidocardium helios* spec. nov.	1	4	2 pv	4 v	C	—	—	—	—	—	—
35	*Frigidocardium iris*	—	—	—	—	?	0	2	—	9 v	—	—
36	*Frigidocardium kirana*	1	9	3 pv	9 v	C	0	1	1 pv	1 v	—	+
37	*Frigidocardium sancticaroli* spec. nov.	1	17	15 pv	483 v	C	0	5	—	52 v	—	+

		PMBP 2004					PANGLAO 2005					
		alive or dead	*number of samples*	*number of specimens*		*habitat category*	*alive or dead*	*number of samples*	*number of specimens*		***CT 2005***	***AURORA 2007***
	Laevicardiinae (continued)											
38	*Frigidocardium torresi*	1	21	7 pv	142 v	C	0	2	—	2 v	—	+
	Fulvia (*Fulvia*) *aperta*	—	—	—	—	—	—	—	—	—	+	—
39	*Fulvia* (*Fulvia*) *australis*	1	24	52 pv	57 v	A, B	0	1	—	1 v	+	—
40	*Fulvia* (*Fulvia*) *boholensis*	1	4	4 pv	—	A	—	—	—	—	—	—
41	*Fulvia* (*Fulvia*) *colorata*	1	7	11 pv	19 v	C	0	1	—	1 v	—	—
42	*Fulvia* (*Fulvia*) *laevigata*	1	20	96 pv	96 v	B	—	—	—	—	+	—
43	*Fulvia (Fulvia) scalata*	1	16	8 pv	36 v	C, D	0	1	—	1 v	—	+
44	*Fulvia* (*Laevifulvia*) *hungerfordi*	1	7	4 pv	61 v	D	—	—	—	—	+	—
45	*Fulvia* (*Laevifulvia*) *lineonotata*	0	1	—	4 v	?	—	—	—	—	—	—
46	*Fulvia* (*Laevifulvia*) *subquadrata*	0	2	—	2 v	D	—	—	—	—	+	—
47	*Fulvia* (*Laevifulvia*) *undatopicta*	0	6	—	15 v	?	—	—	—	—	+	—
48	"*Laevicardium" attenuatum*	—	—	—	—	—	0	1	—	1 v	+	+
49	"*Laevicardium" biradiatum*	0	8	4 pv	3 v	A	—	—	—	—	—	—
50	"*Laevicardium" lobulatum*	1	7	10 pv	21 v	B, D	—	—	—	—	—	—
51	"*Laevicardium" multipunctatum*	0	2	—	2 v	C	—	—	—	—	—	+
	Lyrocardium aurantiacum	—	—	—	—	—	—	—	—	—	—	+
	Lyrocardium lyratum	—	—	—	—	—	—	—	—	—	—	+
52	*Microcardium aequiliratum*	0	3	—	7 v	C	1	13	59 pv	133 v	—	+
53	*Microcardium sakuraii*	0	4	1 pv	3 v	C	1	3	1 pv	3 v	—	—
54	*Microcardium tenuilamellosum*	—	—	—	—	C	0	1	—	2 v	—	+
55	*Microcardium velatum* spec. nov.	—	—	—	—	C	1	10	11 pv	30 v	—	+
	Microcardium spec. nov.	—	—	—	—	—	—	—	—	—	—	+
56	*Nemocardium* (*N.*) *cf. bechei*	0	2	—	3 v	C	—	—	—	—	—	—
57	*Pseudofulvia caledonica*	1	8	6 pv	2 v	A	—	—	—	—	—	—
58	*Trifaricardium nomurai*	—	—	—	—	C	1	3	2 pv	6 v	—	—
	Tridacninae											
59	*Hippopus hippopus*	0	1	—	1 v	A	—	—	—	—	—	—
60	*Tridacna* (*Chametrachea*) *crocea*	0	1	1 pv	—	A	—	—	—	—	—	—
61	*Tridacna* (*Chametrachea*) *maxima*	1	3	2 pv	2 v	A	—	—	—	—	+	—
62	*Tridacna* (*Chametrachea*) *squamosa*	1	3	2 pv	1 v	A	—	—	—	—	+	—
63	*Tridacna* (*Tridacna*) *gigas* [1)]	0	1	—	c.10 v	A	—	—	—	—	—	—
	Incertae cedis											
	Maoricardium pseudolatum	—	—	—	—	—	—	—	—	—	+	—
Total		36(1), 21(0)	694	897 pv	3486 v		4(1), 25(0)	68	75 pv	280 v		
Total number of specimens:					4383					355		

Table 10. Cardiidae recorded during four recent Philippine Expeditions. PMBP 2004, PANGLAO 2005, Cuming Tour 2005 and AURORA 2007. 1 = found alive, 0 = found dead only, + = present, — = absent. Habitat categories relating to PMBP 2004 records only; see page 16 for explanations. A question mark (?) denotes insufficient data to define a habitat category.
[1)] Adult valves observed but not sampled. See under 'Results' for further explanation.


