

Shedding Light onto the Genera (Mollusca: Nudibranchia) *Kaloplocamus* and *Plocamopherus* with Description of New Species Belonging to These Unique Bioluminescent Dorids

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Abstract. Members of the Family Triophinae (Rudman, 1998), Gastropoda: Opisthobranchia, are characterized by having a reduced mantle, a narrow ridge along the sides of the body and a veil surrounding the head. This family is composed by seven genera of which only two have been observed to have bioluminescent species; *Kaloplocamus* Bergh, 1892 and *Plocamopherus* Rüppell & Leuckart, 1831. In order to better understand the evolution of bioluminescence within these dorids a phylogenetic analysis based on morphological and molecular data comprising all genera pertaining to the subfamily Triophinae was undertaken. Because there is great taxonomic confusion regarding *Kaloplocamus* and *Plocamopherus* species, this study is an attempt to do a taxonomic and morphological revision of both genera. Furthermore the description of new species for both *Kaloplocamus* and *Plocamopherus* are included. Five species of *Kaloplocamus* were examined in this study, including three taxa described here: *K. dokte* n. sp.; *K. peuldo* n. sp. and *K. maru* n. sp. Seven species of *Plocamopherus* were examined including four new taxa: *P. pecoso* n. sp., *P. maculapodium* n. sp., *P. margaretae* n. sp. and *P. lemur*, n. s.p. The review of the morphology of these species provides the basis for future phylogenetic studies.

INTRODUCTION

Dorids are marine hermaphroditic slugs that have lost the protective shell of most gastropods. As a result of the loss of this structure and the process of detorsion, dorids exhibit an incredible development of exuberant colors and forms. Color patterns are used as a defensive mechanism. Bright and attractive colors usually indicate that the mantle contains chemicals that are generally toxic to predators (Avila, 1995). Subtler colors may be used as a camouflage strategy (however most cryptic species have chemical defenses, as well). Other modes of protection are behavioral (autotomy of the mantle outgrowths, swimming), presence of spicules and use of their prey defense system (storage of chemical compounds).

Much less common within dorids, is the emission of bioluminescence to startle possible predators. Bioluminescence is the ability to create light as a result of a chemical reaction within a living organism. First noted by Aristotle as light of luminous wood (Johnson & Yata, 1966), early naturalists believed it to be a creation from god, just for the pleasure of the human eye, with no significant function. However, it is well known that the ability to produce such light requires significant expense of energy and, depending on the organism, it has a well-defined function (i.e., communication, prey attraction, defense, etc.) (O'Day & Fernandez, 1974; Day et al., 2004).

Although bioluminescence is known to occur in a di-

versity of organisms such as bacteria, fungi, dinoflagellates, cnidarians, annelids, arthropods, echinoderms, tunicates, fishes and some mollusks (Cephalopoda), it has only been observed within few dorid species: *Kaloplocamus ramosus* (Cantraine, 1835), *Plocamopherus imperialis* Angas, 1864, *P. tilesii* Bergh, 1877 and *P. maderae* (Lowe, 1842) of the two phanerobranch genera (*Kaloplocamus* and *Plocamopherus*). In both cases, the luminescence is intrinsic which means that the production of light is dependent on the animal's own biochemical processes (no symbiotic association with bacteria) (Wilbur & Yonge, 1966). However, in *Kaloplocamus ramosus* the chemical reaction takes place within luminescent cells or photocytes being (intracellular luminescence) whereas in *Plocamopherus* species, it results from the discharge of the luminous chemicals outside the cell where the chemical reaction occurs (extracellular luminescence). It is possible that since these organisms emit light only when disturbed, the role of bioluminescence could be to temporarily distract the attention of potential predators (Wilbur & Yonge, 1966).

Surprisingly, although both *Kaloplocamus* and *Plocamopherus* are the only dorids with this peculiar characteristic, they have been greatly understudied. In order to understand the origin and evolution of bioluminescence in these dorids, it is essential to understand the phylogenetic relationships between them, which cannot be

done unless the taxonomy of both genera is revised. The goal of this study is two-fold. First it includes a taxonomic and morphological revision of the genera *Kaloplocamus* Bergh, 1879 and *Plocamopherus* Rüppell and Leuckart, 1831. Second we provide the descriptions of three new species of *Kaloplocamus* and four new species of *Plocamopherus*.

MATERIALS AND METHODS

Twelve species have been anatomically examined. The specimens used for this study were obtained through several institutions: California Academy of Sciences, Muséum National d'Histoire Naturelle, Paris, Zoologisk Museum, København University, Copenhagen and South African Museum, Cape Town. Most of the specimens were preserved in Bouin's fixative and/or 95% ethanol. All type specimens that were available have been examined. For the newly described species, type material has been designated.

Specimens were dissected with the aid of a Nikon SMZ 10 or a Nikon SMZ zoom 110 dissecting microscope and drawings of the different structures were made with the aid of a camera lucida. For all specimens, an initial description of the external morphology was completed by microscopy to obtain details from the mantle and other external structures. A posteriori, for the internal examination, an incision with a scalpel was made at the right side/ridge of the specimen from the head to the foot to expose the buccal mass and the reproductive system. Within the buccal mass, two structures, radula and jaws, were prepared for further examination. The radula was placed in a 10% sodium hydroxide solution for approximately 48–72 hours, depending on the size and on the strength of the muscular tissue around it. The radula was then rinsed in distilled water and submerged in an ultrasound bath (Branson, 1510) to eliminate any additional tissue. Finally, using fine pointed probes, the radula was mounted on a stub to air-dry. The jaws were opened and mounted on a stub immediately after their extraction from the buccal mass to dry. Stubs were then coated with gold for two minutes using a Hummer 5-sputter coater. Coated samples were viewed by using a LEO scanning electron microscope. All specimens were viewed with a current of 15 kv.

A full external morphological description, SEM pictures of radula and jaws, and drawings of the reproductive system have been completed for all specimens available. The external morphological descriptions are based on photographs and notes made by the collector.

Genus *Kaloplocamus*, Bergh, 1879

Kaloplocamus Bergh, 1879:634; 1884:56
Euplocamus Philippi, 1836:103; Alder, 1845:262; Alder and Hancock, 1855:xix; Bergh, 1879:623, Bergh, 1883:165,

1884:56; Vayssière, 1901:65; Bergh, 1907:70; Vayssière, 1913:341; O'Donoghue, 1929:775
Idalia Leuckart, 1828; Philippi, 1844:76

Type species: *Euplocamus croceus* Philippi, 1836.

The genus *Kaloplocamus* (Opisthobranchia: Doridoidea) is poorly known. All species were described between 1835 and 1955 with the exception of *K. filiosus* (Cattaneo-Vietti & Sordi, 1988). Most of these species have only been reported when originally described. Because several generic names have been attributed to this genus a review of the taxonomic history of the generic name *Kaloplocamus* is necessary.

Cantraine (1835) briefly described the species *Doris ramosa* from the Adriatic Sea. It was characterized as an elongated specimen, with tubercles and bearing six ramified velar appendages and ramified branchial leaves. No illustrations of the animal were provided and because the information regarding the features exhibited by the specimens were scarce; a definitive identification of the species is controversial.

A year later, Philippi (1836) described the genus *Euplocamus* based on a new species: *Euplocamus croceus*. The description was based on two specimens collected in 1832. The genus was characterized by specimens with a probosciform anterior part of the body and presence of branchial leaves of two types, ones shorter and positioned in circle surrounding the anus and the others longer and situated at the sides of the body (referring to the lateral appendages that are characteristic of the group). The aperture of the reproductive system was noted as situated at the right side of the body. The genus was described as intermediate between the dorids (branchial leaves surrounding the anus) and the tritonids (the latter includes genera possessing ramified appendages which function as respiratory systems). Because, until then, the specimens had just one kind of branchial leaves, either in circle or as lateral appendages, Philippi considered the specimen as unique and therefore representative of a new genus, *Euplocamus* (Philippi, 1836).

Forbes, stated that the genus *Euplocamus* should be synonymized with the genus *Triopa* (Johnston, 1838), (Forbes, 1841). He based this judgement on his observation of the lack of cilia on the lateral appendages. This would constitute proof of the misidentification of the function of the lateral appendages (respiration) provided by Philippi, since the genus *Triopa* was composed by specimens that had lateral appendages not involved in respiration as he noted for *E. croceus*.

Cantraine (1841) considered two groups within *Doris*: *Doris planes*, composed of those with the capacity to detach some parts of the body, and *Doris prismatiques*, composed of those that do not have such a capacity. Since he did not consider the lateral appendages of *Euplocamus croceus* as branchial leaves, and he did not observe the ability to lose body parts when disturbed, he included

Polycera and *Euplocamus* in the group of *Doris* prismatiques, and therefore the genus *Doris* (Cantraine, 1841). Cantraine did not refer to the comments that were made by Forbes pertaining to this matter.

Following Forbe's (1841) and Cantraine's (1841) remarks, *Euplocamus* was synonymized with *Idalia* (Philippi, 1844). Even though a note was written on the validity of the genus *Euplocamus*, explaining the differences between the genera *Idalia*, *Triopa* and *Euplocamus* (Alder, 1845), Loven included *Euplocamus* as a synonym of *Idalia*, and reported that the generic name *Euplocamus* had already been given to a lepidopteran (Loven, 1846).

In 1847, Gray created a list of genera that needed (according to him) to be synonymized including the genus *Euplocamus*. After examination of the different species that were described as part of the genus, Gray divided them into two groups. The species that had simple lateral appendages were synonymized with the genus *Idalia* and those that had ramified lateral appendages were synonymized with the genus *Triopa* (Gray, 1847). Several authors, (Alder & Hancock, 1854; Gray, 1857) provided again the necessary evidence to distinguish *Idalia*, *Triopa* and *Euplocamus*. Despite this, Abraham synonymized the latter once more with the genus *Triopa* (Abraham, 1877), where he stated that "the differences between the two genera, however, appear to be more of degree than of kind, and serve better to distinguish sections of one genus"

It was not until much later that Bergh proposed, to use the generic name *Kaloplocamus* to replace *Euplocamus* to avoid any possible confusion with other taxa that had already the same generic name (Bergh, 1879a). The latter had already been given to both a butterfly and a bird. The name *Kaloplocamus* was also chosen because of its similarity with the initial name. However, from 1884 through 1925, even Bergh ignored this designation and published under the generic name *Euplocamus*. The first record of using the name of *Kaloplocamus* dates from 1925 (Thiele, 1925) for the description of *Kaloplocamus orientalis*.

Surprisingly, after all the trial synonymies there is only one attempt to revise the genus, (Baba, 1989). However, this revision only involves two species that are commonly encountered in Japan, *K. ramosus* and *K. acutus*. Even though Cattaneo-Vietti & Sordi (1988) gave an outline of the species included in the genus, no real revision was attempted.

Today the valid generic name considered is *Kaloplocamus* being the type species *Euplocamus crocens*. Sixteen species have been described for this genus: *K. ramosus* (Cantraine, 1835); *K. japonicus* (Bergh, 1879b); *K. principiswalliae* (Collingwood, 1881); *K. pacificus* Bergh, 1884; *K. atlanticus* (Bergh, 1893); *K. maculatus* (Bergh, 1898); *K. longicornis* (Bergh, 1905); *K. tristis* (Bergh, 1905); *K. capensis* (Bergh, 1907); *K. yatesi* (Angas, 1864); *K. orientalis* (Thiele, 1925); *K. aureus*

(Odhner, 1932); *K. acutus* (Baba, 1955); *K. gulo* (Marcus, 1979); *K. filiosus* (Cattaneo-Vietti & Sordi, 1988).

Most of these species were described between 1836 and 1905. However, over time, many of them have been synonymized. Even though Bergh described *K. maculatus* in 1898 and *K. capensis*, *K. tristis* and *K. longicornis* in 1905 and 1907 as new species, in 1908 he states that the only valid species of the genus were *K. croceus*, (var., *K. capensis* and var. *K. atlanticus*); *K. japonicus* and *K. pacificus*. In this article, he also doubted about the validity of the two latter species (Bergh, 1908).

Kaloplocamus differs externally from all other genera included in the subfamily Triophinae, by several features. The lack of a globular structure on the apex of the appendages and the absence of a penial sac in the reproductive system distinguish *Kaloplocamus* from *Plocamopherus*. The shape and length of the lateral appendages, its ramifications, and several radular features (absence of elongated and thin teeth as in *Crimora* or triangular rachidian plates as in *Triopha*) distinguish it from both genera *Crimora* and *Triopha*.

The types of most described species are not available, since most have been lost through the years (misplacement of the specimens, or poor preservation). As a result of the lack of type material and the synonymies proposed over the years, three species are considered as valid in this study, *K. pacificus*, *K. ramosus* and *K. acutus*. Only *K. ramosus* is known to be bioluminescent.

This work includes the description of three new species. Because it is difficult to test that these species are reproductively isolated, the description of new species is based on morphological features such as the external general shape, texture, color and shape of the mantle, lateral appendages and anatomical features such as those present in the radula and the reproductive system.

TERMINAL TAXA

Kaloplocamus ramosus (Cantraine, 1835) (Figures 1A, 2, 3)

Doris ramosa Cantraine, 1835: 383

Type material: *Doris ramosa* Cantraine: the type material is lost. Material examined: CASIZ 072609, one specimen, dissected. Length (preserved): 9 mm. Ilha de São Miguel, Azores, Atlantic Ocean. Depth: 60 feet. 20 July 1988. Collector: T. M. Gosliner. CASIZ 087006, one specimen. Length (preserved): 9 mm. Faial, Azores, Atlantic Ocean. October 1992. Collector: J. Brun.

Distribution: This species is known from the Mediterranean Sea, Japan, Australia, New Zealand, Hong Kong and the Atlantic Ocean including Angola and South Africa.

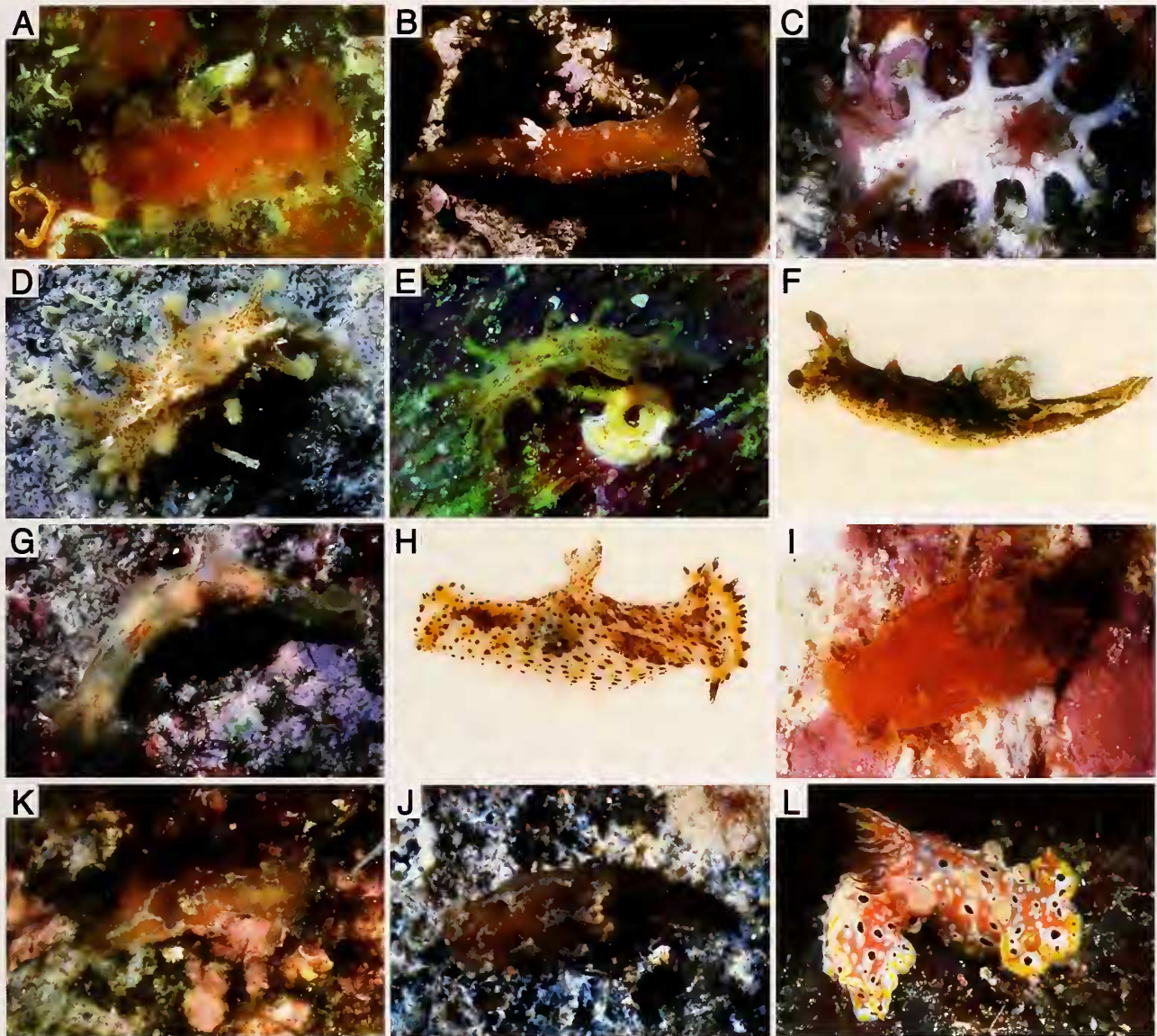


Figure 1. Living animals. A—*Kaloplocamus ramosus* (9 mm). B—*Kaloplocamus acutus* (12 mm). C—*Kaloplocamus dokte* (8 mm). D—*Kaloplocamus peludo* (7 mm). E—*Kaloplocamus maru* (8 mm). F—*Plocamopherus* cf. *imperialis* (13 mm). Photo by B. Bolland. G—*Plocamopherus maculatus* (19 mm). H—*Plocamopherus tilesii* (32 mm). Photo by B. Bolland. I—*Plocamopherus maculapodium* (13 mm). J—*Plocamopherus pecoso* (19 mm). K—*Plocamopherus lemur* (8 mm). L—*Plocamopherus margaretae* (40 mm). Photo by M. Strickland. All lengths were measured from preserved animals. All other photos by T. Gosliner.

