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A revision of the genus *Septaria* FÉRUSSAC, 1803 (Gastropoda: Neritimorpha)

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Abstract

A total of thirteen species of the freshwater neritid limpet *Septaria,* that are found in the Indo - Pacific region, are described. Fifty one nominal taxa are held in European and American Museums of which only 13 are regarded as valid. Specimens were collected from the streams and rivers of Fiji, Samoa, American Samoa, Vanuatu, Solomon Islands, French Polynesia, New Guinea, New Caledonia, Guam, Ponepe, South India, Mauritius, Seychelles and the Philippines between 1983 to 1997. They were dissected to reveal their reproductive anatomy, radula and operculum. Type specimens and other *Septaria* (*Navicella*) specimens held in Natural History Museums were matched with those recently collected. The valid species are: *S. apiata* (LE GUILLOU in RÉCLUZ, 1841), *S. borbonica* (BORY DE ST. VINCENT, 1893), *S. bougainvillei* (RÉCLUZ, 1841), *S. cumingiana* (RÉCLUZ, 1842), *S. janelli* (RÉCLUZ, 1841), *S.livida* (REEVE, 1856), *S. luzonica* (Souleyet in RÉCLUZ), *S. macrocephala* (LE GUILLOU in RÉCLUZ, 1841), *S. porcellana* (LINNAEUS, 1758), *S. sanguisuga* (REEVE, 1856), *S. suffreni* (RÉCLUZ, 1841), *S. taitana* MOUSSON, 1869, *S. tesselata* (LAMARCK, 1816).

Key Words: *Septaria*, freshwater, tropical islands, Neritimorpha.

Introduction

Septaria species are brackish and freshwater neritimorph limpets that inhabit tropical, mainly fast flowing, island streams in the Indo - Pacific region. Species of the genus *Septaria* are easily distinguished from *Neritina* species by their limpet shaped shell with a narrow columellar area, known as a septum, and an operculum, which is embedded in the foot and is unable to shut the animal in the shell. *Neritina*, subgenus Neripteron, which has a similar low rounded single whorl shell, differs by having a wide collumellar area and an operculum that can close the animal inside the shell.

LINNAEUS (1758) made the first mention of a *Septaria* species when he described *Patella porcellana* from India. FÉRUSSAC (1803) was the first to use the generic name *Septaria* when he re-described BORY DE ST. VINCENT's *Patella borbonica*. However, for many years the genus was known as *Navicella*, the junior synonym given by LAMARCK for his *Navicella* lineata and *Navicella tesselata* in 1816. It was not until 1908, when BOURNE resurrected the senior synonym, that the genus became generally known as *Septaria*, although MOUSSON sometimes used the genus *Septaria* in his 1869 catalogue.

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Taxonomic Account

GOLIKOV & STAROBOGATOV (1975) thought the genus *Septaria* was different enough from the other genera of the family Neritidae, to merit a family of its own called Septariidae. VAUGHT (1989) in his classification also placed *Septaria* in the Septariidae, although most authors continued to place the genus in the Neritidae because it shares so many characters with *Neritina*, *Clithon* and *Neritodryas*. This view was reinforced when HOLTHUIS (1997) used 57 characters in a phylogenetic analysis of the Neritimorpha. She found that *Septaria* differed from *Neritina* in only two of the character states – the foot unable to retract into the shell and a strongly bifid epipodium edge. HOLTHUIS (1997) defined Neritidae as including *Septaria*, *Neritina*, *Clithon, Neritodryas* and their subgenera.

Authors have been inconsistent in the name and the geographic range they have given to each species because shell shape and shell markings are variable within species and the difference between shells of each species is not obvious. RÉCLUZ (1841, 1842) described five species and REEVE (1856) added three more, all of which are here deemed to be *S. tesselata*. This variability in shell shape and pattern has lead to authors either lumping several nominal species together (MARTENS, 1881) or dividing the genus into many invalid species (REEVE, 1856). REEVE (1856) described 31 species of *Septaria*, while MARTENS (1881) combined many to establish 19 species. I have found 13 species, but they are not all the same as MARTENS' e.g. he combined *S. sanguisuga* and *S. macrocephala* under the name of *S. macrocephala*. The revision of HAYNES & WAWRA (1989) divided them into two separate species again.

Radulae were used by BAKER (1923) and KOMATSU (1986) to classify the Neritidae. BAKER (1923) did not study any *Septaria* radulae but nevertheless divided the genus into three sections 1. *Septaria* which included *S. borbonica, S. janelli, S. cumingiana* and *S. freycineti* 2. *Navicella* containing *S. lineata* and *S. tesselata* 3. *Sandalium* containing *S. porcellana*. KOMATSU (1986) presented electron micrographs of the radulae of *S. porcellana*, collected from Okinawa Island and Taiwan, and *S. lineata* from Taiwan. He placed *S. lineata* (*S. tesselata*) into a separate subgenus *Navicella* and the other two species he studied, *S. porcellana* and *S. cumingiana*, into another subgenus *Septaria*. The electron micrographs of KOMATSU (1986) and the drawings of STARMÜHLNER (1970, 1976) of neritid radular teeth of the various species are very similar and differences between species are difficult to detect as shown in Figs. 3 a - d.

RIECH (1937) used the name *Septaria borbonica depressa*, LESSON for *S. porcellana* from New Guinea and the Pacific islands. STARMÜHLNER (1970) also used this name for the New Caledonian *Septaria*. STARMÜHLNER (1976) named the same species *Septaria porcellana* f. *depressa*. Other species found by STARMÜHLNER (1976) on Pacific islands were *S. macrocephala, S. suffreni* and *S. lineata* (my *S. livida*). He divided his *S. lineata* into a wide form *apiata* and a narrow form *compressa - clypeolum*. However, the name *apiata* was not available as RÉCLUZ's *Navicella apiata* is a valid species.

The use of the subspecies *depressa* by RIECH (1937) and STARMÜHLNER (1970) was based on shell pattern differences and, often, by incorrect identification e.g. identifying *S. bougainvillei* and female *S. suffreni* as *S. porcellana*.

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If a subgenus were thought desirable, the most appropriate, according to phylogenetic analysis (Fig. 72) would be to use *Navicella* for a subgenus for the two brackish water species, *S. tesselata* and *S. livida* and *Septaria* for the rest of the species.

Morphological Characters

Shell: (Figs. 1 A - B). The shell is thin and cap-like and in one species. The shell of *S. suffreni* is sexually dimorphic (HAYNES, 1991) as the male shell, unlike the female, has a tongue-like projection on the middle of the septum (Fig. 5 b).

Some species have smaller males than females. 95% of all males found in the species *S. porcellana* and *S. bougainvillei* were less than 16 mm long while only 33 - 44 % females were as small as that. The extreme in small males is seen in the protandrous sequential hermaphrodite species *S. macrocephala* where no males were more than 14 mm long and no females less than 11 mm long (HAYNES, 1991). *S. taitana* males from Moorea were also significantly smaller than females (Table 1) and GOVINDAN & NATARAJAN (1972) reported that males of *S. tesselata* were 1.92 mm smaller than females, although I did not find this so (Table 1)

Sex Ratio: Those species with significantly smaller males also have a smaller percentage of males in the population (Table 1).

Ecological Dimorphism: This is found in two species, *S. tesselata* and *S. livida*, that only inhabit brackish water and tidal parts of rivers and streams. Both species have developed two extreme forms that appear to be induced by ecological factors. The form into which the limpet will develop depends on the substratum on which it lives and the strength of the water flow around it. The compressed form lives on grass and reed stems, bamboo and floating logs in calm water while the wider form lives on stones, rocks and concrete in fast flowing water. Intermediate forms are also found.

Operculum: The operculum is nearly square in shape with one or two prongs or ribs extending forward and embedded in the foot. It lies between the visceral mass and the foot and is unable to shut the animal in the shell (Fig. 4 c). The opercula of both *S. sanguisuga* and *S. cumingiana* have two forward projections and are sexually dimorphic. As in *S. suffreni*, the male operculum is narrower than that of the female. (Figs. 5 c, 6 c).

Reproductive Strategies and Anatomy: The reproductive anatomy of both sexes is complex. Males in many species have a large auxiliary gland to produce spermatophores (Figs. 9 - 10) and the females have a vagina and spermatophore sac to receive the spematophores (Fig. 7). All females have a receptaculum seminis to store the sperms before they fertilise the eggs near or in the albumen gland. This in turn opens into the capsule gland (ootype) that leads to the female opening through which the eggs are laid in capsules (Figs. 7).

Copulation was observed in *S. tesselata* by GOVINDAN & NATARAJAN (1972). They observed the penis being introduced 2 - 4 times into the vaginal opening during a period of 3 - 4 minutes at 1 - 1.5 minute intervals.

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Egg laying may cover a period of days when clusters of up to 100 egg cases, each with approximately 100 eggs, are cemented onto rocks, stones or the shells of other gastropods (PÖLLABAUER, 1986).

The life history of *Septaria spp.* is not well understood but free living veligers have been observed to emerge from the egg cases after an interval of 3 weeks to 6 months. When the case becomes soft and rubbery, it becomes detached from the substratum and the veligers are spilled into the water. They swim downwards close to the substratum so that many escape being washed away by the current. However, the wide distribution of many species of *Septaria* indicates that some veligers are carried out to sea to be eventually washed up at the mouth of streams or rivers on other islands. The author has kept *Septaria* veligers for many days in sea water after acclimatizing them in dilutions of sea water.

In *Septaria* species, perhaps because their internal organs are not coiled as they are in *Neritina*, there are considerable differences in reproductive systems and reproductive strategies. Some species of *Septaria* produce spermatophores, and therefore more closely resemble *Neritina*. The spermatophore is different in each species. Both *S. sanguisuga* and *S. cumingiana* produce large complex spermatophores while the spermatophores of *S. tesselata*, *S. livida*, *S. suffreni* and *S. luzonica* are more like those of *Neritina spp. S. apiata* and *S. taitana* have a dorsal spermatophore sac but do not produce spermatophores, while *S. porcellana*, *S. janelli* and *S. borbonica* have a ventral remnant of a spermatophore sac. *S. bougainvillei* and *S. macrocephala* have lost the spermatophore sac altogether.

Males of those species that produce spermatophores have large fleshy auxiliary glands while those that do not have much smaller and flatter auxiliary glands. Most species have a penis with a papilla (Figs. 8, 13) but *S. sanguisuga* and *S. cumingiana* that produce complex spermatophores have no papilla (Figs. 37, 42) and neither do the non - spermatophore producing species *S. bougainvillei* and *S. macrocephala* (Figs. 67, 70).

Radula: Both BAKER (1923) and KOMATSU (1986) used radula to classify the Neritidae, but neritid radular teeth of the various species are very similar and differences are difficult to define because intraspecific differences in radulae are often as great as interspecific differences (Fig. 3 a - d).

Materials and Methods

All *Septaria* types in the Natural History Museum, London (BMNH), Museum National d'Histoire Naturelle, Paris (MNHN), Museum d'Histoire Naturelle, Geneva (MHNG), Zoologisches Museum, Zurich (ZMZ), Museum of Comparative Zoology, Cambridge (MCZ), and the Linnean Society, London were examined. All other *Septaria* specimens held in the above museums as well as those held in the Naturhistorisches Museum Wien (NMW), Zoologische Museum, Amsterdam (ZMA), Museum fur Naturkunde, Berlin (MNB), Natal Museum (NM), Museum of Zoology, University of Michigan (MZM), and the Queensland Museum (QM) were examined.

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Table 1. Size and ratio of the sexes in 13 species of *Septaria*. l = length.

Species	No.	male % l (mm)	female % l (mm)	mean & spread, male	mean & spread, female	X^2	p
S. livida	162	34	66	18.4	22.4	-	-
(Fiji)	-	-	-	11 - 30	9 - 33	3.5	ns
S. tessellata	10	40	60	17	17	-	-
(Tamil Nadu)	-	-	-	13 - 25	13 - 27	-	-
S. bougainvillei	208	24	76	11.4	15.9	-	-
(Fiji)	8 - 17	8 - 22	4.5	0.05			
S. borbonica	74	46	54	15.4	14.4	-	-
(Seychelles)	-	-	-	12 - 23	9 - 22	1.0	ns
S. taitana	59	37	63	13.8	19.3	-	-
(Moorea)	10 - 17	12 - 30	5.5	0.05			
(Tahiti)	35	31	69	16.7	20.0	-	-
	-	-	-	13 - 20	15 - 27	3.3	ns
S. apiata	47	70	30	26.0	24.7	-	-
(Nuka Hiva)	-	-	-	11 - 32	10 - 29	1.3	ns
	31	48	52	15.0	11.9	-	-
	-	-	-	12 - 19	9 - 18	3.1	ns
S. luzonica	124	42	58	13.6	14.3	-	-
(Mindanao)	-	-	-	9 - 26	9 - 23	0.7	ns
S. cumingiana	64	58	42	17.3	19.3	-	-
(Mindanao)	-	-	-	12 - 22.5	15 - 28	2.0	ns
S. janelli	31	52	48	19.2	16.4	-	-
(Mindanao)	-	-	-	14 - 27	11 - 23	2.8	ns
(Camiguin)	21	48	52	20.6	19.6	-	-
	-	-	-	16.- 27	12 - 25	1.0	ns
(Guam)	24	58	42	21.9	18.0	-	-
	-	-	-	18 - 29	14 - 25	3.5	ns
S. porcellana	59	34	66	11.2	17.1	-	-
(Solomon Islands)	-	-	-	9 - 17	11 - 26	5.9	0.05
	35	31	69	10.3	16.5	-	-
(Vanuatu)	-	-	-	8 - 14	11 - 24	6.2	0.05
S. suffreni	129	48	52	16.7	19.7	-	-
(Fiji)	-	-	-	9 - 28	10 - 30	3.2	ns
S. sanguisuga	180	43	57	19.9	18.3	-	-
(Fiji)	-	-	-	11 - 24	10 - 23	1.6	ns
S. macrocephala	192	26	74	10.8	17.5	-	-
(Fiji)	-	-	-	8 - 14	11 - 22	6.7	0.05

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Septaria specimens were collected by the author and others (when stated) from streams and rivers in the following places: Fiji, Samoa, American Samoa, Vanuatu, Solomon Islands, New Guinea (Dan Smits), Society Islands, Marquesas Islands (O. Fossati), New Caledonia (Ch. Pöllabauer), Mindanao, Cumiguin (Philippines), Guam, Ponepe (J.A. Maciolek), Mannanpandal (South India) (M. Sabesan), Mauritius, Seychelles.

The size and number of both sexes from each locality were measured and counted. The length, width and height of shells of each species were measured with calipers to 0.1 mm and l/w and l/h ratios calculated (Figs. 1 A, B; Appendix).

The male and female reproductive organs of at least 10 male and female specimens of each species were dissected.

Radulae from at least four specimens of each species were dissected from material fixed in ethanol. The radulae were soaked in 10% sodium hydroxide solution for 2 hours and the studied under a stereo - microscope (Figs. 3 a - d).

List of Abbreviations

Reproductive Systems

ag albumen gland	fo female opening	rs receptaculum seminis	vd vaginal duct
au auxiliary gland	gp genital pore	sp spermatophore	vo vaginal opening
cg capsule gland	o ovary	sps spermatophore sac	vs vas deferens
de ductus enigmaticus	od oviduct	t testis	
e epididymis	pg prostate	v vagina	

Museums

AM Australian Museum, Sydney
BMNH Natural History Museum, London
LANHM Los Angeles Natural History Museum
LSL Linnaean Society, London
MCZ Museum of Comparative Zoology, Cambridge
MHNG Museum d'Histoire Naturelle, Geneva
MMBS Mukaishima Marine Biological Station, Hiroshima
MNB Museum fur Naturkunde, Berlin
MNHN Museum National d'Histoire Naturelle, Paris
MZM Museum of Zoology, University of Michigan
NM Natal Museum, Pietermaritzburg
NMW Naturhistorisches Museum Wien
QM Queensland Museum, Brisbane
ZMA Zoologische Museum, Amsterdam
ZMZ Zoologisches Museum, Zurich

Systematic Descriptions

Family Neritidae Rafinesque, 1815: 144

Septariidae Golikov & Starabogatov, 1975: 190

Genus *Septaria* Férussac, 1807

Cimber Montford, 1810: 82, *Navicella* Lamarck, 1816: 456, *Sandalium* Schumacher, 1817: 57, *Elara* Adams & Adams, 1854: 386, *Paria* Gray, 1868: 997, *Laodia* Gray, 1868: 995, *Stenopoma* Gray, 1868: 998

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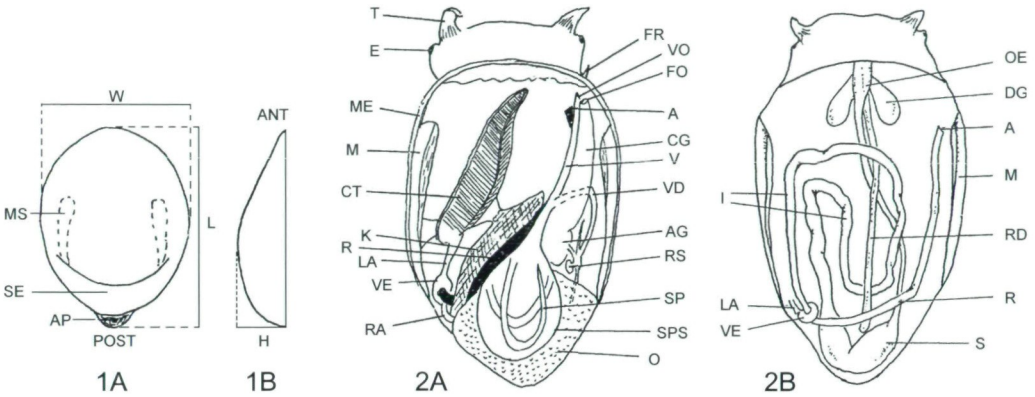

Figs. 1 - 2: (1) *Septaria* shell: (A) ventral view (inside), (B) side view. ANT, anterior; AP, apex; *H*, height; L, length; MS, muscle scar; POST, posterior; SE, septum; W, width. (2) Dissected *Septaria*: (A) Dorsal view of a female *S. luzonica* with the mantle removed and pallial organs exposed. Receptaculum seminis and vaginal duct have been displaced to the right. (B) Alimentary canal of *S. porcellana*. A, anus; AG, albumen gland; CG, capsule gland; CT, ctenidium; E, eye; FO, female opening; FR, female ridge; I, intestine; K. kidney; LA, left auricle; M, muscle; ME, mantle edge; O, ovary; OE, oesophagus; OG, oesophageal gland; R. rectum; RA, right auricle; RD, redula; RS, receptaculum seminis; S, stomach; SP, spermatophore; SPS, spermatophore sac; T, tentacle; V, vagina; VD, vagina duct; VE, ventricle; VO, vagina opening.

Description of the Genus

Shell: Shell symmetrical, cap-shaped and oval with length up to 33 mm (Fig. 1). Apex at the posterior margin (Fig. 1 A). Aperture very large, columella narrow forming a septum which is wide, shallow and unserrated (Fig. 1 A). Ground colour olive brown to yellowish or pinkish brown, with dark markings of triangles, tongues or concentric, horizontal, zigzag or longitudinal lines (Figs. 4 a, 5 a, 6 a). Shell interior white-gray with left and right muscle scars showing (Fig. 1 A).

Operculum: Much smaller than the aperture, calcareous with a clear red-brown horn margin at posterior. Squarish in shape with usually one projection embedded in the foot. It lies between the pallial organs and foot and cannot function as a lid to close the shell (Fig. 4 c, 5 c, 32 c).

Anatomy: The gut and reproductive organs are not coiled. It has a large mantle cavity and when the mantle is removed the animal's asymmetry is revealed. To the left is the bipectinate ctenidium, heart and kidney while the reproductive complex fills the right side in both males and females (Fig. 2 A).

Septaria, like other neritids, has a rhipidoglossan radula where the lateral teeth nearest the marginals become enlarged (Fig. 3 a). They are the most powerful teeth and their broad semicircular flange has a shovelling action while the marginals sweep up particles of periphyton on the backstroke of the radula.

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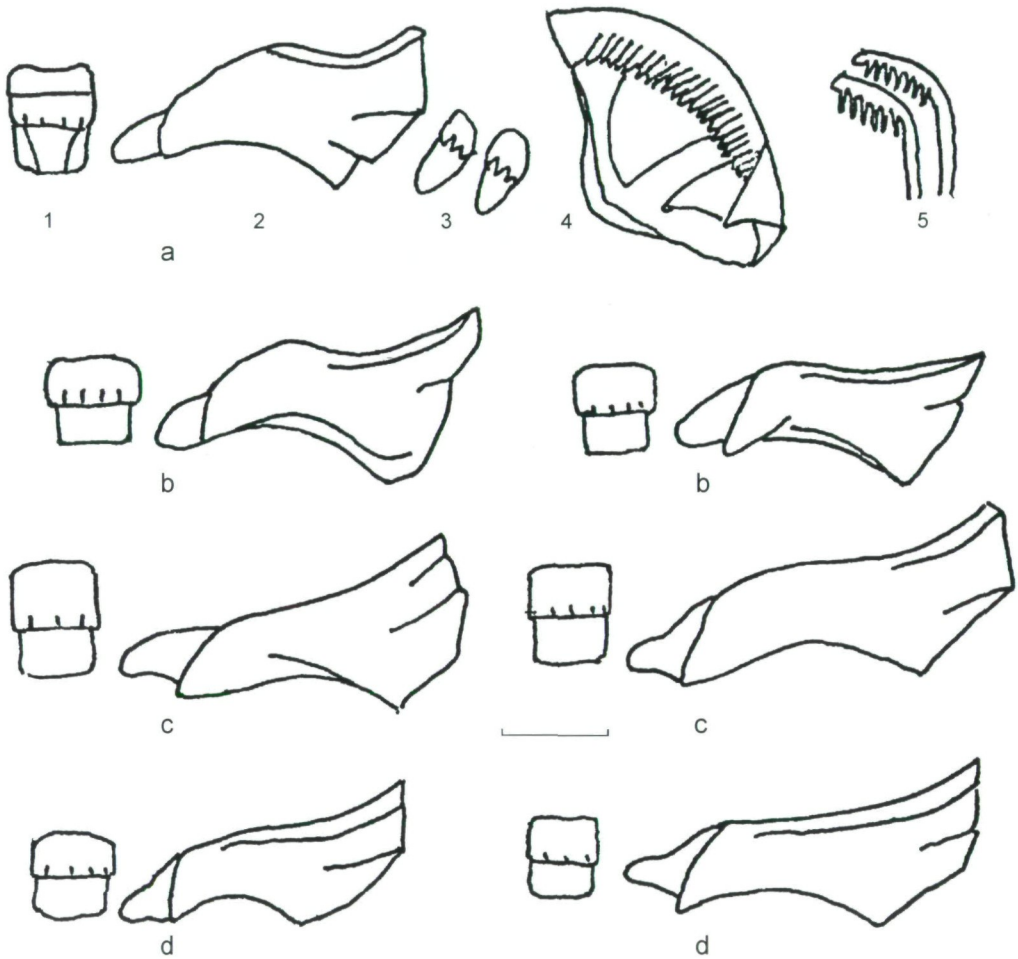

Fig. 3: (a) Right transverse row of *S. macrocephala* radula 1 - 3 central teeth, 4 lateral, 5 marginals, b - d: Right central teeth of the radula from two specimens of: (b) *S. cumingiana*, (c) *S. luzonica*, (d), *S. sanguisuga*. Scale bar 75 µm.

