Taxonomic revision of the Indo-Pacific *Vasticardium flavum* species group (Bivalvia, Cardiidae)

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ABSTRACT
The group of *Vasticardium flavum* (Trachycardiinae) includes four species of medium size, with a slightly elongate or rounded shell of circa thirty ribs, and a characteristic sculpture: rounded ribs elaborately ornamented with transverse ridges. The identity of *Cardium flavum*, until now rather enigmatic, is revised based on Linné's descriptions and the designation of a lectotype. Three subspecies of *V. flavum* are recognized: the nominal subspecies (Carolines to eastern Indonesia and the Solomons), *V. flavum subrugosum* (India to the Philippines, China, South Japan) and *V. flavum dupuchense* (north-western Australia). *Vasticardium pectiniforme* (Born, 1780), better known as *V. rugosum* (Lamarck, 1819) and often erroneously considered a synonym of *V. flavum*, is the most common and widespread trachycardiine in the Indo-Pacific. Two additional species have restricted ranges in Australia: *Vasticardium vertebratum* (Jonas, 1845) [= *V. reeveanum* (Dunker, 1852)], and *Vasticardium ornatum* (Sowerby, 1877) [= *V. fultoni* (Sowerby, 1916)].

KEY WORDS
Mollusca,
Bivalvia,
Trachycardiinae,
Vasticardium,
Indo-Pacific.

RÉSUMÉ
Le groupe de *Vasticardium flavum* (Trachycardiinae) comprend quatre espèces de taille moyenne, avec une coquille légèrement allongée ou arrondie, d'une trentaine de côtes et une sculpture caractéristique : côtes arrondies fortement ornées de barres transversales. L'identité de *Cardium flavum*, restée jusqu'ici plutôt énigmatique, est révisée grâce aux descriptions de Linné et à la désignation d'un lectotype. Trois sous-espèces de *V. flavum* sont reconnues : la sous-espèce nominale (des Carolines à l'Indonésie orientale et les îles Salomons), *V. flavum subrugosum* (de l'Inde aux Philippines, Chine et sud du Japon), et *V. flavum dupuchense* (Australie du nord-ouest). *Vasticardium pectiniforme* (Born, 1780), plus connue sous le nom de *V. rugosum* (Lamarck, 1819) et souvent considérée à tort comme synonyme de *V. flavum*, est le plus commun et le plus répandu des Trachycardiinae de l'Indo-Pacifique. Deux autres espèces ont des répartitions limitées en Australie: *Vasticardium vertebratum* (Jonas, 1845) [= *V. reeveanum* (Dunker, 1852)], et *Vasticardium ornatum* (Sowerby, 1877) [= *V. fultoni* Sowerby, 1916].

MOTS CLÉS
mollusques,
bivalves,
Trachycardiinae,
Vasticardium,
Indo-Pacifique.

INTRODUCTION

Cardium flavum and *C. rugosum* are among the names most frequently used in the literature on Indo-Pacific Cardiidae. Considered together, they constituted the absolute record in Fischer-Piette's chresonymy (1977), with more than one hundred usages in the literature. Both names are practically always used to designate the same species of Trachycardiinae, one of the most common in the littoral zones of these two oceans. About half the authors use the name *Cardium flavum* Linné, 1758. The others think that this name is enigmatic, and use the name *Cardium rugosum* Lamarck, 1819, which is defined without ambiguity. Nevertheless, as far as I know, no author since 1819 has expressed the view that *C. flavum* could be anything but *C. rugosum*.

The main aim of this paper is to show that Linné's description of *C. flavum* does not fit *C. rugosum* and that type material exists that stabilizes the name *C. flavum* without ambiguity. There are in fact two easily separable species, *C. flavum* and *C. rugosum*, which have consistently been confused for more than 170 years. There are three contributing factors. First, the two species are similar in size, shape, number of ribs and, as far as rib morphology is concerned, only a detailed observation can separate them. Second, they are very widely sympatric. A third reason could be that the confusion was initially made by two leading malacologists in the beginning of the nineteenth century, Lamarck (1819) and Sowerby (1841).

The majority of authors immediately subsequent to Linné correctly identified *C. flavum* Linné, following Schröter who gave good description and figures (1784: pl. 7, fig. 11a, b; 1786: 43; figured specimen still present in ZUMC, Spengler collection, here Fig. 2A). This accurate identification could have survived but Lamarck (1819: 10) introduced a new species, *Cardium rugosum,* with the comment "an *Cardium flavum* Linné?". This erroneous assumption was also made by Sowerby who mentions (1841b: No. 58): "*C. rugosum* yellow var.= *C. flavum* Linn?". Following these two authoritative opinions, *C. flavum* has mainly been interpreted as being the same as *C. rugosum* Lamarck, and named either *flavum* or *rugosum*.

The few authors who dealt with the identification of Linné's bivalves (mainly Hanley 1855 and Dodge 1952) were not very thorough in their investigations. None examined the Reginae Ulricae collection (now in Uppsala, Sweden). Dodge (1952: 62) stated about *C. flavum*: "There is no internal evidence of its identity" [= no specimen, no synonymy, no locality], and dismissed Linné's description which was short (but mentionned at least three characters never present together in any other Cardiidae, see below).

MATERIAL, METHODS AND TEXT CONVENTIONS

The material used for this paper comes from the following museums:

AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BISHOP	Bernice P. Bishop Museum, Honolulu
BMNH	The National History Museum, London
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
LACM	Los Angeles County Museum of Natural History, Los Angeles
MHNG	Muséum d'Histoire Naturelle de Genève, Geneva
MNHN	Muséum national d'Histoire naturelle, Paris
NHMW	Naturhistorisches Museum, Vienna
NMW	National Museum of Wales, Cardiff
QM	Queensland Museum, Brisbane
USNM	National Museum of Natural History, Washington DC
WAM	Western Australian Museum, Perth
ZMA	Zoölogisch Museum, Amsterdam
ZMUC	Zoologisk Museum, Copenhagen

Museum investigations include also the examination of Linné's private collection held by the Linnean Society, London, and of syntypes of *Cardium flavum* Linné from the Louisa Ulricae collection in the Zoological Museum, Uppsala University, Sweden.

For convenience, the shells are divided externally into four radial "quarters":

AQ	Anterior Quarter
MAQ	Medio-Anterior Quarter
MPQ	Medio-Posterior Quarter
PQ	Posterior Quarter

In the description of the shells particular attention was devoted to rib morphology (profile and ornamentation of the ribs), by taking into account these elements in the first formed parts of the shell (juvenile or umbonal part) and the variations towards the latest formed parts (adult parts).

The ribs are described as follows with regard to their ornamentation:

Single-ridged. Presence of "vertical" or oblique ridges, more or less tubercular, only on the posterior flank of the rib; top and anterior flank smooth (not illustrated here).
Double-ridged. Ridges or tubercles on both flanks; top smooth (Figs 1B, 2D).
Full-ridged. The flank ridges join from one side to the other and develop also across the top zone; this typically happens in ribs that are more or less rounded in section and the ridges form successive portions of circles (Fig. 2E-G). Sometimes not all the lateral ridges reach the top; sometimes the lateral ridges are irregularly connected by obliquely oriented top ridges. In both cases the ribs are called *irregularly full-ridged* (Fig. 2G).
Top-ridged. In ribs that are low and flat, the lateral ridges are little developed, and the rib appears to be ridged only on the top (Fig. 1D, on left).
Crush-ridged. Sometimes some or many ridges widen in the top zone, taking a triangular shape, with apex towards the ventral margin, appearing to be "crushed" (Fig. 2H).

SYSTEMATICS

Family CARDIIDAE Lamarck, 1809
Subfamily TRACHYCARDIINAE Stewart, 1930

Genus *Vasticardium* Iredale, 1927

TYPE SPECIES. — *Cardium elongatum* Bruguière, 1789; Original Designation (Iredale 1927: 75).

DIAGNOSIS
Shell medium to large (maximum height ranging from 37 to 140 mm according to species); ovoid and symmetrical to asymmetrical and posteriorly expanded, obliquely or not, "winged" or truncated; often appreciably elongated and inflated. Hinge line moderately angled (average angle about 130°). Cardinal teeth in right valve separated or merely touching at their base and never connected by a high and narrow dorsal saddle. Rib number small to medium (22-45, exceptionally 50). Ribs enlarge quickly in juvenile median and anterior parts, becoming square-sided and fully ornamented, directly following small, smooth, postmetamorphic very early shell. In PQ, ribs always high and square-sided in juvenile shells, always simple rather than divided into two parts; top scales or nodules always arranged in a single row along the apex of these ribs. In other quarters of adult shells, ribs generally high, often squared and overhanging interstices, rarely triangular, often bearing scales or tubercles with crenulated margins in MPQ, cross-bars in anterior half. Interstices rather deep and wide, with a flat bottom, smooth or finely striated independently from flanks of ribs, never notched.

REMARK
Four generic names have been utilized for the Indo-West Pacific Trachycardiinae: *Trachycardium* Mörch, 1853, *Acrosterigma* Dall, 1900, *Vasticardium* Iredale, 1927 and *Regozara* Iredale, 1936. *Regozara* should be considered as a synonym of *Vasticardium* (see Wilson & Stevenson 1977: 76). For the time being it is difficult to choose among the other three names because this subfamily certainly needs generic revision, particularly in the Indo-Pacific where a lot of valid species remain not covered in recent monographs. It is not beyond the scope of this paper to reevaluate the supraspecific taxonomy and *Vasticardium* is used provisionally.

THE GROUP OF *Vasticardium flavum* (Linné, 1758)

This group is characterized by shells medium-sized (maximum height varying from 37 to 86 mm according to the species), often symmetrical but with anterodorsal margin always more raised than posterior, sometimes more or less

expanded backwards and asymmetrical, with ribs curved backwards in projection, but very rarely markedly truncated in the posterior margin. Rarely appreciably elongated: mean L/H = 0.91 (range 0.80-0.99). Moderately and rather variably depressed: mean W/L = 0.73 (range 0.63-0.95). Hinge generally at an angle with main axis of shell, moderately angled (angle between main cardinal and laterals range 125-135°). External colours generally light, internally white to purple. Ventral margin coloured only in one species (*V. vertebratum*). Rib number small to medium, range 22-35.