External Morphology: The living animal has a bright orange-red color (Figure 1A). The entire dorsum has small tubercles that are translucent orange. *Kaloplocamus ramosus* has eight velar ramified appendages, which are thin and have secondary sharp, elongate ramifications. The oral tentacles are flat and wide. The rhinophores are the same color as the rest of the body. The clavus is slightly speckled with small white dots. The rhinophoral sheath is very short and speckled similar to the clavus of the rhinophore. The dorsum has four pairs of ramified

lateral appendages. These appendages are not as thin as the ones on the veil, being somewhat flat and wide with sharp and elongate ramifications at the apex. The branchial leaves are of the same color as the rest of the body, tripinnate.

Radula and Jaws on Buccal Armature: The radular formula of the specimen dissected is $17 \times (17.6.0.6.17)$. Two well-differentiated types of teeth are observed in the radula (Figure 2A, C). The six inner lateral teeth are sim-

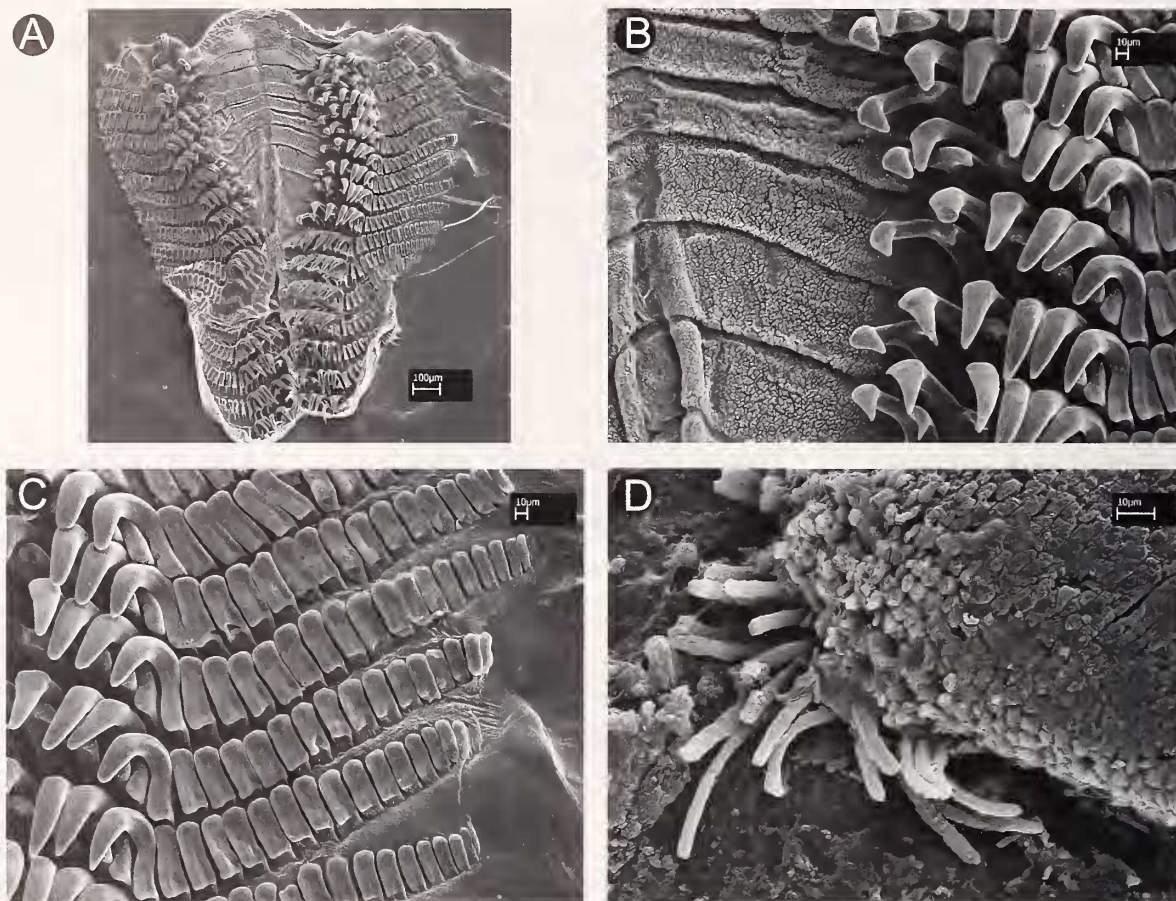


Figure 2. *Kaloplocamus ramosus* (CASIZ 072609) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

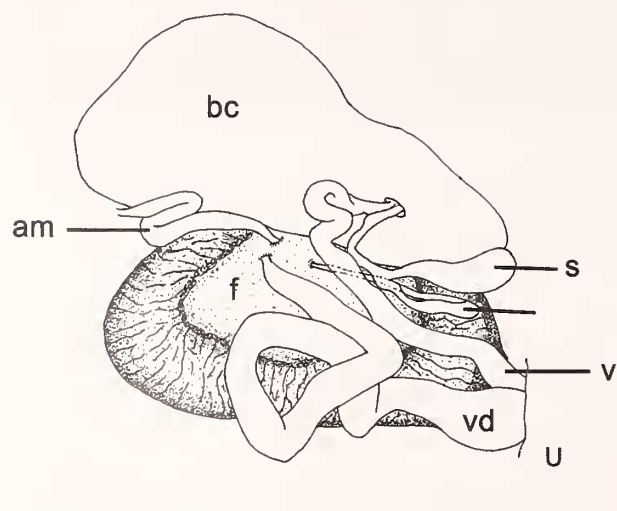


Figure 3. Reproductive system of *Kaloplocamus ramosus* (CASIZ 072609). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

ilar in shape, sharply hook-shaped with a secondary cusp well developed (Figure 2B). This secondary cusp is more developed in the innermost tooth and becomes less evident towards the outer lateral. There are seventeen outer lateral teeth, which are rectangular in shape and flat (Figure 2C). The size of the outer lateral teeth decreases from the innermost to the outermost. The rachis is papillated and separated in different rectangular plates, which are wider in the upper part of the radula. Presence of jaws with thin, rounded, elongate and densely packed rodlets (Figure 2D).

Reproductive System: The reproductive system (Figure 3) is triaulic. The vas deferens is not differentiated into a prostate. The female gland is oval somewhat elongate. The vagina is half as wide as the vas deferens and is two-thirds its length. It is connected to the bursa copulatrix. From the bursa copulatrix merges a thin and elongate duct that divides into two equally thin ducts. The first duct leads to the receptaculum seminis and second one, the uterine duct connects to the female gland mass. The latter is very thin but twice as long as the duct of the recep-

taeculum seminis. The ampulla, which is thinner than the vagina and almost as long, connects to the female gland mass near the connection of the vas deferens and the bursa copulatrix ducts.

Remarks: The morphological features exhibited by the specimen dissected correspond exactly to those described by Cantraine (1835). *Kaloplocamus ramosus* and *K. acutus* differ primarily in their external morphology. Both of them have lateral appendages, but in the case of *K. acutus* the appendages are not as ramified at the apex, and are sharper. The white tips at the top of the clavus of the rhinophores, as well as the red-purple coloration on the lateral appendages present only in *K. acutus*, distinguish them. The length of the duct leading from the receptaculum seminis to the female gland mass, which is twice as long as the one leading to the bursa copulatrix in *K. ramosus* and of the same length in *K. acutus*, separates these species. In a similar sized specimen, *K. ramosus* always has a larger number of both types of teeth. Also the hook shaped portion of the inner lateral teeth is much longer and sharper in *K. ramosus* than *K. acutus*. *Kaloplocamus ramosus* differs from *K. pacificus* in the external morphology by not having a dorsal keel (present in *K. pacificus*). Anatomically they differ by the presence of rodlets in the jaws of *K. ramosus* and the absence in *K. pacificus* (Bergh, 1884). We have followed Marshall and Willan's synonymy of *K. yatesi* to *K. ramosus* (Marshall & Willan, 1999).

Kaloplocamus japonicus and *K. ramosus* were synonymized (Eliot, 1913) since there were very few differences between them, based mostly on the number of appendages. Thiele (1925) described *K. orientalis* based on a different number of teeth. Since the variation in the number of teeth in the radula is highly variable within species in the genus it cannot be considered as a good character to establish new species. Therefore, *K. orientalis* should also be regarded as a synonym of *K. ramosus*. *Kaloplocamus principiswallie* was synonymized with *K. japonicus* (Pruvot-Fol, 1935) based on the poor description given by Collingwood (1881). Nordsieck suggested that the form *K. aureus* of Odhner 1932 should be synonymized with *K. ramosus* (Nordsieck, 1972) and *K. filus* was synonymized with *K. ramosus* (Vallès et al., 2000).

Kaloplocamus acutus Baba, 1955
(Figures 1B, 4, 5)

Kaloplocamus acutus Baba, 1955: 45

Type material: *Kaloplocamus acutus* Baba. Material examined: CASIZ 116905, two specimens, one dissected. Length (preserved): 12 mm. Depth: unknown. Puako in cave at night, Hawaii. 3 May 1981. Collector: Scott Johnson. CASIZ 065370, one specimen, dissected. Length (preserved): 8 mm. Madang, Papua New Guinea. Depth: 23 m. 22 May 1988. Collector: R. C. Willan.

Distribution: *Kaloplocamus acutus* was first described from Sagami Bay, Japan (Baba, 1955). It has been reported from the Indo-Pacific. Reported from Papua New Guinea and Hawaii (present study).

External Morphology: The body shape of the living animal is elongate (Figure 1B). The anterior part of the body is somewhat wider than the rest of the body. The head bears six velar appendages, which are semi-translucent. Opaque white coloration is present on the basal third of the velar appendage, with the remainder being translucent. These appendages have acute, simple, and elongate ramifications, each of which is bright red-carmine in color. The body has a background coloration of orange-red, with white dots over the entire dorsum. Both rhinophores are orange-red as the body, with a white line on the anterior part of the clavus. There are four lateral appendages along each lateral side of the body. The first three pairs of appendages are situated between the rhinophores and the branchial leaves. The fourth pair is located just behind the branchial leaves. The lateral appendages are similar to the veil appendages in that they have the same coloration pattern. There are five bipinnate branchial leaves. The branchial leaves have an opaque white coloration throughout their whole length when observed from an anterior angle. However, when viewed from a posterior angle, they have the same coloration as the rest of the body. As with all the appendages, the branchial leaves have sharp and simple elongated ramifications that are red carmine in color. The posterior part of the foot is elongate, acutely pointed and red-orange in color, speckled with white dots.

Radula and Jaws on Buccal Armature: The radular formula of the specimen dissected is $16 \times (11.3.0.3.11)$. Two different types of teeth are observed in the radula (Figure 4A–C). The three innermost teeth are similar in shape and hook-shaped with a secondary cusp developed in a lower position of the tooth. This secondary cusp is more pronounced in the lateral innermost teeth and disappears by the third inner lateral tooth. All three inner lateral teeth are long and the hook portion is sharp. The eleven outer lateral teeth are flat and rectangular in shape (Figure 4A, C). Their size decreases towards the outer margins. The papillated rachis has a series of transverse plates that decrease in size towards the base of the radula. The jaws have rodlets that are thin, rounded, elongate and densely packed (Figure 4D).

Reproductive System: The reproductive system (Figure 5) is triaulic. The vas deferens is not differentiated into a prostate. The vagina, although it is almost as wide as the vas deferens, is half as long. It is connected directly to the bursa copulatrix. The bursa copulatrix is similar in size to the receptaculum seminis to which is connected by a duct that enlarges and divides itself into two ducts. One duct opens into the receptaculum seminis and the other, is the uterine duct that opens into the female gland mass. The

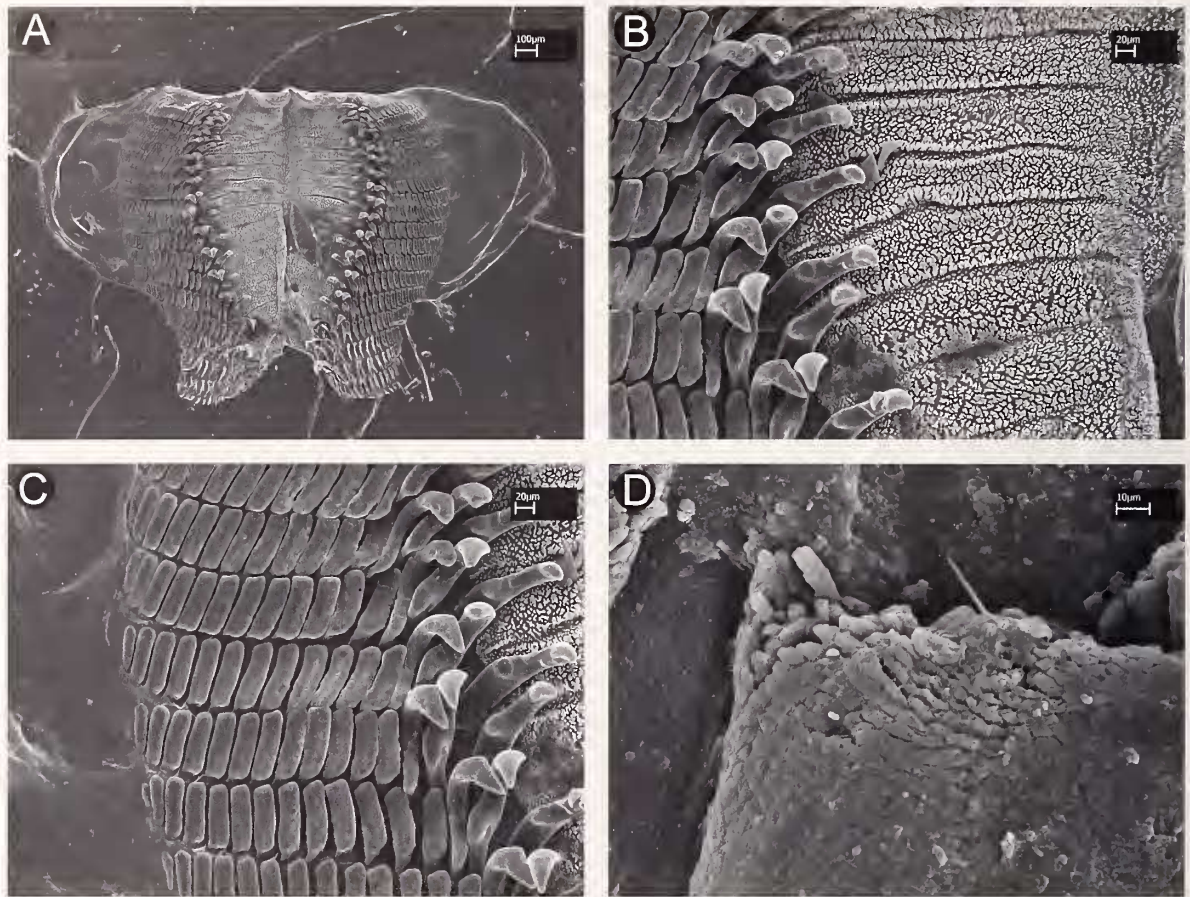


Figure 4. *Kaloplocamus acutus* (CASIZ 116905) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

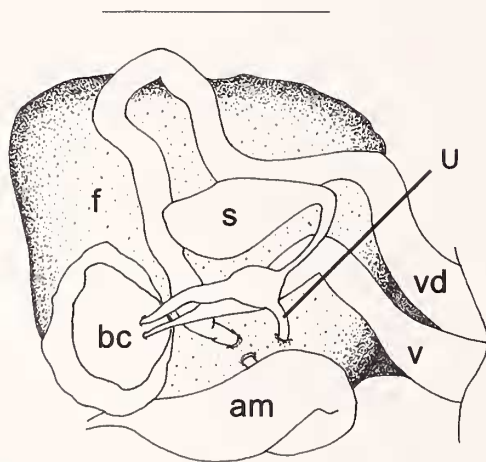


Figure 5. Reproductive system of *Kaloplocamus acutus* (CASIZ 116905). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

ampulla, wider than the vas deferens, and as long as the vagina, penetrates into the female gland near the connection of the vas deferens and the bursa copulatrix ducts. The connection between the ampulla and the vas deferens occurs within the female gland mass.

