

REFLECTIONS ON THE DISTRIBUTION OF POLYTYPIC SPECIES OF THE GENUS *VASTICARDIUM* (MOLLUSCA, CARDIIDAE) FROM THE INDO-PACIFIC

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ABSTRACT

Vasticardium rugosum (Lamarck, 1819) is a junior synonym of *V. pectiniforme* (Born, 1780), which is the valid name for this species. Much confusion exist in the literature because *Vasticardium rugosum* has erroneously been considered a synonym of *Vasticardium flavum* (Linné, 1758), which, however, is a polytypic species occurring as three subspecies in the Indo-Pacific. I have examined the characters and the distribution of the three subspecies *Vasticardium flavum flavum* (Linné, 1758), *V. flavum subrugosum* (Sowerby, 1840) and *V. flavum dupuchense* (Reeve, 1845). The transition zone between *V. flavum flavum* and *V. flavum subrugosum* occurs along the eastern coast of Sulawesi, while *V. flavum dupuchense* apparently is parapatric with the others. Distribution of the four subspecies of *Vasticardium orbita* (Broderip & Sowerby, 1833), the three subspecies of *Vasticardium luteomarginatum* (Voskuil & Onverwagt, 1991), and the six subspecies of *Vasticardium elongatum* (Bruguière, 1789) shows that the relations between the different forms (subspecies and even species) are sometimes difficult to understand. However, the available data indicate that the presence of the Sunda Shelf in the Neogene could account for the differentiation and distribution of these taxa.

INTRODUCTION

This paper concerns shells which have been grouped into the subfamily Trachycardiinae Stewart, 1930. I have particularly studied the representatives of this group in the Indo-Pacific. The taxa have been often placed in the genus *Trachycardium* Mörch, 1853. However, I think that this genus concerns only the American species, and I place the Indo-Pacific shells into the two genera *Acrosterigma* Dall, 1900 and *Vasticardium* Iredale, 1927 (Vidal, 1999). The latter genus includes the largest shells of the group. Another difference is that *Vasticardium* includes several polytypic species, *i.e.*, that the shells are variable in characters (polymorphic *sensu* Mayr), and that shells with comparable characters are geographically grouped, forming different subspecies. However, in practice the demarcation of subspecies and the differentiation between species and

subspecies often constitute difficult taxonomic problems.

I am going to show and comment on three examples, which particularly concern Indonesia. First, the group of *Vasticardium flavum* (Linné, 1758), second the group of *Vasticardium orbita* (Broderip & Sowerby, 1833), third the group of *Vasticardium elongatum* (Bruguière, 1789).

THE GROUP OF *VASTICARDIUM FLAVUM*

Because the two taxa *flavum* Linné, 1758 and *rugosum* Lamarck, 1819 have very often been considered to be synonyms, the first necessary step is to examine Lamarck's species to clearly separate it from the true *V. flavum*. In fact they constitute two different species where *V. flavum* is polytypic while Lamarck's species is perfectly

monotypic.

VASTICARDIUM PECTINIFORME

The species *Cardium rugosum* was defined by Lamarck in 1819 without ambiguity. Several good syntypes exist in Lamarck's collections, both in Paris and Geneva. However, previously to Lamarck, this shell had already been named *Cardium pectiniforme* Born, 1780, which is the valid name.

Vasticardium pectiniforme is one of the most common shells in the Indo-Pacific, widespread from Natal to Japan and Fiji (Fig. 1).

It lives exclusively in the intertidal zone, apparently in all sedimentary environments, and valves of this species are rarely absent in any beach of the area of distribution. As already mentioned the shell is monotypic in all this area, that means it is rather constant in characters and that some minor differences existing between populations do not allow to separate subspecies.

The shell is of medium size, moderately elongated, with circa 30 ribs which are rounded and rugose on the top.

Several other names have been given to this species, in addition to the valid name *pectiniforme*, viz., *regulare* Bruguière, 1789,

peregrinum Jousseaume, 1888, *nigropunctatum* Habe & Kosuge, 1966, and above all *flavum* in more than 55% of the cases.

VASTICARDIUM FLAVUM

Cardium flavum was defined by Linné in 1758, but with no references, no marked type in his collection, with only a short description in Latin. These poor indications gave a rather enigmatic character to this species.

