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Revision of the living *Pustularia* (Mollusca: Gastropoda: Cypraeidae) with the description of *P. chiapponii* n. sp.

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Abstract

The genus *Pustularia* represents a distinctive unit in the Cypraeid subfamily Erosariinae. The species are very similar to each other and their taxonomy has been subject of recent debates. This study clarifies some of the points in question and gives a comprehensive analysis of conchological features on the basis of populations from selected localities. A new species from the Philippines is described as *P. chiapponii*.

Contents

1. Remarks on the shell shape of the family Cypraeidae

An ancient systematic criterion for subdividing the animal kingdom is body symmetry. The Radiata comprise radially symmetrical animals (e.g. Cnidaria). The Bilateria are the large group of bilaterally symmetrical animals, to which the phylum Mollusca belongs. Its orders comprise animals with a longitudinal axis of symmetry dividing the animal into two nearly equal portions. In most families of the order Gastropoda, this symmetry is lost due to torsion of the visceral sac and the subsequent coiling of the shell. These animals have attained a secondarily asymmetrical appearance, often emphasized visually by special shell processes on only one side (e.g. Strombidae).

There are a few gastropod families in which one side of the shell is the mirror image of the other dorsally–the differences between the two halves are apparent only in the basal view. In those cases we observe a change from an asymmetrical to a seemingly symmetrical shell. This phenomenon can be observed in the family Ovulidae, Triviidae and Cypraeidae, in which the species display a certain degree of bilateral symmetry in shell shape and ornamentation. Good examples are the genera *Luria* (e.g. *pulchra* (Gray, 1824)), *Bistolida* (e.g. *stolida* (Linné, 1758)) and, not least, *Pustularia* (e.g. *bistrinotata*). Perhaps this symmetry in the appearance confuses molluscivore crustaceans which detect food by sight. In their habitat of narrow coral crevices, the species of *Pustularia* are usually inaccessible to molluscivore fish which search for food by chemical rather than optical stimuli.

2. General notes on the natural history of the genus *Pustularia*

The species of *Pustularia* are highly specialized, mostly sublittoral reef dwellers. The peculiar shape of the shell in all species of the genus makes it a well-defined systematic subunit within the family Cypraeidae. The genus *Pustularia* has ancestral forms mainly in the Caribbean Oligocene. Comparing living and fossil species, *Pustularia* might have evolved from *Proadusta*-like forms (Fig. 1); this hypothesis makes the sole survivor of the old genus *Proadusta surinamensis* (Perry, 1811), the closest living relative in the Atlantic. In the Indo-Pacific there is the widespread genus *Staphylaea* whose granulose surface and dentition are similar to those of *Pustularia*. The relationship of the five living species of *Staphylaea* to *Pustularia* is uncertain, but probably close. Both genera seem to have evolved from a common pustulose ancestor.

Living species of the genus *Pustularia* have distributions from the Red Sea, the Indian Ocean and the western and central Pacific to the Hawaiian Islands. An Indo-Pacific species similar to *Pustularia* is *Nesiocypraea lisetae* Kilburn, 1972 (Fig. 1). It differs by having a distinctly curved aperture and a distinctly denticulate fossula, which is narrow and smooth in all *Pustularia* species. In adult shells of *Nesiocypraea lisetae* there is a callus ridge

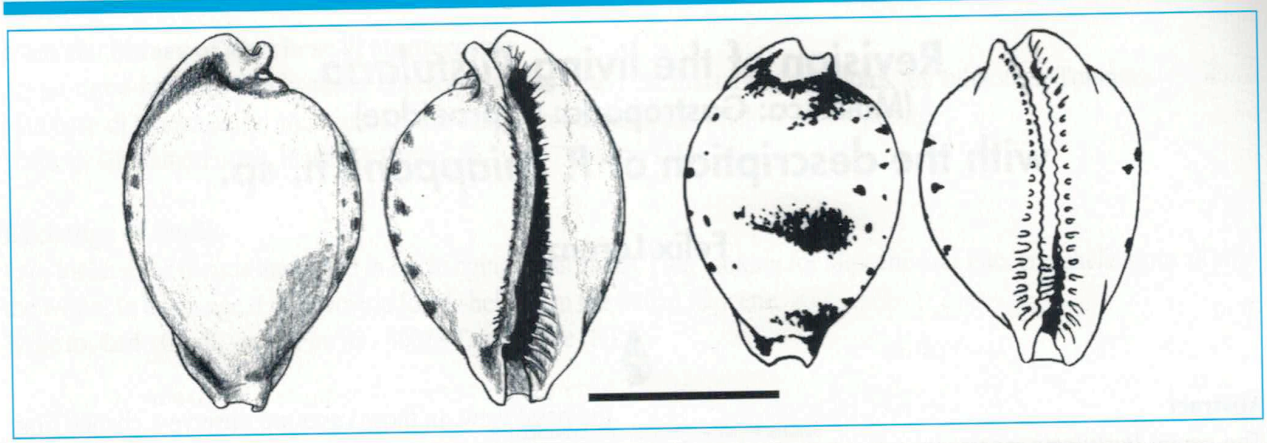


Fig. 1 (left): *Proadusta moloni*, Vicenza, Late Eocene (20 mm), (right): *Nesiocypraea lisetae*, Richardsbay, Natal (15 mm)

connecting both labral and columellar teeth. In *Pustularia*, a comparable ridge may be present on the columellar side, especially in subadult specimens of *P. cicercula* and *P. margarita*, but it is not found towards the extremities as in *N. lisetae*. Adult shells of all *Pustularia* species form a noteworthy posterior extremity composed of an accumulation of callus and two marginal spines formed by the posterior terminal ridges (Fig. 3). This type of posterior extremity characterizes the shell of *Pustularia*. It is not found in any other living cypraeid species and also lacks in the Caribbean fossil species assigned to *Pustularia*.

3. Comments on the taxonomy of some living *Pustularia*

A great deal of confusion was caused by SCHILDER (1966) concerning the type species of *Pustularia*, *P. cicercula* (LINNÉ, 1758). He studied the Linnean collection in the British Museum in 1936 and based his later descriptions of subspecies (SCHILDER & SCHILDER 1938) on this experience, whereas the results from the 1936 visit were published only thirty years later.

Linné hardly ever designated type specimens, and in many cases it has been difficult to derive sufficient information from his brief descriptions. The correct usage of names such as *labrolineata* and *flaveola* is still being debated: just two examples from the Cypraeidae.

Schilder did not find specimens of *cicercula* in the remains of the Linnean collection, but he located two shells he identified as *bistrinotata bistrinotata*: those were reported to be badly corroded, without basal blotches, but with very faint spots and blotches dorsally. There are traces of a dorsal groove. Schilder concluded that these two shells were Linné's types of *cicercula*, hence synonymous with *bistrinotata*. He proposed to change the usage of the name *cicercula* for the shell formerly known as *bistrinotata*. In the brief description of *cicercula*, Linné does not mention any dorsal blotches, but to Schilder there seemed no doubt that the two eroded shells in the Linnean collection were the types of *cicercula*.

Linné was a very accurate observer, and it therefore appears unlikely that dorsal blotches would have escaped his attention or were considered insignificant.

For many reasons, later authors did not accept the taxonomic changes postulated by Schilder, and indeed they appear too forward. Schilder himself admitted in the 1966 work: "For though we cannot be absolutely sure that the specimens preserved in Linnaeus' collection are the same shells which Linnaeus faced when he composed his descriptions, there is a probability in different degrees that it was so." Taking this into account, it is confusing why SCHILDER & SCHILDER described *bistrinotata* in 1937, only one year after studying the questionable shells in the Linnean collection.

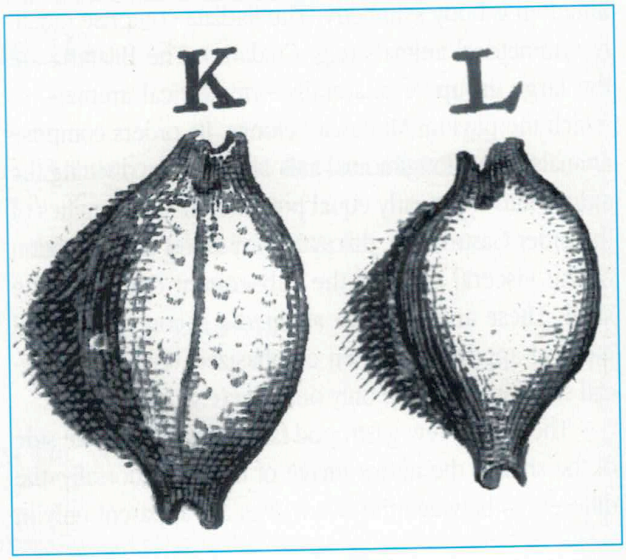


Fig. 2: Type Figures from RUMPHIUS (1705) Plate 39. K: *cicercula*, L: *margarita*

There is no explicit holotype specimen of *cicercula*. The figures and the text of the original description are all we have at hand. Linné, like many other later taxonomists, based many of his taxa on illustrations from other publications, and in the case of Mollusca, the work by RUMPHIUS (1705) was a frequently used source. A famous example is *Conus aurisiacus* LINNÉ, 1758 which is depicted in perfection in this monumental work. In the case of *cicercula*, the figure Linné based his description on is also in RUMPHIUS plate 39 Fig. K (see also DODGE, 1953). This illustration shows a pustulose shell with a distinct dorsal groove and a spire blotch. Apparently, this figure in RUMPHIUS shows a *cicercula* in the sense the name is in use today, as the combination of a dorsal groove and a spire blotch is specific. Schilder himself did not follow his own proposal of 1966, as in the "Catalogue" of 1971 the traditional usage of *cicercula* and *bistrinotata* is maintained (see also BURGESS, 1977).