Remarks: *Kaloplocamus acutus* was first described by Baba (1955). It was shortly described as having orange-yellow background coloration. Characterized by the presence of six velar processes, four pairs of lateral appendages with a small number of sharp pointed branches that were always carmine red and a radula with two inner lateral teeth (Baba, 1955). The dorsum of the present specimen has four pairs of ramified appendages that are larger and longer than those of the veil. The branchial leaves have the same orange coloration as the rest of the body. All appendages have a pink-red-purple coloration at the apex of the ramifications and the rhinophores are red. Both, the red carmine coloration on the apex of the lateral and oral veil ramifications and the white lines on the anterior part of the clavus of the rhinophores are characteristic of the species. Also typical of the species is the presence of the

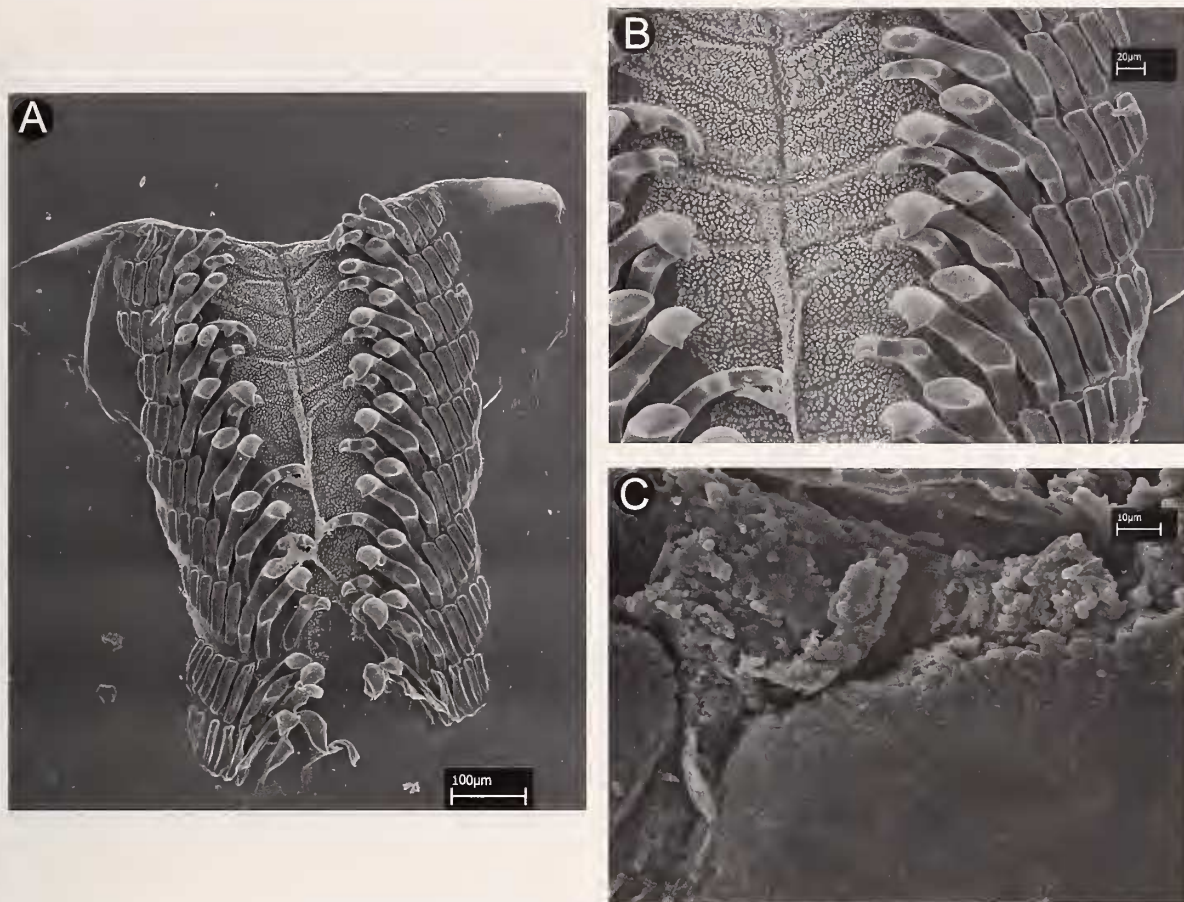


Figure 6. *Kaloplocamus dokte* (CASIZ 146066) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Jaws.

simple and sparse ramifications on the veil and lateral appendages. *Kaloplocamus acutus* differs from *K. pacificus* in its external morphology by not having a dorsal keel (present in *K. pacificus*) by having lateral and frontal appendages that have simple ramifications.

Kaloplocamus dokte n. sp.
(Figures 1C, 6, 7)

Type and examined material: Holotype, CASIZ 086448, one specimen. Length (preserved): 4 mm. Depth: 3 m. Barracuda Point, Madang, Papua New Guinea. 9 June 1992. Collector: T. M. Gosliner. Paratypes: CASIZ 146066, one specimen, dissected. Length (preserved): 8 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 30 January 1988. Collector: T. M. Gosliner. CASIZ 078586, one specimen. Length (preserved): 3 mm. Depth: unknown. Bwaken Island, Manado, Sulawesi, Indonesia. Date: unknown. Collector: P. Fiene. CASIZ 146060, one specimen. Length (preserved): 4 mm. Depth: 8 m. St 52, Barracuda Point, Madang, Papua New Guinea. 5 July 1989. Collector: T. M. Gosliner. CASIZ 146068, one specimen. Length

(preserved): 4 mm. Depth: 8 m. Barracuda Point, Papua New Guinea. 16 July 1989. Collector: T. M. Gosliner. CASIZ 146057, one specimen. Length (preserved): 5 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 27 August 1989. Collector: T. M. Gosliner. CASIZ 075887, one specimen. Length (preserved): 6 mm. Depth: 6.6 m. Barracuda Point, Madang, Papua New Guinea. 19 November 1990. Collector: T. M. Gosliner. CASIZ 146065, one specimen. Length (preserved): 2 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 14 August 1984. Collector: T. M. Gosliner. CASIZ 146067, three specimens. Length (preserved): 2–3 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 31 August 1989. Collector: T. M. Gosliner. CASIZ 146059, one specimen. Length (preserved): 5 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 22 July 1989. Collector: T. M. Gosliner. CASIZ 146063, one specimen. Length (preserved): 3 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 14 August 1989. Collector: T. M. Gosliner. CASIZ 146064, one specimen. Length (preserved): 5 mm. Depth: 8 m. Barracuda Point, Madang, Papua New Guinea. 4 February 1988. Collector: unknown. CASIZ 146061, one

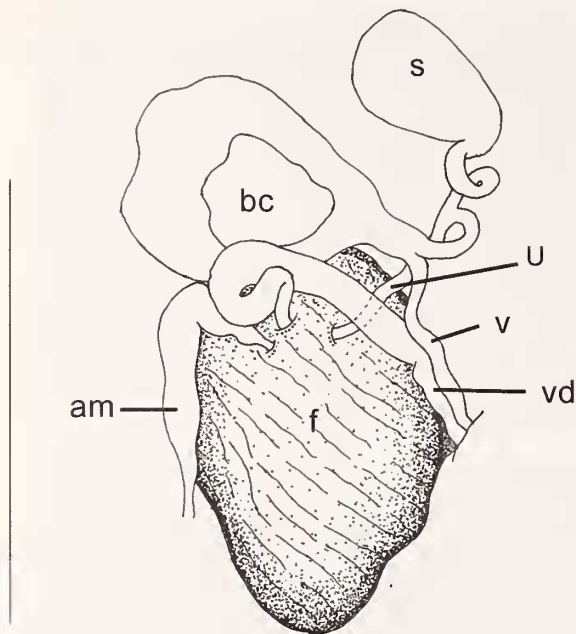


Figure 7. Reproductive system of *Kaloplocamus dokte* (CASIZ 146066). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

specimen. Length (preserved): 5 mm. Depth: unknown. Rasch Passage, Madang, Papua New Guinea. 20 August 1989. Collector: T. M. Gosliner. CASIZ 083657, one specimen. Length (preserved): 6 mm. Depth: unknown. Luzon Island, Philippines. 19 February 1992. Collector: T. M. Gosliner.

Distribution: Specimens of this species have been found in Papua New Guinea, Indonesia and the Philippines.

External Morphology: When alive, this species appears to be ovoid in shape but upon a closer view, the posterior portion of the foot is elongated (Figure 1C). Most of the animal is opaque white except for the posterior end of the foot and the eight velar appendages, which are highly transparent. The dorsal and central portions of the body are translucent and the digestive gland is visible. The three tripinnate branchial leaves, are a translucent red-carmine. The rhinophores are of the same color as the branchial leaves, but more translucent with white dots on the apex. The long, large, lateral appendages are totally opaque white except at the apex, where they ramify and become more cream in tone. There are four pairs of lateral appendages. They are smooth with ramifications in the apex only. Instead of being sharp and long these ramifications are rounded, almost globular and there are many of them resembling in shape to a bunch of grapes. These ramifications only occur on the exterior portion of the lateral appendage, with the interior portion being smooth over its entire length.

Radula and Jaws on Buccal Armature: The specimen dissected had a radula formula of $10 \times (5.3.0.3.5)$. The radula is characterized by the presence of two different types of teeth (Figure 6A, B). The three inner lateral teeth, (Figure 6A, B) similar in shape, are elongated and hook-shaped at the apex. The hook-shaped portion of the teeth is short. The innermost lateral tooth has a smaller secondary cusp near the primary one. The outer lateral teeth (Figure 6A, B), five per side, are flat and rectangular in shape. The size of these rectangular teeth diminishes from the innermost to the outermost. The papillated rachis has a series of transverse plates that are regular in shape and size for the whole length of the radula. There are an equal number of rachidian plate rows, as rows of teeth. Presence of jaws with thin, elongate, rounded rodlets that are densely packed (Figure 6C).

Reproductive System: The reproductive system (Figure 7) is triaulic. The vas deferens is not differentiated in its distal portion into a prostate. The thin vagina is half the length of the vas deferens and before entering into the bursa copulatrix joins the duct from the receptaculum seminis. The duct connecting receptaculum seminis and bursa copulatrix, divides into two ducts, one leading to the oval receptaculum seminis and the other, the uterine duct, entering into the female gland mass. The ampulla is thin and short, and enters into the female gland mass near the connection of the vas deferens and the bursa copulatrix ducts. It presumably bifurcates into the vas deferens and oviduct within the female gland.

Remarks: This species is distinguished by the opaque white coloration, never reported before for a *Kaloplocamus* species. The presence of four ramified appendages that are of the same length and are ramified are typical of the genus. However the ramifications shape (similar to a bunch of grapes) makes this species unique. Another interesting feature that distinguishes *K. dokte* from other *Kaloplocamus* is the small radula with a small number of teeth. *Kaloplocamus dokte* differs from *K. pacificus* in the absence of a keel as well as differences on the lateral and frontal appendages that are not tripinnate. As in *K. ramosus* and *K. acutus*, four lateral appendages were observed as well as a total of eight veil appendages, which are shorter and smaller than the former. However, *K. dokte* has lateral appendages that bear small secondary ramifications that instead of being sharp and elongated as in *K. acutus* or ramified as in *K. ramosus*, they are rounded. The radula is different from the typical structure of the *K. ramosus* and *K. acutus* specimens in that the three innermost lateral hook-shaped teeth are large relative to the size of the radula.

Etymology: This species is named "*dokte*" for the father of the senior author, whose nickname in Haitian kreol is Dokte.

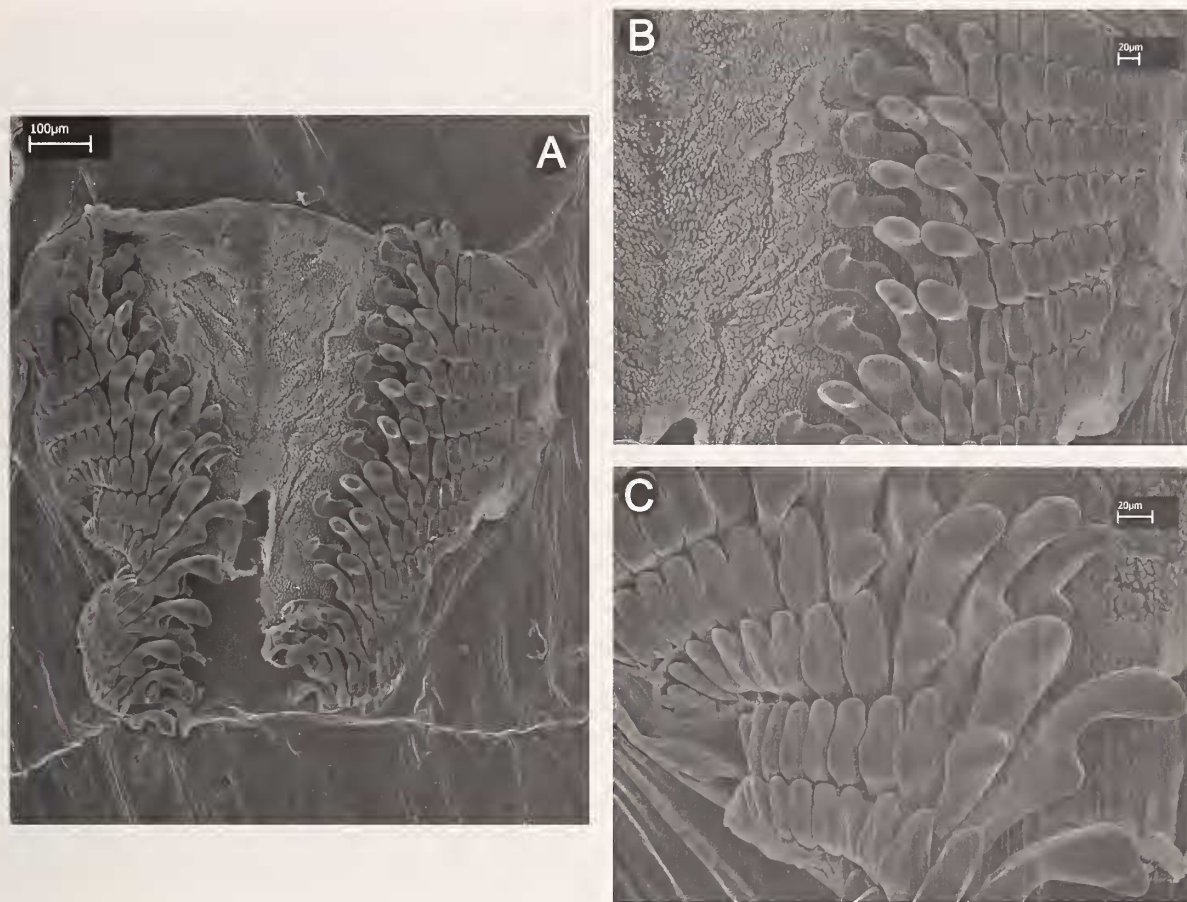


Figure 8. *Kaloplocamus peludo* (CASIZ 085981) SEM photographs of the radula. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth.

