

Review of the genus *Pachy bathron* Gaskoin, 1853 (Gastropoda : Cystiscidae)

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ABSTRACT. The species of the genus *Pachy bathron* Gaskoin, 1853 are studied. Four species are revised, all recorded from the southern Caribbean sea, and a new species, *P. olssoni* sp. n., is described from Panama. The external anatomy and the radula of the majority of the animals are presented. Information is given on the habitat and distribution of each species. The biogeographical aspects are discussed.

RESUME. Les espèces du genre *Pachy bathron* Gaskoin 1853 sont étudiées. Quatre espèces sont révisées, toutes rapportées du sud de la mer Caraïbe, et une nouvelle espèce, *P. olssoni* sp. n., est décrite du Panama occidental. L'anatomie externe et la radula des animaux sont présentées. Des informations sont données sur l'habitat et la distribution des espèces. Les aspects biogéographiques sont discutés.

INTRODUCTION

The genus *Pachy bathron* was described by Gaskoin (1853, p.356-358), and was based upon two species : *P. cassidiforme* Gaskoin, 1853 and *P. marginelloideum* Gaskoin, 1853. *P. cassidiforme* was described first, and must therefore be considered as the type species. This species remained very elusive for more than a century, with even the holotype being apparently lost. It was neither figured nor recorded in collections after its description until a photograph of a shell from the Coen Collection (HUI) was presented by Coomans (1973, p. 12). In the same paper, Coomans demonstrated that the type locality recorded by Gaskoin ('Island of St. Vincent') should be interpreted as a Caribbean locality as opposed to a West African one.

Since its description by Gaskoin, the familial placement of the genus *Pachy bathron* has been much discussed. Gaskoin himself (1853, p.356) declined to associate the genus with the Marginellidae, Cassidae or Cypraeidae. Coomans (1972) presented, in chronological order, the different stages of this discussion by previous authors but failed to add the important comments of Sowerby (1852, re-ed) to this debate. Sowerby stressed the resemblance of the species he illustrated (*P. marginelloides*) to those of the genus *Marginella* (*sensu lato*), and he characterised the original features of the genus *Pachy bathron* thus : '....the columellar lip spread

over the body whorl and the teeth continued across it in folds.' Sowerby also noted that *Marginella kieneriana* Petit, 1838 was close to *P. marginelloides* and commented that this could associate the genus *Pachy bathron* with the 'Marginellae'.

Six taxa, all described from Caribbean localities, present a shell morphology which allow their placement into the genus *Pachy bathron* :

Marginella kieneriana Petit, 1838

Erato cypraeoides C.B. Adams, 1845

Pachy bathron cassidiforme Gaskoin, 1853

Pachy bathron marginelloideum Gaskoin, 1853

Pachy bathron tayrona Diaz and Velasquez, 1987

Microcassis colettae Paulmier, 1997

They all share the shell features of a very long and narrow aperture, a moderate to heavily callused columella, callused parietal surface traversed by continuations of columellar plaits, a strongly denticulated inner lip, marked transverse lirae regularly spaced along the internal apertural wall, and a tendency to form a pattern of chevrons of various configurations on the body whorl.

During the last 30 years, several partial revisions of the genus have been published. Coomans (1972 and 1973) recognised two species ; *P. cassidiforme* Gaskoin and *P. cypraeoides* C.B. Adams (Synonym : *P. marginelloideum* Gaskoin) assigning them to 'the

Marginellid genus *Pachy bathron*, related to *Persicula* (1973, p. 12).

Diaz and Velasquez (1987) attributed the same two species to the 'Marginellid genus *Pachy bathron*' and described as new a third species, *P. tayrona*, from northern Colombia.

More recently, however, Coovert and Coovert (1995) declined to assignate generic status to *Pachy bathron*, for the moment preferring instead to place it within the genus *Persicula* as part of the family Cystiscidae Stimpson, 1865.

The obtaining and observation of living specimens corresponding to the six taxa quoted above, together with the re-evaluation of the available type material, has enabled the current authors to propose a general revision of the genus *Pachy bathron*.

During the preparation of this work, several new *Pachy bathron* populations have been discovered off the coasts of Panama. One is possibly a western population of *P. tayrona*, whereas the other has sufficient original features to allow its description as a new species.

MATERIAL AND METHODS

Living specimens of four species of *Pachy bathron* were collected by several means:

- *P. kieneriana* was collected by small boat dredging in Central Venezuela by F. Boyer and later by F. Hennequin. T. McCleery also dredged this species in Central Venezuela, and in addition scuba dived for it (hand sieve technique) in Los Testigos Islands.

- *P. cypraeoides* was collected by diving and snorkelling in the Netherlands and Venezuelan Antilles by T. McCleery (a suction technique being used to extract sand and sediment, which was then hand sieved).

- *P. cassidiforme* was collected by diving in Martinique by P. Clovel, and in St. Vincent, Grenadines and Grenada by G. Mackintosh.

- *P. aff. tayrona* was collected by snorkelling (using suction apparatus and hand sieve technique) in the San Blas Islands, Eastern Panama by T. McCleery.

Numerous shells of a new species were obtained from Marcos Alvarez (Panama City). These shells were presented as several lots, variously labelled as coming from either the Caribbean region of Bocas del Toro, the Veraguas region with coasts both on the Caribbean and Pacific sides of Panama, or three localities from West Panama namely the Azuero Peninsula, and the Montuosas and Ladrone Islands. Taking natural variability into account, these shells were found to be conchologically conspecific. Due to the referred localities and to the depths and dates of the samples taken, most of these data are considered to be credible, and they are used as such for the determination of a specific distribution on both sides of the isthmus of Panama.

Field sketches and photography of the living animals were performed in most cases, and several specimens of each species were preserved in 70% isopropyl alcohol for later radular studies.

The radulae were extracted by E. Rolán and scanning electron microscope images produced (C.A.C.T.I., University of Vigo, Spain.)

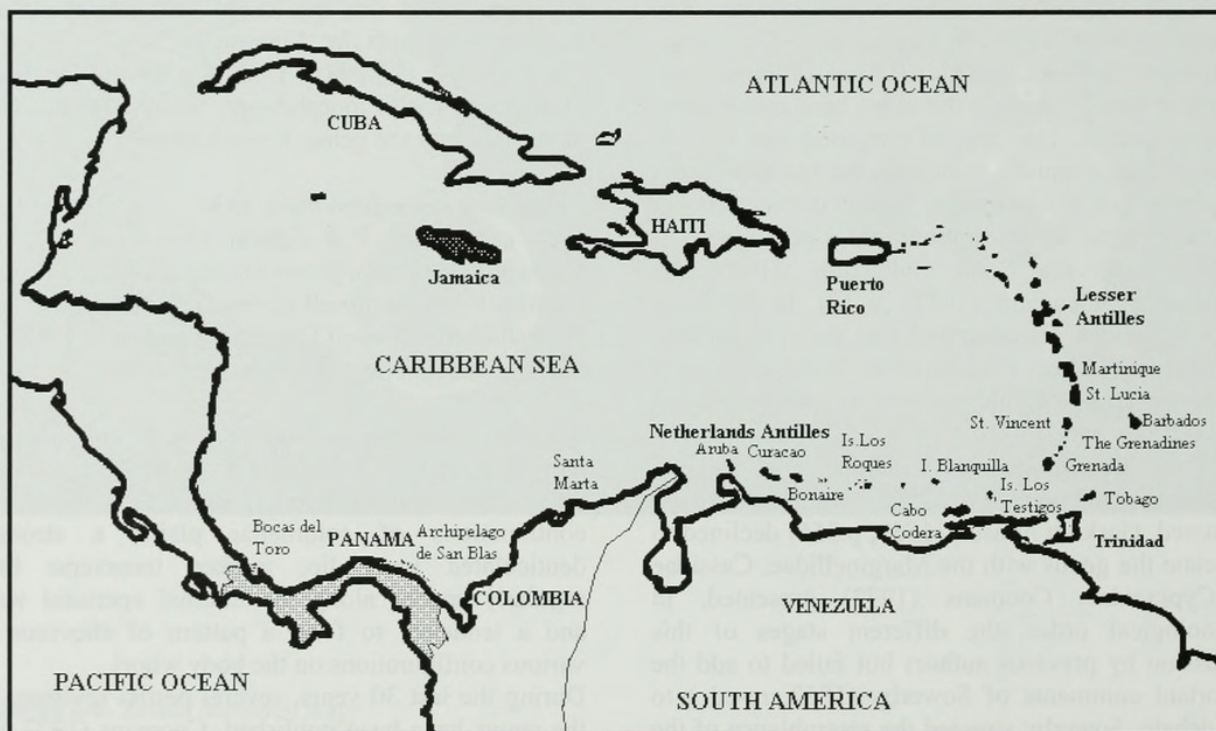


Fig. 1.