Depth in meters
0 25 50 75 100 125 150 175 200 225 250 275 300 325 350 375 400
Trachyardiinae
Acrosterigma dianthinum
Acrosterigma hobbsae
Acrosterigma maculosum
Acrosterigma punctolineatum
Acrosterigma simplex
410
Acrosterigma transcendens
410
Vasticardium angulatum
Vasticardium flavum subrugosum
Vasticardium kenyanum
Vasticardium papuanum
Vasticardium pectiniforme
Vasticardium philippinense
410
Vasticardium sewelli
Cardiinae
Vepricardium incarnatum
Orthocardiinae
Afrocardium exochum
Afrocardium richardi
Freneixicardia victor
Fraginae
Corculum cardissa
Ctenocardia fornicata
Ctenocardia gustavi
Ctenocardia translata
Ctenocardia virgo
Fragum fragum
Fragum grasi spec. nov.
Fragum mundum
Fragum scruposum
453
Fragum sueziense
Fragum unedo
669
Lunulicardia hemicardium
Microfragum erugatum
Microfragum festivum
Microfragum subfestivum

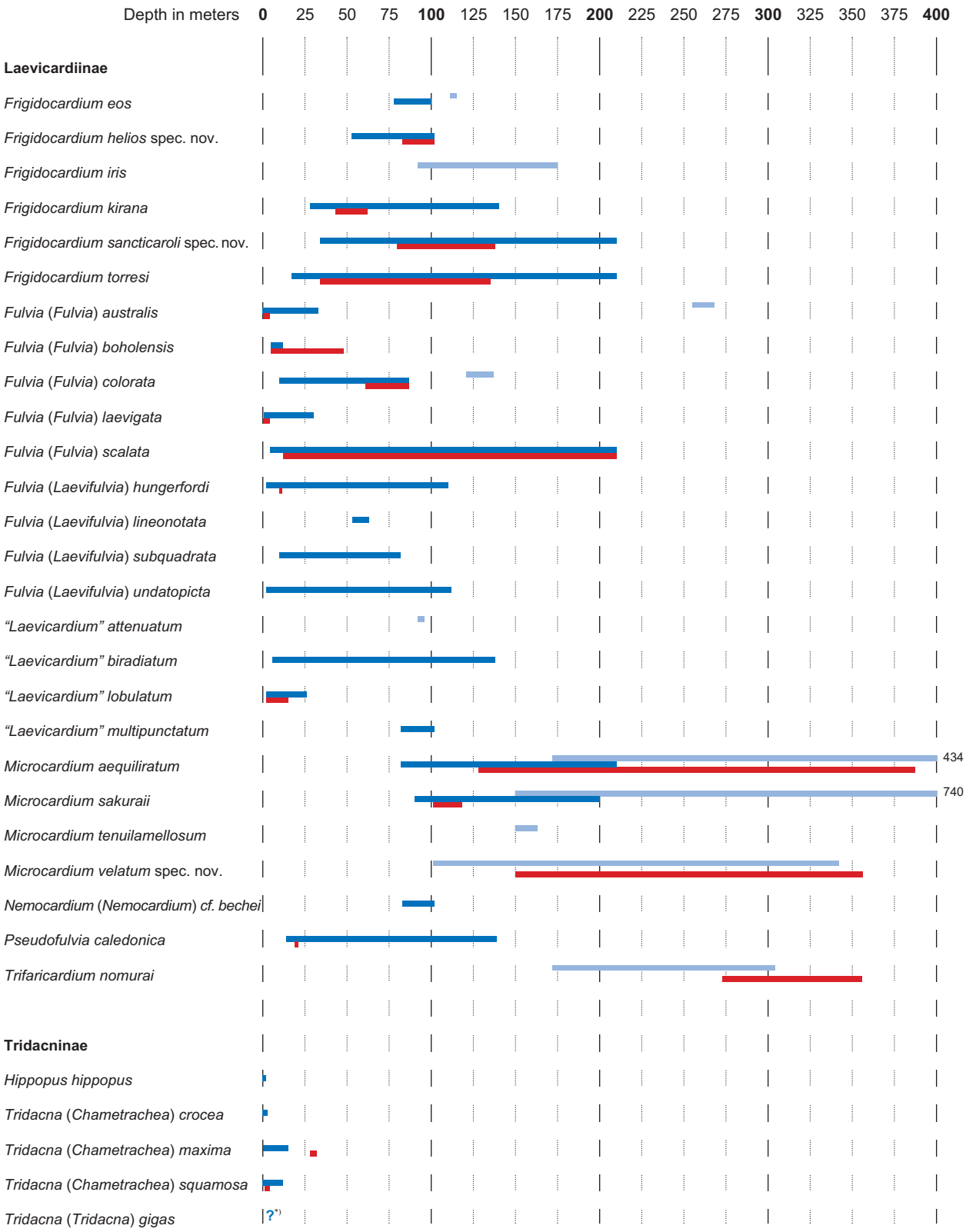


Table 11. Bathymetrical range of PMBP 2004 and PANGLAO 2005 Cardiidae. For taxa with recordings over 400 m the maximum depth is given.