JUVENILE RIB MORPHOLOGY

Rib morphology is the same in juvenile specimens of all the forms of group, except *V. ornatum* (see below).

PQ. Ribs high, roughly square-sided (Fig. 2C). Flattened top zone ornamented with large, slightly twisted regularly set transverse scales, occupying almost all width of rib. Anterior margin of rib top bears numerous smaller bent scales (three or four in number between each large top scale), more or less joined together, forming a sharp, festooned edge, a little overhanging interstice. Posterior flank of rib finely, vertically ridged. [In *V. ornatum,* secondary ornamentation of ribs (small scales and ridges) absent]. Interstices, as wide as ribs, flat-bottomed and always finely but decidedly striated.

Other parts of shells. MPQ, MAQ, AQ: ribs high with upper part of flank having, on both sides, a succession of regularly disposed swellings which touch more or less together on rib tops, and overhang a little interstices which are flat, a little narrower than ribs, and concentrically striated.

ADULT RIB MORPHOLOGY

PQ. Rib morphology is similar to this of juveniles (Fig. 4F), except in *flavum* (Fig. 2B) where they are lower, progressively losing their edge ornamentation and relief, progressively separated into two parts by a thin longitudinal furrow; large top scales become smaller and limited to posterior half, and eventually disappear.

Other parts of shells. MPQ, MAQ, AQ: both rib profile and ornamentation are variable among species, populations, or growth stages in an individual. Rib profile changes, becoming more or less rounded, symmetrically or not, with lower part a little narrower (characteristic basal constriction: Fig. 4E); then becoming more or less symmetrically triangular with a rounded top zone and progressively lowering, loosing their basal constriction and, eventually, becoming flatly rounded, then hardly marked. Interstices remain generally flat, about as wide as ribs, markedly striated except sometimes in fully adult parts. Ornamentation generally changes when profile changes, with various possible sorts of ridging as defined above. *V. vertebratum* and *V. ornatum* (Fig. 5F, G) have a more elaborate rib morphology, with additional phenomena of flank constriction and division of flank ridging, only rarely and imperfectly observed in *V. flavum* and *V. pectiniforme*.

THE STATUS OF THE NAMES *Cardium flavum* AND *Cardium rugosum*

Cardium flavum Linné, 1758

LINNÉ'S ORIGINAL DESCRIPTION

"*C. testa subovata sulcata: latere anteriore scabro, posteriore dentato. Testa subovata, flava, latere anteriore alba. Sulci crenati nodulis in latere posteriore; margo non rubens.*"

[*C.* shell subovate ribbed: posterior (for Linné *posterior* = anterior and *anterior* = posterior) side rough, anterior toothed. Shell subovate, yellow, posterior side white. Ribs ornamented with small nodes on anterior side; margin not red.]

Linné (1764) added: "*Margines subserrati: exteriore dentato, non rubro. Color intus albus, fundo interdum rufescente. Rima hians, nymphis nudis. Anus impressus, oblongus, clausus.*"

[Margin subserrated: exterior toothed, not red. Internal colour white, sometimes turning russet in the bottom. Posterior dorsal margin gaping, nymph nude. Lunule impressed, oblong, closed.]

TYPE MATERIAL (Table 1)

Authors appear to have restricted the search of a type specimen to Linné's personal collection, now in the Linnean Society in London, and have neglegted to search in the Museum Ulricae collection, now in Uppsala. A contributing factor

TABLE 1. — Characters of *V. rugosum* and *V. subrugosum* compared with Linné's description of *C. flavum*.

Linné's description of *C. flavum*	*V. rugosum* = *V. pectiniforme*	*V. subrugosum* = *V. flavum*
Testa subovata sulcata; sulci crenati nodulis in latere posteriore; margo non rubens (1758). Shell subovoid ribbed; ribs with nodular ridges anteriorly; margin [internal ?] not red.	**Fits**	**Fits**
Margines subserrati; exteriore [emended in *posteriore* as in 1767] *dentato, non rubro* (1764). [Posterior?] margins subserrated; anterior dentate, not red.	**Fits**	**Fits**
Rima hians (1764). [Posterior] slit gaping.	**Can fit**: slit below ligament variable; shell slightly gaping.	**Can fit**: slit below ligament variable; shell slightly gaping.
Latere anteriore scabro (1758). Posterior side rough.	**Could fit**: but "scaly" (= *squamoso* used by Lamarck) would have fitted better.	**Fits better**: ornaments often degenerate, but the PQ remains always "rough".
Anus impressus, oblongus, clausus (1764). Lunule impressed, oblong, closed.	**Could fit**: but lunule generally narrow to non existent, never markedly impressed.	**Fits perfectly**: lunule wider, oblong, more or less deeply hollowed.
Testa flava (1758). Shell yellow.	**Does not fit**: very exceptionally yellowish stains. Lamarck writes "*albida immaculata*" (immaculate white).	**Fits**: often nicely lemon-yellow coloured.
Latere anteriore alba (1758). Posterior side white.	**Does not fit with above**: posterior same colour as the rest.	**Fits**: all shells, even the coloured ones, white posteriorly.
Color intus albus, fundo interdum rufescente (1764). Internal colour white, sometimes turning russet in the bottom.	**Does not fit**: interior always entirely white.	**Fits**: interior almost always more or less partially coloured mainly in the bottom.

(see Dodge 1952: 16, 17) is that the specimens of this collection were never labelled by Linné, identification and labelling being made by Swartz, after 1789. However Linné (1758: 680) states that *C. flavum* is in MLU [Museum Louisae Ulricae], which is confirmed by the published description of that collection (1764: 490). So, it is extremely probable that no specimen ever existed in Linné's personal collection (Dodge 1952: 62) and that, if any specimen still remains, it is likely to be searched in the Ulricae collection. There are two specimens labelled *C. flavum* in that collection. But the presence of this label, not placed by Linné, is not sufficient for these specimens to be granted the qualification of types. It is necessary they fit Linné's description. It is why an "exegesis" of the descriptive data left by Linné has been considered as necessary. Table 1 compares these data with the characters of *C. rugosum* and those of *C. subrugosum* Sowerby, 1838. This comparison shows that at least three characters of *C. flavum* are incompatible with *C. rugosum*, but are shared by *C. subrugosum*. Additionally, one of the two specimens labelled *C. flavum* in Uppsala fits the descriptions perfectly and must be considered as a type with certitude. [It is not the case of the other which is a small specimen of *Vasticardium*

assimile (Reeve, 1845)]. The condition of the first specimen thus conforms to that recommended by Dodge (1952: 17):

"If a given description unequivocally and exclusively agrees with a specimen in the collection now in Upsala, it can be safely identified as the species described. If, further, this description in the Museum Ulricae refers specifically to a listing in the tenth edition of the 'Systema', we can be sure that the specimen is, in fact, the type of the 'Systema' species."

LECTOTYPE DESIGNATION

The first specimen above cited (Fig. 1A) is here selected as lectotype of *Cardium flavum*. It is kept in the Uppsala University Zoological Museum, Linnésamlingen nr. 411; no locality; dimensions: 55.0 × 47.2 × 36.0 mm, with thirty-two ribs.

REMARK

In Linné's personal collection, in London, a shell labelled *C. flavum,* is referenced under No. 68 in the Linnean Society list. A manuscript note (by Hanley?) says: "Hanley has isolated one complete, unmarked specimen [Linné used to 'mark' his specimens inside with a number]. He says however that Linnaeus did not himself possess the type". This shell is a specimen of *V. rugosum*, in rather fair state of preservation, dimensions 43.6 × 37.5 × 29.7 mm, with thirty ribs, uniform, washed out, beige external colour, internal colour whitish, with a practically non-existent lunule. It does not fit Linné's descriptions at all and certainly belongs to the numerous specimens added to the collection by post-Linnean examiners (see Dodge 1952: 8).

Cardium rugosum Lamarck, 1819

LAMARCK'S ORIGINAL DESCRIPTION

"23. Bucarde ridé. *Cardium rugosum.*[Ridged cockle]. *C. testa ovato-rotundata, inaequilatera, albida, immaculata; costis rotundatis, transverse rugosis: lateris antici squamoso scabris.*"
[Shell roundly-ovate, inequilateral, white, immaculate; ribs rotund, transversally ridged: posterior side roughly scaly].
"*An Cardium flavum.* Lin.?
Schroet. einl. in Conch. 2. t. 7. f. 11. a. b.
Card. magnum. Chemn. Conch. 6. p. 196. t. 19. f. 191.
Seba, Mus. 3. t. 86. f. 7.
Encyclop. pl. 297. f. 2.
[2] *Var. testa minore, subaequilatera.*
Habite l'Océan Indien. Mon cabinet. Espèce tranchée, très-distincte. La coquille est blanche, quelquefois teintée de fauve ou d'un roux ferrugineux. Ses côtes, au nombre de 28 à 32, sont arrondies, un peu arquées, sillonnées et comme ridées transversalement. Largeur 69 millimètres. Le *Cardium regulare,* Brug. Dict. n°. 24, n'est qu'une variété de cette espèce. Elle n'est pas réellement équilatérale ; on la dit d'Amérique."