Incidentally, in the same work by RUMPHIUS there is the well-recognizable original type figure of *margarita* (DILLWYN, 1817) (Pl. 39 Fig. L), explicitly described as being completely smooth compared to the granulose shell ("knorrelige Kopje") of Fig. K on the same plate (= *cicercula*). These illustrations from RUMPHIUS are reproduced here (Fig. 2).

In the above-mentioned 1966 article, Schilder described the supposed types of *globulus* from the Linnean collection. These shells show the characteristics of the typical *globulus globulus* from Sri Lanka and Thailand and correspond with Linné's description. This is one case in which the assignment of a Linnean name is referable to actual specimens in his collection and most likely correct, even at the subspecific level.

The taxa introduced by SCHILDER & SCHILDER are: *bistrinotata bistrinotata* (1937), *b. mediocris*, *b. sublaevis*, and *globulus sphaeridium* (all 1938) and finally *bistrinotata keelingensis* (1940). Their characteristics and measurements, along with the type localities are compared precisely in the "Prodrome of a Monograph" p. 126-127. The interpretation of those names, as well as their correct assignments to the various series of shells investigated therein present no problem.

The recently described *Pustularia jandeprezi* POPPE & MARTIN, 1997 will be discussed below.

Finally, *mauiensis* BURGESS was based on a series of shells. The species was illustrated and described and compared carefully and accurately.

4. The conchological features of *Pustularia*

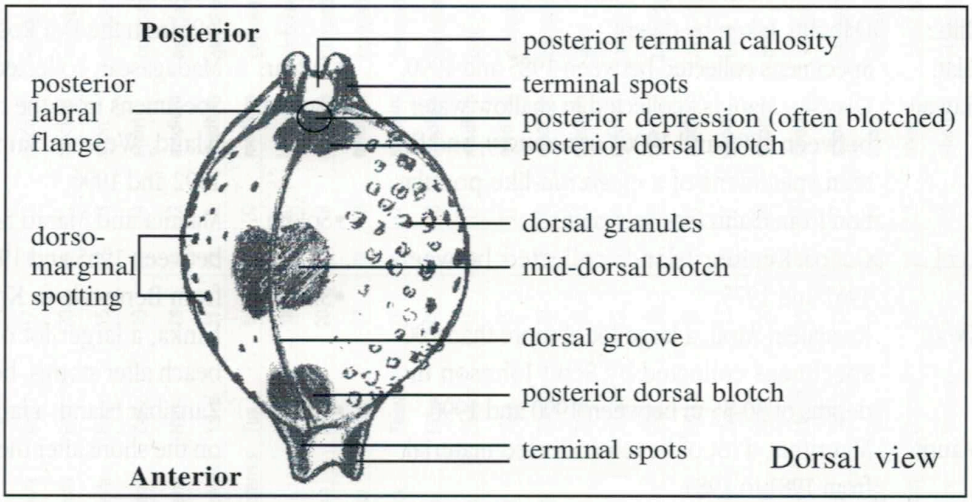
The shells of *Pustularia* can readily be separated from others in the family Cypraeidae by the globular body, with the above-mentioned spiny-rostrated extremities in combination with an extremely narrow aperture framed by fine dentition. A pustulose surface is common. A second ridge formed by the teeth on the columellar side is sometimes found inside the aperture, while the edge of the moderately narrow fossula is always smooth. The spire is slightly projecting in the subadult, but completely concealed by callus in the adult stage. The species of *Pustularia* differ from each other mainly by different combinations of very few features, some of which are not found in other Cypraeidae. The terminology for the *Pustularia* shell is shown in Fig. 3.

The most important features for taxonomic distinction are the presence or absence of

a) the spire blotch
b) dorsal granules
c) the four basal blotches
d) the three dorsal blotches

To judge the value of the various shell features, it proved necessary to examine larger series of specimens

Fig. 3a: Terminology of the shell of *Pustularia* (dorsal view)



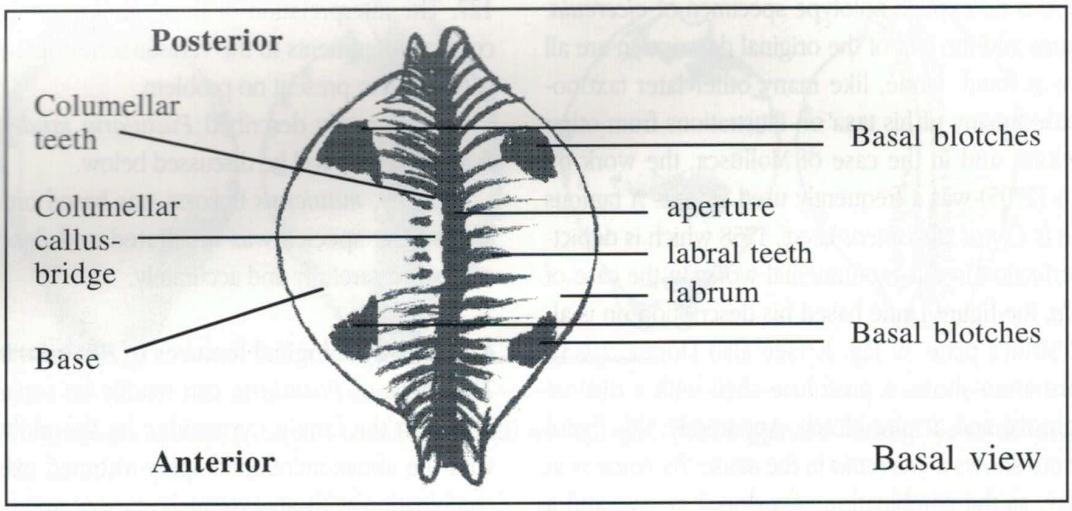


Fig. 3b: Terminology of the shell of *Pustularia* (basal view)

from defined geographic origins. The comparisons were made on series consisting of at least ten specimens. Table 1 shows the results of this study of 32 lots of more than 1100 specimens from 20 localities. Values printed in bold letters are those of highest consistency, denoting that 100% of the examined specimens of the respective lots show the feature. Those entries printed in standard letters describe lots in which 75% or more of the examined specimens show the particular feature. The remark "variable" denotes that a feature was found to be highly variable and hence of no value for distinction. For the comparative analysis, a consistent feature (100%) is an argument in favor of a distinction at the species level, while in a subspecies or a forma, a certain number of qualitative (75%) features may be sufficient.

Explanation of the categories (features) in Table 1:

THE LOTS AND LOCALITIES (IN ALPHABETICAL ORDER):

- •And: Andaman Sea, a small lot of shells collected by divers between 1991 and 1994.
- •Djib.: Djibouti, taken by divers
- •Eilat: Specimens collected between 1985 and 1990.
- •Hawaii: Olavalu, Maui Is., collected in shallow water between 1983 and 1990 (*mauiensis*), and fifteen specimens of a *cicercula*-like population from Oahu (see section 6)
- •Keel.: Cocos/Keeling Island, collected between 1967 and 1975.
- •Kwa.: Kwajalein Atoll, a large lot of more than 200 specimens collected by Scott Johnson in depths of 30-35 m between 1990 and 1996.
- •Maurit: Mauritius, a lot of beach-collected material from 1981 to 1984.
- •NCal.: Noumea, New Caledonia (1983-1986).
- •Phil.: Philippines. The lot of *P. chiapponii* n. sp. from Borongan, E. Samar Island, collected between 1985 and 1990. In addition to this lot of twelve specimens, there are an additional 40 specimens supplied by the company TRIDAGNA (Spain) who could not give details about their origin except "Philippines". Those shells correspond exactly with those from ascertained origins so that they were included in the study. The other lot marked "Philippines" is from Samar Island, collected between 1979 and 1995.
- •Taiwan: A lot of shells collected between 1990 and 1992 in the south of Taiwan.
- •Tahiti: Specimens collected by divers in the area around Hitiaa, Tahiti between 1986 and 1995.
- •Thail.: Specimens from Phuket Island, Thailand, collected between 1985 and 1990.
- •Tua.: Tuamotu, a lot of shells labeled "Tuamotu '69" from the Eva Roscoe collection.
- •Tuléar: Madagascar, collected by snorkeling, 1996.
- •Samoa: Specimens from the northwest coast of Savaii Island, Western Samoa, collected between 1992 and 1996.
- •Solom.: Malaita and Marau Sound Islands, collected between 1965 and 1975.
- •Sri La.: from Beruwala to Kosgoda Beach, S. W. Sri Lanka, a larger lot of shells collected on the beach after storms, between 1990 and 1997.
- •Zanz.: Zanzibar Island, a large lot of shells collected on the shore after the cyclone of 1967.

