

On the identity of “*Vermetus*” *roussaei* Vaillant, 1871 (Mollusca, Caenogastropoda, Vermetidae), with the description of a new species

Stefano SCHIAPARELLI

Dipartimento per lo Studio del Territorio e delle sue Risorse,
Viale Benedetto XV, 5, I-16123 Genova (Italy)
steschia@dipteris.unige.it

Bernard MÉTIVIER

Laboratoire de Biologie des Invertébrés marins et Malacologie, CNRS-ESA 8044,
Muséum national d’Histoire naturelle,
55 rue de Buffon, F-75231 Paris cedex 05 (France)
metivier@mnhn.fr

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ABSTRACT

The status of two vermetid species is reassessed after examining the type of *Vermetus roussaei* Vaillant, 1871 from the malacological collection of the Muséum national d’Histoire naturelle, Paris. *Vermetus roussaei* is referred to genus *Petalconchus* Lea, 1843, subgenus *Macrophragma* Carpenter, 1857, on the basis of shell morphology. Records of this species from the Philippines and the Indian Ocean actually refer to a new species, *Vermetus (Thylaeodus) enderi* n. sp., which shares with the previous taxon only the external appearance. This new species is commonly found on the axial branches of reefphytic anthozoans, as black corals (*Antipathes* spp.) or gorgonaceans.

KEY WORDS

Indian Ocean,
ecology,
Vermetidae,
taxonomy,
new species.

RÉSUMÉ

L’identité de « Vermetus » roussaei Vaillant, 1871 (Mollusca, Caenogastropoda, Vermetidae), avec description d’une espèce nouvelle.

La position systématique de deux espèces de vermetes est redéfinie après l’examen du type de *Vermetus roussaei* Vaillant, 1871, de la collection malacologique du Muséum national d’Histoire naturelle de Paris. L’espèce *roussaei*, par la morphologie de sa coquille, se rattache au genre *Petalconchus* Lea, 1843 et au sous-genre *Macrophragma* Carpenter, 1857. Actuellement, les citations des Philippines et de l’océan Indien sous ce nom spécifique concernent une espèce nouvelle, *Vermetus (Thylaeodus) enderi* n. sp., qui ne partage avec le précédent taxon que son aspect extérieur. Cette nouvelle espèce est commune sur les branches axiales d’anthozoaires, comme le corail noir (*Antipathes* spp.) ou de gorgonacés.

MOTS CLÉS

océan Indien,
écologie,
Vermetidae,
taxonomie,
nouvelle espèce.

INTRODUCTION

The family Vermetidae Rafinesque, 1815 is a group of caenogastropods whose taxonomy remains in a state of flux, despite two centuries of malacological studies. This is due in part to the resemblance of the shells to those of polychaetes serpulid, which has made the family an unpopular research subject.

Little is known about the biology, ecology and geographical distribution of many of these worm-like gastropods and, for that matter, about the actual number of living species.

Much of the taxonomic confusion was resolved by Keen (1961; 1971) and Morton (1955; 1965), who identified some sound diagnostic characters. However, some of their assumptions have been shown to be incorrect (Gould 1994; Bieler 1995) and thus the problem of sound morphological characters useful for generic placement has re-emerged.

In recent years, attention has mainly focused on vermetid ecology (e.g., Miloslavich & Penschaszadeh 1992; Calvo *et al.* 1998) and functional morphology (Savazzi 1990, 1996; Gould 1994; Schiaparelli & Cattaneo-Vietti 1999); only one author dealing with historical problems of nomenclature (Bieler 1996).

In this contribution, two vermetid species are defined. Their generic placement, however, must be considered provisional pending a comprehensive revision of the entire family.

One of these species, *Vermetus roussaei* Vaillant, 1871, is reassigned to the genus *Petalococonchus* Lea, 1843, subgenus *Macrophragma* Carpenter, 1857, based on shell morphology. The other, a very common Indian Ocean species, misidentified as *Serpulorbis roussaei* (Vaillant, 1871) by Springsteen & Leobrera (1986), is defined as new species and placed in the genus *Vermetus* Daudin, 1800, subgenus *Thylaeodus* Mörch, 1860.

Some peculiar ecological features of the new species, which lives on the axial branches of the black coral (*Antipathes* spp.), are given.

ABBREVIATIONS

MNHN Muséum national d'Histoire naturelle, Paris;

MZB Zoological Museum of Bologna, University of Bologna;

MSNG Museo di Storia Naturale di Genova.

MATERIALS AND METHODS

A *Vermetus* n. sp. shell aggregate was accidentally brought up with fishing lines by local fishermen in October 1995. They were fortunately discovered, the same day they were collected, on the bottom of a dhoni (maldivian boat) from the first author. Vermetids, due to epibionts' covering, were still alive when examined. The aggregate was then preserved in alcoholic liquid before the final fixation in formaldehyde.

Further SCUBA-diving investigations in the type locality and in other areas, allowed to discover the particular niche of this species. Underwater photographs were taken, in the type locality, on March 1996, by Cerrano Carlo.

Preserved animals were dissected under a stereomicroscope and sketches were made using a camera lucida apparatus. Protoconchs, radulae and opercula were cleaned with hydrogen peroxide, dehydrated in alcohol then coated with gold for Philips E 515 SEM observations.