One of the first interpretations of *Vasticardium flavum* was made by Lamarck, who thought it could be a synonym of *V. rugosum*. In 1819, he wrote about *V. rugosum*: "an *Cardium flavum* Linné". Later, Sowerby had a similar opinion and wrote in 1841 that *C. flavum* could be a "yellow var." of *C. rugosum*.

Following these two authoritative opinions, *Cardium flavum* has been interpreted as being the same species as *Cardium rugosum* and named either *flavum* or *rugosum* in the literature. I have estimated that Lamarck's species was cited about 50 times with its correct name *rugosum*, and about 60 times with the name *flavum* which, in my opinion, corresponds to another species, which is examined in the

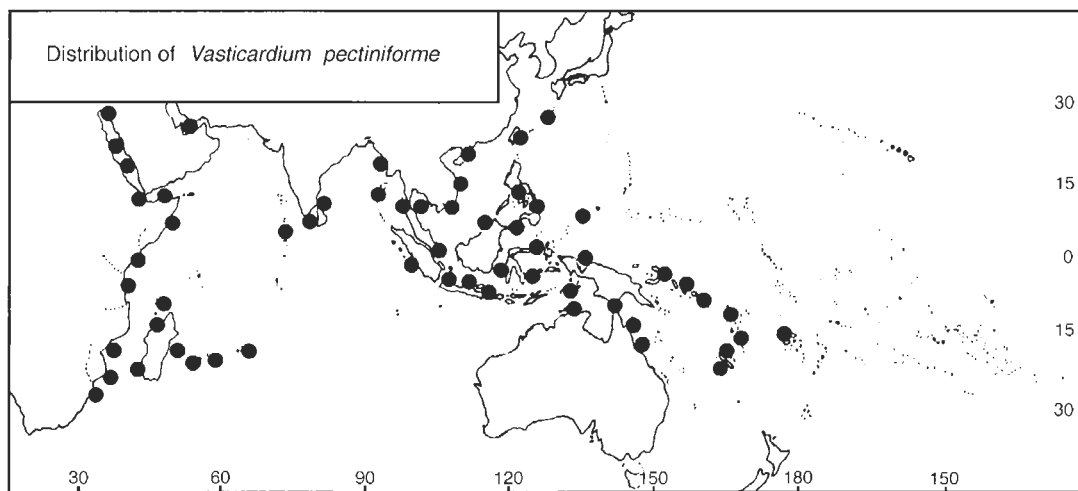


Fig. 1 - Distribution of *Vasticardium pectiniforme* (formerly *Vasticardium rugosum*).

next paragraph.

I have shown (Vidal 1997b) that the short description of *C. flavum* given by Linné does not fit at all the characters of *C. pectiniforme*. Linné indicates for *C. flavum* “*testa flava, latere anteriore alba*” what is to say “shell yellow, anterior (= posterior) side white”. *V. pectiniforme* is exteriorly never yellow but practically always entirely uniformly white or light beige.

Linné also indicates: “*fundo interdum rufescente*” what is to say “umbonal cavity sometimes turning russet”. *V. pectiniforme* is always perfectly white interiorly.

Linné (1764) stated that *C. flavum* is present only in Queen Ulrica’s collection, now in Uppsala (Sweden), and not in his personal collection, now in London. Only this latter collection was correctly investigated by authors for a type specimen of this species, without success. But an enquiry into the Uppsala collection allowed me to discover a shell which fits Linné’s descriptions, as far as colours are concerned. It was also catalogued as *flavum* in this museum (posthumous to Linné).

I have selected this shell as lectotype of

Cardium flavum Linné, 1758 (Vidal 1997b). It resembles *V. pectiniforme*, with the same shape and size, same rib number, but differs by its colours, but above all by the cross-section of the ribs (flatly triangular instead of well rounded) and their ornamentation (ribs smoother). Another difference with *V. pectiniforme* is that *V. flavum* has some variable characters of ribs and colours; the combination of these characters allows to define three subspecies, geographically separated: *V. flavum s.s.*, *V. flavum subrugosum* Sowerby, 1838, *V. flavum dupuchense* (Reeve, 1845) (Fig. 2).