species/ssp/form	origin/series	⦰ (mm)	avg .no. teeth · lab.	col.	length of teeth	general shape	dorsal color	dorsal blotches	terminal spots	dors.-marg. spots	basal blotches	blotch at spire	dorsal groove	dors. granule	aperture	shape of extremities	dental color	col. bridge callus
cicercula	Zanz.	16	25	20	long	globular	cream	**absent**	**absent**	faint abs.	**absent**	**dark**	distinct	**distinct**	variable	thick rostrate	variable	variable
cicercula	Thail.	20	25	21	**long**	globular	cream	**absent**	**absent**	faint	**absent**	**dark**	distinct	**distinct**	variable	**rostrate**	as base	absent
cicercula	Phil.	20	26	21	**long**	globular	cream	**absent**	**absent**	crowded	**absent**	**dark**	indist.	**distinct**	variable	**thin, rostr.**	variable	absent
cicercula	Djib.	15	27	24	**long**	elongate	oran/brown	**absent**	**absent**	crowded	**absent**	**dark**	distinct	**distinct**	variable	**thin, rostr.**	**darker**	absent
cicercula	Kwa.	17	26	20	**long**	elongate	cream	**absent**	**absent**	faint - abs.	**absent**	**dark**	distinct	**distinct**	straight	**thin, rostr.**	variable	variable
?cicercula	Hawaii	16	27	21	medium	elongate	cream	**absent**	**absent**	crowded	**absent**	**faint**	indist.	**indist.**	straight	**thin, rostr.**	as base	variable
marg.margarita	And.	17	26	22	medium	elongate	cream	**absent**	**absent**	**crowded**	**absent**	**faint**	**absent**	**absent**	sl. curved	**thin, rostr.**	sl. darker	variable
marg.margarita	Phil.	20	26	21	medium	elongate	cream	**absent**	**absent**	**crowded**	**absent**	**faint**	**absent**	**absent**	straight	**thin, rostr.**	sl. darker	variable
marg.margarita	Kwa.	15	26	23	short	elongate	cream	**absent**	**absent**	**crowded**	**absent**	**faint**	**absent**	**absent**	sl. curved	**thin, rostr.**	sl. darker	variable
marg. "africana"	Zanz.	16	26	24	**short**	humped	cream	**absent**	**absent**	**crowded**	**absent**	**faint**	**absent**	**absent**	straight	**produced**	as base	**massive**
marg. "africana"	Natal	18	24	22	**medium**	humped	cream	**absent**	**absent**	**crowded**	**absent**	**faint**	**absent**	**absent**	straight	**produced**	variable	**massive**
marg. tuamotensis	Tahiti	11	22	21	**medium**	globular	**white**	**absent**	**absent**	very sparse	**absent**	**dark**	**absent**	**absent**	straight	**thick rostr.**	**as base**	absent
marg. tuamotensis	Tua.	10	22	20	**medium**	globular	**white**	**absent**	**absent**	very sparse	**absent**	**dark**	**absent**	**absent**	sl. curved	**thick rostr.**	**as base**	absent
chiapponii	Phil.	18	24	20	**long**	globular	yellow	**very faint**	**absent**	**absent**	**absent**	**none**	**distinct**	**distinct**	**curved**	**rostrate**	**as base**	**absent**
b. bistrinotata	Phil.	20	20	18	**medium**	humped	oran.:brown	**distinct**	variable	**crowded**	**distinct**	**none**	variable	distinct	sl. curved	**rostrate**	**darker**	**massive**
b. bistrinotata	Keel.	17	19	18	**medium**	humped	orange	variable	absent	**crowded**	**distinct**	**none**	variable	distinct	straight	**rostrate**	**darker**	narrow
b. bistrinotata	Taiwan	19	19	17	**medium**	humped	orange	**distinct**	absent	**crowded**	variable	**none**	variable	distinct	sl. curved	**rostrate**	**darker**	variable
b. mediocris	NCal.	18	17	16	**medium**	elongate	yellow	faint/abs.	**absent**	sparse	variable	**none**	**indist.**	**indist.**	straight	rostrate	variable	**absent**
b. mediocris	Solom.	15	20	17	**medium**	oval	yellow	**faint**	faint abs.	**dense**	variable	**none**	**indist.**	**indist.**	straight	rostrate	variable	absent
b. mediocris	Kwa.	15	21	17	**medium**	elongate	**orange/red**	**sm. distinct**	absent	sparse	variable	**none**	indist.	**distinct**	straight	**rostrate**	darker	**absent**
b. sublaevis	Samoa	13	19	19	medium	elongate	**orange**	**sm. distinct**	absent	sparse	**distinct**	**none**	indist.	distinct	**curved**	blunt	**darker**	**absent**
b. sublaevis	Tahiti	15	22	21	**medium**	oval	**orange**	distinct	faint	crowded	**distinct**	**none**	absent	**indist.**	**curved**	blunt	**darker**	variable
g. globulus	Thail.	22	22	21	**medium**	cylindrical	oran/brown	**absent**	distinct	**crowded**	absent	**none**	**absent**	**absent**	straight	thick rostr.	darker	**absent**
g. globulus	Phil.	19	25	23	**short**	oval / glob.	maroon	absent	**distinct**	**crowded**	variable	**none**	**absent**	**absent**	straight	rostrate	**darker**	narrow
g. globulus	Sri La.	16	22	21	**medium**	oval / glob.	orange	absent	distinct	**crowded**	absent	**none**	**absent**	**absent**	straight	rostrate	darker	narrow
g. brevirostris	Zanz.	14	20	17	**short**	oval	orange	absent	**absent**	**sparse**	**absent**	**none**	**absent**	**absent**	sl. curved	**blunt**	**as base**	variable
g. brevirostris	Eilat	13	24	21	**short**	oval	oran/brown	absent	**absent**	**sparse**	**absent**	**none**	**absent**	**absent**	sl. curved	rostrate	darker	variable
g. brevirostris	Maurit.	13	18	17	**short**	elongate	pale	absent	**absent**	**sparse**	**absent**	**none**	**absent**	**absent**	straight	**blunt**	**as base**	**massive**
g. brevirostris	Tuléar	11	19	17	**short**	elongate	orange	**absent**	**absent**	**sparse**	**absent**	**none**	**absent**	**absent**	straight	**blunt**	as base	narrow
g. sphaeridium	Kwa.	16	25	21	**short**	elongate	**brown**	faint	**distinct**	**sparse**	**distinct**	**none**	**absent**	**absent**	straight	**thin, rostr.**	**darker**	**absent**
g. sphaeridium	Solom.	18	25	22	short	oval / glob.	**brown**	faint/absent	distinct	**crowded**	variable	**none**	**absent**	**absent**	straight	thin, rostr.	**darker**	variable
g. sphaeridium	Samoa	15	23	21	**short**	elongate	**brown**	faint	**distinct**	**sparse**	**distinct**	**none**	**absent**	**absent**	straight	**thin, rostr**	**darker**	**absent**
mauiensis	Hawaii	13	18	17	**medium**	**pyriform**	**cream**	pale	variable	**sparse**	**absent**	**none**	**absent**	**indist.**	sl. curved	**blunt**	**as base**	**massive**

SIZE:
Obtained from the average measurement of all available adult specimens (average length).

AVERAGE NUMBER OF LABRAL AND COLUMELLAR TEETH:
The teeth of each specimen of the lot were counted excluding indistinct crenulations towards the extremities. The numbers given here are the actual number of teeth counted, not the normalized number after SCHILDER & SCHILDER 1938 (relative number of teeth in a hypothetical shell of 25 mm length).

LENGTH OF TEETH AND COLUMELLAR CALLUS BRIDGE:
The length of the teeth is described as short = not reaching the middle of the labrum or mid-base, medium = reaching onto the middle of the labrum or base, or long = reaching far across the labrum and base, touching the margins. In some shells, there is an accumulation of callus more or less covering the teeth. This cover may be present only along the aperture, forming a narrow bridge across the teeth. In some cases, the callus is massive and covers all of the teeth in the mid-third along the aperture.

GENERAL SHAPE:
Although shape in *Pustularia* is rather similar in all species compared with other cypraeids, the tendency of the shell's body (not considering the extremities) was compared.

DORSAL COLOR:
The ground color of the dorsum varies little throughout the genus; it was found to range from cream to brown, with variable shades of yellow or orange. Plain white shells were found to be an exception.

DORSAL BLOTCHES:
These actually consist of three pairs of darker staining on either side of the dorsal line (the name bis-tri-notata refers to these). The mid-dorsal pair is often missing while traces of the anterior dorsal blotch are rather common. The complete absence of any trace of dorsal blotches safely separates a number of species from those groups which occasionally have such traces. Caution: In *P. cicercula*, for instance, there may be an accumulation of brown pattern along the dorsal line, but this is not the same feature, as it is formed by the secondary (adult) pattern. The three pairs of dorsal blotches described here are already formed by the subadult shell (see below), they are always absent in *P. cicercula*.

TERMINAL SPOTS:
Some species show a darker staining of the extremities visible only in the dorsal view. In *Pustularia*, this feature seems of little importance for species and subspecies characterization.