SYSTEMATICS

Subclass CAENOGASTROPODA
Family VERMETIDAE Rafinesque, 1815
Genus *Petalococonchus* Lea, 1843
Subgenus *Macrophragma* Carpenter, 1857

Petalococonchus (Macrophragma) roussaei
(Vaillant, 1871)

Vermetus sipho Rousseau in Chenu, 1844: pl. 4, fig. 3 (top right only, not bottom left) [not Lamarck 1818].

Vermetus (Aletes) sipho Lam – Mörch 1862: 364 [not Lamarck 1818].

Vermetus Roussaei Vaillant, 1871: 197. – Tryon 1886: 175, pl. 51, fig. 43.

TYPE MATERIAL. — Holotype MNHN.

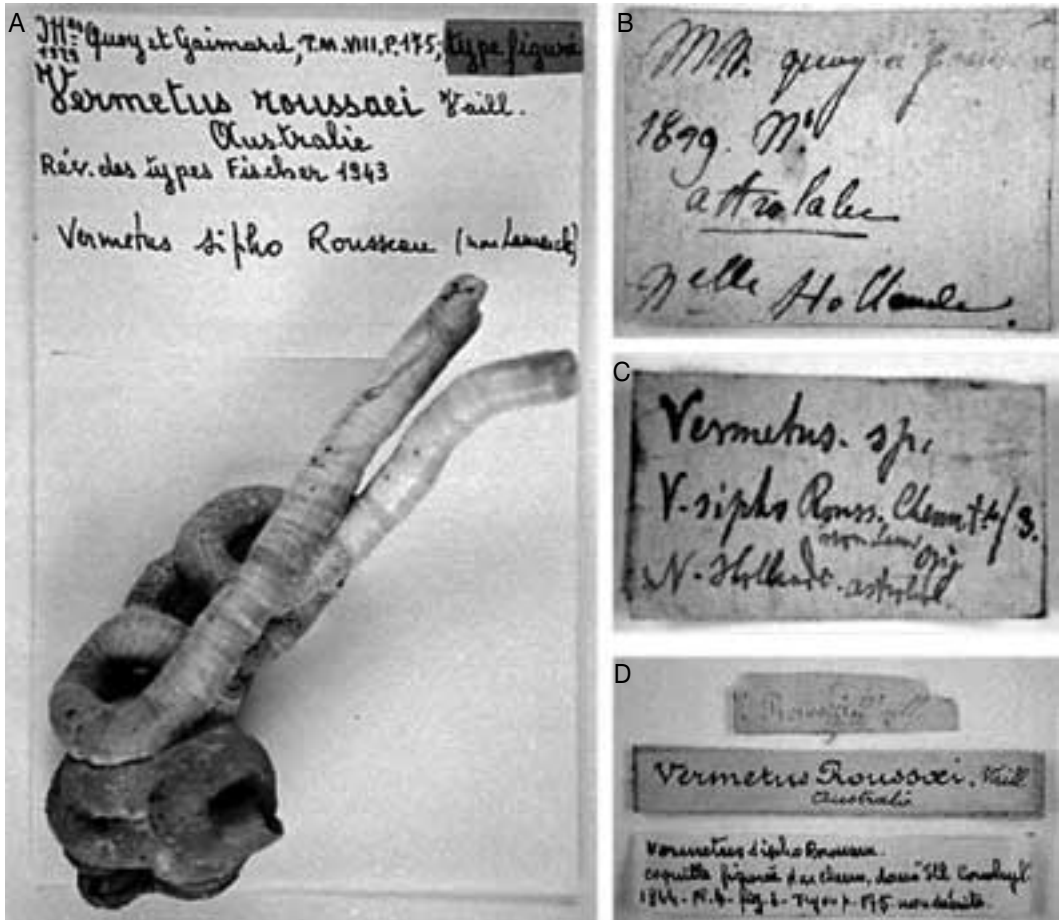


FIG. 1. — **A**, syntypes of *Petalococonchus* (*Macrophragma*) *roussaei* with the actual label; **B**, original label of the Quoy & Gaimard "Astralabe" expedition; **C**, Mörch's original label (in red ink); **D** other more recent MNHN labels.

TYPE LOCALITY. — "Nouvelle Hollande [= Australia]."

MATERIAL EXAMINED. — Holotype (Fig. 1A; original label: fig. 1B).

DISTRIBUTION. — Not known.

ORIGINAL DESCRIPTION (HOLOTYPE)

BY VAILLANT (1871)

"*Testa juvenilis...* *Testa adulta spiraliter contorta, anfractibus inter se laxè conjunctis, ultimo porrecto; externe et intrinsecus castanea. Costulis longitudinalibus 15 ad 17 circiter, et lamellis incrementi tenuibus interruptis ornata, quasi decussata. Lira columellaris parva, distincta. Testa grandaeva plus minusve recta, laevigata, albida vel lentissime rubra. Diam. aperturæ 0^m,008 ad 0^m,009*".

REMARKS

The species is known only from the type material.

HISTORY

This species has a strange and tortuous history. In fact it has been named two times, first by Rousseau (*in* Chen 1844) with the name "*siphon*" (preoccupied by another Lamarckian vermetid taxon), then it was considered a synonym of *Vermetus siphon* (Lamarck, 1818) [*Serpula*] by Mörch (1862), and finally described, correctly, as a new species by Vaillant (1871).

