PSEUDOCEROS AND *PSEUDOBICEROS* (PLATYHELMINTHES, POLYCLADIDA, PSEUDOCEROTIDAE) FROM EASTERN AUSTRALIA AND PAPUA NEW GUINEA

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Newman L.J. & Cannon L.R.G. 1994 12 01: *Pseudoceros* and *Pseudobiceros* (Platyhelminthes, Polycladida) from eastern Australia and Papua New Guinea. *Memoirs of the Queensland Museum* 37(1): 205-266. ISSN 0079 - 8835.

The large tropical polyclad genus *Pseudoceros* Lang, 1884 is reviewed and of the over 150 species recognised by Faubel (1984) and Prudhoe (1985, 1989) only 26 are considered members of *Pseudoceros* sensu stricto. *Pseudobiceros* Faubel, 1984 is upheld and 14 species are recognised. For the Great Barrier Reef and eastern Papua New Guinea, 23 *Pseudoceros* (17 new species) and 11 *Pseudobiceros* (8 new species) have been found. Collectively these polyclads are not uncommon on coral reefs and feed mainly on colonial ascidians. Observations on feeding and copulatory behaviour, and larval development are given.The simple hypodermic insemination observed in these animals supports anatomical analyses that clearly demonstrates intraspecific homogeneity of the reproductive structures within species of a genus. Genera may be determined on gross morphology of the pseudotentacles, eyes, pharynx and number of male pores. Specific determinations rely primarily on colour pattern, as suggested by Hyman (1954, 1959a) and Prudhoe (1985). □ *Polycladida, Cotylea, Pseudocerotidae, Pseudoceros, Pseudobiceros, flatworm, taxonomy.*

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Large, flamboyantly coloured flatworms have been known from tropical seas, and especially from coral reefs for nearly 150 years (Prudhoe, 1985); most have been assigned to *Pseudoceros* Lang, 1884 (Polycladida). These species have been recorded from few specimens, often only a single one, and sometimes only from coloured paintings (Schmarda, 1859; Lang, 1884; von Graff, 1893; Stummer-Traunfels, 1933). More often than not, type specimens have not been designated and specimens have rarely been deposited in museums. A serious contributing factor to their poor representation in collections is the ability of these worms to self-destruct under stress. Before fixation is complete, worms often autolyse, breaking into mucous fragments, or contract and contort making examination impossible; and most invariably have lost their colour and pattern.

Despite this, Marcus (1950) and Hyman (1954, 1959a) listed over 100 species of *Pseudoceros* distinguished primarily on colour and pattern. Although details of the reproductive anatomy are the most widely used characters for classifying turbellarian flatworms (Cannon, 1986) only about 25 worms assigned to *Pseudoceros* have been investigated in this way. Both Hyman (1954, 1959A) and Prudhoe (1985, 1989) maintained that within *Pseudoceros* only colour pattern is required to distinguish species, so lack of reproductive details has not been considered an impediment to the erection of new species.

A contrary view was proposed by Faubel (1984) who based his classification of the polyclads largely on anatomical characters, mainly of the male reproductive system. Faubel erected several new genera to accommodate *Pseudoceros* sensu lato and these are distinguished on details of the male reproductive system. Prudhoe (1985, 1989) disagreed believing, for example, that the number of male complexes (one or two) could vary within species. He was influenced largely by the view of Lang (1884) that *P. maximus* was found in the Bay of Naples with three variations: either one or two separate male complexes or two male complexes opening into one antrum.

No comprehensive taxonomic account of free-living marine flatworms from Australian waters exists. Polyclads have not received attention although they are conspicuous reef inhabitants (Hyman, 1954; 1959a; Prudhoe, 1985; 1989; Newman & Cannon, 1994); are symbionts and pests of a variety of reef invertebrates (Prudhoe, 1985), including giant clams (Newman et al., 1993) and soft corals (Cannon, 1990); and are mimics of toxic nudibranchs (Newman et al., 1994). Less than 20 studies have considered Australian polyclads, several are popular or deal with them as pests (Stead, 1907) or potential parasite vectors (Anderson et al., 1993) and only

seven taxonomic papers have been published since 1898 (Woodworth, 1898; Haswell, 1907; Hyman, 1959b; Prudhoe, 1977; 1982; Cannon, 1990; Newman et al., 1994). Of the 16 nominal species recorded from the GBR only three have been described as new in that time (Cannon & Newman, 1993).

This study set out to examine the tropical '*Pseudoceros*' fauna from the Great Barrier Reef (GBR) and eastern Papua New Guinea (PNG). We wanted to ascertain the relative merits of the proposals of Faubel (1984) and Prudhoe (1985) for the determination of genera and species within *Pseudoceros* sensu lato by making use of observations of live animals, in situ photography and examination of new taxonomic characters. We were significantly assisted by the development of a new fixative regime (Newman & Cannon, in press) which produces consistently well fixed, flat specimens with minium loss of colour pattern.

METHODS

Animals were either hand collected from under coral boulders at the reef crest or under ledges on the reef slope by SCUBA from Heron Island (23° 27' S, 151°55' E) and One Tree Island (23°30' S, 152°05' E) southern GBR and Madang (5°14' S, 145°45' E) and Laing Island (4°16' S, 144°56' E), eastern Papua New Guinea. Unless otherwise stated all animals were collected during the day and photographed by L.J. Newman and A.E. Flowers. Flatworms were kept in separate containers and brought back to the laboratory live, and retained in 1 litre plastic ice cream containers (non-aerated to avoid physical damaged to these delicate worms from the bubbles). Photographs were taken either in situ using Nikonos III & V cameras, extension tubes and underwater strobes, or in the laboratory using Nikon F4 and Canon T70 & T90 with 50 & 105mm macro lenses, extension tubes and TTL flashes.

Full details of specimen fixation and preparation are given by Newman & Cannon (in press). In brief, polyclads were fixed by coaxing them onto filter paper which was then transferred to frozen fixative (formaldehyde, calcium acetate - propylene glycol, propylene phenoxytol). After fixation for 12 to 24 hours, specimens were preserved in 70% ethanol for histological preparation. Whole mounts were prepared by first staining with Mayer's Haemalum, then dehydrating in graded alcohols and mounting in canada balsam. Longitudinal serial sections of the reproductive region were prepared by embedding excised tissue in Paraplast (56°C), sectioning at 5 - 7µm, and staining with haematoxylin and eosin. Only mature animals were prepared for serial sections and wholemounts, when possible.

Drawings and measurements were made with the aid of a camera lucida by L.J. Newman. Measurements given in descriptions are from type specimens. These provide a guide to relative size of animals but because of the plasticity of form, differences in specimen size cannot be considered absolute. Body measurements are expressed in mm (length x width) and were taken from live animals in a relaxed state. Abundance data are expressed as the number of animals collected: R = rare, 1 - 5 animals; C = common, 6 - 20 animals; A = abundant, > 21 animals. Presentations of the reproductive anatomy derived from sections are given with minimal interpretation and, as far as practical, are taken directly from single sections. Only one side of the reproductive apparatus was drawn for *Pseudobiceros*.

Descriptions of colour patterns are based on living animals. Colours and colour number in parenthesis refer to Pantone Colors by Letraset 1989 Series U. Unless otherwise stated all material and colour transparencies are lodged at the Queensland Museum (QM): wet specimens in 70% ethanol are designated (S), wholemounts (WM), serial sections (LS) and colour transparencies (CT). Material examined from other institutions includes that from the British Museum (BMNH), United States National Museum (USNM) and the Australian Museum (AM).

Legends for all figures are as follows: a, auricular groove; c, cement glands; ce, cerebral eyespot; cp, cement pouch; e, ejaculatory duct; f, female pore; i, intestine; m, marginal ruffling; ma, male pore; mo, mouth; o, oviducts; p, pharynx; pe, pseudotentacular eyes; pr, prostate; ps, pseudotentacles; s, sucker; sc, scattered ovaries & testes; se, seminal vesicle; st, stylet; v, vas deferens; va, vagina.

TAXONOMY

THE PROBLEM WITH *PSEUDOCEROS*

Pseudoceros is the dominant genus within the family Pseudocerotidae which contains about 200 species in seven genera. Pseudocerotids are characterised and distinguished by a ruffled pharynx from the next most speciose family of tropical polyclads, the Euryleptidae, which have

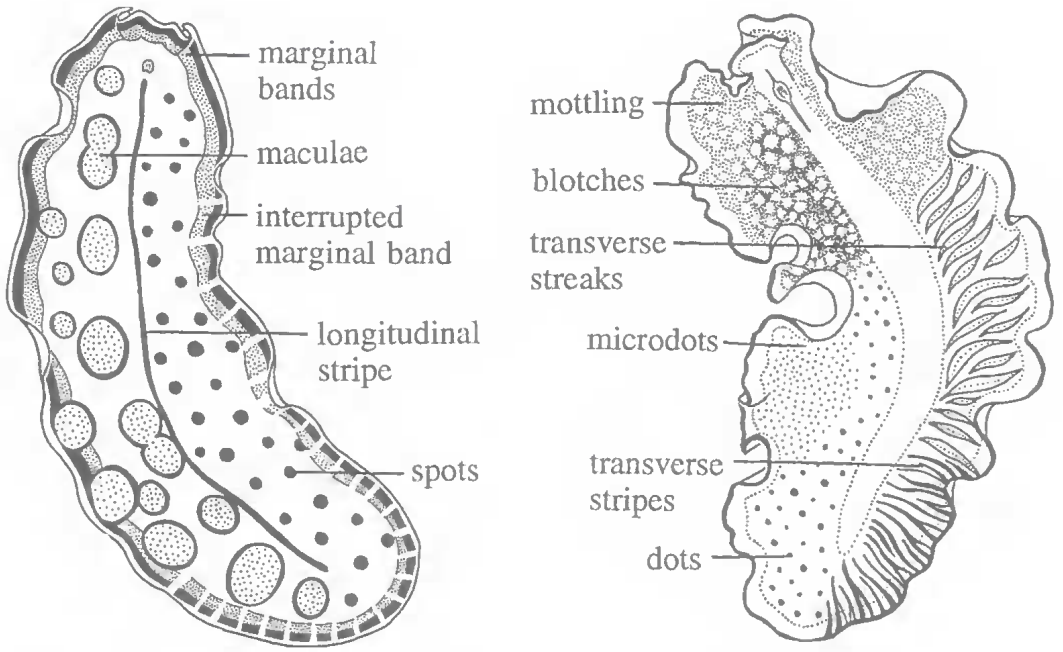


FIG. 1. Dorsal surface colour patterns found in *Pseudoceros* and *Pseudobiceros*.

a tubular pharynx (this latter family has about 130 species in 12 genera; Prudhoe, 1985). The other genera of pseudocerotids are less speciose (most are monospecific) and poorly known (Cannon, 1986).

Genera within the Pseudocerotidae are distinguished by characteristics of the male reproductive system (presence or absence of prostate and seminal vesicle), the female system (number of complexes), the alimentary system (presence or absence of anal pores) and external characters (presence or absence of dorsal papillae and tentacular eyes).

According to Prudhoe (1985, 1989) *Pseudoceros* is by far the biggest genus with about 150 named species (75% of the family). Marcus (1950) listed all known species distinguished on colour pattern alone. Both Hyman (1954, 1959a) and Prudhoe (1985, 1989) considered reproductive anatomy too homogeneous within the genus to be useful in classification and reaffirmed the belief that within *Pseudoceros* species determination could be made solely on the basis of colour pattern. Prudhoe (1985) further pointed out that although colours fade on preservation or change through diet (Crozier, 1917), the pattern still remained.

It is well established among turbellarian flatworms (and probably within the phylum Platyhelminthes) that the anatomy of the reproductive system is of major significance in classification (Cannon, 1986). Basing his work substantially on reproductive anatomy, Faubel (1984) erected a new scheme for the Polycladida at variance with the more conventional view of Lang (1884), Bresslau (1933) and Marcus and Marcus (1968) which Prudhoe (1985) continued to follow. A consequence of this was the separation of *Pseudoceros* into five genera. Working mainly from the literature Faubel (1984) found it difficult to assign many taxa to these new genera and so established a list of incertae sedis. Prudhoe (1985, 1989) knew of Faubel's work and rejected it, maintaining variability was an inherent part of *Pseudoceros* and that changes due to maturation could also be reflected in differential morphology of some organs.

We analyse here some of the characters (established and new) within *Pseudoceros* sensu lato which we believe can elucidate the taxonomy of this large genus. Although the genus was split by Faubel (1984), the genera other than *Pseudoceros* were not accepted by Prudhoe (1985, 1989). However, we have ascertained that by examining extensive material from the GBR and PNG, the genus *Pseudobiceros* Faubel, 1984 is valid. Based on our re-examination of these two genera we find we can only reliably place a limited

TABLE 1. Colour pattern groups for recognised and new species of *Pseudoceros* .

	Colour Pattern	Recognised Species	New Species
1	Even Colour	***perviolaceus*** - purple	***bolool*** - black
2	Marginal Bands	***bimarginatus**** - white; orange & black & yellow margin ***gamblei*** - white; blue margin ***litoralis*** - brown; orange & black margin	***depiliktabub*** - black; green & cream & yellow margin ***jebborum*** - orange; black & orange margin ***periaurantius*** - black; orange margin ***peripurpureus*** - black; violet & purple magin ***prudhoei*** - brown; blue & yellow margin ***sapphirinus*** - black; blue laterlal band ***verecundus*** - cream; orange & black interrupted margin
3	Longitudinal Stripes	***bifasciatus*** - purple; 2 black stripes, orange & white margin ***bifurcus*** - blue; 1 median stripe, orange & white ***dimidiatus**** - black; 2 yellow stripes, orange margin ***gravieri**** - blue; many yellow stripes ***violaceus*** - purple; 1 yellow median stripe, yellow margin ***kelaartii*** - purple mottled; 3 white stripes tristriatus - blue, 3 orange stripes	***laticlavus*** - black; 1 median white stripe, white margin ***monostichos*** - cream; narrow black median line, blue & purple & green margin ***paralaticlavus*** - black; 1 median white stripe, white & yellow margin
4	Spots, Dots & Mottling	***atropurpeus*** - purple; white dots ***concinnus*** - cream; blue spots ***ferrugineus*** - red; white dots ***interruptus*** - brown mottled, blotches of red-brown, interrupted margin ***leptostictus**** - cream; orange & black spots, interrupted margin ***memoralis*** - white; brown dots & interrupted margin ***mossambicus*** - black; greenish spots ***pardalis*** - brown; yellow spots ***pius*** - yellow mottled; red & black spots ***vinosus*** - red; yellow & white dots	***goslineri*** - cream & brown mottling; pink & purple spots & dots ***heronensis*** - cream; brown & white dots, yellow margin ***ouini*** - cream mottled; pink spots at margin
5	Maculae	***glaucus*** - grey; black maculae	***lindae*** - burgundy; yellow & blue maculae ***scintillatus*** - black; yellow maculae, orange margin
6	Transverse Streaks & Stripes	***zebra*** - yellow; black streaks, orange margin	***felis*** - grey mottled; black bifurcating stripes & spots
†	Colour indeterminate	***fuscogriseus, langemaakensis, tomiokensis***	

*collected during this study, † colour pattern not given in original description, but sufficient detail provided from preserved specimens for generic determination.

number of species in each. A discussion of morphological and anatomical characters is given here for *Pseudoceros* and comparisons are made with *Pseudobiceros.*

Colour & pattern. Due to incomplete species descriptions in the past literature, we have defined and illustrated colour patterns for both *Pseudoceros* and *Pseudobiceros* based on living animals (Fig. 1). We have created six groups of colour patterns to aid in species identifications and comparisons are made where possible with the previous literature (Tables 1, 2). Although these divisions may be somewhat arbitrary, they provide a basis for the description of these flatworms.

Pseudoceros contains the most diversified colour groups and the colour patterns are usually opaque. The majority of species were found to be spotted, dotted or mottled (Group 4). Species with an even background colour (Group 1) and distinct maculae (Group 5) were not common. In contrast, the majority of *Pseudobiceros* were flamboyantly patterned either possessing a dark (usually black) background with distinct marginal bands (Group 2) or stripes (Groups 3 & 6). It appears that *Pseudobiceros* are generally more strikingly coloured when compared to *Pseudoceros* which possesses many cryptically coloured species.

The ovaries are sometimes bright red or deep purple and can influence the colour of the dorsal surface. The pharynx, intestine and reproductive organs are white in both genera.