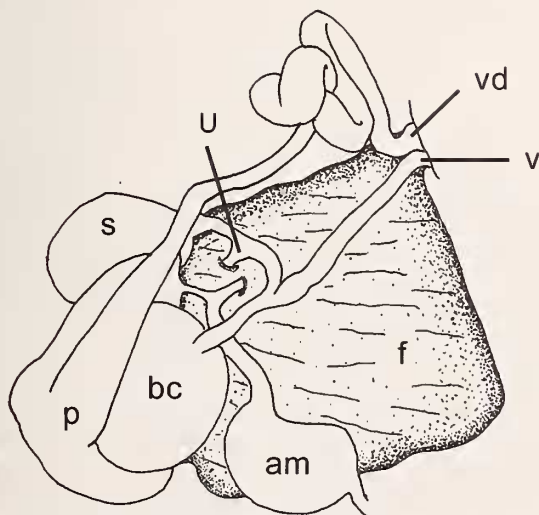


Figure 9. Reproductive system of *Kaloplocamus peludo* (CASIZ 085981). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

Kaloplocamus peludo n. sp.
(Figures 1D, 8, 9)

Type and examined material: Holotype, CASIZ 083828, one specimen. Length (preserved): 6 mm. Depth: 20 m. Batangas, Luzon Island, Philippines. 23 February 1992. Collector: T. M. Gosliner. Paratypes: CASIZ 085981, four specimens, two dissected. Length (preserved): 8–4 mm. Depth: 33 m. Kirby's Rock, NW side of the Maricaban Island, Batangas, Luzon Island, Philippines. 26 March 1993. Collector: T. M. Gosliner. CASIZ 118946, one specimen. Length (preserved): 11 mm. Depth: unknown. Batangas, Luzon Island, Philippines. March 1995. Collector: Mike Miller. CASIZ 085934, two specimens. Length (preserved): 9–11 mm. Depth: 23 m. Mindanao, Philippines. 31 March 1993. Collector: T. M. Gosliner. CASIZ 086294, two specimens. Length (preserved): 6–7 mm. Depth: 3 m. Madang, Barracuda Point, Papua New Guinea. 9 June 1992. Collector: T. M. Gosliner. CASIZ 115384, two specimens. Length (preserved): 7–10 mm. Depth: 55 m. Seragaki, Okinawa, Ryukyu Island, Japan. 127°52.60'E;

26°30.40'N, 26 March 1997. Collector: R. F. Bolland. CASIZ 099222, one specimen. Length (preserved): 11 mm. Depth: unknown. Mtwara, Tanzania. 31 October 1994. Collector: T. M. Gosliner. CASIZ 121138, one specimen. Length (preserved): 6 mm. Depth: 13 m. Marshall Islands: Kwajalein Atoll. Ennubuj Island: Gea Island: ocean side of island. 24 October 1992. Collector: S. Johnson.

Distribution: Several specimens of this new species have been found in many different localities ranging from the Philippines, Papua New Guinea, Palau, Marshall Islands and Japan in the Western Pacific to Tanzania in the Western Indian Ocean.

External Morphology: The living animal has a general orange coloration (Figure 1D). The whole dorsum has brown dots except at the apices of the lateral appendages, which are pale yellow. These brown dots are similar and size and regularly distributed. The dorsum has an opaque white, irregularly shaped line, which runs from the front of the head to the posterior end of the notum. This line bifurcates at the level of the branchial leaves, where it surrounds them and reemerges again behind the branchial leaves. The posterior end of the foot is thin and acute and has a yellow color similar to that of the lateral appendage apices. Two types of appendages are observed in the specimen. The first type of appendages is the longest and widest. There are three pairs of these lateral appendages situated along the margin of the sides. These appendages have a ramified apex. Each ramification of the apex has a rounded base and a long, thin and sharp prolongation. The whole length of each of these appendages is covered by little and acute ramifications. The second type of appendages, are thin, long with many small sharp, thin and long simple ramifications. These appendages are present on the sides of the body, foot, dorsum and oral veil in number 15–17 per side with 6 on the oral veil. The rhinophores have a lamellate clavus and a peduncle with little, thin and sharp ramifications. Each rhinophoral sheath edge has three ramifications. The middle one is virtually identical to the lateral appendages. The other two ramifications are similar to the smaller tentacles of the rest of the body. The oral tentacles are simple folds of the mantle that have a cylindrical shape. There are three tripinnate branchial leaves. They present long, simple, and thin ramifications as the smaller appendages.

Radula and Jaws on Buccal Armature: The radular formula of the specimen is $11 \times (8.3.0.3.8)$. Two different types of teeth are present in the radula (Figure 8A–C). The three inner lateral teeth similar in shape have a blunt hook with a secondary cusp (blunt as well) developed in a lower position of the tooth. The outermost eight teeth are rectangular in shape and their size decreases from the innermost to the outermost. The papillated rachis is not well

separated into different plates being just one whole plate for the radula. No rodlets were observed on the jaws.

Reproductive System: The reproductive system (Figure 9) is triaulic. The vas deferens is differentiated in its distal portion into a wide, translucent prostate. A thin short oviduct emerges from the prostate joining the oval ampulla before entering into the female gland mass. The vagina is very thin and is a fourth of the length of the vas deferens. Before entering into the bursa copulatrix it joins the duct from the receptaculum seminis. The duct connecting receptaculum seminis and bursa copulatrix, divides into two ducts, one leading to the oval receptaculum seminis and the other, the uterine duct, entering into the female gland mass.

Remarks: This species is characterized by the several features, which make it very different from the other known species of *Kaloplocamus*. The presence of two kinds of lateral appendages which bear on the apex long, thin and simple filaments; the presence of tubercles with thin and long ramifications as well all over the body; and the particular shape of the rhinophores sheaths disguising themselves as lateral appendages are unique of *K. peludo*. Even though the general morphology of the radula is typical of the genus *Kaloplocamus*, several differences are found. The inner lateral teeth have a blunt apex instead of the typical sharp hook shaped. The presence of a granulated rachis characteristic of the genus, differs by not been transversally divided in rachidian plates rows. Other important differences are the absence of rodlets in the jaws and the presence of a distinctive wider prostate gland.

Etymology: This species is named *peludo* for the long and thin filaments (hair-like) present on the apex of the lateral appendages. *Peludo* is a Spanish adjective to indicate that something or someone has a lot of hair.

Kaloplocamus maru n. sp.
(Figures 1E, 10, 11)

Type and examined material: Holotype, CASIZ 170939. Length (preserved): 6 mm. Depth: 0–27 m. Badeldoab Island, Ngerduais Island, Palau. 21 September 1996. Collector: T. M. Gosliner. Paratype: CASIZ 109685, two specimens, two dissected. Length (preserved): 6–10 mm. Depth: 0–27 m. Badeldoab Island, Ngerduais Island, Palau. 21 September 1996. Collector: T. M. Gosliner.

Distribution: This species has been collected in Palau.

External Morphology: The living animal has a general orange color (Figure 1E). The whole dorsum has brown dots except the tips or apex of the lateral appendages, which are pale yellow. The dorsum has a white diamond shaped spot that runs from the behind of the rhinophores to the tail (just behind the branchial leaves). The end of the foot is acute and has a similar color to the appendage apices. Two types of appendages are observed. The first

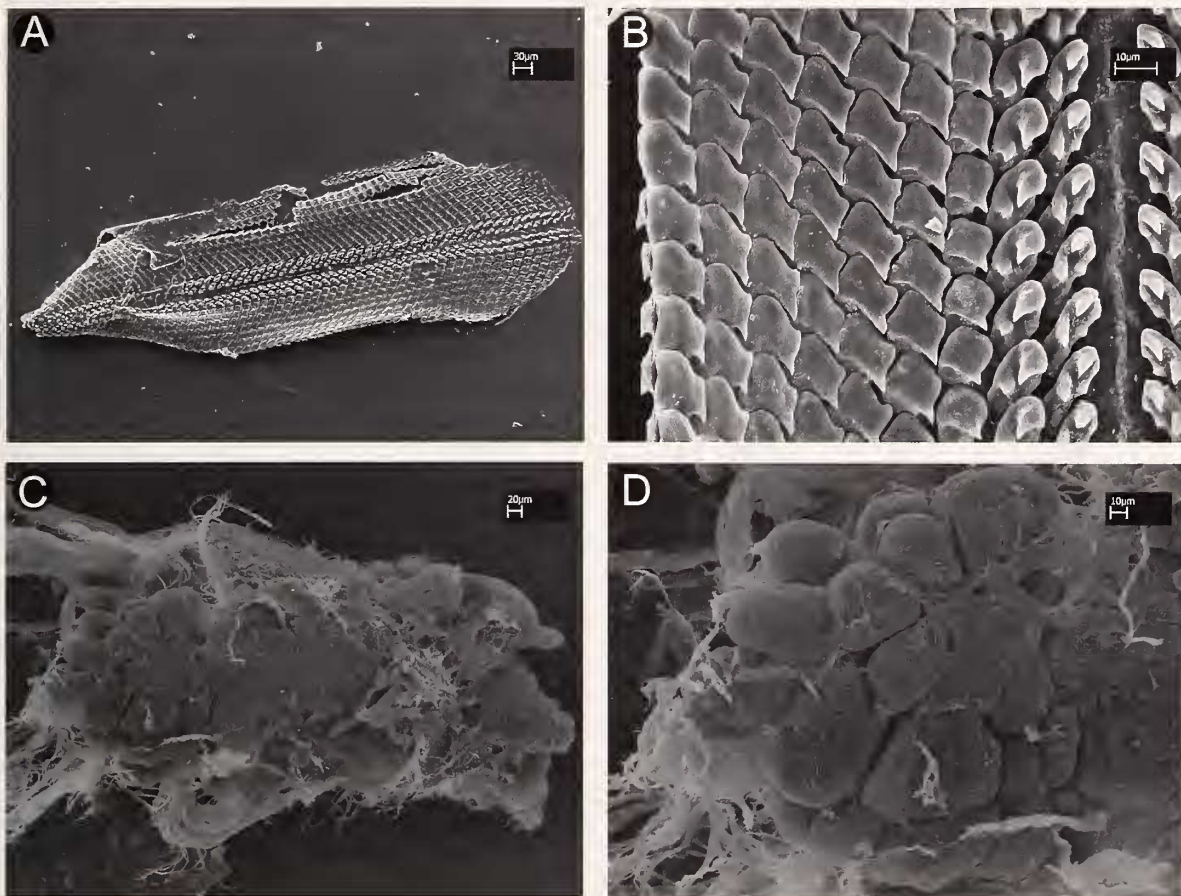


Figure 10. *Kaloplocamus maru* (CASIZ 109685) SEM photographs of the radula and glands. A. Whole radula. B. Inner lateral teeth. C & D. Buccal glands.

type of appendages are longer and wider and are positioned at the margin of the sides of the animal. These appendages have apical ramifications that are rounded at the base with a long, thin and sharp prolongation. Small acute ramifications cover the remaining parts of the appendage. The second type of appendage is thin, long with many small sharp, thin and long simple ramifications. These appendages are present on the entire body, sides, foot, and dorsum. The oral veil has four appendages, two of which are longer, situated at the lateral edges of the oral veil and two that are shorter situated in the center. The rhinophores have a lamellate clavus and a peduncle with acute ramifications. Each rhinophoral sheath edge has three ramifications. The middle one is virtually identical to the lateral appendages. The other two ramifications are similar to the smaller tentacles of the rest of the body. The oral tentacles are simple folds of the mantle with the appearance of cylinders. The three branchial leaves are tripinnate. They have the same simple and thin ramifications as the smaller appendages.

Radula and Jaws on Buccal Armature: The radula is enveloped in a cylindrical buccal mass, that has large glandular structures at both sides (Figure 10C, D). Their function has not yet been identified. The radular formula of this species is $68 \times (7.2.0.2.7)$. The radula of *Kaloplocamus maru* is characterized by being a long ribbon of teeth (Figure 10A). There are two types of teeth. There are two inner lateral teeth with similar shape with the inner one being smaller than the outer one (Figure 10A, B). Both teeth are hook-shaped at the apex but the remaining tooth body seems to be folded forward, having each folded edge developed into a protuberance in the middle of their length. The outer lateral teeth are flat and have an irregular shape. The rachis is reduced to a line between both sides of the radula (Figure 10B). No jaws were observed.

Reproductive System: The reproductive system is triaulic (Figure 11). The vas deferens is not differentiated into a prostate. It is as long and almost as wide as the vagina but becomes thinner in its proximal portion. Proximally the

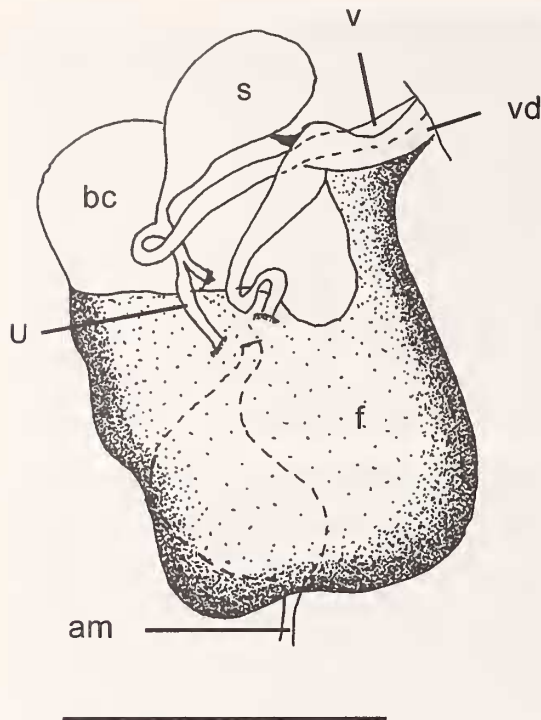


Figure 11. Reproductive system of *Kaloplocamus maru* (CAS-IZ 109685). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

vagina joins the duct coming from the receptaculum seminis, becoming a single duct. The latter splits into two other ducts, one of which enters into the bursa copulatrix and the other (uterine duct) connects with the female gland mass. The ampulla is wide and oval in shape and the upper part differentiates into a narrow and short duct that connects with the female gland mass near the connection of the vas deferens and the bursa copulatrix ducts.

Remarks: *Kaloplocamus maru* is very similar to *Kaloplocamus peludo* in the general external morphology. *Kaloplocamus maru* is characterized by features such as the presence of long, thin and simple ramifications present in the apex of the lateral appendages; the presence of tubercles with thin and long ramifications as well all over the body (but many fewer than those present in *K. peludo*); and the particular shape of the rhinophoral sheaths disguising themselves as lateral appendages. Even though both species (*K. peludo* and *K. maru*) are externally very similar, anatomical differences clearly separate them. The radula of *Kaloplocamus maru* is atypical of the genus *Kaloplocamus*. Two types of radular teeth are present in both species but differ markedly in their features. In *K. maru* the inner lateral teeth have a much shorter, blunt cusp than in *K. peludo*. The outer lateral teeth are irregular in *K. maru* but are rectangular in *K. peludo*. The absence of a wide granulate rachis is also atypical for the genus, in this

case it is observed only as a very narrow line that runs longitudinally the radula. Usually, *Kaloplocamus* radular general morphology is wider than longer in contrast to that of *K. maru*, which is much longer than wider. Because of the atypical features of the radula two specimens were examined having both the same radula. Other differences are the presence of a distinct prostate in *K. peludo* versus its apparent absence in *K. maru*.

Etymology: This species is named "maru" after the mother of the senior author, whom we all call Maruxa.

GENUS *PLOCAMOPHERUS* RÜPPELL AND LEUCKART, 1831

Historiophorus Pease, 1860:35

Peplidia Lowe, 1842:51

Plocamophorus Whitelegge, 1889

Plocamorphorus Fewkes, 1889

Plocamoceros J. E. Gray, 1857

Plocamophorus Okada and Baba, 1938:276

Type species: *Plocamopherus ocellatus* Rüppell & Leuckart, 1831.

The genus *Plocamopherus* was described based on a new species, *Plocamopherus ocellatus* characterized by having a shell-less body, elongate, doridiform, convex dorsum, and armed at both sides with simple tentacles (Rüppell & Leuckart, 1831). The anterior margin has ramified appendages, retractile rhinophores, a mid-dorsal anus surrounded by the branchial leaves, and a reproductive system opening on the right side. *Plocamopherus ocellatus* (type species) was characterized by a shaded color, dorsal oval spots of a sulfur color, and presence of conical papillae at both. This species was described from the Red Sea (Rüppell & Leuckart, 1831).