TYPE MATERIAL

Lamarck refers to four illustrations in the literature, and to shells from his own collection:
1. Schröter (1784: pl. 7, fig. 11a, b). This shell, from Nicobar, later identified by Schröter himself (1786: 43) as *C. flavum* is in ZMUC (here Fig. 2A); dimensions 60.6 × 46.4 × 46.7 mm, with twenty-six ribs. It is identifiable as *V. flavum subrugosum.*
2. *Cardium magnum* – Chemnitz (1782: 196, pl. 19, fig. 191). This shell (Fig. 3D) is also in ZMUC; dimensions 71.1 × 60.4 × 41.5 mm, with thirty-two ribs. It is a weakly coloured form of *V. angulatum* (Lamarck) (see Vidal 1991).
3. Seba (1758: pl. 86, fig. 7). Its whereabouts are unknown and the identification is doubtful.
4. Encyclopédie méthodique, Lamarck (1816: pl. 297, fig. 2). The illustrated shell could be in Geneva (see below).
5. Lamarck's collection, three lots of *C. rugosum*:
– two shells in MNHN, about 35 mm high, hand labelled by Lamarck as "*individus jeunes*" (young individuals);
– one lot in MHNG (1085-55) of two large shells; one (Fig. 4C) possibly the 69 mm specimen cited by Lamarck, and one 74.5 × 72 × 51 mm, possibly figured with a reduced scale in Lamarck (1816: pl. 297, fig. 2).
– one lot in MHNG (1085-56) of three specimens, H = respectively 48, 39, 20 mm, corresponds to "[2] *Var. testa minore, subaequilatera".*

LECTOTYPE DESIGNATION

Cardium rugosum is based on ten **syntypes**, belonging to three different species and it is necessary to select a **lectotype**. I select as lectotype of *Cardium rugosum* Lamarck the shell in Geneva cited by Lamarck, in the lot 1085-55: H = 73, L = 70, W = 50 mm (Fig. 4C).

VALID SPECIES AND SUBSPECIES OF THE *Vasticardium flavum* GROUP

Vasticardium flavum s. l. (Linné, 1758)

Cardium flavum Linné, 1758: 680. – Schröter 1784: pl. 7, fig. 11a, b; 1786: 43. – Bruguière 1789: 232. – Spengler 1799: 22, pl. 1, fig. 2a, b. – Römer 1869: 56 [description only, not figures]. – Hidalgo 1903: 335.

Cardium fucatum Spengler, 1799: 30.

Cardium subrugosum Sowerby, 1838: fig. 34; 1840: fig. 71; 1841a: 108.

Cardium gratiosum Deshayes, 1854: 331.

Cardium tumidum Deshayes, 1854: 331.

Cardium dupuchense Reeve, 1845: Sp. 67.

Regozara flava – Habe & Kosuge 1966a: 154, pl. 59, fig. 7.

Vasticardium (*Regozara*) *flavum* – Habe 1967: pl. 55, fig. 3.

Trachycardium flavum – Springsteen & Leobrera 1986: fig. 12.

Not *Cardium flavum* – Born 1780: 47, fig. 8. [= *C. crassum* Gmelin, 1791]. – Chemnitz 1782: 86, pl. 17, fig. 178 [= *C. muricatum* Linné, 1758]. – Römer 1869: the figures [pl. 5, fig. 10 = *C. pectiniforme* Born; pl. 7, figs 7, 8 = *C. angulatum* Lamarck, 1819].

Not *Cardium* (*Trachycardium*) *flavum* – Abrard 1942: 25, pl. 3, fig. 1 [= *Trachycardium luteomarginatum* Voskuil *et* Onverwagt, 1991].

Not *Acrosterigma flava* – Coleman 1975: 15, fig. 11 [= *C. vertebratum* Jonas, 1844].

Not *Trachycardium flavum* – Sharabati 1984: pl. 47, fig. 3a, c [= *Trachycardium luteomarginatum* Voskuil *et* Onverwagt, 1991]. – Oliver 1992: 125, pl. 23, fig. 6a, b [= *C. pectiniforme* Born, 1780].

DISTRIBUTION AND SUBSPECIES. — *V. flavum* has a narrower distribution in the tropical zone than *V. pectiniforme*. In the Indian Ocean it seems to be limited to the north-east part. In the Pacific it ranges to western Carolines and the Solomons, but is absent south-east of these islands.
V. flavum is rather constant in dimensions, shape, characters of lunule and hinge. Three subspecies are recognized based on differences in colour, number of ribs and above all rib morphology: *flavum s.s.*, *subrugosum* and *dupuchense*.

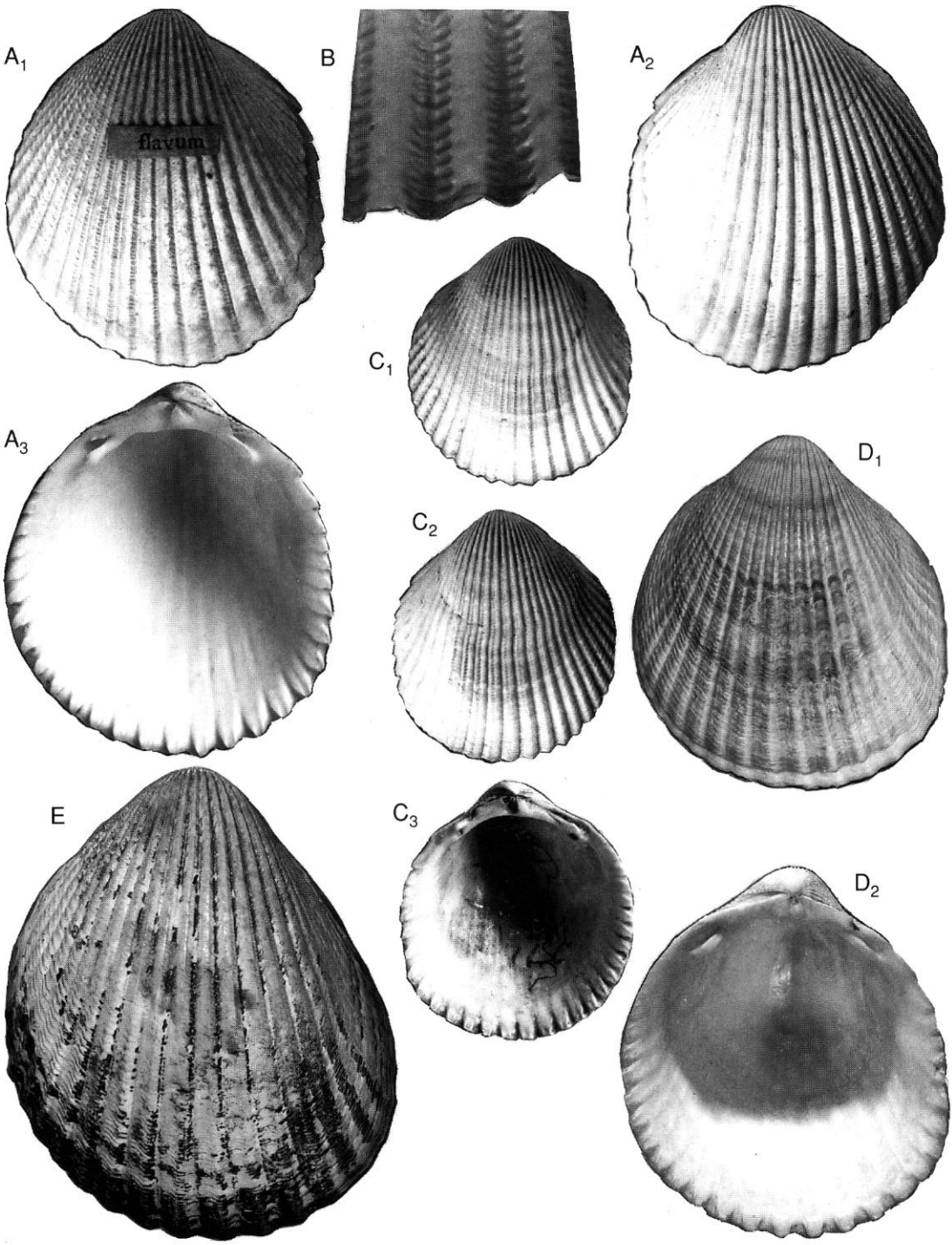
DIAGNOSIS
Shell generally 40 to 60 mm high when adult (maximum observed = 72.4 mm); average L/H = 0.90 (range 0.80-0.96); average W/L = 0.75 (range 0.66-0.84). Lunule variable, but generally well developed, mainly in the right valve, oblong and hollowed, sometimes very deeply. Shell covered by a uniformly light brown thin periostracum without (or very exceptionally with) black spots, covering all shell, thicker in MPQ than in other quarters. External shell colour, without periostracum, is entirely white to partially yellow to purple, continuous and not in shape of irregular, discontinuous, more or less concentric splashes. Posterior zone AQ almost always entirely white. Interior partially to entirely yellow to dark purple, rarely entirely white. Rib number variable according to subspecies, range 22-34.

Adult rib morphology
PQ. Ribs become lower, progressively less ornamented, and generally divided into two parts often becoming very flat, smoothed and hardly identifiable. Sometimes anterior half of rib lowers more than posterior half which can remain relatively high and keep more or less its ornaments, the surface remaining always "rough".
Other parts of shell. MPQ, MAQ, AQ: profile and ornamentation of ribs vary according to subspecies (see details in each subspecies description). Schematically: ribs high, subrounded to subtriangular and well ornamented in *subrugosum* and *dupuchense* subspecies; ribs low, flattened, ornaments disappearing in nominal subspecies.

Vasticardium flavum flavum (Linné, 1758) (Figs 1, 4A)

Cardium flavum Linné, 1758: 680, No. 71.
Cardium fucatum Spengler, 1799: 30.
Cardium gratiosum Deshayes, 1854: 331.
Cardium tumidum Deshayes, 1854: 331.

TYPES SPECIES. — *Cardium flavum*: lectotype here selected, Uppsala University Zoological Museum, Linnésamlingen nr. 411 (see above).
Cardium fucatum: holotype in ZMUC, a shell labelled "Guinea" (= probably New Guinea), 38.4 × 33.7 × 27.2 mm, 32 ribs (Fig. 1C).


A1
flavum
B
A2
C1
A3
D1
C2
E
C3
D2

Cardium gratiosum: three syntypes in BMNH from Moluccas, not catalogued: 66.5 × 55.8 × 50.0 mm, with 30 ribs; 64.7 × 52.0 × 40.6 mm, with 32 ribs; 55.0 × 45.6 × 37.3 mm, with 29 ribs (Fig.1D).
Cardium tumidum: two syntypes in BMNH from Moluccas, not catalogued, 72.4 × 58.0 × 52.0 mm, with 28 ribs (Fig. 1E); 65.0 × 57.5 × 43.5 mm, with 30 ribs (Fig. 4A).