DORSO-MARGINAL SPOTS:
The marginal spotting in *Pustularia* species usually extends also onto the dorsum, where it mixes with a very fine brown mottling or spotting. The latter is a very variable feature and was not compared, while the coarser spotting itself was found to be of relative importance. In granulose species, a spot usually occurs together with a granule.

BASAL BLOTCHES:
In some *Pustularia* species there are two marked blotches on either side of the aperture. This feature was found to be of considerable importance for separation of species and subspecies. In some taxa, the blotches may be small, incomplete, or faint, and sometimes present only in a certain percentage of specimens. In those cases a statistical comparison may be important for identification, especially on the subspecific level.

DORSAL GROOVE:
This feature is usually correlated with the degree of dorsal granulation. Heavily granulose specimens usually have a well-defined and deeply cut dorsal groove. This feature is important for separating species in those cases where it is never found vs. those taxa where it occurs at least occasionally.

BLOTCH AT SPIRE:
Even if a dorsal groove does not exist there is a more or less distinct depression left of the spire in adult shells. In two species, this depression is distinctly blotched darker while it is not in all other taxa.

DORSAL GRANULES:
The degree of granulation and the areas of the dorsum showing granules may vary considerably. The mere fact whether granules may ever be found or not is important for species distinction. The taxa compared in Table 1 are thus interpreted as either granulose ("distinct", "indistinct" or "variable") or smooth ("absent").

APERTURE:
The aperture of all *Pustularia* is very narrow and of the same width throughout. In most taxa, it is rather straight or very slightly curved to the left. There are some taxa, however, in which the aperture shows a distinct curve to the left in the posterior third of the shell.

SHAPE OF EXTREMITIES:
Although in all species of the genus, the extremities have about the same structure, the degree of rostration and the thickness of the terminal spines varies. The data in the table reflect the general impression gained from comparison of the various series.

DENTAL COLOR:
Darker staining of the teeth usually varies considerably within a single lot, but there are certain groups in which this feature is highly consistent. Comparison of the dental color is always made with the color of the middle of the base.

The data in Table 1 reveal that at least five species can be defined on the basis of consistent features. It is also apparent that a population of aberrant shells was examined whose conchological relationship to *bistrinotata* is obvious, apart from very constant features that suggest a distinction at the species level. This population is described below as *Pustularia chiapponii* n. sp.

5. A new species of *Pustularia* from the Philippines

Material
Two lots of live-collected shells were obtained recently from commercial shell dealers. One lot of twelve specimens is from Borongan, Samar, and the other lot of 40 specimens reached the author without locality data except "Philippines". Both lots were mixed with larger quantities of *cicercula*, *margarita* and *globulus*, as well as typical *bistrinotata bistrinotata*, suggesting that the origin is indeed the Philippines. Since both lots of shells show identical shell features, it is assumed that they were collected in the same area. It is astonishing that despite the vast exploitation of the Philippines Islands, even today shells appear which have never before been illustrated or studied.

The new taxon is described here in honor of Dr. Marco Chiapponi of Lecco, who has contributed for a long time to the study of the interesting genus *Pustularia*.

Pustularia chiapponii n. sp.

Description
Greatly inflated, globular. The extremities are distinctly rostrated but barely margined. The spire is large, somewhat projecting, completely covered by a thick callus. Dorsum and margins are densely granulose; those granules are less distinct towards the middle of the dorsum. There is a deep dorsal groove running longitudinally across the shell, forming a Y-shaped depression bordering the posterior extremity. The posterior terminal callosity is well developed. The aperture is narrow and conspicuously curved to the left in the posterior third.

The teeth on both sides are fine, rather weak, but well defined throughout their way across both labrum and base and far onto the margins on both sides where they meet the dorsal pustules. The posterior labral margin is crossed by the teeth, which thus are visible as spiny processes in the dorsal view. The entire shell is pale yellow, there are no traces of basal blotches, nor is there any staining of the teeth. The yellow color is slightly paler only towards the aperture. There are three barely perceptible darker patches dorsally, which may be interpreted as

Pustularia chiapponii n. sp. : Borongan, Philippines. Series of the types. The holotype is on the left.

blotches. These are, however, not separated by the dorsal groove. There are no traces of smaller marginal or dorsal spots.

The paratypes correspond exactly with the holotype; none of the features described above are subject to perceptible variation.

Designated types

Length x width x height (mm), (labral teeth: columellar teeth), depository

Holotype:	19.1 x 12.6 x 11.4	(24 : 22)
	coll. HDN Cismar	
Paratype 1:	19.1 x 12.6 x 11.6	(24 : 18)
	coll. Chiapponi	
Paratype 2:	16.4 x 10.4 x 9.4	(25 : 18)
	coll. Chiapponi	
Paratype 3:	17.7 x 11.5 x 10.2	(24 : 18)
	coll. Lorenz	
Paratype 4:	19.4 x 12.3 x 11.0	(22 : 18)
	coll. Lorenz	
Paratype 5:	18.7 x 11.5 x 10.3	(25 : 19)
	coll. Lorenz	
Paratype 6:	19.7 x 12.3 x 11.0	(25 : 19)
	coll. Chiapponi	
Paratype 7:	17.9 x 11.1 x 9.9	(24 : 18)
	coll. Chiapponi	

Type locality

The only ascertained locality of the new species is Borongan, Eastern Samar Island, Philippines. The habitat is unknown but suspected to be rather shallow water.

Discussion

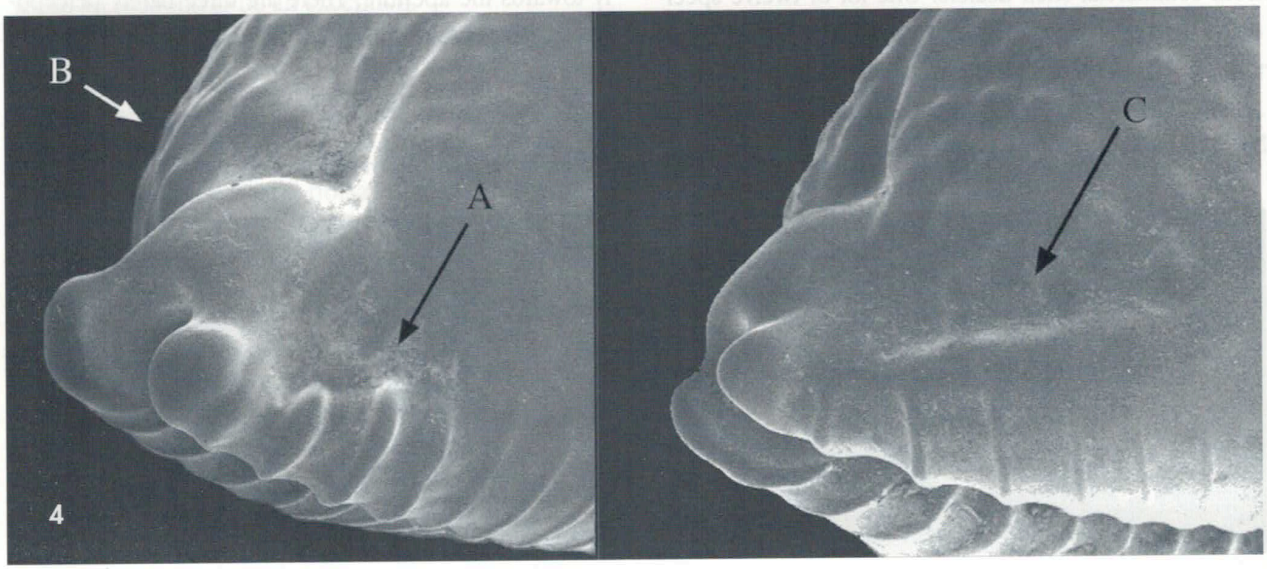
Pustularia chiapponii belongs to the group of pustulose species without a spire blotch. The only similar species, therefore, is *P. bistrinotata* from which it differs by the following features: complete absence of basal blotches in all specimens known. There are some specimens of *bistrinotata*, especially of its Melanesian subspecies *mediocris*, in which the basal blotches are reduced, incomplete, or even absent. In *mediocris*, the percentage of specimens without basal blotches is 40% for Solomon populations and 25 % for New Caledonian populations. In 60% of the Solomon specimens and 75% of the New Caledonian specimens, there are at least apparent remnants of basal blotches.

In *chiapponii*, the teeth are long, extending far across the base and the labrum, they are never interrupted by a callus bridge, and in no specimen are they shorter mid-way on either side. In none of the populations of *bistrinotata* are there teeth of comparable length. Furthermore, the teeth meet with the dorsal granules, which are often connected.

In *P. bistrinotata*, the pustules are usually separate and distinct from each other (Fig. 5). The posterior labral teeth cross the terminal margin (Fig. 4, left). This feature is seen only in exceptional specimens of *bistrinotata*. All populations of *bistrinotata* show a brown spotting of the margins as well as the dorsum. Smaller spotting is not developed in *chiapponii*.