VASTICARDIUM FLAVUM FLAVUM

Vasticardium flavum flavum (*flavum s.s.*) is present from Solomon Islands in the east to Maluku and part of Sulawesi and Nusa Tenggara in the west (Fig. 2). It is not necessarily coloured yellow but generally well coloured, outside and inside. The ribs are flat and smooth. It has been also been described under the names *Cardium fucatum* Spengler, 1799, *C. gratiosum* Deshayes, 1855, and *C. tumidum* Deshayes, 1855.

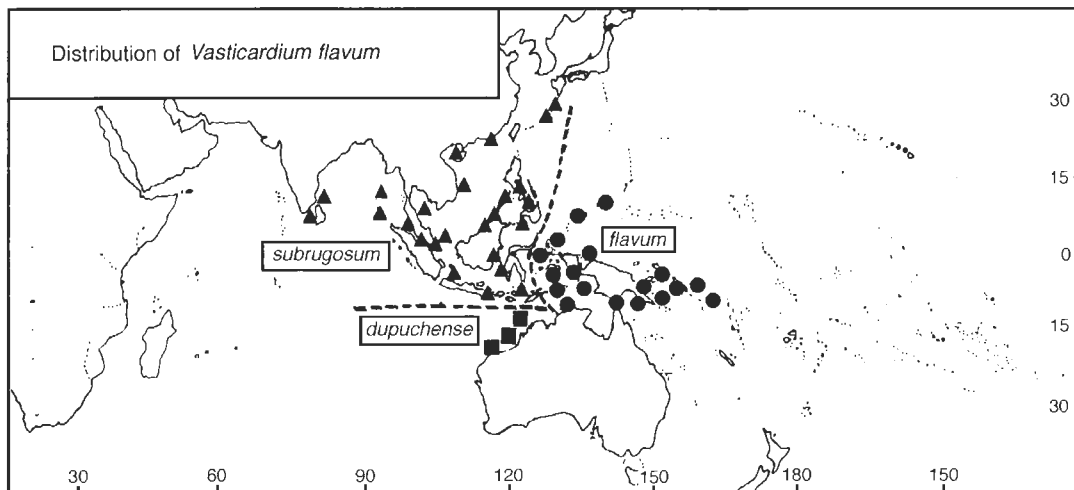


Fig. 2 - Distribution of *Vasticardium flavum*.

VASTICARDIM FLAVUM SUBRUGOSUM
SOWERBY, 1840

Figures of *V. flavum subrugosum* and its description fits entirely the characters of *C. flavum*. Sowerby writes: "testâ posticè albâ, anticè flavidâ," what means "shell posteriorly white, anteriorly yellowish".

There is no doubt that *subrugosum* is the same species as *flavum* (existence of intermediate and transitional forms). The ribs are higher and stronger, the colours often less intense, and the ribs wear stronger, typical ornaments in the subspecies *flavum subrugosum*. Since Sowerby's specimen has been lost, I have selected a shell from Phuket as neotype of *Cardium subrugosum* Sowerby, 1840 (Vidal 1997b).

The subspecies *flavum subrugosum* is present in the intertidal zone from south Japan, Philippines, Sulawesi and Nusa Tenggara to south India, (Fig. 2). It is very abundant in the Philippines.

Towards the west, the shells are less coloured. When the subspecies *subrugosum* is little coloured, or when the shells are covered with a periostracum, it can be confused with the species *pectiniforme*. However, the discrimination will be easy if

details of the rib structure are examined: The subspecies *subrugosum* carries transverse ridges on the ribs and these ridges are thick and very regular in the anterior part. In comparison the species *pectiniforme* has thinner and irregularly arranged transverse ridges. The ribs are smoother and often longitudinally divided into two parts in the posterior part of *subrugosum*. With very few exceptions, these criteria allow separation of the species *rugosum* from the subspecies *flavum subrugosum*. The two shells are almost always sympatric, and in some localities they look very much alike, for example in south China.

VASTICARDIUM FLAVUM DUPUCHENSE
(REEVE, 1845)

This subspecies occurs only in North-western Australia (Fig. 2). It has numerous characters of *V. flavum*, but one character of *V. pectiniforme* is present in the posterior part (Vidal 1997b). The subspecies *V. flavum dupuchense* differs from both *V. flavum flavum* and *V. flavum subrugosum* in having a smaller number of ribs (mean number 25 against 31).