In 1818 (vol. 5: 367), Lamarck introduced "*siphon*" for the first time, describing the vermetid

Serpula sipho with the following diagnosis: “*S. testa tereti, longa, undato-curva, versus basim obsolete cancellata; spira baseos congesta, subtus planulata*. An Gualt. Conch. t.10. fig. L. Dargenv. Conch. t.4 fig. H. Masier. Adans. Seneg. pl. 11.f.5. Habite l’Océan des Indes, à Timor. Mus. n.o. Elle varie beaucoup, et néanmoins je la crois distincte de la suivante [*Serpula arenaria*]”.

Three lots (MNHN) can be considered syntypes of *Serpula sipho* Lamarck. These are: 1) a specimen, glued on cardboard, and labelled: [front] “M. Peron 1803. Type. M³ 24^d. *Vermetus sipho*. Lamk. Timor”. (unidentified but relatively modern handwriting); [back] “*Serp. Sipho* (Type de Lk.)” (Vaillant’s handwriting) and “*Vermetus (Thylacodes) sipho* Lam. = *V. dentiferus* Lam. Timor Peron.” (red ink, Mörch’s handwriting); 2) a specimen, glued on cardboard, labelled: [front] “Type de Lamarck. M³ 24^a. *Vermetus sipho*. Lamk. Timor.” (Unidentified but modern handwriting); [back] “*S. sipho*” (Lamarck’s handwriting) and “Timor” (unidentified modern handwriting); 3) a specimen illustrated by Adanson (1757) as Le Masier (Fischer-Piette 1942: pl. 10, fig. 1). Gualtieri’s specimen (Gualtieri 1742) cannot be considered a syntype because Lamarck used “an” when referring it to *Serpula sipho*, while the one illustrated by Dezallier d’Argenville (1757) may be a syntype but cannot be traced.

As mentioned above, the first nomenclatural error was made by Rousseau (Chenu 1844: pl. 4, fig. 3, top right and bottom left), who introduced a new taxon, *Vermetus sipho* Rousseau (not Lamarck), figured in, for two specimens that do not belong to the Lamarckian type series.

Since no text was ever published to explain Rousseau’s use of “*sipho*”, it is not clear whether Rousseau intended to use Lamarck’s *Serpula sipho* for these specimens, which he might have considered conspecific with Lamarck’s taxon, or whether he intended to establish a new nominal species (*Vermetus sipho* Rousseau, 1844). Sherborn (1922-1932) listed *Vermetus sipho* L. Rousseau in J. C. Chenu, 1844 and *Serpula sipho* Lamarck, 1818 as different species, but the name *Vermetus sipho* Rousseau, 1844, even if available (ICZN,

1999, Art. 12.2.7), is invalid because it is a secondary homonym (ICZN, 1999, Art. 52.3).

It is these specimens figured by Chenu (1844) (MNHN) that are the subject of this study.

The top right specimens figured by Chenu (1844: pl. 4, fig. 3) carry several labels. They are: 1) “MM. Quoy et Gaimard 1829. N° Astrolabe N.elle Hollande” (original label in handwriting of Quoy or Gaimard, fig. 1B); 2) “*Vermetus*. sp. *V. sipho* Rouss. Chenu t.4 f. 3 non Lam. N. Hollande Astrolabe” (red ink; Mörch’s label, fig. 1C); 3) “*V. Roussei* Vaill.” (unidentified modern handwriting, fig. 1D, upper labels).

Mörch wrote his label during a visit to MNHN in 1869 (Vaillant 1871: 187), but in his major work on vermetids (Mörch 1862), he wrote about this specimen: “Of the figures quoted by Lamarck, none agree with the description”. Yet, in the same text, Mörch stated: “the upper figure 3 of Chenu’s plate seems to me to correspond exactly with Lamarck’s descriptions”, thus suggesting that he considered it to be Lamarck’s material. However, this is not the case for the specimen illustrated by Rousseau (*in* Chenu 1844: pl. 4, fig. 3 top right), which was obtained during the Astrolabe expedition. The Astrolabe sailed from Toulon in 1826, returned to Marseille 24 February 1829 and the samples were accessioned by the Muséum in 1829. Accordingly, this specimen could not possibly be Lamarck’s syntype of *Serpula sipho*, published in 1818. This specimen is thus a syntype of *Vermetus sipho* Rousseau, 1844.

Moreover, Mörch (1862) also stated that Deshayes (1843: 65) had regarded Le Masier of Adanson as “the type” of *Serpula sipho*. But Deshayes had merely synonymized *Serpula sipho* Lamarck, 1818 with Le Masier of Adanson, 1757 on the grounds of priority. Deshayes was also wrong, since Adanson’s work is both non-binominal and pre-Linnean, and in doing so he did not designate a “type” [= lectotype] in the sense of the ICZN.

The latest chapter of this story was written by Vaillant (1871), who, while reorganising the MNHN vermetid collection with the help of M. L. Rousseau, recognized that *Serpula sipho*

Lamarck and *Vermetus sipho* Rousseau were not only different nominal species, but also different taxa. He separated from the "*sipho*" complex the specimens illustrated by Chenu (1844: pl. 4, fig. 3, top right), naming them *Vermetus Roussaei*. It is thus only these specimens illustrated in Rousseau/Chenu's pl. 4, fig. 3 top right, that are the syntypes of *Vermetus roussaei* Vaillant, 1871. Their type locality is "Nouvelle Hollande" (Australia).