Shape, texture & size. Both genera are extremely delicate, elongate oval and have a smooth

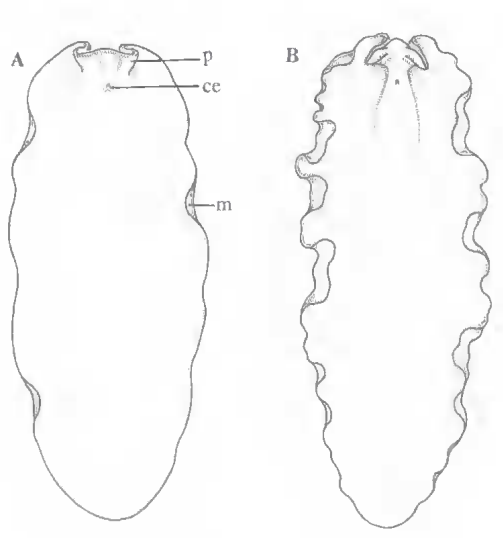


FIG. 2. General morphology of the dorsal surface. A, *Pseudoceros* ; B, *Pseudobiceros*..

dorsal surface without dorsal papillae as found in *Acanthozoon* and *Thysanozoon.*

Pseudoceros are flat with few, shallow marginal ruffles (tending to increase in number with size) and blunt posteriorly or tapering only slightly when extended (Fig. 2A). Species range in size from a few millimetres (juveniles) to a maximum of 70 × 35mm. In contrast, *Pseudobiceros* are narrower, raised medially, possess deep marginal ruffles (often crenulated when the animal is resting) and taper posteriorly when extended (Fig. 2B). Most species are extremely fragile and readily fall apart when disturbed. Species which are black or mainly black are opaque but most other species are transparent and their internal organs can be seen through the epidermis. *Pseudobiceros* are undoubtedly the largest of the pseudocerotids reaching a maximum of 140 × 80mm; twice the maximum size of *Pseudoceros.*

Pseudotentacles. The 'tentacles' are clearly folds of the anterior margin and not separate as in Euryleptidae. These pseudotentacles must be examined from living animals as they loose their distinctive shape during fixation.

In *Pseudoceros*, the pseudotentacles are simple folds occurring in two forms; either square blunt, simple, tubular folds (Fig. 3A) or pointed broad flaps (Fig. 3B). It appears that differences between these two forms are due to size since both forms have been observed in a single species. Conversely in *Pseudobiceros*, the pseudotentacles are further developed, held more erect and are more conspicuous. Two distinct pseudotentacular types are found being either ear-like and pointed (Fig. 3C) or square with lateral ruffles (Fig. 3D). The degree of lateral ruffling of the pseudotentacles can also vary from slight to deep ruffles. Differences observed between these two forms of pseudotentacles in *Pseudobiceros* are species specific.

Cerebral eyes. Prudhoe (1989) noted that the number of eyes increased with size. Within the cerebral eyespot the eyes are arranged in a horseshoe shaped cluster with concentric rows (not two distinct elongate clusters as found in Euryleptidae). There is little difference in the arrangement of cerebral eyes between *Pseudoceros* and *Pseudobiceros* although the latter tends to possess a larger number of eyes, especially in mature animals. Occasionally the cerebral eyes appear to form a round cluster in both genera.

The cerebral eyespot is often found in the clear area which in *Pseudoceros* is an inverted heart shape (Fig. 3A, B) and in *Pseudobiceros* an elongate oval extending anterior and posteriorly, sometimes becoming an indistinct median line in large specimens (Fig. 3C, D). The presence and shape of this clear area is evident in live animals but lost during fixation. Occasionally a few precerebral eyes are found in *Pseudoceros.*

Pseudotentacular eyes. Pseudotentacular eyes are present in both genera (not absent as in *Parapseudoceros*) although they are difficult to see in animals with black backgrounds or marginal bands. The dorsal pseudotentacular eye arrangement differs between *Pseudoceros* and *Pseudo-*

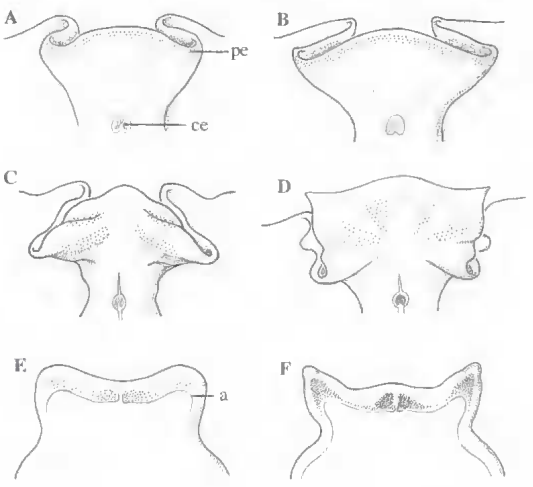


FIG. 3. A-D, Dorsal pseudotentacles and eye arrangement. A, B, *Pseudoceros*; C,D, *Pseudobiceros*. E, F, ventral pseudotentacular eye arrangement. E, *Pseudoceros*; F, *Pseudobiceros.*

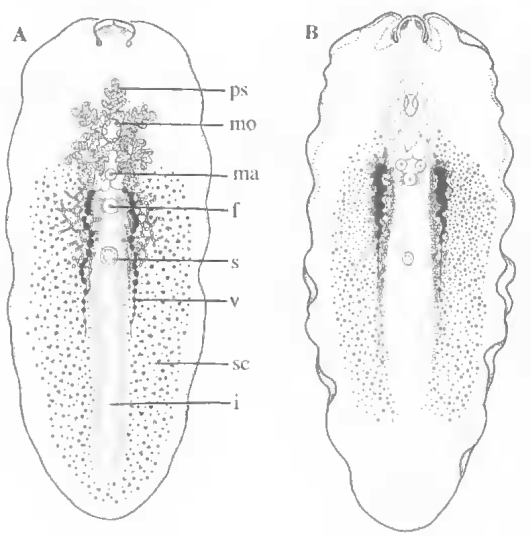


FIG. 4. General morphology of the ventral surface. A, *Pseudoceros*; B, *Pseudobiceros*.

biceros: in *Pseudoceros*, the dorsal pseudotentacular eyes are arranged in two to three scattered lines across the anterior pseudotentacular rim (Fig. 3A, B), but in *Pseudobiceros* the eyes are arranged in four loose longitudinal clusters across the pseudotentacles (Fig. 3C, D). The ventral pseudotentacular eyes occur in two loose clusters in *Pseudoceros*, but in four dense clusters in *Pseudobiceros* (Fig. 3E, F).

An auricular ciliated groove is found ventrally and terminates at the lateral limit of the pseudotentacles in *Pseudoceros* but extends laterally along the margin in *Pseudobiceros* (Fig. 3E, F). According to Prudhoe (1985) the function of this groove is unknown but it is probably used for chemoreception.

Pharynx. The pharynx is clearly ruffled in *Pseudoceros* and *Pseudobiceros* (not tubular as found in Euryleptidae and Prosthiostomidae). Hyman (1959a) first noted differences in pharynx shape in *Pseudoceros* and used the phrase 'butterfly shape' to describe a pharynx with 'lateral lobulations that increase in length in the anteroposterior direction'. Hyman further stated that pharynx shape may be decisive in species determination but this has not been investigated in any detail. Prudhoe (1989) apparently did not agree with Hyman and stated that differences in pharynx shape were simply due to growth whereby 'in a young worm the pharynx has a compact outline, but as the worm grows so the pharynx finally assumes a butterfly shape'. Furthermore, Prudhoe believed that differences in pharynx shape within the genus could be due to fixation.

Our studies clearly show a difference in pharynx shape between *Pseudoceros* and *Pseudobiceros*. The pharynx in *Pseudoceros* is round and oval with about seven (one anterior, four lateral and two posterior) complex pharyngeal lobes, each dividing ('butterfly shaped') and extending laterally (Fig 4A, 5A). In comparison, the pharynx in *Pseudobiceros* is generally relatively smaller, narrower and elongate-oval with about 10 to 20 shallow simple pharyngeal folds which do not divide (Figs 4B, 5B). Obvious differences in pharynx shape between these two genera have probably been overlooked since the pharynx shape can be drastically distorted in preserved specimens.

Intestine. The intestine extends posteriorly to just near the posterior margin of the body in *Pseudoceros* (Fig. 4A): it does not extend as far in *Pseudobiceros* (Fig. 4B). Numerous lateral anastomosing intestinal branches can be seen clearly in *Pseudoceros* as they evenly branch off the intestine trunk. It is difficult to see the numerous lateral branches of the intestine in *Pseudobiceros* since the intestine is much wider and often inflated. These intestinal branches appear to be finer and more numerous than in *Pseudoceros* and do not extend to the posterior limit of the intestine. It should be noted that the majority of *Pseudobiceros* collected during this study were velvety black and anatomical details were difficult to see in whole mounts.

Sucker. The sucker (or adhesive organ) is characteristic of the cotyleans but is sometimes difficult to see in preserved specimens. Prudhoe (1985) maintained that the purpose of the sucker was not known. Our in situ observations clearly show that the sucker is used to adhere animals to their substrate and is not used during copulation.

In *Pseudoceros* the small, round sucker is found posterior to the female pore in the mid-body (or just anterior to the mid-line when animals are alive) (Fig. 4A). The sucker and gonopores are generally equally spaced. In *Pseudobiceros* the sucker is less pronounced and is well separated from the male and female gonopores (Fig. 4B). Specimens of both genera were occasionally found with two unequal sized suckers.

Gonopores. In *Pseudoceros* the single male pore is found between or just posterior to the last pair of pharyngeal folds and the female pore is clearly separated from the male pore (Figs 4A,

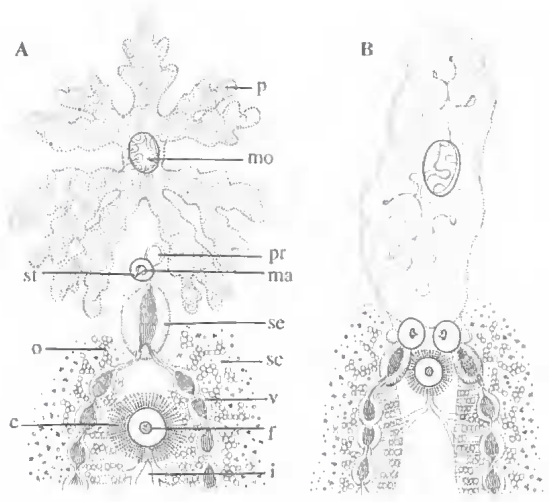


FIG.5. Details of the pharynx and gonopores. A, *Pseudoceros*; B, *Pseudobiceros*.

5A). In *Pseudobiceros* the symmetrical male pores are found just posterior to the end of the pharynx (Figs 4B, 5B), and they are clearly separate. The two male antra and penis papillae are usually directed towards each other making interpretations of the penial stylet from longitudinal sections often difficult and several animals may need to be sectioned.

In *Pseudoceros* and *Pseudobiceros* there is a single female pore (not multiple as in *Nymphozoon*) found posterior to the male pore(s). In *Pseudoceros* the female pore is well separated from the male pore (Figs 4A, 5A) whereas in *Pseudobiceros* the female pore is clearly found between the male pores (Figs 4B, 5B). It should be noted that the position of the gonopores and sucker can change dramatically with fixation.

Testes. The scattered testes are found ventrally, occasionally occurring with the ovaries in the dorsal parenchyma (Prudhoe, 1985). Testes and ovaries often mature simultaneously.

Male pore(s). The presence of a double male reproductive system was first noted by Lang (1884). He described three varieties of *Pseudoceros maximus* Lang, 1884; one with a single male pore, one with two male pores and a double male apparatus, and one with two male systems but only one male pore. Stummer-Traunfels (1895) considered these three varieties to be different species but did not separate them. Later, Stummer-Traunfels (1933) figured two specimens of *Pseudoceros latissimus* (Schmarda, 1859), with one and two male pores.

Hyman (1959a) also noted that the presence of a single or paired male apparatus in Pseudocerotidae was a useful character and predicted that the details of the male copulatory apparatus may be of value in specific diagnosis, but she rarely gave these details. Prudhoe (1989) maintained that the number of male copulatory apparatuses was questionable as a diagnostic feature. He explained that the occurrence of supernumerary of organs is well known among certain families of polyclads and he refrained from accepting Faubel's (1984) reclassification of the family Pseudocerotidae, including the diagnosis of *Pseudobiceros*, and instead recognised the systematics given by Bresslau (1933).

The double anatomy of the male reproductive system is characteristic of *Pseudobiceros* (Figs 4B, 5B). There can be no question that this represents merely supernumerary of male organs as suggested by Prudhoe (1989). Significant differences in other morphological characters (such as the pseudotentacles, eyes and pharynx) exists between *Pseudoceros* and *Pseudobiceros* to confirm the distinction between these genera.

Vas deferens. Prudhoe (1989) believed that a diagnostic feature for *Pseudoceros* is whether each vas deferens opens into the seminal vesicle separately or whether they unite to form a single duct. In *Pseudoceros* the seminal vesicle and vas deferens change shape dramatically depending on maturity. In the early stages of development of the male phase the ducts unite to open into the seminal vesicle by a common duct, but as the vesicle becomes swollen with sperm, the duct disappears and each vas deferens appears to open into the seminal vesicle separately (Figs 5A, 6).

In both genera, species were found with branching vas deferens. It is assumed that rather than being of taxonomic significance this is due to sexual maturity where fully developed vas deferens form an anastomosing network.

Seminal vesicle & ejaculatory duct. The seminal vesicle is basically elongate and oblong and there are no apparent generic or specific differences (Figs 5, 6, 7A). The walls are thick and muscular (circular muscle) and the development of musculature depends on sexual maturity since the walls are thinner when the seminal vesicle is swollen with sperm.

The ejaculatory duct is directed antero-dorsally and varies considerably in length and in the amount of coiling, but there is no apparent significant difference between the two genera (Fig. 6).

Prostate & prostatic duct. The prostate is free or independent (not interpolated into the seminal vesicle) and varies from oval to round. The muscular wall contains extraepithelial glands which

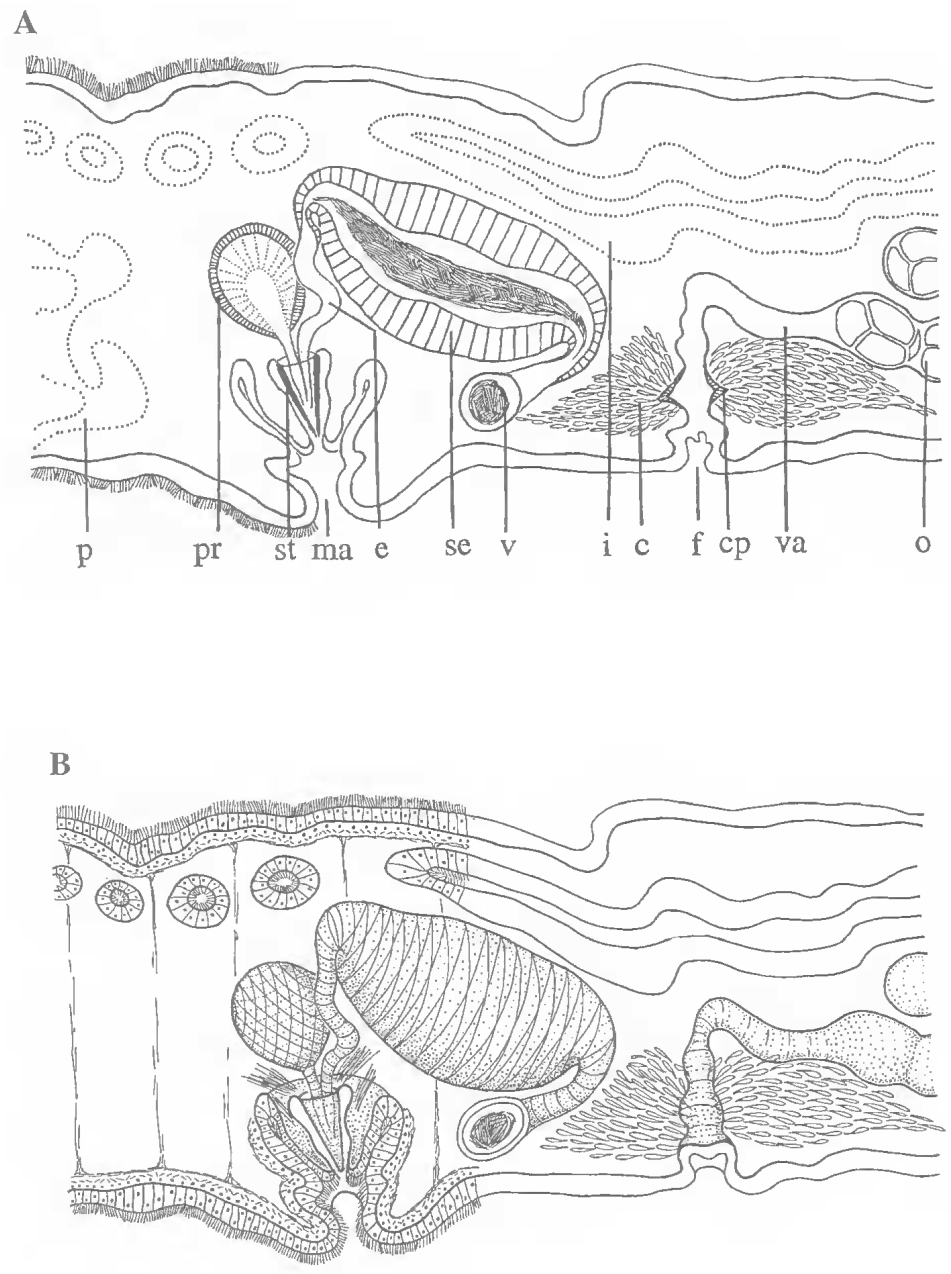


FIG. 6. Diagrammatic reconstruction of the body in the genital region showing the reproductive anatomy for *Pseudoceros* and *Pseudobiceros*. A, general distribution of organ systems; B, details of musculature. (In *Pseudobiceros*, which may be similarly diagrammatically represented, the male and female systems are not in line so they are shown separately in the descriptions).