The dorsal blotches characteristic of *bistrinotata* are almost absent in *chiapponii*, in which the darker zone is not split in two by the groove mid-dorsally. The spire of

Fig. 4: The characteristic posterior extremity of a *Pustularia*. Left: *P. chiapponii* n. sp., right: *P. bistrinotata*. (SEM photos)



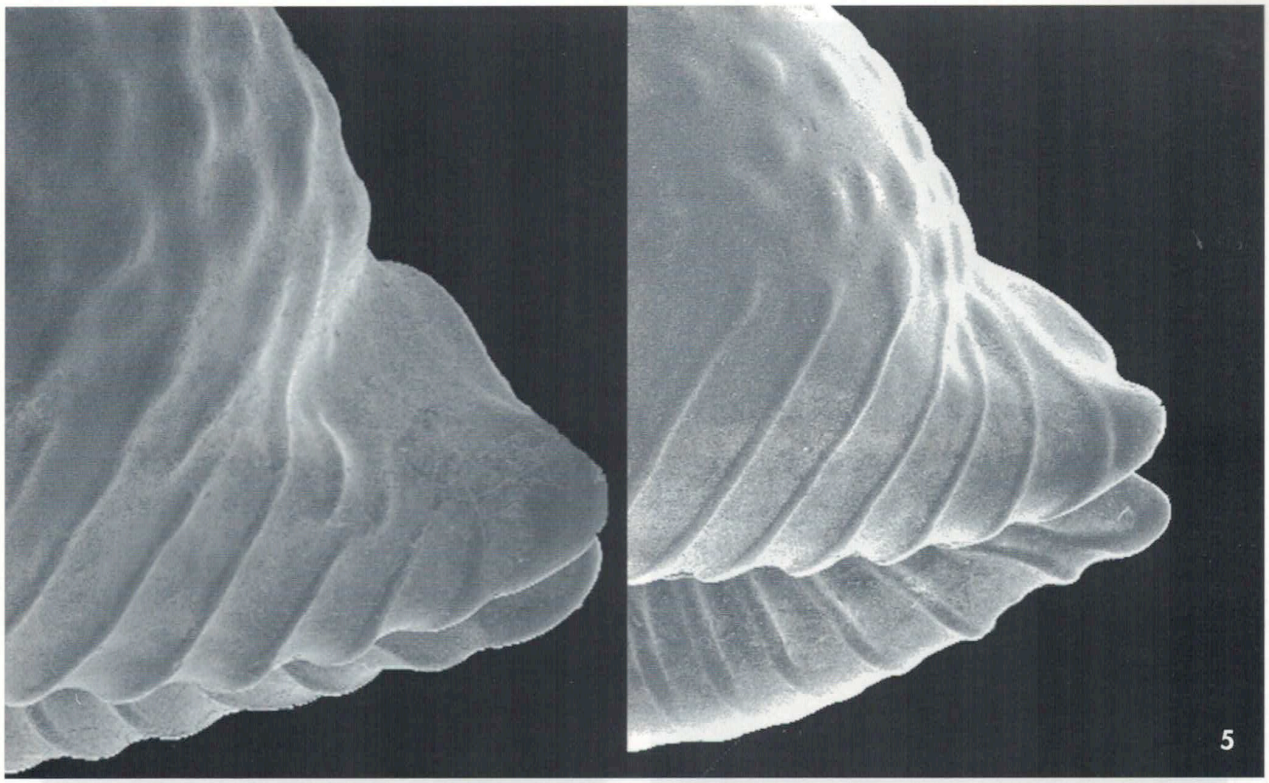


Fig. 5: The characteristic posterior extremity of a *Pustularia* (columellar view) Left: *P. chiapponii* n. sp., right: *P. bistrinotata*. (SEM photos). Note the connected pustules in *P. chiapponii*.

chiapponii is large, situated right of the posterior extremity, and despite being covered by callus, is still visible as a slight projection (Fig. 4, right). This is usually not seen in *bistrinotata*. The distinctly curved aperture is typical in the Polynesian *sublaevis* but rarely in populations of the Western Pacific. Finally, the general shape of *chiapponii* differs by being more globular, with the extremities being coarser and rather knobby.

The pale yellow color all over is only found in southeastern Melanesian populations of *mediocris*, and especially in New Caledonian shells. Those, however, are less inflated, their dorsal groove is indistinct, the basal blotches are faint but visible, the teeth are coarser and much shorter, and the posterior columellar teeth do not cross the posterior labral margin towards the dorsum.

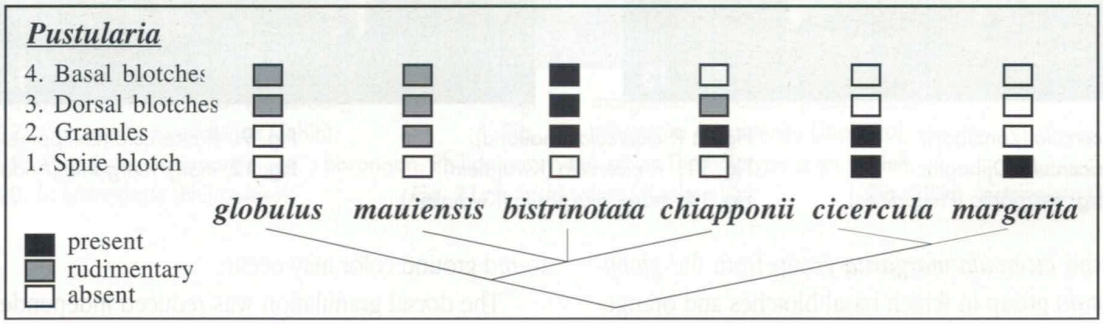
There is no problem distinguishing *chiapponii* from other members of the genus.

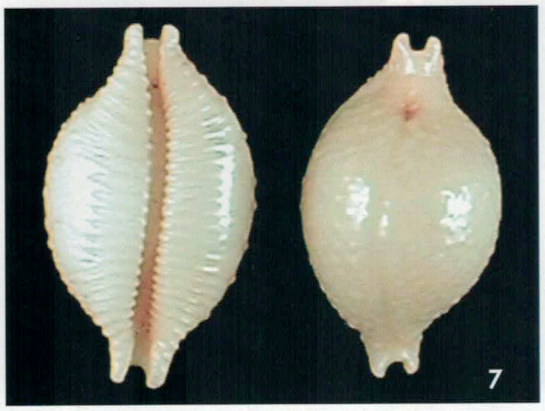
6. The living species of *Pustularia*

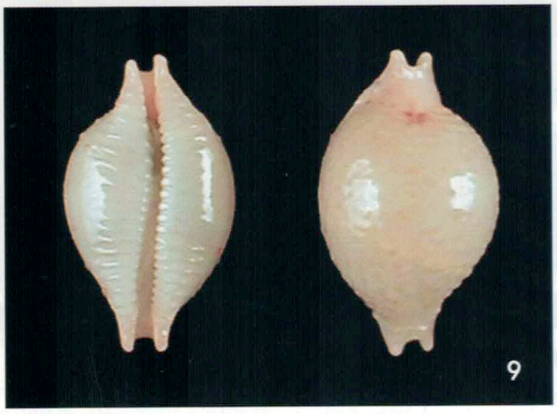
A cladographic comparison of all species and subspecies of the genus based on those features whose statistic consistency is greatest, would produce relationships given in Fig. 6.

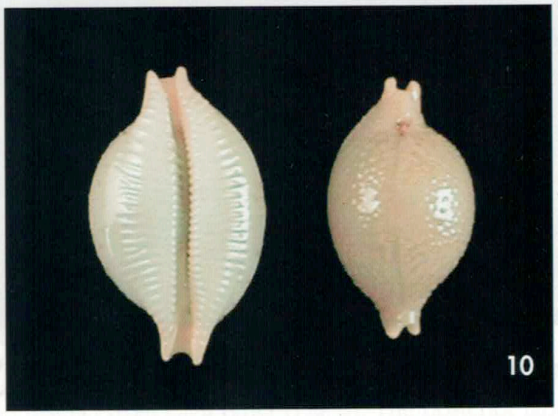
According to this interpretation, the presence or absence of a spire blotch is ranked as a conservative feature that has been lost completely in one lineage while it was retained in the other. It is the most consistent and apparent feature, along with a number of linked characteristics

Fig. 6: A possible cladographic interpretation of the living species of *Pustularia*









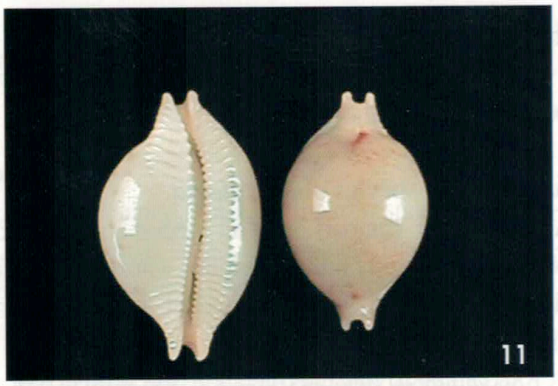


Fig. 7: *P. cicercula* (Zanzibar);
Fig. 8: *P. cicercula* (Thailand);
Fig. 9: *P. cicercula* (Philippines);
Fig. 10: *P. cicercula* (Djibouti);
Fig. 11: *P. cicercula* (Kwajalein);
Fig. 12: *marg. margarita* (Andam.)
Fig. 13: *marg. margarita* (Philippines)
Fig. 14: *marg. margarita* (Kwajalein)

separating the *cicercula/margarita* group from the *globulus/bistrinotata* group in which basal blotches and orange-to-red ground color may occur.