One of the species illustrated by Chenu (1844: pl. 4, fig. 3, bottom left) is wrongly numbered on the plate "n° 3" but should have been "n° 5", a conclusion also reached by Rousseau, who ascribed it to *Serpulorbis polyphragma* Sassi, 1827 (Vaillant 1871: 197), now regarded as a synonym of *Serpulorbis arenaria* (Linnaeus, 1767).

The syntypes of *Vermetus roussaei* Vaillant, 1871 possess an internal lamina (visible at the inside of the broken earlier whorls), ornamentation formed by a regular reticulate sculpture of longitudinal striae intersecting finer axial ones, and middle whorls forming a hollow cylinder and dark brown shell, characters that are typical of the genus *Petalococonchus* Lea, 1843, subgenus *Macrophragma* Carpenter, 1857, as defined by Keen (1961).

Hughes (1993) reported the ecological and anatomical features of a species, found in western Australia, identified as *Serpulorbis* (*Serpulorbis*) *sipho* (Lamarck, 1818).

Even if no comparison with the type material was made by this author, the examination of the potential holotype (MNHN) of *Serpula sipho* leads to correctly ascribe the specimen to the genus *Serpulorbis* Sassi, 1827.

Genus *Vermetus* Daudin, 1800
Subgenus *Thylaeodus* Mörch, 1860

Vermetus (*Thylaeodus*) *enderi* Schiaparelli n. sp.

Serpulorbis roussaei Vaillant, 1871. – Springsteen & Leobrera 1986: 44, pl. 8, fig. 10 (not Vaillant 1871).

Serpulorbis (*s.s.*) *roussaei* (Vincent) (sic) – Savazzi 1996: 160, fig. 2A (not Vaillant 1871).

Serpulorbis roussaei of authors (not Vaillant 1871).

TYPE MATERIAL. — Holotype and paratypes: in an aggregate of specimens (MNHN) (Fig. 2C); paratypes: one aggregate of specimens (MZB 14024) (Fig. 2B), one aggregate of specimens (MSNG) (Fig. 2A), one aggregate of specimens on *Lopha* sp., coll. Schiaparelli.

TYPE LOCALITY. — Kudarah Thila (Shoal of Kudarah), 72°55'E, 3°34'N, South Kudarah Island, Ari Atoll, Maldives, Indian Ocean.

ETYMOLOGY. — From the Divehi (Maldivian language) name (*ènderi*) of the black coral (*Antipathes* spp.), on which this species is commonly found.

MATERIAL EXAMINED. — Several specimens from type locality, Philippines and Indonesia.

KNOWN DISTRIBUTION. — Maldives, Philippine Islands (Cebu) and Indonesia (Bunaken Marine Park, North Sulawesi).

DESCRIPTION

The holotype is part of a bigger cluster of specimens (Fig. 2C). The shell consists of an isolated tube (Fig. 2C, arrow), which is cemented and spirally coiled only in its apical portion (Fig. 2D, E, K, L), straight thereafter, as it is typical in this species.

Shell aperture diameters have an average size of 3 to 4 mm. Shells may be completely white or pale yellowish-beige with longitudinal orange-brown lines twisted in some specimens (Fig. 2F). The ornamentation is formed by simple scaly growth stages (Fig. 2G), more evident in juveniles. In some specimens scaly ornamentation organised in long longitudinal ridges, which delimit other completely smooth longitudinal portions. In coloured shells, the scaly ridges correspond to coloured lines. Feeding-tube scars (Keen 1961; Schiaparelli & Cattaneo-Vietti 1999) are practically absent: of more than 250 specimens examined only a juvenile showed a clear arrangement of the tube (Fig. 2E). The shape of the protoconch, with quite disjunct whorls, is uncommon for a vermetid. It has a tip that tends to be erect (Fig. 2H, I) and lacks sculpture; the length is of 600 µm, while the diameter is of 500 µm.

ANATOMY

The body (Fig. 4) is very long and shows no tendency to coil after extraction from the shell. The