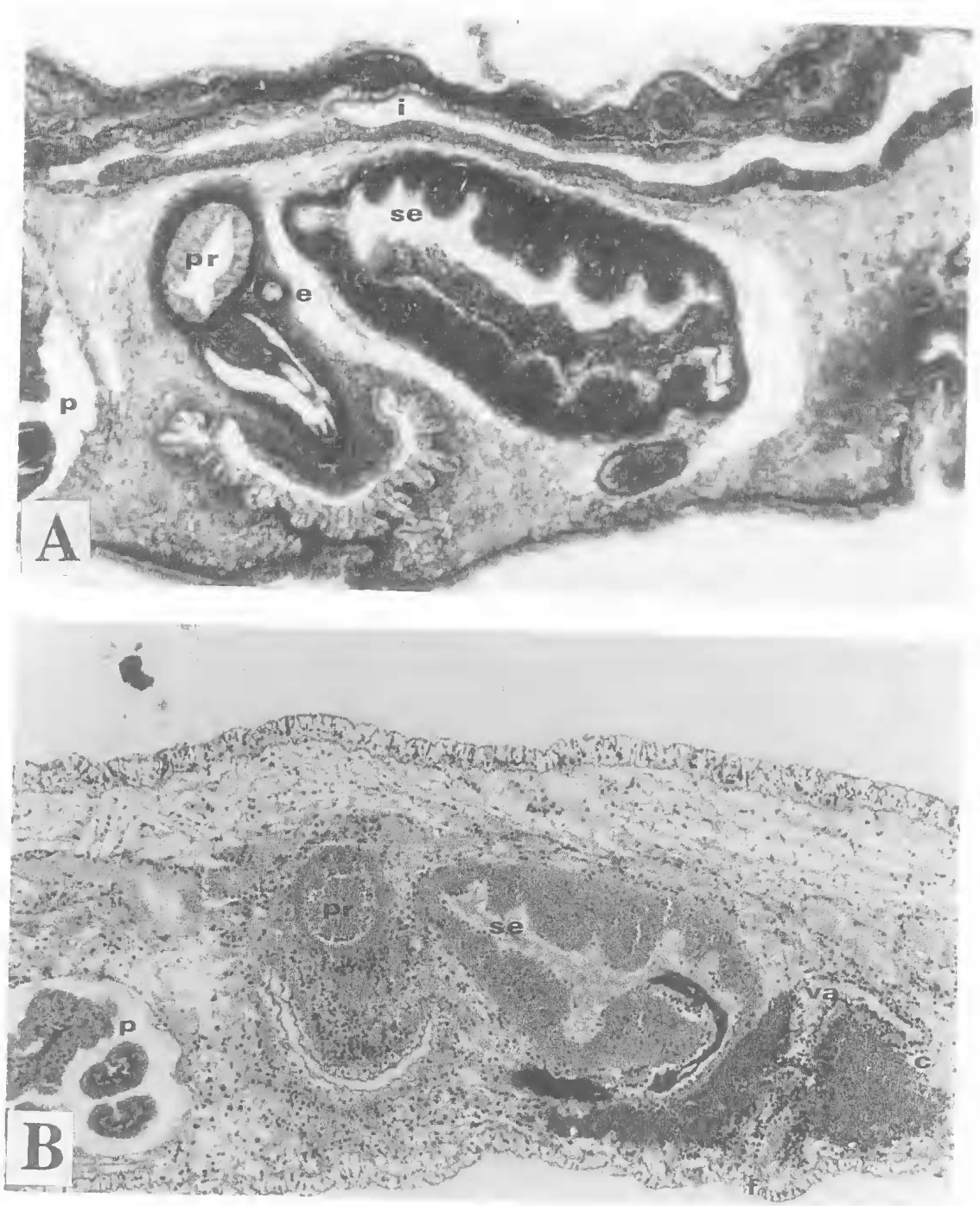


FIG. 7. Photomicrographs of the reproductive system in *Pseudoceros.* A, male; B, female.

discharge into the interior. In two large species the prostate had either an involuted lining or two separate chambers but these variations appear to be due to size. The prostatic duct is short, straight and joins the ejaculatory duct in the penis.

Penial stylet & male antrum. Although the stylet varies in width at its base, there is no apparent difference in shape between the two genera (Figs 6, 7A, 8A). The male antrum is usually wide and folded in *Pseudoceros* and deep (almost tubular) in *Pseudobiceros*. Variation in the size and shape of the penis pocket, penial sheath and antrum appear to be due to fixation, as no specific or generic differences have been determined.

Ovaries. The ovaries are scattered dorsally and extend anteriorly to the mid-pharynx region and posteriorly to the posterior margin in *Pseudoceros*, but only to the posterior end of the intestine in *Pseudobiceros* (Fig. 4).

Oviducts & vagina. The distal oviducts anastomose postero-laterally along the intestine and extend to about 1/3 the body length when the animal is fully mature, finally joining the short posteriorly directed muscular vagina (Figs 4, 5, 6). The anatomy of the female system appears to be similar between species and genera as no notable differences have been found.

Cement glands & female antrum. The cement (or 'shell') glands extend outward from the lining of the cement pouch which is located within the folded female antrum. These glands are compressed dorso-ventrally and appear to be relatively more extensive in *Pseudoceros* than in *Pseudobiceros*.

Musculature. In *Pseudoceros* the body has a thin circular muscle layer, a weak diagonal muscle layer and a more prominent longitudinal muscle layer (Fig. 6B). In *Pseudobiceros* there is an extra, though not well-defined, longitudinal muscle layer directly beneath the basement membrane. Dorso-ventral muscles are more prominent in the larger *Pseudobiceros*.

In both genera, the prostate is surrounded by crossed longitudinal muscle bands which lie over weak circular muscles (Fig. 6B). The seminal vesicle has distinct crossed circular muscle bands. There are several retractor muscles around the base of the penis sheath and there appear to be slightly more of these muscles in *Pseudobiceros*. The vagina has only weak, occasional, circular muscle bands.

Size and state of fixation appeared to contribute to slight variations observed in these patterns. No specific differences were found in the muscle layers of the copulatory organs or in the body wall of the reproductive region.

Pseudoceros Lang, 1884

Proceros velutinus Blanchard, 1847; type unknown, painting only?

Type Locality

Genoa, Italy.

Emended Diagnosis

Flamboyantly or cryptically coloured. Body soft, oval, flat medially, few marginal ruffles, blunt or tapering slightly posteriorly (Fig. 2A). Pseudotentacles simple folds or broad flaps formed from the anterior margin (Fig. 3A, B). Cerebral eyespot horseshoe shaped with 20 to 60 eyes in semicircular rows, usually in an inverted heart shaped clear area. Dorsal pseudotentacular eyes in two to three scattered lines; ventral pseudotentacular eyes more numerous, extending medially to the pseudotentacular tips in two loose clusters (Fig. 3E). Pharynx anterior with about seven (one anterior, four lateral and two posterior) highly ruffled, deep, complex pharyngeal folds (Figs 4A, 5A). Intestine narrow, extends towards the posterior margin, numerous lateral branches. One male pore posterior to pharynx, between last pair of pharyngeal lobes. Female pore well separated from male pore, equidistant from it and sucker. Sucker distinct, midbody. Male copulatory apparatus single with seminal vesicle and armed penis papilla, prostate orientated antero-dorsally.

Taxonomic Remarks

Lang (1884) first described the genus *Pseudoceros* as pseudocerotids with sharp or blunt (acute or rounded) marginal pseudotentacles, without dorsal papillae, with single or double male copulatory organs and no anal pores (pores from the gut branches) dorsally.

Faubel (1984) diagnosed *Pseudoceros* as 'Pseudocerotidae with smooth dorsal surface, tentacular and cerebral eyespots present, male copulatory apparatus single with seminal vesicle and armed penis papillae, prostatic vesicle orientated antero-dorsally'. Prudhoe (1985, 1989) added that the pharynx has four or five pairs of lateral folds and that the male copulatory complex may be single or double: in the latter case they are arranged symmetrically.

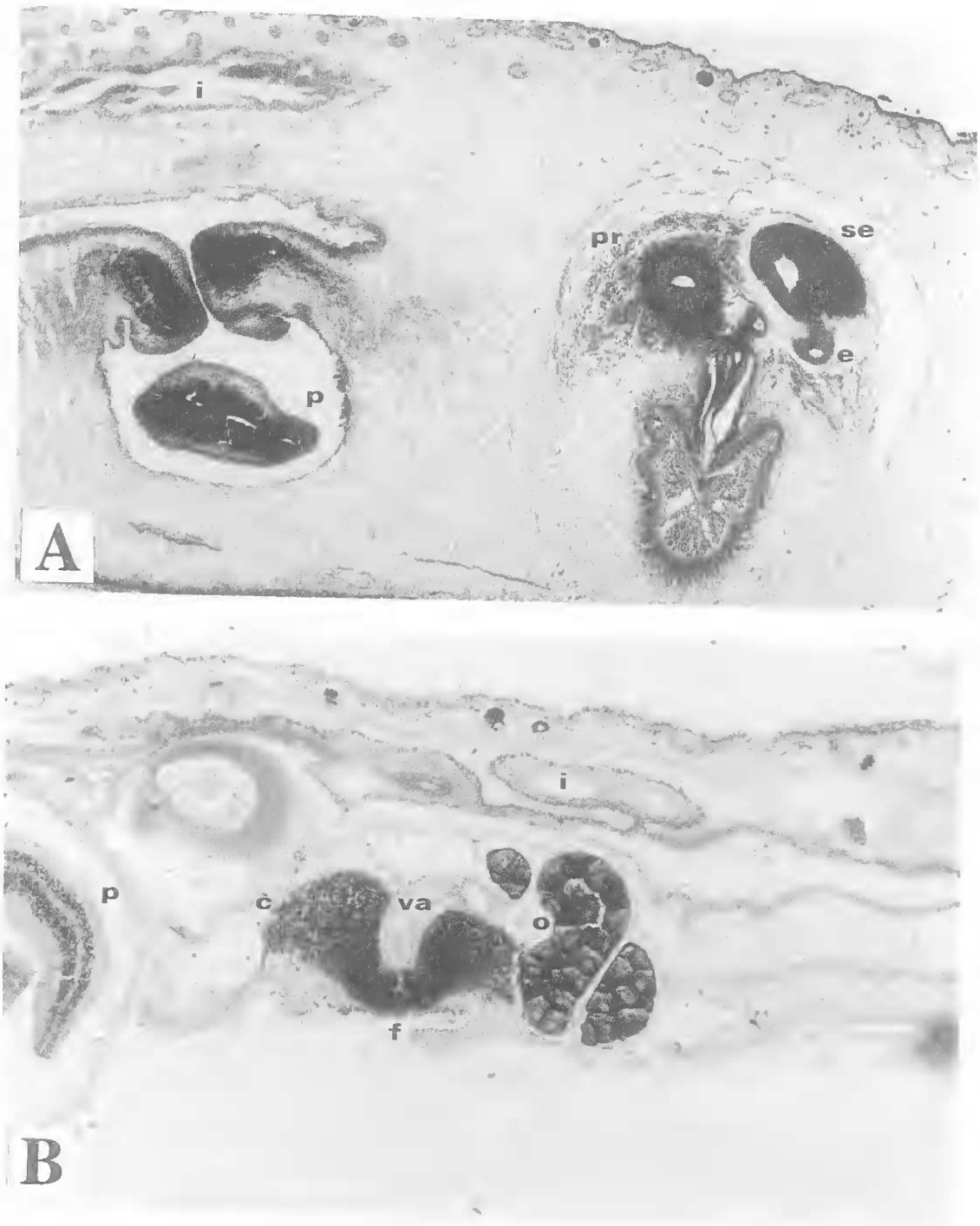


FIG. 8. Photomicrographs of the reproductive system in *Pseudobiceros*. A, male; B, female.

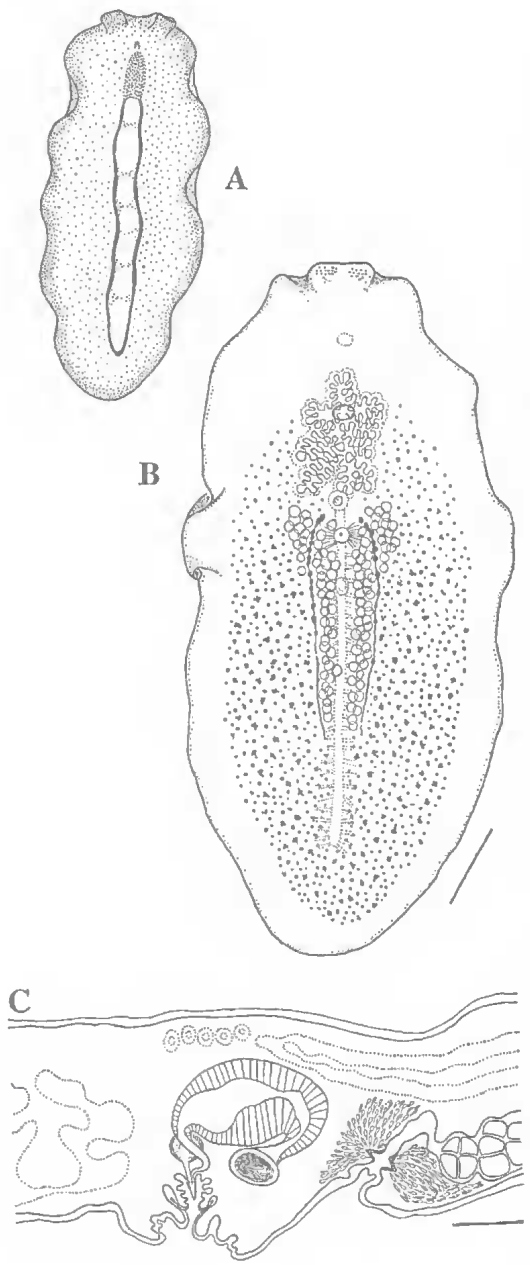


FIG. 9. *Pseudoceros bifurcus* Prudhoe, 1989. A, diagram of the dorsal colour pattern; B, QMG210332, wholemount showing the morphology from the ventral surface; C, QMG210323, reconstruction of the reproductive anatomy . Scales: B, 2.5mm; C, 500µm.

LIST OF RECOGNISED SPECIES

The following 26 known species we believe may be reliably placed in *Pseudoceros* sensu stricto based on the morphology of the pharynx, eyes, pseudotentacles or reproductive anatomy (Table 1):*atropurpeus* Kato, 1939; *bifasciatus* Prudhoe, 1989; *bifurcus* Prudhoe, 1989*; *bimarginatus* Meixner, 1907*; *concinnus* (Collingwood, 1876); *dimidiatus* von Graff, 1893*; *ferrugineus* Hyman, 1959*; *fuscogriseus* Hyman, 1959 ; *gamblei* Laidlaw, 1902; *glaucus* Prudhoe, 1989; *gravieri* Meixner, 1907*; *interruptus* (Stimpson, 1855); *kelaartii* (Collingwood, 1876); *langemaakensis* Faubel, 1984; *leptostictus* Bock, 1913*; *litoralis* Bock, 1913; *memoralis* Kato, 1938; *mossambicus* Prudhoe, 1989; *pardalis* Verrill, 1900; *perviolaceus* (Schmarda, 1859); *pius* Kato, 1944; *tomiokaensis* Kato, 1938; *tristriatus* Hyman, 1959a; *vinosus* Meixner, 1907; *violaceus* (Kelaart, 1858); *zebra* (Leuckart, 1928)(*collected during this study).