Map showing the area of distribution of the genus *Pachy bathron*

ABBREVIATIONS AND TERMINOLOGY

The following abbreviations are used in this paper:

NHM: Natural History Museum, London, England.
 HJ: Hebrew University of Jerusalem, Israel.
 IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles.
 MCZ: Museum of Comparative Zoology, Harvard, Massachusetts, U.S.A.
 MHNLR: Muséum d'Histoire Naturelle, La Rochelle, France.
 MNHN: Muséum national d'Histoire naturelle, Paris, France.
 MOL: Instituto de Investigaciones Marinas de Punta de Betin, 'INVEMAR', Santa Marta, Colombia.
 SMF: Seckenberg Museum, Frankfurt, Germany.
 ZMA: Zoologische Museum, Amsterdam, The Netherlands.
 AWC: Andrew Wakefield Collection.
 FBC: Franck Boyer Collection.
 TMC: Tony McCleery Collection.
 JCC: Jacques Colomb Collection, Marseilles, France
 LBC: Luigi Bozzetti Collection, Milan, Italy.
 ABC: The Islands of Aruba, Bonaire and Curacao which together comprise the Netherlands Antilles.

For the purposes of this paper, 'specimen' refers to a live taken specimen, whereas 'shell' refers to a dead collected shell.

SYSTEMATICS

Family **CYSTISCIDAE** Stimpson, 1865

Genus *Pachyathron* Gaskoin, 1853.

Type species : *Pachyathron cassidiforme* Gaskoin, 1853 (subsequent designation by Adams and Adams, 1858).

Pachyathron kieneriana (Petit, 1838)

Figs. 2-3, 18, 22-27, 50-51.

Marginella kieneriana Petit, 1838, p.20.

Type material. One syntype, considered to be the holotype, in MNHN, 11.5 x 7.6mm (Figs. 2-3).

Other material examined. - Puerto Frances, Cabo Codera, Central Venezuela, dredged and dived September 1999 on coarse muddy sand at 20 m. 8 adult specimens (8.3 x 5.2mm to 12.0 x 8.7mm), AWC.

- Puerto Frances, Cabo Codera, Central Venezuela, dredged February 1997 in sticky black mud at 25 m, 1 adult specimen (9.65 x 5.9 mm), AWC.

- Puerto Frances, Cabo Codera, Central Venezuela, dredged and dived September 1999 on coarse muddy sand at 20 m, 16 adult specimens (9.3 x 5.9 mm to 13.3 x 9.5 mm), TMC, (Figs. 22-24).

- Puerto Frances, Cabo Codera, Central Venezuela, dredged February 1997 from coarse coral sand at 15

m to sticky mud at 25 m, 12 adult specimens (9.1 x 5.7mm to 13.4 x 9.1mm), 3 juvenile specimens (6.0 x 4.0mm to 12.5 x 8.5 mm) and 1 adult shell (12.0 x 7.85mm), FBC.

- Isla Grande, Is. Los Testigos, Venezuela, dived June 1999 on coarse clean sand at 20 – 21m, 4 adult specimens (8.0 x 4.5mm to 8.9 x 5.3mm), AWC, and 3 adult specimens (7.5 x 4.4 mm to 8.6 x 5.1 mm), TMC, (Figs.25-27).

- Tobago, 2 large shells, Dautzenberg Collection (IRSNB).

Original description. '*Marginella kieneriana*, Petit. Long:12 mill. Larg:9 mill. – Testa parva piriforme, fulva, maculis albis transverses per quarto series dispositis ornate : spira brevissima, exsertiuscula, labro crasso, vix intus crenulato plicis columella octonis.'

Complementary Notes. Shell glossy, rarely completely smooth, usually with heavy growth lines. Medium to large sized for the genus (length 8mm to 12.5mm, possibly larger) comprising 2.5 whorls (excluding protoconch of 1.5 whorls) and presenting variety of outlines from globular, ovoid or pyriform, to sub-cylindric (Los Testigos). Spire slightly elevated and smooth with glazed suture. Aperture curved, narrow and parallel sided with very little anterior flare. Inner aspect of lip with 22-24 denticles. Lip thickened internally with no external callus formation. 8 columellar plaits. Weak parietal callus traversed by 8 plaits. Strong parietal callus ridge at entrance to aperture. All of parietal callus blends into glaze of body whorl with no posterior groove to separate the two.

Colour variable. Base colour tan. Olive green bands encircle body whorl either concentrated as one main central band, or as three or four narrower ones. These bands form the background to the spiral chevron pattern. Spiral chevron pattern of 5-7 evenly spaced rows from sub-sutural level to anterior extremity. Pattern comprises white blotches with rounded to pointed black chevrons pointing towards the growing edge of the shell. Nearer to the lip, extra white marks and associated chevrons are formed between the regular rows, disrupting the regular pattern. Spire colour reddish tan, becoming paler towards protoconch, which is translucent at the nucleus (Figs. 22-27). Specimens which retain the basic pattern but are weakly coloured, appearing yellowish to pinkish tan overall, are often found amongst the typical darker shells.

The following description of the animal is based on the study of several specimens from Puerto Frances (Fig. 18): Typical Cystiscid Type 4 animal (after Coover & Coover 1995). Foot reddish brown with opaque white blotches, some fusing together to form larger irregular edged patches. Bilobed head opaque white, each half having a streak of reddish brown running from slightly behind the small black eye,

medially and anteriorly to meet the other at its tip. Eyes situated at the base of the two short reddish brown tentacles. Siphon short, opaque white, and fringed at its tip with reddish brown.

The radula was extracted from a specimen from Puerto Frances (Figs. 50-51) : Type 3 Cystiscid radula (after Coover & Coover 1995). Very thin (10 μ m), cord like, uniserial radula with approximately 400 strongly arched and overlapping rachidian plates. Each plate has 9 sharply pointed cusps, the strongest being the single central cusp. The lateral cusps are slightly smaller, with the most lateral tooth being diminutive.

Type locality. Les Plages de la Guayra, Venezuela.

Distribution. The species has been found from La Guayra (central mainland coast of Venezuela) to Los Testigos Islands and Tobago. Due to its various habitats, it could well have a wider distribution in Venezuelan mainland coastal locations as well as in offshore island groups. Unconfirmed reports that this species has been found in Brazil require verification.

Habitat. Available records indicate an important variability of habitats, from sticky black mud to coarse clean white coral sand. The bathymetric range of distribution of the species is currently known to be from 15 to 25 m.

Remarks. This species has the most distinctive shell of all the group, and has until now been considered to be a member of the genus *Persicula* by most authors. It does possess, however, all of the defining characteristics of the genus *Pachy bathron* (ovoid to pyriform shell shape, slightly elevated spire, parietal callus with horizontal plaits, labial denticles, chevronned pattern, body whorl often with numerous growth lines, and similarities in the chromatism of the soft parts of the animal), and therefore the authors consider that its correct taxonomic assignation should be within this genus.

The central Venezuelan coastal populations exhibit considerable variability of size, morphology and colour pattern. Specimens from Los Testigos Islands, however, all appear to have more constant characters (size, very regular rows of chevrons, and a very dark brown parietal callus and anterior notch). This may be a phenotypic expression of the smaller genetic pool found within relatively smaller isolated colonies in the offshore island localities. The minor differences in shell shape and colour pattern between

both populations are not considered of sufficient magnitude to permit separation into different species, unless further analysis of the animals suggests this is indicated.

***Pachy bathron cypraeoides* (C.B. Adams, 1845)**

Figs. 4-10, 19, 28-37, 52-53, 56-58.

Erato cypraeoides C.B. Adams, 1845, p.1-2.

Pachy bathron marginelloideum Gaskoin, 1853, pp. 357 – 358, figs. 4-6.

Type material. Two syntypes are deposited in MCZ and were examined by the authors. Though badly worn and faded, one syntype is clearly recognizable as being representative of the species (Figs. 5-7). This specimen was figured as a black and white photograph by Clench and Turner (1950, p.271, fig. 11) in their revision of the species described by Adams. This selection by Clench and Turner must be considered as the designation of a lectotype. The paralectotype is in fact the shell of another species, *Persicula chrysomelina* (Redfield, 1848). The lectotype, ref. No. 186065, measures 7.9 x 5.2mm. The holotype of *P. marginelloideum* is recorded as being deposited in Cabinet Gaskoin in the NHM but no trace of it can be found there and so it is presumed lost. It measured 7.1 x 4.1mm.