MATERIAL EXAMINED. — The type material above listed. Other lots:
W Carolines. Palau-Yap group, 6 (USNM), 1 (BISHOP), 5 (ANSP).
E Indonesia. Moluccas, 2 (BMNH), 3 (IRSNB), 7 (ZMA), 9 (USNM). — Irian Jaya, 3 (LACM), 1 (MNHN), 1 (ZMA), 10 (ANSP).
NE and E Papua-New Guinea. 1 (MNHN), 2 (IRSNB), 4 (ZMA), 3 (AMS), 1 (USNM).
S Papua-New Guinea. Samarai, 1 (AMS). — Torres Strait, 1 (USNM).
Solomons. 1 (BMNH), 1 (AMS), 1 (LACM), 1 (USNM), 2 (ANSP).

DISTRIBUTION. — Eastern Indonesia (Moluccas and Irian Jaya), the Carolines, Papua-New Guinea and the Solomons and western Carolines.

DIAGNOSIS
Largest subspecies, reaching more than 70 mm in height (maximum 72.4, a syntype of *C. tumidum*). Under periostracum, colour partly or totally yellow to purple, except for posterior part (PQ and part of MPQ) which is more or less white. Interior almost always brownish to purple stained by zones, mainly in umbonal cavity. Mean rib number 31.0, range 27-34.

Adult rib morphology
PQ. Sculpture quickly degenerates distally from umbo, and often becomes virtually smooth, ribs being often represented only by cicatricial slits.
MPQ. Ribs very low, flatly rounded, much wider than interstices, firstly symmetrical but becoming onwards more and more asymmetrically and obtusely triangular; no traces of basal constrictions; single-ridged, then often becoming entirely smooth distally in large shells.

FIG. 1. — **A_{1-3}**, *Cardium flavum* Linné, lectotype here selected; L = 47.2 mm. **B**, *Vasticardium flavum flavum*, from Papua-New Guinea, MNHN. Flattened low ribs with biridged ornamentation in medial part; scale: × 3.6. **C_{1-3}**, *Cardium fucatum* Spengler, holotype; L = 33.7 mm. **D_{1-2}**, *Cardium gratiosum* Deshayes, syntype No. 3; L = 40.6 mm. **E**, *Cardium tumidum* Deshayes, syntype No. 1; L = 58 mm.

MAQ. Ribs low, becoming flat or asymmetrically triangular, with anterior side shorter and steeper; no trace of basal constrictions. Rarely irregularly top-ridged, generally double-ridged to single-ridged or entirely smooth.
AQ. Ribs low becoming flat or obtusely asymmetrically triangular; no basal constrictions; always top-ridged or full-ridged, more or less regularly (perfect regularity of ridging in this quarter, which characterizes other subspecies, disappears in many specimens).

REMARKS
This nominal subspecies of *V. flavum* differs from the others by its smoother ribs, and often more vivid colours, with more purple. Characters of colour and ribbing allow separation of this subspecies from the two others but may vary progressively and independently. Intermediate specimens of uncertain subspecific status are rare.

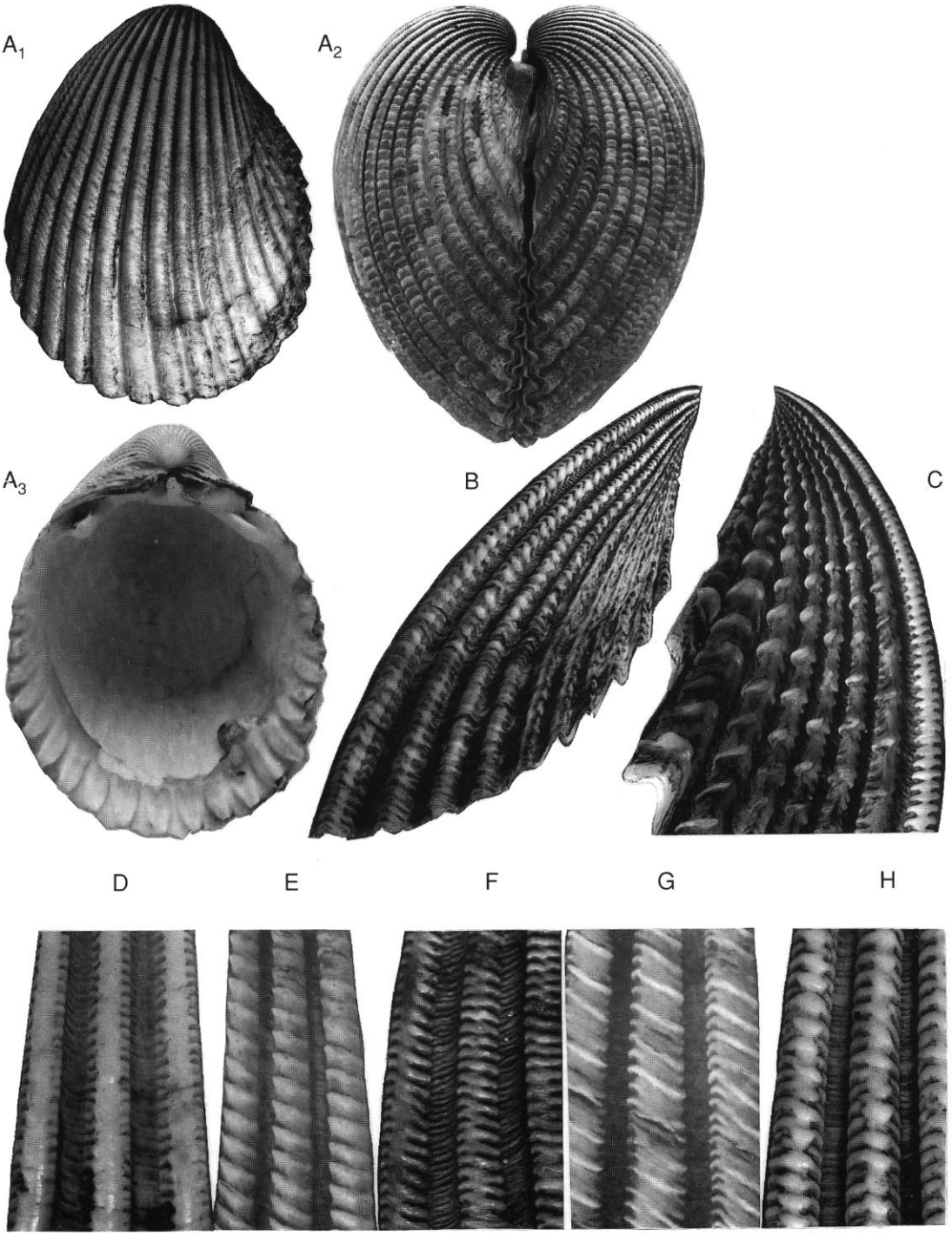
Vasticardium flavum subrugosum
(Sowerby, 1838)
(Figs 2A, B, D, E, H, 3B, C)

Cardium subrugosum Sowerby, 1838: fig. 34; 1840: fig. 71; 1841a: 108.

Not *C. subrugosum* – Abrard 1942: 25, pl. 2, fig. 28 [= *V. pectiniforme*]. – Reeve 1845: Sp. 55. – Lamy 1927: 519 and 1941: 565 [= *V. luteomarginatum* (Voskuil *et* Onverwagt, 1991)].

TYPES SPECIES. — Sowerby's figured specimen (1840a: fig. 71), from Ceylon, cannot be traced in BMNH. Neotype here selected, a shell from Phuket, in MNHN (Fig. 3C); dimensions: 48.7, × 43.5 × 33.7 mm; rib number: 29.

MATERIAL EXAMINED. — The following lots:
Sri Lanka. 1 (NHMW), 2 (IRSNB), 1 (AMS).
E India. Andaman Island, 1 (NMW), 1 (LACM). — Nicobar Island, 1 (ZMUC: 2 Schrîter's shells), 1 (NHMW). — Riam, 1 (USNM).
Thailand. Phuket, 2 (MNHN). — Gulf of Siam, 4 (USNM), 2 (ANSP).
N W Malaysia. 2 (AMS).
Singapore. 2 (MNHN), 1 (BMNH), 1 (AMS), 2 (USNM), 4 (LACM), 2 (ANSP).
Malaysia. E coast, 1 (AMS), 2 (USNM). — N Borneo, 1 (BMNH), 1 (ZMA), 2 (AMS), 4 (USNM), 2 (ANSP).
W Indonesia. Sumatra, 1 (MNHN), 1 (USNM). — Java, 4 (MNHN), 1 (ZMA), 1 (AMS), 1 (LACM). —


A1
A2
A3
B
C
D
E
F
G
H

Bali, 2 (MNHN), 3 (AMS), 1 (USNM), 1 (ANSP). — Flores, 1 (MNHN), 1 (ZMA). — Alor, 1 (MNHN). — Borneo, Balikpapan, 1 (AMS). — Sulawesi, 3 (MNHN), 1 (AMS), 1 (USNM), 1 (ANSP).
Philippines. 5 (MNHN), 1 (BMNH), 4 (AMS), 19 (LACM), 3 (BISHOP), 42 (USNM), 15 (ANSP).
Viet Nam. 4 (MNHN), 1 (LACM).
S China. 2 (MNHN), 2 (BMNH), 1 (IRSNB).
S Japan (Ryukyu). Okinawa Island, 1 (LACM), 3 (BISHOP), 3 (USNM). — Amami Island, 1 (LACM).

DISTRIBUTION. — Sri lanka to the Philippines, South China and Ryukyu-Amami Islands. Replaced southeastwards in the Pacific by *V. flavum flavum*.