SPECIES FROM EASTERN AUSTRALIA & PAPUA NEW GUINEA

Pseudoceros bifurcus Prudhoe, 1989 (Figs 9A - C; 46A)

Pseudoceros dimidiatus von Graff, 1893; George & George, 1979: 43, pl. 49 fig. 7.

Pseudoceros unidentified species; Stummer-Traunfels, 1933: pl. 1, fig. 17.

P. liparus Marcus, 1950; Coleman, 1990: 30.

Pseudoceros bifurcus Prudhoe, 1989: 78, fig. 20.

MATERIAL EXAMINED

HOLOTYPE: Mayotte, Comoros Islands, Madagascar, 38m, P. Bouchet, 29.03.77, WM, BMNH1984.10.6.7-8.

PARATYPE: same data as holotype.

OTHER MATERIAL: Heron Is., reef slope, 3 to 15m, 12.07.89, WM, QMG210320; 12.90, WM, QMG210323; 18.02.91, S, QMG210439; 11.06.91, WM, QMG210325; WM, QMG210326; S, QMG210365; 20.06.91, LS, QMG210321; S, 4 spec., QMG210322; LS, QMG210330; 26.06.91, S, 3 spec., QMG210331; 06.91, LS, QMG210327; WM, QMG210328; 02.02.92, WM, QMG210329; 13.02.92, LS, QMG210332; 23.02.92, S, 7 spec. QMG210336; J. Tanner, 28.08.92, LS, QMG210333; 09.92, WM & LS, QMG210335; One Tree Is., reef slope, 18m, 12.09.02, LS, QMG210334. Records: Broadhurst Reef, central GBR, 15m, I. Loch, 14.10.73, CT.

DESCRIPTION

Colour & pattern. Background varies from blue (279) to light mauve (250) (cream in the largest animals) intensifying to purple (252) at the margin; lacks distinct marginal band. Pseudotentacles mauve. Bright orange (1655) regular elongate spot posterior from the cerebral eyespot

fading into an irregularly shaped white median stripe which ends before the posterior margin; stripe bordered by dark burgundy (221). Ventrally light mauve or cream, marginal band mauve.

External features. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes, occasionally with a few scattered precerebral eyes. Size: mature from 23 × 10mm to 60 × 35mm; juveniles from 1.0 × 0.4mm.

Reproductive anatomy. Seminal vesicle rounded oblong (888µm long); ejaculatory duct short, coiled. Prostatic vesicle round (185µm wide). Stylet short (130µm long). Male antrum moderately deep and voluminous. Female antrum shallow.

REMARKS

This species belongs to Group 3 where the majority of species possess a dark purple or black background. Only *P. gravieri* (Table 1) and *P. tristriatus* have a similar background colour but *P. bifurcus* has one white medial stripe not multiple yellow or orange longitudinal stripes.

Prudhoe (1989) described this species from two immature specimens and based his diagnosis on the colour pattern observed from a colour transparency (not located). Specimens from Heron Is. are identical in colour pattern to Prudhoe's description with the exception of a white marginal band. This band may be an artefact resulting from the lighter ventral surface exposed due to ruffling of the margin. Although the pharynx was not described by Prudhoe, the holotype and paratype possess complex pharyngeal folds. The reproductive anatomy was not examined by Prudhoe (1989).

Stummer-Traunfels (1933) may have first figured this species from Indonesia but it was not named. In the colour plate the animal is shown as blue with an orange median stripe bordered by black. This pattern is similar to *P. bifurcus* with the exception that the median stripe is only orange anteriorly in *P. bifurcus*.

BIOLOGY

Animals were commonly observed feeding during the day on ascidians especially *Eudistoma laysani* (Sluiter, 1900), under ledges on the reef slope. Animals were also observed copulating in situ and in the laboratory.

HABITAT & DISTRIBUTION

Found under ledges (usually on ascidian prey) on reef slope. Abundant from Heron Is., rare from One Tree Is. Records: Central GBR, Madagascar.

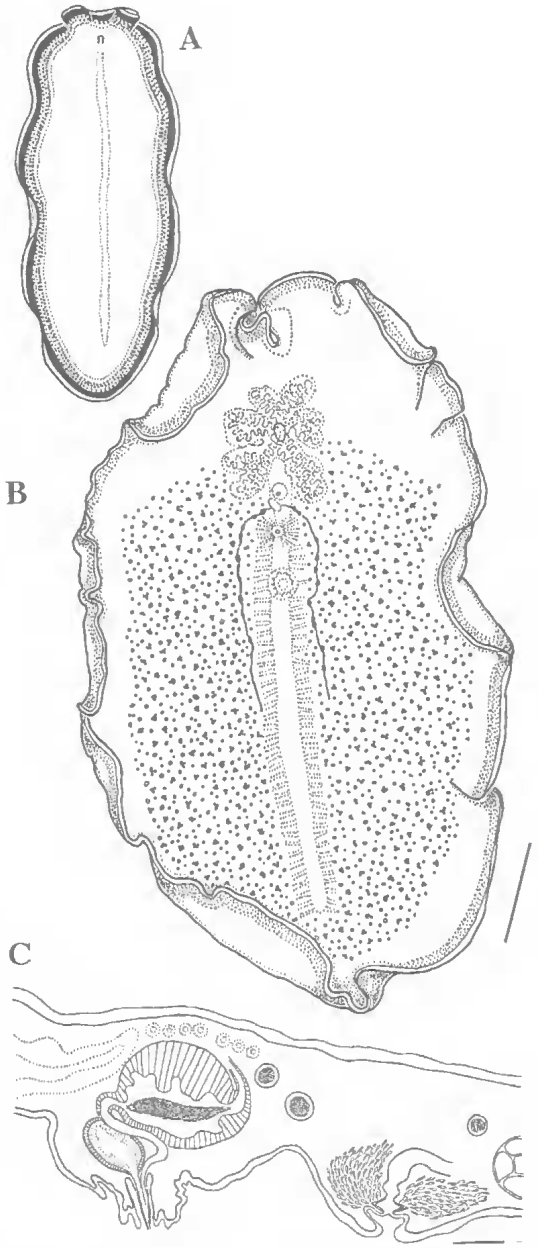


FIG. 10. *Pseudoceros bimarginatus* Meixner, 1907. A, diagram of the dorsal colour pattern; B, QMG210374, wholemount showing the morphology from the ventral surface; C, QMG210375, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250µm.

Pseudoceros bimarginatus Meixner, 1907
(Figs 10A - C; 46B)

Pseudoceros bimarginatum Meixner, 1907: 465 - 468, pl. XXV figs 5, 6; pl. XXVI, figs 17, 18; Marcus,

1950: 84; Prudhoe, 1985: 194; Prudhoe, 1989: 78 - 79.

Pseudoceros - undescribed species Stummer-Traunfels, 1933: pl. 7.

Pseudoceros corallophilus Hyman, 1954: 223, fig. 2; Faubel, 1984: 207; Coleman 1990: 31; Cannon & Newman, 1993: 83, pl. 4.

MATERIAL EXAMINED

HOLOTYPE: Unknown, Somalia.

OTHER MATERIAL: Heron Is., reef crest, 17.08.89, WM, QMG210372; 11.06.91, WM, QMG210374; 31.01.92, LS, QMG210375; 21.02.92, S, QMG210377; 10.08.92, S, QMG210381; 14.08.92, WM, QMG210382; 09.09.92, LS, QMG210383. Records: Anilao, Philippines, Stn. 13, 31.03.93, T. Gosliner, CT.

DESCRIPTION

Colour & pattern. Background white or white-cream (sometimes faint purple anteriorly) with three distinct marginal bands; inner wide orange (151) , middle opaque black, narrow bright yellow-green (102) rim. Fine narrow, median white line (sometimes faint or absent), not extending to the posterior margin and along the inside of the orange marginal band. Ventrally vibrant pink-orange (135) with the same marginal bands.

External features. Pseudotentacles simple folds. Cerebral eyespot with 30 to 40 eyes. Marginal eyes obscured due to black pigmentation of the marginal band. Size: mature from 23 × 12mm to 32 × 18mm; juvenile from 12 × 6mm.

Reproductive anatomy. Seminal vesicle round (638µm long), ejaculatory duct long, coiled; vas deferens dorsally directed. Prostate small, oval (323µm wide). Stylet short (187µm long). Male and female antra wide.

REMARKS

This species belongs in Group 2. Only one other species is white, *P. gamblei. P. bimarginatus* has three distinct marginal bands not one as in *P. gramblei. P. heronensis* sp. nov. (Group 4) also somewhat resembles this species (see below).

Meixner (1907) described and illustrated this species from Gravier's original description which is as follows, 'Face dorsale rose pâle, face ventrale, même teinte, plus foncée. Sur le poutour bandes jaune d'or, brune, avec un liseré vert.' Although this colour description of the marginal bands differs slightly from ours, it is difficult to know whether the original description was based on a living or preserved animal. From the original description the relative width of the marginal bands and deeper colour of the ventral surface convince us of the similarity in these animals.

Subsequently, Stummer-Traunfels (1933) figured this same species in a colour plate yet it remained unnamed. Hyman (1954) obviously overlooked this species when describing *P. corallophilus* 'with some hesitation' based on one preserved immature specimen from Heron Island.

The dorsally directed vas deferens and round seminal vesicle are unusual for the genus.

BIOLOGY

The vibrant orange, black and yellow marginal bands suggest that this species is displaying aposematic or warning colouration.

HABITAT & DISTRIBUTION

Found moving across boulders or sand during the day at the reef crest. Common from Heron Is. Records: Central GBR, Somalia, Philippines.

Pseudoceros bolool sp. nov.
(Figs 11A - C; 46C)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 28.12.90, WM, QMG210386.

PARATYPE: Heron Is., reef crest, 06.09.92, LS, QMG210395.

OTHER MATERIAL: Heron Is., reef crest, 29.08.89, S, 2 spec., QMG210384; 17.10.89, LS, QMG210385; 06.11.90, S, QMG210441; 02.01.91, S, QMG210387; 19.01.92, S, QMG210399; 27.01.92, LS, QMG210389; 04.02.92, S, QMG210390; 19.02.92, LS, QMG210391; WM, QMG210487; 24.08.92, LS, QMG210394; 18.02.93, S, QMG210396; 21.02.93, S, QMG210397; One Tree Is., reef crest, 19.08.93, WM, QMG210630; Madang, reef crest, 2 - 3m, 08.06.92, WM, QMG210392; 16.06.92, LS, QMG210393.

DESCRIPTION

Colour & pattern. Background velvety black, no markings, grey when extended or dark brown if gut diverticula full of food. Ventrally light grey medially, darker marginally.

External features. Pseudotentacles simple folds. Cerebral eyespot with about 60 eyes in clear area. Size: mature from 16 × 9mm to 45 × 22mm; immature from 6 × 3mm.

Reproductive anatomy. Seminal vesicle elongate, oblong (638µm long), ejaculatory duct coiled. Prostate round (203µm wide). Stylet short (113mm long). Male antrum wide.

DIAGNOSIS

Even black dorsally, with no other markings.

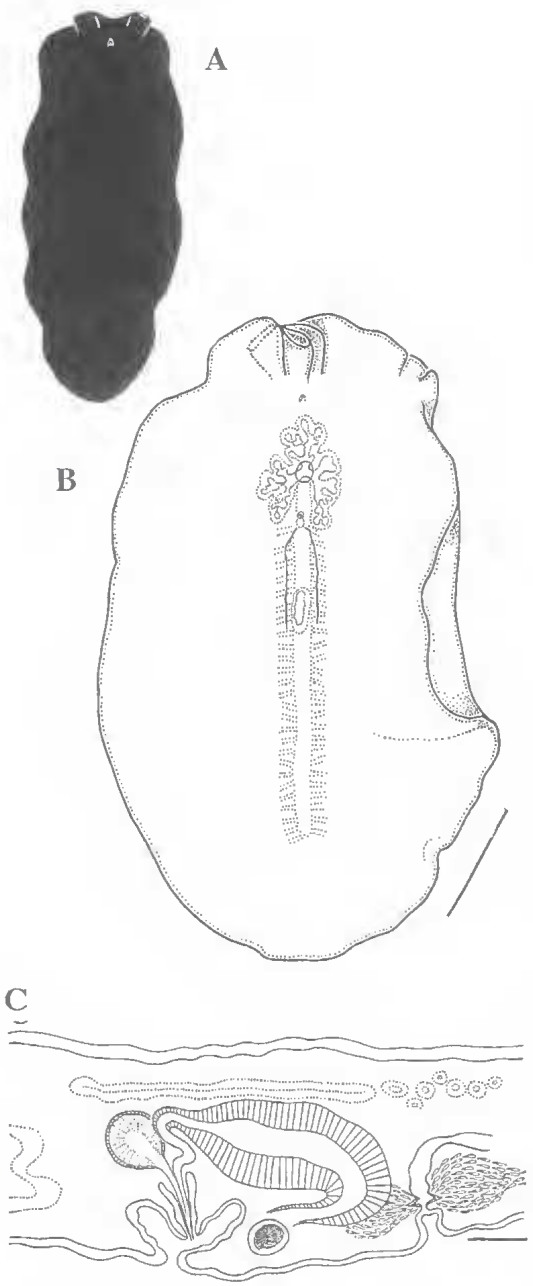


FIG. 11. *Pseudoceros bolool* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210386, wholemount showing the morphology from the ventral surface; C, QMG210395, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250µm.

ETYMOLOGY

From an Australian aboriginal word for night 'bolool'.

REMARKS

This species belongs in Group 1 with the violet coloured *P. periviolaceus.*

Hyman (1959a) described *Pseudoceros ater* from Palau as uniform dark greyish or practically black without any markings. Examination of the holotype of *P. ater* (USNM28655) showed that the pharynx had simple rather than complex pharyngeal folds and may be referable to *Pseudobiceros.*

Both *P. bolool* and the nudibranch *Dendrodoris nigra* (Stimpson, 1855) are evenly black, of similar size and are often found under the same boulders. These animals are possible mimics.

HABITAT & DISTRIBUTION

Usually found on colourless, transparent, encrusting colonial ascidians under boulders at the reef crest or from under rubble on the reef slope. Common (especially juveniles) from Heron Is., rare from One Tree Is. and Madang.

Pseudoceros depiliktabub sp. nov.
(Figs 12A - C; 46D)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, under rubble, 4m, 24.06.92, WM, QMG210473.

PARATYPE: Madang, reef crest, under rubble, 3m, 26.06.92, LS, QMG210474.

DESCRIPTION

Colour & pattern. Background velvety black fading into three marginal bands; inner marginal band black-green (556) fading to yellow-cream (127) with distinct bright orange (109) rim. Ventrally purple-black, same marginal bands.

External features. Pseudotentacles simple folds. Body sometimes with few deep marginal ruffles, tapering slightly posteriorly. Cerebral eyespot with about 30 eyes. Size: mature from 25 × 11mm; juvenile from 20 × 6mm.

Reproductive system. Seminal vesicle elongate oblong (795µm long), ejaculatory duct coiled. Prostate round (285µm wide). Stylet short (195µm long). Male antrum deep, female antrum shallow.

DIAGNOSIS

Dark green with three marginal bands; inner wide, dark green; middle wide cream; and narrow orange at rim.

ETYMOLOGY

From the Rewo Village language (Madang, PNG) name of the reef where it was collected.

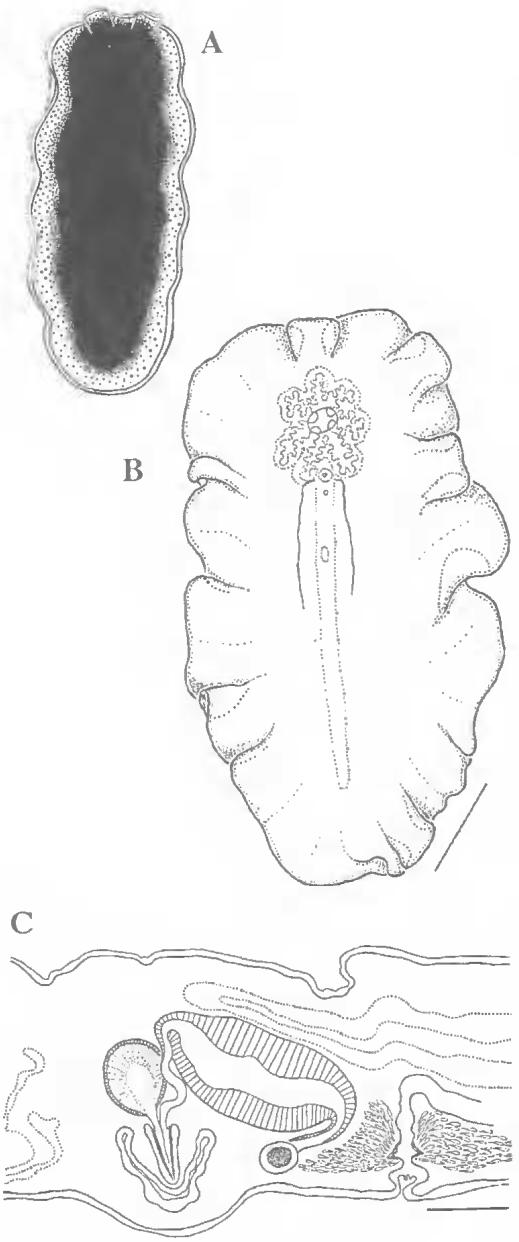


FIG. 12. *Pseudoceros depiliktabub* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210473, wholemount showing the morphology from the ventral surface; C, QMG210474, reconstruction of the reproductive anatomy. Scales B, 2.5mm; C, 250µm.