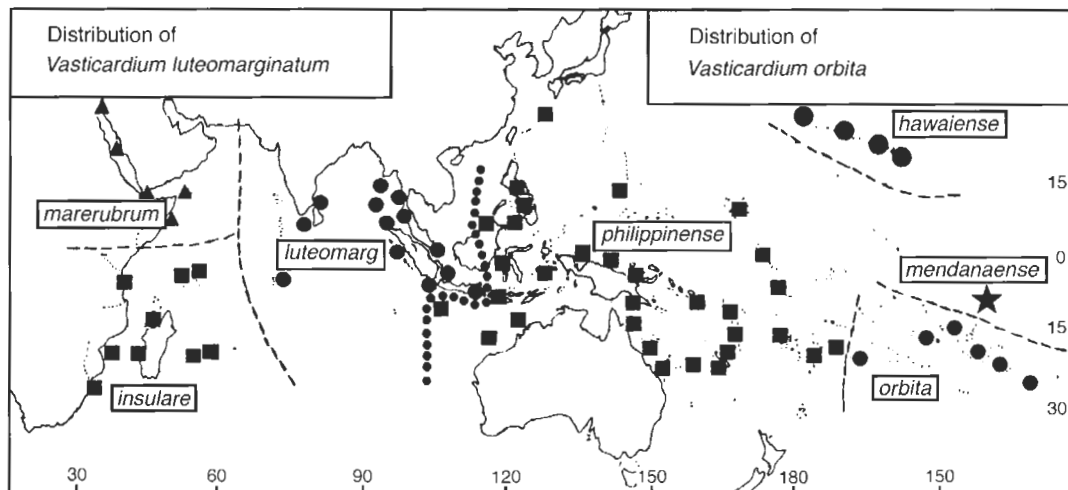


Fig. 3 - Distribution of *Vasticardium orbita* and *Vasticardium luteomarginatum*.

THE GROUP OF *VASTICARDIUM ORBITA*

In this group I have placed taxa which have common characters of shape, colour, hinge and, above all, rib morphology. I have provisionally separated two polytypic species in this group: *Vasticardium orbita* with four subspecies and *Vasticardium luteomarginatum* with three subspecies.

The type subspecies *Vasticardium orbita orbita* (Broderip & Sowerby, 1833) came from the Tuamotu Archipelago. *V. orbita s.s.* has numerous ribs and it is the largest cockle in the group. The type subspecies is endemic to Polynesia. I consider that three other forms represent subspecies of *V. orbita* (Fig. 3): *V. orbita mendanaense*, *V. orbita hawaiiense*, and *V. orbita philippinense*

V. orbita mendanaense (Sowerby, 1897) differs by its small size, higher ribbing, and strong contrast between posterior part and the rest. It is endemic to the Marqueses.

V. orbita hawaiiense (Dall, Bartsh & Rheder, 1938) has typical conical scales in the whole posterior half. It is endemic to the Hawaiian Islands.

V. orbita philippinense (Hedley, 1899) has a wider distribution in the Indo-Pacific. It

is less elongated, with ribs flatter and often smoother. It has been described also as *C. angulatum* Lamarck *sensu* Reeve, 1845, and *C. pseudoangulatum* Bülow, 1905.

All the subspecies have comparable characters of the interior, with typical hooked lateral teeth in the hinge and strongly purple coloured ventral margin. Taking account of the lots I have observed, all the subspecies are isolated, and there are no obvious intermediate forms. This isolation is understandable for the subspecies found in Hawaii and Marqueses, but not for *V. o. orbita s.s.* and *V. o. philippinense*. The change between the two subspecies (which are really different), happens abruptly in the middle of Polynesia, exactly between Niue and Aitutaki-Rarotonga in the Cook Islands. I could not find any explanation for this perfect parapatry.

THE GROUP OF *VASTICARDIUM LUTEOMARGINATUM*

Other forms belonging to the "*Vasticardium orbita* complex" are present exclusively in the Indian Ocean. I have considered the forms as constituting one species, *Vasticardium luteomarginatum* Voskuil &