The alimentary system of *S. borbonica* was described in detail by BOURNE (1908) and other *Septaria* species have essentially similar alimentary systems (Fig. 2 B).

The anatomical features of the kidney, circulatory and nervous systems were also described by BOURNE (1908).

Septaria luzonica (SOULEYET in RÉCLUZ, 1841) (Figs. 4, 7 - 10, 11)

Navicella luzonica SOWERBY, 1850: 532; SOULEYET, 1850: 573; REEVE, 1856: pl.3, 11a, b; MARTENS, 1881: 16, pl2, figs. 9-18; KABAT & FINET, 1992: 238. *Septaria luzonica* RIECH, 1937: 67

Type Material *Navicella luzonica* SOULEYET in RÉCLUZ, 1841: 375 (2 syntypes MNHN, 4 syntypes MHNG 1520 0, Luzon, Philippines); *Navicella parva* MOUSSON, 1849: (holotype ZMZ, Bima, Indonesia).

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Description

Shell: (Figs. 4 a, b) Size up to 26 mm long, mean w/l ratio 0.71, mean h/l ratio 0.36. Symmetrical, boat-shaped as the apex curves towards the ventral side and the apex is ground flat on the ventral surface. Apex is small, pointed and outside the posterior shell margin. Shell widest in front of the septum, which is deeply concave and curved towards the apex.

Ground colour yellow brown with faint darker markings forming long, narrow stripes changing to small triangles on the apex. When the animal is in the shell, the foot is dark gray. The shell inside is gray and the septum white turning bright pink or yellow-orange near the small apex.

Male and female individuals are approximately the same size and populations have the same number of each sex (Table 1).

Operculum: (Fig. 4 c) Robust, rib and anterior white turning yellow and black at the posterior. Has a clear, dark orange horn margin.

Reproductive Anatomy: (Figs. 7 - 10) The female has a spermatophore sac which can contain several long spermatophores with a definite filament. Males have a wide blunt penis with a prominent papilla and a large fleshy auxiliary gland.

Habitat: On stones and boulders in fast flowing streams from near the sea to a few kilometers inland.

Range: (Fig. 11) Philippines, Indonesia and West New Guinea.

Records: PHILIPPINES: Mindanao, Camiguin (author), Luzon (MHNG, MNHN, NM), Mindoro (MCZ), Panay I. (MNHN), INDONESIA: Batjan I., Irian Djaya (MCZ, ZMA), Bima, Sumbawa (ZMZ).

Remarks: *S. luzonica* can be confused with female *S. suffreni* as its shape and yellow-orange septum are similar. I believe that FRANC (1957) confused the two and that his *S. luzonica* from New Caledonia is in fact *S. suffreni*. Others e.g. STARMÜHLNER (1970) and POLLABAUER (1986) did not find *S. luzonica* in New Caledonia.

Septaria suffreni (RÉCLUZ, 1841) (Figs. 5, 6, 12 - 15, 16)

Navicella freycineti REEVE, 1856: Fig .4; *Para freycineti* GRAY, 1867: 997; *Navicella freycineti* MARTENS, 1881: 21 Figs. 11-26; *Septaria suffreni* RIECH, 1937:64; STARMÜHLNER, 1976: 70, 543; HAYNES, 1984: Fig. 35; HAYNES, 1985: 204; HAYNES, 1987: 377; HAYNES, 1990: 237; HAYNES, 1991: Figs. 1, 2C, 3B, 4C; *Navicella freycineti* KABAT & FINET, 1992: 235; *Navicella suffreni* KABAT & FINET, 1992:248; *Septaria suffreni* STARMÜHLNER, 1993: 265, Figs. 34, 36; HAYNES, 1997: Fig. 1; *Septaria freycineti* COWIE, 1998: 18

Type Material *Navicella suffreni* RÉCLUZ, 1841: 374 (3 probable syntypes in Delessert's collection MHNG 16385 var. a; 16386 var. b; 16387 var.c, Levuka, Fiji); *Navicella freycineti* RÉCLUZ, 1841: 375; (possible holotype MHNG 15099, Makassar, Sulawesi); *Navicella psittacea* REEVE, 1856; (4 syntypes BMNH, Australian Islands); *Navicella haustrum* REEVE, 1856: Fig. 18 a, b; (4 syntypes BMNH); *Navicella pala* MOUSSON, 1865: 13; (holotype ZMZ, Samoa); *Navicella excelsa* GASSIES, 1870: 18; (holotype BMNH, New Caledonia).

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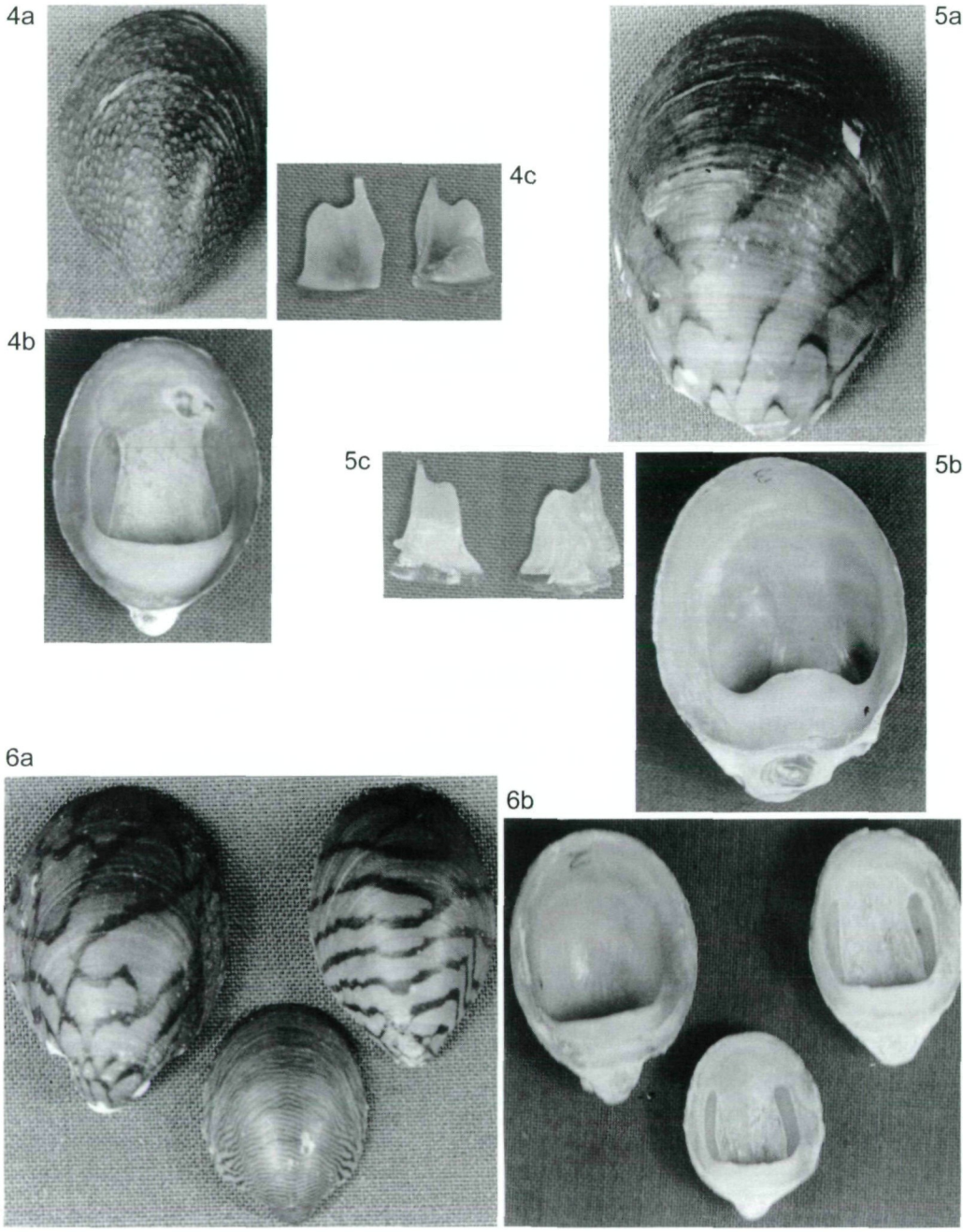

Figs. 4 - 6: (4) *S. luzonica* shells (a) dorsal side; (b) ventral side; Length: 22, 24 mm; (c) operculum: Width: 7.5 mm. (5) *S. suffreni* shell, male (a) dorsal side; (b) ventral side; Length: 34, 27 mm; (c) operculum; Width: 7 mm. (6) *S. suffreni* shell, female (a) dorsal side; (b) ventral side; Length: 15 - 26 mm; (c) operculum; Width: 10 mm.

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Description

Shell: (Figs. 5 a, b, 6 a, b) The only *Septaria* species with obviously sexually dimorphic shells. Shell up to 30 mm long, mean w/l ratio 0.74, mean h/l ratio 0.34. Shell symmetrical, cap-like, apex outside the posterior edge of the shell. Ground colour yellow-green with variable markings - transverse wavy lines, fine triangles fading in older individuals, zigzags to only a few lines. Ventral surface of shell white to gray, muscle insertion scars prominent and darker. Septum on posterior edge orange. Apex small and often eroded.

Dimorphism: Male shell often narrower than the female and the inner edge of its septum has a central tongue-like projection (Fig. 5 b). Female septum edge straight (Fig 6 b).

Male and female individuals are the same size and populations have the same number of each sex (Table 1).

Operculum: (Figs. 5 c, 6 c) Orange-pink and narrower in male. The posterior edge has a dark orange horn border and it is wider than the anterior end with the rib.

Reproductive Anatomy: (Figs. 12 - 15) The female has a spermatophore sac which can contain several long spermatophores. Males have a fleshy penis with a long inner papilla and a large fleshy auxiliary gland.

Habitat: On stones and rocks from tidal regions to well inland (50 km).

Range: (Fig. 16) Fiji, Samoa, New Caledonia, Vanuatu, It is the most abundant *Septaria* species in Samoa.

Records: FIJI: Viti Levu (NMW, MNHN) Lami R., Sabeto R., Wairoro Ck. (author); Vauua Levu, Nasekawa R. (author); Ovalau (author, ZMZ), *N. pala* (MNHG); Taveuni (author); Kadavu (author); SAMOA (author, NMW, MCZ, MNHN), *S. pala* and *S. haustrum* (MNHG), *S. freycineti* (MNB, MNHN); NEW CALEDONIA (MNHN, NMW, MCZ); VANUATU *S. freycineti* (BMNH, ZMA, MCZ).

Remarks: MARTENS (1881) considered that RÉCLUZ's *N. suffereni* and *N. freycineti* were synonyms and chose the name N. *freycineti*. RIECH (1923), on the other hand, thought the South East Asian *N. freycineti* from Sulawesi was a synonym of *N. cumingiana* and therefore used *S. suffreni* for the South Pacific species. The probable type specimens of *N. suffreni* are from Ovalau, Fiji. And the only other records of this species are from the South Pacific islands of Fiji, Samoa, New Caledonia and Vanuatu. The holotype of *N. freycineti* is the only record from Indonesia or anywhere else in South East Asia. RÉCLUZ gives its locality as 'Les marais de Makassar' – the swamps of Macassar –, Sulawesi. On the other hand, *S. suffreni* of the Pacific islands occurs on stones and rocks in fast flowing streams, and not in swamps. It is, therefore, not likely that RÉCLUZ's *N. freycineti* is a synonym of *S. suffreni* or is a valid species.

Shell dimorphism in the species has led authors to confuse the females with *S. porcellana*, *S. bougainvillei* and *S. macrocephala* (STARMÜHLNER, 1976; HAYNES, 1988). *S. suffreni* is the only one of these four species that produces spermatophores. FRANC (1957) confused female *S. suffreni* with *S. luzonica* because both have a pointed apex and a yellow-orange septum. Male *S. suffreni* can be mistakenly identified as *S. cumingiana* as its shell also has a similar, although usually smaller, projection on its septum (Figs. 5 b, 32 b). If the operculum is present there is no confusion as the operculum of *S. cumingiana* has two ribs while that of *S. suffreni* has only one.

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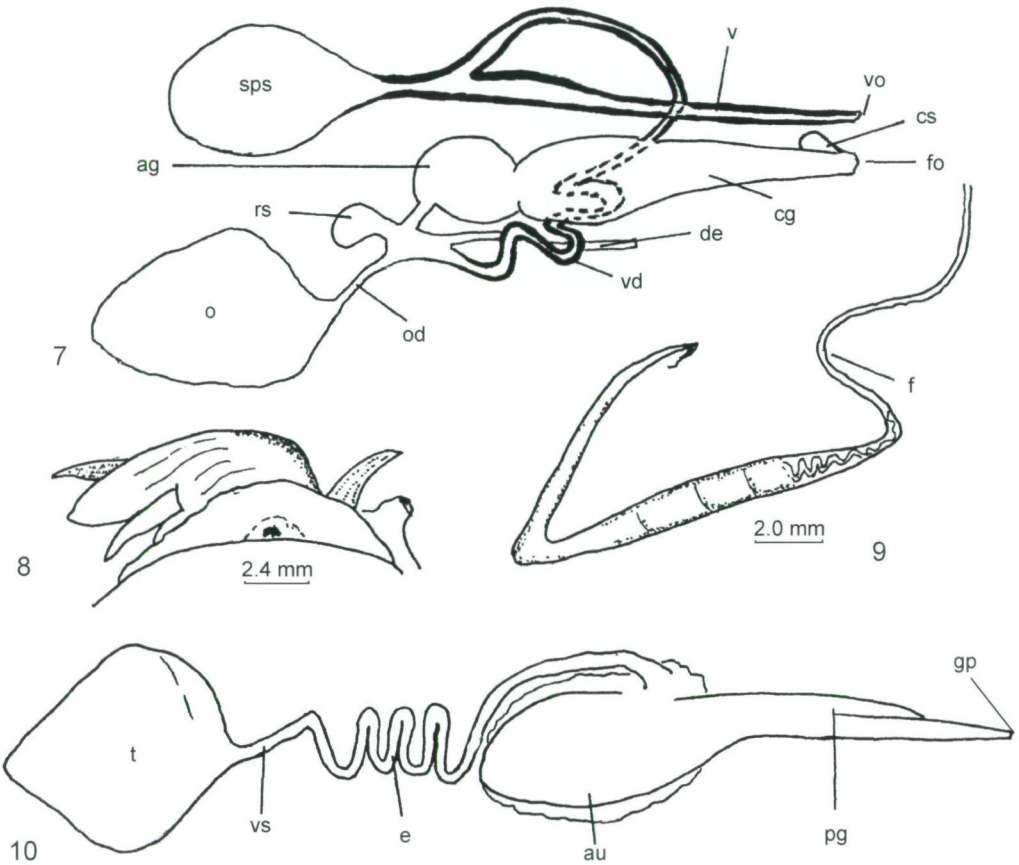

Figs. 7 - 10: *S. luzonica* reproductive system: (7) female. (8) penis. (9) spermatophore (f, filament). (10) male.

Septaria tesselata (LAMARCK, 1816) (Figs. 17 - 19, 23 - 26, 27)

Navicella lineata RÉCLUZ, 1841: 377; *Navicella tesselata* RÉCLUZ, 1841: 380; MARTENS, 1881: pl.7, Figs. 8 - 17, pl. 8, Figs 1 - 9; TRYON, 1888: 81, Fig. 57; *Navicella lineata* TRYON, 1888: Fig. 58; *Septaria (Navicella) lineata* BAKER, 1923: 77; *Septaria tesselata* RIECH, 1937: 68; *Septaria lineata* BENTHEM-JUTTING, 1956: 314, Fig.33; STARMÜHLNER, 1974: Pl. 11, Figs. 9-13; *Septaria (Navicella) lineata* KOMATSU, 1986: 171, Fig. 12; KOMATSU, 1986: Pl. 8, Fig. 6; *Septaria tesselata* HAYNES, 1993: 287.

Type Material *Navicella tesselata* LAMARCK, 1816: 456, Figs. 3, 4 (changed from *tesselaria* on the same page) (2 syntypes MHNG 1094/5 no.3, India; *Navicella lineata* LAMARCK, 1816: 456, Fig.2 (holotype MHNG 1094/4 no. 2, India); *Navicella entrecastauxi* RÉCLUZ, 1841: 380 (type MHNG, New Holland); *Navicella clypeolum* RÉCLUZ, 1842:157 (type BMNH, Philippines); *Navicella variabilis* RÉCLUZ, 1842: 155 (type MHNG, Philippines); *Navicella maculifera* MOUSSON, 1848: 268 (type ZMZ, Java); *Navicella coerulescens* RÉCLUZ, 1850: 376 (type MHNG, Bengal); *Navicella eximia* REEVE, 1856: Fig. 26 (type BMNH, Sri Lanka); *Navicella reticulata* REEVE, 1856: Fig. 20 (type BMNH, Sri Lanka); *Navicella insignis* REEVE, 1856: (type BMNH, Sumatra).

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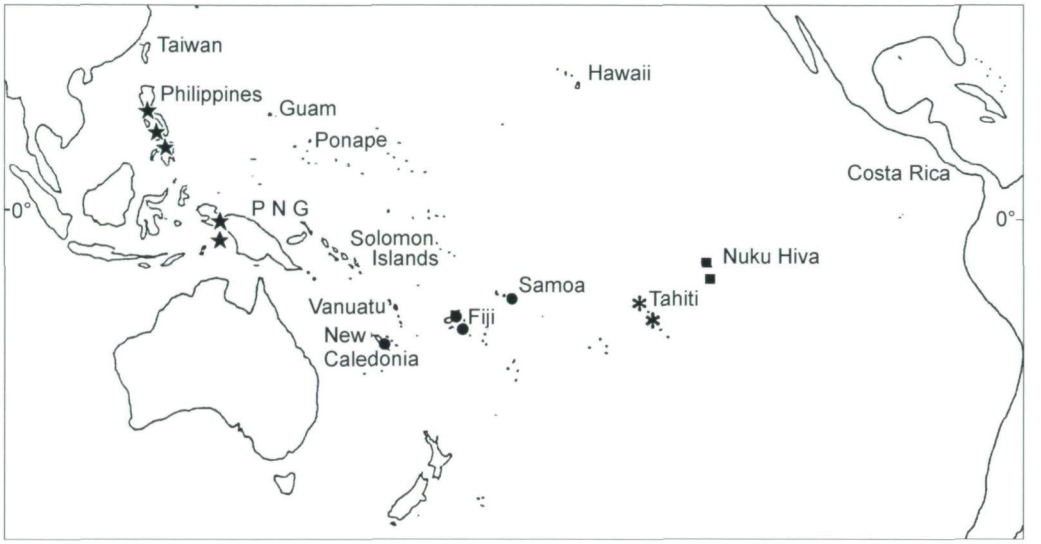

Fig. 11: Distribution of *S. luzonica* ★, *S. macrocephala* ●, *S. taitana* ✻ and *S. apiata* ■.

Description

Shell: (Figs. 17 a, b, 18 a, b, 19 a, b)

Wide Form: Shell length up to 27 mm, mean w/l ratio 0.67, mean h/l ratio 0.29 (compressed form w/l ratio 0.45, h/l ratio 0.23). Shell symmetrical, oval cap-like, apex inside the posterior margin (fig. 17 a). Posterior straight or rounded, anterior rounded. Shell widest across the center.

Ground colour yellow-brown or yellow-green, with black or purple lines arranged around the apex. May instead have small triangles or zig-zag lines. Septum white or gray, flat to concave, deep and with a curved margin. Interior of shell white/gray.

Males smaller than females according to GOVINDAN & NATARAJAN (1972) (Table 1).

Operculum: (Fig. 17 c) Delicate, pale yellow, oblong with a rib angled inwards, horn margin transparent.

Compressed Form: Shell fragile, narrow and compressed sideways with apex protruding over the posterior margin. Shell pattern of black or purple lines and triangles or pink longitudinal lines. Septum very narrow and operculum pale yellow, fragile, long and thin and rib angled inwards (Figs. 19 a, b).

Intermediate forms also occur (Fig. 18 a, b)

Reproductive Anatomy: (Figs. 23 - 26) The female has a spermatophore sac which contains several long spermatophores (20 mm long). The male has a large auxiliary gland and a relatively long , thin penis with a long papilla.

Habitat: In brackish water or in tidal parts of rivers and streams. Wide form is found on stones in fast flowing water, while the compressed form is found on plant material such as logs and grass stalks in quiet backwaters.

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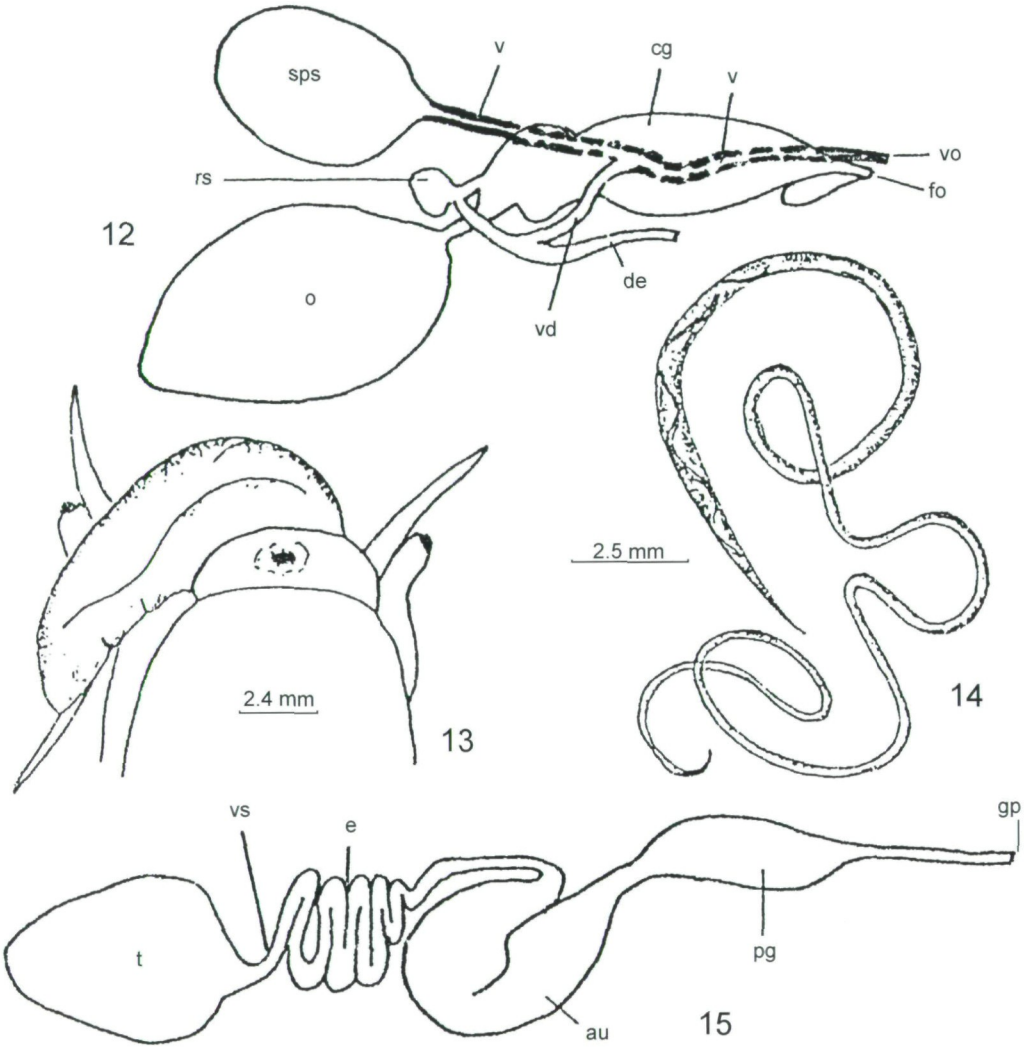

Fig. 12 - 15 (after HAYNES, 1991): *S. suffreni* reproductive system: (12) female., (13) penis. (14) spermatophore. (15) male.