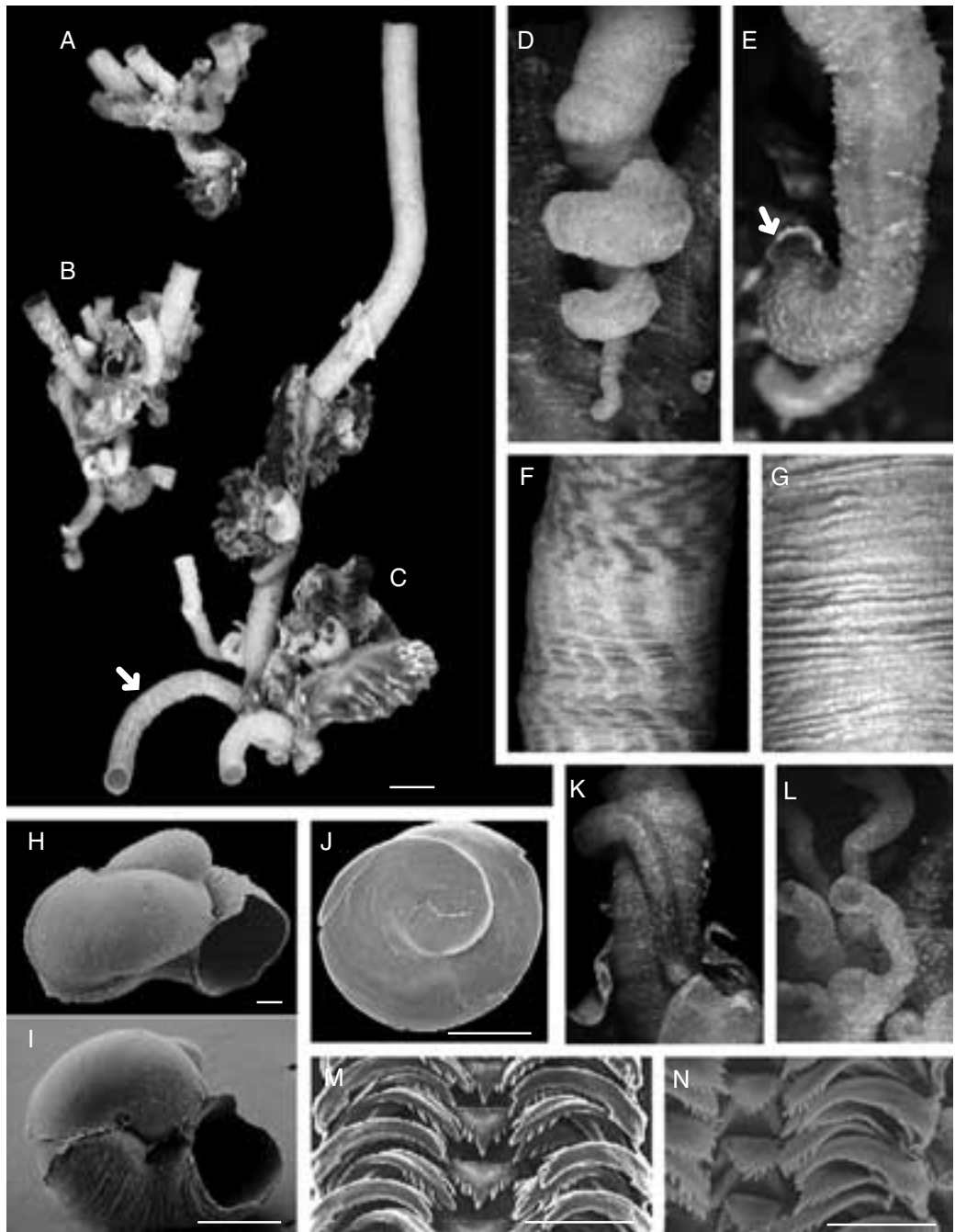


FIG. 2. — *Vermetus (Thylaeodus) enderi* Schiaparelli, n. sp.; **A**, paratypes 2 (MSNG); **B**, paratypes 1 (MZB); **C**, holotype (arrow) and paratypes (MNHN); **D**, juvenile shell on the paratype 3 (first author's collection); **E**, same sample: juvenile with a feeding-tube scar; **F**, adult shell colour pattern; **G**, ornamentation formed by simple squamulose growth stages; **H**, protoconch lateral view; **I**, protoconch basal view; **J**, operculum; **K**, reptant growth in a juvenile; **L**, erect growth in other juveniles; **M**, *V. (T.) enderi*, taenioglossate radula; **N**, freak radula. Scale bars: A-C, 1 cm; H, M, N, 0.1 mm; I, 0.5 mm; J, 1 mm.

columellar muscle is well-developed and robust, adapted for deep and fast retreat into the long shell (e.g., Fig. 2C).

The foot possesses a slightly concave yellowish-beige operculum that covers the entire surface of the foot. The operculum, which tightly fits the shell aperture (ratio operculum/shell diameter: 8-9/10), has a dirty-white spiral lamina externally (Figs 2J; 3F) that contrasts with the darker background of the body colouration. The interior has a low, but distinct attachment scar.

The head is squat with two short cephalic tentacles; the pedal ones small and very difficult to detect, at least in our preserved material. The ctenidium extends for about one-fourth of the total body length and comprises triangular lamellae; at its base an evident osphradium is present. The near absence of pedal tentacles, which are commonly used in vermetids both to spread and to re-collect the mucous net, and the well-developed ctenidium indicate that feeding is exclusively ciliary.

The visceral sac has a digestive acinose portion that is light-brown in colour and shows superficial black spots, both in male and females. The female ovary has racemous blind orange sacs clearly visible due to the transparency of the body in this region; the male gonad is uniformly yellow.

The radula is taenioglossate (2:1:1:1:2) (Fig. 2M). One specimen has an abnormal central cusp in all rows (Fig. 2N).

The mantle of the female has no dorsal slit and the egg capsules lie free inside the mantle cavity. In one female we have found two egg capsules containing unsegmented embryos. Only one of the two was not damaged, the other being accidentally squeezed during dissection. The egg capsules are almost spherical and transparent. The diameter of the intact one is of about 600 µm and it is possible to count 21 embryos inside (Fig. 5A). The damaged egg capsule revealed in the inside the presence of smaller globular cells, which are probably polar bodies (Fig. 5B).

The dominant colour of the soft parts beneath the operculum, observed on fresh collected specimens, is a deep orange-red, scattered with yellow

small dots on outer mantle margin and around the head (Fig. 3E). The inner mantle margin is yellowish-white, with orange spots that corresponds, on the shell surface, to the coloured scaly processes. A narrow yellow band, regularly interrupted by red squared spots, encircle the foot margin. A yellow "V" encircles the cephalic tentacles.