Even though several changes of the spelling of the name *Plocamopherus* have been published throughout the history of the genus (Lowe, 1842; Gray, 1857; Pease, 1860; Fewkes, 1889; Whitelegge, 1889; Okada & Baba, 1938), its validity has never been questioned, with the exception of Risbec, who synonymized it with *Triopha* and *Triopa*, because he found it impossible to distinguish the three genera (Risbec, 1928). Subsequent authors did not accept this synonymy.

Plocamopherus has been considered as very closely related to the genera *Kaloplocamus* and *Triopha*. Included as well in the subfamily Triophinae, *Plocamopherus* has several characteristics that allow its unequivocal identification. A limaciform body usually with up to three pairs of lateral appendages characterizes it. In most cases, the most posterior pair of appendages have a bioluminescent structure on their apices composed of columnar cells that produce a secretion that, when excreted produces light. This structure is sometimes also present in some species, on the other two pairs of appendages, but when present, it is usually much smaller. This structure is unique to *Plo-*

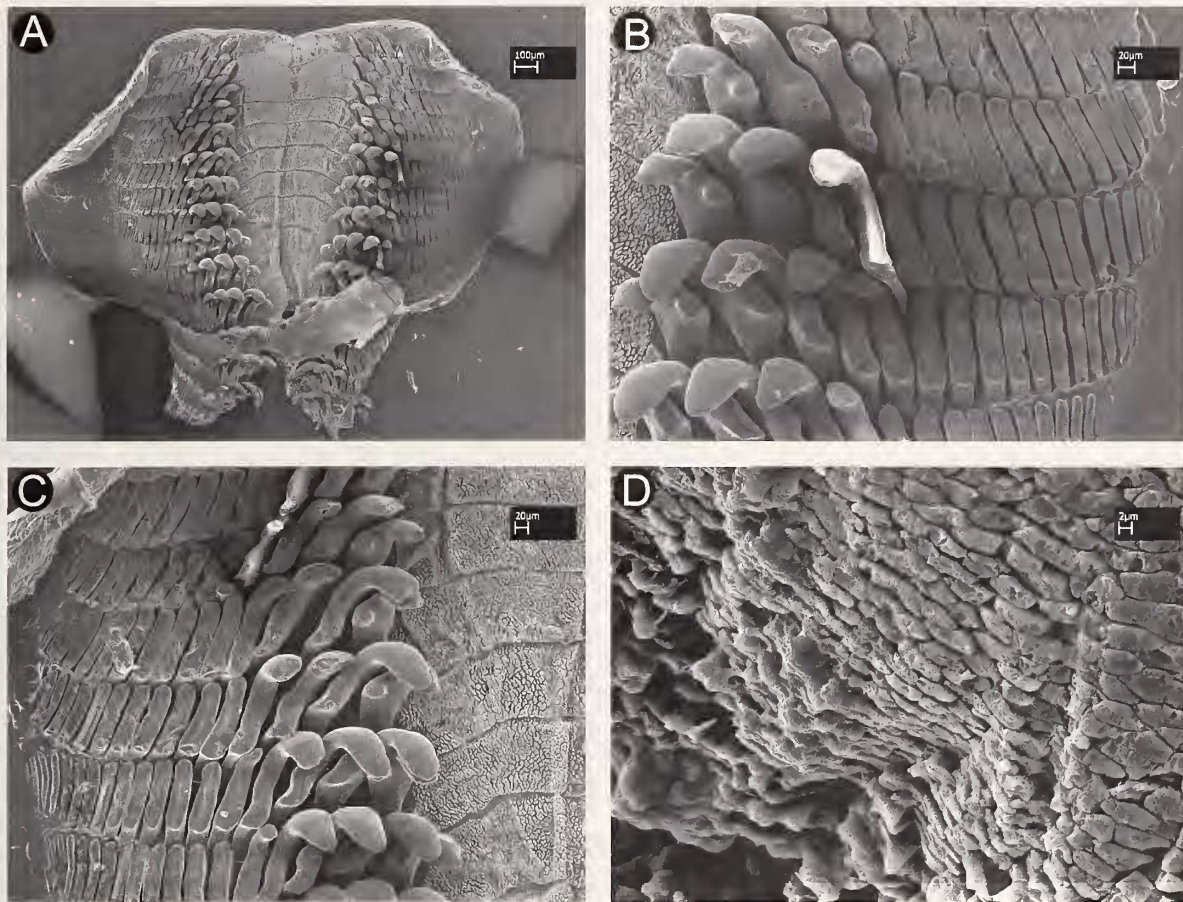


Figure 12. *Plocamopherus* cf. *imperialis* (CASIZ 079194) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

camopherus species. However the production of bioluminescence is not limited to the bioluminescent structures. The head and the sides of the body as well as the crest of the tail emit a less intense light than the bioluminescent structures (as occurs *Kaloplocamus ramosus*). Another feature of *Plocamopherus* is their ability to swim (Lowe, 1842, 1843). Most species of this genus have a vertically flattened postero-dorsal keel on the foot that allows them to swim by lateral undulation.

There are seventeen described species: *Plocamopherus amboinensis* (Bergh, 1890); *P. apheles* (Barnard, 1927); *P. ceylonicus* Kelaart, 1858; *P. flagellatus* (Kruzenstern, 1813); *P. fulgurans* (Risbec, 1928); *P. imperialis* Angas, 1864; *P. indicus* (Bergh, 1890); *P. insignis* (Smith, 1884); *P. levivarius* (Abraham, 1876a); *P. lucayensis* Hamann and Farmer, 1988; *P. maculatus* Pease, 1860; *P. maderae* Lowe, 1842; *P. naevatus* (Abraham, 1876b); *P. ocellatus* Rüppell and Leuckart, 1831; *P. pilatecta* Hamann and Farmer, 1988; *P. ramulosus* (Stimpson, 1855); and *P. tilesii* Bergh, 1877.

Plocamopherus uaeavatus was synonymized with *Plocamopherus imperialis* (Bergh, 1883). Thompson in 1975

proposed *P. amboinensis*; *P. apheles*, *P. flagellatus*; *P. fulgurans*, *P. indicus*, *P. levivarius* as dubious species. These descriptions were based on preserved material (Thompson, 1975). The descriptions not only lack data on the external coloration, but anatomical details as well, since most of them were not dissected. Thompson determined the following valid species: *Plocamopherus ocellatus*, *P. maderae*, *P. maculatus*, *P. ceylonicus*, *P. imperialis*, and *P. tilesii*.

TERMINAL TAXA

Plocamopherus cf. *imperialis* Angas, 1864
(Figures 1F, 12, 13)

Plocamopherus imperialis Angas, 1864:59

Type material: *Plocamopherus imperialis* Angas, was lost. Material examined: CASIZ 079194, one specimen, dissected. Length (preserved): 13 mm. Depth: 1.5 m. Seragaki Beach, Ryukyu Islands, Okinawa. 25 March 1991. Collector: R. F. Bolland. CASIZ 089062, one specimen. Length (preserved): 8 mm. Depth: 3 m. Seragaki Beach,

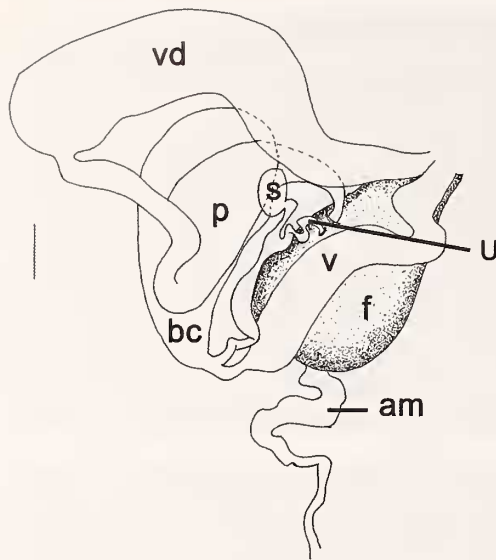


Figure 13. Reproductive system of *Plocamopherus* cf. *imperialis* (CASIZ 079194). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

Ryukyu Islands, Okinawa. 1 January 1993. Collector: R. F. Bolland.

Distribution: Known from temperate Southeastern Australian waters and northern New Zealand (Rudman 1998) and from Okinawa.

External Morphology: In life, its body shape is elongate, limaciform and anteriorly rounded (Figure 1F). The oral veil is wide, flattened and has eight velar processes. The presence of flat oral tentacles was observed. The present specimen has a yellowish background color. The entire body is highly speckled with brown dots that are more intense on the dorsum than the sides of the body. There are larger blotches of brown coloration surrounding the lateral appendage bases. The rhinophoral peduncles are pink with a brownish clavus. The rhinophoral sheaths are short with the margins minutely papillated. There are three pairs of lateral appendages, the first two being conical in shape and having small-branched papillae on the tip. Both tips are pink as is the globular structure on the third pair. The same structure and coloration is presented by the velar appendages. There are five tripinnate branchial leaves, which are very elongate and elevated. The posterior portion of the foot is elongated and thin and has a small keel that is slightly fringed on its upper margin. The posterior end of the foot is flattened laterally.

Radula and Jaws on Buccal Armature: The specimen dissected had a radula formula of $15 \times (12.5.0.5.12)$. Two types of teeth are present. The five inner lateral teeth (Figure 12A–C) are similar in shape, slightly broad and hook-shaped at the apex. The apex is very short, flattened and

almost blunt. The five innermost teeth have a small secondary cusp. The outer lateral teeth (Figure 12A–C), twelve per side, are flat and rectangular in shape. The size of these rectangular teeth decreases from the innermost to the outermost. The rachis has a series of papillated transverse plates, whose size decreases towards the base of the radula. There is an equal number of rachidian plates rows as rows of teeth. The jaws have thin, elongate and flattened rodlets that are densely packed (Figure 12D).

Reproductive System: The reproductive system is triaulic (Figure 13). The vas deferens is differentiated in its proximal portion into a wide penial sheath. On its distal portion the vas deferens becomes half as thick and differentiates into the prostate. The massive prostate is connected to the female gland by a thin and short duct. The vagina is almost as wide as the vas deferens but half as long. From the large and oval bursa copulatrix, emerges a short and thin duct that divides into two ducts, one of which is connected to the receptaculum seminis and the other is connected to the vagina. The uterine duct emerges from the receptaculum duct and connects with the female gland mass near the prostate duct. The ampulla is narrow, convoluted and long and enters into the female gland mass in a position distal relative to the penetration of both the vas deferens and the uterine ducts.

Remarks: Even though Angas (1864) did not give any details of the anatomy *P. imperialis* in the original description, this species has a rather unique external coloration characterized by the presence of the three lateral pink appendages, a yellow-brown background color and the presence of irregular brown dots all over the body. However some differences are found in the color pattern (brown blotches on the lateral appendages apices) and the geographical distribution. In order to be certain that both species are the same, an analysis of the Australian species would be necessary. Anatomical details as a non-enveloped bursa copulatrix (by the prostate) differentiates them from *P. ceylonicus*, *P. tilesii*, *P. maculatus*, where the bursa is totally enveloped by the prostate.

Plocamopherus maculatus (Pease, 1860)
(Figures 1G, 14, 15)

Plocamopherus maculatus (Pease, 1860): 35

Type material: *Plocamopherus maculatus* Pease, was not available. Material examined: CASIZ 116824, three specimens, one dissected. Length (preserved): 19–20 mm. Depth: 10 m West side Pig Island, Madang, Papua New Guinea. 7 February 1988. Collector: T. M. Gosliner. CASIZ 073147, one specimen. Length (preserved): 8 mm. Depth: 20 m. Cement Mixer Reef, Madang, Papua New Guinea. 22 October 1986. Collector: T. M. Gosliner. CASIZ 071152, one specimen. Length (preserved): 15 mm. Depth: 9 m. Pig Island, Madang, Barracuda Point Papua

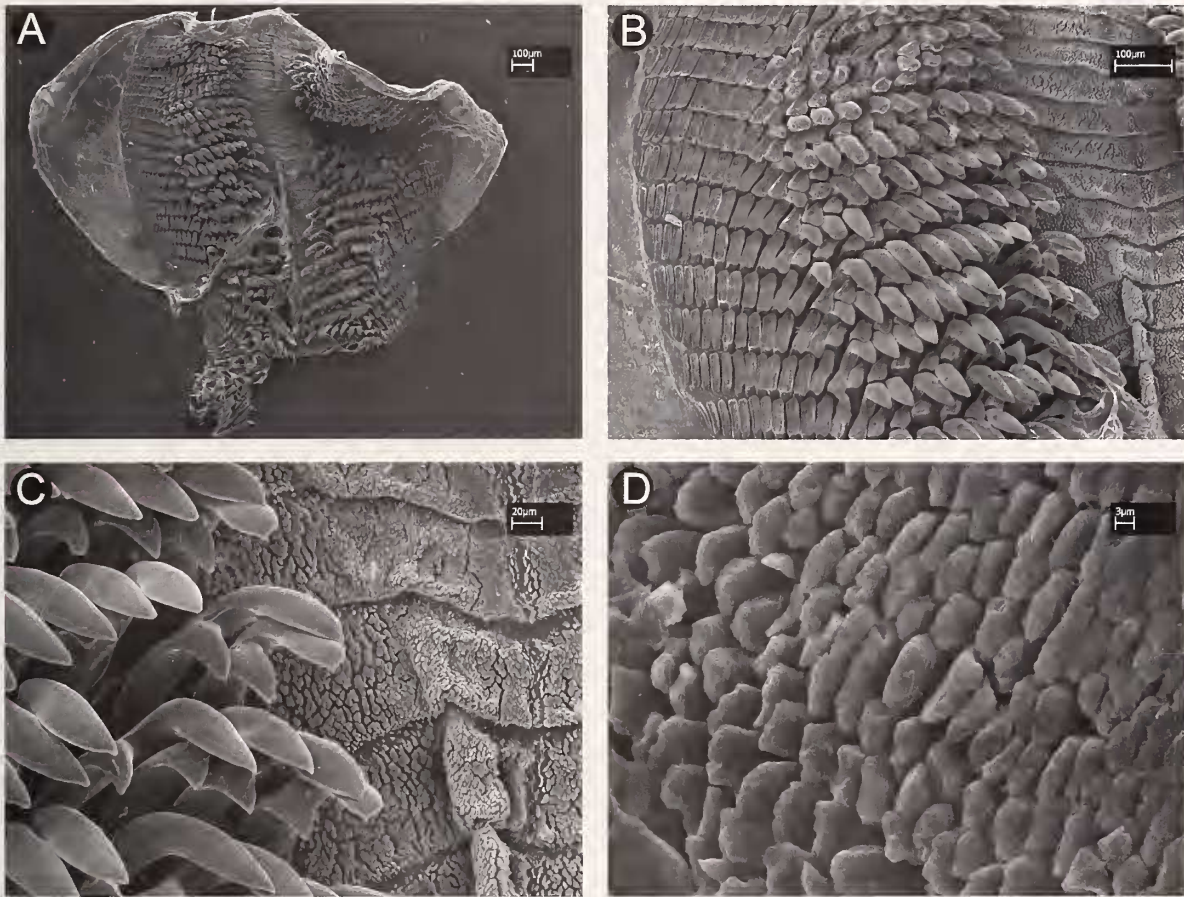


Figure 14. *Plocamopherus maculatus* (CASIZ 116824) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

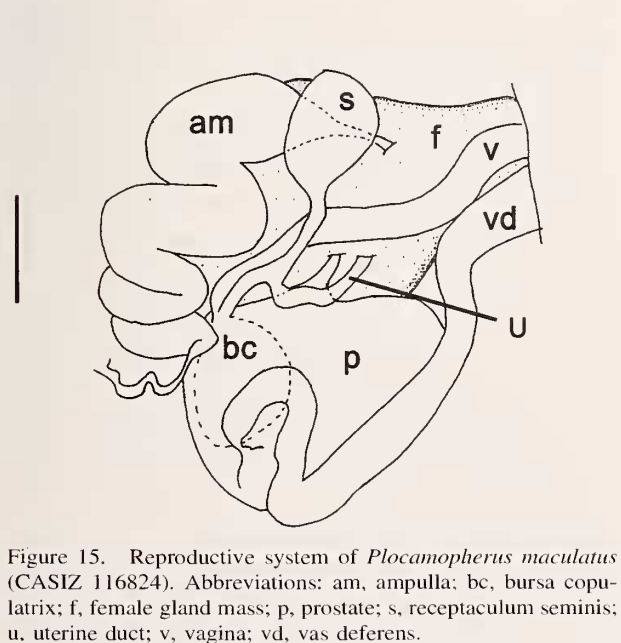


Figure 15. Reproductive system of *Plocamopherus maculatus* (CASIZ 116824). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

New Guinea. 7 February 1988. Collector: T. M. Gosliner. CASIZ 086317, three specimens. Length (preserved): 4–12 mm. Depth: 10 m. South side Rasch Passage, Madang, Papua New Guinea. 16 June 1992. Collector: T. M. Gosliner. South African Museum, Cape Town, A35560, one specimen. Length (preserved): 18 mm. Depth: unknown. K 212. 14 May 1981. Collector: unknown.