Other material examined. - Aruba harbour, Netherlands Antilles. Suction, followed by hand sieving, September 1999 from grass and rubble at 0.5-1m, numerous adult specimens (6.5 x 4.5mm to 8.5 x 5.5mm.), TMC, (Figs. 28-30).

- Aruba harbour. Dived and hand sieved September 1999 from sand and coral rubble at 0.5 – 1m, two adult specimens (measuring 8.4 x 5.4mm and 7.4 x 4.8mm), and one juvenile specimen, used for radular examination (5.2 x 3.2mm), AWC.

- East of Aruba harbour. Snorkelled and hand sieved September 1999 from sand and coral rubble at 2-2.5m, one adult specimen, TMC.

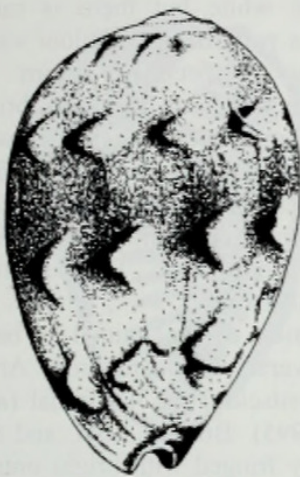
- Malmok bay, Aruba. Dived and hand sieved September 1999 from sand and coral rubble at 7- 8m, seven adult specimens (6.0 x 4.0mm to 7.4 x 4.6mm), TMC, (Figs 31-33).

- Malmok, Aruba. On clean sand at 7m. One specimen (6.8 x 4.1mm) and one shell (8.0 x 5.15mm), FBC.

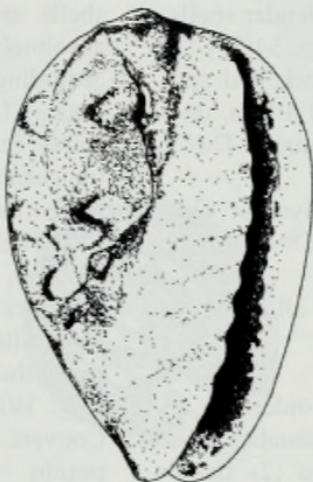
- Arasji, Aruba. Two adult shells and two juvenile shells, FBC.

Figures 2-10.

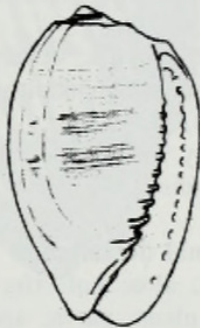
2-3. *P. kieneriana* Petit, 1838, syntype (MNHN), 11.5x7.6mm; **4.** *P. cypraeoides* C.B. Adams, 1845, La Blanquilla, Venezuelan Antilles, 4.35x2.8mm; **5-7.** *P. cypraeoides* C.B. Adams, 1845, lectotype (MCZ), 7.9x5.2mm; **8-10.** *P. cypraeoides* C.B. Adams, 1845, original figures.



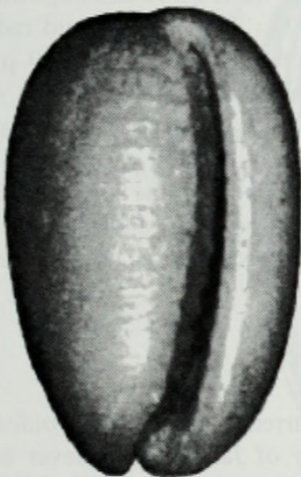
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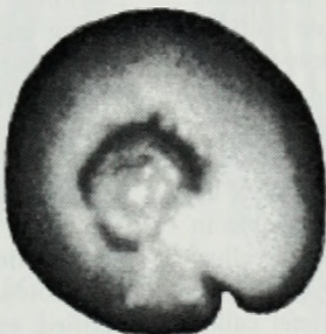
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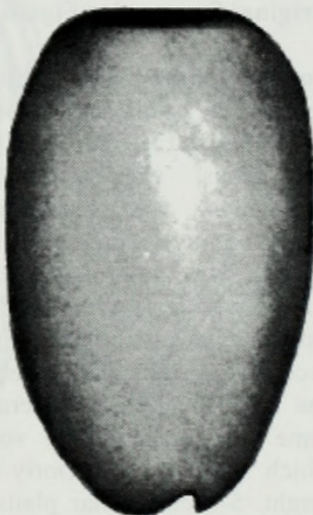
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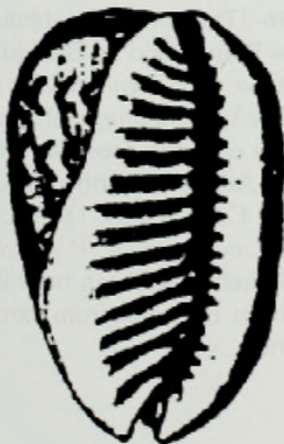
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- Lac Bay, Bonaire, Netherlands Antilles. Snorkelled and hand sieved 1998 from grass and rubble at 2m, one adult specimen (7.0 x 4.1mm), TMC.
- Curacao, Netherlands Antilles. Eight slender shells (5.3 x 3.2mm to 6.2 x 3.6mm), LBC, (Figs. 34-35).
- Los Roques, Venezuelan Antilles. Snorkelled and hand sieved July 1999 from white sand at 1m, one adult specimen measuring (6.5 x 4.1mm), TMC, (figs. 36-37).
- La Blanquilla, Venezuelan Antilles. Dived at 12m on sand, one subadult specimen (4.35 x 2.8mm), JCC (Fig. 4).
- Many specimens and shells in ZMA, all listed in Coomans (1972, p.91).

Original description. 'Erato (?) cypraeoides M. t. solida, alba; anf. ifra suturam fusco-canaliculis; spira plana, parva; apertura lineari, pro (2) funde emarginata; labro extra crasso, intus exile crenulato; labio per totum transversum exile plicato. Long. .325 poll.; lat. .2 poll. Jamaica.'

Original figures. See Figs. 8-10.

Complementary notes. Shell glossy, medium to heavily callused and ribbed with growth lines. Medium sized (length from 5.2 mm to 8.5 mm) for the genus. Comprising 2 whorls (excluding protoconch), and presenting an ob-ovate outline. Spire slightly depressed with a low lens-shaped, translucent white protoconch, comprising 1.5 whorls. Suture irregular, glazed over.

Aperture narrow, slightly curved and parallel sided except for a slight flare anteriorly. Inner aspect of lip has 15-18 denticles, obliterated and uncountable in some specimens due to very heavy labial callus, which extends posteriorly slightly beyond spire height. 5-9 columellar plaits. Strong parietal callus with 12-14 plaits lying horizontally across it, commencing from the parietal callus ridge. Edge of parietal callus demarcated in its posterior half by a deep groove. Anterior half gradually merges into glaze of body whorl.

Base colour of shell pure white. General appearance is yellowish off-white, due to presence of fine axial pattern which extends to cover the whole of the body whorl except the internal and external labial callus, and the parietal callus and columella which are all white. Microscopically the fine axial yellow brown lines are drawn sharply towards the lip forming 4-5 rows of sharp arrowheads. Macroscopically these are visible as spiral bands which appear slightly darker than the area in between. In many specimens the

pattern can be extremely faint, and is then reduced to 4 -5 fine double rows of tiny brown spots representing the bases of the arrowheads. Occasional shells are almost pure white but there is rarely absolutely no trace of a pattern. Spire colour varies according to locality ; specimens from the Aruba, Malmok Bay population all have dark brown spires (excluding the protoconch which is always translucent white), whereas other populations from Aruba have colour absent from the spire (Figs. 28-33). The specimen from Klein Curacao (Coomans 1972, p. 92) also has a dark spire. This feature is therefore in need of further study.

The following description of the animal is based upon the study of several specimens from Aruba (Fig. 19) : Typical Cystiscid Type 4 Animal (after Coover & Coover, 1995). Bilobed head, and foot peachy - orange, finely fringed with bright orange. Midline and posterior part of foot also marked with bright orange. Tentacles short, completely orange. Eyes tiny, black, situated medially at base of tentacles.

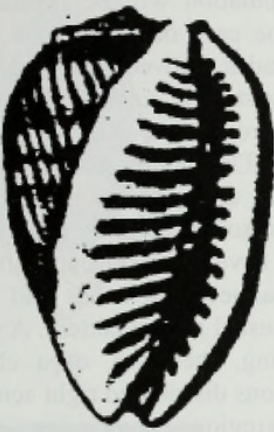
The radula was extracted from a sub-adult specimen from Aruba (Figs. 52-53) : Type 3 Cystiscid radula (after Coover & Coover 1995): Very thin (9 µm), cord like, uniserial radula with approximately 400 strongly arched and overlapping rachidian plates. Each plate has 7 - 9 sharply pointed cusps along the cutting edge, the strongest being the single central cusp. The lateral cusps can be of unequal size and are slightly smaller, the most lateral tooth being diminutive.