ECOLOGY

This species forms dense aggregates (> 20 individuals) (Fig. 3D), commonly at 15-20 m depth, on the axial branches of a black coral *Anthipates* spp. and in association with bivalves as such as *Lopha cristagalli*, *Dendrostrea* cf. *folium* (Ostreidae) (Fig. 3C), and *Pteria* cf. *penguin* (Röding, 1798) (Pteriidae) (Fig. 3A), which adhere with byssus threads or cement themselves to the branches.

This association of vermetids and bivalves is covered by several species of sponges (Fig. 3B, D, E) and undetermined colonial Ascidiacea (Fig. 3A, F).

Many long (up to 40 cm; diam. 1 cm) feeding-tubes characterize the shell of the oldest specimens (Fig. 3B). This length is probably reached in order to avoid competition for food created by the dense branches of the black coral.

Strangely this vermetid does not show any evidence of old abandoned feeding-tubes (Keen 1961) and its growth (except for the very first coils) is practically straight.

Feeding tube scars were erroneously considered as a character of taxonomic value by Keen (1961), as discussed by Bieler (1995), but they are expressed only in some situations (Schiaparelli 1996; Schiaparelli & Cattaneo-Vietti 1999). Their absence could be due to encrusting sponges, which may prevent the mollusc from cutting away the shell edges.

Aggregates of shells up to 1 metre in length have been observed in the Philippines (Springsteen & Leobrera 1986), and their ecology seems to be the same as the Maldivian specimens, as exemplified by the colony figured by Springsteen & Leobrera (1986: pl. 8, fig. 10) growing on a coral or gorgonacean branch.

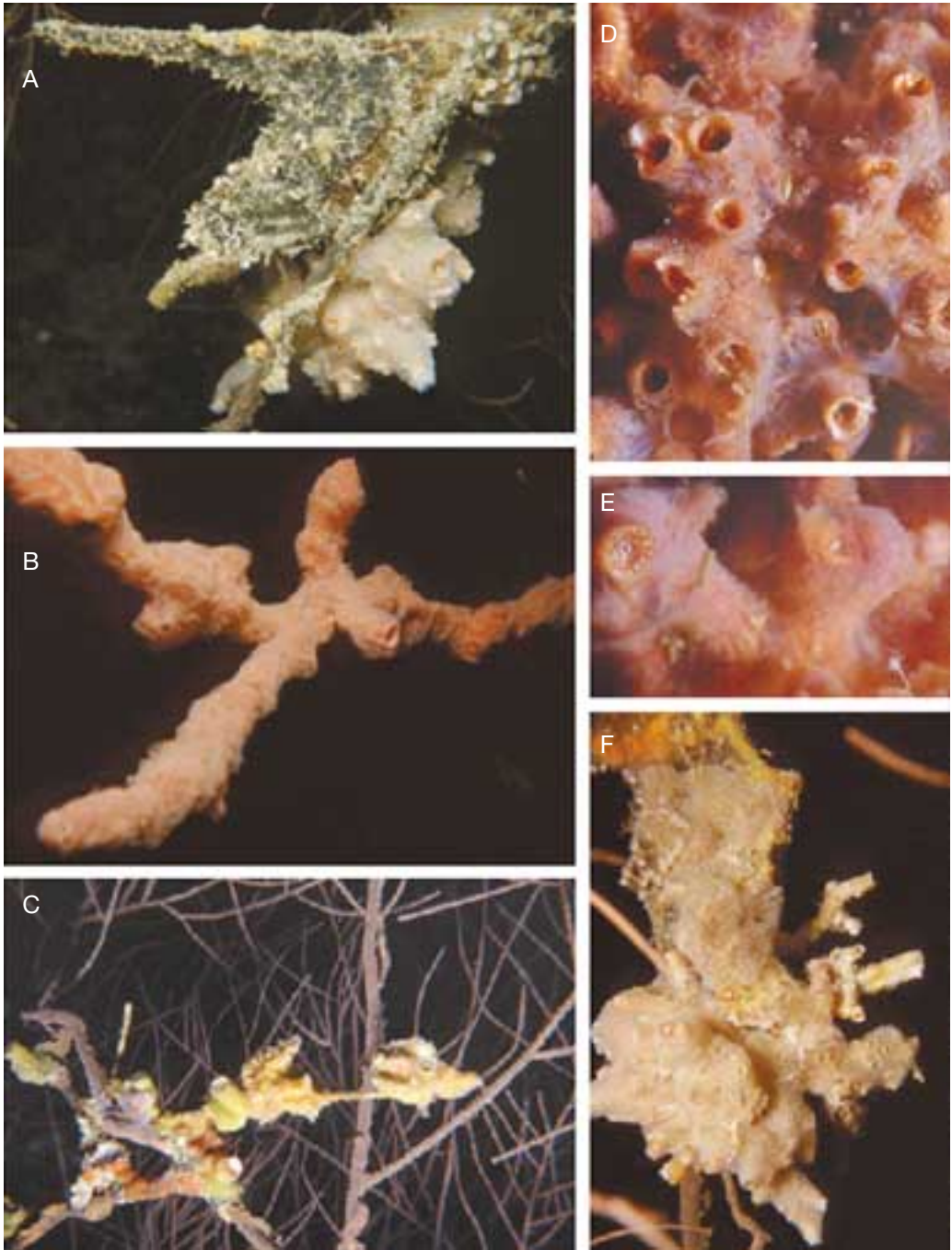


FIG. 3. — *Vermetus (T.) enderi* Schiaparelli n. sp. in association with the black coral *Antipathes* spp. and others epizoic organisms; **A**, on the axial branch, embedded in a colonial Ascidiacea and in association with *Pteria* cf. *penguin*; **B**, specimens with very long feeding tubes embedded in a sponge; **C**, specimens cemented both on *Antipathes* spp. axial branches and on *Dendrostroma* cf. *folium*; **D**, *V. enderi* dense framework of specimens embedded in a sponge; **E**, a more isolated individual (top left) with in evidence the colour pattern; **F**, a dense cluster of specimens embedded in a colonial Ascidiacea.