REMARKS

This species belongs to Group 2 in which several species possess a black background with vibrantly coloured marginal bands. *P. bimarginatus* also possesses three marginal bands, however, the bands are orange, black and yellow not green, cream and yellow as in *P. depiliktabub.*

HABITAT & DISTRIBUTION

Found under rubble at the reef crest. Rare from Madang.

Pseudoceros dimidiatus von Graff, 1893
(Figs 13A - C; 46E, F)

Pseudoceros dimidiatus von Graff, 1893: 362, pl. VIII; Faubel, 1984: 238, incerta sedis.
unidentified flatworm; Steene, 1990: 322, pl. 184.

MATERIAL EXAMINED

HOLOTYPE: Painting only, GBR, Australia.
OTHER MATERIAL: Madang, reef slope, 10m, M. Ghiselin, 03.06.92, LS, G210489. Records: Wistari Reef, off Heron Is., reef slope, 20m, R. Riechelt, 16.11.80, CT; north Sulawesi, M. Severns, CT.

DESCRIPTION

Colour & pattern. Background velvety black with two median yellow (Process Yellow) stripes which vary from narrow to extremely wide, stripes begin at the pseudotentacles and continue posteriorly to join just prior to the posterior margin. Narrow black median stripe. Distinct wide orange (021) marginal band. Ventrally grey-black with orange marginal band.

External features. Large species with several deep marginal ruffles. Pseudotentacles simple folds (Fig. 46E) or broad flaps (Fig. 46F). Cerebral eyespot with 100's of eyes. Size: mature at 70 × 25mm.

Reproductive anatomy. Seminal vesicle large (2.36mm long); ejaculatory duct short, coiled. Prostate oval (473µm wide) with numerous chambers resulting from an involuted lining. Stylet relatively long (225mm). Male antrum wide, female antrum narrow and shallow.

REMARKS

This species belongs in Group 3. Its flamboyant colour pattern of black with yellow longitudinal stripes and orange margin is distinct. *P. dimidiatus* is somewhat similar to *P. violaceus* which is purple with a yellow stripe and marginal band, however, the former species has two wide yellow median stripes and a distinct bright orange margin. It is surprising that this large conspicuous species has rarely been recorded since 1893. The unusual prostate with its involuted lining may be due to this species' large size.

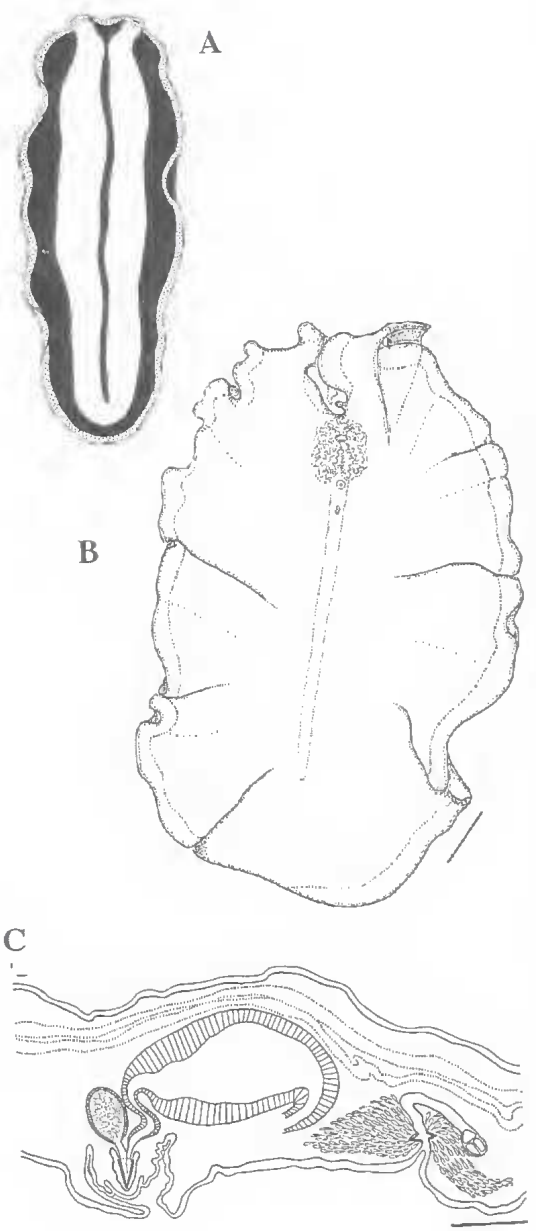


FIG. 13. *Pseudoceros dimidiatus* von Graff, in Saville-Kent, 1893. A, diagram of the dorsal colour pattern; B, QMG210489, wholemount showing the morphology from the ventral surface; C, QMG210489, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500μm.

HABITAT & DISTRIBUTION

Found under rubble from the reef slope. Rare from Madang. Record: Heron Is., N. Sulawesi.

Pseudoceros felis sp. nov.
(Figs 14A - C; 46G)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 07.02.92, WM, QMG210449.

PARATYPE: Heron Is., reef crest, 21.01.92, LS, QMG210448.

DESCRIPTION

Colour & pattern. Background grey with an intricate reticulate pattern of cream, pale yellow and dark brown blotches medially; irregular black spots medially, black blotches laterally. Narrow black bifurcating stripes extending laterally to the margin, interrupted occasionally. Margin indistinct, orange (136) with an extremely narrow black rim. Ventral surface grey medially, brown laterally and orange marginally.

External features. Small species. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes. Size: mature from 20 × 15mm; juvenile from 16 × 6mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle rounded oblong (645μm long), ejaculatory duct coiled. Prostate oval (255μm wide). Stylet short (143μm long). Male and female antra shallow.

DIAGNOSIS

With narrow, transverse, bifurcating black stripes; brown and cream mottling, faint orange margin.

ETYMOLOGY

From the Latin *felis* = cat, for its wildcat-like colour pattern.

REMARKS

This species belongs in Group 6 with one other species, *P. zebra*. *P. felis* differs from *P. zebra* in possessing narrow, transverse, bifurcating stripes and distinct mottling not a few broad stripes without mottling. This colour pattern is cryptic.

HABITAT & DISTRIBUTION

Found on the topside of algal covered boulders at the reef crest. Rare from Heron Is.

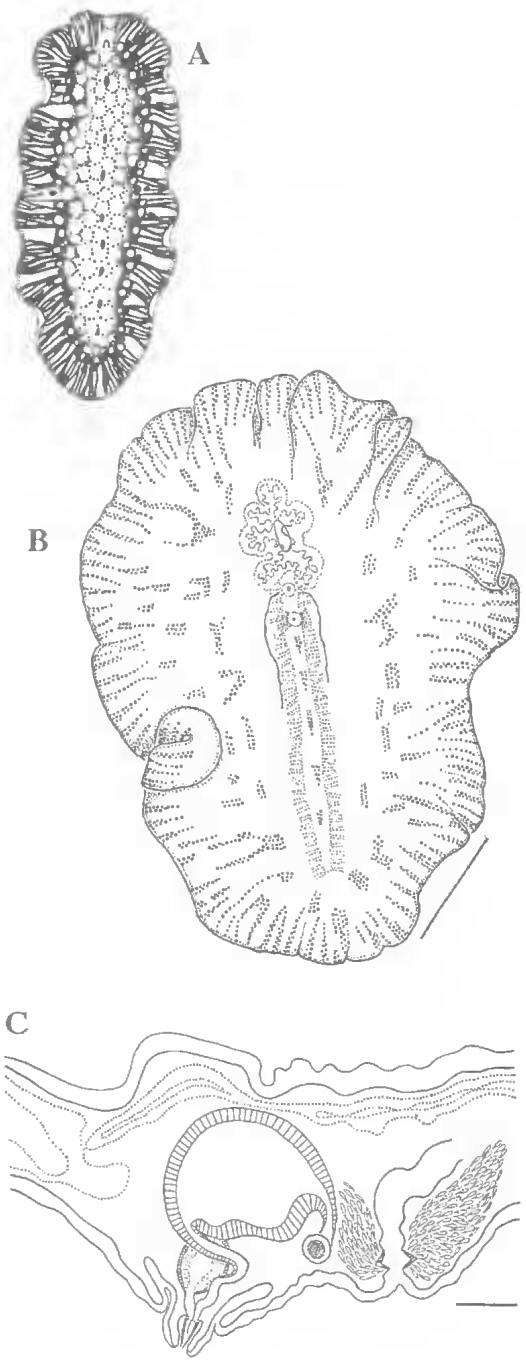


FIG. 14. *Pseudoceros felis* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210449, wholemount showing the morphology from the ventral surface; C, QMG210448, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250µm.

Pseudoceros ferrugineus Hyman, 1959
(Figs 15A - C; 47A)

Pseudoceros ferrugineus Hyman, 1959a: 571, fig. 9 b,c; Prudhoe, 1977: 586; Cannon & Newman, 1993: 83, pl. 4.
Pseudobiceros ferrugineus Faubel, 1984: 216.
Pseudoceros kentii von Graff, 1893: 362, pl. XIII, fig. 1; Poulter, 1987: 48, pl. 2.1.3.a.

MATERIAL EXAMINED

HOLOTYPE: Palau, Micronesia, Stanford Team, 20.10.55, S, USNM 28652.

OTHER MATERIAL: Heron Is., reef crest, 31.07.89, WM + eggs, QMG21036; WM, QMG210486; 17.10.89, LS & WM, QMG210365; WM, QMG210366; 26.06.91, S, QMG210440; 07.02.92, WM, QMG219367; 19.02.92, LS, QMG210368; 03.09.92, LS, QMG210369. Records: Broadhurst Reef, central GBR, reef slope, 15m, I. Loch, 29.06.74, CT; Philippines, 31.03.93, T. Gosliner, CT.

DESCRIPTION

Colour & pattern. Background dark red (186) with many small, compacted white dots covering the entire surface (making it appear brilliant purple-pink); dots more concentrated laterally. Two distinct marginal bands; inner marginal band red without dots (varies from narrow to wide), outer band bright orange (021). Ventral surface red intensifying to burgundy (220) towards the margin. Juveniles with same pattern except the white dots are fewer and relatively larger.

External features. Large species, margin with several deep ruffles. Pseudotentacles simple folds or broad flaps. Cerebral eyespot with a very large number of eyes. Size: mature from 60 × 35mm to 45 × 21mm; juvenile from 6 × 3mm.

Reproductive anatomy. Vas deferens branched. Seminal vesicle long (1.5mm), ejaculatory duct short. Prostatic vesicle small (285µm wide) with two chambers, highly muscular prostatic duct. Stylet small (158µm long). Male and female antra shallow.

REMARKS

This species belongs in Group 4 where only one other species possesses a red background, *P. vinosus*; however, *P. ferrugineus* possesses numerous, minute, white dots not white and yellow flecks.

Hyman (1959a) originally described this species as having two male pores. Examination of the holotype revealed only one male pore and complex pharyngeal folds which is characteristic

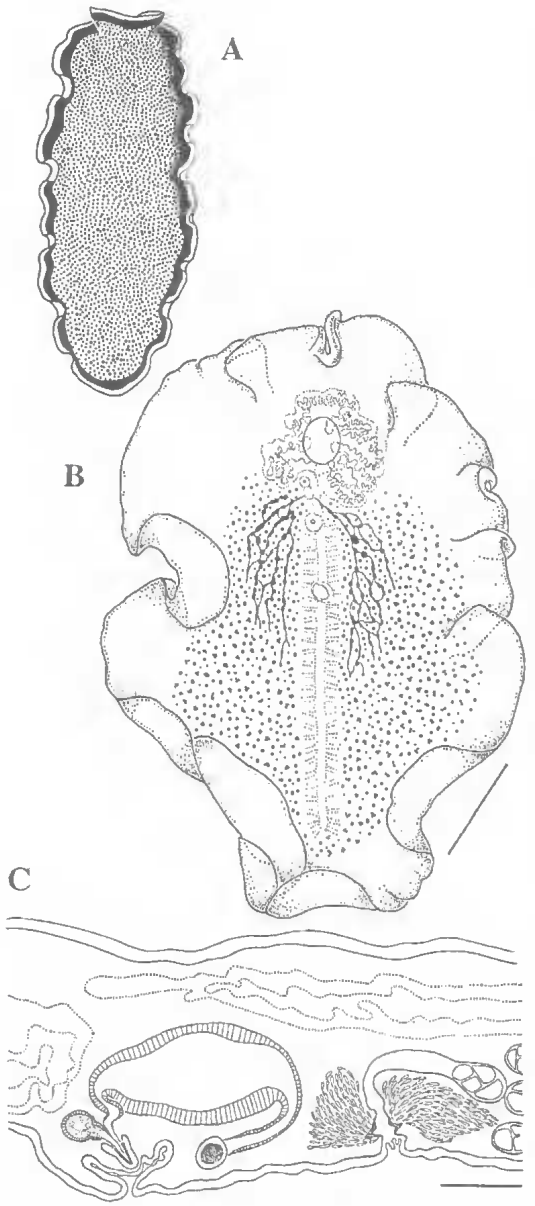


FIG. 15. *Pseudoceros ferrugineus* Hyman, 1959. A, diagram of the dorsal colour pattern; B, QMG210364, wholemount showing the morphology from the ventral surface; C, QMG210369, reconstruction of the reproductive anatomy. Scales: B, 1mm; C, 250µm.

of the genus. The two chambered prostate is unique to this species.

BIOLOGY

One animal was observed laying a thin layer of red eggs on an empty bivalve shell in an aquarium. Similar eggmasses have also been observed when an animal was removed from colonial ascidians under boulders.

HABITAT & DISTRIBUTION

This flamboyant species is found under boulders (sometimes on pink encrusting colonial ascidians) at the reef crest. Common from Heron Is. Records: Central GBR, Micronesia, Philippines.

Pseudoceros goslineri sp. nov.
(Figs 16A - C; 47B)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef slope, under sponge, 30m, 19.06.92, WM, QMG210454.

PARATYPE: Madang, reef crest, 3m, T. Gosliner, 15.06.92, LS, QMG210453.

OTHER MATERIAL: Heron Is., reef crest, 04.02.92, WM, QMG210452; reef slope, 12m, 02.02.93, LS, QMG210455. One Tree Island, reef crest, 16.08.93, S, QMG210493. Other Record: Wheeler Reef, central GBR, reef slope, 12m, I. Loch, 28.07.74, CT.

DESCRIPTION

Colour & pattern. Colour pattern variable. Background cream mottled with orange, pink and brick red dots (PNG animals darker brown medially, brown not orange dots); concentrated brick red dots medially appearing as irregular elongate blotches. Margin composed of purple (240) and pink (236) irregular dots and spots, marginal spots closer together anteriorly across pseudotentacles. Ventrally light violet (263).

External features. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes. Size: mature from 70 × 28mm to 14 × 8mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle elongate (623µm long); ejaculatory duct short, coiled. Prostate round (225µm wide). Stylet extremely short (98µm long). Male and female antra deep.