Type locality. Jamaica.

Distribution. The occurrence of *P. cypraeoides* in the quoted type locality of Jamaica has never been verified, and in fact remains distinctly unlikely. This can be concluded for the following reasons. Firstly, all the records from the date of the original description to the present day are from the ABC islands of the Netherlands Antilles, except two new recent records (Figs. 4, 36-37) from the neighbouring Venezuelan Antilles (Los Roques and La Blanquilla). Secondly, the paralectotype of *P. cypraeoides* is in fact a shell of *Persicula chrysomelina*, well known as a Netherlands Antillean endemic species. Finally, in the same paper C.B. Adams described another species (*Volvarina rubella* C.B. Adams, 1845) citing the same type locality as *P. cypraeoides*. *V. rubella* is well known from the Southern Caribbean but like *P. cypraeoides* has never been recorded from Jamaica since its original description.

Figures 11-17.

11-13. *P. cassidiforme* Gaskoin, 1853, original figures; **14-15.** *Microcassis colettiae* Paulmier, 1997, original figures; **16-17.** *P. tayrona* Diaz & Velasquez, 1987, paratype MOL895, 8.7x5.0mm.



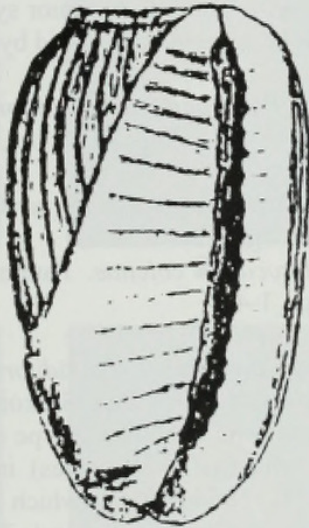
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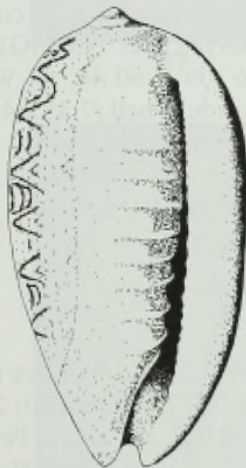
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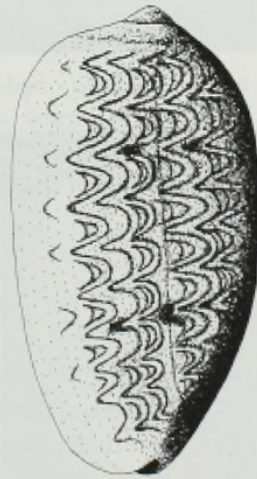
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It can therefore be assumed that C.B. Adams described *P. cypraeoides* from a lot of shells collected in the ABC islands. At this period in history, there was an active shipping trade between Jamaica and the ABC Island group, and Adams could have procured this particular lot of shells from a merchant vessel or similar source. The lectotype has a distinctly dark spire, and it is possible that it could have originated from the dark spired Malmok population (Aruba).

Based upon current collecting records, and the above albeit circumstantial evidence, we propose to provisionally consider that the distribution of *P. cypraeoides* is restricted to the Southern Antilles (ABC Islands to La Blanquilla). The apparent scarcity of the species in the Venezuelan Antilles (although this area has been reasonably well sampled during the last decade) is probably an indication that this archipelago could represent the extreme eastern edge of the geographical range of the species. The practically unexplored Paraguana Peninsula of mainland Venezuela is in close proximity to the Netherlands Antilles, and the presence of supposed endemic species from the ABC Islands must be investigated there. For example, two specimens of *Volvarina vokesi* de Jong & Coomans, 1988 were collected in the Park of Morocoyo, State of Falcon, 100km south of Bonaire Island (AWC).

In the collection of one of the authors (FBC) is a shell resembling *P. cypraeoides* which belonged to a lot of dead collected material from an old collection, with the label 'Callao, Peru'. This shell is identical to the material examined from the ABC islands, and was mixed with shells of several undetermined species of *Volvarina*, apparently not from the ABC islands. Future sampling of the molluscan fauna along the western coasts of Colombia, Ecuador and Peru should reveal if a sibling species of *P. cypraeoides* really does occur in the Panamic province.

We propose the Islands of the Netherlands Antilles (Aruba, Bonaire, Curacao) as the revised type locality of *P. cypraeoides*.

Habitat. In coral rubble and *Thalassia* beds. Compact communities were observed in Aruba at 0.5-3m and again at 7-8m. Coomans (1972, p. 92) quotes a fresh specimen taken at 60m near Klein Curacao (deposited in NNM).

Figures 18-33.

18. *P. kieneriana* Petit, 1838, live animal; 19. *P. cypraeoides* C.B. Adams, 1845, live animal. 20. *P. cassidiforme* Gaskoin, 1853, live animal; 21. *P. aff. tayrona* Diaz & Velasquez, 1987, live animal; 22-24. *P. kieneriana* Petit, 1838, Puerto Frances, Cabo Codera, Venezuela, 10.5x6.8mm. 25-27. *P. kieneriana* Petit, 1838, Isla Grande, Los Testigos, Venezuela, 8.7x5.1mm; 28-30. *P. cypraeoides* C.B. Adams, 1845, Aruba Harbour, Netherlands Antilles, 8.5x5.5mm; 31-33. *P. cypraeoides* C.B. Adams, 1845, Malmok, Aruba, Netherlands Antilles, 7.4x4.6mm.

Remarks. The lot of small slender shells from Curacao (Figs. 34-35) could simply represent a local form of *P. cypraeoides*. The obtaining of live specimens of this population will be necessary to determine if this is the case or if they are in fact morphological intergrades between the eastern *P. cassidiforme* and the western *P. tayrona*. In addition, the two specimens from Los Roques and La Blanquilla (Figs. 4, 36-37), though assigned here to the taxa *P. cypraeoides*, are certainly not typical of that species. They have some morphological affinity with *P. cassidiforme*, have a translucent white shell with seven narrow opaque spiral bands and only a faint suggestion of the usual zigzag pattern. A picture appears to be emerging, therefore, of a cline of *Pachyathron* populations distributed right across the Southern Caribbean region, comprising several sibling species distributed at geographic intervals. The original description and the type figures of *P. marginelloideum* (Figs. 8-10) are a perfect match for the species *P. cypraeoides*, thereby making *P. marginelloideum* its junior synonym. This synonymy has been previously stated by Coomans (1972).

Pachyathron cassidiforme Gaskoin, 1853

Figs. 11-13, 20, 38-39, 54.

Pachyathron cassidiforme Gaskoin, 1853, pp. 356-357, figs 1-3.

Microcassis colettae, Paulmier 1997, pp. 733-748. Figs. 1-4, 9.

Type material. *P. cassidiforme* is recorded as being deposited in Cabinet Gaskoin, British Museum, but there is no trace of the type specimen (nor any other specimen of this species) in the collections at the NHM. The holotype (which measured 6.3 x 3.8mm) is therefore presumed lost. The specimen from HUI (ref. No. 31.587/1 ex. Coll. Coen 2008), figured in Coomans (1973, p. 12) is here designated as neotype. Length 6.8mm. Locality: Grenadines, Lesser Antilles.

The type material of *M. colettae* is as follows:

- Holotype.(Ref. No. MG1): Insular shelf, Martinique 14 36' 06 N-60 46' 44 W dredged in white sand at 60m. Adult shell (7.55 x 4.35mm), MHNLR.

- Paratypes (Ref. No. MG2): Same locality as holotype. Six adult shells (from 5.75 x 3.5mm to 7.4 x 4.2mm), MHNLR.



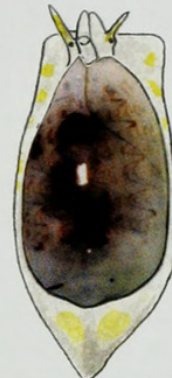
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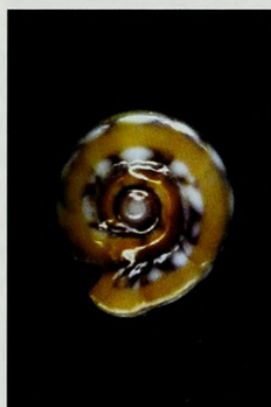
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Other material examined. - Isle de Ronde, Grenada (north end of bay), dived 1998 in coral rubble at 7m, one adult shell (5.8 x 3.6mm), TMC, (Figs. 38-39).