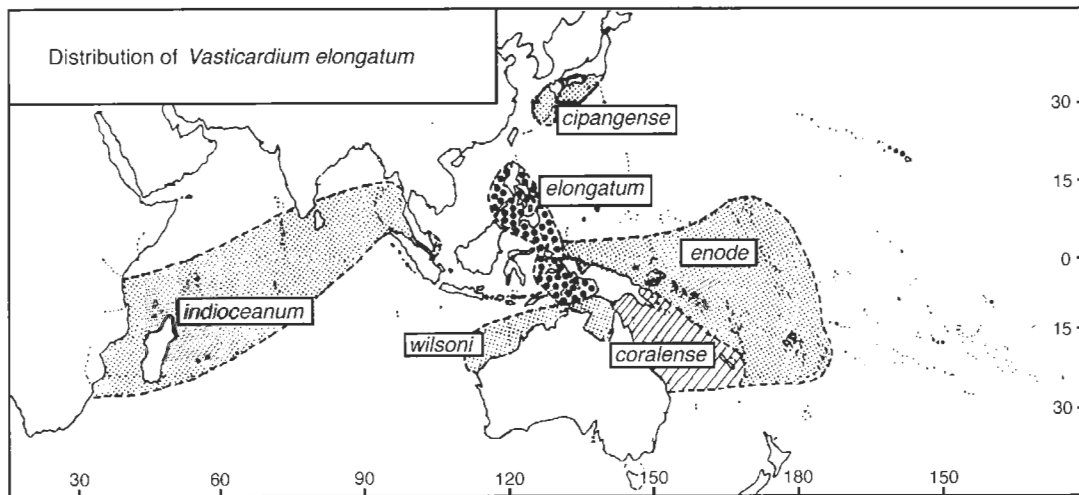


Fig. 4 - Distribution of *Vasticardium elongatum*.

Onverwagt, 1991, with three subspecies. The species has been known for a long time, but numerous invalid or inadequate names have been utilized for it, particularly the name *Cardium leucostoma* Born, which in reality is an American Atlantic species.

The subspecies of *V. luteomarginatum* (Fig. 3), are geographically isolated. The taxa are well defined, although rare, more or less intermediate forms can be present as individual variants in the populations, mainly in the subspecies *insulare*.

The type subspecies *V. luteomarginatum luteomarginatum* is present in western Indonesia, Andaman Sea, south India and Chagos Is. The holotype and several paratypes of this taxon are said by Voskuil and Onverwagt to come from Samar Is (Philippines). I consider that this locality is not easily acceptable, for three reasons: (1) It is the only record known to me of this shell in the Philippines. (2) These shells are identical to all the ones present in Andaman Sea and north Sumatra, which have particular local characters. (3) These shells come from a dealer (personal communication).

Exteriorly, *V. luteomarginatum* s.s. has low, rounded-smooth to triangular ribs, instead of square-sided ribs characteristic of the following two subspecies. Interiorly it is strongly coloured on the ventral margin, not necessary yellow (as its name indicates) but also purple.

The subspecies *V. luteomarginatum marerubrum* (Voskuil & Onverwagt, 1991) was recently described as a species (*Trachycardium marerubrum*). In my opinion it is a subspecies, which is rather colourless on the ventral margin, usually only slightly light yellow. The rib ornamentation is rather elaborate. It is present in the Red Sea, Gulf of Oman and northern Somalia.

The subspecies *V. luteomarginatum insulare* Vidal, 1997 is always purple coloured on the interior margin (Vidal 1997a). It is present in east Africa, from Kenya to north Natal, in Madagascar and

surrounding islands.

THE GROUP OF *VASTICARDIUM ELONGATUM*

Vasticardium elongatum (Bruguière, 1789) is a polymorphic species when adult (the young shells being very similar). The taxon has a wide distribution in a large part of the Indo-West Pacific. I have defined six subspecies (Vidal 1993) (Fig. 4):

Vasticardium elongatum elongatum
(Bruguière, 1789)

Vasticardium elongatum coralense
Vidal, 1993

Vasticardium elongatum enode
(Sowerby, 1840)

Vasticardium elongatum wilsoni
(Voskuil & Onverwagt, 1991)

Vasticardium elongatum cipangense
Vidal, 1993

Vasticardium elongatum indioceanum
Vidal, 1993

Among these six subspecies, three have numerous intermediate forms, viz. the type subspecies *V. elongatum* s.s., and the two subspecies *V. elongatum coralense* and *V. elongatum enode*. The taxon *V. elongatum wilsoni* in north western Australia is more morphologically unique, but rare intermediate forms exist. On the other hand, the subspecies *V. elongatum cipangense* is totally unique. As far as the taxon *V. elongatum indioceanum* is concerned, it is rather unique. Geographically, it is separated from the other subspecies by a large zone in Indonesia including Sumatra, Java, Borneo, Nusa Tenggara and Sulawesi, from where I have never observed any lot nor see any record in the literature.