DIAGNOSIS

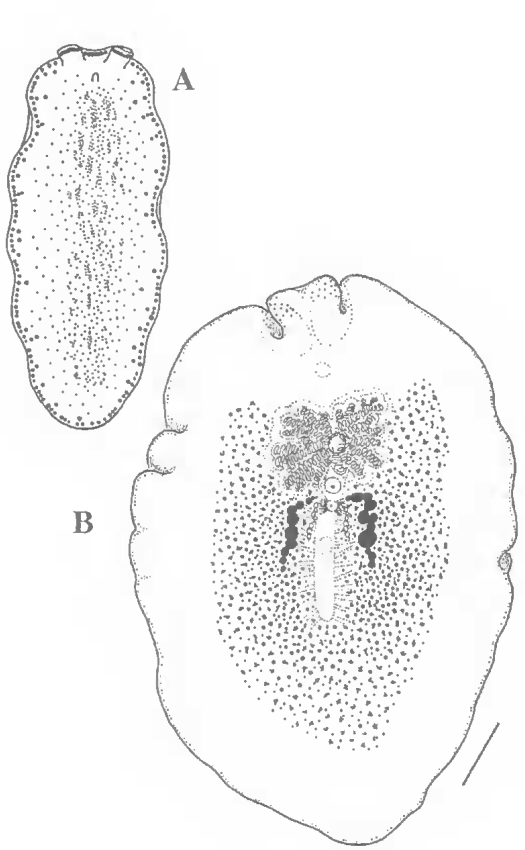
Cream with purple, pink and orange spots; margin with purple and pink spots and dots.

ETYMOLOGY

For Dr Terry Gosliner.

REMARKS

This species belongs in Group 4 in which several species possess a cream background, however, *P. goslineri* most closely resembles *P. ouini* sp. nov.



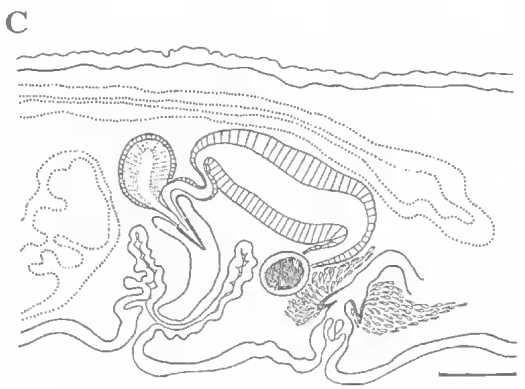


FIG. 16. *Pseudoceros goslineri* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210453, wholemount showing the morphology from the ventral surface; C, QMG210454, reconstruction of the reproductive anatomy. Scales: B, 1mm, C, 500µm.

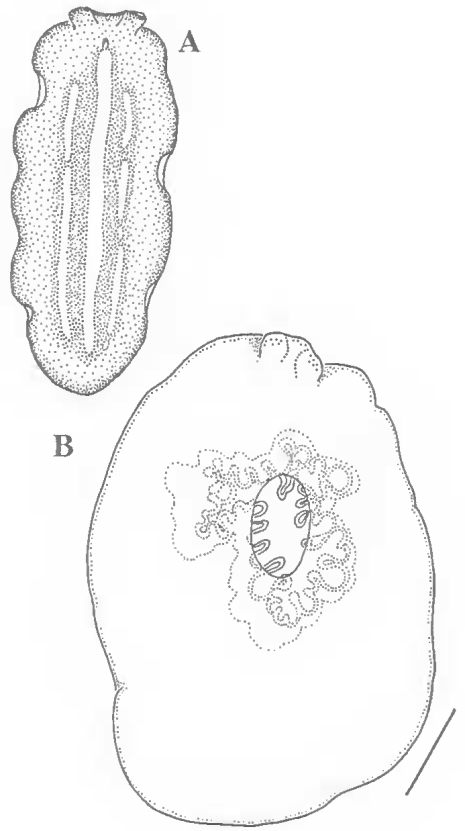


FIG. 17. *Pseudoceros gravieri* Meixner, 1907. A, diagram of the dorsal colour pattern; B, QMG210345, wholemount showing the morphology from the ventral surface. Scales: B, 2.5mm; C, 250µm.

HABITAT & DISTRIBUTION

Found under boulders from the reef crest to the reef slope (one animal found on a sponge at 30m). Rare from Heron, One Tree Is. and Madang. Record: Central GBR.

Pseudoceros gravieri Meixner, 1907
(Figs 17A, B; 47C, D)

Pseudoceros gravieri Meixner, 1907: 468-469, Pl. XXVI, figs 7a, 7b, 12; Prudhoe, 1989: 83.

MATERIAL EXAMINED

HOLOTYPE: Unknown, Djibouti.

OTHER MATERIAL: Heron Is., reef slope, 9m, 12.07.89, WM, QMG210345. Record: GBR, G. Allan, CT.

DESCRIPTION

Colour & pattern. Background blue-purple (279 or 2715), darker medially, intensifying to purple (252) at margin. Three bright yellow (122) longitudinal stripes in immature specimen; central stripe wide; two lateral stripes narrower, shorter and discontinuous (Fig. 47C). Larger specimens (Fig. 47D) with numerous discontinuous longitudinal yellow stripes. Ventrally light mauve.

External features. Pseudotentacles simple folds. Size: juvenile at 6 × 3mm.

Reproductive anatomy. The only specimen collected was immature.

REMARKS

This species belongs in Group 3 where the majority of species possess a dark purple or black background. Only *P. gravieri*, *P. bifurcus* and *P. tristriatus* are blue as mentioned above.

According to Meixner (1907), Gravier first described this species as having, 'bandes jaune d'or encadrées par des bandes bleu foncé. Un liseré bleu plus clair sur tout le poutour'. The figure given by Meixner shows that this species possesses a complex pharynx and simple folded pseudotentacles which is characteristic of the genus.

This species could be easily confused with *P. tristriatus* Hyman, 1959a which is described as blue with three longitudinal orange stripes, each stripe bordered by black and extending almost to the posterior end. However, *P. gravieri* has a variable number of yellow longitudinal stripes that are clearly not bordered by black.

HABITAT & DISTRIBUTION

Found on blue-purple ascidians (*Clavelina* sp.) under ledges on the reef slope. Rare from Heron Is. Record: GBR, Djibouti.

Pseudoceros heronensis sp. nov.
(Figs 18A - C; 47E)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 17.08.92, WM, QMG210462.

PARATYPE: Heron Is., reef crest, 08.09.92, LS, QMG210465.

OTHER MATERIAL: Heron Is., reef crest, 22.02.92, S, QMG210460; 29.07.92, LS, QMG210461; 06.09.92, WM, QMG210463; WM, QMG210464; 21.02.93, WM, QMG210466.

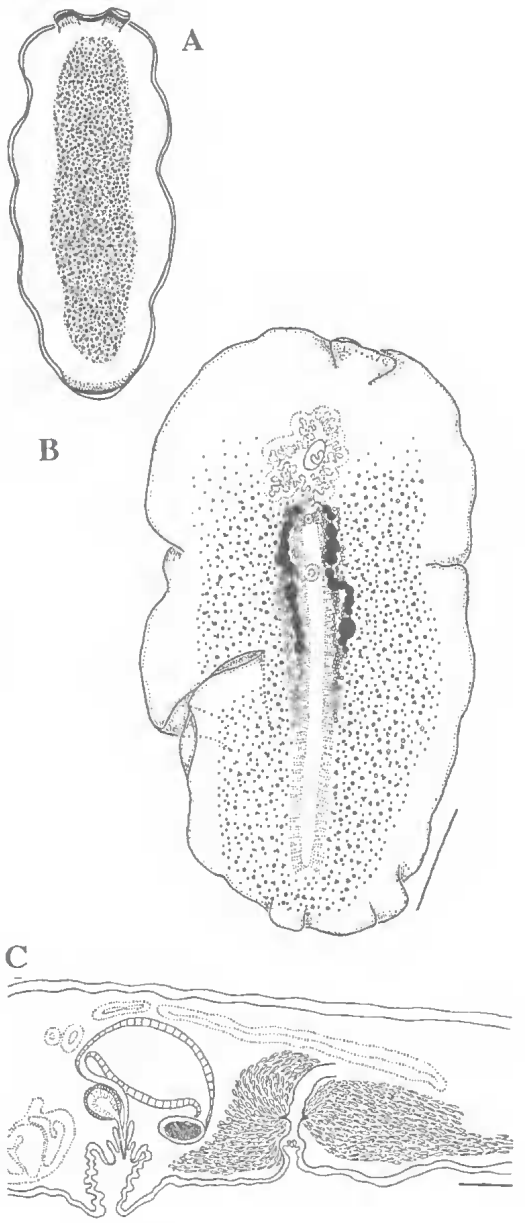


FIG. 18. *Pseudoceros heronensis* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210462, wholemount showing the morphology from the ventral surface; C, QMG210465, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

DESCRIPTION

Colour & pattern. Background cream-yellow; medially with small chocolate brown (483) and

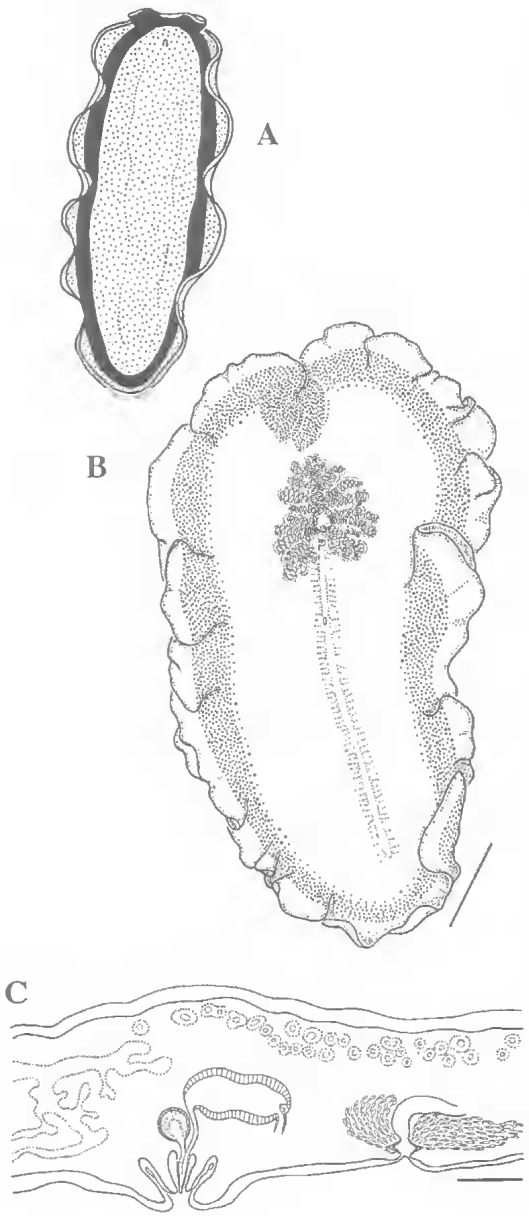


FIG. 19. *Pseudoceros jeòborum* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210470, wholemount showing the morphology from the ventral surface;C, QMG210471, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

white dots (clusters of microdots). Margin extremely wide, cream, covered in orange (172) microdots; narrow yellow-green (394) rim. Three narrow marginal bands found only anteriorly on pseudotentacles and along the posterior margin; inner band orange (165), middle band black and yellow-green at rim. Gut diverticula usually orange.

External features. Small species. Pseudotentacles simple folds. Cerebral eyespot with about 20 eyes. Size: mature from 18 × 8mm to 28 × 12mm; juvenile from 14 × 6mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle round oblong (600µm long); ejaculatory duct long, not coiled. Prostate round (188µm width). Stylet short (135mm long). Male antrum deep and voluminous; female antrum deep, cement glands extensive.

DIAGNOSIS

Cream with orange, black and yellow short marginal bands occurring only anteriorly along the pseudotentacles and along the posterior margin, mottled medially.

ETYMOLOGY

For the Heron Island Research Station.

REMARKS

This species belongs in Group 4 in which several other species possess a cream, yellow or white background. *P. heronensis* is somewhat similar to *P. bimarginatus* which also possesses orange, black and yellow marginal bands, however, *P. heronensis* has these marginal bands restricted to the anterior and posterior end not around the entire margin. This species also resembles *P. verecundus* sp. nov. Cryptic on colonial ascidians.

HABITAT & DISTRIBUTION

Found under boulders, usually feeding on orange and pink colonial ascidians. Common from Heron Is.

Pseudoceros jebborum sp. nov.
(Figs 19A - C; 47F)

Pseudoceros sp. Poulter, 1987: 48, pl. 2.I.2.f

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 3m, 01.02.93, WM, QMG210470.

PARATYPE: Heron Is., reef slope, 10m, 06.02.93, LS, QMG210471.

OTHER MATERIAL: Madang, reef crest, 3m, 23.06.92, WM, QMG210467; 26.06.92, LS, QMG210468; 28.06.92, WM, QMG210469; Heron Is., reef slope, 10m, 06.02.93, S, QMG210472.

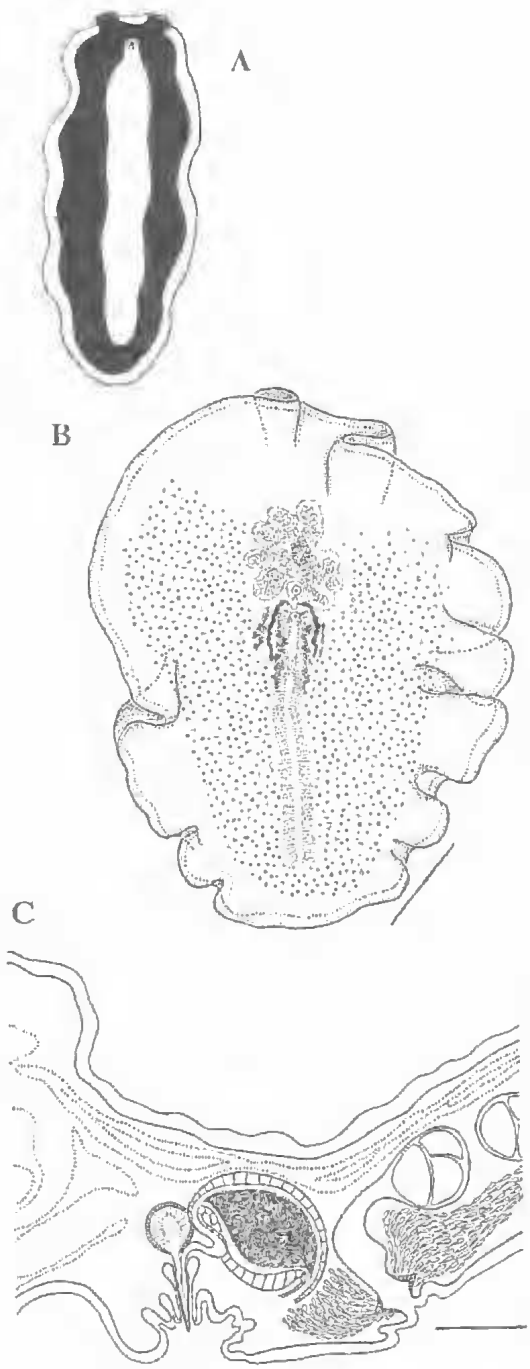


FIG. 20. *Pseudoceros laticlavus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210354, wholemount showing the morphology from the ventral surface; C, QMG210353, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250µm.

DESCRIPTION

Colour & pattern. Background cream-orange (121), grey black laterally near the margin and across the pseudotentacles. Marginal band wide, cream with a narrow distinct bright yellow (102) rim. Ventrally same colour pattern, pharyngeal lobes usually dark purple.

External features. Margin with shallow ruffles, tapering slightly posteriorly. Pseudotentacles simple folds. Cerebral eyespot relatively small with about 60 eyes. Size: mature from 70 × 30mm to 40 × 30mm; juvenile (or not mature) from 27 × 10mm to 70 × 32mm.

Reproductive anatomy. Seminal vesicle long (850µm); ejaculatory duct short, not coiled. Prostate small, round (240µm wide). Stylet relatively large (278µm long), larger than prostate. Male and female antra shallow.

DIAGNOSIS

Cream-orange medially with two distinct marginal bands; inner wide black, outer cream-orange.

ETYMOLOGY

For the Jebb family (Christensen Research Institute, Madang).

REMARKS

This species belongs in Group 2 and is the only one possessing an orange background. *P. jebborum* somewhat resembles *P. paralaticlavus* sp. nov. (Group 3) in pattern, however, the former species has a narrow black marginal band, not a black background. Several animals were found to be immature although they were relatively large (i.e. 70 × 32mm).

HABITAT & DISTRIBUTION

Found under rubble on the reef slope. Rare from Heron Is., Madang. Record: Hawaii.