- Anse d'Arlet, Martinique. Scuba and hand sieved January 1999 under flat coral rock in sand at 22-30m, one adult specimen (5.2 x 3.6mm), TMC ; two adult specimens (6.0 x 3.8mm and 5.65 x 3.5mm), AWC ; one specimen (3.3mm long) and four shells (from 5.1 to 5.35mm in length), FBC.

- Baliceaux Island, St. Vincent. Dived and sieved May 1997 from sand at 13m, one specimen (measuring 6.1 x 3.9mm), AWC.

- Frigate Is, Grenada. Dived at night in sand at 8m. One specimen (5.3mm long), FBC.

Original description. 'Shell subcylindrico-ovate, opaque-white colour, three continuous bands a few shades darker than the shell traverse the dorsum ; dorsum coarsely striated longitudinally ; spire rather depressed, subacuminated, volutions four, irregularly crenulated ; the posterior edge of the last whorl forms a coronated ridge at the base, of which a deep depression surrounds the shell terminating at the outer part of the aperture ; base rather round, broad and very thick, abrupt at its outer border, and extends over the anterior third of the side of the shell, terminating on the columellar extremity ; aperture rather narrow, slightly curved ; outer lip thick and finely denticulated along the inner edge ; columellar side, about twelve or fourteen distant linear teeth transvers the entire base and terminate on the inner margin of the columellar groove ; columellar groove shallow ; extremities flat (perpendicularly), rather prominent and keeled, posterior end of aperture not rostrated ; channel deep and rather short.'

Original figures. See Figs. 11-13 for *P. cassidiforme* and Figs. 14, 15 for *M. colettiae*.

Complementary notes. Shell small for the genus and has the original feature of an unglazed body whorl, even in fresh specimens. The regular growth lines are the most numerous of the genus, and result in a distinctly axially costate body whorl.

The following description of the animal is based upon a study of a single specimen from Martinique (Fig. 20) : Typical Cystiscid Type 4 animal (after Coover & Coover 1995). The foot, which does not extend very far out of the shell, is translucent grey with yellowish patches of various sizes, and on the specimen examined, two large yellow patches

situated either side of the midline on the posterior part of the foot. Tentacles translucent grey except the middle third which is bright orange. Lateral surfaces of each head lobe also bright orange, this extending to surround the tiny black eyes which are situated on the medial aspect of the base of the tentacles.

The radula was extracted from a specimen from Martinique (Figs. 54) : Type 3 Cystiscid radula (after Coover & Coover 1995): Very thin (7 μ m), cord like, uniserial radula with 425 strongly arched and overlapping rachidian plates. Each plate has 9 sharply pointed cusps, the strongest being the single central cusp. The lateral cusps are slightly smaller, the most lateral tooth being diminutive.

Type locality. Island of St. Vincent.

Distribution. Known only from the southeastern Antilles, from Martinique to Grenada.

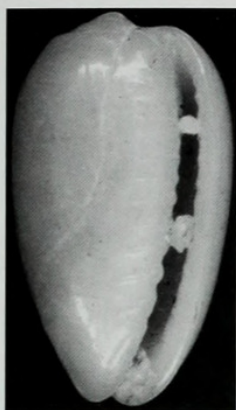
Habitat. Found by divers in coral rubble and sand under coral slabs at 7-30m. The species seems to be a sand dweller, moving at night (G. Mackintosh, pers. comm.). Its bathymetric range of distribution must be considered as deeper than this as *M. colettiae* was found as deep as 123m (Paulmier, 1997).

Remarks. Living specimens of this species were only discovered in the Grenadines as recently as 1997 by G. Mackintosh, and a short time later by P. Clovel in Martinique. The axial costae, unglazed body whorl and dark blotch at the base of the columella enable this species to be easily identified, and there does not appear to be any distinguishing feature by which specimens from Martinique can be separated from Grenadian examples.

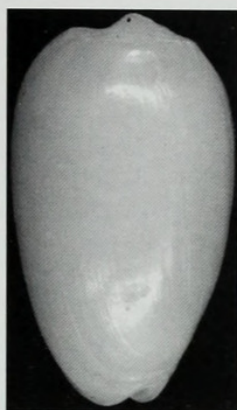
Paulmier (1997) makes no mention of the possibility of the animal being a Marginelliform gastropod, but instead considers it to be associated with the *Cassidae*. The study of dead shells only may be partly responsible for this. Paulmier therefore not only assigns an invalid species name, but also erroneously creates a new Genus, *Microcassis*. Nevertheless, Paulmier's work is useful in that it presents new information on the bathymetric range of the species, which can be considerably extended to 123 metres. It has been confirmed herein that the species is in fact a Cystiscid, and is the same as that described in 1853 by Gaskoin as *Pachyathron cassidiforme*. *Microcassis colettiae* Paulmier, 1997 is therefore a junior synonym of *P. cassidiforme*, Gaskoin, 1853.

Figures 34-49.

34-35. *P. cypraeoides* C.B. Adams, 1845, Curacao, Netherlands Antilles, 6.2x3.6mm; **36-37.** *P. cypraeoides* C.B. Adams, 1845, Los Roques, Venezuelan Antilles, 6.5x4.1mm; **38-39.** *P. cassidiforme* Gaskoin, 1853, Isle de Ronde, Grenada. 5.8x3.6mm; **40-42.** *P. aff. tayrona* Diaz & Velasquez, 1987, Porvenir, San Blas Archipelago, East Panama, 6.5x3.9mm; **43-45.** *P. olssoni* sp. n., Escudo de Veraguas Is, Bocas del Toro, East Panama. Holotype (NHM) 5.0x3.4mm; **46-47.** *P. olssoni* sp. n., Escudo de Veraguas Is, Bocas del Toro, East Panama. Paratype 6, 5.4x3.5mm; **48-49.** *P. olssoni* sp. n., Peninsula de Azuero, West Panama, Paratype 7, 5.9x4.0mm.



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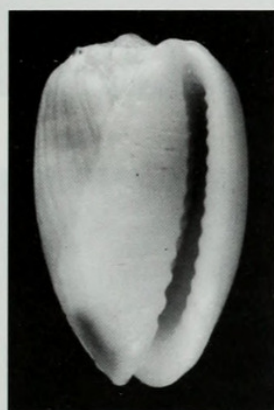
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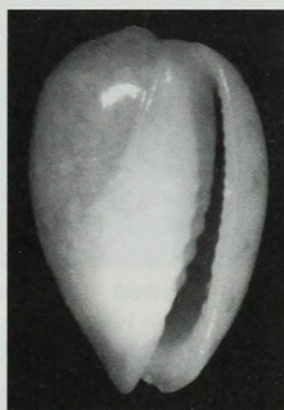
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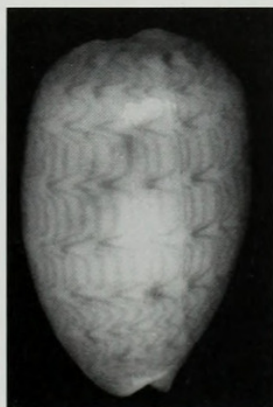
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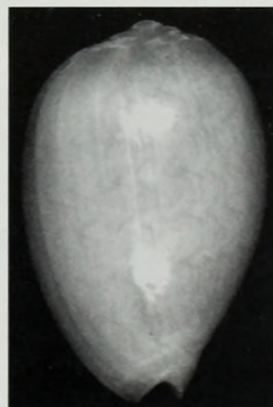
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***Pachy bathron tayrona* Diaz & Velasquez, 1987**

Figs. 16-17, 21, 40-42, 55.

Pachy bathron tayrona Diaz & Velasquez, 1987, pp. 217 – 221.**Type material.** - Holotype (Ref. no. 305966): Bahía de Chengue, Colombia, in *Thalassia* meadow at 0.5m. Adult specimen (10.2 x 5.8mm), SMF.- Paratypes (Ref. nos. 305967 / 305968): Bahía de Chengue, Colombia, in *Thalassia* meadow at 0.5m. One adult shell (8.2 x 4.7mm), and one juvenile shell (no dimensions given), SMF.- Paratypes (Ref. nos. 895 / 896): Bahía de Chengue, Colombia, in *Thalassia* meadow at 0.5m. One adult specimen (9.4 x 5.2mm), and one adult shell (11.5 x 6.3mm), MOL.**Other material examined** - Porvenir, San Blas Archipelago, East Panama. In erosions in *Thalassia* beds in 1.5-2m. 36 adult specimens (from 5.6 x 3.4mm to 7.3 x 4.3mm), TMC, (Figs. 40-42) ; 11 specimens (from 6.4 x 3.6mm to 7.0 x 4.1mm), AWC; two adult and one juvenile shells, FBC.**Original Description.** 'Shell medium sized (up to 11.5mm total length), obovated, thick shelled, glossy, with a rather blunt, low but unconcealed spire. Nucleus rather blunt, tan, apparently with two whorls, and covered by an irregular line. Surface of the spire may present some enamellous bulges along the suture. Body whorl smooth and polished; some fresh specimens (over 5.0mm long) bear four to six fine longitudinal scissulations on the body whorl, which can be better recognised on the dorsal side and near the outer lip.