DIAGNOSIS

Shell of medium size reaching a maximum of about 50 mm high, generally slightly asymmetrical, rarely appreciably elongated. Under periostracum, colour from entirely white to pure light lemon-yellow, except for PQ which is always white. Interior rarely entirely white, almost always partially (very rarely totally) yellow-orange to dark purple stained. Sometimes this purple colour seems to pass through the shell and is externally locally discernible on white zones, in PQ and MPQ. Internal margin always white. Mean rib number 31.0, range 28-34.

Adult rib morphology

PQ. Ribs, although dividing into two parts and losing their relief, are still well discernible, sometimes keeping the anterior marginal small bent scales and top scales more or less reduced, leaving surface always "rough" (Fig. 2B).

MPQ and MAQ. Ribs variable in profile but always relatively high, sometimes rounded or symmetrically roundly triangular, but more often asymmetrically (anterior side rounded, posterior side becoming flat and steeper); basal constrictions present, or replaced by two thin basal stripes (Figs 2B, 3B). Ornamentation variable. ribs crush-ridged, rather rarely full-ridged, often double-ridged with a more or less smooth, widened, central zone formed by shortening of anterior ridging, posteriorly remaining normally developed.

AQ. Ribs high, generally rounded, sometimes a little squared by top flattening; almost always symmetrical with marked basal constrictions (Figs 2E, 3B). Always full-ridged, with wide conical ridges very regularly set. Ridging in AQ is in continuity with MAQ.

REMARKS

V. flavum subrugosum differs from the nominal sub-species by its generally lighter colour, and, more important, by its more markedly ornamented and often crush-ridged ribs. It differs from *V. flavum dupuchense* mainly by a higher rib number and a less markedly ornamented PQ.

The name *subrugosum* has been much less used than *rugosum* or *flavum*. The reason is certainly because *V. flavum subrugosum* may resemble *V. pectiniforme*, particularly when the shells are covered by a periostracum. Additionally *V. flavum subrugosum* is almost everywhere sympatric with the other. Numerous authors (*e.g.* Wilson & stevenson 1977: 86) do not mention its name and probably do not recognize its existence in the Indo-Pacific.

FIG 2. — **A_{1-3}**, *Vasticardium flavum subrugosum*, from Nicobar (India), historical "Schröter's shell", cited as *C. flavum* Linné. ZMUC, Spengler collection; **A_2**, anterior side; L = 46.4 mm. **B**, *Vasticardium flavum subrugosum*, from Cebu, Philippines, MNHN, detail of the PQ and four ribs of the MPQ; scale: × 2.2. **C**, *Vasticardium pectiniforme*, from the Red Sea, MNHN: detail of juvenile PQ; scale: × 4.8. **D**, *Vasticardium flavum subrugosum*, from Cebu, Philippines, MNHN: double-ridged rib ornamentation; scale: × 3.4. **E**, *Vasticardium flavum subrugosum*, from Cebu, Philippines: full-ridged rib ornamentation in the MAQ, MNHN; scale: × 3.6 (same specimen as in figure 15). **F**, *Vasticardium pectiniforme*, from the Red Sea: full-ridged rib ornamentation in MPQ, MNHN; scale: × 3.5 (same specimen as in figure 3A). **G**, *Vasticardium pectiniforme* from the Red Sea, MNHN: irregularly full-ridged rib ornamentation in the MAQ; scale: × 3.7. **H**, *Vasticardium flavum subrugosum* from Cebu, Philippines, MNHN (same specimen as in figure 3B): crush-ridged rib ornamentation; scale: × 4.0.

Vasticardium flavum dupuchense
(Reeve, 1845)
(Fig. 5A)

Cardium dupuchense Reeve, 1845: Sp. 67.

TYPES SPECIES. — Three syntypes in BMNH No. 1971-25, Cuming's collection, from Dupuch Island, Torres Strait (locality emended to Depuch Island, Western Australia, by Wilson & Stevenson 1977: 86). One of them, 50.2 × 48.8 × 40.0 mm, with 27 ribs, fits Reeve's figure 67 and is designated on the labels as lectotype, probably by Wilson & Stevenson, but they never published this selection. I confirm here the selection of this specimen as lecto-

type. Paralectotypes, 55.3 × 47.0 × 39.5 mm, with 23 ribs and 47.2 × 41.2 × 32.3 mm, with 25 ribs.

MATERIAL EXAMINED. — The type material. Other lots: **Western Australia.** Dampier, 1 (MNHN), 1 (WAM). — Port Hedland, 1 (MNHN), 1 (WAM). — Exmouth Gulf, 1 (MNHN), 1 (WAM); Montebello Island, 1 (WAM). — Faise Cap Creek, 1 (ANSP).

DISTRIBUTION. — "Northern Western Australia, from Broome South to Point Cloates. Fossil records at Shark Bay", according to Wilson & Stevenson (1977: 87).

DIAGNOSIS

Shell of medium size (maximum height 54.5 mm, Wilson & Stevenson 1977: 86), not elongated, almost always asymmetrical, with expanded posterior part. Under periostracum (which sometimes bears some black spots), shell exteriorly white to light yellow; sometimes light purple in MPQ and PQ. Interior vividly dark purple in large concentrical zones in posterior three quarters, mainly in adult parts. Internal margin white. Mean rib number 25, range 22-28.

Adult rib morphology

PQ. Anterior part of ribs lowers and more or less degenerates; posterior part remains generally high and still bears more or less reduced scales.

MPQ. Ribs high, rounded but with a tendency to become slightly triangular. Basal constrictions more or less discernible. Generally full-ridged to slightly crush-ridged.

Anterior half. Ribs high, rounded; basal constrictions present. Regularly full-ridged with wide ridges, more or less conical.

REMARK

V. flavum dupuchense resemble *V. pectiniforme* in having black spots on the periostracum, high ribs and scales well developed in PQ. It is even more similar to many specimens of *V. flavum* in its colour and above all in the regular rib ridging in the anterior part. It differs from the other subspecies of *V. flavum* and also from *V. pectiniforme* by its lower rib number. Although it is treated here as a subspecies of *V. flavum*, its taxonomic status is questionable. Because it does not co-occur with *V. pectiniforme*, it could conceivably also be considered as a form of that species.

Vasticardium pectiniforme (Born,1780)
(Figs 2C, F, G, 3A, 4B-F)

Cardium pectiniforme Born, 1780: 49, pl. 3, fig. 10 (*non* fig. 9).

Cardium regulare Bruguière, 1789: 227.

Cardium rugosum Lamarck, 1819: 10.

Trachycardium peregrinum Jousseaume, 1888: 212.

Vasticardium nigropunctatum Habe *et* Kosuge, 1966a: 324, pl. 29, fig. 16; 1966b: 154, pl. 59, fig. 9.

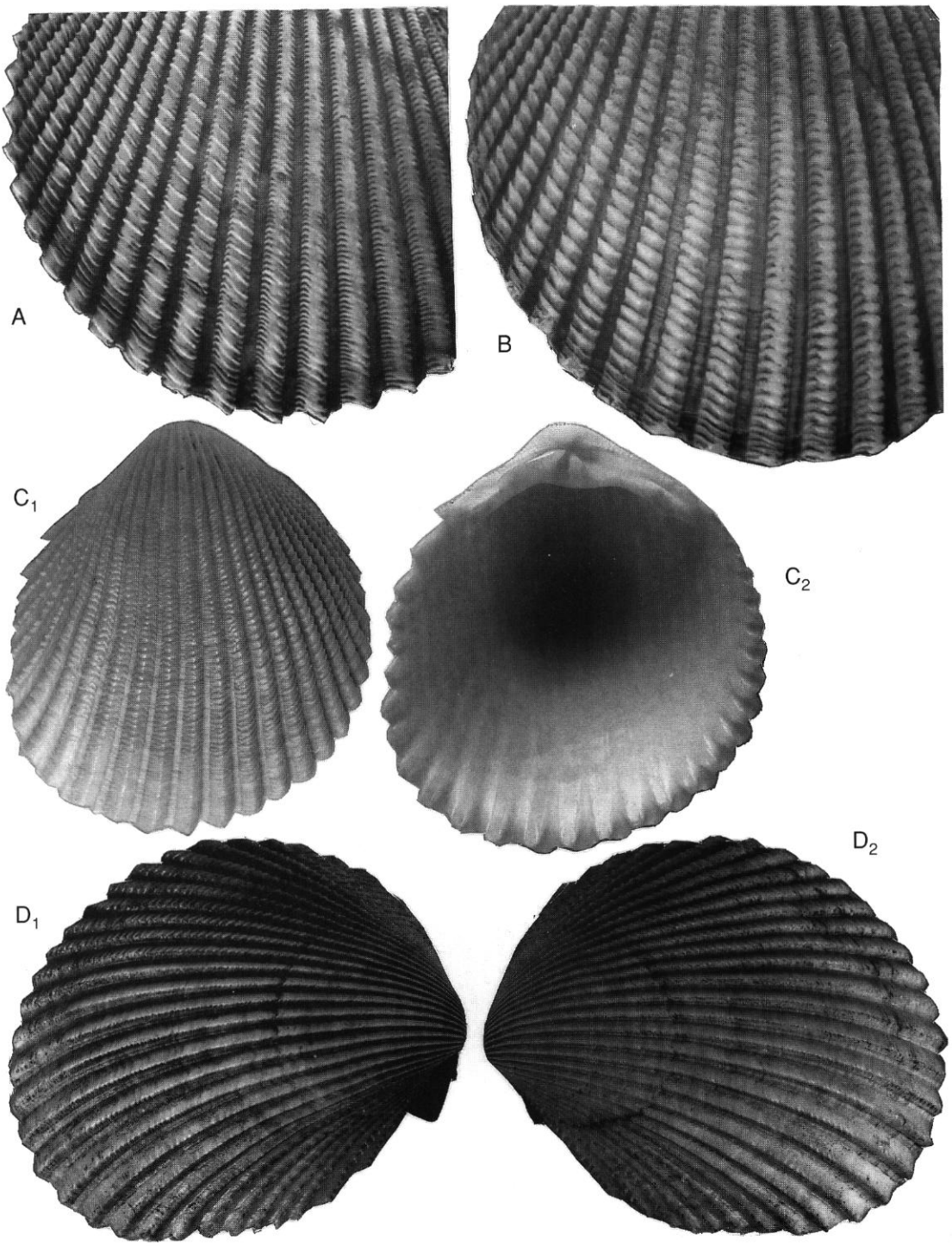
Not *C. rugosum* Reeve, 1845: Species 68 [= *V. luteo-marginatum* (Voskuil *et* Onverwagt, 1991)].