Distribution: *Plocamopherus maculatus* has been reported from Hawaii (Kay & Young, 1969), Western Australia (Wells & Bryce, 1993), South Africa (Gosliner, 1987) and is here reported from Papua New Guinea.

External Morphology: In life the body is elongate, limaciform and anteriorly rounded (Figure 1G). The head has a wide flattened and fringed oral veil with numerous papillae. The oral tentacles are flat. *Plocamopherus maculatus* has translucent white background coloration. Typical of the species are the red-orange dots on the dorsum between the rhinophores and in the central part of the dorsum as well as crimson and white pigment surrounding the base of the branchial leaves. The whole body is slightly and regularly speckled with minute brown-orange dots.

The rhinophores are for their entire length translucent white and are speckled with minute crimson dots as is the rest of the body. The rhinophoral sheaths are short. There is only one pair of lateral appendages situated behind the branchial leaves that bears the white globular structure. There are two pairs of slightly ramified conical tubercles at the tip at each side of the body. There are five tripinnate branchial leaves, which are elongate. The posterior portion of the foot is elongate and thin, and has a small keel that is slightly fringed on its upper margin.

Radula and Jaws on Buccal Armature: The specimen dissected had a broad radula with formula of $28 \times (11.11.0.11.11)$. Two types of teeth are present. The eleven inner lateral teeth (Figure 14A–C), similar in shape, are elongate and slightly hook-shaped at the apex. The apex is very elongated, somewhat flattened and fairly sharp. All inner lateral (except for the two outermost) have a well-developed secondary cusp. The outer lateral teeth (Figure 14A, B), eleven per side, are flat and rectangular in shape. The size of these rectangular teeth decreases from the innermost to the outermost. The rachis has a series of papillated transverse plates that are very regular in shape and size through the whole length of the radula. There is an equal number of rachidian plates rows, as rows of teeth. The jaws have thin, elongate and flattened rodlets that are densely packed (Figure 14D).

Reproductive System: The reproductive system is triaulic (Figure 15). The vas deferens is differentiated in its distal portion into a well-developed and glandular-looking prostate. The prostate is connected to the female gland by a thin and short duct. The vagina is almost as wide as the vas deferens in its proximal portion, and connects directly into the bursa copulatrix. The vagina is one-third the length of the vas deferens. From the rounded and small bursa copulatrix, emerges a short and thin duct that divides into two ducts, one of which is connected to the receptaculum seminis and the other penetrates into the female gland mass. Both ducts are of similar length and width. The ampulla is wide, long and convoluted and enters into the female gland mass in a position distal relative to the connection of both the vas deferens and the uterine ducts.

Remarks: Described under the generic name *Histiophorus* (Pease, 1860), it was synonymized with the genus *Plocamopherus* by Bergh (1879b). *Plocamopherus maculatus* was characterized by the whitish background coloration with the orange speckles and the crimson dots at the base of the branchial leaves. The coloration of this species is rather unique among the *Plocamopherus* species. The features exhibited by the radula are also characteristic of the species where the number of innermost and outer lateral is identical (usually the former being more numerous).

Plocamopherus tilesii Bergh, 1877
(Figures 1H, 16, 17)

Plocamopherus tilesii Bergh, 1877:433

Type material: *Plocamopherus tilesii* Bergh, was not found. Material examined: CASIZ 079251, one specimen, dissected. Length (preserved): 32 mm. Depth: 50 m. Seragaki Beach, Ryukyu Islands, Okinawa. 7 July 1991. Collector: R. F. Bolland. CASIZ 97426, one specimen. Length (preserved): 11 mm. Depth: unknown. Oman Arabian Sea: Ra's ad Duqm: tidepool. October–November 1993. Collector: J. L. Earle.

Distribution: Known from Japan, China, Arabian Sea. Also reported occasionally from New South Wales, although no published records (www.seaslugforum.net).

External Morphology: In life its body shape is oval and anteriorly rounded (Figure 1H). The oral veil is wide, flattened and bears numerous short somewhat flattened appendages that vary in length. The presence of flat oral tentacles was observed. *Plocamopherus tilesii* has a translucent, yellowish background color and the whole body is homogeneously speckled with regular black and white spots. There are yellow patches that are irregular in size with distribution over the entire body. Also present are large brownish spots that are fewer in number. The oral veil margin is lined by a yellow coloration, however the oral appendages are black for their entire length. The rhinophores are translucent for their whole length, speckled extensively with brown dots. The rhinophoral sheaths are short and have large, irregular, black spots on the margin. There are three pairs of short lateral appendages, with the last two pairs having a prominent globular structure that is white in color. There are three tripinnate branchial leaves. The posterior portion of the foot is short and flattened forming a keel that has a small crest.

Radula and Jaws on Buccal Armature: The dissected specimen had a radular formula of $18 \times (8.10.0.10.8)$. The radula of *P. tilesii* is characterized by the presence of two different types of teeth (Figure 16A–C). The inner lateral teeth, (Figure 16A–C) similar in shape, are hook-shaped. The primary cusp is elongated and sharp. Only the first three innermost teeth have a well-developed secondary cusp. The base of the innermost lateral teeth becomes less rectangular and more triangular towards the lower teeth rows of the radula. The outer lateral teeth (Figure 16A, C), eight per side, are flat and rectangular in shape. The size of these rectangular teeth decreases from the innermost to the outermost. The papillated rachis has a series of transverse plates that decrease in size towards the base of the radula. The jaws were lost.

Reproductive System: The reproductive system is triaulic (Figure 17). The vas deferens is differentiated in its distal portion into a well-developed and glandular looking pros-

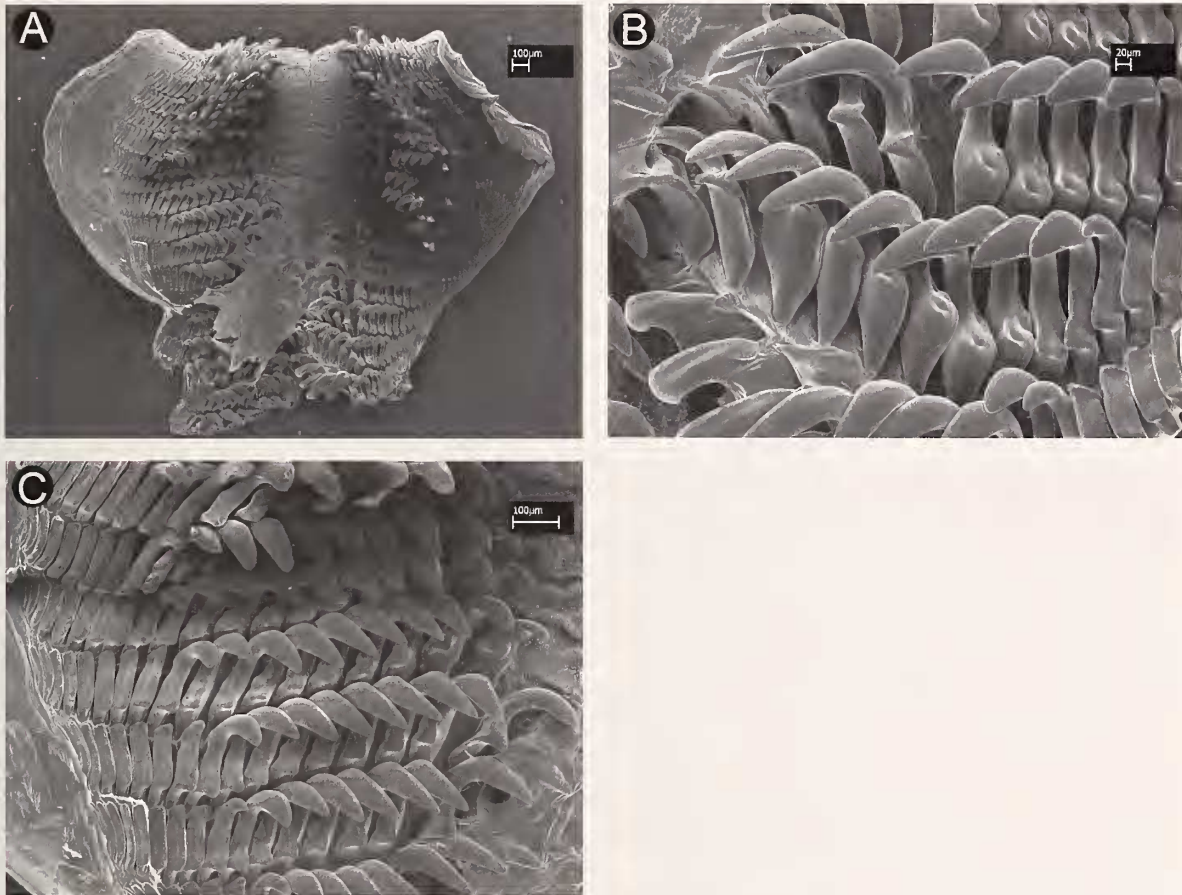


Figure 16. *Plocamopherus tilesii* (CASIZ 079251) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth.

tate that envelops the whole bursa copulatrix. The prostate is connected to the female gland by a very short and thin duct. The vagina is as half as wide as the vas deferens but is almost the same length. From the rounded bursa copulatrix, emerges a short duct that divides into two ducts, one, which is connected to the vagina and the other to the receptaculum seminis. This second duct before entering into the receptaculum seminis splits again into the uterine duct that penetrates the female gland mass. The ampulla is very elongate and convoluted and enters the female gland mass in a position distal relative to the penetration of both the vas deferens and the uterine ducts.

Remarks: According to the original description (Bergh, 1877) this species has a light brown-gray background color speckled with dark purple and yellow spots all over the body. The yellow spots are larger and may be found at the margins of the mantle. Characteristic of the species is the black color present on the appendages of the oral veil whereas its margin is lined with yellow. The radula of *P. tilesii*, as in *P. maculatus*, has more innermost teeth than typically found in other species of *Plocamopherus*.

Plocamopherus maculapodium n. sp.
(Figures 11, 18, 19)

Type and examined material: Holotype, CASIZ 099307, one specimen. Length (preserved): 25 mm. Depth: unknown. Ras Nungwi, Zanzibar, Tanzania. 6 November 1994. Collector: Don Pisor. Paratypes: CASIZ 070421, one specimen, dissected. Length (preserved): 13 mm. Depth: 3–6 m. Cement Mixer Reef, Madang, Papua New Guinea. 11 January 1988. Collector: T. M. Gosliner. CASIZ 073403, one specimen. Length (preserved): 11 mm. Depth: 33 m. Cement Mixer Reef, Madang, Papua New Guinea. 22 October 1986. Collector: T. M. Gosliner.

Distribution: This new species has been collected from Papua New Guinea and Zanzibar, Tanzania.

External Morphology: In life the body shape is elongate, limaciform and anteriorly rounded (Figure 11). The head bears a fringed oral veil without distinct appendages. The presence of flat oral tentacles was observed. *Plocamopherus maculapodium* has a red background color and the

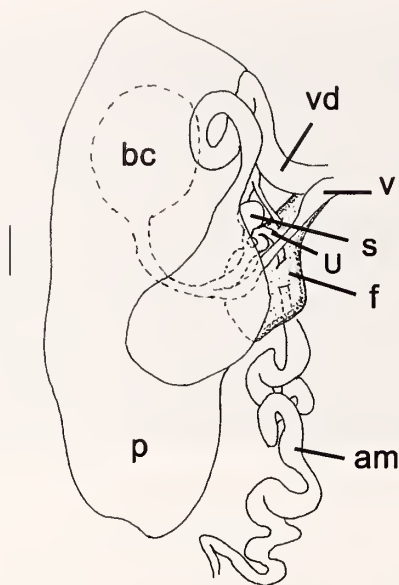


Figure 17. Reproductive system of *Plocamopherus tilesii* (CASIZ 079251). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

notum is slightly speckled with minute white dots. The white dots are usually situated on the notum along a line at the margin of both sides of the animal and joining behind the branchial leaves. They are also present along the margin of the fringed oral veil, on the tip of the posterior portion of the foot, tips of branchiae, clavus of the rhinophores, dorsal tubercles and oral veil appendages. There are a few black larger spots on the sides of the animal at the base of the foot. The rhinophores are elongate and at the peduncle have the same red background coloration. However, the clavus is red-brown with a white spot at the tip. The rhinophoral sheath is short. There are three pairs of short lateral appendages, with the last pair having a prominent rounded globular structure that is white in color. All lateral appendages are slightly ramified and whitish at the tip. At both sides of the body, four small tubercles are found in both sides situated at a regular distance from each other. There are three tripinnate branchial leaves. The posterior portion of the foot is elongated and thin forming a keel that has a small crest tipped with white. The specimens examined were 11–25 mm long after being preserved.

Radula and Jaws on Buccal Armature: The specimen dissected had a radular formula of $14 \times (7.3.0.3.7)$. The radula of *P. maculapodium* is characterized by the presence of two different types of teeth (Figure 18A–C). The inner lateral teeth, (Figure 18A, B) similar in shape, are broad and curve towards the rachis. There are three of them and the innermost tooth has a well-developed secondary cusp. These hook-shaped teeth are blunt at the

apex, not sharp. There are seven outer lateral teeth per side, (Figure 18A, C) which are flat and rectangular in shape. The size of these rectangular teeth diminishes from the innermost to the outermost. The papillated rachis has a series of transverse plates that decrease in size towards the base of the radula. The jaw rodlets are thin, elongate, flattened and densely packed (Figure 18D).

Reproductive System: The reproductive system is triallic (Figure 19). The vas deferens is differentiated in its distal portion into a well-developed and glandular-looking prostate that envelops the whole bursa copulatrix. The prostate is connected to the female gland by a very short and thin duct. The vagina is as wide as the vas deferens but half its length. From the oval bursa copulatrix merges a short duct that divides into two ducts, one that is connected to the vagina and the other to the receptaculum seminis. This second duct before entering into the receptaculum seminis splits into the uterine duct that penetrates the female gland mass. The ampulla is very short and enters into the female gland mass in a position distal relative to the penetration of both the vas deferens and the uterine ducts.

Remarks: The most similar species in their external morphology to *P. maculapodium* are *P. lucayensis* and *P. pilatecta*. All three have red background coloration and are speckled with white small dots. However several characteristics distinguish them. First, in both *P. maculapodium* and *P. pilatecta* the white dots are situated at the margins of the body, along a line joining behind the branchial leaves whereas in *P. lucayensis* they are scarce and regularly distributed over the whole notum (Hamann & Farmer, 1988). These white dots are also present in *P. maculapodium* and *P. pilatecta* along the margin of the fringed oral veil on the margin of the keel, tips of branchiae, clavus of the rhinophores, dorsal tubercles and oral veil appendages as opposed to in *P. lucayensis*. Radular differences are found in the inner lateral teeth, where the curved portion of the teeth is much longer and wider in *P. maculapodium* than in *P. pilatecta*. Externally, *P. maculapodium* and *P. pilatecta* differ by the presence in the former of three lateral appendages whereas the latter has only one. The reproductive system of *P. maculapodium* differs from that of *P. pilatecta* by the presence of a convoluted prostate that totally envelops the bursa copulatrix, as opposed to the naked bursa copulatrix in *P. pilatecta* and by the shape of the vagina which is flat in *P. pilatecta*.

Etymology: This species is named *maculapodium* referring to the black spots present on the sides of the foot.

Plocamopherus pecoso n. sp.
(Figures 1J, 19, 20)

Type and examined material: Holotype, CASIZ 110378, one specimen. Length (preserved): 20 mm.