The dorsal granulation was reduced independently

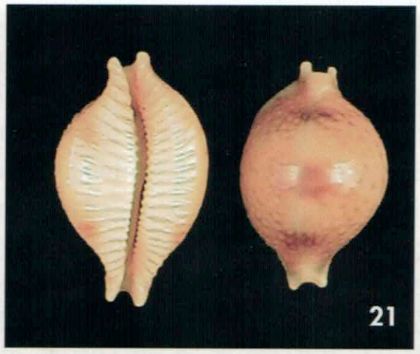


Fig. 15: *margarita "africana"* (Zanzibar); **Fig. 16:** *margarita "africana"* (Natal);
Fig. 17: *margarita tuamotensis* (Tahiti); **Fig. 18:** *margarita tuamotensis* (Tuamotu);
Fig. 19: *Pustularia chiapponii* n. sp. : Borongan, Philippines. Types series.The holotype is on the left.
Fig. 20: *b. bistrinotata* (Philippines) **Fig. 21:** *b. bistrinotata* (Keeling Isl.) **Fig. 22:** *b. bistrinotata* (Taiwan)

(as a secondary adaptation) in both lineages: in the *cicercula/margarita* group (*margarita*) and in the *globulus/bistrinotata* group (*globulus*, and to a high degree in *mauiensis*). It is a feature shared with the related Indo-Pacific *Staphylaea*, but not with the older ancestral Atlantic forms, such as *Proadusta*.

In *mauiensis*, rudimentary granulation is present in occasional specimens, as is the basal and dorsal blotching. This places *mauiensis* in close proximity to *bistrinotata*. In all three, *globulus*, *bistrinotata*, and *mauiensis*, the basal blotching is either well-produced or at least rudimentary, whereas in *chiapponii* it is lost.

The number of features that are not found in *chiapponii* (blotches on base and dorsum, marginal spotting, no columellar callus bridge) weigh against those which are specific for *chiapponii* (longer teeth, connecting granules, curved aperture, projecting spire, denticulate posterior labral margin). The features compared in the cladogram are merely of a conchological nature and do not necessarily reveal biological relationships. This particular cladogram is not the only possible one, but a consequence of the above-made interpretations.

The group of shells with a distinct spire blotch consists of two species, *cicercula* and *margarita*. Both have a distinct spire blotch that is not found in the other taxa. Furthermore, both have no trace of basal or dorsal blotches. Recent radula studies confirm their status (LORENZ, 1998). BRADNER & KAY (1996) also illustrate the radulae of *cicercula* and *margarita*. Their illustrations show radulae of a certain variability but with apparent differences between the taxa.

In specimens from Kwajalein, the mantle of *cicercula* shows a darker spotting, the papillae are rather thin and short. In *margarita* from the same locality, the mantle is translucent, with only few white spots encircling the somewhat thicker and longer papillae. How well these features can be used to draw conclusions, however, is so far uncertain. Interestingly, the somewhat rarer *margarita* has a wider distribution and a far greater geographic variability compared to *cicercula*. Three forms are compared in the table. The rare western *africana* hardly differs from typical *margarita*, whereas the features of *tuamotensis* are rather constant and remarkable. It is suggested that *tuamotensis* deserves subspecific rank.

As can be seen by comparing the data in Table 1, *P. cicercula* shows little variation throughout its wide distribution. Specimens from the western Indian Ocean are occasionally distinguished as subspecies or form *lienardi* (JOUSSEAUME 1874). The features assigned to this taxon by SCHILDER & SCHILDER 1952 simply cannot be ascertained for East African or Red Sea specimens, merely the smaller average size is relatively constant.

A set of shells from Oahu, Hawaii should be mentioned here, provisionally incorporated as "*?cicercula*" in Table 1. Conchologically, these specimens have intermediate features between *cicercula* and *margarita*, as the dorsum is usually smooth on top but faintly pustulate towards the rostrated extremities. The teeth are very fine and unstained. The most striking feature is the reduction of the spire blotch, which is barely visible in some specimens. The systematic position of this population is so far still under study.

The group of shells without spire blotch is split into four species, *chiapponii*, *bistrinotata*, *mauiensis* and *globulus*.

P. chiapponii, in which no basal blotches, no marginal spotting, but a distinct granulation are found. It is the least variable species with a very limited distribution in the Philippines.

P. bistrinotata, the most variable species, with a number of geographic subspecies and varieties which are compared in Table 1. Generally, the species is characterized by the combination of four basal blotches, three pairs of dorsal blotches separated by a more or less distinct sulcus, and the pustulose surface. In the western *b. bistrinotata* the dorsum is rather humped, the teeth are nearly always stained darker, the basal blotches are distinct and large, the dorsal blotches are dark and wide, the dorsal ground color is a saturated reddish-brown and the marginal spots are dense and dark. The name *keelingensis* was introduced for specimens from the Indian Ocean. It is described as being more humped, less granulose, without distinct dorsal sulcus and less produced teeth, the basal blotches are described as being well-marked. Such shells are found throughout the Philippines, and mainly in Samar and Bohol, but the shell differences claimed to distinguish *keelingensis* by SCHILDER & SCHILDER (1952) could not be verified on the basis of shells from Cocos/Keeling Island and other western localities. In Melanesia and Micronesia, the paler and more elongate *mediocris* occurs. In Micronesian populations the shells are rather small, rostrated, and bright orange, while Melanesian

specimens are usually yellowish. Callused, larger and rather pale New Caledonian specimens have been separated as forma *cicerculaeformis* RAYBAUDI, 1993. The less granulose, more distinctly curved and blotched Polynesian *sublaevis* is considered a subspecies here, judging from the series examined. However, the separation from *mediocris* is sometimes difficult and only possible when larger numbers of shells from known localities are compared.

As already mentioned, the Hawaiian *P. mauiensis* occasionally shows two or even all four basal blotches and, more commonly, three dorsal blotches. This phenomenon reveals a close relationship with *bistrinotata.* In many specimens, a very indistinct granulation is visible on the anterior portion of the dorsum. The status of *mauiensis* as a valid species can be confirmed by this study, mainly because of the coarser, shorter, and always unstained teeth, as well as a different dorsal and basal ground color.

P. globulus is subdivided into three geographical subspecies: The western *brevirostris* SCHILDER & SCHILDER, 1938 is characterized by smaller size, absence of staining on the teeth, and lack of basal blotches. It is a well-distinguished geographic subspecies ranging from the East African coast to Mozambique, the Seychelles to the Mascarenes, maintaining the characteristic features.

Specimens from the Red Sea show a dark staining of the teeth, which suggests that (despite smaller size) these belong to *g. globulus* rather than *brevirostris.* The shells of *g. globulus* from the northern and Central Indian Ocean are often cylindrical rather than globular, the teeth are only faintly marked with brown, the extremities are short and rather solid, four basal spots are seen but rarely.

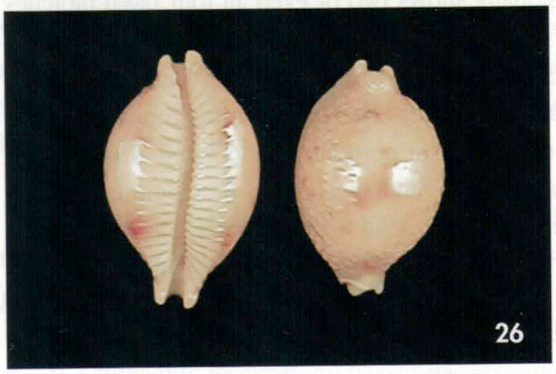
Smaller, more rostrated shells with darker teeth and four distinct basal spots are found in Pacific regions, especially Melanesia and western Polynesia. This eastern form is well known as *P. globulus sphaeridium* SCHILDER & SCHILDER, 1938. The development of typical *globulus* to *sphaeridium* is rather gradual, as can be seen from the data in the table.

Philippine specimens may resemble those from the Solomons which can be assigned to *sphaeridium.* Still, the status of *sphaeridium* might be considered as a geographical subspecies with a considerable overlapping zone in the western Pacific, while the populations from western Polynesia and Micronesia are consistent in their features and have little resemblance to classic specimens from Sri Lanka or Thailand.