Range: (Fig. 27) South India, Sri Lanka, Taiwan, Philippines, Indonesia, New Guinea, Solomon Islands, Natal (East Africa).

Records: INDIA: (MHNG; Calcutta (BMNH); Bengal (MHNG, ZMZ, MCZ); Tamil Nadu (author); SRI LANKA: Southern and Western Provinces (NMW, BNHM, ZMZ, MCZ); PHILIPPINES: Bislig (ZMZ), Salana R., Mindanao (author, MNHN); Luzon (ZMZ; Negros (ZMZ, BMNH, MNHG); INDONESIA: Java (ZMZ, ZMA, MCZ); Moluccas (ZMZ); Sumatra (ZMA); Sulawesi (ZMZ); Flores (ZMA); Buru (MNB); SOUTH AFRICA: Kwazulu Natal - Kwo Makosi Lagoon, Umbogintwini Lagoon, Mbizana R., Illovo R. Karridene (NM); NEW GUINEA: (MHNG), Irian Jaja (author);

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SOLOMON ISLANDS: New Georgia (author); Choiseul (MCZ); Malaita (MCZ); TAIWAN (MMBS).

Remarks: In 1816 LAMARCK described *Navicella tesselata* and *Navicella lineata* as two species of brackish water limpets from India. MARTENS (1881) considered that the two species were synonymous and chose the name *Navicella tesselata*. Subsequent authors have used both names but *Navicella tesselata*, the choice of MARTENS, the first reviser, should be used. Type specimens in the Museum d'Histoire Naturelle, Geneva confirm that LAMARCK's two types are the same species and that the holotype labelled *N. lineata* is the narrow or compressed form, as is one of the syntypes of *N. tesselata*. Further examination of specimens from Vanuatu and Fiji has shown that they differ from *Septaria tesselata* in shell and operculum shape and more importantly in reproductive anatomy. Examination of the *Septaria* type specimens in the various Natural History Museum showed that this South Pacific species was *Navicella livida* REEVE, 1856 held in the Natural History Museum, London. It, like *S. tesselata* has a narrow or compressed form and it is abundant near the mouth of rivers and streams, usually in brackish water. *Septaria livida*, the Fijian species, has been referred to as *Septaria* lineata by STARMÜHLNER (1976) and HAYNES (1984, 1985, 1987, 1990, 1994).

The shells of the compressed forms of *S. tesselata* and *S. livida* are very similar. Both have fragile, long, thin shells with longitudinal lines (Figs. 19 a, 20 a). The wide forms are easier to tell a part as the apex of *S. tesselata* is low and inside the posterior margin of the shell. It is not found in the Pacific south of the Solomon Islands.

Septaria livida (REEVE, 1856) (Figs. 20 - 21, 28 - 31, 27)

Septaria lineata STARMÜHLNER, 1976: Figs. 45, 46; HAYNES, 1984: Figs. 33, 34, 36; HAYNES, 1985: 204; HAYNES, 1987: 377; HAYNES, 1991: Figs. 2 D, 3 A, 3 D; HAYNES, 1997: Fig. 1 A.

Type Material *Navicella livida* REEVE, 1856: figs. 13 a, b (2 syntypes BMNH 1974 107, unknown); *Navicella schmeltziana* MOUSSON, 1870: (2 syntypes ZMZ, Ovalau, Fiji); *Navicella picturata* GARRETT, 1872: (paratypes MCZ, Vanua Levu, Fiji); *Navicella splendens* MOBILLE, 1895: 399 (3 syntypes MNHN, Vanuatu); *Navicella francoisi* MOBILLE, 1895: 400 (holotype MNHN, Vanuatu).

Description

Shell: (Figs. 20 a, b, 21 a, b)

Wide Form: Shell length up to 33 mm, mean w/l ratio 0.79, mean h/l ratio 0.37; compressed form mean w/l ratio 0.56, mean h/l ratio 0.25. Shell wide and straight at the posterior, narrower and rounded at anterior end. The apex is high above or in front of the posterior margin. Septum edge straight or slightly curved.

Ground colour yellow-brown or olive-brown with black/brown markings, which form yellowish triangles or tongues. Interior white/gray and septum often yellowish. The two muscle scars are darker and often prominent.

Males and females are approximately the same size and are present in equal numbers (Table 1).

Operculum: (Fig. 21 c) Nearly square, pink-orange with a clear horn at the posterior margin. Anterior rib angled slightly inwards.

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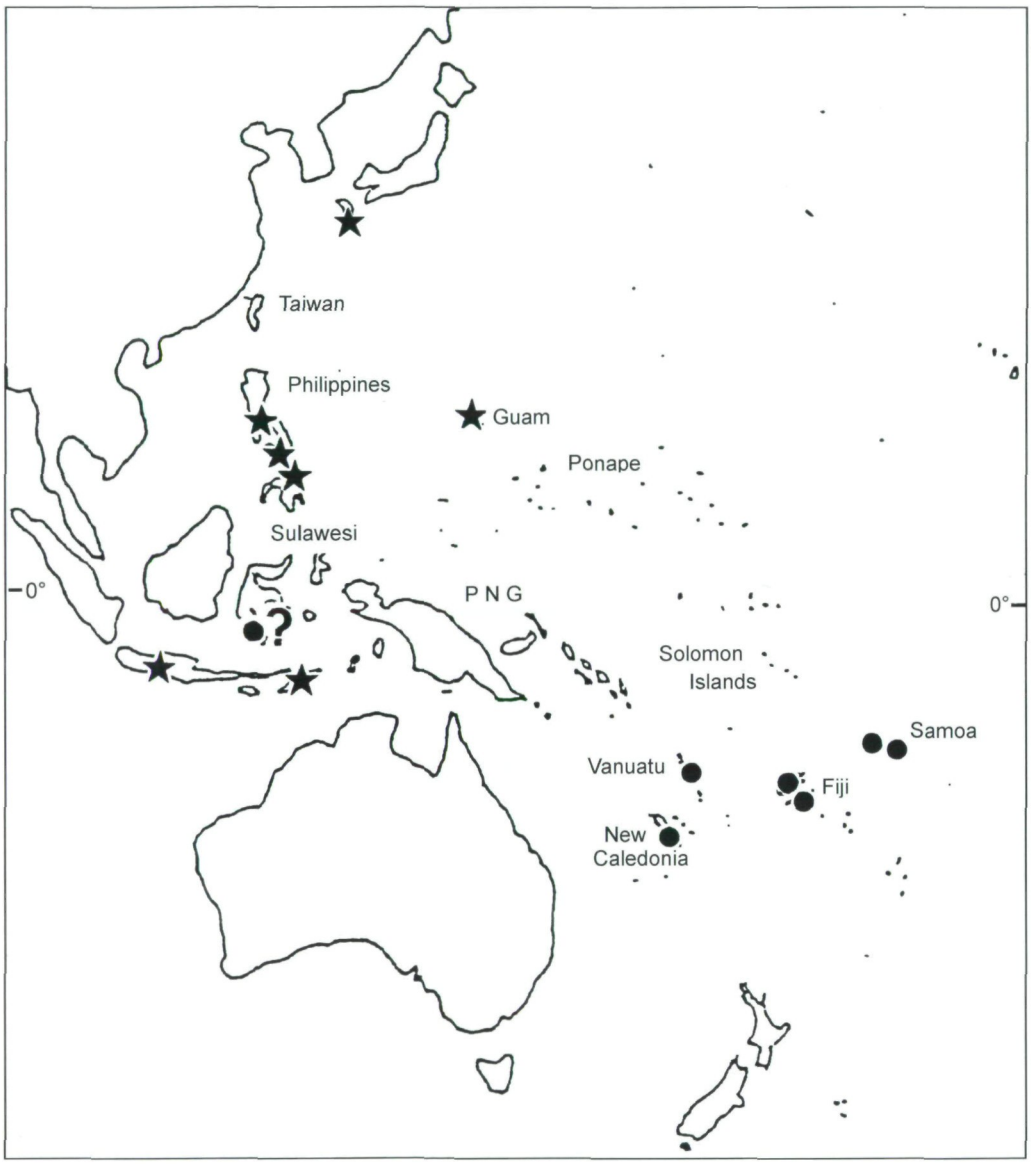

Fig. 16: Distribution of *S. suffreni* ● and *S. cumingiana* ★.

Compressed Form: Shell fragile, narrow, pointed and with apex outside shell margin. Back ground colour yellow/brown with black or purple longitudinal lines or with lines and triangles. The septum is deep with a curved margin (Figs. 20 a, b).

Operculum: fragile, yellow and rectangular.

Reproductive Anatomy: (Figs. 28 - 31) Females have many short spermatophores, 8 mm long in their spermatophore sac. The penis is well tucked away, fleshy but relatively small, with a papilla.

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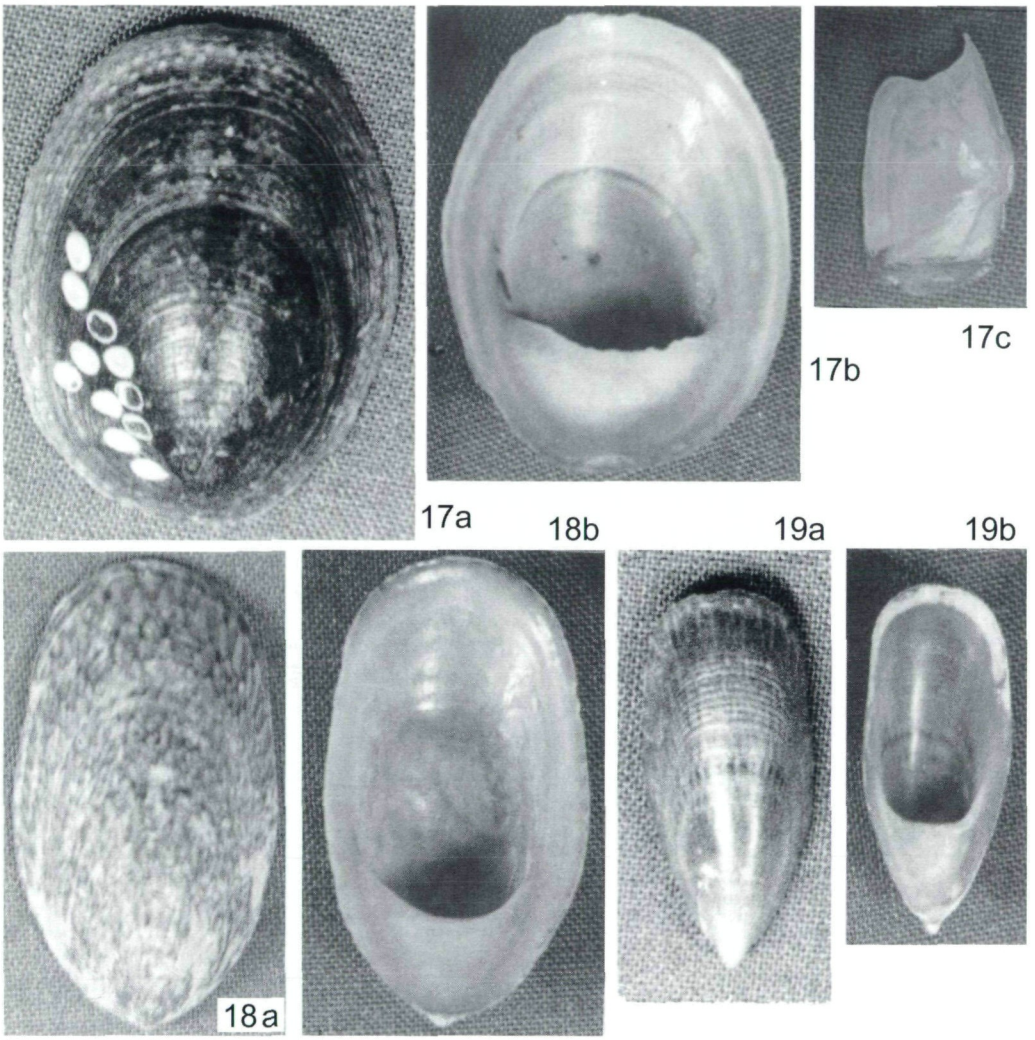

Figs. 17 - 19: *S. tesselata* shells: (17) wide form: (a) dorsal side; (b) ventral side; Length: 23, 24 mm; (c) operculum; Width 9 mm. (18) intermediate form: (a) dorsal side; (b) ventral; Length: 25 mm. (19) compressed form: (a) dorsal side; (b) ventral side; Length: 20 mm.

Habitat: In brackish water and in tidal parts of rivers and streams. Wider form found on stones, rocks and concrete bridge abutments in fast flowing water. Compressed form found on sticks, bamboo, grass stalks and floating wood in quiet tidal backwaters. Intermediate forms are found on bamboo and logs.

Range: (Fig. 27) Has a restricted range and has only been reported from Viti Levu, Vanua Levu, Ovalau (Fiji) and Vanuatu.

Records: FIJI: Viti Levu (NMW), Rewa R. Lami R. Sigatoka R, Waidalice R. (author); Vanua Levu: (MCZ), Nasekawa R., Buca Bay (author); Ovalau (ZMZ, author); VANUATU: (MNHN).

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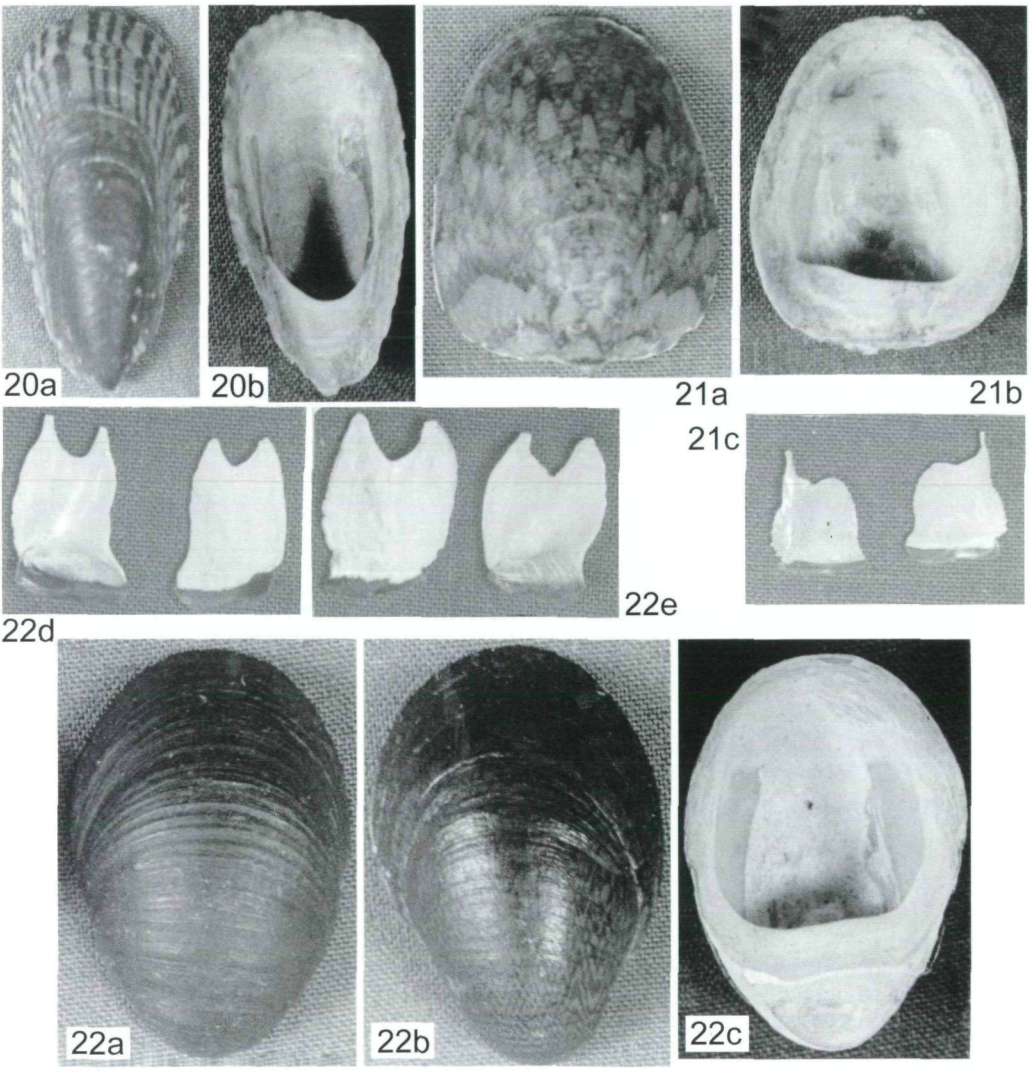

Figs. 20 - 22: (20) *S. livida* shell, compressed form: (a) dorsal side; (b) ventral side; Length: 25 mm. (21) *S. livida* shell, wide form: (a) dorsal side; (b) ventral side; Length: 25 mm; (c) operculum; Width: 7 mm. (22) *S. sanguisuga* shell (a) (b) dorsal side; (c) ventral side; Length: 24 mm; (d) male operculum; Width: 6 mm; (e) female operculum; Width: 9 mm.

Remarks: This species has previously known as *Septaria* lineata but it is not synonymous with LAMARCK' *S. tesselata/lineata*. The Mann - Whitney U test showed that the shells of *S. livida* were significantly wider than those of *S. tesselata*. The males are the same size while *S. tesselata* males are sometimes smaller than the females, and *S. livida* has short (8 mm long) spermatophores while *S. tesselata* has comparatively long ones (20 mm long). In the wide form, the shell apex of *S. livida* is on or outside the shell margin unlike that of *S. tesselata*.

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REEVE's *Navicella livida* was the oldest type conforming to the characteristics of this species. REEVE's type closely resembles specimens I have collected from mouths of rivers and streams in Viti Levu and Vanua Levu, Fiji. The compressed form has also been given names (*N. picturata* and *N. francoisi*) but these are not valid as intermediate specimens between the two extremes, wide and compressed, can be found.

The wide form of *S. livida* was thought by STARMÜHLNER (1976) to be a form of *S. lineata* which RÉCLUZ (Le Guillou) 1841 had described as *Navicella apiata*. STARMÜHLNER called this wide form *S. lineata* f. *apiata*. However RÉCLUZ (1841) gave the locality of *N. apiata* as Noukahiva and mistakenly placed it in the Fiji islands. Nuka Hiva is an island in the Marquesas Archipelago (French Polynesia). The types (10 syntypes MHNG, 3 syntypes MNHN) from Nuka Hiva are similar to those recently collected by O. FOSSATI from Nuka Hiva, Marquesas Islands. FOSSATI ET AL. (1992) refers to this species as *Septaria porcellana*, but *S. apiata* is a valid species differing from both *S. porcellana* and *S. livida*.

Septaria sanguisuga (REEVE, 1856) (Figs. 22, 36 - 39, 40)

Navicella macrocephala MARTENS, 1881: 14; *Navicella sanguisuga* SMITH, 1885: 588; *Septaria sanguisuga* HAYNES, 1984: Fig. 38; HAYNES, 1988: 377-383; HAYNES & WAWRA, 1989: Figs. 1 - 4; HAYNES, 1990: 243; HAYNES, 1991: Figs. 2 E, 3 C, 4 E, 5 D; STARMÜHLNER, 1993: 263 Fig. 37; HAYNES, 1997: 71, Fig. 1; Cowie, 1998: 19.

Type Material *Navicella sanguisuga* REEVE, 1856: Fig. 17 (4 syntypes BMNH 1974 119, New Caledonia); *Navicella magnifica* REEVE, 1956: Fig. 16 (Holotype BMNH, Hammond's I. now Rendova I., Solomon Islands); *Navicella scarabeus* REEVE, 1856: Fig. 12 (4 syntypes BMNH, Solomon Islands).

Description

Shell: (Figs. 22 a - c) Shell up to 30 mm long, mean w/l ratio 0.69, mean h/l ratio 0.32. Shell oblong-ovate and deep with a large apex that erodes horizontally and forms a flat surface across the ventral end. The shell widens in front of the septum. Coloured brown, sometimes with black wavy lines that follow the growth ridges that are prominent. The shell inside is bluish and the sloping septum and apex are often orange.

Males and females are approximately the same size (Table 1).

Operculum: (Figs. 22 d, e) Pink with two ribs of nearly equal length, projecting forward. The horn edge is orange and male operculum is narrower than the female.

Reproductive Anatomy: (Figs. 36 - 39) The females have a spermatophore sac which can contain 2 - 3 large, complex purple stained spermatophores. Males have a long fleshy penis without a papilla and a large auxiliary gland.

Habitat: In fast flowing streams on stones and rock faces, from near the sea (Vanuatu) to well inland (Fiji).

Range: (Fig. 40) Fiji, Samoa, Vanuatu, New Caledonia, Solomon Islands, Ponepe, Philippines.

Records: FIJI: Ovalau (ZMZ, author); Taveuni (LANHM, author); Vanua Levu, Gau, Kadavu (author); SAMOA: Upolu (NMW, ZMZ, author); VANUATU: Tanna (author) ; NEW CALEDONIA (BMNH, MNHN, MNW); SOLOMON ISLANDS: New Georgia (AM, author); N, magnifica Rendova I. (Hammond's I.)(BMNH); *N. scarebeus* (BMNH); PONEPE: (author); PHILIPPINES: Lubang (MCZ); Luzon (MCZ).