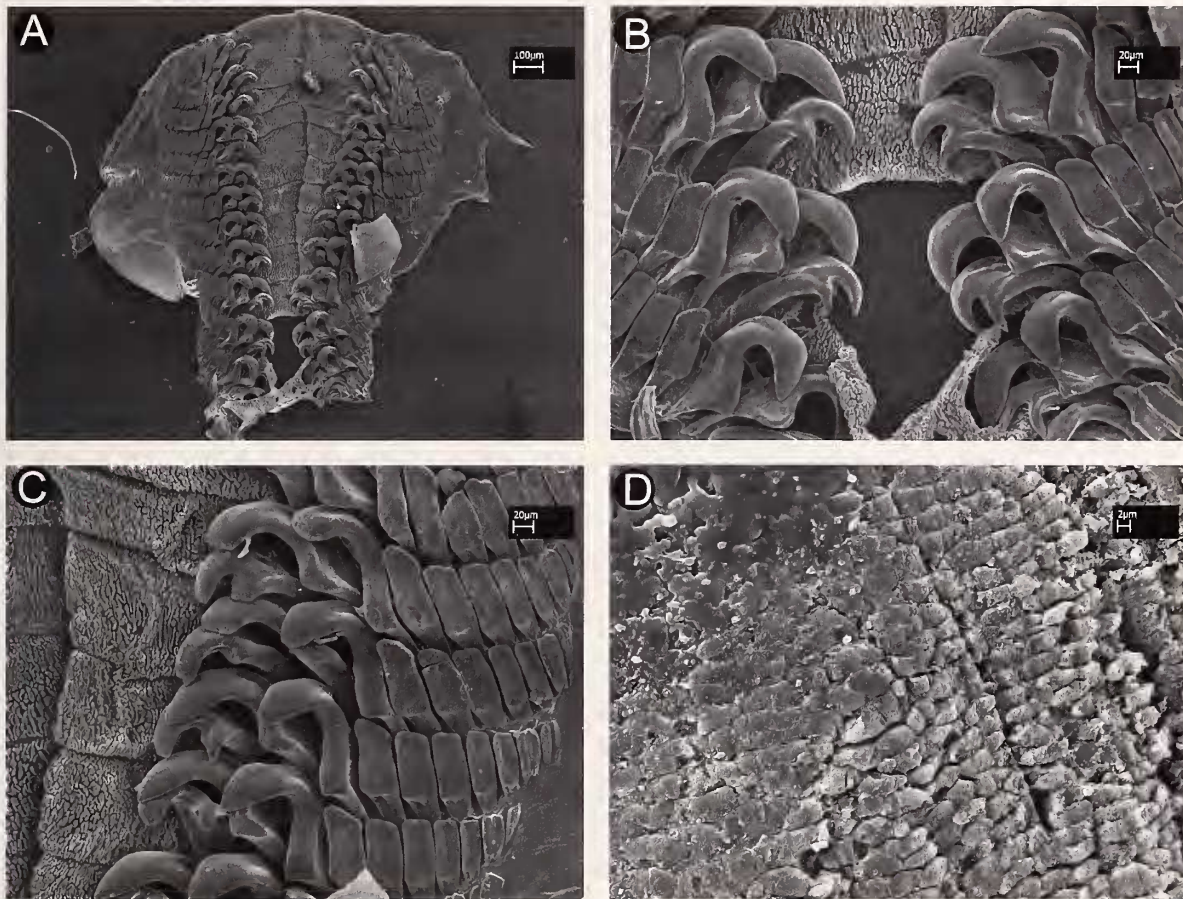


Figure 18. *Plocamopherus maculapodium* (CASIZ 070421) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

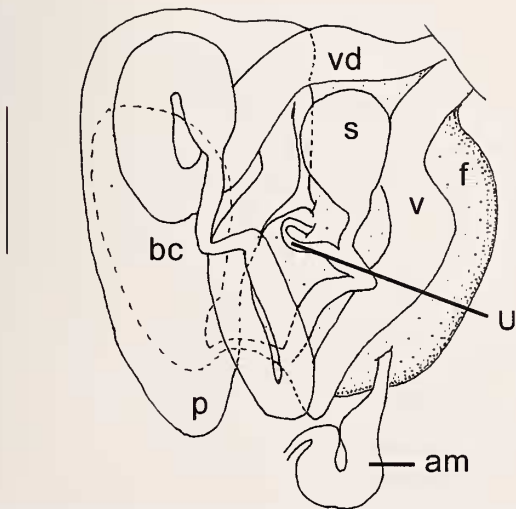


Figure 19. Reproductive system of *Plocamopherus maculapodium* (CASIZ 070421). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

Depth: unknown. Caban Island, Batangas, Luzon, Philippines. 21 April 1997. Collector: T. M. Gosliner. Paratypes: CASIZ 106548, one specimen, dissected. Length (preserved): 19 mm. Depth: 0–10 m. Polonpoli, Marican Island, Batangas, Luzon, Philippines. 19 April 1996. Collector: T. M. Gosliner. CASIZ 083738, one specimen. Length (preserved): 8 mm. Depth: unknown. Balayan Bay, Batangas, Luzon Island, Philippines. 19 February 1992. Collector: T. M. Gosliner. CASIZ 097401, one specimen. Length (preserved): 4 mm. Depth: 31 m. Balayan Bay, Batangas, Luzon Island, Philippines. 15 March 1994. Collector: T. M. Gosliner. CASIZ 088077, one specimen. Length (preserved): 11 mm. Depth: 10 m. Bus Stop Reef, Balayan Bay, Batangas, Luzon Island, Philippines. 24 March 1993. Collector: T. M. Gosliner.

Distribution: This species has been collected only in the Philippines.

External Morphology: In life its body shape is elongate, limaciform and anteriorly rounded (Figure 1J). The head bears a fringed oral veil with eight short, small and ramified appendages. The oral tentacles are flat. *Plocamo-*

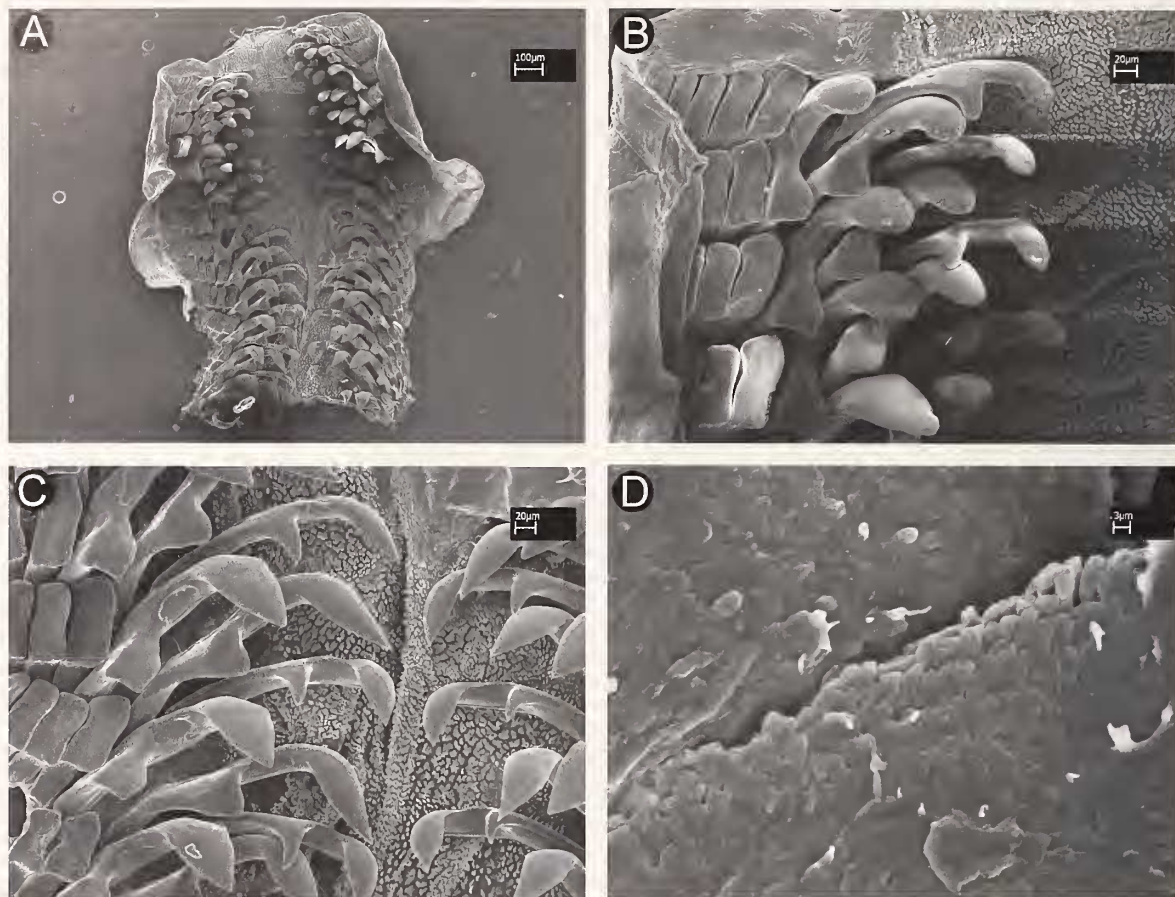


Figure 20. *Plocamopherus pecosus* (CASIZ 106548) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

pherus pecosus has a transparent white background color heavily speckled all over the body with small orange dots. These orange dots become much larger and fewer at the base of the foot. The presence of minute brown dots surrounding the lateral appendages base and along the keel was observed (these brown dots are present all over the body in other specimens of this species). There are some white dots that are usually situated on the notum along a non-continuous line at the margin of both sides of the animal and joining behind the branchial gills. They are also present along the margin of the fringed oral veil on the tip of the tail, tips of branchiae, clavus of the rhinophores, dorsal tubercles and oral veil appendages but they are slightly larger and scarce. The long rhinophores are translucent and speckled with brown at the peduncle and clavus. A white spot is present at the tip of the clavus. The rhinophoral sheath is long. There are three pairs of short lateral appendages; the two posterior pairs have a prominent, brown, rounded globular structure. Usually the posterior most pair has the larger globular structure, although exceptions have been observed. All lateral ap-

pendages are slightly ramified and whitish at the tip. There are three principal tripinnate branchial leaves, which do not form a complete circle around the anus. The posterior portion of the foot forms a well-developed keel that has a small crest tipped with white.

Radula and Jaws on Buccal Armature: The specimen dissected had a radular formula of $14 \times (6.3.0.3.6)$. The radula of *P. pecosus* is characterized by the presence of two different types of teeth (Figure 20A–C). The inner lateral teeth, (Figure 20A, B) similar in shape, are thin, elongated and hook-shaped. There are three of them and the innermost tooth has a well-developed secondary cusp while in the other two it is prominent but somewhat less pronounced. These hook-shaped teeth are acute apically. The outer lateral teeth (Figure 20A, C), six per side, are flat and rectangular in shape. The size of these rectangular teeth decreases from the innermost to the outermost. The papillated rachis has a series of transverse plates that are regular in size along the whole length of the radula. The jaw rodlets are thin, elongate, flattened and densely packed (Figure 20D).

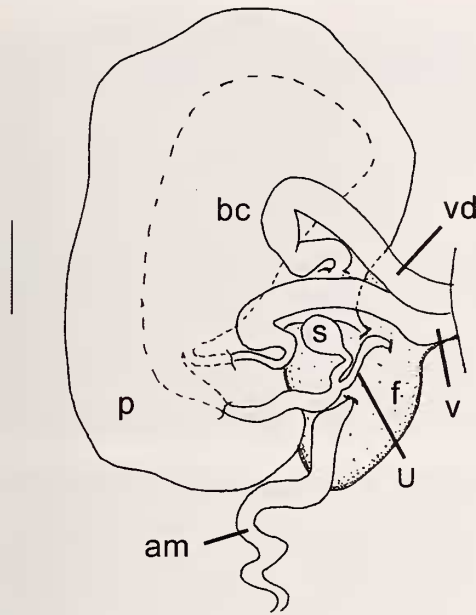


Figure 21. Reproductive system of *Plocamopherus pecoso* (CASIZ 106548). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

Reproductive System: The reproductive system is triallic (Figure 21). The vas deferens is differentiated in its distal portion into a well-developed and glandular-looking prostate. The prostate is connected to the female gland by a short duct. The vagina, although almost as wide as the vas deferens in its proximal portion, becomes half as wide at its distal part and penetrates directly into the bursa copulatrix. The vagina is as long as the vas deferens. The bursa copulatrix is totally enveloped by the massive prostate. From the oval bursa copulatrix, emerges a somewhat flattened duct that divides into two ducts, one which is connected to the receptaculum seminis and the other (the uterine duct) that penetrates into the female gland mass. Both ducts are of similar length and width. The ampulla is thin and elongated and enters into the female gland mass in a position distal relative to the entrance of both the vas deferens and the uterine ducts.

Remarks: The most similar species to *Plocamopherus pecoso* are *P. ceylonicus* and *P. maderae*. Even though all of them are mottled with orange dots, *Plocamopherus pecoso* has a background color of translucent brown as opposed to the pale dull red of *P. maderae*. *Plocamopherus pecoso* does not have the brown pattern typical of *P. ceylonicus* nor the white pattern along margin edge of the body sides (Kelaart, 1858). The orange dots are slightly larger in *Plocamopherus pecoso* with smaller and more numerous ones in *P. maderae* and yellowish in *P. ceylonicus*. No white dots are present on *P. maderae*. *Plocamopherus pecoso* has two pairs of lateral appendages

with the globular structure whereas only one is found in *P. maderae*. Differences are found in the radula as well. In *Plocamopherus pecoso* the innermost teeth have a long and acutely pointed cusp, in *P. maderae* the innermost cusp is elongated wide and slightly blunt.

Etymology: This species is named *pecoso* due to the presence of dots over its entire body appearing as freckles. In Spanish the word *pecoso* means to have a lot of freckles.

Plocamopherus lemur n. sp.
(Figures 1K, 22, 23)

Type and examined material: Holotype, CASIZ 146056, one specimen. Length (preserved): 9 mm. Depth: unknown. Les Cocotiers Hotel, Ile Ste. Marie, Madagascar. 17 April 1989. Collector: T. M. Gosliner. Paratype: CASIZ 074152, one specimen. Length (preserved): 12 mm. Depth: unknown. patch reef, Grand Passe, Aldabra Island, Seychelles. 21 March 1986. Collector: T. M. Gosliner. CASIZ 146058, one specimen, dissected. Length (preserved): 9 mm. Depth: unknown. North side, Andilana Beach, Madagascar. 15 April 1989. Collector: T. M. Gosliner. CASIZ 146062, one specimen. Length (preserved): 10 mm. Nosy Komba, Madagascar. 16 April 1989. Collector: T. M. Gosliner.

Distribution: This species has been collected from both East and West coasts of Madagascar and the Seychelles.