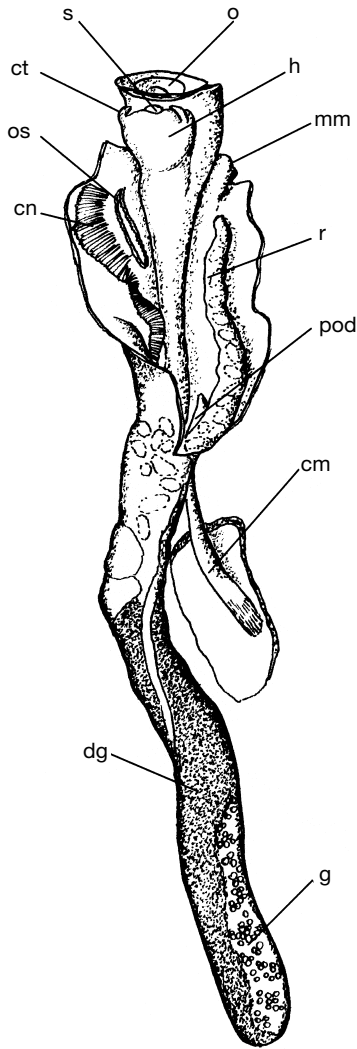


FIG. 4. — Gross anatomy of a female specimen of *Vermetus* (*T.*) *enderi*. Abbreviations: **cm**, columellar muscle; **ct**, cephalic tentacles; **cn**, ctenidium; **dg**, digestive gland; **g**, gonad; **h**, head; **mm**, mantle margin; **o**, operculum; **os**, osphradium; **pod**, pallial oviduct; **r**, rectum; **s**, sole foot.

REMARKS

V. enderi n. sp. is readily distinguishable from the known Indo-pacific vermetid species both for its shell features and the particular ecological niche. In general, it differs from Hong Kong *Vermetus* (*Vermetus*) sp. (Hughes, 1985) in having a bigger operculum and no evident pedal tentacles; from the western Australian *Vermetus* (*V.*) sp. (Hughes

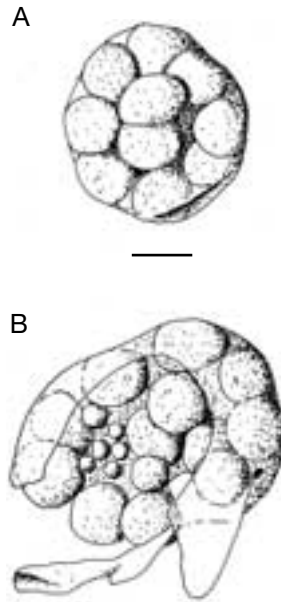


FIG. 5. — *Vermetus* (*T.*) *enderi* egg capsules: **A**, intact egg capsule; **B**, a damaged one with smaller globular bodies (polar bodies?). Scale bar: 0.2 mm.

1993) in having females without mantle slit and brooding free eggs capsules; from the Hawaiian *Vermetus alii* Hadfield & Kay, 1972 in having an operculum with only one to two volutions, instead of more than eight, and a protoconch with erected tip.

The South Californian species *V. (Thylaeodus) contortus* (Carpenter, 1857) (Keen 1961; Morton 1965) and the Mediterranean *V. (T.) rugulosus* Monterosato, 1878 (Bieler 1995), both belonging to the same subgenus of this new species, show instead similarities either in anatomical organisation (e.g., brood protection in mantle cavity) and general shape. However they differ in whorls development, sculpture and dimensions.

DISCUSSION

The new species *Vermetus (Thylaeodus) enderi* has no internal lamina and so can be placed, following the last monographs on the Vermetidae

published by Keen (1961) and Morton (1955, 1965) in the genus *Vermetus* Daudin, 1800, subgenus *Thylaeodus* Mörch, 1860.

The generic placement of both species herein discussed, *Vermetus (Thylaeodus) enderi* n. sp. and *Petalococonchus (Macrophragma) roussaei* (Vaillant, 1871), should however be considered provisional due to the problems still existing in the definition of sound taxonomic characters for this family (Gould 1994).

The two genera *Vermetus* and *Petalococonchus* in fact are closely allied, the unique morphological feature of the latter, an internal longitudinal lamina (Keen 1961), being completely absent in some specimens (Gould 1994).

The works of Keen & Morton certainly need to be updated and the taxonomy of the whole family needs a global revision.