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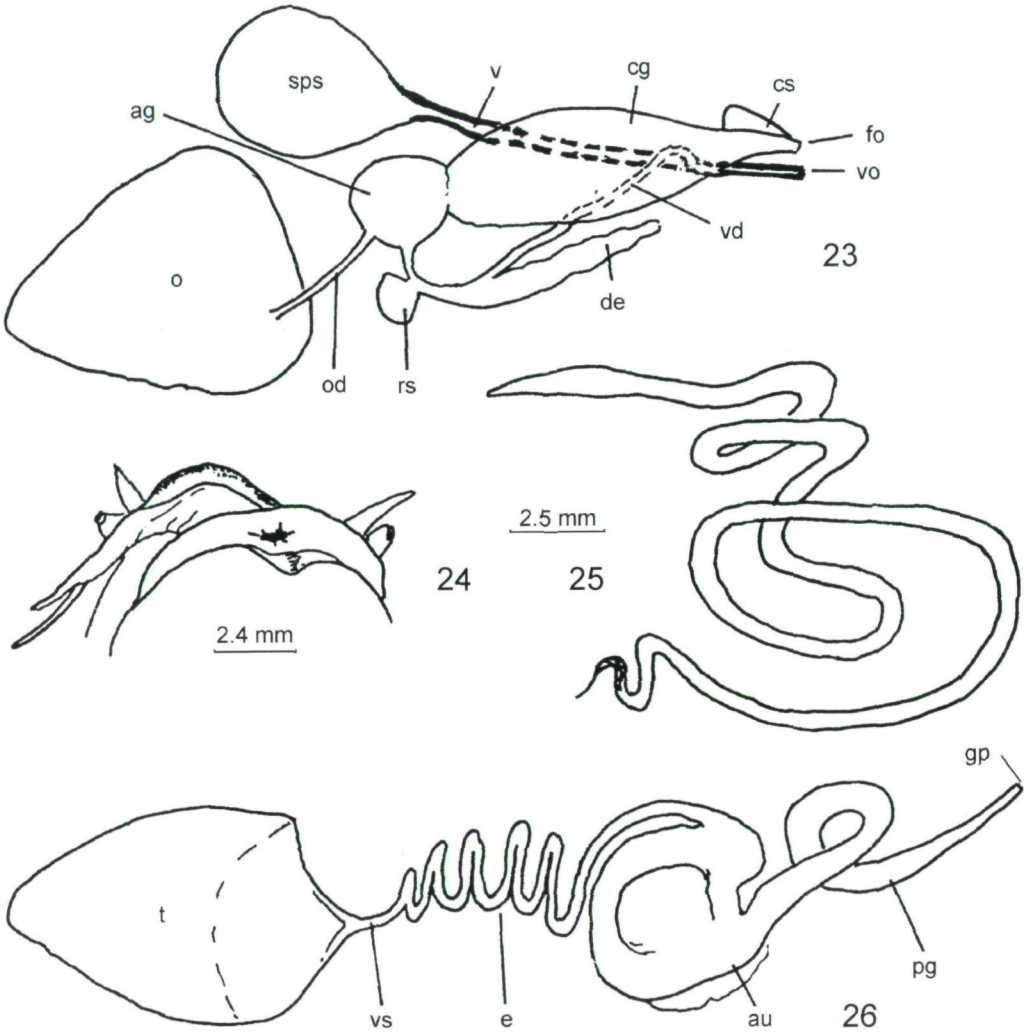

Figs. 23 - 26: *S. tesselata* reproductive system: (23) female., (24) penis., (25) spermatophore., (26) male.

Remarks: *Septaria sanguisuga* has often in the past been confused with *Septaria macrocephala*. MARTENS (1881) combined the four species *N. sanguisuga* (REEVE, 1856), *N. scarebeus* (REEVE, 1856), *N. magnifica* (REEVE, 1856) and *N. macrocephala* (RÉCLUZ, 1841). However, HAYNES & WAWRA (1989) described both *S. sanguisuga* and *S. macrocephala*, highlighting their differences, and establishing that they were two distinct species. Both species have a large apex extending well beyond the posterior edge of the shell, but in *S. macrocephala* the apex is nearly always eroded away, while that of *S. sanguisuga* is rarely eroded. The operculum of *S. sanguisuga* has two prongs of nearly equal length projecting forward while that of *S. macrocephala* has only one. *S. cumingiana* has a two pronged operculum like *S. sanguisuga*, but its shell is widest across the septum while *S. sanguisuga*'s is widest across the centre.

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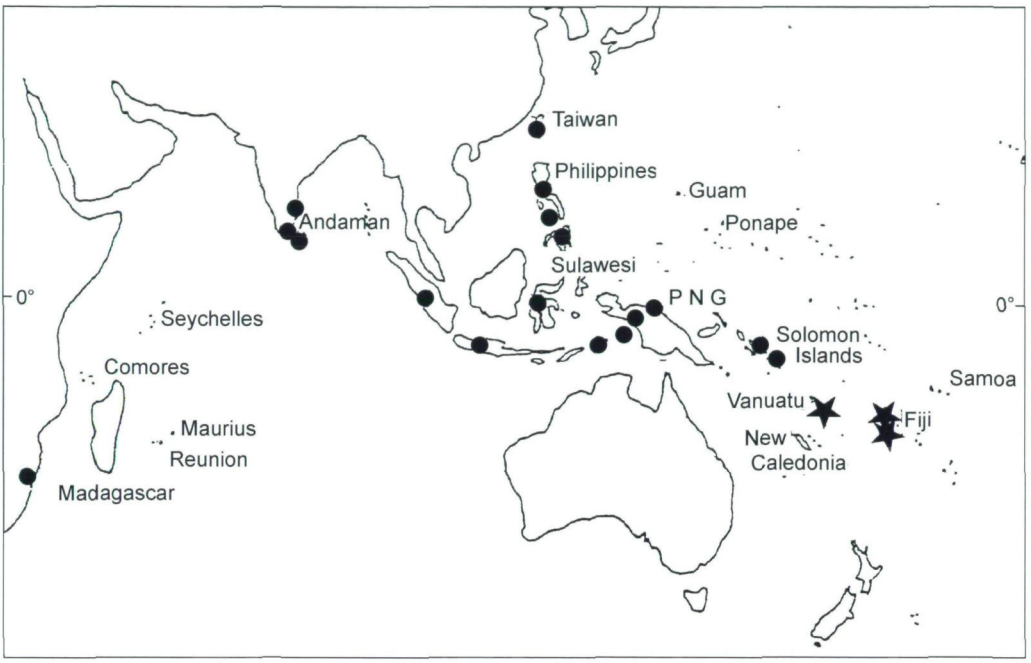

Fig. 27: Distribution of *S. tesselata* ● and *S. livida* ★ .

MARTENS (1881) appears to have been correct in combining *N. scarebeus* and *N. magnifica with N. sanguisuga*. As the shell increases in size, *S. sanguisuga* becomes more variable in shape and the apex becomes less pronounced. The types of *N. scarebeus* and *N. magnifica* are very large shells, between 35 - 45 mm long and with a relatively short apex. The small one pronged opercula housed with *S. scarebeus* types are not big enough to belong to any of the shells and probably do not belong to the *N. scarebeus* shells.

Septaria cumingiana (RÉCLUZ, 1842) (Figs. 16, 32, 41 - 44)

Navicella cumingiana SOWERBY, 1850: pl. 118 Figs 16 - 18; REEVE, 1856: pl.2 Figs 7 a, b; MARTENS, 1881: pl. 4 Fig. 19; *Septaria freycineti* RIECH, 1937: 67; *Septaria borbonica* BENTHEM JUTTING, 1956: 313 Fig. 32; *Septaria cumingiana* KOMATSU, 1986: pl. 10 Fig. 10; KOMATSU, 1991: Figs. 1 - 4; *Navicella cumingiana* KABAT & FINET, 231.

Type Material *Navicella cumingiana* RÉCLUZ, 1842: 157 (4 syntypes BMNH 1974 120, 2 syntypes MNHN, Mindanao, Philippines).

Description

Shell: (Figs. 32 a - c) Shell length up to 28 mm, mean w/l ratio 0.77, mean h/l ratio 0.33. Shell symmetrical with a small pointed apex outside the posterior shell margin. Shell widest across the septum. Septum deep with a small, wide tongue-like projection in the centre.

Ground colour yellow brown with thick wavy black and light concentric lines. The lines are narrower and fainter in larger shells (Fig. 32 a). When the animal is in the shell, the foot is white with black around the upper surface. Inside of shell is gray/white.

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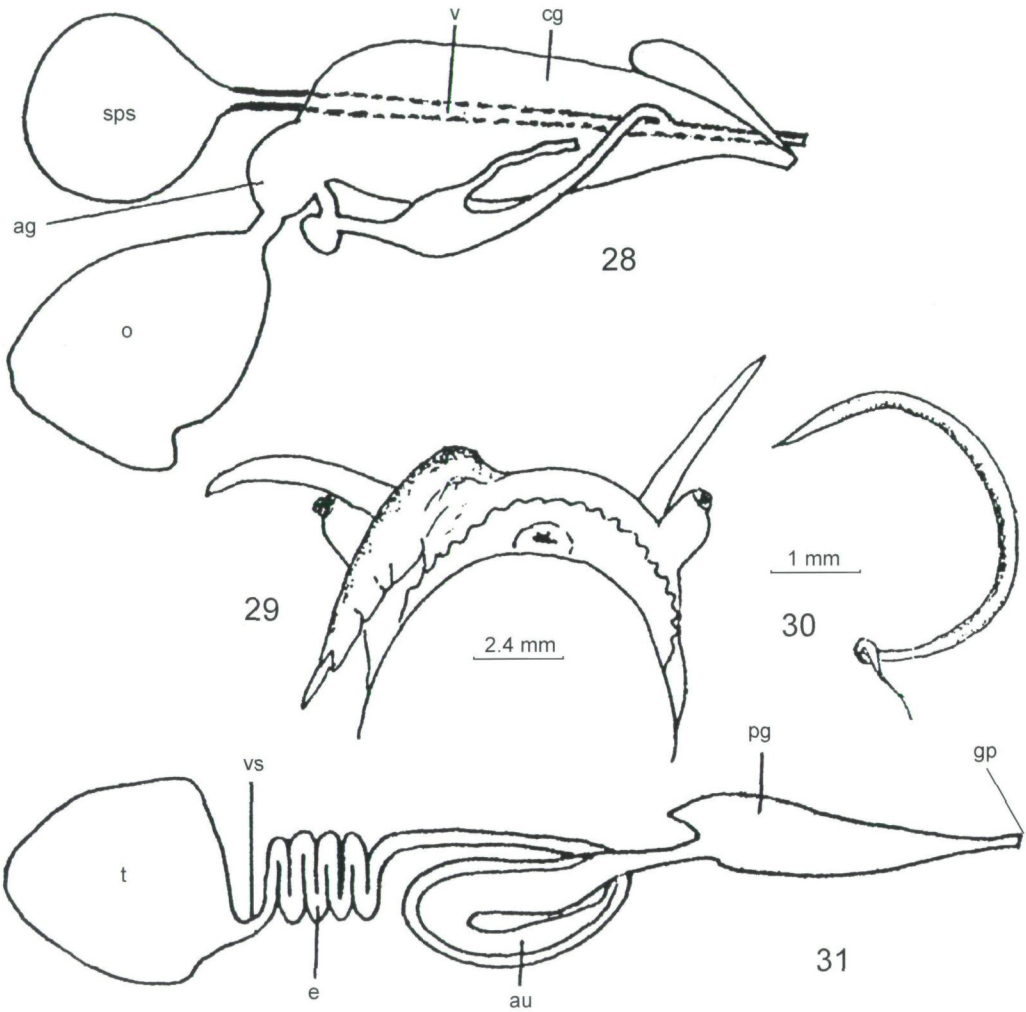

Figs. 28 - 31: *S. livida* (HAYNES, 1991 as *S. lineata*) reproductive system: (28) female. (29) penis., (30) spermatophore. (31) male. Figs. 28 - 31

Males and females are approximately the same size and populations have the same number of individuals of each sex (Table 1).

Operculum: (Figs. 32 d, e) Pink-white, horn margin dark orange-pink and like the operculum of *S. sanguisuga* it has two nearly equal length prongs. Male operculum is narrower than the female's.

Reproductive Anatomy: (Figs. 41 - 44) The females have a spermatophore sac that can hold 2 - 3 spermatophores. The spermatophores are large and complex and the filament extends well into the vagina from the spermatophore sac. Males have a blunt, flat penis with no papilla and a large solid auxiliary gland.

Habitat: In fast flowing streams and rivers on stones and concrete.

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Range: (Fig. 16) Mindanao , Camiguin (Philippines); Bali, Java, Sulawesi (Indonesia); Asfines R., Guam; Iriomate I. (Okinawa).

Records: PHILIPPINES: (NM); Mindanao & Cumaguin (BMNH, MNHN, author); Mindanao (MNHN, MZM. ZMZ, MCZ, author); Marioles (MHNG); Pandon (MHNG = *N. undulata*; Luzon, Lilimbon R. (MZM); Subic Bay (MCZ); Mindora (MCZ, ZMA); INDONESIA: Java (AZM), Bali (ZMZ); GUAM Asafines R. (author); OKINAWA, Iriomata I. (MMBS).

Remarks: *Septaria cumingiana* is usually characterized by obvious dark and light concentric lines that follow the growth ridges. However, a specimen collected from Guam had a pattern of faint large, light triangles. Because of the projection on the septum, it can be mistaken for male S, *suffreni* and because of similar opercula, it can be confused with *S. sanguisuga*. However, the shell of *S. sanguisuga* is widest anterior to the septum, while the shell of *S. cumingiana* is widest across the septum (Figs. 32 a, b).

Septaria apiata (LE GUILLOU in RÉCLUZ, 1841) (Figs. 11, 33, 45 - 47)

Navicella apiata RÉCLUZ, 1850: 375; REEVE, 1856: pl. 5 Fig.22 a; MARTENS, 1881: pl.7 Figs. 1 - 4; *Septaria porcellana* POINTIER & MARQUET, 1990: 227, pl. 2 Fig. 2; FOSSATI et al., 1992: 45 - 56; *Navicella apiata* Kabat & Finet, 1992: 227.

Type Material *Navicella apiata* RÉCLUZ, 1841: 376 (10 syntypes MHNG 15031, 15032, 15033, 3 syntypes MNHN, Nuka Hiva, Marquesas Archipelago).

Description

Shell: (Figs. 33 a, b) Shell length up to 32 mm, mean w/l ratio 0.67, mean h/l ratio 0.32. Shell oblong-ovate. Apex is well outside the posterior shell margin and is long and pointed, especially in young, and often eroded on the ventral surface. Septum wide with a straight edge.

Ground colour yellow-brown, crossed by many fine dark lines that form a pattern of fine triangles or ovals. Inside shell is gray with prominent darker muscle impressions. Septum yellow-orange.

Males and females approximately the same size and populations with the same number of each sex (Table 1).

Operculum: (Fig. 33 c) Nearly square, pink-orange, thick and brittle with a stout rib.

Reproductive Anatomy: (Figs. 45 - 47) Females have no spermatophores but have a spermatophore sac with compartments that contain shiny bundles of sperms, Males have a large auxiliary gland and a penis with a large , long papilla.

Range: (Fig. 11) Marquesas Islands, French Poynesia.

Habitat: From a few metres from the sea to well inland in fast flowing streams.

Records: MARQUESAS ISLANDS: Nuka - Hiva (MHNG, MNHN, ZMZ, author), *N. crepiduloides* (BMNH); Fatu Hiva, Ua - Pou, Ua - Huka, Hiva - Oa, Tahuata (author).

Remarks: *Septaria apiata* is endemic to the Marquesas Islands. RÉCLUZ described *N. apiata*'s habitat as 'Noukahiva, l'une des iles Fidgi', but undoubtedly meant Nuka Hiva,

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one of the larger islands in the Marquesas Archipelago. The type specimens conform to those collected from Nuka Hiva and other Marquesas Islands by O. FOSSATI in 1990. FOSSATI et al. (1992) called the species *Septaria porcellana. Septaria* from both the Marquesas and the Society Islands have been previously regarded as *S. porcellana* (STARMÜHLNER 1976, POINTIER & MARQUET 1990, RESH et al.1990, FOSSATI et al. 1992). However, *Septaria* from both groups of islands differ from one another and from *S. porcellana* in shell shape and pattern and in reproductive anatomy. Young *S. apiata* have a long pointed apex and resemble *S. sanguisuga*.

Septaria taitana MOUSSON, 1869 (Figs. 11, 34, 48 - 50)

Septaria borbonica depressa RIECH, 1937: 65; *Septaria porcellana* f. *depressa* STARMÜHLNER, 1976: 537; *Septaria porcellana* HAYNES, 1990: 237 - 248; POINTIER & MARQUET, 1990: 227, pl2 Fig. 1; RESH et al., 1990: 195 - 214.

Type Material *Septaria taitana* MOUSSON, 1869: MOUSSON Catalogue 236 (4 syntypes ZMZ 529697, Tahiti).

Description

Shell: (Figs. 34 a - c) Shell length up to 30 mm, w/l ratio 0.70 (but variable, see appendix), mean h/l ratio 0.30. Shell slightly skewed, apex small and outside the posterior shell margin.

Ground colour orange-brown with a pattern of thick black lines radiating from the apex and crossing one another, forming a pattern of triangles and oblongs.

Shell inside white/gray, muscle scars darker and prominent. Septum yellow-orange and wide with a nearly straight edge.

Males smaller than females and there are fewer males in a population (Table 1).

Operculum: (Fig. 34 d) Pink with a short rib and an orange-pink horn border.

Reproductive Anatomy: (Figs. 45 - 47) Females have no spermatophores but have a small dorsal spermatophore sac with ill-defined compartments. Males with a relatively large auxiliary gland. Penis short and broad with a long papilla.

Habitat: From a few metres from the sea to 3 - 4 km inland on stones and rocks in fast flowing streams.

Range: (Fig. 11) Tahiti, Moorea, Huahine, Raiates (Society Islands, French Polynesia)

Records: SOCIETY ISLANDS: Tahiti (ZMZ, author), *S. borbonica depressa* (MCZ), *S. porcellana depressa* (NMW), *S. depressa* (MNHN), *S. porcellana* (MNHN); Moorea *S. porcellana* (author, MNHN), *S. depressa* (ZMA), *S. bougainvillei* (ZMZ); Raiates S. *porcellana* (MNHN).

Remarks: *Septaria taitana* MOUSSON 1869 was the only *Septaria* type specimen found in the Natural History Museums from the Society Islands. It conforms to specimens recently collected from Tahiti and Moorea. The *Septaria* species from Tahiti have been called *S. depressa*, *S. borbonica depressa*, *S. porcellana depressa* and more recently *S. porcellana* (HAYNES, 1990, POINTIER & MARQUET, 1990, RESH et al., 1990). The shell pattern of *S. taitana* is similar to one of the type specimens of *N. depressa* LESSON, 1832

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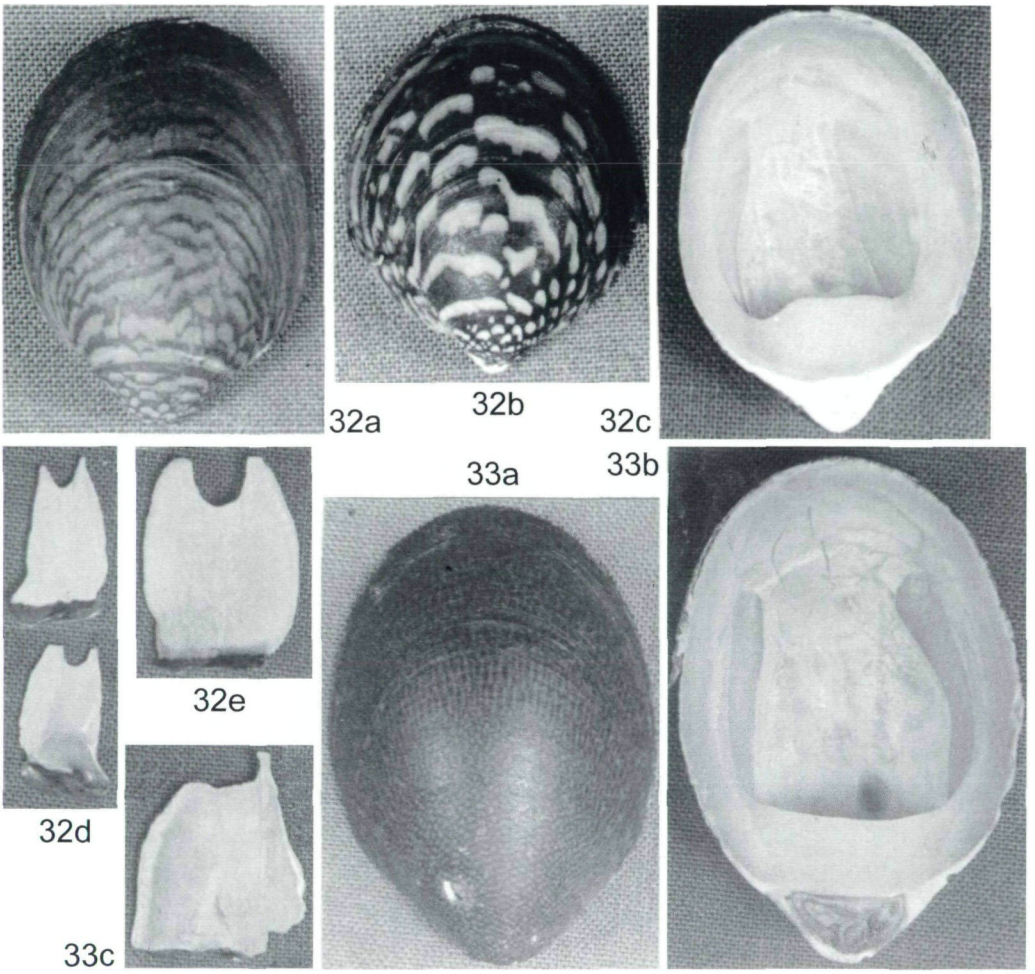

Figs. 32 - 33: (32) *S. cumingiana* shells: (a) (b) dorsal side; (c) ventral side; Length: 20, 23 mm; (d) male operculum;Width: 5 mm; (e) female operculum; Width: 9 mm. (33) *S. apiata* shells: (a) dorsal side; (b) ventral side; Length: 21, 24 mm; (c) operculum; Width: 8 mm.

held in MNHN and collected from New Guinea. However *N. depressa* types are more likely to be *S. porcellana* whose shells are variable. *S. taitana* differs from *S. porcellana* in shell shape and reproductive organs but resembles it in having small males.