Found dead during PANGLAO 2005 (covered depth range 64-2323 m)
Note that the indicated depth range for many taxa is partly related to *post-mortem* downslope transportation
Found dead during PMBP 2004 (covered depth range essentially 0-150 m; sporadically down to 210 m)
Combined live recordings of PMBP 2004 and PANGLAO 2005

*) Empty valves observed but not sampled; exact depth range not recorded.

Material examined. — **Philippines**: PANGLAO 2005, Stn CP 2343, 273-356 m, 2 pv (A/DNA), 4 v; Stn DW 2365, 303-304 m, 1 v; Stn DW 2371, 172-175 m, 1 v.

Description. — Shell medium (H 20-23 mm), rather thick shelled, inflated, roughly quadrangular with rounded anterior and ventral margins but slightly truncated posterior margin. Heterogeneous rib structure, surface divided into two very differently sculptured and unequally sized zones. Both zones with numerous minute radial ribs (c. 110-120 in total). Rib interstices of posterior zone with transverse bars, every second to fourth bearing small, blunt spinelets. Many low and unsculptured rounded radial ribs confined to anterior quarter on anterior zone, crossed by coarse, strongly undulating, anastomose commarginal threads. Lunular area vaguely bordered, smoothish or with a few commarginal furrows on larger shells; lunular heart a simple ovate and rounded bulge of dorsal margin, slightly larger on right valve. Shell exterior and interior entirely white, sometimes with a slight hue of lemon-yellow on the posterior slope. In the early shell, demarcation line dividing both zones rather clear, curved, and strongly oblique to radial sculpture (pl. 22 fig. 9a). The anterior zone has a more glossy appearance than the posterior zone.

Distribution and ecology. — Imperfectly known, recorded from mainland Japan, South China Sea (Higo *et al*., 1999), the Philippines (Ter Poorten & Huber, 2007), Indonesia (J.-M. Poutiers, pers. comm., 06.2009) and north-western Australia (Ter Poorten & Huber, 2007). Found in sublittoral and upper bathyal environments. Present material, exclusively from PANGLAO 2005, recorded from 273-356 m (alive) and 172-304 m (dead).

Remarks. — The differences in shell morphology between Philippine and Japanese material appear to be trivial and can safely be regarded as falling within the range of intraspecific variation.

CONCLUDING REMARKS

The concentration in the Philippines of 85 cardiid taxa as presently known is very similar to the number in Indonesia and confirms the species richness of the Coral Triangle centre of marine biodiversity. This number is considerably higher than the 60 species estimated by Crame (2000: fig. 7) at latitude 10°N, suggesting a substantially higher latitudinal diversity gradient, but otherwise does not deviate from the general bivalve pattern of higher diversity in lower latitudes as ascertained by Crame (2000). However, apart from the clear dependency of species richness on habitat diversity, it should be kept in mind that the sampling strategies used and the sampling effort expended also heavily influence the numbers of species collected (Bouchet *et al*., 2002; Hoeksema, 2007; Bouchet *et al*., 2009). The absence of virtually any endemics is in accordance with results of other workers, and reinforces the fact that the Philippine archipelago cannot be considered as supporting a geographically isolated biota.

Detailed analysis of samples in combination with ecological data made available by large scale expeditions, greatly adds to our knowledge of cardiid environmental preferences. Inclusion of these preferences contributes to a more complete understanding of species concepts, thus forming a broader basis for taxonomic work at (supra)specific level and (palaeo) ecological studies. Moreover, it can validate or refute earlier results, e.g. the recent transfer of *Afrocardium* from Fraginae to Orthocardiinae, which is confirmed by the present ecological data.

Although the habitat type A defined herein is the most common cardiid habitat, the four new species described in this paper originate from habitat type C (3 species) and B (1 species), suggesting that future sampling activities that more strongly emphasize these habitats may result in additional new taxa and more balanced knowledge of cardiid ecological preferences. More targeted sampling, covering various depth intervals, is needed in order to gain insight into the taxonomic status of several taxa, e.g. supposed forms of *Corculum cardissa* (Linnaeus, 1758). Repeated sampling to overcome problems caused by seasonal or long-term fluctuations in the occurrence of taxa, should result in more comprehensive distributional knowledge. For cardiids, suction sampling generally proved to be a highly rewarding and efficient collecting technique.

The large number of Indo-Pacific cardiids newly described during recent decades, the large number of range extensions reported in this paper and other recently published regional faunal overviews as well as the various range contractions resulting from repeated misidentifications in the literature, make it clear that despite recent extensive research, our knowledge of cardiid diversity and distributions is still far from adequate. Further sampling and taxonomic investigations are therefore necessary in order to develop a well-founded basis for future studies of biogeography, ecology, biodiversity, etc. One of the many supraspecific investigations still to be dealt with is the generic placement of the taxa herein provisionally referred to *Laevicardium*, which is unsatisfactory from a morphological point of view.

An interdisciplinary approach that includes fossil assemblages also leads to a more comprehensive understanding of taxonomy. For cardiids, this is exemplified by the present referral of *Cardium* (*Ctenocardia*) *victor* Angas, 1872 to the hitherto considered extinct *Freneixicardia* Schneider, 2002.

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