Aperture rather narrow, extending about 6/7 of total length. It becomes anteriorly somewhat wider, twists lightly to the left and forms a distinct anterior notch, visible from the dorsal view. A callous formation along the parietal wall is poorly developed but visible: it extends above the end of the aperture towards the upper suture of the penultimate whorl and is minutely pitted.

There are nine to thirteen linear folds on the pillar whorl, the upper ones becoming nearly or completely obsolete. These pillar folds continue undiminished into the interior of the columella. Outer lip thickened, minutely pitted and bearing 18 – 20 denticulations.

Shell tan to dirty white, highly polished, spire occasionally with light brown to chestnut streaks or mottlings at the suture. Body whorl shows numerous microscopical wavy or interrupted longitudinal

brown lines, which become widely spaced towards the outer lip. Some side by side running and uninterrupted lines form simultaneously a single arrow – pointed mark at regular intervals. Some other lines are weaker coloured and interrupted at the same intervals where the darker ones form the arrow – like flexures, leaving thus whitened spaces between two arrow series. Macroscopically this colour pattern is expressed as eight to nine spiral rows of whitened mottlings alternating with brown stains on a tan background. Some rows are usually more conspicuously coloured than others. In young and worn specimens, the colour pattern fades away, leaving a light tan or pure white shell.'

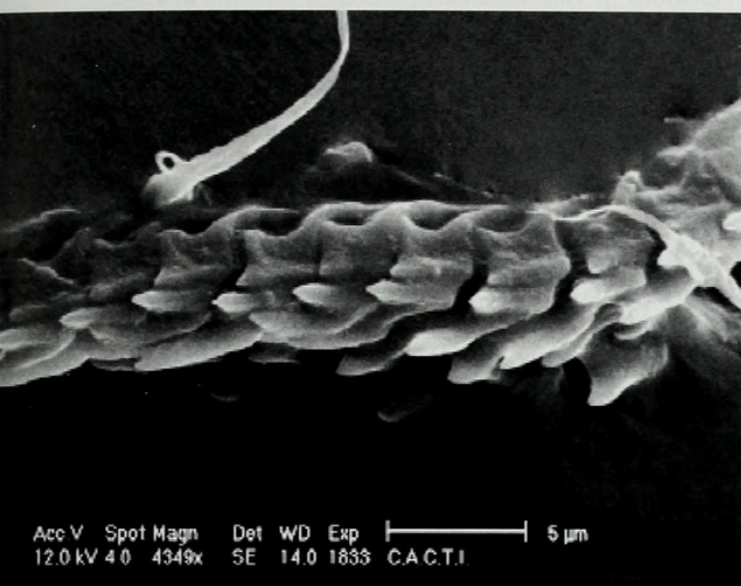
Original figures. The holotype (SMF 305966) and two paratypes (SMF 305967 and SMF 305968) are figured in the original paper.

Another paratype (MOL 895), 8.7x5.0mm, is figured here (Figs. 16-17).

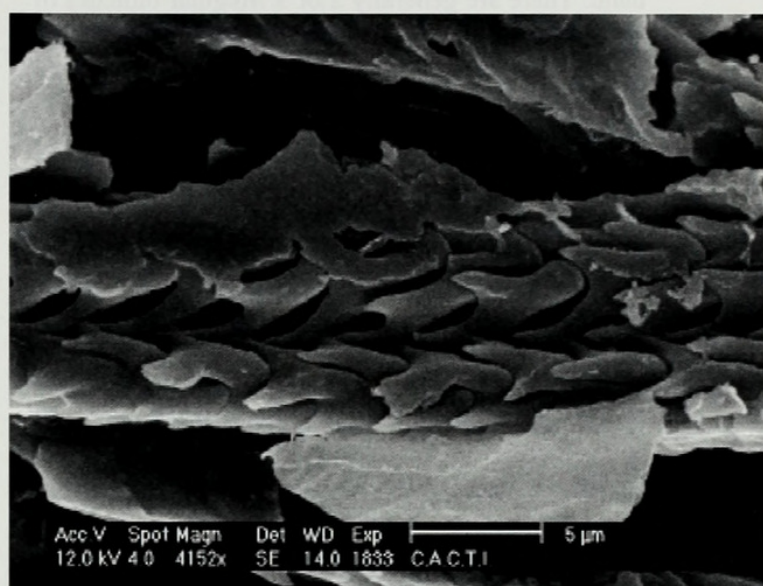
Complementary notes. Northern Colombian shells are large for the genus (up to 11.5mm long) whereas San Blas specimens (Figs. 40-42) are much smaller in size (up to 7.3mm). Both of these populations have a L/W ratio of 55-57% which is slender for the genus and comparable only to the two specimens of *P. cf. cypraeoides* from Paloe Lechi, Bonaire (Coomans, 1972) at 56.5% and the eight slender shells of *P. cf. cypraeoides* from Curacao in LBC (Figs. 34-35). These may be found to form a link in a cline of morphologies from *P. cypraeoides* to *P. tayrona*.

It is well known that shells from continental mainland coastal areas can be larger than those of populations from offshore islands where food supply is less abundant.

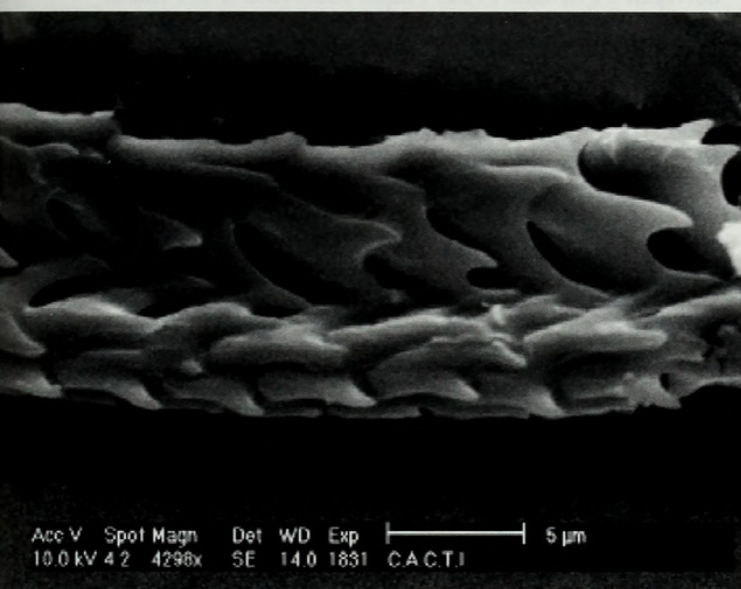
P. tayrona from Northern Colombia is typically light tan to cream across the whole of the body whorl (Diaz & Velasquez 1987). This is the impression when viewed from a distance, but on closer inspection it becomes apparent that it is the pattern of axial wavy lines which gives this effect, the base colour being either white or off white. In the vast majority of the San Blas specimens this pattern is reduced to a central band occupying 70% of the body whorl. The pattern is completely absent from the posterior 20% of the shell and also from the anterior 10%. The axial wavy lines in the central section lie parallel to each other and at 6 or 7 places along their length are drawn forwards to form an extra large arrowhead shape. This has the effect of creating 6 or 7 spiral rows of arrowheads encircling the central**Figures 50-55.****50-51.** *P. kieneriana* Petit, 1838, Radula, scale bar 5 µm; **52-53.** *P. cypraeoides* C.B. Adams, 1845, Radula, scale bar 5 µm; **54.** *P. cassidiforme* Gaskoin, 1853, Radula, scale bar 5 µm; **55.** *P. aff. tayrona* Diaz & Velasquez, 1987, Radula, scale bar 10 µm.