DISCUSSION

In my opinion, several conditions are necessary to define a subspecies:

First, a specimen or population of specimens must be identifiable as belonging

to a given subspecies without knowledge of its geographical provenance.

Second, populations of a given subspecies must occur in a same geographical area.

Third, co-occurrence of shells with characters of two different subspecies can exist geographically in a transitional area, but in that case shells with intermediate combinations of characters must exist to confirm that the separation between both forms is not really specific.

Fourth, if there is no transitional area between two adjacent areas with different subspecies, there must be a reason for the genetic isolation of these areas. However, in that case, and without any other taxonomic tool other than the observation of the shell, the qualification "subspecies" or "species" is subjective, and depends on the attitude of mind of the taxonomist. In case of uncertainty, I prefer myself to choose the subspecies rank: this allows the problem not to be eluded; the rank of the subspecific taxon can easily be changed into specific, if necessary.

I maintain that the main criteria to classify two different groups of shells as two subspecies of the same species are their isolation (allopatry) and the existence of intermediate forms. In comparison, the main criteria to classify two different groups of shells as two species are their existence together (sympatry) and the absence of intermediate forms. Consequently, there are two sorts of groups of shells, which can be considered as subspecies:

1) The unquestionable subspecies with progressive evolution of characters from the nominal subspecies, with intermediate forms and eventually a transitional geographical zone.

2) The questionable subspecies, which are geographically isolated or "perfectly parapatric" (adjacent but not interdependent), without transitional zone nor intermediate forms. These can be true subspecies still genetically connected to the nominal subspecies, or can be subspecies in

the process of speciation, or already true species.

The subspecies *V. flavum subrugosum* belongs to the first group. There is a progressive variation from east to west of the characters of *V. flavum flavum*. A transition zone with mixing of forms and intermediate forms occurs in Sulawesi and Nusa Tenggara. However, a more precise demarcation of the two subspecies, defined by application of a percentage rule, has to wait for more abundant sampling. The reasons of this partition should also be investigated in more detail.

The isolated and perfectly parapatric subspecies *V. flavum dupuchense* seems to belong to the second group of questionable subspecies. In any case (subspecies or species) the absence of intermediate forms as well as the isolation need explanations, such as strong marine currents influencing the distribution of planktonic larvae.

RELATIONS BETWEEN *V. LUTEOMARGINATUM* AND *V. ORBITA*

My finding that *V. luteomarginatum* is absent in the Philippines is in accordance with J. Hylleberg (pers. com.), indicating that the two species *V. luteomarginatum* and *V. orbita* never co-occur. The two taxa have common characters of morphology (shape and ribbing), particularly in the young specimens, and some specimens of both groups do appear similar, but so far intermediate forms have not been recorded. However, the parapatric occurrence of these two species is an important argument for possible conspecificity of the two forms. If further evidence shows that there is only one species, it can be subdivided into seven subspecies.

By courtesy of R. Kilburn, the Natal Museum, South Africa, I have recently received lots of local *V. luteomarginatum insulare*, which are identical to specimens of *V. orbita philippinense*, particularly those from New Caledonia, as far as colours and detailed rib morphology are concerned.

However, they differ definitely from *V. orbita orbita* in the rib number. The rib number in *V. orbita philippinense* (range 36-44) is always higher than in *V. luteomarginatum* (range 29-35) while the rib number in *V. orbita orbita* ranges from 42-50. Does this difference in rib number, appearing rather abruptly between adjacent forms, exclude a possibility of conspecificity? I maintain that the forms are conspecific. Of course, this opinion of mine is solely based on morphological analyses. Other methods (molecular techniques) may help in solving the questions about relationships between species and subspecies. Certainly, phenomena of strict parapatry and abrupt changes exist, and these matters need enquiries and explanations.

CONCLUSIONS

The present review shows that there are several polytypic species in the genus *Vasticardium*, but that many problems still remain to be solved. The main cause of these problems is the possible existence of what I have named "perfect or strict parapatric forms" for which paradoxically the fact of not living together would argue for being subspecies (and not species), and, at the same time, the absence of intermediate forms would argue for being species (and not subspecies).