Not *C. rugosum* var. *gortanii* Nardini, 1937 [= *Vasticardium gortanii* (Nardini, 1937)].

TYPES SPECIES. — *Cardium pectiniforme*: two syntypes in NHMW, Ref. G23-875a, no locality. Dimensions: 30.7 × 29.2 × 19.4 mm, with 30 ribs and 26.3 × 25.4 × 15.2 mm, with 31 ribs, (figured by Born, pl. 3, fig. 10; and this paper Fig. 4B), here selected as lectotype.
Cardium regulare: no type located, no reference cited. Bruguière's detailed description fits the characters of *V. pectiniforme*. The type locality was said to be "American Atlantic", but this is probably a mistake.
Cardium rugosum: lectotype MHNG 1085-55 (see above).
Trachycardium peregrinum: ten syntypes (six conjoined and four odd valves) in MNHN, from Aden and several Red Sea localities. Largest specimen is 55.1 × 47.2 × 37.1 mm, with 30 ribs (Fig. 4D).
Vasticardium nigropunctatum: holotype 45.4 × 39.2 × 32.0 mm, and one paratype 36.6 × 31.3 × 23.8 mm in NSMT from Amami Island (South Japan) (Habe & Kosuge 1966b: 154, pl. 59, fig. 9; material not seen).

MATERIAL EXAMINED. — The syntypes of *C. rugosum*, *C. pectiniforme*, *C. peregrinum*. Other lots:
S and E Africa. Natal, 1 (MNHN), 1 (BMNH), 1 (USNM). — Mozambique, 1 (MNHN), 2 (LACM), 1 (ANSP). — Tanzania, 2 (BMNH), 1 (ANSP), 4 (USNM). — Zanzibar, 1 (MNHN), 3 (BMNH), 2 (LACM), 4 (ANSP), 2 (USNM). — Kenya, 9 (MNHN), 4 (BMNH), 1 (ANSP). — E Somalia, 1 (MNHN), 1 (ANSP).
W Indian Ocean. Madagascar, 54 (MNHN), 2 (BMNH), 5 (ANSP). — Mauritius, 8 (MNHN), 2

FIG. 3. — **A**, *Vasticardium pectiniforme*, from the Red Sea, MNHN; scale: × 1.8. **B**, *Vasticardium flavum subrugosum*, from Cebu, Philippines, MNHN; scale: × 2.5. **C_{1-2}**, *Cardium subrugosum* Sowerby, neotype here selected; L = 43.5 mm. **D_{1-2}**, *Vasticardium angulatum* Lamarck, a specimen from Tranquebar (India), cited and figured by Chemnitz as *C. magnum* Linné, ZMUC, Spengler collection; L = 60.4 mm.

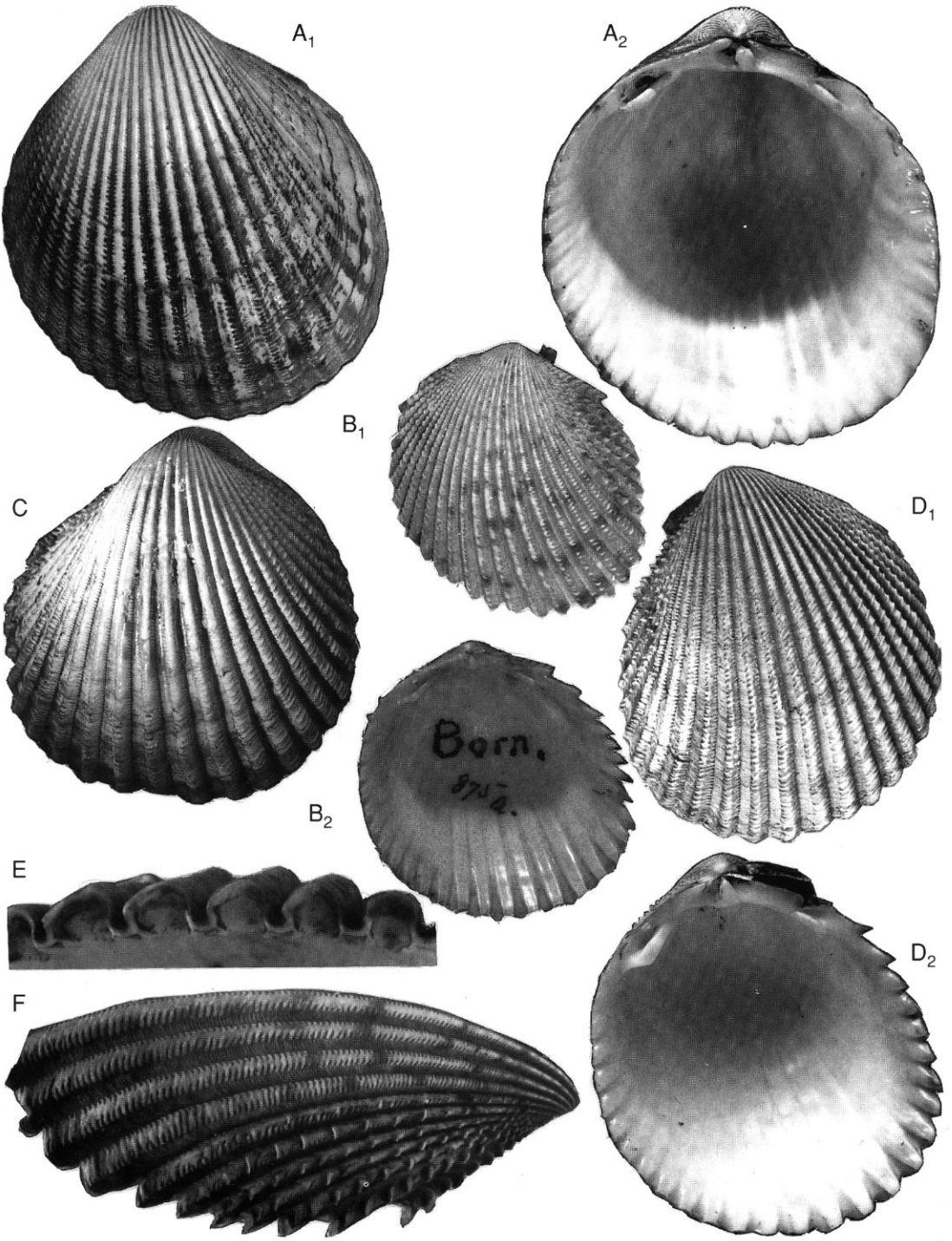

A
B
C1
C2
D2
D1

(MHNG), 2 (BMNH), 2 (IRSNB), 1 (LACM), 1 (ANSP), 1 (USNM). — Rodrigues, 1 (BMNH). — Comores, 3 (MNHN). — Seychelles, 4 (MNHN), 2 (BMNH), 1 (LACM), 2 (ANSP), 1 (USNM).
Gulf of Aden. N Somalia, 1 (MNHN). — Yemen, 3 (MNHN), 2 (USNM). — Djibouti, 5 (MNHN).
Red Sea. N Yemen, 2 (MNHN). — Ethyopia, Dalhak arch., 1 (MNHN). — Saudi Arabia, 1 (MNHN), 1 (USNM). — Egypt, fossils 2 (MNHN). — Israel, Aqaba, 3 (MNHN).
N Indian Ocean. Pakistan, Karachi, 1 (BMNH). — Maldives, 1 (BMNH). — India, Manaar, 1 (BMNH), 2 (ANSP); Riam, 1(USNM); Andaman, 2 (BMNH). — Sri Lanka, 2 (BMNH), 1 (IRSNB), 1 (ANSP). — Burma, 1(BMNH), 2 (ANSP).
W Thailand. Phuket, 4 (MNHN), 3 (BMNH), 1 (USNM), 1 (LACM), 1 (ANSP); Butan group, 1 (USNM).
Malaysia. NW, 1 (BMNH); N Borneo, 1 (USNM).
Singapore. 1 (MNHN), 1 (BMNH), 1 (USNM), 1 (USNM), 1 (ANSP).
Gulf of Siam. 2 (USNM).
Indonesia. Sumatra, 1 (USNM). — Java, 1 (MNHN), 2 (IRSNB), 5 (USNM); Bali, 2 (MNHN), 1 (LACM). — Lombok, 2 (LACM). — E Borneo, 1 (AMS). — Sulawesi, 1 (MNHN), 1 (LACM), 1 (USNM). — Moluccas, 1 (ZMA), 1 (LACM), 1 (USNM). — Irian Jaya, 6 (LACM), 1 (USNM), 3 (ANSP). — Tanimbar, 2 (USNM).
Philippines. 8 (MNHN), 30 (USNM), 10 (LACM), 3 (ANSP).
Asia. Viet Nam, 5 (MNHN), 3 (LACM). — S China, 2(MNHN). — Taiwan, 1 (ANSP). — S Japan, Okinawa Island, 1 (MNHN), 6 (LACM), 3 (BISHOP), 6 (USNM), 2 (ANSP); Amami Island 1 (BMNH), 1 (ANSP), 1 (LACM).
Pacific. Papua-New Guinea, 1 (MNHN), 3 (IRSNB), 1 (WAM), 1 (LACM), 1 (ANSP). — Australia, Torres Strait, 1 (BMNH), 2 (LACM); Northern Territory, Port Essington, 1 (USNM); N Queensland, 6 (MNHN), 3 (QM), 2 (LACM), 1 (USNM), 1 (ANSP). — New Caledonia, 50 (MNHN), 2 (ANSP), 1 (USNM). — Vanuatu, Efate Island, 3 (MNHN); Santos Island, 3 (USNM). — Fiji, 1 (LACM). — Solomons, 1 (BMNH), 1 (ANSP), 1 (USNM). — W Carolines, Palau group, 2 (USNM), 1 (BISHOP), 3 (ANSP).