***Septaria porcellana* (LINNAEUS, 1758)** (Figs. 35, 51 - 53, 57)

Navicella porcellana RÉCLUZ, 1841: 373; *Navicella depressa* RÉCLUZ, 1841:373; *Navicella suborbicularis* RÉCLUZ, 1841: 377; *Navicella haustrum* REEVE, 1856: pl. 1 Fig. 3; pl. 4 Fig. 18; *Navicella depressa* MARTENS, 1881: pl. 5 Figs 1 - 9; *Septaria Sandalium porcellana* BAKER, 1923: 152; *Septaria borbonica depressa* RIECH, 1937: 65; *Septaria porcellana* BENTHEM JUTTING, 1956: 315 Fig.31; *Septaria borbonica depressa* STARMÜHLNER, 1970: Figs. 26 - 29; *Septaria janelli* PACE, 1970: Fig. 1; *Septaria por-*

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cellana f. depressa STARMÜHLNER, 1976: 537 Figs. 131 - 137, 150 - 154; STARMÜHLNER 1986: 380 - 384; *Septaria porcellana* KOMATSU, 1986: Fig. 11; KOMATSU, 1986: pl. 5 Figs. 1 - 3, pl. 8 Fig. 5; HAYNES, 1990: 237 - 248; HAYNES, 1993: 285 - 290; HAYNES, 1996: Figs. 4, 8, 12.

Type Material *Patella porcellana* LINNAEUS, 1758: 781 (holotype LSL 657 Ed. 10, India); *Navicella depressa* LESSON, 1832: 150 (2 syntypes MNHN, New Guinea); *Navicella zebra* LESSON, 1832: 151 (2 syntypes MNHN, New Ireland.

Description

Shell: (Figs. 35 a - d) Shell length up to 27 mm, mean w/l ratio 0.79, mean h/l ratio 0.39. Shell symmetrical, cap-like and relatively deep and wide. Apex outside the posterior shell margin and often eroded.

Ground colour yellow-brown with a black or purple-pink pattern of triangles and horizontal lines. When the periostracum flakes off the shell, a purple pattern remains. Shell inside white to light gray, septum narrow and its edge curved and tinged yellow.

Male shells significantly smaller than females and fewer males in the populations (Table 1).

Operculum: (Fig. 35 e) Pale pink, nearly square, robust with a relatively long rib. Horn margin yellow-orange.

Reproductive Anatomy: (Figs. 51 - 53) Female with a small, thin walled, ventral spermatophore sac without spermatophores. Males small (up to 15 mm long) with large flap-like penis with a papilla and a small auxiliary gland.

Habitat: In still and swift current on stones from a few metres from the sea to 5 - 6 km inland.

Range: (Fig. 57) New Guinea, Solomon Islands, Vanuatu, New Caledonia, India, Andaman Islands, Indonesia, Philippines, Taiwan, Okinawa, Guam, Saipan, Northern Australia.

Records: NEW GUINEA: Uriami R. (Int. Landsnail Soc.); *S. depressa* (MNHN), New Ireland; *S. zebra* (MNHN), New Britain (MCZ); Bougainville (MCZ); SOLOMON ISLANDS, New Georgia (author), Guadalcanal (author, NM), Makira (author, MCZ); VANUATU, Efate, Espiritu Santo, Tanna, Pentecost (author); NEW CALEDONIA (MNHN, MNW), *N. haustrum*, *N. morelatana* (BMNH); INDIA (LSL), Andaman Islands (NMW); TAIWAN (MMBS, NM); JAPAN, Okinawa (MNHN); INDONESIA, Sulawesi, East Flores, Java (ZMA), Molucca Islands (MCZ), Ambon (NM); GUAM (MCZ), Saipan I. (MCZ); PHILIPPINES, Negros, Batan (MCZ); AUSTRALIA, Northern Territory, Anson Bay, Port Darwin (QM).

Remarks: *S. porcellana* has been confused with other *Septaria* species with a similar shell and this suggested that it had a wider distribution than it actually has. At one time its distribution was thought to extend from the Indian Ocean, across South East Asia, the Philippines, Indonesia to Taiwan and down across the Pacific to Fiji and French Polynesia.

RÉCLUZ (1841) erroneously combined it with the Indian Ocean species under the name of *S. borbonica* and later RIECH (1937) continued the practice. Various *Septaria* species have been mistakenly identified as *S. porcellana* – female *S. suffreni* by STARMÜHLNER (1976), *S. bougainvillei* by STARMÜHLNER (1976), HAYNES (1985, 1988, 1990, 1991), *S. taitana* by STARMÜHLNER (1976), POINTIER & MARQUET (1990), RESH et al. (1990), *S. apiata* by FOSSATI ET AL. (1992) and *S. janelli* by MACIOLEK & FORD (1987).

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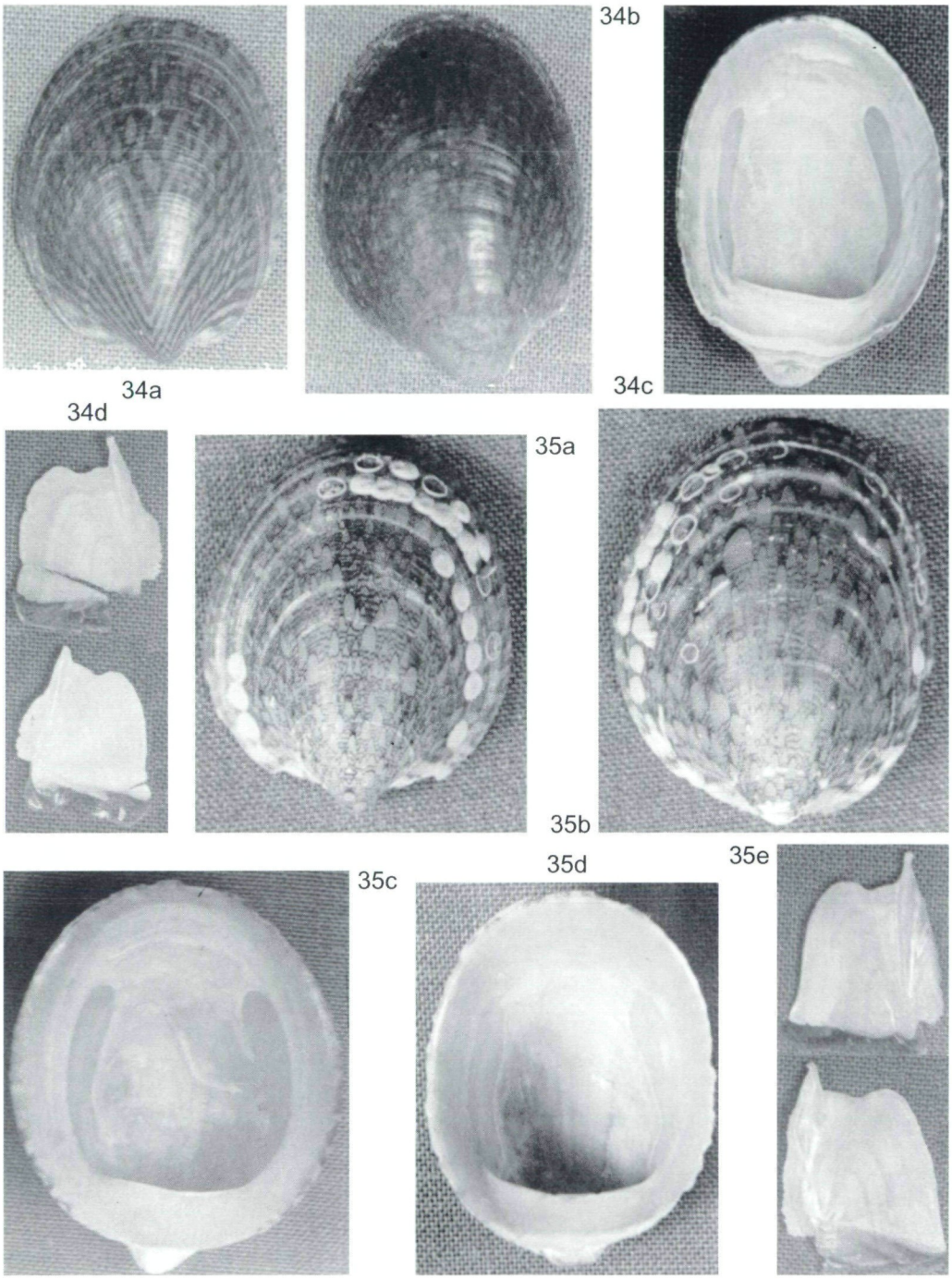

Figs. 34 - 35: (34) *S. taitana* shells: (a) (b) dorsal side; (c) ventral side; Length: 23, 24 mm; (d) operculum; Width: 8 mm. (35) *S. porcellana* shells: (a) (b) dorsal side; (c) (d) ventral side; Length 24, 25 mm; (e) operculum; Width: 10 mm..

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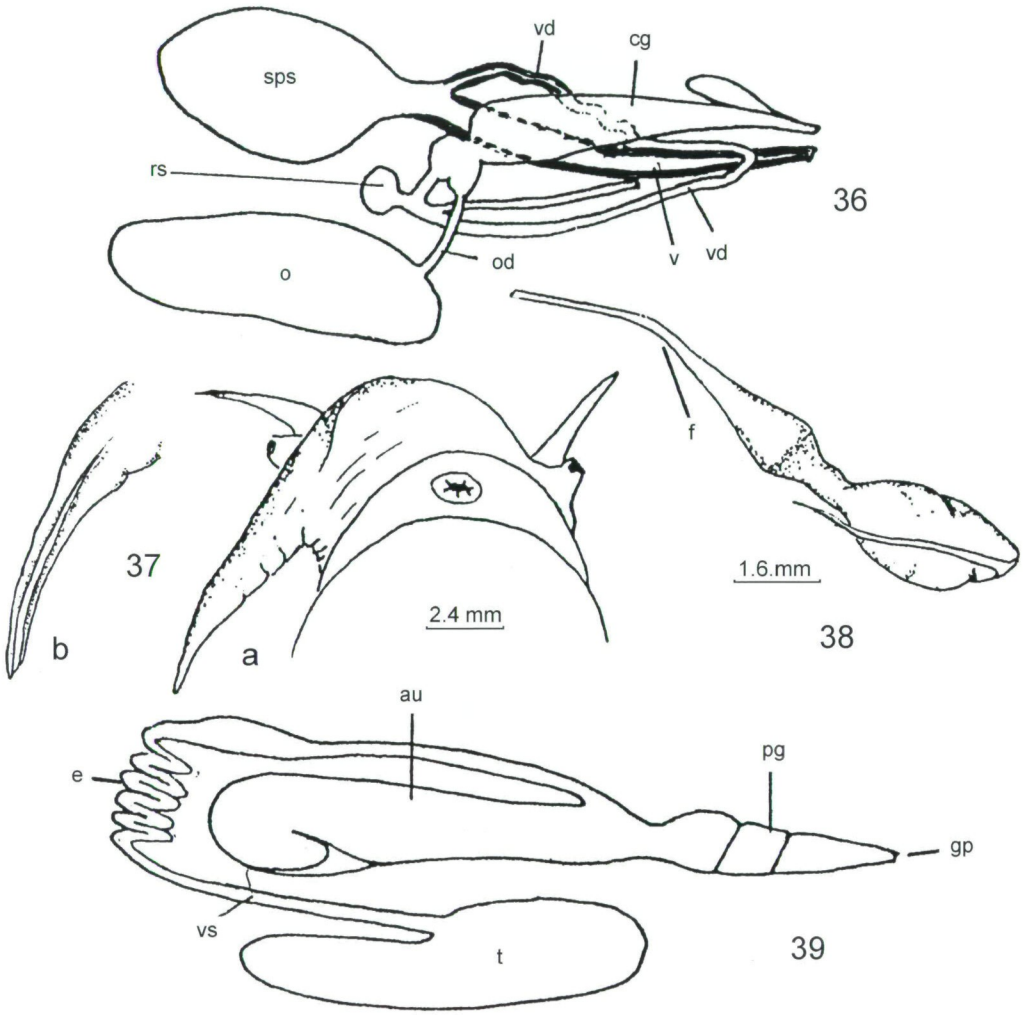

Figs. 36 - 39: *S. sanguisuga* reproductive system: (36) female. (37) penis (a) ventral view; (b) dorsal view. (38) spermatophore (f, filament). (39) male (Figs. 36 - 39: HAYNES, 1991).

The holotype of *S. porcellana*, held in the Linnaean Society, London is a deep robust shell that has lost its periostracum and is, therefore, white with a pink pattern of triangle and horizontal lines. It is not much like the illustration of *Patella porcellana* in Rumphius, Georgius Everhaus, Amsterdam, 1705, which is cited by LINNAEUS. It has a few dark triangular lines. However, the *P. porcellana* holotype is like specimens collected from Solomon Islands, New Guinea, Vanuatu and New Caledonia which have a similar black-red pattern of triangles and lines. Specimens from Andaman Islands, India, Indonesia, Philippines, Taiwan and Northern Australia also conform to the holotype.

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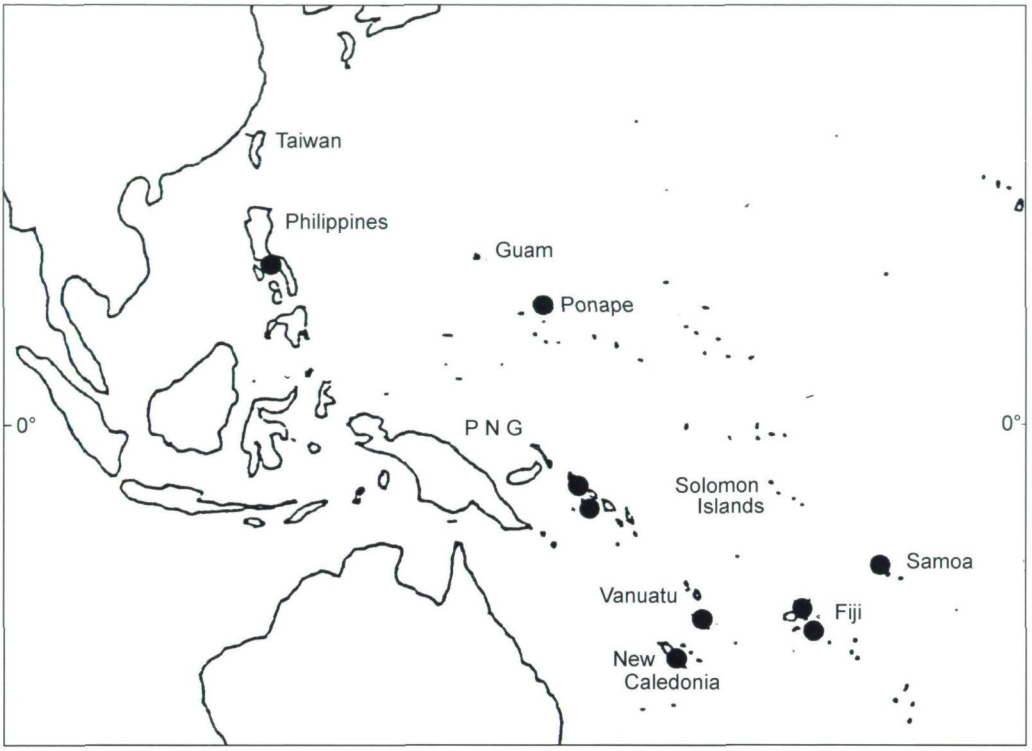

Fig. 40. Distribution of *S. sanguisuga* ●.

The two syntypes of *Navicella depressa* LESSON (MNHN) were collected from New Guinea. The larger of the syntypes is certainly *S. porcellana* although the smaller is less typical. As there is variation of shell pattern in all *Septaria* species, *S. depressa* should be considered a synonym of *S. porcellana* and not a subspecies.

Some *S. janelli* shells have a similar pattern to those of *S. porcellana*, but *S. janelli* shells are more green in colour, the apex is off centre and the males are the same size as the females.

Septaria borbonica (BORY DE ST VINCENT, 1803) (Figs. 54 - 56, 57, 58)

Navicella elliptica QUOY & GAIMARD, 1832: 206 pl. 58. Fig. 2534; *Navicella porcellana* RÉCLUZ, 1841:372; SOWERBY, 1849: pl. 127 Figs 1 - 2; REEVE, 1856: Figs. 6, 10; CROSSE, 1874: 242; *Navicella borbonica* MARTENS, 1881: pl.1 Figs 4 - 18; *Navicella (Cimber) borbonica* TRYON, 1888: pl. 27 Fig. 212; *Septaria borbonica* BOURNE 1908: 810 pl.46 Figs 1 - 3, pl. 52 Fig. 23; ANDREWS, 1937: 525 pl. 4 Fig. 23; *Septaria (Septaria) borbonica* STARMÜHLNER, 1969: 85 - 152; *Septaria borbonica* STARMÜHLNER, 1983: Figs. 16, 17; HAYNES, 1996: Figs. 3, 7, 11.

Type Material *Patella borbonica* BORY DE ST VINCENT, 1803:287 pl. 37 Fig. 2 (type lost); *Septaria borbonica* FÉRUSSAC, 1807: 70 (2 probable syntypes MNHN, Reunion); *Navicella elliptica* LAMARCK, 1822: 177 pl. 456 (7 syntypes MHNG, Mauritius); *Navicella bimaculata* REEVE, 1856: Figs. 6, 10 (5 syntypes BMNH, Mauritius).

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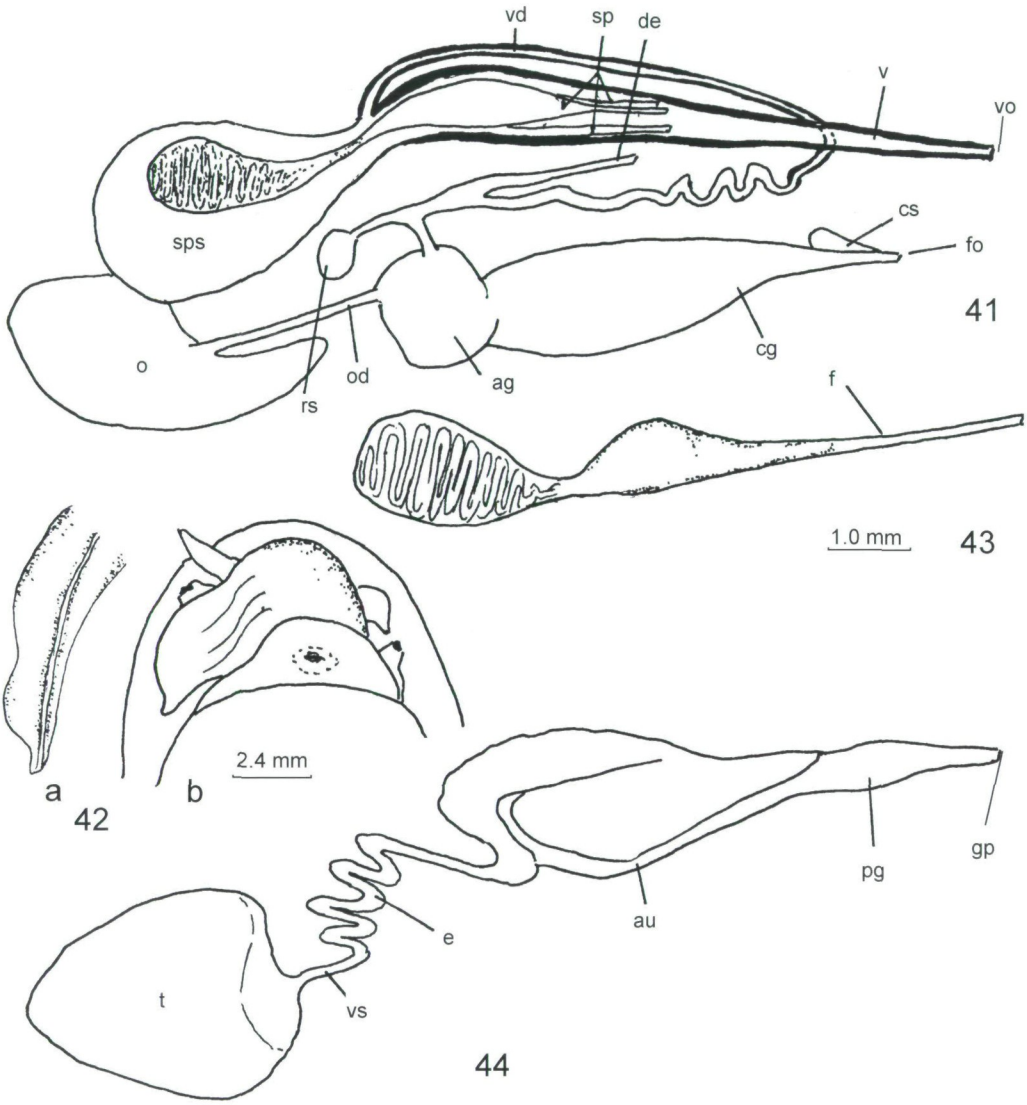

Figs. 41 - 44: *S. cumingiana* reproductive system: (41) female. (42) penis (a) ventral view; (b) dorsal view; (43) spermatophore (f filament). (4) male.

Description

Shell: (Figs. 58 a - c) Length up to 23 mm, mean w/l ratio 0.74, mean h/l ratio 0.33. Shell symmetrical, cap-like with apex outside the posterior margin of the shell, but often eroded. Widest across the septum.

Dorsal pattern is often covered by a dark encrustation. Ground colour Yellow-brown with dark lines making a pattern of small intricate triangles and/or ovals. Inside dark gray with a yellow, narrow septum.