The systematics of the living members of the genus *Pustularia* according to this study appear as follows:

Genus: *Pustularia*

1. *cicercula* (LINNÉ, 1758)
   syn.: *lienardi* JOUSS. 1874, *vulavula* STEADM. & COTT. 1943
2.1 *margarita* (DILLWYN, 1817)
   syn.: *tricornis* JOUSS. 1874
2.2 *margarita tuamotensis* LORENZ & HUBERT, 1993
3.1. *bistrinotata bistrinotata* SCHILDER & SCHILDER, 1937
   syn.: *quadrimaculata* DAUTZ. & BOUGE 1933,
   keelingensis SCH. & SCH. 1940, *jandeprezi* POPPE& MARTIN, 1997
3.2. *bistrinotata mediocris* SCHILDER & SCHILDER, 1938
3.3. *bistrinotata sublaevis* SCHILDER & SCHILDER, 1938
4.1. *globulus globulus* (LINNÉ, 1758)
   syn.: *affinis* GM. 1791, *tetsuakii* KIRA 1959
4.2. *globulus brevirostris* SCHILDER & SCHILDER, 1938
4.3. *globulus sphaeridium* SCHILDER & SCHILDER, 1938
5. *mauiensis* (BURGESS, 1967)



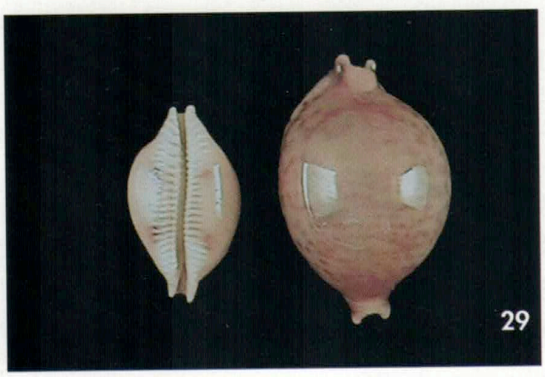
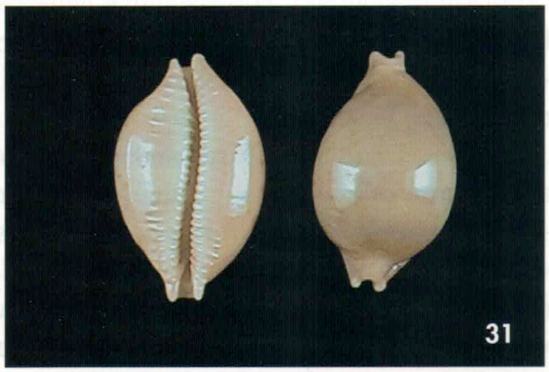


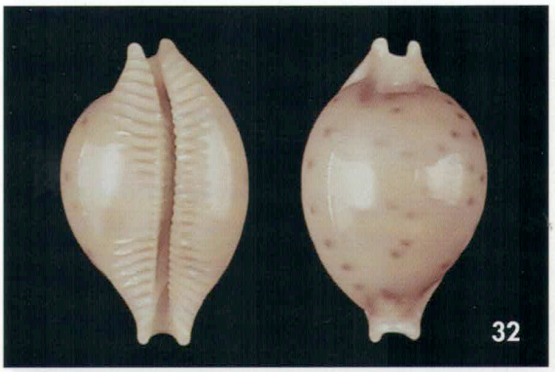
Fig. 23: *b. mediocris* (N. Caledonia);
Fig. 24: *b. mediocris* (Solomon Isl.);
Fig. 25: *b. mediocris* (Kwajalein);
Fig. 26: *b. sublaevis* (Samoa);
Fig. 27: *b. sublaevis* (Tahiti);
Fig. 28: *g. globulus* (Thailand)
Fig. 29: *g. globulus* (Philippines)
Fig. 30: *g. globulus* (Sri Lanka)

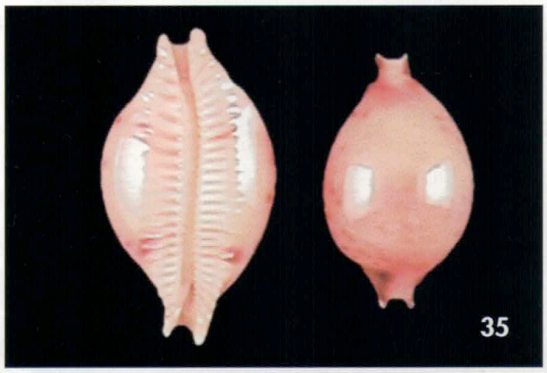
6. *chiapponii* n. sp.

7. The subadult shells of *Pustularia*

Subadult *bistrinotata* show three blurred darker basal blotches, which later become encircled by darker spot-







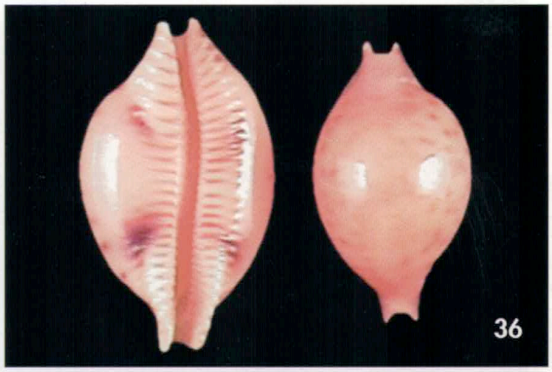


Fig. 31: *b. brevirostris* (Zanzibar)
Fig. 32: *b. brevirostris* (Bilat)
Fig. 33: *b. brevirostris* (Mauritius)
Fig. 34: *b. brevirostris* (Tuléar)
Fig. 35: *g. sphaeridium* (Kwajalein)
Fig. 36: *g. sphaeridium* (Solomon Isl.)
Fig. 37: *g. sphaeridium* (Samoa)
Fig. 38: *mauiensis:* (Hawaii)

ting rising upward from the margins. The basal blotches form rather late in development, as do the dorsal granules. In general, subadult shells of *Pustularia* have shorter teeth, a high gloss, no development of granules, a partly exposed spire and a posterior extremity without the characteristic structure seen in all adult *Pustularia.*

Recently, *P. jandeprezi* Poppe & Martin, 1997 was described from the Philippines and compared with *bistrinotata.* First impression of the diagnosis suggests

that it is based entirely on subadult specimens of *bistrinotata*. In fact, subadult specimens of *bistrinotata* are found throughout its distribution, and they do resemble the holotype of *jandeprezi* in every respect. The authors explain that their type is a fully adult shell with well-formed dentition and extremities and a callused base.

The description reads as follows:

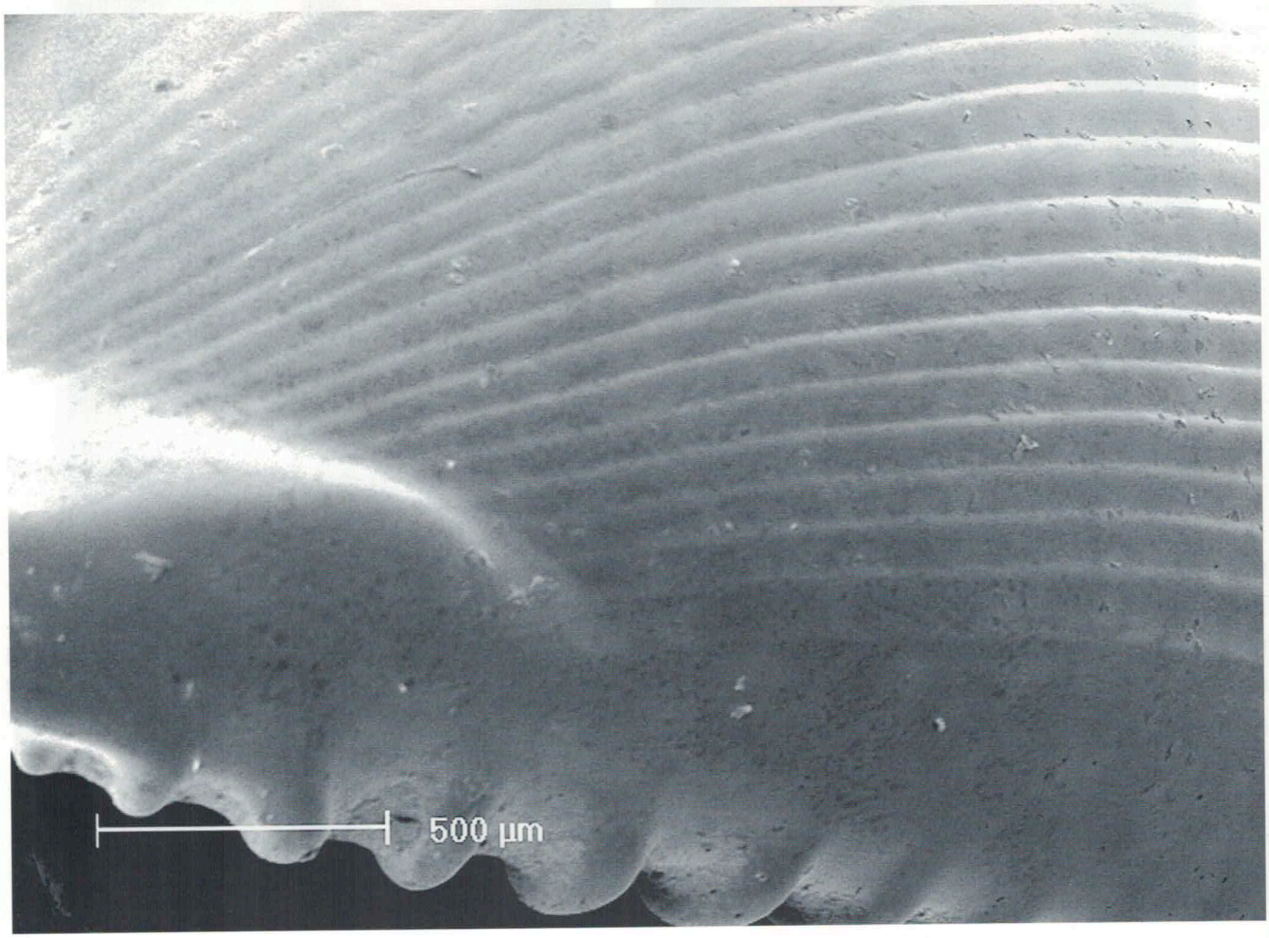
"Shell thin, solid, very globose. The general shape is oval-globular. The extremities are thin, solid and long. The teeth are fine and short. The callus on the base is thick, white to slightly olive colored. Basal blotches may be present or absent. The dorsal color varies from cream-white to olive-brown, most often with a mid-dorsal blotch. The rounded dorsum is smooth and no specimens with dorsal granules are known. The teeth on the columellar side number between 20 and 25. The labial teeth between 21 and 28. The spire is prominent, even in heavy adults. A dorsal line is absent. One paratype [No. 11] is almost entirely white colored, without marginal spotting, and with a pale mid-dorsal blotch (...)" [I suspect that latter specimen, which shows absolutely no similarity to any of the other types might be *P. chiapponii*].