DISTRIBUTION AND ECOLOGY. — *Vasticardium pectiniforme* is generally abundant through most of all the tropical Indian Ocean, Red Sea, and western Pacific. Its eastern limit seems to be the Ryukyus (South Japan), the western Carolines, Solomons and Fiji.
It seems to be rare in the Persian Gulf (Melvill & Standen 1906: 837; Smythe 1982: 99), and on the southern coast of Oman. It seems to be absent from the western coast of Australia (Western Australia and Northern Territory).
V. pectiniforme prefers reef environment in very shallow water: it is abundant intertidally but is rarely collected by dredging. In New Caledonia, not a single specimen or valve has been found at any of the 1200 stations of the dredging program in the lagoon, 7 to 100 m depth, yet it is abundant on all the beaches around the main island.

DIAGNOSIS
Shell of medium size, generally 40 to 60 mm high when adult. Largest specimen observed 76.0 × 65.3 × 40.7 mm (MNHN, Ballot collection 1887, no locality); largest record, a Pleistocene fossil from Port Sudan 86 × 68 mm, figured by Nardini (1937: pl. 17, fig. 1). Shell often symmetrical (except that anterodorsal margin is always more raised than posterior), sometimes more or less expanded posteriorly and asymmetrical with ribs curved backwards in projection, but very rarely markedly truncated in posterior margin. Rarely appreciably elongated: mean L/H = 0.92 (range 0.86-0.97). Moderately and rather variably depressed: mean W/L = 0.71 (range 0.63-0.84). Lunule variable in size but always small to very small, sometimes practically non existent; never markedly hollowed. Periostracum light brown, thin, uniform, often with small black spots more or less concentrically aligned (*nigropunctatum*), more abundant in MPQ. Shell uniformly white to beige, very rarely yellowish to light brown, generally light, lusterless, under periostracum. Occasionally, shell has some reddish spots (see for example Sowerby 1838: fig. 41). Interior almost always entirely white, very rarely slightly yellowish coloured around the lateral teeth, and exceptionally very slightly in the umbonal cavity. In Papua-New Guinea some forms can be partly slightly yellow, particularly in internal and external margins (but PQ is not white). Secondary anterior lateral tooth in right valve (tooth AIII) always regularly elongated and never crushed in its middle or

FIG. 4. — $\mathbf{A}_{1\text{-}2}$, *Cardium tumidum* Deshayes, syntype; L = 57.5 mm. $\mathbf{B}_{1\text{-}2}$, *Cardium pectiniforme* Born, lectotype here selected; L = 25.4 mm. **C**, *Cardium rugosum* Lamarck, lectotype here selected; L = 70.0 mm (reduced). $\mathbf{D}_{1\text{-}2}$, *Trachycardium peregrinum* Jousseaume, largest syntype; L = 47.2 mm. **E**, *Vasticardium pectiniforme*, from Mauritius, MNHN: detail of profile of ribs in median ventral margin; scale: × 3.2. **F**, *Vasticardium pectiniforme*, from the Red Sea, MNHN: detail of PQ and part of MPQ; scale: × 1.8.


A1
A2
B1
C
D1
Born.
B2
E
D2
F

divided into two teethlets. Mean number of ribs 30.6, range 26-35.

Adult rib morphology

PQ. No significant change from juvenile shells: ribs remain high, square-sided, well ornamented on top and flanks. Interstices wide (Fig. 4F).

MPQ. Change from PQ abrupt. Ribs generally rounded, more or less symmetrically, rarely roundly triangular, always basally constricted, generally full-ridged (Figs 2F, 3A, 4F) but sometimes double-ridged; rarely crush-ridged.

MAQ. Generally very irregularly full-ridged (Figs 2G, 3A) with many lateral ridges not reaching top zone; thus ridges on top zone less numerous, narrower and with wider, irregular spaces between them, sometimes forming a herringbone pattern. Below these "top-ridges", short remaining lateral ridges progressively disappear also, onwards, but can still be present in all the zone and in AQ.

AQ. Ribs well rounded, ornamented with full ridges; full ridges thin, relatively widely and regularly spaced.

REMARK

Differences between *V. pectiniforme* and *V. flavum*: the smooth and coloured *V. flavum flavum* is easily separated from the "rugose" and whitish *V. pectiniforme*. The other two subspecies of *V. flavum* can sometimes, at first glance and mainly when the periostracum is present, look very much like *V. pectiniforme*. Nevertheless they can be separated by the observation of four characters:

1. Lunule: the lunule in *V. flavum* is wider and deeper.

2. Colours: *V. pectiniforme* is almost always "colourless" outside and entirely white inside and very often bears black spots on the periostracum. These spots may rarely be present in *V. flavum* which is often partially vividly coloured, outside and inside.

3. PQ: in *V. pectiniforme* (Figs 2C, 4F) the ribs always remain high, square-sided and well ornamented in the adult as in the juvenile, when they degenerate in the adult part in two subspecies of *V. flavum* [subsp. *flavum* and subsp. *subrugosum* (Fig. 2B)].

4. The ornamentation of the ribs in the anterior half of the shell can also, and exclusively, separate the two species. The ribs of the anterior half of the shell in *pectiniforme* have irregular ornamentation: narrow and irregularly set full-ridges in AQ; in MAQ these ridges are irregular and are often combined with numerous small lateral ridges (Figs 2G, 3A). The ribs of the anterior half of the shell in *flavum* have regular ornamentation; the full-ridges are everywhere wide (wider than the grooves separating them), more numerous, very regularly set, often conical, with virtually no intermediate lateral ridgelets in MAQ (Figs 2E, 3B).

Vasticardium vertebratum (Jonas, 1844)
(Fig. 5C, E, F)

Cardium vertebratum Jonas, 1844: 33; 1846: 119, pl. 9, fig. 9a-c.

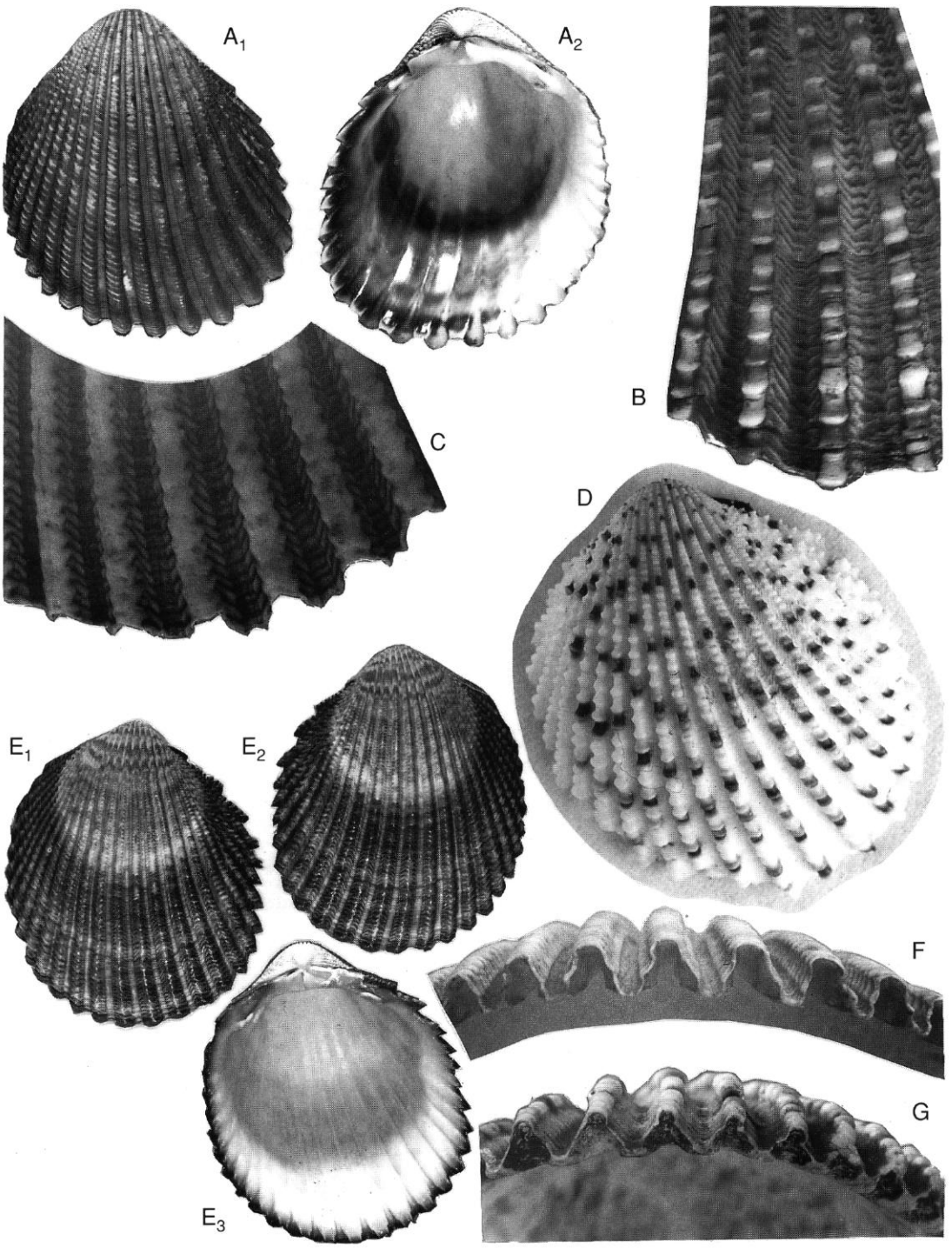
Cardium reeveanum Dunker, 1852: 54; 1858: 22, pl. 6, figs 6-8.

Regozara olivifer Iredale, 1936: 275, pl. 20, fig. 8.