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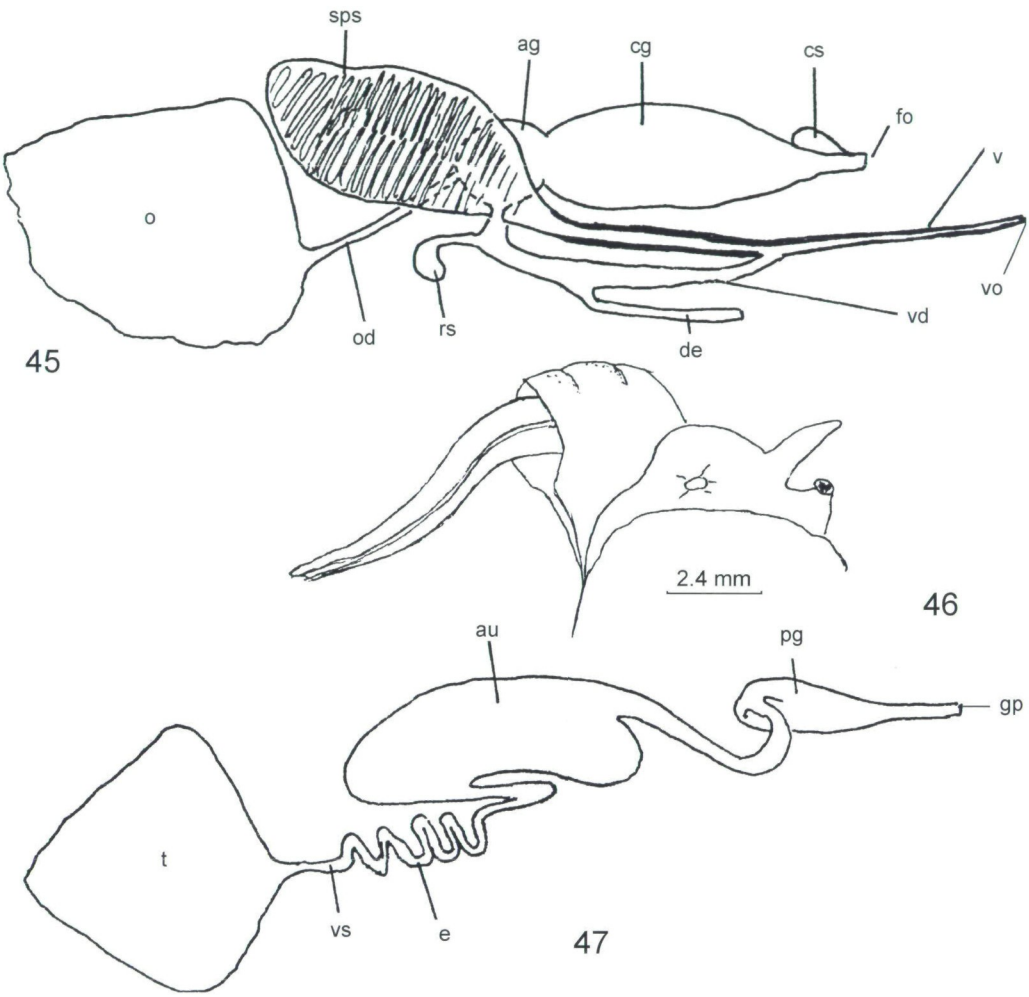

Figs. 45 - 47: *S. apiata* reproductive system: (45) female. (46) penis. (47) male.

Males and females the same size and the same number of each sex in populations.

Operculum: (Fig. 58 d) Fragile, thin, pale pink-orange and wider at the posterior. Horn margin darker pink-orange and the rib short and often knobbly or crooked.

Reproductive Anatomy: (Figs. 54 - 56) Females with a small ventral spongy remnant of a spermatophore sac without spermatophores. Males have a broad grooved penis with a long papilla. Auxiliary gland quite large.

Habitat: In still and swift water on stones and rocks from a few metres from the sea to 4 - 5 km inland.

Range: (Fig. 57) Indian Ocean Islands - Seychelles, Mauritius, Rodriguez, Reunion, Comoros, Madagascar, East Coast of Africa e.g. Kwazulu Natal.

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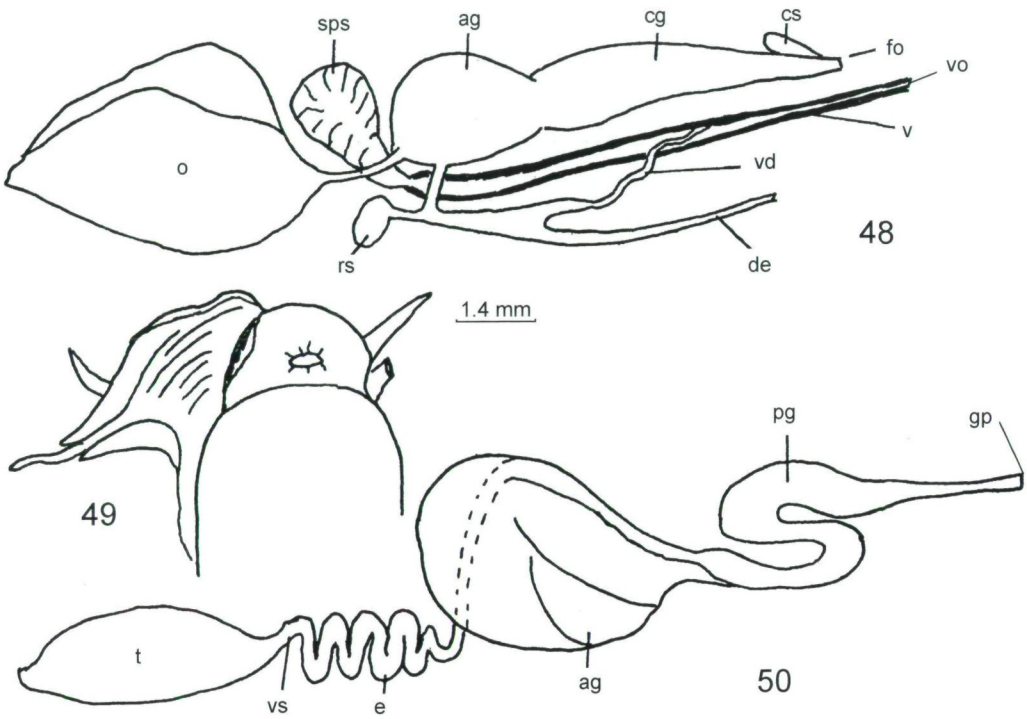

Figs. 48 - 50: *S. taitana* reproductive system: (48) female. (49) penis. (50) male.

Records: SEYCHELLES: Mahe, Grande Anse R. (NMW, author); MAURITIUS: (author, NM, NMW, ZMA); *N. elliptica* (MHNG); *N. bimaculata* (BMNH); COMOROS, Anjouan (NMW, NM); RODRIGUEZ (NM); REUNION (NMW, MNHN, MCZ, NM); MADAGASCAR (NMW); SOUTH AFRICA, Kwazulu Natal (NM).

Remarks: *Septaria borbonica* and *Septaria porcellana* have been confused by many authors. Although the shells of the two species are somewhat similar, *S. borbonica*'s shell is flatter and more shovel-shaped and its anatomy and geographic distribution is different as *S. borbonica* is confined to the Indian Ocean. I have collected it from Mauritius and Seychelles, while STARMÜHLNER found it in Madagascar (1969), Comoros, Rodriguez and Reunion (1983). The Natal Museum has specimens collected from Transkei and Zululand on the Kwazulu Natal coast. BENTHEM-JUTTING (1956) mistakenly called *S. cumingiana* from Java *S. borbonica* (Figures of shell and operculum show this).

Confusion between *S. borbonica* and *S. porcellana* began when RÉCLUZ (1841) combined the two species. As he correctly stated, BOURNE (1908) studied the anatomy of *S. borbonica* and not that of *S. porcellana*. RIECH (1937) and STARMÜHLNER (1970) used the name *S. borbonica* depressa when referring to the New Guinea and New Caledonian *S. porcellana*.

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Septaria janelli (RÉCLUZ, 1841) (Figs. 59, 62 - 64, 65)

Navicella suborbiculus RÉCLUZ, 1842:155; *Navicella janelli* SOWERBY, 1850: 547 - 552; REEVE, 1856: pl.1 Figs 1 a, b; MARTENS, 1881: pl.4 Figs 19 - 19; *Septaria porcellana* MACIOLEK & FORD, 1987: 628; HAYNES, 1990: 242 - 243.

Type Material *Navicella janelli* RÉCLUZ, 1841: 376; 1842: 154 (type may be lost, but possible syntypes MHNG, Luzon, Philippines; *Navicella d'urvillei* RÉCLUZ, 1841: 378 (lectotype MHNG and paralectotype MHNG selected from probable syntypes in the Delessert collection by Kabat & Finet (1992)); *Navicella laperousi* RÉCLUZ, 1841: (2 syntypes MNHN, Guam; syntypes MHNG mixed with *S. bougainvillei*).

Description

Shell: (Figs. 59 a - c) Shell length up to 27 mm, mean w/l ratio 0.79, mean h/l ratio 0.37. Apex just outside the posterior of shell margin and often eroded. Shell deep and widest just anterior to the septum. On the dorsal side the apex is skewed slightly to the left.

Ground colour yellow-brown or yellow-green with black markings that are typically longitudinal black lines or long thin oblongs or triangles or triangles but more often the pattern is composed of acute triangles and wavy lines, similar to those of *S. porcellana* (Fig. 35 a). Inside shell white-gray, septum narrow and cream-yellow, changing to orange at the edge.

Males and females the same size and with the same number of each sex in populations (Table 1).

Operculum: (Fig. 59 d) Delicate, white-pale yellow, horn margin colourless but may be stained dark red-brown. Rib thin and narrow, and the rib side is serrated.

Reproduction Anatomy: (Figs. 62 - 64) Females with a small ventral wrinkled spermatophore sac with no spermatophores but there is a relatively large receptaculum seminis. Males have a broad grooved penis with a long papilla.

Habitat: From a few metres from the sea to well inland on stones in fast flowing streams.

Range: (Fig. 65) Philippines, (Luzon, Mindanao, Camiguin); Indonesia (Ambon); Guam, Ponepe, (Taiwan?).

Records: PHILIPPINES: Luzon (NM, MHNG, ZMZ, BMNH); Bataan, Lubang (MCZ); Mindanao, Cagayan (MHNG, author); Camiguin (MHNG, author); GUAM: (MHNG, MNHN), Umatec R. (MCZ), Yling R. (author); PONEPE: (author); INDONESIA: Ambon (MHNG).

Remarks: RÉCLUZ, 1841 described one individual shell from M. Janelle's collection that came from the river Umata, Guam. It was a robust shell with oblique longitudinal lines. The summit was skewed off centre. The type is lost, but MHNG has 2 specimens from Cuming's Philippines collection that RÉCLUZ described in1842. The slight lack of symmetry of the shells, with the apex off centre, helps to distinguish *S. janelli* from *S. porcellana*.

The lectotype and paralectotypes of *N. d'urvillei* from Amboine (MHNG) are *S. janelli*, as are the two syntypes (MNHN) of *N. laperousi* from Umata R., Guam. I found no *S. porcellana* at Cagayan or Camiguin I. (Mindanao, Philippines) or on Guam or Ponepe

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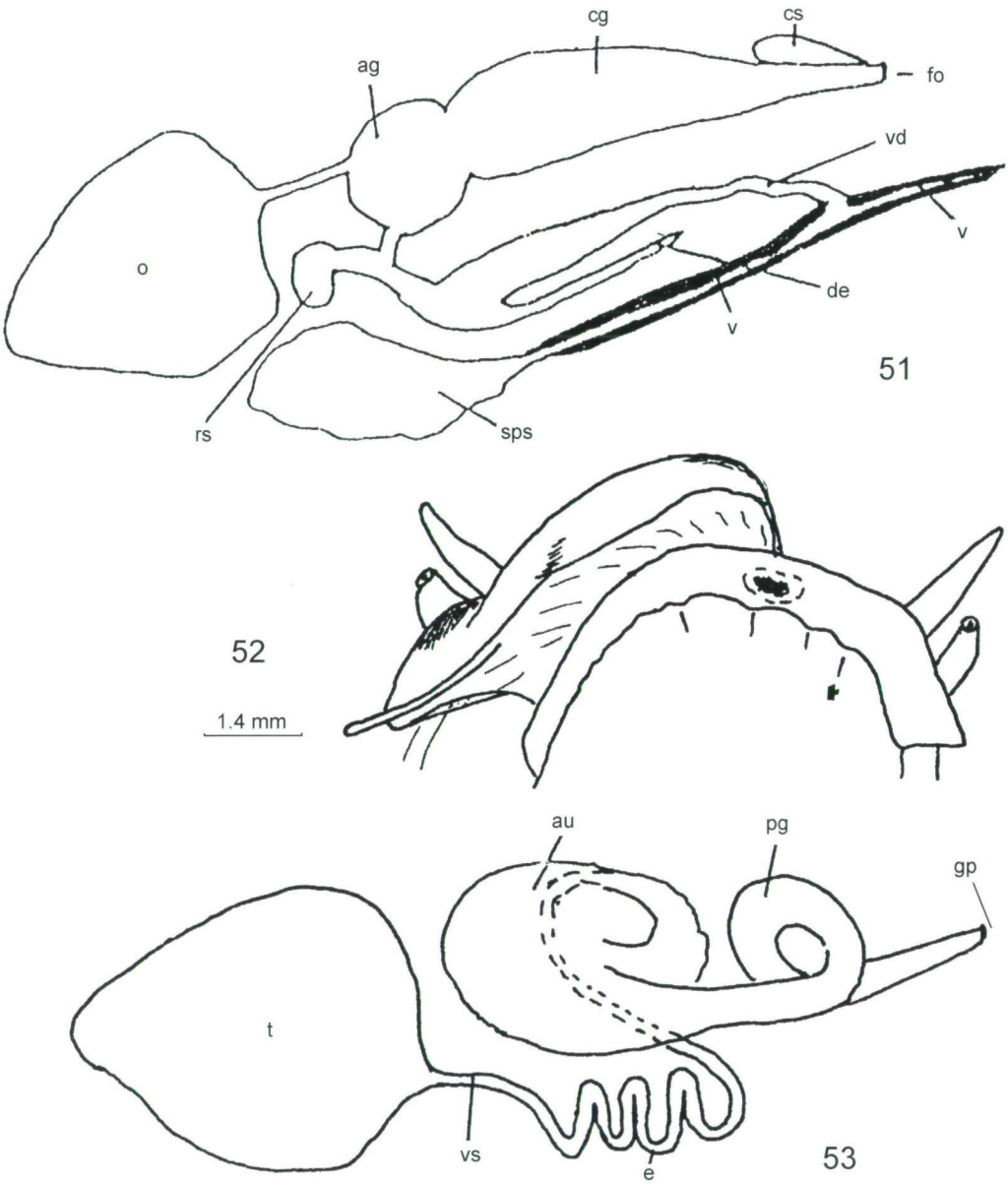

Figs. 51 - 53: *S. porcellana* reproductive system: (51) female (after HAYNES, 1996). (52) penis. (53) male.

in the North Pacific, although others have found them there. *S. janelli* is easily identified when it has characteristic longitudinal lines but otherwise it can be mistaken for *S. porcellana*, as both have a pattern of acute triangles (tongues) and horizontal lines. *S. janelli* can be distinguished by its slightly skewed shell, black markings rather than pink and males that are the same size or larger than females. These two species are often con-

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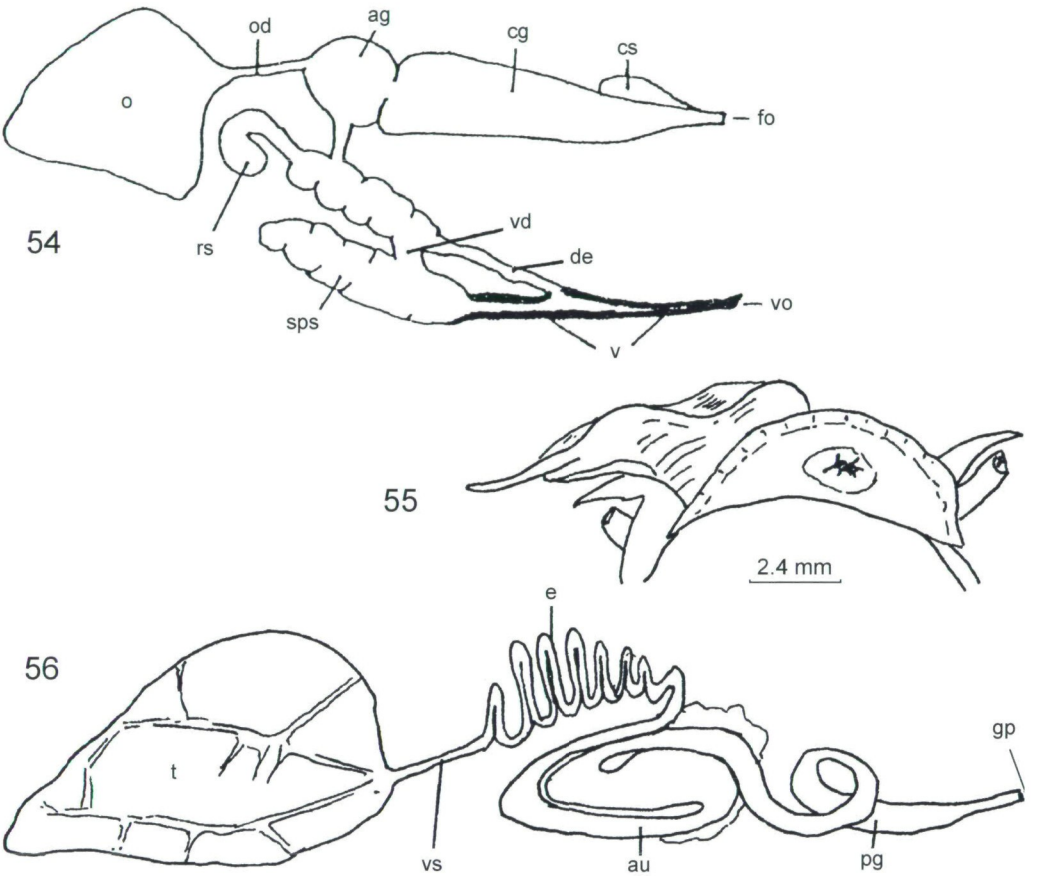

Figs. 54 - 56: *S. borbonica* reproductive system: (54) female (after HAYNES, 1996). (55) penis. (56) male.

fused because of the similarity of their shells , but the reproductive anatomy of *S. janelli* is more like that of *S. borbonica*.

Remarks: Early authors treated *S. bougainvillei* as a separate species, but more recently it has been considered a synonym of *S. porcellana*. FRANC (1956) and STARMÜHLNER (1970) used *S. borbonica depressa* to include both both *S. bougainvillei* and *S. porcellana* in New Caledonia and Vanuatu. From 1984 - 1991, HAYNES used the name *S. porcellana* for the Fijian species when in fact she was referring to *S. bougainvillei*. In 1996, HAYNES described the differences in the reproductive anatomy of these two species and established that *S. bougainvillei* was a valid species endemic to the south Pacific islands. Both *S. porcellana* and *S. bougainvillei* are found in Vanuatu and New Caledonian streams and this has added to the confusion. Female *S. suffreni* have been mistakenly identified as *S. bougainvillei*, which they resemble, but *S. bougainvillei* females unlike *S. suffreni* have no spermatophores or spermatophore sac.

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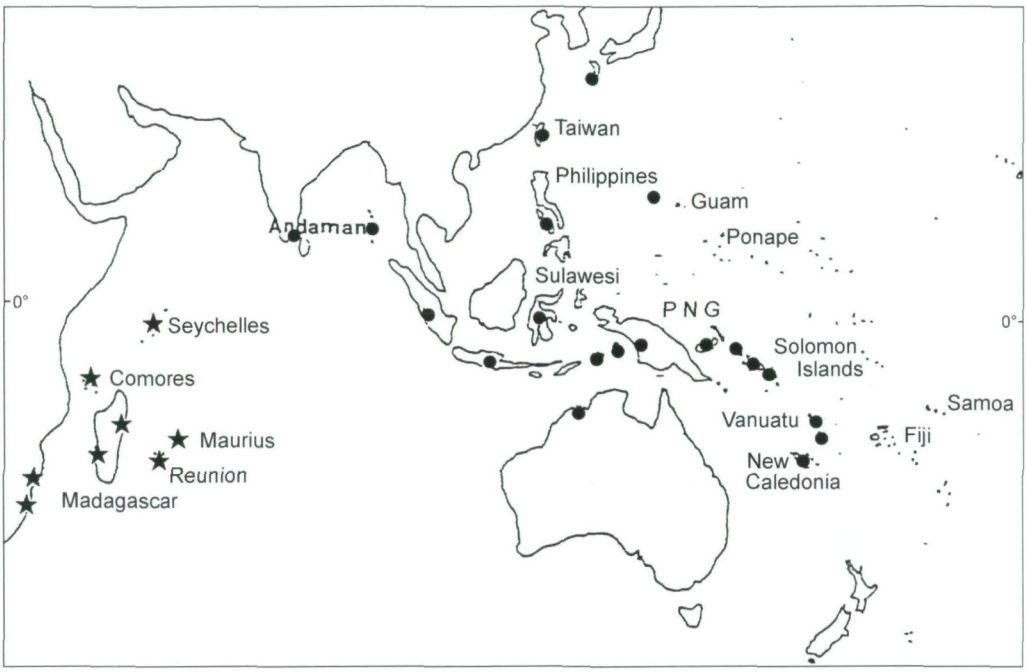

Fig. 57: Distribution of *S. porcellana* ● and *S. borbonica* ★.

Septaria bougainvillei (Recluz, 1841) (Figs. 60, 65, 66 - 68)

Navicella bougainvillei Martens, 1881: pl. 3 Fig. 110; *Septaria borbonica depressa* Franc, 1956: 200; Starmühlner, 1970: Fig. 26 d, e; *Septaria porcellana depressa* Starmühlner, 1970; Haynes, 1984: Fig. 37; *Septaria porcellana* Haynes, 1985: 206 - 208; Haynes, 1991: Figs. 2 B, 3 B, 5 B, 6 B; *Navicella bougainvillei* Kabat & Finet, 1992: 229; *Septaria porcellana depressa* Starmühlner, 1993: 259; *Septaria bougainvillei* Haynes, 1996: Figs. 5, 9, 13; Haynes, 1997, 71 - 76.

Type Material *Navicella bougainvillei* Recluz, 1841: 374 (type lost, neotypes MHNG, Ovalau, Fiji) *Navicella hupeiana* Gassies, 1863: pl. 8 Fig. 13 (2 syntypes BMNH, MNHN, New Caledonia); *Navicella nana* Montrouzier, 1879: 135 (holotype BMNH, New Caledonia).

Description

Shell: (Figs. 60 a -c) Shell length up to 25 mm, mean w/l ratio 0.75, mean h/l ratio 0.32. Shell ovate, symmetrical, cap-like with apex extending a little way outside the shell edge. Apex often eroded. Septum narrow, yellowish with a straight edge.

Ground colour yellow to yellow-brown with black nearly horizontal or transverse lines across the shell. Where the lines cross they form obtuse triangles. Inside the shell is white-gray, muscle scars not prominent.

Males significantly smaller than females and fewer males in populations (Table 1).

Operculum: (Fig. 60 d) Pale pink, horn at posterior margin orange-brown, fragile and rib relatively long.