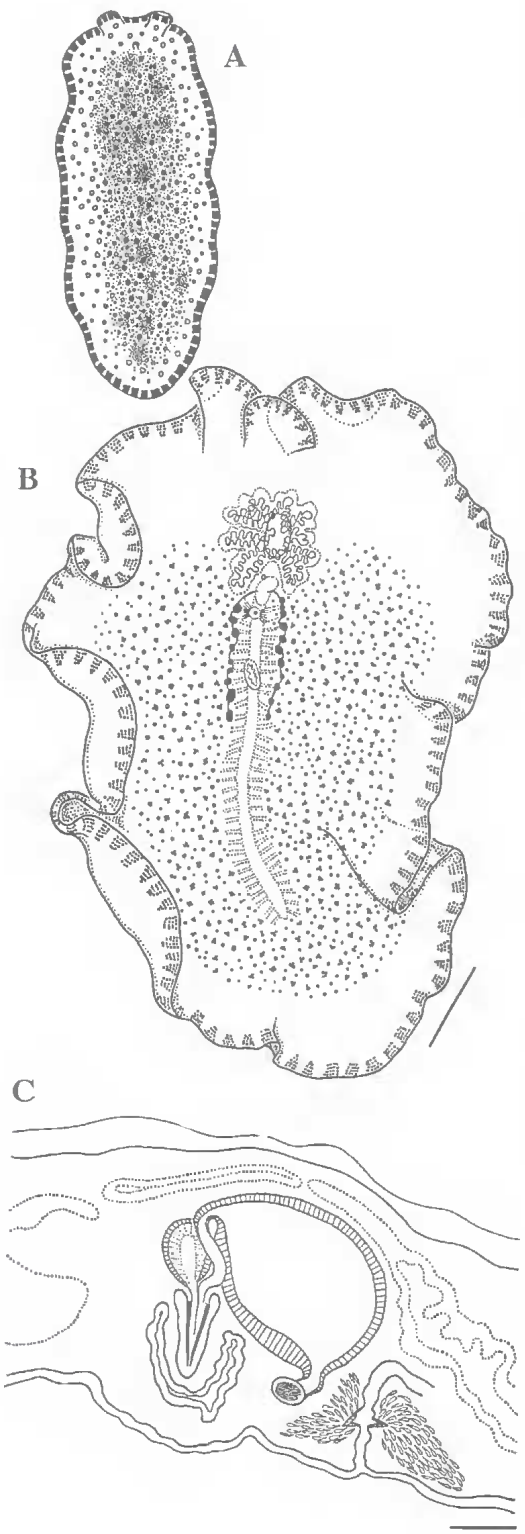
Pseudoceros laticlavus sp. nov.
(Figs 20A - C; 48A)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 31.07.89, WM, QMG210346.

PARATYPES: Heron Is., reef crest, 31.07.89, WM, QMG210347; t4.02.92, LS, QMG210353; WM, QMG210348; S, QMG210349.

OTHER MATERIAL: Heron Is., reef crest, 06.t1.90, S, QMG210443; 20.06.91, S, QMG210350; 21.01.92, LS, QMG21035; 31.01.92, WM, QMG210352; 19.02.92, WM, QMG210354; S, QMG210358; 26.08.92, WM, QMG210355; S, QMG210356;



31.08.92, WM, QMG210357; S, 2 spec., QMG210438; 04.02.93, WM, QMG210359; LS, QMG210360; 17.02.93, WM, QMG210361; 20.02.93, S, QMG210362; One Tree Is., reef crest, 16.08.93, QMG210492.

DESCRIPTION

Colour & pattern. Background black (not velvety) with a single wide white median stripe; marginal band wide white, discontinuous over the pseudotentacles. Ventrally same pattern.

External features. Relatively small species. Pseudotentacles simple folds. Cerebral eyespot with about 15 eyes. Size: mature from 14 × 8mm to 30 × 10mm; juvenile from 3 × 2mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle small, rounded oval (338µm long); ejaculatory duct coiled. Prostate extremely small (113µm wide). Stylet narrow (158µm long), larger than prostate. Male and female antra shallow and wide.

DIAGNOSIS

Black with a single white median stripe and wide white margin.

ETYMOLOGY

From the Latin *laticlavus* = broad stripe, referring to the distinct median stripe.

REMARKS

This species belongs in Group 3 in which several species possess a dark purple or black background but only one other species also has white stripes, *P. paralaticlavus* sp. nov.

HABITAT & DISTRIBUTION

Found on colonial ascidians, under boulders at reef crest. Common from Heron Is., rare from One Tree Is.

Pseudoceros leptostictus Bock, 1913
(Fig. 21A - C; 48B)

Pseudoceros leptostictus Bock, 1913: 256 - 257, pl. III, fig. 12, 13; Marcus, 1950: 86; Prudhoe, 1977: 597 - 598; Faubel, 1984: 239, incerta sedis.

FIG. 21. *Pseudoceros leptostictus* Bock, 1913. A, diagram of the dorsal colour pattern; B, QMG210341, wholemount showing the morphology from the ventral surface; C, QMG210342, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250µm.

MATERIAL EXAMINED
HOLOTYPE: unknown, Western Australia.
PARATYPE: Western Australia, not located, AM W.5457.
OTHER MATERIAL: Heron Is., reef crest, 29.09.89, WM, QMG210338; reef slope, 6m, 30.02.92, LS, QMG210342; reef crest, 29.07.92, WM, QMG210341; 23.08.92, LS, QMG210343; 06.09.92, WM, QMG210344; Motupore Is., off Port Moresby, PNG, reef slope, D. Brunckhorst, 17.06.88, S, QMG210339; Madang, reef crest, 26.06.92, WM, QMG210340.

DESCRIPTION

Colour & pattern. Background cream-white: pale yellow (127) medially with orange-brown (158) blotches; entire surface covered with small scattered spots, spots orange laterally, black medially, interspersed with smaller white spots. Marginal band interrupted, narrow black with an extremely narrow, yellow-green (387) rim. Ventrally pink (211) with an uninterrupted black marginal band.

External features. Pseudotentacles simple folds. Cerebral eyespot small with about 40 eyes. Pseudotentacular eyes obscured due to black pigment. Size: mature from 16 × 9mm to 26 × 10mm; juvenile 10 × 5mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle rounded oblong (825µm long), ejaculatory duct coiled. Prostate oval (263µm wide), same size as stylet (263µm long). Male and female antra deep.

REMARKS

This species belongs in Group 4 in which four other species possess a cream background colour. Only two species have an interrupted marginal band, *P. interuptus* and *P. memoralis*. *P. leptostictus* differs from *P. interruptus* by its cream colour and narrow black and yellow-green marginal bands, not brownish with mottles of reddish brown and four marginal bands, and differs from *P. memoralis* in having two distinct marginal bands not three.

Bock (1913) originally described this species (from a preserved specimen) as sandy yellow, brighter yellow medially becoming reddish towards the margins, black stippling over the dorsal surface, margin with a band of quadrangular blackish markings, bounded by a thin band of yellow. The pharynx and the reproductive structures were not described by Bock or Prudhoe (1977) but the description of the characteristic colour pattern is similar to our specimens.

HABITAT & DISTRIBUTION

Found on purple colonial ascidians under boulders at the reef crest and under ledges on the reef slope. Rare from Heron Is., Madang and Motupore Is. (9°31' S, 147°10' E), south PNG. Records: Northern GBR, Western Australia.

Pseudoceros lindae sp. nov.
(Figs 22A - C; 48C)

MATERIAL EXAMINED
HOLOTYPE: Heron Is., reef slope, 10m, 23.02.93, WM, QMG210417.
PARATYPES: Heron Is., reef slope, 10m, 17.02.90, WM, QMG210413; 23.02.93, LS, QMG210416.
OTHER MATERIAL: Heron Is., reef slope, 3 - 12m, 07.10.89, WM, QMG210412; 26.06.91, WM & LS, QMG210414; 27.01.93, LS, QMG210415.

DESCRIPTION

Colour & pattern. Dramatic pattern of maculae in vivid colours. Background burgundy (214) intensifying towards the margin; numerous large golden-yellow (116) oval to round shaped maculae medially, becoming larger and blue laterally and blending into the marginal band. Background fading to turquoise (311) then sky blue (2975) towards the margin; margin composed of large turquoise and sky blue maculae which form an irregular wide band. Ventral surface light purple-violet (2635).

External features. Body thick and fleshy. Pseudotentacles broad flaps. Pharynx with highly ruffled complex pharyngeal folds. Size: mature from 32 × 12mm to 44 × 12mm; juvenile from 25 × 17mm.

Reproductive anatomy. Vas deferens branched. Seminal vesicle elongate oblong (1.5mm long); ejaculatory duct short, coiled. Prostate large oval (444µm wide). Stylet short (185µm long). Male and female antra deep.

DIAGNOSIS

Burgundy background with large golden yellow maculae medially and blue maculae marginally.

ETYMOLOGY

In honour of Mrs Linda Newman.

REMARKS

This species belongs in Group 5 with two other species. *P. lindae* differs from these species by having a burgundy background not grey background as in *P. glaucus* nor black as in *P. scintillatus* sp. nov.

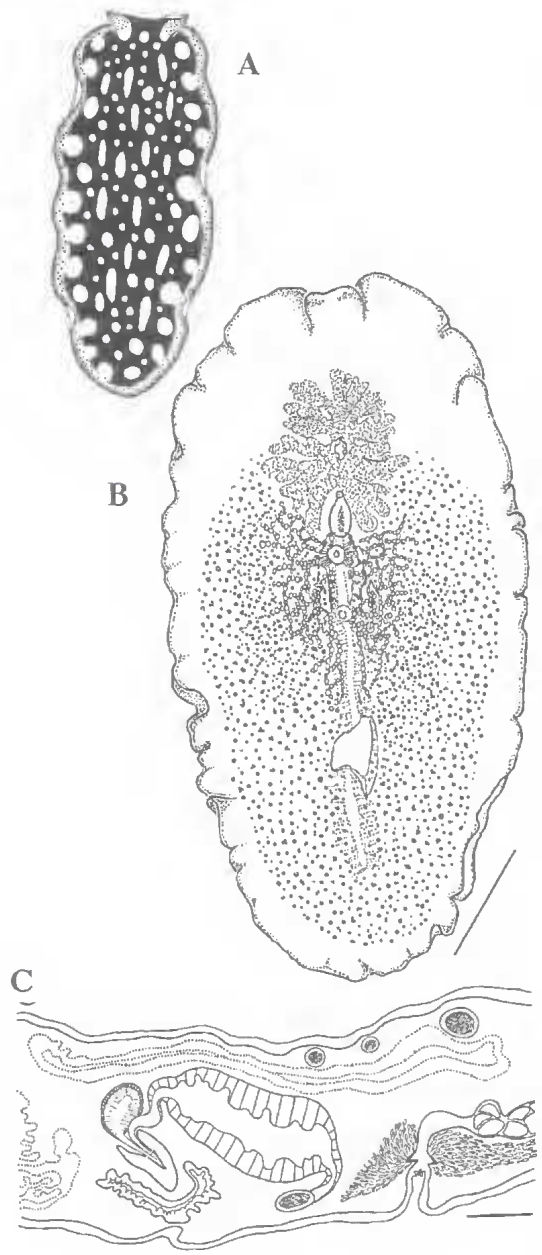


FIG. 22. *Pseudoceros lindae* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210417, wholemount showing the morphology from the ventral surface; C, QMG210416, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

BIOLOGY

Animals were observed copulating in situ and in the laboratory, both animals showing damage from copulation (Fig. 48C).

HABITAT & DISTRIBUTION

This species tends to be more common under ledges on the reef slope especially at night. Common from Heron Is.

Pseudoceros monostichos sp. nov.
(Figs 23A - C; 48D)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, 26.06.92, WM, QMG210451.

OTHER MATERIAL: Wistari Reef, off Heron Is., reef slope, 10m, 28.01.92, LS, QMG210450.

DESCRIPTION

Colour & pattern. Background cream with a distinct narrow black-brown median line; line bisects the cerebral eyespot anteriorly, does not extend to the posterior margin; line bordered laterally by white and then light brown. Narrow margin with four indistinct bands; inner band yellow (106) intensifying to green (367) then sky blue (298) then purple (257) at rim. Ventrally cream with same marginal bands, wide dark purple-black median stripe, dark grey laterally.

External features. Dorsal surface with numerous dimples only observed when resting, tapering slightly posteriorly. Pseudotentacles broad flaps. Cerebral eyespot obscured due to dark pigment of the median line. Size: mature 35 × 12mm; juvenile 25 × 9mm.

Reproductive anatomy. Seminal vesicle large (1.5mm long), ejaculatory duct not coiled. Prostate oval (300µm wide). Stylet extremely small (113µm long). Male and female antra shallow.

DIAGNOSIS

Cream with a single narrow dorsal median black-brown median stripe, wide brown ventral median stripe and unusual dimpled texture of the dorsal surface.

ETYMOLOGY

From the Latin *mono* = one, *stichos* = line, for its characteristic narrow median stripe.

REMARKS

This species belongs in Group 3. No other species from this group has a cream background colour. *P. bifurcus* has a wide median stripe, however, this white stripe is bordered by burgundy and is not a fine black median line as in *P. monostichos*. This species is unusual as the ventral surface is more strikingly patterned than the dorsal surface.

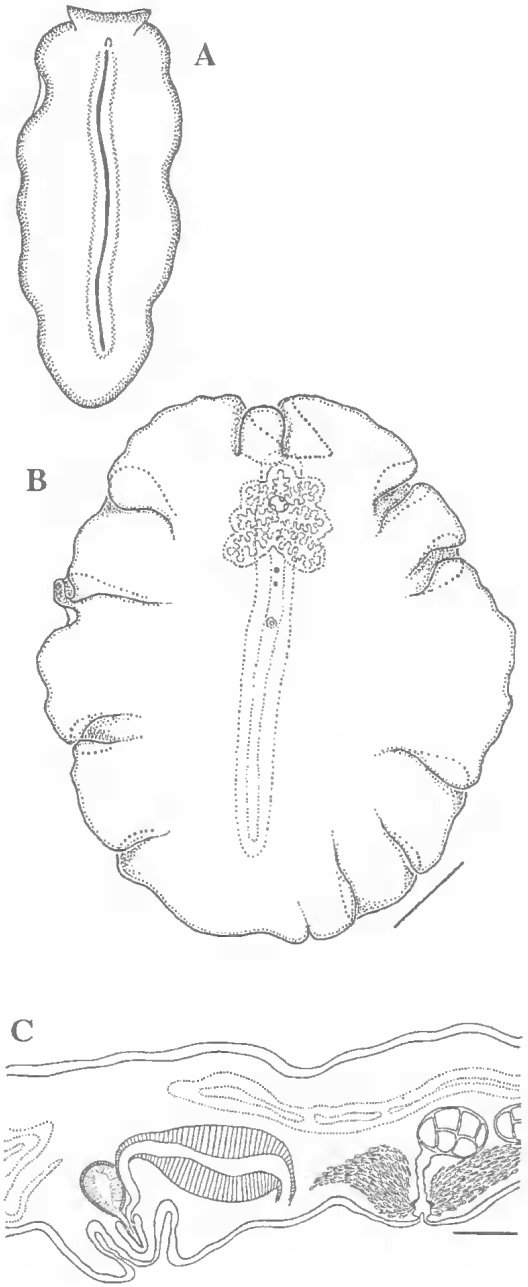


FIG. 23. *Pseudoceros monostichos* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210451, wholemount showing the morphology from the ventral surface; C, QMG210450, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250µm.

HABITAT & DISTRIBUTION

Found under rubble at the reef crest and under ledges on the reef slope. Rare from Heron Is. and Madang.

Pseudoceros ouini sp. nov.
(Figs 24A - C; 48E)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, 27.06.92, WM & LS, QMG210631.

DESCRIPTION

Colour & pattern. Background transparent beige and opaque cream-white with faint orange mottling medially and laterally. Margin with well spaced, evenly sized, bright pink (232) spots, spots more concentrated anteriorly to form a band across the pseudotentacles. Ventrally white, margin with same spotted pattern.

External features. Pseudotentacles broad flaps. Cerebral eyespot with about 30 eyes. Size: mature at 20 × 10mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle small (638µm long); ejaculatory duct short, not coiled. Prostate small round (240µm wide). Stylet short (128µm long). Male and female antra deep.

DIAGNOSIS

Cream background with widely spaced, evenly sized, pink marginal spots.

ETYMOLOGY

For Mr Jean-Marc Ouin.

REMARKS

This species belongs in Group 4. Several other species possess a cream background colour, but only *P. concinnus* and *P. goslineri* have spots along the margin. *P. concinnus* (Collingwood, 1876) was originally described as 'cream coloured with an edging of blue all around, composed of small and larger spots running into one another'. The margin is distinctly different in *P. ouini* since the spots are widely spaced and pink rather than blue. *P. goslineri* is similarly coloured but the pink dots and spots along the margin are more numerous and irregular, with distinct brown blotches medially.

DISTRIBUTION

Found under rubble at the reef crest. Rare from Madang.