TYPES SPECIES. — *Cardium vertebratum*: holotype, according to Jonas, a shell from West Australia, 63.5 × 46.6 × 38.1 mm, with 28 ribs, not traced.
Cardium reeveanum: holotype, according to Dunker, a shell deposited in Bremen, from New Holland [Australia], H = 2 inches [= 50.8 mm], with 28 ribs, not traced.
Regozara olivifer: holotype from Sydney Harbour in AMS C60606, 66 × 56 × 46 mm, with 28 ribs.

MATERIAL EXAMINED. — The holotype of *Regozara olivifer* and the following lots:
Australia. Western Australia, Swan River, 1 (BMNH); Admiral Bay, 1 (WAM). — Northern Territory, Port Darwin, 1 (BMNH); Port Essington, 4 (BMNH);

FIG. 5. — **A_{1-2}**, *Vasticardium flavum dupuchense*, from Dampier (W. A.), MNHN; L = 43.0 mm. **B**, *Vasticardium ornatum*, from Dampier Salt (W. A.): detail of rib morphology in median adult part, MNHN; scale: × 3.7 (shell artificially dark coloured). **C**, *Vasticardium vertebratum*, from Kurrimine Beach (Queensland), MNHN: detail of rib morphology in median adult part; scale: × 3.8. **D**, *Vasticardium ornatum*, from Dampier Salt (W. A.), MNHN; L = 28.4 mm (same specimen as B, G). **E_{1-3}**, *Vasticardium vertebratum*, from Tin Can Bay (Queensland), MNHN; L = 42.2 mm. **F**, *Vasticardium vertebratum*, from Kurrimine Beach (Queensland), MNHN: detail of profile of ribs in the median ventral margin; scale: × 3.8 (same specimen as C). **G**, *Vasticardium ornatum*, from Dampier Salt (W. A.), MNHN: detail of profile of ribs in the median ventral margin; scale: × 3.8 (same specimen as B).


A1
A2
B
C
D
E1
E2
E3
F
G

Cape Arnhem, 2 (USNM). — Queensland, Torres Straits, 1 (BMNH). — North Queensland, 6 (MNHN), 2 (BMNH), 6 (LACM). — Central Queensland, 3 (MNHN), 2 (BMNH), 2 (QM), 5 (LACM), 3 (USNM). — South Queensland, 5 (MNHN), 2 (QM). — New South Wales, 5 (AMS).
Singapore. 1 (AMS).
Viet Nam. 1 (MNHN).

DISTRIBUTION. — "Western, northern and eastern Australia; south to Geographe Bay in Western Australia and Sydney, New South Wales. The species is a Quaternary fossil in South Australia", according to Wilson & Stevenson (1977: 83).
My observations do not fully confirm this limited distribution, with five deviating records:
1. Melvill & Standen (1906: 837) cite *Cardium* (*Trachycardium*) *vertebratum* at Dubai, Persian Gulf. This material is not in NMW.
2. Bosch (1982: 171) cites and figures *Cardium reeveanum* from Salalah, southern coast of Oman. The figured shells resemble *V. pectiniforme*. It is no longer mentioned in Oliver, 1995.
3. Oliver (1992: 126, pl. 23, fig. 4a, b) figured a shell *Trachycardium vertebratum* in BMNH with no mentioned locality and records it from Aden, Port Sudan, Perim, Obock. The identification of the BMNH specimen (which I have examined) is good, but there is no material from Aden, Perim and Obock in Jousseaume's and Lavranos' collections (MNHN) that is attribuable to the present species, and the occurence of *V. vertebratum* in the Red Sea cannot be as large as indicated by Oliver.
4. Presence of a valve labelled from Nhatrang (Viet Nam) in MNHN, coll. Saurin.
5. A valve from Pulau Sudong (Singapore) in AMS, C310526.

DIAGNOSIS
Shell of medium size generally reaching 55-60 mm (largest specimen observed 98.2 × 79.5 × 67.1 mm in AMS from Broken Bay, near Sydney). Shape transversally ovoid, rarely symmetrical. Rather elongated for group: mean L/H = 0.83 (range 0.80-0.87); variably depressed: mean W/L = 0.84 (range 0.77-0.95). Lunule very narrow to practically non existent. Hinge typical of group, but in right valve secondary anterior lateral tooth (AIII) almost always depressed in its middle and divided into two more or less independent small teeth. Shell is of a characteristic superb orange to coral red colour. Colours disposed in regular concentric, bands, darker in adult zones. Combination of this vivid reddish colour with brown periostracum can give a greenish shade (*olivifer*). Interior white, except for a narrow, dark, reddish ventral margin. Mean rib number: 28.4 range 26-33.

Adult rib morphology
PQ. Same sculpture as well in adult shells as in juvenile: square-sided ribs, large oblique scales on top, small bent scales on anterior margin, vertical ridges on posterior margin.
Median part of shell. MPQ and MAQ: characteristic juvenile rib morphology of group restricted to umbonal region, and sculptures switches to that characterizing adult portion of shell very early. Specific characteristics of adult part of these two zones (Fig. 5C, F): (1) quasi-perfect symmetry in sculpture of roundly triangular ribs, in profile as well as in ornamentation; (2) two sets of constrictions on ribs, one at base of lateral ridging (as in many forms of group), another one in middle of flank. Ribs generally irregularly full-ridged, or rather crush-ridged. "Crushing" of top ridges is so marked that in many cases top zone becomes almost smooth. A very regular line of tubercular ridges lies in lower part of flank between middle and basal rib constrictions, on both flanks. This latter perfect arrangement is a little disturbed in most distal part of adult zone.
AQ. Ribs rounded, symmetrical, becoming regularly full-ridged towards anterior, by loss of numerous lateral ridges and tubercles. Full ridges rather wide, slightly obliquely set, generally less densely packed than in other species of group.

REMARKS
V. vertebratum mainly differs from the other species of the group by three characters: colour, quasi-perfect symmetry of the ribs in the median half with two constrictions, regular line of tubercular ridges on both flanks of the ribs in the median half (beaded ribs).
V. vertebratum can be confused with *V. rubicundum* (Reeve, 1845) because of similarity in colours and the "beaded" ornementation of the ribs. However these two species belong to two different groups, and have many different characteristics, particularly in rib number and morphology.

Vasticardium ornatum (Sowerby, 1877)
(Fig. 5B, D, G)

Cardium ornatum Sowerby, 1877: 755, pl. 75, fig. 2.

Cardium fultoni Sowerby, 1916: 76, pl. 3, fig. 7.

Acrosterigma sowerbyorum Voskuil *et* Onverwagt, 1992: 34, fig. 6 [a *nomen novum* for *C. ornatum*, erroneously considered as unavailable: see Remarks].

TYPES SPECIES. — *Cardium ornatum*: holotype in NMW, Melvill-Tomlin collection 55-158-1242, labelled "Hong-Kong", 19.0 × 18.2 × 12.8 mm, with 29 ribs.
Cardium fultoni: holotype in BMNH 1919-12-31-69, labelled "Philippines", 37.0 × 32.6 × 24.2 mm, with 28 ribs.

MATERIAL EXAMINED. — The type material and the following lots:
Natal. 1 (NMW).
North Western Australia. 1 (MNHN), 2 (ANSP); Yampi Sound, 1 (WAM), 1 (USNM); Cape Frezier, 1 (WAM); Heywood Island, 1 (WAM); Scorpion Island, 1 (WAM).

DISTRIBUTION. — Apparently endemic to northern Western Australia, approximatively from Capricorn tropic to latitude 15°S. Wilson & Stevenson (1977: 88) concluded that "Sowerby's locality [Philippines] was probably incorrect and that the holotype came from Western Australia". The same arguments apply to the localities Natal and Hong-Kong (holotype of *C. ornatum*) which are also probably erroneous.

DIAGNOSIS
Shell of small to medium size, reaching 37 mm in height. Shape rotund (*ornatum*) to obliquely ovate (*fultoni*). Anterior edge rounded, posterior edge slightly flared, rarely slightly truncated. A little elongated [according to Wilson & Stevenson (1977: 88), mean ratio L/H = 0.91 (range 0.86-0.99)], and moderately inflated [mean W/L = 0.76 (range 0.68-0.84)]. Lunule narrow to practically non existent. External colour uniform, white to cream (periostracum never seen); tops of ribs here and there bear dark red-purple spots almost regularly placed and roughly concentrically aligned. Internally white. Rib number: according to Wilson & Stevenson, mean number 29, range 25-33.

Adult rib morphology
PQ. Different from other species of group: ribs high with regularly set, conical, scales occupying all upper half of rib top; no secondary ornamentation like in other species. In most adult part ribs bifurcate into a lower anterior part and a higher scaled posterior part, with the latter slightly overhanging interstice backwards.
Other parts of shell. Ribs with a symmetrical profile comprising two parts from top to base: (a) a rounded upper part, full-ridged with wide ridges, sometimes a little flattened on top, and (b) two lower flanks, triangularly disposed, obliquely striated, separated from rounded summital zone by a constriction, and becoming vertical at their base (Fig. 5B, G). Interstices open, trapezoidal, with a flat bottom regularly striated, more or less independently of flanks.

REMARKS
D'Orbigny (1850: 79) used the combination *Cardium ornatum* for the taxon originally named *Pinnopsis ornatus* Hall, 1843: 244, fig. 8. *Pinnopsis ornatus* and *P. acutirostra*, also named by Hall, 1843, in the same formation, are Devonian fossils, very similar to each other. The latter is now classified in *Lunulacardium* Münster, 1840, family Lunulacardiidae Fischer, 1887 (see Newell *et al.* 1969) and there is neither primary nor secondary homonymy with *Cardium ornatum* Sowerby, 1877. Under Art. 59d of the Code this latter name is an available name and *Acrosterigma sowerbyorum* is a junior objective synonym.
Vasticardium ornatum has been placed in the *V. flavum* species group, because of comparable dimensions, shape, rib number, and above all because of an adult rib morphology of the same type, although different.

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