External Morphology: The body shape is elongate, limaciform and anteriorly rounded (Figure 1K). The oral veil has 18 ramified appendages that differ in length. The oral tentacles are flat. *Plocamopherus lemur* has a brownish background color heavily speckled all over the body with minute brown dots, and minute orange dots that are clustered to form orange patches. White pigment is present in front of the branchial leaves, around the lateral appendages, at the base of the rhinophores and along the crest. This white coloration is situated on the notum along a non-continuous line at the margin of both sides of the animal and joining behind the branchial leaves. White pigment is also present along the margin of the sides of the body, the oral veil, tips of branchiae and clavus of the rhinophores. At the peduncle, the rhinophores are translucent and the clavus is translucent with a white apex. The rhinophoral sheath is short with clusters of orange dots. There are three pairs of lateral appendages, with only the last pair forming a rounded, brown, and prominent globular structure. All lateral appendages are conical having a short but highly ramified prolongation at the apex. The first two lateral appendages are very short and the last pair is very elongate. Six to eight small tubercles are present at each side of the animal. There are three principal tripinnate branchial leaves. The posterior

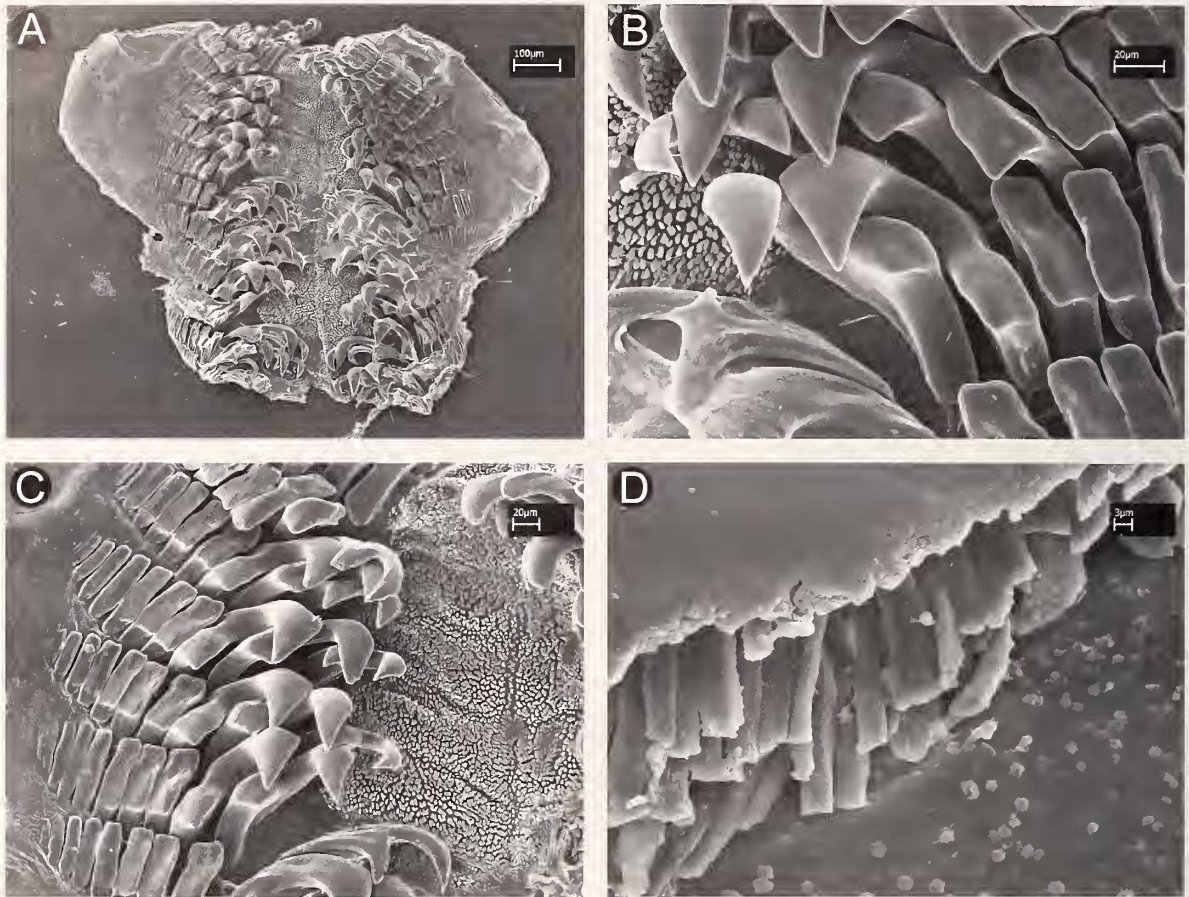


Figure 22. *Plocamopherus lemur* (CASIZ 146056) SEM photographs of the radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

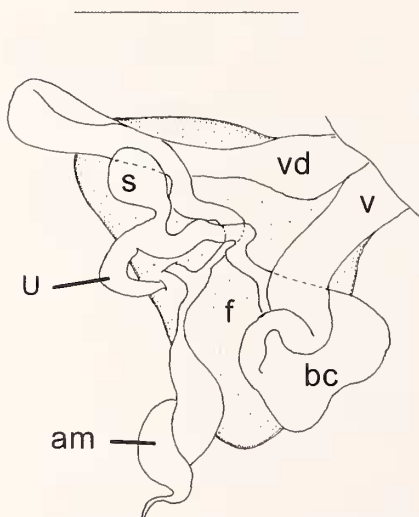


Figure 23. Reproductive system of *Plocamopherus lemur* (CASIZ 146056). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

portion of the foot forms a well-developed but short keel that is fringed on its upper margin.

Radula and Jaws on Buccal Armature: The specimen dissected had a radular formula of $13 \times (6-7.3.0.3.6-7)$. The radula of *P. lemur* is characterized by the presence of two different types of teeth (Figure 22A-C). The inner lateral teeth (Figure 22A, B), similar in shape, are thin, elongate and hook-shaped. There are three of them and only the innermost tooth has a well-developed secondary cusp. These hook-shaped teeth have an acute apex. The outer lateral teeth (Figure 22A, C), six to seven per side, are flat and rectangular in shape. The size of these rectangular teeth decreases from the innermost to the outermost. The papillated rachis has a series of wide transverse plates that are regular in size along the whole length of the radula. The jaws have rodlets that are thin, elongate, flattened and densely packed (Figure 22D).

Reproductive System: The reproductive system is triaulic (Figure 23). The vas deferens is not differentiated into a prostate. The vagina is as wide as the vas deferens and penetrates directly into the bursa copulatrix. The vagina

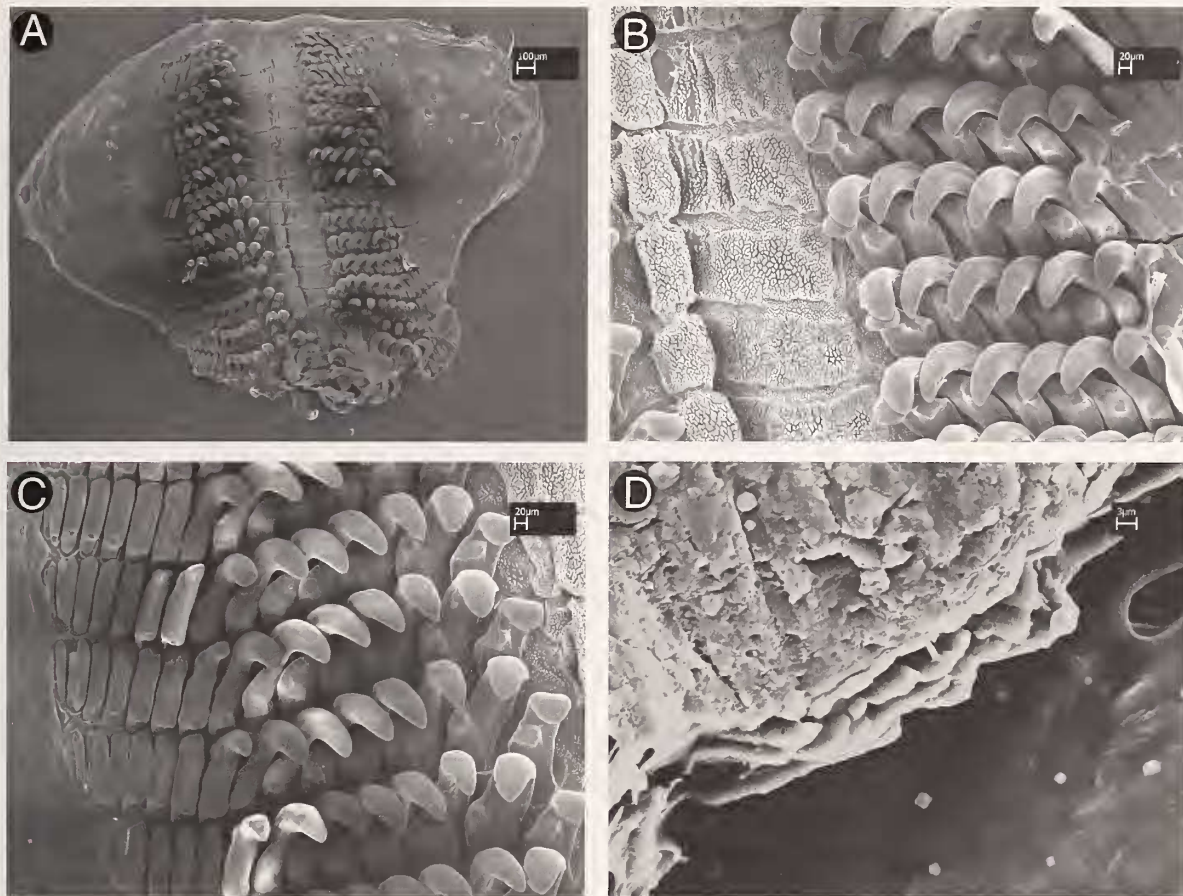


Figure 24. *Plocamopherus margaretae* (CASIZ 162208) SEM photographs of radula and jaws. A. Whole radula. B. Inner lateral teeth. C. Outer lateral teeth. D. Jaws.

is half as long as the vas deferens. From the oval bursa copulatrix, emerges a wide duct that splits into two ducts, one of which is connected to the small oval receptaculum seminis, and the other (the uterine duct) that penetrates into the female gland mass. The ampulla, is externally connected to the vas deferens entering into the female gland mass in a position proximal relative to the penetration of the uterine duct.

Remarks: *Plocamopherus lemur* resembles *P. ceylonicus* and *P. pecosus*. All three species have a brownish translucent background color with orange and brown dots on the notum. However, in *P. lemur* these dots are not distributed regularly, but in patches. No branched papillae or yellow coloration are present on the notum of *P. lemur*, which are characteristic of *P. ceylonicus*. Only the last pair of lateral appendages, which is extremely long in *P. lemur*, has the globular structures while both *P. pecosus* and *P. ceylonicus* have two pairs of globular structures. In both *Plocamopherus pecosus* and *P. ceylonicus* the prostate envelops the bursa copulatrix, while the prostate

is not a discrete structure leaving the bursa copulatrix exposed in *P. lemur*.

Etymology: This species is named lemur owing to similarity of coloration with the cryptic primates that are characteristic of its type locality, Madagascar.

Plocamopherus margaretae n. sp.
(Figures 1L, 24, 25)

Type and examined material: Holotype, CASIZ 162208, one specimen. Length (preserved): 35 mm. Depth: unknown. Myanmar. Collector: Mark Strickland. Paratype: CASIZ 162207, one specimen, dissected. Length (preserved): 40 mm. Depth: unknown. Dubai, United Arab, Emirates. Collector: C. Harris.

Distribution: This new species has been collected in Dubai and Myanmar.

External Morphology: In life, its body shape is elongate and anteriorly rounded (Figure 1L). The oral veil is wide,

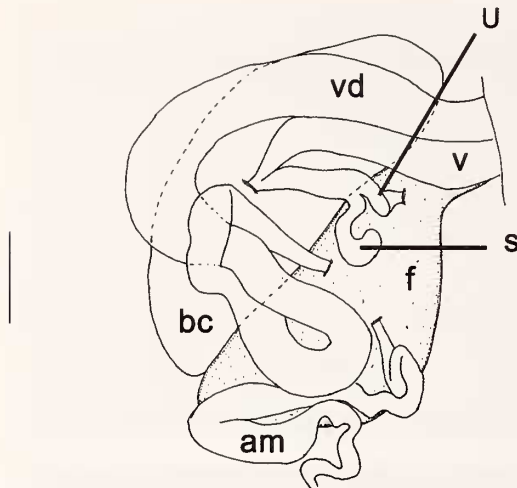


Figure 25. Reproductive system of *Plocamopherus margaretae* (CASIZ 162208). Abbreviations: am, ampulla; bc, bursa copulatrix; f, female gland mass; p, prostate; s, receptaculum seminis; u, uterine duct; v, vagina; vd, vas deferens.

flattened and fringed. The oral tentacles are flat. *Plocamopherus margaretae* has a pink or red background color heavily speckled all over the body with large white spots and black, almost oval spots. The white spots are of various sizes and are regularly scattered on the notum. The black spots appear always surrounded by white, and are much fewer than the white spots. A yellow-orange line runs along the margin of the foot, the margin of the oral veil and the margin of the keel. The rhinophores are yellow-pink for their whole length. At the tip of the clavus there is a short white line. The rhinophoral sheath is the same background color as the body and is short with its margin lined by white and yellow pigment. There are three pairs of lateral appendages, which are rounded and form prominent globular structures. These globular structures are much larger in the posterior most pair of appendages. The anterior pairs are very short and rounded. All are pink-yellowish in color. There are three tripinnate branchial leaves that each insert separately into the dorsum. The posterior portion of the foot forms a well-developed elongated keel that is slightly fringed in its upper margin.

Radula and Jaws on Buccal Armature: The specimen dissected had a radula formula of $16 \times (7.7.0.7.7)$. The radula of *P. margaretae* is characterized by the presence of two different types of teeth (Figure 24A–C). The inner lateral teeth, (Figure 24A, B) similar in shape, are wide and hook-shaped with a blunt apex. There are seven of them and the three innermost teeth have a well-developed secondary blunt cusp while in the other four is less pronounced. The outer lateral teeth (Figure 24A, C), seven per side, are flat and rectangular in shape. The size of these rectangular teeth diminishes from the innermost to

the outermost. The papillated rachis has a series of transverse plates that are regular in size along the whole length of the radula. The jaws have rodlets that are thin, elongate, flattened and densely packed (Figure 24D).

Reproductive System: The reproductive system is triaulic (Figure 25). The vas deferens is not differentiated into a prostate. The vagina, although almost as wide as the vas deferens, is a third of its length. The bursa copulatrix is large and oval, from which, emerges a duct that divides immediately into two ducts, one of which connects to the vagina and the other connects to the receptaculum seminis. From the latter also emerges the uterine duct that penetrates the female gland mass. The ampulla is thin convoluted and elongated entering into the female gland mass in a position proximal relative to the penetration of both the vas deferens and the uterine ducts.

Remarks: The most similar species to *P. margaretae* is *P. tilesii*. However the differences between both are obvious. While *P. margaretae* has pink-red background coloration, *P. tilesii* is whitish or yellowish. Both have black dots all over the notum, however they are more regularly distributed and scarcer in *P. margaretae* than in *P. tilesii*. Another external characteristic that differentiates both species is the number of lateral appendages and globular structures that are present, with three pairs in *P. margaretae* and two in *P. tilesii*. Even though the number of teeth may be somewhat variable, in *P. tilesii*, the number of innermost teeth exceeds the number of outer lateral teeth, whereas in *P. margaretae* the outermost are more numerous than the inner lateral. In *Plocamopherus margaretae* the prostate is not differentiated and therefore the bursa copulatrix is exposed whereas in *P. tilesii* the prostate is massive and totally enveloping the bursa copulatrix.

Etymology: This species is named for Carol Harris' mother. Carol collected the first specimens of this species.

CONCLUSION

The ability of living organisms to produce light has multiple functions depending on the organism. Fishes, like the Malacosteidae, produce red light to see their prey without alerting either prey or other possible predators (O'Day & Fernandez, 1974). Several beetles use light to communicate with their potential mates (Day et al., 2004), etc. In mollusks, light production has already been studied within cephalopods (Young, 1977; Johnsen et al., 1999). In dorids, bioluminescence has only been reported from the two genera *Kaloplocamus* and *Plocamopherus*. Both genera are phanerobranchs (having non-retractable branchial leaves) and have taxonomically been included in the same subfamily Triophinae. Both genera are almost exclusively Atlantic and Indo-Pacific and share several morphological and anatomical features: six to eight lateral processes, presence of a large rachis in the radula, similar

outer and inner lateral teeth and the ability (of several species) to emit light among others.

We have revised the taxonomy of both genera. As a result, we considered that there are six valid species for the genus *Kaloplocamus* (*K. pacificus*, *K. ramosus*, *K. acutus*, *K. maru*, *K. peludo* and *K. dokte*). However we believe that a comprehensive study of all *K. ramosus* specimens, of their external and internal morphology is necessary as well as a molecular phylogenetic analysis, allowing us to understand the distribution patterns shown by this spectacular species. Within the genus *Plocamopherus* we suggest that the valid species are the following: *P. ocellatus*, *P. maderae*, *P. maculatus*, *P. ceylonicus*, *P. imperialis*, *P. tilesii*, *P. lucayensis*, *P. pilatecta*, *P. pecosus*, *P. maculapodium*, *P. lemur* and *P. margaretae*.

Interestingly not all species of both genera have been reported to be bioluminescent. Whether they are bioluminescent or not remains to be observed both in the wild and by TEM studies of the body wall and the globular structure tissues of both genera. It is important to note that it may not have been observed in the wild because although a stimulation provokes the animal into swimming and emitting light, when the animal is stressed or receives a continuous mechanical stimulation it stops emitting light, suggesting that there is some kind of product that it stores, that is used for the light emission and therefore its availability is limited (Wilbur & Yonge, 1966). It is possible that since these animals emit light only when disturbed and for a short span of time, the role could be to temporally distract the attention of potential predators (Wilbur & Yonge, 1966).

In order to better understand the evolution of bioluminescence within these dorids a phylogenetic analysis based on morphological and molecular data comprising all genera pertaining to the subfamily Triophinae must be done. If *Kaloplocamus* and *Plocamopherus* were sister taxa, a plausible explanation could be that bioluminescence evolved just once. However, the information available regarding the light production in such organisms is very limited. Even though Wilbur and Yonge (1966) established the different type of light emitting systems, there was no description of the cellular tissue of the mantle (also capable of emitting light) of *Plocamopherus* species. Wilbur and Yonge stated that the light from the globular processes is much more intense than that of the rest of the body wall, which raises the question whether it is, or not, the same type of cells that produce the light in the body wall and the globular structure.

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