In the discussion, POPPE and MARTIN stress the absence of any dorsal granules and color differences compared to *bistrinotata* from the same area, as well as the exposed spire even in callused shells of *jandeprezi*. The latter is always concealed in adult *bistrinotata*. There is, according to the authors, also a difference in shape and number of teeth compared to *bistrinotata*.

Comparison made between subadult specimens of *bistrinotata* from various localities with the illustrations of the *jandeprezi* types did not reveal any significant difference, but as the holotype is claimed to be an adult shell, the status of *jandeprezi* remains an open question.

Subadult shells of other *Pustularia* species are translucent and mostly white. The western

Fig. 39: *Pustularia margarita*, subadult. SEM-Photograph (500x)



brevirostris is plain white, the extremities short and spiny. On the columellar side, a longitudinal denticulate ridge forms prior to the strong dentition. It is soon covered by callus and teeth, which extend onto the base as the shell reaches maturity. Also in *cicercula* and *margarita*, the young shells are white, translucent, with a comparable columellar ridge. The latter is typical in adult specimens of the rare *Nesiocypraea lisetae*, for which subadult *cicercula* or *margarita* are occasionally "mistaken" by dealers. In early stages of all *Pustularia*, the spire is still exposed. In such shells, the surface (especially on the labral side) shows longitudinal growth ridges visible under magnification (Fig. 39). In *cicercula* and *margarita*, the subadult shells show two darker transverse bands that are never preserved in fully adult shells.

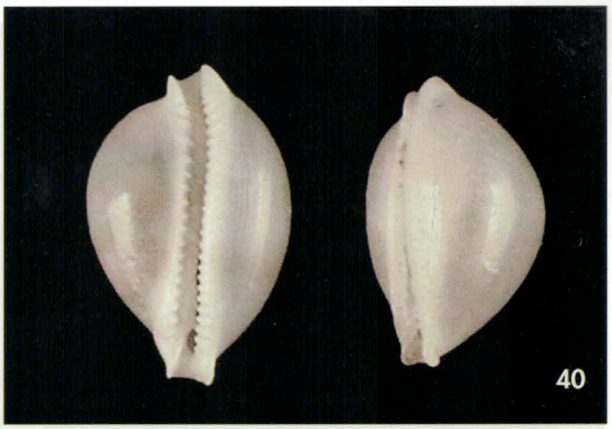
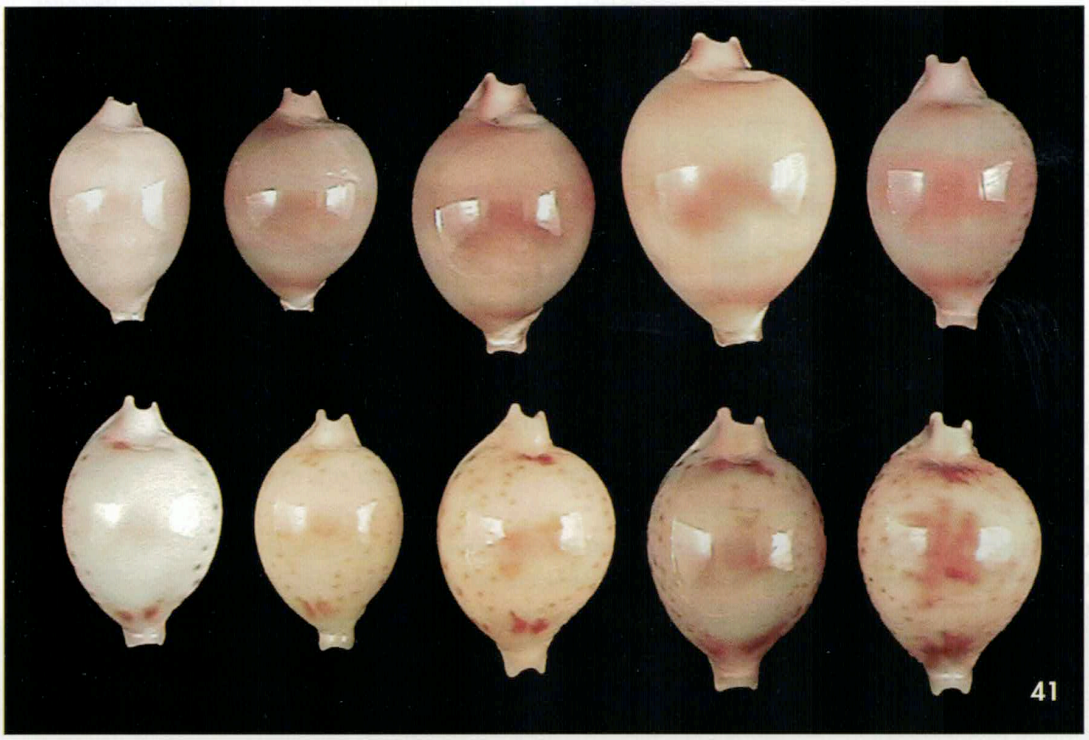


Fig. 40: *margarita:juvenile specimen* (Kwajalein); note the fine longitudinal striae on the labral side

Fig. 41: *bistrinotata* : growth stages from subadult to adult showing gradual development, from *"jandeprezi"* = subadult (left) to the typical form



8. Relationship between locality and average shell length

Another interesting aspect that can be derived from Table 1 is the change in average size from western to eastern localities. Splitting the Indo-Pacific into five sectors, the average shell lengths of each sector vary considerably within a species: shells from the western Pacific are largest, while those from East Africa and eastern Polynesia are considerably smaller (Fig. 43).

The reasons for this phenomenon are so far unknown. In other genera of Cypraeidae a similar increase in size from western to eastern localities has so far not been confirmed.

Acknowledgements

The present study could not have been carried out without the assistance of colleagues and friends. Many thanks to Prof. Dr. Alex HUBERT†, Scott JOHNSON (Kwajalein) Prof. em. Dr. Dr. hc.

Fig. 42: *? cicercula*: (Hawaii)

Günther STERBA (Markkleeberg); Dr. Hans Werner KOYRO (Gießen); Prof. Dr. Klaus-Jürgen GÖTTING (Pohlheim); Prof. Dr. Erhard SCHULTE (Alten-Buseck), Mohammed MAKUNGU (Zanzibar); Guido POPPE (Berchem); Dr. Marco CHIAPPONI (Lecco), Ludwig GABRIELLI (Neuss), Dr. Vollrath WIESE (Cismar), Manfred BLÖCHER (Duisburg), Capt. Felix and Ingrid LORENZ (Lauenburg), and Jana KRATZSCH (Buseck-Beuern).

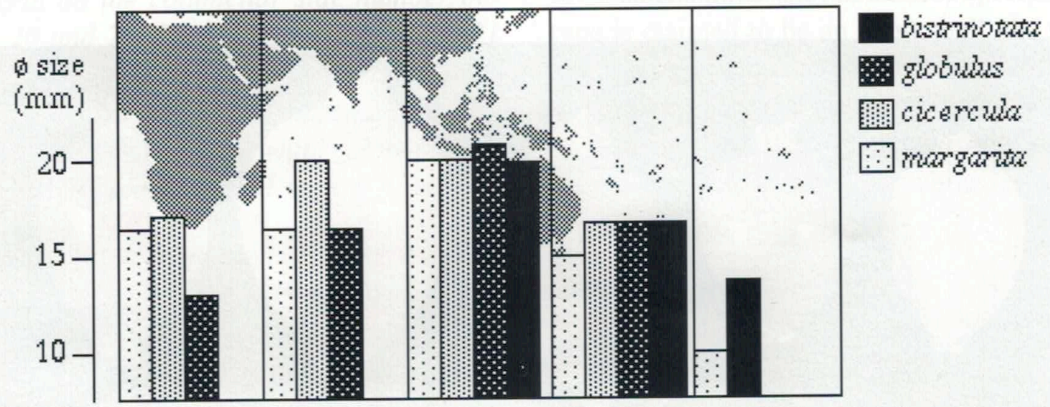


Fig. 43: Change of average shell size with geographic region

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