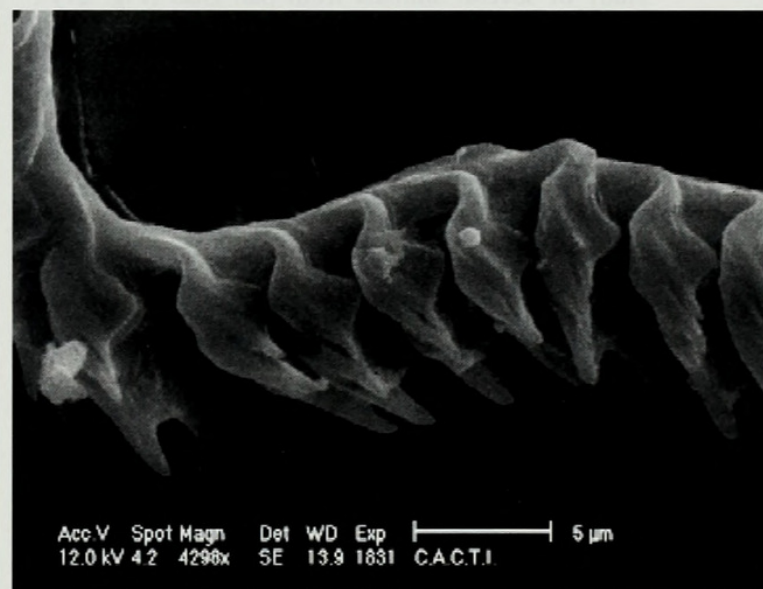
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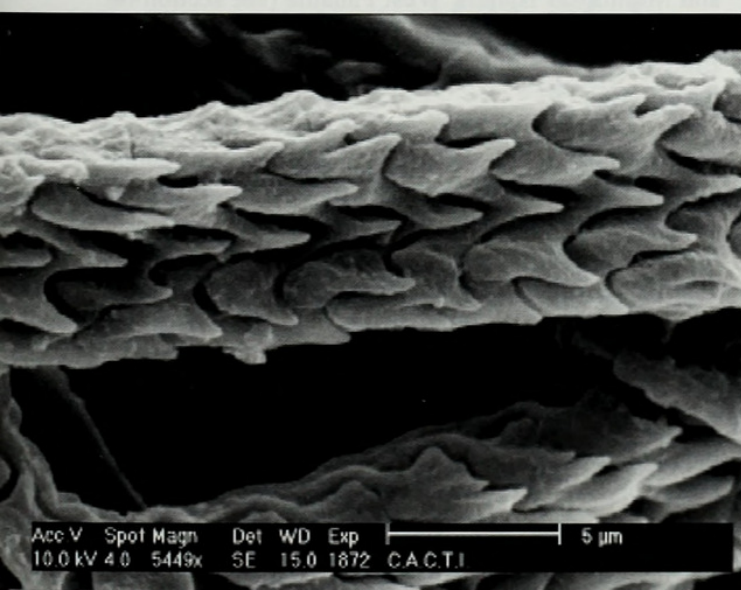
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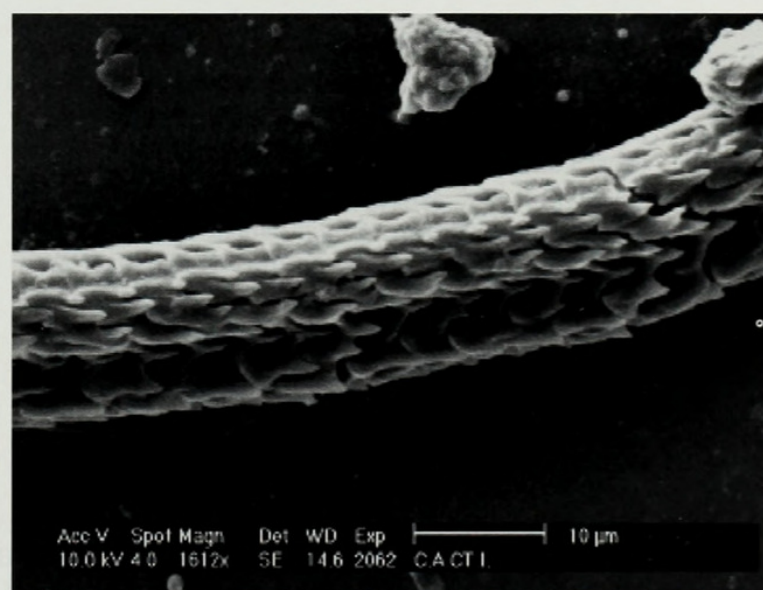
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band. There are generally 2 or 3 irregular blotches of the same colour on the arrowhead row closest to the posterior end, and the same on the penultimate row at the anterior end. When viewed from a distance, these blotches appear to merge somewhat, giving the impression of two rows of brown markings. On occasional specimens, very faint traces of axial pattern can be detected in the light zones, but never on the spire itself, yet even then the overall effect of a darker central band remains. The intensity of the pattern varies slightly with the growth lines which form slightly raised ribs. There are only two specimens from San Blas which do not follow the above rule and exhibit a full length light brown axial pattern with 8 or 9 rows of chevrons (as in Colombian examples).

There are 16 or so countable labial denticles, fading out anteriorly into 6-8 internal lirae, as the lip begins to flare.

The following description of the animal is based on a study of several animals from San Blas (Fig. 21) : Typical Cystiscid Type 4 animal (after Coovert & Coovert 1995). All soft parts are medium grey-brown with small paler blotches. There are two larger pale patches situated either side of the midline on the posterior part of the foot. The short tentacles are a darker brown colour. The overall appearance is of rather a drab looking animal compared to the bright orange markings of some other species in the genus. Radulae were extracted from two specimens from San Blas (Fig. 55) : Type 3 Cystiscid radula (after Coovert & Coovert 1995): Very thin (12 µm) cord like uniserial radula with, in the two specimens examined, 298 and 310 strongly arched and overlapping rachidian plates. Each plate has 9 sharply pointed cusps, with the central cusp being the strongest.

Type locality. Bahia de Chengue, Parque Nacional Natural Tayrona, Caribbean coast of Colombia.

Distribution. Initially thought to be restricted to the Northern Caribbean coast of Colombia, between the Bays of Santa Marta and Nenguange, but recently a population has been found in the San Blas Islands (East Panama). Once the population from San Blas was discovered at Porvenir, a search for other populations occupying similar habitat was instigated throughout the rest of the northwestern part of the archipelago, with no success. This population therefore seems quite isolated. However, it remains possible that other populations occur between the San Blas Archipelago and Santa Marta, as the intervening coastline has never been sampled for micromolluscs.

Habitat. In Northern Colombia, living specimens are found only in turtle grass beds (*Thalassia testudinum*) and under corals in shallow water to 3 metres. The specimens from the San Blas Archipelago were found in the banks of pit-like

erosions in *Thalassia* beds, amongst its roots in 1.5-2 metres.

Remarks. The differences between the populations of San Blas and Santa Marta are mainly based on features not considered to be of major taxonomic importance (minor colour variation and size differences). The authors therefore feel that further exploration of the Colombian coastline West of Santa Marta is required before the specific status of both populations can be clarified. It is therefore proposed, for the time being, to refer to the San Blas population as *P. aff. tayrona*.

***Pachy bathron olssoni* sp. n.**

Figs. 43-49.

Type material. -Holotype. Escudo de Veraguas Island, Bocas del Toro Province, East Panama (Caribbean). Dredged 40-490 ft. in sand and red mud between 1976 and 1982. Adult shell (5.0 x 3.4 mm), NHM ref. no. 20001283, (Figs. 43-45).

-Paratype 1. Same locality as holotype. Adult shell (5.3 x 3.45 mm), NHM ref. no. 20001284.

-Paratypes 2 - 5. Ladrões Island, Gulf of Chiriqui, West Panama (Pacific). Dredged 200-300 ft. 1988. Four adult shells (5.6 x 3.5 mm, 5.4 x 3.4 mm, 5.5 x 3.5 mm, 5.0 x 3.2 mm), TMC.

-Paratype 6. Same locality as holotype. Adult shell (5.4 x 3.5 mm), TMC, (Figs. 46-47).

-Paratype 7. Peninsula de Azuero, West Panama. Dredged 200-400 ft. on sand and mud. 1986. Adult shell (5.9 x 4.0 mm), TMC, (Figs. 48-49).

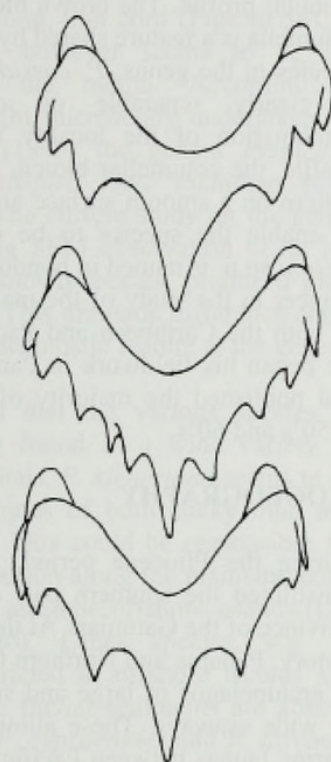
-Paratype 8. Ladrões Island, Gulf of Chiriqui, West Panama. One adult shell (5.6 x 3.7 mm), AWC.