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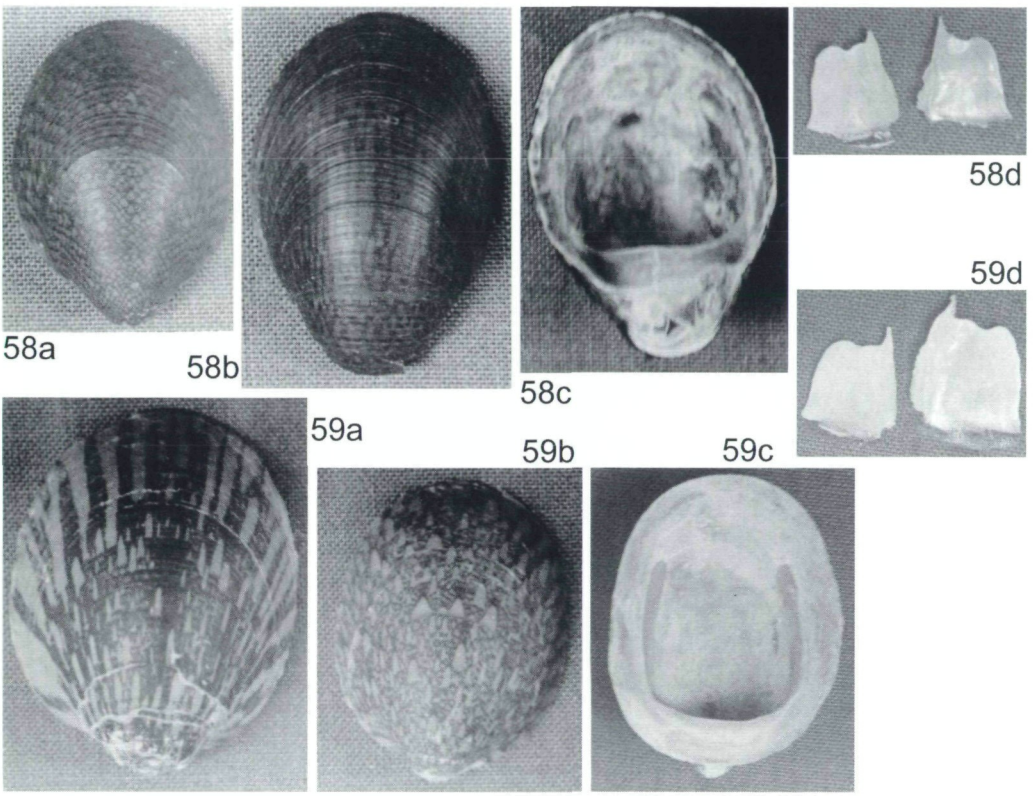

Figs. 58 - 59: (58) *S. borbonica* shells: (a) (b) dorsal side; (c) ventral side; Length: 22, 25 mm; (d) operculum; Width: 7 mm. (59) *S. janelli* shells: (a) (b) dorsal side; (c) ventral side; Length: 22, 25 mm; (d) opercula; Width: 8, 10 mm.

Reproductive Anatomy: (Figs. 66 - 68) Females without spermatophores or any remnant of a spermatophore sac. Males small (up to 15 mm long) with a small auxiliary gland and with a large flat, furrowed penis that has no papilla.

Habitat: From a few metres from the sea to 3 - 4 km inland on rocks and stones in swift flowing streams.

Range: (Fig. 65) Fiji, New Caledonia, Vanuatu, (Samoa?).

Records: FIJI: Ovalau (MHNG, ZMZ, author); Viti Levu (MNB, author); Vanua Levu (ZMZ, author); Taveuni, Kadavu, Gau, Beqa, Waya (author); NEW CALEDONIA: (MNW, MNHN, MCZ); *N. hupaena* (BMNH, MNHN); Vanuatu: (ZMA); Tanna (author); (SAMOA MNW, author - both may be female *S. suffreni)*

Remarks: Early authors treated *S. bougainvillei* as a separate species, but more recently it has been considered a synonym of *S. porcellana.* FRANC (1956) and STARMÜHLNER (1970) used *S. borbonica depressa* to include both both *S. bougainvillei* and *S. porcellana* in New Caledonia and Vanuatu. From 1984 - 1991, HAYNES used the name *S. porcellana* for the Fijian species when in fact she was referring to *S. bougainvillei.* In 1996,

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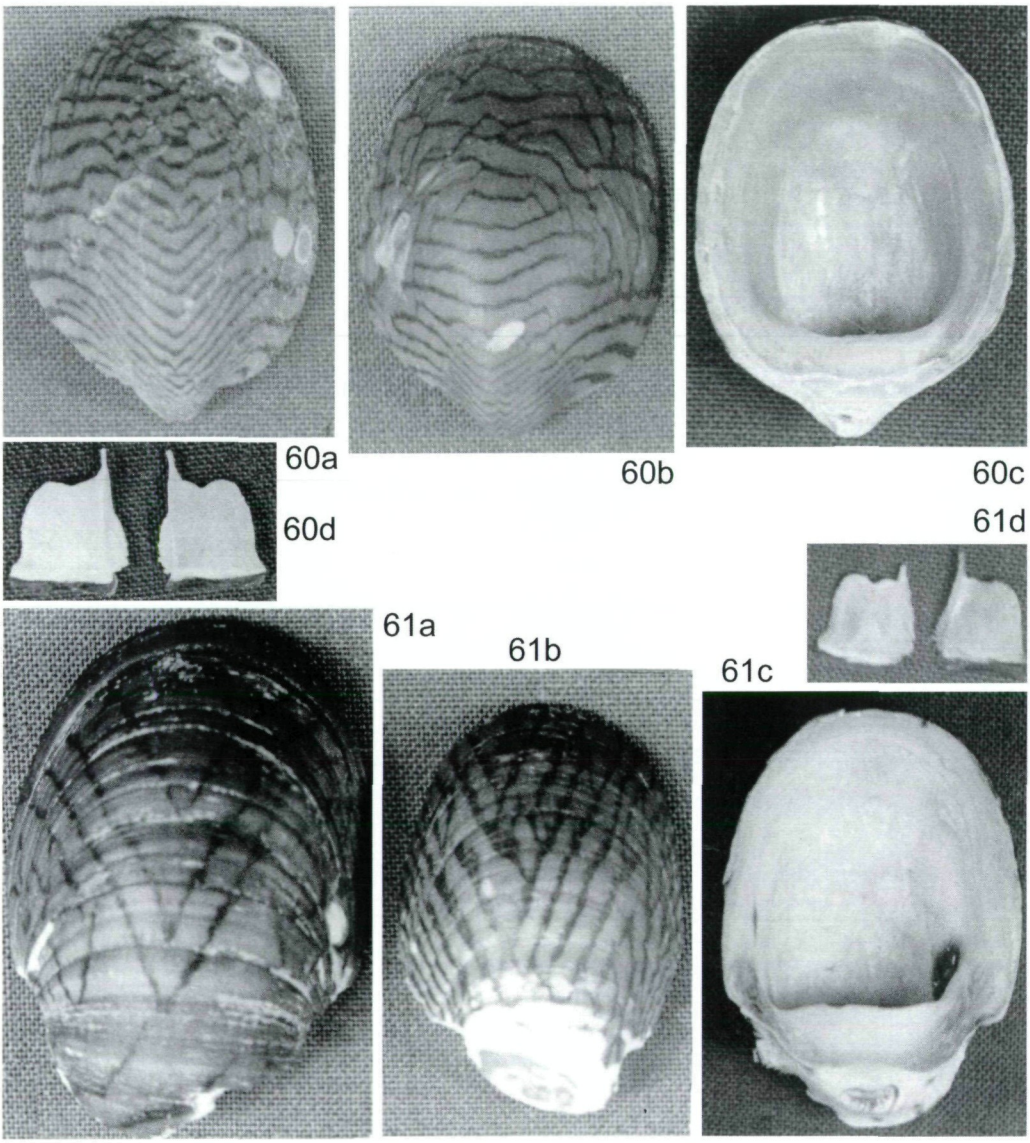

Figs. 60 - 61: (60) *S. bougainvillei* shells: (a) (b) dorsal side; (c) ventral side; Length: 22 mm; (d) operculum; Width: 8 mm. (61) *S. macrocephala* shells: (a) (b) dorsal side; (c) ventral side; Length: 28, 22 mm; (d) operculum Width: 8mm.

HAYNES described the differences in the reproductive anatomy of these two species and established that *S. bougainvillei* was a valid species endemic to the south Pacific islands. Both *S. porcellana* and *S. bougainvillei* are found in Vanuatu and New Caledonian streams and this has added to the confusion. Female *S. suffreni* have been mistakenly identified as *S. bougainvillei,* which they resemble, but *S. bougainvillei* females unlike *S. suffreni* have no spermatophores or spermatophore sac.

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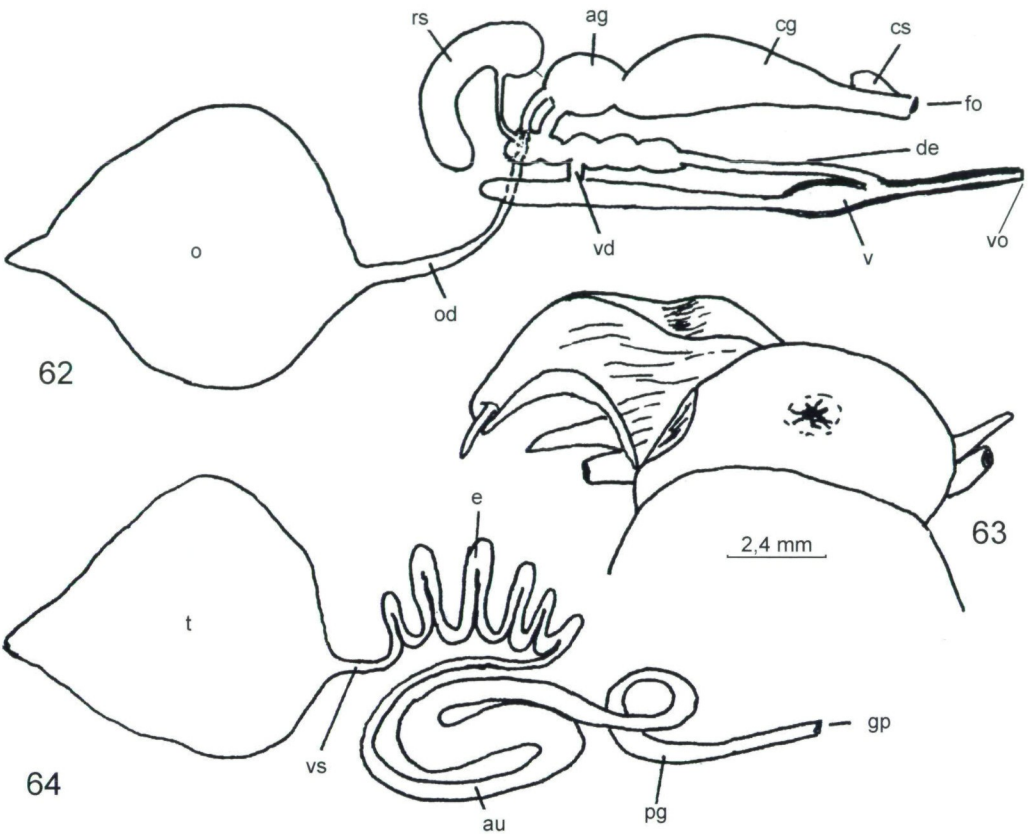

Figs. 62 - 64: *S. janelli* reproductive system: (62) female. (63) penis. (64) male.

Septaria macrocephala (LE GUILLOU in RÉCLUZ, 1841) (Figs 11, 61, 69 - 71)

Navicella sanguisuga GASSIES, 1863: pl 8 Fig. 12; *Navicella macrocephala* MARTENS, 1881: pl.11 Fig. 4; CROSSE, 1894: 161 - 473; *Septaria macrocephala* RIECH, 1937: 68; FRANC, 1956: pl 11 Fig 27; STARMÜHLNER, 1976: 542 - 3, pl 14 Fig. 155; HAYNES, 1984: Fig. 39; HAYNES, 1985; 206 - 208; HAYNES, 1988: 377 - 383; HAYNES, & WAWRA, 1989: Figs. 1 a, b, 3a; HAYNES, 1990: 242 - 243; HAYNES, 1991: Figs, 2 A, 4 A, 5 B; *Navicella macrocephala*, KABAT & FINET, 1992: 238; *Septaria macrocephala*, HAYNES, 1997: Fig. 1 E; COWIE, 1998: 18.

Type Material *Navicella macrocephala* RÉCLUZ, 1841: 374 (2 possible syntypes MHNG 15201, syntypes mixed with *S. sanguisuga* MNHN, Ovalau, Fiji).

Description

Shell: (Figs. 61 a - c) Shell length up to 25 mm , mean w/l ratio 0.75, mean h/l ratio 0.32. Shell ovate relatively narrow, with a large protruding apex but it is nearly always eroded.

Ground colour yellow-green or yellow-brown with a pattern of black lines in wide triangles formed from lines radiating from the apex and crossing one another. Interior white-gray, muscle scars prominent but narrow.

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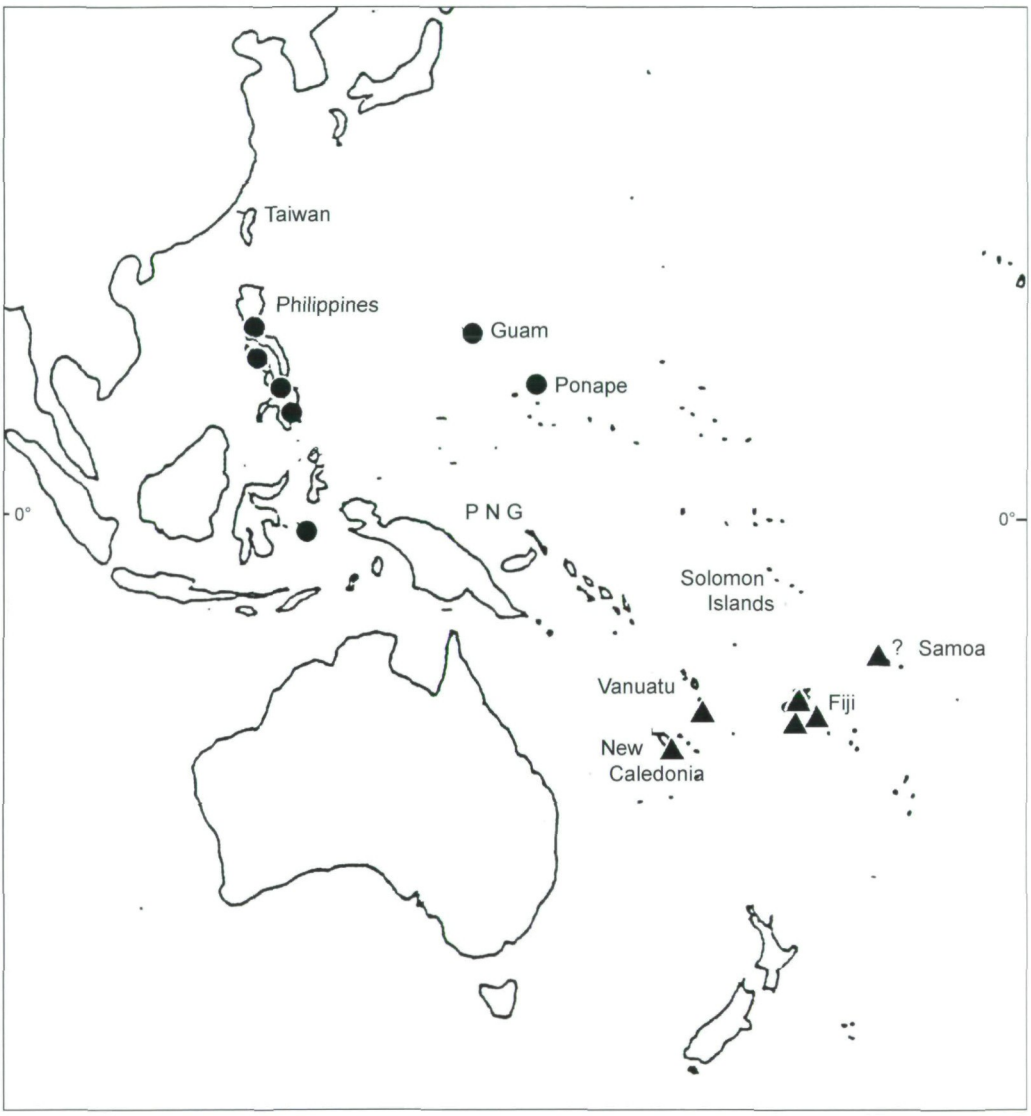

Fig. 65: Distribution of *S. janelli* ● and *S. bougainvillei* ▲.

S. macrocephala is a protandrous sequential hermaphrodite. Males are less then 15 mm long and females are never less than 12 mm long and there are fewer males in populations (Table 1) (HAYNES, 1991).

Operculum: (Fig. 61 d) White-pink, squarish with a narrow rib and yellow-orange to black posterior horn margin.

Reproductive Anatomy: (Figs. 69 - 71) Females without spermatophores or a spermatophore sac, males with a small auxiliary gland and a large flat grooved penis without a papilla.

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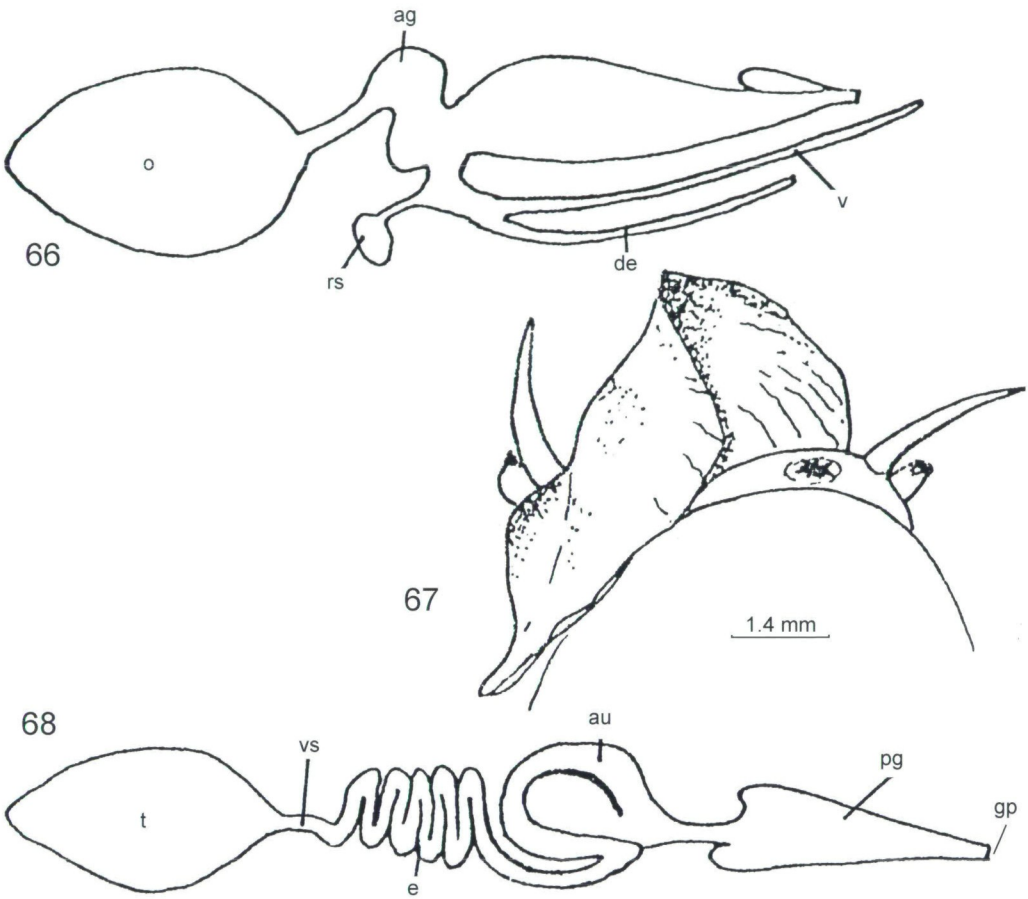

Figs. 66 - 68: *S. bougainvillei* reproductive system: (66) female. (67) penis. (68) male. (after HAYNES, 1991).

Habitat: In swift flowing streams on stones and rocks well above the influence of the sea.

Range: (Fig. 11) Fiji, New Caledonia, Samoa.

Records: FIJI: (ZMZ, MNB); Ovalau (MNHN, MHNG, MCZ, author); Vanua Levu, Taveuni, Gau, Kadavu (author); NEW CALEDONIA (MNHN, MNW); AMERICAN SAMOA: Tutuila (author)

Remarks: *S. macrocephala* (RÉCLUZ, 1841) and *S. sanguisuga* (REEVE, 1856) were combined under the older name by MARTENS (1881) and the two species have been confused often since then because both have a large protruding apex. *S. macrocephala* can be distinguished by the obvious pattern of radiating lines forming large triangles, its strongly eroded apex, its greater width across the apex and an operculum that has only one rib. It is not as easy to distinguish *S. macrocephala* from *S. bougainvillei* as both have shells that erode at the apex and an operculum with one rib. However, the pattern on *S. bougainvillei* shells consist of transverse or horizontal lines while the lines on *S.*

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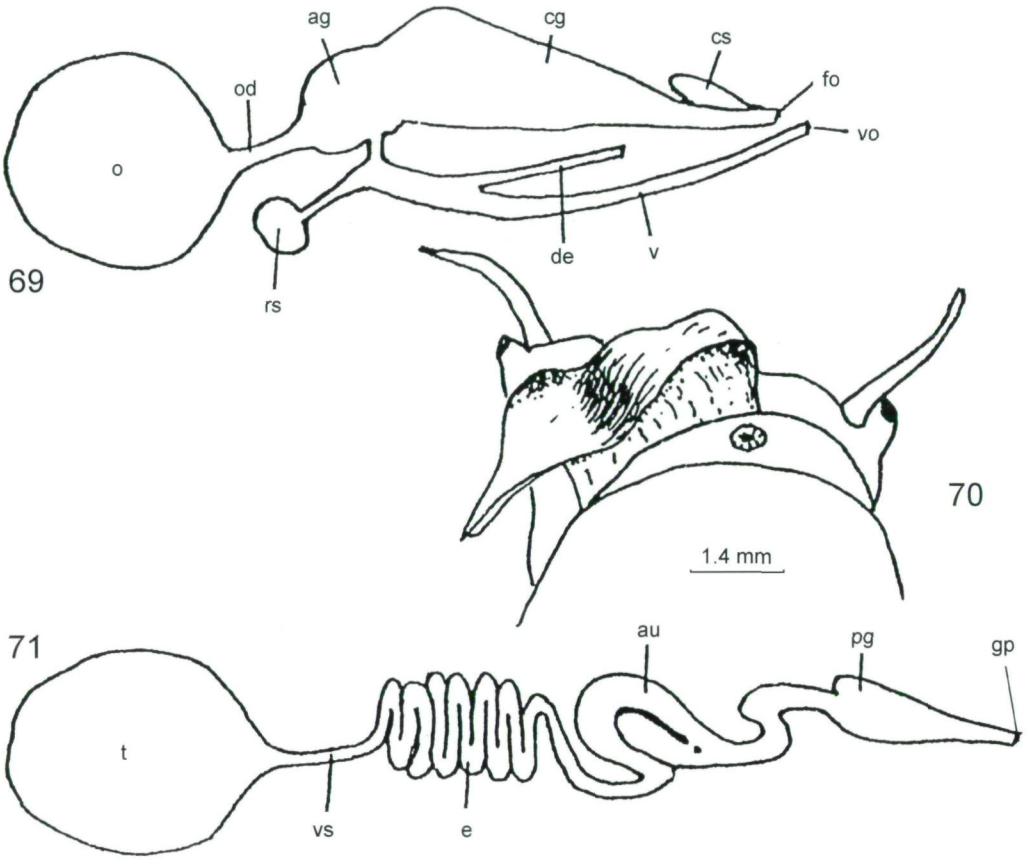

Figs. 69 - 71: *S. macrocephala* reproductive system: (69) female. (70) penis. (71) male. (after HAYNES, 1991).

macrocephala shells tend to radiate downwards from the summit. Both species are present in fast flowing streams on high Fijian islands. *S. macrocephala* has also been mistaken for female *S. suffreni* and the spermatophores claimed to have been from *S. macrocephala* by HAYNES & WAWRA (1989) are those from *S. suffreni*. The error was corrected in HAYNES (1991) when it was established that *S. macrocephala* has no spermatophores.