I have established that Indonesia plays a particular role in each one of the four polytypic species examined (Fig. 5):

1) The transitional zone between *Vasticardium flavum s.s.* and *V. flavum*

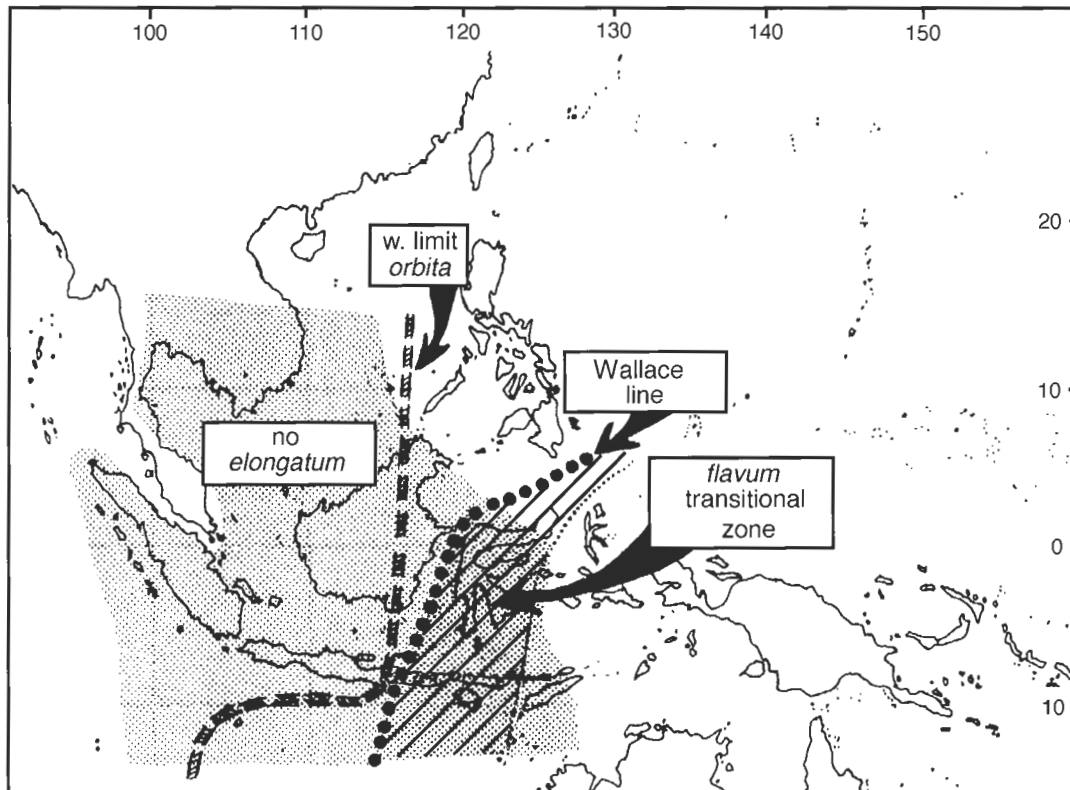


Figure 5. Distribution in relation to the Wallace Line.

subrugosum is situated in Sulawesi and Nusa Tenggara.

2) The western limit of *Vasticardium orbita* seems to run through Borneo and the western part of Nusa Tenggara (with an indentation west of Christmas Is.

3) The eastern limit of *Vasticardium luteomarginatum* is very probably the same line as above.

4) A wide part of western Indonesia seems to lack *Vasticardium elongatum* and separates the area of *V. elongatum indioceanum* from the other subspecies in the Pacific.

One reaction, with regard to this distribution of taxa, could be to think the Wallace Line. However it seems that such an explanation must be given up, for two reasons. First, the Wallace Line, crossing Indonesia in its middle, separates two zones with different land fauna and vegetation, not two marine zones. Second, although the palaeontology of the genus *Vasticardium* is far from being clear, it is probable that this genus is not older than the Miocene. The „Wallace effect“, due to a continental drift, is certainly much older.

The only explanation I see, is the existence in the past where the Sunda Shelf would have separated two marine basins where some species would have had slightly different evolution. Such a scenario would be comparable to the Panama Isthmus, where some taxa have become different on the Atlantic and the Pacific sides. A shelf certainly existed in the late Quaternary, at glacial ages. The ethnologists attribute the first migration of people to Australia, ca. 40,000 years ago.

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