-Paratype 9. Ladrões Island, Gulf of Chiriqui, West Panama. One adult shell (5.25 x 3.1mm), FBC.

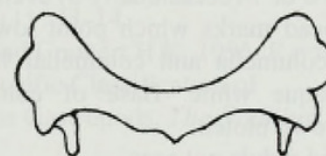
Other material examined. - Veraguas Province, without further precision. Also Peninsula de Azuero and Montuosas Islands, West Panama (see section on Materials and Methods). Dredged in 30-120m. Eighty nine shells (from 5.0 x 3.2 mm to 7.3 x 4.5 mm), TMC.

Description. Shell glossy and small for the genus (length from 5 to 7.3 mm, averaging 5.4mm) with an average L/W ratio of 65%, comprising two whorls (excluding protoconch), presenting an outline varying from globular to oval-pyriform. Spire slightly elevated with a distinct, slightly irregular suture. Smooth, translucent, slightly raised protoconch of 1.5 whorls.

Aperture narrow and curved, approximately 9/10 of the total length of the shell, parallel sided for the posterior half, then flaring a little anteriorly. Inner aspect of lip has approximately 22 fine denticles which vary in size. Anteriorly the denticles are fine and small, gradually becoming larger and coarser centrally, then are fine and irregularly spaced



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58

10 μ m

Figures 56-58

56. Variation in a series of 3 rachidian plates (non-repeating pattern) of *P. cypraeoides* C.B. Adams, 1845. **57.** End view of single rachidian plate of *P. cypraeoides* C.B. Adams, 1845; **58.** three dimensional representation of a single rachidian plate of *P. cypraeoides* C.B. Adams, 1845.

towards the posterior end of the lip. Internal lirae visible through the thin shell of the body whorl on dorsal aspect.

Outer aspect of lip weakly callused, with a shallow external groove running its full length, and continuing around the siphonal notch. Siphonal notch 'V' shaped and deep, curving towards central axis of shell when viewed from anterior end.

Anterior half of columella internally bearing 5 or 6 distinct plaits, which fade out in the posterior half. Plaits emerge more clearly on apertural parietal callus ridge and extend across parietal callus almost horizontally as 10-12 evenly spaced plaits.

Edge of parietal callus demarcated along its posterior third by a deep groove. Anterior two thirds merges smoothly into body whorl as a clear glaze.

Colour pattern consists of light yellow-brown zig-zag pattern on a pale background, extending the full length of the shell giving an overall impression of a golden brown shell (in the majority of unfaded shells). The pattern varies in detail but generally comprises 6 or 7 (occasionally 8) evenly spaced rows of arrowhead marks which point towards the outer lip. Lip, columella and columellar half of parietal callus opaque white. Base of columella with a distinct brown blotch.

Animal and radula not seen.

Type locality. Bocas del Toro Province, East Panama (Caribbean).

Distribution. A number of identical shells selected from several tens of examples were labelled as coming from Ladrões Islands and Peninsula de Azuero on the Pacific side of Panama, more or less opposite Bocas del Toro Province. These are almost identical to the Caribbean shells, falling within their size range and exhibiting comparable shell features. In the present state of our documentation, it seems that the new species is distributed along both Caribbean and Pacific shores of Panama. Many species (or sibling species) of marine molluscs are known to range on both sides of Panama, so the case is quite likely. One point remains to be clarified, that is to know whether the Caribbean and the Panamic populations of *P. olssoni* sp. n. are truly conspecific, or if they belong to two sibling species. Further investigations of the soft parts of the animals (chromatism, variability of proteins, etc.) would provide the answer to this question.

Habitat. Unknown.

Remarks. *P. olssoni* sp. n. differs from other *Pachyathron* species in several respects. The body whorl is usually devoid of strong growth lines and is smooth and glossy. Due to the lack of growth marks

the colour pattern remains very clear. Morphometric analysis reveals a L/W ratio of about 65%, which is very high for the genus and represents a very globular profile. The brown blotch at the base of the columella is a feature shared by only one other species in the genus, *P. cassidiforme*, from which it is clearly separable on other grounds. The combination of the locality data, a distinct shell profile, the columellar blotch, and the intricate axial pattern on a smooth surface are sufficient characters to enable the species to be described as new. *P. olssoni* sp. n. is named in honour of Axel A. Olsson, a pioneer in the study of the marine molluscan faunas of both the Caribbean and Pacific sides of Panama. He began his fieldwork in Panama as early as 1917 and published the majority of his work during the 1950's and 60's.

BIOGEOGRAPHY

During the Pliocene period, the Panamanian area constituted the southern part of the Limonian sub-province of the Gatunian. At this period in geological history, Panama and Northern Colombia formed a set of archipelagos of large and small islands separated by wide seaways. These allowed free exchanges of marine faunas between Pacific and Caribbean zones. At the end of the Zanclean and beginning of the Piacenzian stages of the Pliocene (Petuch, 1988), approximately 3 million years ago, the isthmus of Panama was formed, initially at the level of the Balboa Seaway, situated at the present level of Costa Rica and West Panama (close to the type locality of *P. olssoni* sp. n.). By the end of the Piacenzian era at the end of the Pliocene, only the Atrato Seaway remained open, situated at the level of the Darien Peninsula (close to the area of distribution of *P. tayrona*). The Isthmus of Panama was finally completed at the Pliocene-Pleistocene boundary, around 2 million years ago.

Due to the relatively recent (in geological terms) completion of the land bridge, it is hardly surprising that within many molluscan groups, similar phenae occur on both the Caribbean and Pacific sides. Some of these separated populations have been subject to gradual genetic drift (or even sudden mutation) which has led to reproductive incompatibility and specific separation. These newly evolved species, though genotypically different from each other may have retained similar phenotypic characteristics and therefore appear almost identical to each other. Alternatively there may have been little or no genetic change and the separated populations could still have retained their mutual reproductive potential, despite being physically isolated from each other. Both of these scenarios could apply to populations of sibling *P. olssoni* and *P. cypraeoides* (if the both are confirmed as currently living on the Pacific side).

TAXONOMIC DISCUSSION

As expected, *Pachyathron* shares the same features of its radular apparatus with *Persicula*, namely strongly arched, overlapping, multicuspid rachidian plates, arranged as a long, thin cord (Figs.50-58). A significant difference however seems to be the relative lengths of the radula. According to observations under light microscopy undertaken by Coover & Coover (1995) the genera *Persicula*, *Gibberula* and *Canalispira* have rachidian plate counts of 80 to 209. The current study on the genus *Pachyathron*, utilising SEM observation of all but one of the currently known species, produced plate counts from 293-425. This dramatic difference could prove to be a reliable diagnostic feature at the generic level.

It has been observed that the various species of *Pachyathron* can be found in a wide variety of environments and habitats. *P. kieneriana* seems to be able to tolerate substrates of both sticky mud and coarse coralline sand. This could be responsible for its wide area of distribution along the mainland coast of Venezuela, as well as some offshore islands (Los Testigos and Tobago). Other species, e.g. *P. cassidiforme*, are restricted to offshore islands and found in places where fluvial sediments are absent. At least two species (*P. cypraeoides* and *P. tayrona*) appear to be restricted to environments comprising of coral sand and seagrass. The habitat of *P. olssoni* sp. n. is presently unknown (all the available material being dredged dead). As *P. olssoni* sp. n. is currently understood to be found on Pacific as well as the Caribbean sides of Panama, it demonstrates its ability to survive in two somewhat different environmental conditions, since the Pacific coast of Tropical West America nearly always has a Pacific swell which makes for turbid shallow water with a notable absence of *Thalassia* beds. The absence of *P. olssoni* sp. n. from Caribbean Southeast Panama (San Blas Archipelago) seems to be well established by recent enquiries. However, the general distribution of the species remains to be clarified, both along the Caribbean side (towards the coasts of Costa Rica and Nicaragua) and along the Panamic side (towards Costa Rican protected bays and the Gulf of Panama), as all these areas have not been checked for micromolluscs.

ACKNOWLEDGEMENTS

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We are also indebted to Adam Baldinger (Museum of Comparative Zoology, Harvard), Kathie Way and Joan Pickering (Natural History Museum, London), and Virginie Heros (Museum national d'Histoire naturelle, Paris) for access to type material, and to Juan M. Diaz (Instituto de Investigaciones Marinas y

Costeras, Santa Marta, Colombia) for information on the Colombian population of *P. tayrona*.

Special thanks to Emilio Rolán (Vigo, Spain) who extracted all the radulae and provided SEM photographs.

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