The small males are most often found clinging to the shells of larger females.

Phylogenetic Analysis

The phylogenetic analysis is based on my own investigations and previous authors evaluation and observations of the family Neritidae. The phylogenetic analysis of the 13 *Septaria* species used 15 morphological characters, with 31 character states, derived from shell, operculum and reproductive anatomy. The reproductive anatomy is particularly important as it shows evolutionary changes that resulted in the loss of spermatophore production by males and the disappearance of a spermatophore sac in famales.

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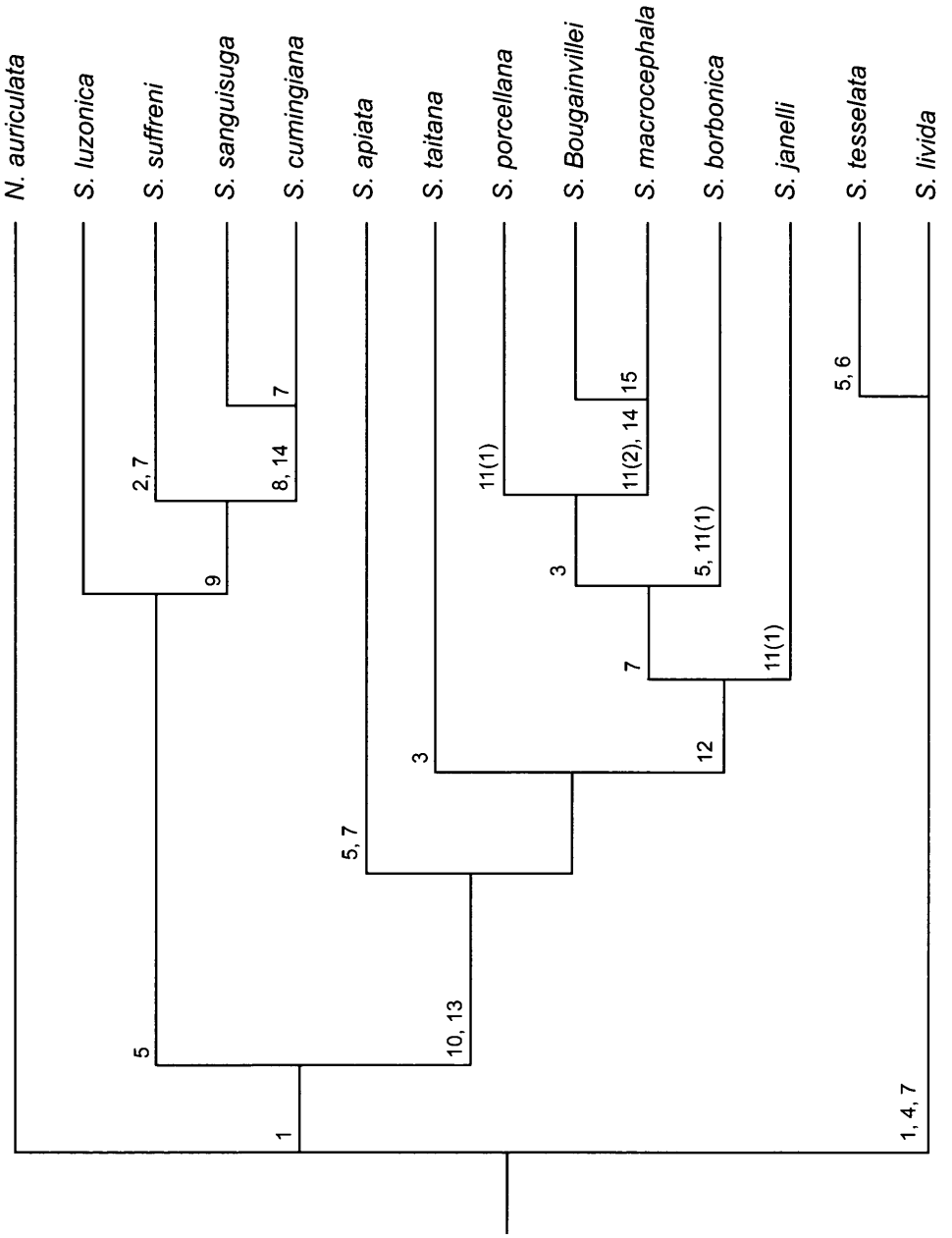

Fig. 72: Most parsimonious consensus tree for species of *Septaria* based on majority rule. Numbers refer to characters listed within the text.

All characters were treated as undirected and unordered and, therefore, the character polarity is determined by the rooting. A search for optimal tree(s) was carried out by using the branch - and - bound algorithm.

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The outgroup used was the brackish water species *Neritina auriculata*, the *Neritina* species HOLTHUIS (1996) found closest to *Septaria* in her phylogenetic analysis. She credited both *N. auriculata* and *Septaria* species as having in common a looped vaginal canal, no distinction between the body and filament of the spermatophore and the presence of a papilla in the penis. These character states are considered plesiomorphies but they are not present in all *Septaria* species e.g. the spermatophores of *S. luzonica* have a distinct filament. The penis is without a papilla in the more derived non- spermatophore producing species, *S. bougainvillei* and *S. macrocephala* and also in *S. sanguisuga* and *S. cumingiana*, producers of complex spermatophores.

The character states present in *Neritina auriculata* and other species of *Neritina* are considered to be plesiomorphies. The main difference between *Neritina* and *Septaria* species is the narrow columella or septum and a modified operculum in *Septaria* that make it impossible for *Septaria* species to retract into their shell as do *Neritina* species.

The characters used in the phylogenetic analysis are explained in the following (numbers refer to Tables 2 and 3 and to the cladogram Fig. 72):

1. All genera in the Neritidae, except *Septaria*, are able to retract into their shell as the operculum can close the shell aperture with the animal inside. *Septaria* are true limpets with a large aperture and narrow septum. The operculum is elongated and at the posterior it is embedded in the foot and anteriorly it lies in a sac between the foot and visceral mass. Presumably it is used as a skeleton for muscles of the foot to act on but it cannot close the aperture.
2. Male and female individuals of the Neritidae in general have similar shell shape. All species of *Septaria*, except *S. suffreni*, also have the same shaped shells. Male *S. suffreni* shells are characterized by having a tongue-like projection in the middle of the septum (Fig. 5 b). Female *S. suffreni* have no such projection and for a long time were not recognized as *S. suffreni* but were thought to be specimens of *S. porcellana*, *S. bougainvillei* or *S. macrocephala*. Male *S. suffreni* shells are also generally narrower than female shells. This may help them cling to females when transferring spermatophores in fast flowing water.
3. Shells of both sexes are the same size in the Neritidae in general but in some species of *Septaria* the males are significantly smaller. These species are *S. taitana*, *S. porcellana*, *S. bougainvillei* and *S. macrocephala* and they do not produce spermatophores.
4. The only species with ecologically dimorphic forms within the Neritidae are the two brackish water limpets, *Septaria tesselata* and *Septaria livida*. The compressed form lives on vegetation in still water, while the wide form lives on stones and boulders in flowing water.
5. The shells of non-limpet shaped Neritidae are widest across the base of the columella. It is therefore assumed that *Septaria* species that are widest across the septum have the plesiomorphic state.
6. The apex at the posterior of the shell protrudes past the columella (*Neritina*) or septum (*Septaria*) in all species except in *S. tesselata*.
7. *Neritina* species have a skewed shell that shows some trace of the coiled embryonic shell. A skewed shell is, therefore, the plesiomorphic state.

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8. The operculum of most species of *Septaria* have only one rib (prong or peg) embedded in the foot. This is derived from the epophysis of other Neritidae and is the ancestral state.
9. Male and female shells of *Neritina* are similar in shape and their opercula are also similar in shape. *S. suffreni* male shells are narrower than females and as would be expected the male operculum is also narrower. Although male and female shells are similar in *S. sanguisuga* and *S. cumingiana* the male opercula are narrower than the female ones.
10. *Neritina* species and other neritids produce spermatophores that are stored in the female in a large spermatophore sac. The presence of spermatophores is the plesiomorphic state.
11. The presence of a dorsal spermatophore sac is also ancestral. *Septaria* species show a reduction of this sac to a small dorsal chambered sac without spermatophores in *S. apiata* and *S. taitana* , to a smaller rudimentary ventral chamber in *S. porcellana*, *S. borbonica* and *S. janelli* and finally to a loss of the sac altogether in *S. bougainvillei* and *S. macrocephala*.
12. A large fleshy auxiliary gland in the male is associated with the production of spermatophores. Those species that no longer produce spermatophores have a smaller flatter auxillary gland.
13. The manipulation of spermatophores from the genital opening into the vaginal opening of the female requires a requires a fleshy or long penis as is found in *Neritina* and *Septaria* with spermatophores. The more derived species of *Septaria* that do not produce spermatophores have the apomorphy, a ridged flap-like penis for conveying free sperms from male to female.
14. A papilla is present in the penis of *N. auriculata* and some other Neritidae but not all. A penis with a papilla is considered the plesiomorphic state but it is absent only from *S. sanguisuga* and *S. cumingiana* and the two species that have undergone the most reproductive anatomy simplification, *S. bougainvillei* and *S. macrocephala*.
15. All neritid species, with the exception of the protandrous sequential hermaphrodite *S. macrocephala*, are diecious.

These characters (Table 2) were placed in a data matrix (Table 3) and analysed by means of Phylogenetic Analysis Using Parsimony (PAUP) version 4 (Swofford, 1998) using the branch - and - bound algorithm. Eleven most parsimonious trees were obtained and a single majority-rule consensus tree was produced from them. This tree had a length of 23 steps, a consistency index (CI) of 0.6957 and a retention index (RI) of 0.8333 (Fig. 72).

The consensus tree divides *Septaria* into two clades, one containing the brackish water species, *S. tesselata* and *S. livida* which have ecologically dimorphic shells, and another clade containing the remaining species. This division agrees with LAMARCK (1816) who placed *S. tesselata* in the genus *Navicella* and BAKER (1923) and KOMATSU (1986) who placed it in the subgenus *Navicella*. The rest of the genus is monophyletic and is divided into, two further clades, those with spermatophores and those without. The joining of these two clades has only 27% confidence according to the phylogenetic tree, probably because the species producing spermatophores have many individual apamorphies. *S. luzonica*

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Table 2: Characters and their states used in the phylogenetic analysis.

Shell

1. With a wide columella and able to retract into their shell: yes (0): no (1).
2. Shell shape sexually dimorphic: no (0): yes: (1).
3. Shell size sexually dimorphic: no (0): yes, males smaller (1).
4. Shell shape ecologically dimorphic: no (0): yes, shell has a wide and compressed form: (1).
5. Shell width greatest; across the septum (0): in front of the septum (1).
6. Apex of shell: outside the shell margin: (0): inside the shell margin (1).
7. Apex position: skewed from centre: (0): in the centre (1).

Operculum

8. Number of ribs: one (0): two: (1).
9. Operculum sexually dimorphic : no (0): yes, male narrower than female (1).

Reproductive Anatomy

10. Spermatophores present in a spermatophore sac: yes (0): no, absent (1).
11. Spermatophore sac or remnant present: dorsal (0): ventral (1): absent (2).
12. Male auxiliary gland: large and fleshy (0): small and flat (1).
13. Penis: long or freshy (0): wide and flap-like (1).
14. Penis with a papilla: yes (0): no (1).
15. Reproductive system: dioecious (0): protandrous sequential hermaphrodite (1).

Table 3: *Septaria* data matrix. 0, plesiomorphy; 1, 2, apomorphy.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
N. auriculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
S. luzonica	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
S. suffreni	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0
S. tessellata	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
S. livida	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
S. sanguisuga	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0
S. cumingiana	1	0	0	0	1	0	1	1	1	0	0	0	0	1	0
S. apiata	1	0	0	0	1	0	1	0	0	1	0	0	1	0	0
S. taitana	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0
S. porcellana	1	0	1	0	0	0	1	0	0	1	1	1	1	0	0
S. borbonica	1	0	0	0	1	0	1	0	0	1	1	1	1	0	0
S. janelli	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0
S. bougainvillei	1	0	1	0	0	0	1	0	0	1	2	1	1	1	0
S. macrocephala	1	0	1	0	0	0	1	0	0	1	2	1	1	1	1

has the most plesiomorphic character states and is closest to the outgroup *N. auriculata*, while *S. suffreni*, *S. sanguisuga* and *S. cumingiana* have the apomorphy, sexually dimorphic opercula. *S. sanguisuga* and *S. cumingiana* have the apomorphies, a two pronged operculum and the absence of a papilla on the penis. However, the existence of such species as *S. apiata* and *S. taitana*, with a dorsal spermatophore sac without sper-

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matophores, intermediate between the species that produce spermatophores and those that have completely lost the spermatophore sac, suggests that they are all closely related. In the clade containing the non-spermatophore producing species, *S. apiata* is joined to the other species with 55% confidence while the tree for the others has a confidence of 100%.

Discussion

The consensus tree that places *S. tesselata* and *S. livida* in one clade and the remaining *Septaria* species in another makes the genus polyphyletic. This agrees with the concept that the genus should be placed in the family Neritiidae and not a separate family Septariidae. Although *S. tesselata* and *S. livida* are placed in a different clade, their exclusion is based on a single unique apomorphy, ecologically dimorphic shells and not all most parsimonious trees placed them in a separate clade.

Evolutionary change within the genus is towards the loss of spermatophores and the simplification of the reproductive anatomy. This has progressed furthest in the South Pacific. Most species that retain spermatophores (*S. luzonica*, *S. cumingiana*, *S. sanguisuga* and *S. tesselata*) are found in South East Asia although the more derived forms *S. porcellana* and *S. janelli* are also present. Species with modifications of reproductive systems and loss of spermatophores radiate out from the South East Asian region. *S. borbonica* and *S. janelli* from the Indian Ocean and North Pacific respectively have a ventral remnant of a spermatophore sac, *S. apiata* and *S. taitana* from the Eastern Pacific retain a dorsal pleisiomorphic, but much reduced, spermatophore sac while *S. bougainvillei* and *S. macrocephala* in the South Pacific have completely lost the spermatophore sac. The last two together with *S. taitana* and *S. porcellana* have significantly smaller males.

The southern species, *S. livida* with its two ecological shell forms appears to have evolved from the similar northern species *S. tesselata*. *S. suffreni* with the apomorphies, sexually dimorphic shell and operculum, is also a South Pacific species.

The only species that is found throughout South East Asia (Philippines) and the North and South Pacific is *S. sanguisuga* which retains a complex spermatophore but has an apomorphic operculum that is both two pronged and sexually dimorphic.

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Appendix

Shell Dimensions

Specimen(s) / Locality	Mean SD	Mean SD	Mean SD	w/l	h/l	Length (mm)	width (mm)	height (mm)
S. luzonica								
12 / Salana R., Mindanao	14.2	2.07	10.2	2.07	5.2	1.42	0.72	0.37
12 / Jasa-an-Cubilig R., Mindanao	17.0	4.01	11.8	2.7	6.1	1.73	0.69	0.36
12 / Dinangason R., Camiguin	14.8	3.04	10.2	1.86	5.0	1.10	0.69	0.34
S. suffreni								
15 / Lami R., Viti Levu.	21.7	4.90	15.8	3.51	7.6	1.55	0.73	0.35
15 / Nasekawa R., Vanua Levu.	18.3	2.92	13.3	2.44	5.8	1.26	0.73	0.32
5 / Naivika R., Taveuni	16.5	1.77	12.6	1.82	5.7	1.04	0.76	0.35
6 / Naisogo Ck., Ovalau.	19.8	2.56	14.8	1.46	6.8	0.68	0.75	0.34
S. livida								
2 syntypes / Unknown	24	-	18.0	-	8.4	-	0.75	0.35
8 / Rewa R., Viti Levu	16.9	3.08	12.7	2.40	6.0	1.48	0.75	0.35
23 / Lami R., Viti Levu	19 5	5.01	15.7	4.2	7.3	2.50	0.81	0.37
23 / Nasekawa R., Vanua levu	20.4	3.68	16.8	2.91	8.0	1.82	0.82	0.39
Compressed form:								
4 / Buca Bay, Vanua Levu	13.2	5.6	6.9	3.15	3.6	1.10	0.52	0.27
4 / Rewa R., Viti Levu	17.6	5.49	8.6	2.75	3.8	1.47	0.49	0.22
S. macrocephala								
20 / Naisogo Ck., Ovalau.	19.7	2.94	14.6	1.94	6.18	1.24	0.74	0.35
20 / Naivika Ck., Taveuni.	16.5	2.98	11.6	2.41	5.3	1.08	0.70	0.32
(N.B. The length could not be measured accurately as most specimens were eroded at the apex)								
S. tesselata								
6 / Tamil Nadu, India.	20.8	5.77	12.9	2.96	5.4	1.40	0.62	0.26
8 / Kai Woru, N. Guinea	17.1	3.12	12.4	2.52	5.2	0.90	0.72	0.30
3 / Baga Vaga, Philippines	24.8	4.25	17.0	3.00	8.0	1.00	0.68	0.32
8 / Sri Lanka (STARMÜHLNER, 1974)	15.2	2.79	9.9	1.90	3.9	0.90	0.65	0.26
Compressed forms:								
1 / Salana R., Mindanao.	18.0	-	7.5	-	4.2	-	0.42	0.23
1 / Sri Lanka (STARMÜHLNER, 1974)	11 1	-	5.2	-	2.5	-	0.47	0.23
S. bougainvillei								
20 / Naivika Ck., Taveuni	16.1	3.24	11.7	2.63	5.3	1.24	0.73	0.33
20 / Naisogo Ck., Ovalau	17.7	2.98	13.2	1.17	5.6	0.92	0.75	0.32
6 / Nubulevu Ck. Kadavu, Fiji.	19.3	1.88	14.8	1.66	6.0	0.73	0.77	0.31
S. sanguisuga								
20 / Naivika Ck. Taveuni	19.9	3.63	14.1	2.9	6.4	1.51	0.71	0.32
20 / Naisogo Ck. Ovalau	18.3	2.07	12.4	1.68	6.0	0.69	0.68	0.33
12 / Puha R. Solomon Is.	18.2	4.45	12.0	2.66	5.5	1.38	0.66	0.30
5 / Noh-keni Str. Tanna	14.1	2.0	9.9	0.96	5.3	0.45	0.70	0.32
5 / Kwamera Str. Tanna, Vanuatu	19.0	2.58	13.3	1.71	6.0	0.61	0.70	0.32
S. janelli								
21 / Salana R. Mindanao	15.9	2.85	12.3	2.44	5.8	1.31	0.81	0.36
10 / Jasa-an-Cabulig R., Mindanao	21.3	3.43	17.2	2.32	8.7	1.16	0.79	0.39
11 / Dinangasa R. Camiguin	21.5	4.54	16.9	3.76	8.3	2.36	0.79	0.39
10 / Cotcot Str. Camiguin	18.4	2.19	14.5	1.57	6.7	0.74	0.79	0.36
10 / Yling R., Guam	21.9	2.77	17.1	2.20	7.9	1.35	0.78	0.36

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Specimen(s) / Locality	Mean SD	Mean SD	Mean SD	w/l	h/l	Length (mm)	width (mm)	height (mm)
S. porcellana								
6 / Uriami R. New Guinea	20.8	5.93	16.7	3.74	8.3	2.54	0.80	0.40
4 / Borora R. N. Georgia, Sol. Is.	19.3	1.19	15.2	3.28	7.7	2.24	0.79	0.40
6 / ICLARM Guadalcanal, Sol. Is.	22.8	5.11	16.8	2.79	8.8	1.70	0.74	0.39
9 / Makira, Sol. Is.	19.2	2.79	15.5	2.75	7.1	1.47	0.81	0.37
6 / Ewor R. Efate, Vanuatu	22.4	6.14	17.7	3.67	8.2	2.07	0.79	0.37
6 / Wailapa R. Santo, Vanuatu	24.5	3.43	19.5	3.51	9.7	2.36	0.80	0.40
12 / Airport R. Pentecost, Vanuatu	25.7	4.43	20.6	3.77	10.5	2.44	0.80	0.41
S. cumingiana								
12 / Salana R. Mindanao	17.4	4.90	13.4	3.68	5.8	1.81	0.77	0.33
12 / Jasa-an-Cobulia R., Mindanao	15.9	2.38	12.3	1.93	5.3	0.94	0.77	0.33
5 / Tapsin pegeuno R., Mindanao	14.2	3.10	10.8	2.45	4.8	1.15	0.76	0.34
4 / Dinangasan R. Camiguin	13.2	4.10	9.9	2.74	4.1	1.19	0.75	0.31
1 / Asmafines R., Guam	26.0	-	9.0	-	?	0.79	0.35	
S. apiata								
11 / Hukaui Nuku Hiva	25.5	3.32	18.4	1.92	8.3	0.94	0.72	0.33
4 / Taipivai-croite, Nuku-Hiva	25.4	3.12	17.3	1.85	7.8	0.96	0.68	0.31
10 / Taipivai Nuku Hiva	19.2	8.88	13.1	5.58	5.9	3.00	0.68	0.31
10 / Hotuatua Nuku Hiva, Marquesas	15.3	1.89	9.4	1.37	4.8	0.69	0.61	0.31
S. taitana								
10 / Opunohu R., Moorea	21.1	2.19	16.6	2.17	6.6	0.95	0.76	0.31
10 / Afareaitu R. Moorea	14.1	3.15	9.2	2.41	3.8	1.01	0.65	0.27
9 / Maatea R. Moorea	20.8	4.83	16.6	5.54	6.4	1.85	0.79	0.31
15 / Trois Cascades, Tahiti	19.3	2.96	13.2	2.39	6.1	0.99	0.68	0.32
S. borbonica								
10 / Grande Anse R., Seychelles	17.3	3.39	12.7	2.63	5.6	1.19	0.73	0.33
20 / Bae du Cap R., Mauritius	16.4	5.29	12.3	3.46	5.3	2.10	0.75	0.32
20 / Pailles, Mauritius	18.5	2.94	13.6	2.42	6.3	1.03	0.74	0.34

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