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REFERENCES

- Adanson M. 1757. — *Histoire naturelle du Sénégal. Coquillages, avec la relation abrégée d'un voyage fait en ce pays, pendant les années 1749, 50, 51, 52 et 53*. C. J. B. Bauche, Paris, XCVI-275 p., 19 pl., 1 map.
- Bieler R. 1995. — Vermetid gastropods from São Miguel, Azores: comparative anatomy, systematic position and biogeographic affiliation. *Açoreana* suppl. 1995: 173-192.
- Bieler R. 1996. — Mörch's worm snail taxa (Caenogastropoda: Vermetidae, Siliquariidae, Turritellidae). *American Malacological Bulletin* 13 (1-2): 23-35.
- Calvo M., Templado J. & Penchaszadeh P. E. 1998. — Reproductive biology of the gregarious Mediterranean vermetid gastropod *Dendropoma petraeum*. *Journal of the Marine Biology Association U.K.* 78: 525-549.
- Chenu J. C. 1844. — *Illustrations conchyliologiques ou Description et figures de toutes les coquilles connues vivantes et fossiles, classées suivant le système de Lamarck modifié d'après les progrès de la science, et comprenant les genres nouveaux et les espèces récemment découvertes*. A. Franck, Paris: pl. 4 (*Vermetus*), livraison 26-27.
- Deshayes G. P. 1843. — in Lamarck J. B. de, *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent...* 2nd éd. Vol. 9 : *Histoire des Mollusques*. J. B. Baillière, Paris, 728 p.
- Dezallier d'Argenville A. J. 1757. — *L'Histoire naturelle éclaircie dans une de ses parties principales, la conchyliologie qui traite des coquillages de mer, de rivière et de terre...* Nouvelle édition. De Bure, Paris: XXII-380-84-CVIII p., 29-9 pl.
- Fischer-Piette E. 1942. — Les mollusques d'Adanson. *Journal de Conchyliologie* 85: 101-366.
- Gould S. J. 1994. — *Petalococonchus sculpturatus alaminatus*, a new Pliocene subspecies of vermetid gastropods lacking its defining generic character, with comments on vermetid systematics in general. *Journal of Paleontology* 65 (5): 1025-1036.
- Gualtieri N. 1742. — *Index testarum conchyliorum quae adservantur in museo Nicolai Gualtieri et met hodice distributae exhibentur tabulis CX*. Ex typographia Caietani Albizzini, Florentiae, 33 p., 110 pl.
- Hughes R. N. 1993. — The vermetid gastropods of Rottneest Island, Western Australia: 193-205, in Wells F. E., Walker D. I., Kirkman H. & Lethbridge R. (eds), *Proceedings of the Fifth International Marine Biological Workshop: the Marine Flora and Fauna of Rottneest Island, Western Australia*. Western Australian Museum, Perth.
- ICZN 1999. — *International Code of Zoological Nomenclature*. 4th ed. International Trust for Zoological Nomenclature, London, 306 p.
- Keen M. 1961. — A proposed reclassification of the gastropod family Vermetidae. *Bulletin of the British Museum (Natural History), Zoology* 7 (3): 183-213.
- Keen M. 1971. — *Sea Shells of Tropical West America; Marine Mollusks from Baja California to Peru*. 2nd ed. Stanford University Press, Stanford, California: 1064p.
- Lamarck J. B. de 1818. — *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent...* Vol. 5. Deterville; Verdier, Paris, 622 p.
- Miloslavich P. A. & Penchaszadeh P. E. 1992. — Reproductive biology of *Vermetus* sp. and

- Dendropoma corrodens* (Orbigny, 1842): two vermetid gastropods from the southern Caribbean. *The Veliger* 35: 78-88.
- Mörch O. A. L. 1862. — Review of the Vermetidae. Part II. *Proceedings of the Zoological Society of London for the Year 1861*: 326-365.
- Morton J. E. 1955. — The evolution of vermetid gastropods. *Pacific Sciences* 9: 3-15.
- Morton J. E. 1965. — Form and function in the evolution of the Vermetidae. *Bulletin of the British Museum (Natural History), Zoology* 11: 585-630.
- Savazzi E. 1990. — Biological aspects of theoretical shell morphology. *Lethaia* 23: 195-212.
- Savazzi E. 1996. — Adaptations of vermetid and siliquariid gastropods. *Palaeontology* 39 (1): 157-177.
- Schiaparelli S. 1996. — Contribution to the knowledge of Vermetidae (Mollusca: Gastropoda) from the Ligurian Sea. *Bollettino Malacologico* 31 (9-12): 267-276.
- Schiaparelli S. & Cattaneo-Vietti R. 1999. — Functional morphology of vermetid feeding-tubes. *Lethaia* 32: 41-46.
- Sherborn C. D. 1922-1932. — *Index Animalium Sive Index Nominum quae ab A.D. MDCCLVIII Generibus et Speciebus Animalium Imposita Sunt, sectio secunda, 1801-1850*. British Museum, London.
- Springsteen F. J. & Leobrera F. M. 1986. — *Shells of the Philippines*. Carfel Seashell Museum, Manila, 377 p., 100 pls.
- Tryon G. W. 1886. — *Manual of Conchology; Structural and Systematic. With Illustrations of the Species*. Vol. 8. G. W. Tryon, Philadelphia, 461 p., 79 pls.
- Vaillant L. 1871. — Recherche sur la synonymie des espèces placées par de Lamarck dans les genres Vermet, Serpule, Vermilie appartenant à la famille des Tubispirata. *Nouvelles Archives du Muséum d'Histoire naturelle de Paris* 7: 181-200.

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