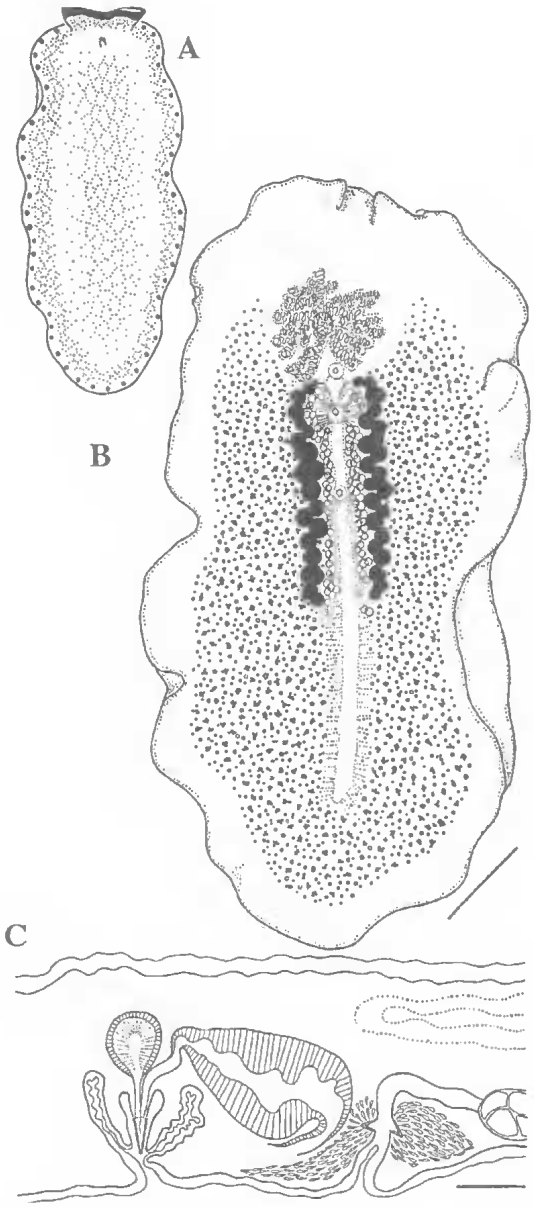


FIG. 24. *Pseudoceros ouini* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210631, wholemount showing the morphology from the ventral surface; C, QMG210631, reconstruction of the reproductive anatomy. Scales: 2mm; C, 250µm.

Pseudoceros paralaticlavus sp. nov.
(Figs 25A - C; 48F)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 07.02.93, WM, QMG210432.

PARATYPES: Heron Is., reef crest, 07.09.92, WM, QMG210428; reef slope, 3m, 01.02.93, LS, QMG210431.

OTHER MATERIAL: Heron Is., reef crest, 17.10.89, WM, QMG210418; LS, QMG210459; 21.01.92, S, QMG210419; WM, QMG210420; 19.02.92, S, QMG210422; 07.08.92, WM, QMG210426; 03.09.92, WM, QMG210427; 17.02.93, S, QMG210435; One Tree Is., reef crest, 12.09.92, WM, QMG210429. Madang, reef crest, 3 - 5m, 01.06.92, LS, QMG210423; 08.06.92, LS, T. Gosliner, QMG210424; 11.06.92, WM, QMG210425; Planet Rock, S. Madang, reef slope, 6m, 26.05.92, S, QMG210436; Hansa Bay, Laing Is., reef crest, J. - M. Ouin, 15.06.92, WM, QMG210430.

DESCRIPTION

Colour & pattern. Background velvety black with wide cream-white median band and a narrow white median stripe. Two marginal bands; inner band wide, white; rim narrow, bright yellow (Process Yellow) or orange-yellow (109); pseudotentacles black with yellow rim. Ventrally same pattern. Pharynx sometimes dark purple (2695); ovaries and oviducts bright red-purple (226).

External features. Pseudotentacles simple folds. Cerebral eyespot with about 30 eyes. Size: mature from 22 × 10mm to 50 × 22mm; juvenile 9 × 6mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle oblong (593µm long); ejaculatory duct long, coiled. Prostate round, extremely small (113µm wide). Stylet (165µm long) larger than prostate. Male and female antra shallow and wide.

DIAGNOSIS

Black with broad white longitudinal median stripe, margin with two bands: inner wide, white; outer narrow, yellow-orange.

ETYMOLOGY

From the Latin *para* = like, *laticlavus* = broad stripe, for its similarity in colour pattern to *P. laticlavus*.

REMARKS

This species belongs in Group 3 and is similar to *P. laticlavus*. However, *P. paralaticlavus* possesses a distinct yellow or orange marginal band and this band is absent in *P. laticlavus*. As well, *P. paralaticlavus* reaches a larger size at maturity (22 × 10mm to 50 × 22mm) compared to *P. laticlavus* (14 × 8mm to 30 × 10mm).

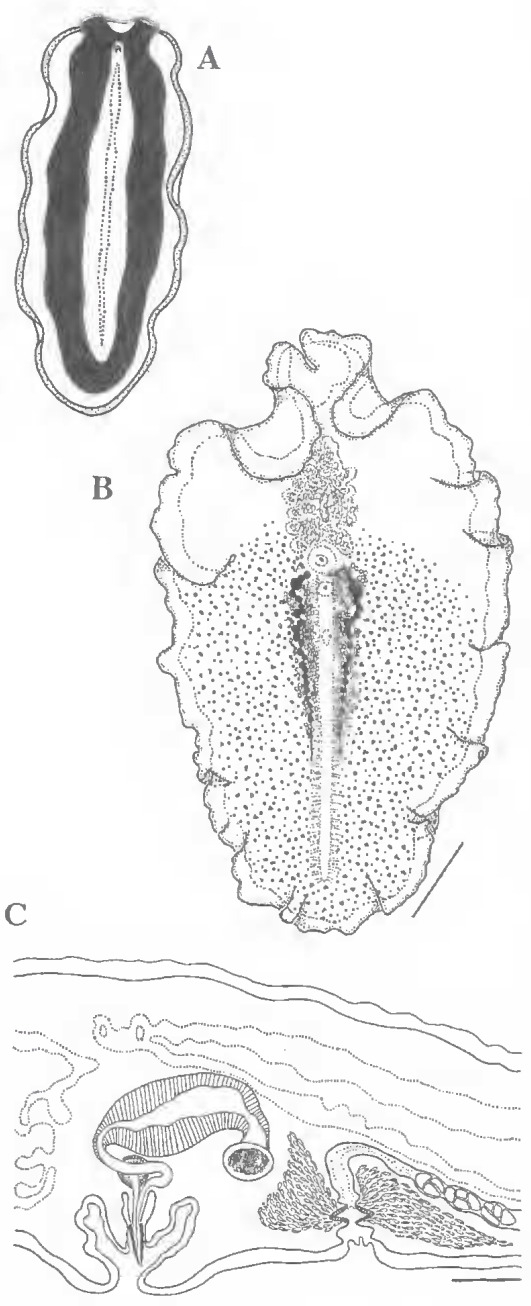


FIG. 25. *Pseudoceros paralaticlavus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210432, wholemount showing the morphology from the ventral surface; C, QMG210431, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250µm.

HABITAT & DISTRIBUTION

Found on yellow colonial ascidians under boulders at the reef crest. Common from Heron Is., rare from Madang.

Pseudoceros periaurantius sp. nov.
(Figs 26A - C; 49A)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 6m, 30.07.92, WM, QMG210475.

PARATYPE: Heron Is., reef slope, 3m, 05.02.93, LS, QMG210476.

DESCRIPTION

Colour & pattern. Background velvety black with a distinct wide brilliant orange (136) marginal band. Ventrally dark grey with a lighter grey marginal band.

External features. Pseudotentacles broad flaps. Relatively small cerebral eyespot with about 50 eyes. Size: mature at 18 × 12mm; juvenile at 30 × 16mm.

Reproductive anatomy. Vas deferens not observed. Seminal vesicle small, round (413µm long); ejaculatory duct long, coiled. Prostate large, rounded oval (262mm wide). Stylet narrow (225µm long), similar in size to prostate. Male and female antra shallow.

REMARKS

This species belongs in Group 2. Several other species possess a black background and vibrantly coloured marginal bands. Only one other species has an orange marginal band, *P. litoralis*, but *P. periaurantius* is black with an orange marginal band not brown with an orange inner marginal band and brown rim.

DIAGNOSIS

Black background with brilliant, wide orange marginal band.

ETYMOLOGY

From the Latin *peri* = around, *aurantius* = orange, for its distinct orange marginal band.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Rare from Heron Is.

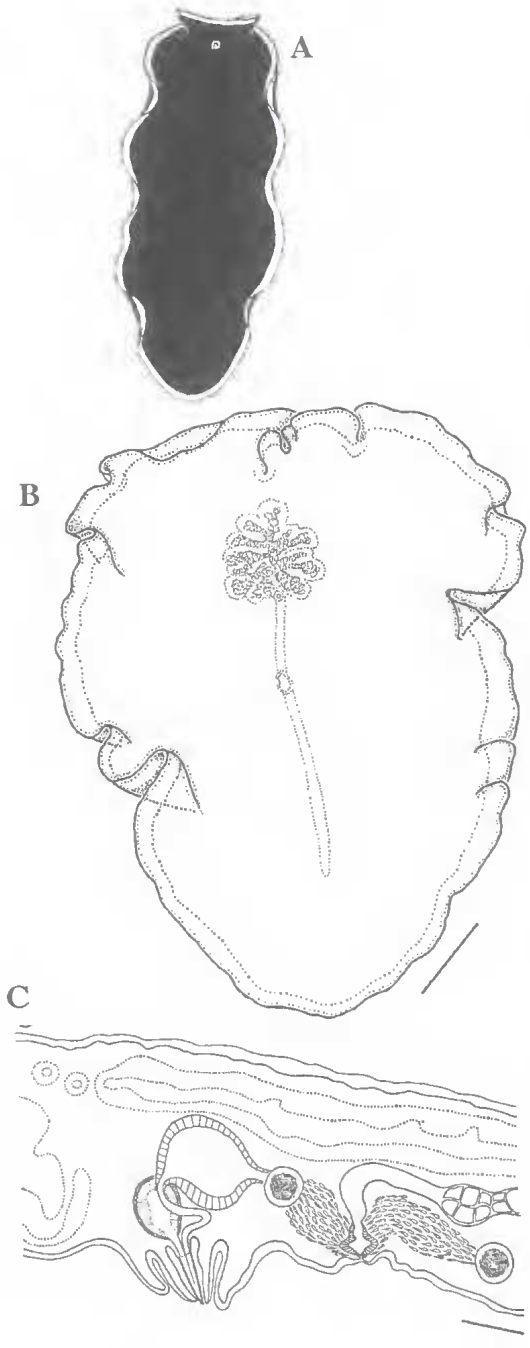


FIG. 26. *Pseudoceros periaurantius* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210475, wholemount showing the morphology from the ventral surface; C, QMG210476, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 250µm.

Pseudoceros peripurpureus sp. nov.
(Figs 27A - C; 49B)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 21m, WM, 06.02.92, QMG210457.

PARATYPES: Heron Is., reef slope, 21m, LS, QMG210456; 10m, night, 25.02.92, LS, QMG210458.

DESCRIPTION

Colour & pattern. Background velvety black with two distinct narrow marginal bands; inner band violet (245), dark purple (2735) at rim. Ventrally dark blue-black, same marginal bands.

External features. Large species, body thick and fleshy, tapering slightly posteriorly. Pseudotentacles broad flaps. Eyes obscured by black pigment. Size: mature from 40 × 25mm to 60 × 35mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle large, oblong (1.8mm long); ejaculatory duct coiled. Prostate oval (398µm wide). Stylet long (223µm long). Male and female antra shallow.

DIAGNOSIS

Black with two narrow marginal bands; inner violet, outer purple.

ETYMOLOGY

From the Latin *peri* = around, *purpureus* = purple, for its purple marginal bands.

REMARKS

This species belongs in Group 2 in which several species possess a black background with vibrantly coloured marginal bands, however, no other species has a purple marginal band. Hyman (1959a) described *Pseudoceros caeruleocinctus* as having a brilliant blue marginal band but it is uncertain whether this species belongs to *Pseudoceros* since morphological details were not given. Although the holotype was examined, the shape of the pharynx could not be ascertained due to the black pigmentation and the contracted nature of the specimen.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Rare from Heron Is.

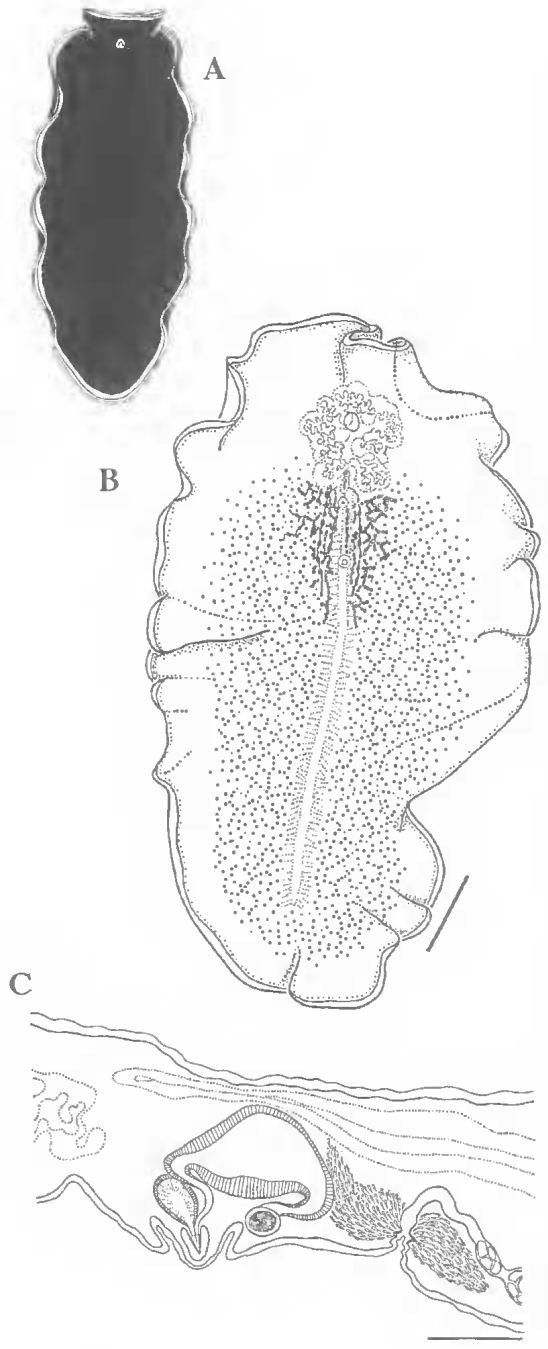


FIG. 27. *Pseudoceros peripurpureus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210457, wholemount showing the morphology from the ventral surface; C, QMG210458, reconstruction of the reproductive anatomy. Scales: B, 5mm; C, 500µm.

Pseudoceros prudhoei sp. nov.
(Figs 28A - C; 49C)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 14.09.89, WM, QMG210398.

PARATYPES: 23.08.92, LS, QMG210402; 23.02.93, LS, QMG210403.

OTHER MATERIAL: Heron Is., reef crest, 05.02.92, WM, QMG210399; Madang, reef crest, 2 - 5m, T. QMGosliner, 06.06.92, S, QMG210442; 09.06.92, WM, QMG210400; WM, QMG210401; 01.06.92, S, 2 spec., QMG210434; 24.06.92, S, 2 spec., 24.06.92, QMG210433.

DESCRIPTION

Colour & pattern. Background brown-orange (143) with two marginal bands: inner band wide, sky blue (290 or 306) or mauve (5315); outer band distinct, narrow, yellow (102 or 393) or cream. Entire dorsal surface covered in dark brown microdots. Ventrally same colour pattern.

External features. Margin with few ruffles. Pseudotentacles simple folds. Cerebral eyespot relatively small with 30 to 50 eyes. Size: mature from 30 × 8mm; juvenile from 7 × 3mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle elongate oblong (638µm long); ejaculatory duct short, not coiled. Prostate round (248µm wide). Stylet long (225µm long), similar size to prostate. Male antrum deep, voluminous. Female antrum deep.

DIAGNOSIS

Brown covered in brown microdots: two marginal bands; inner band wide, blue or light purple; outer band narrow, bright yellow.

ETYMOLOGY

In honour of the late Mr Stephen Prudhoe.

REMARKS

This species belongs in Group 2. Only *P. litoralis* also possesses a brown background colour with two marginal bands, however, in *P. prudhoei* the marginal bands are blue and yellow not orange and black.

HABITAT & DISTRIBUTION

Found under boulders and under rubble at reef crest. Rare from Heron Is. and Madang.

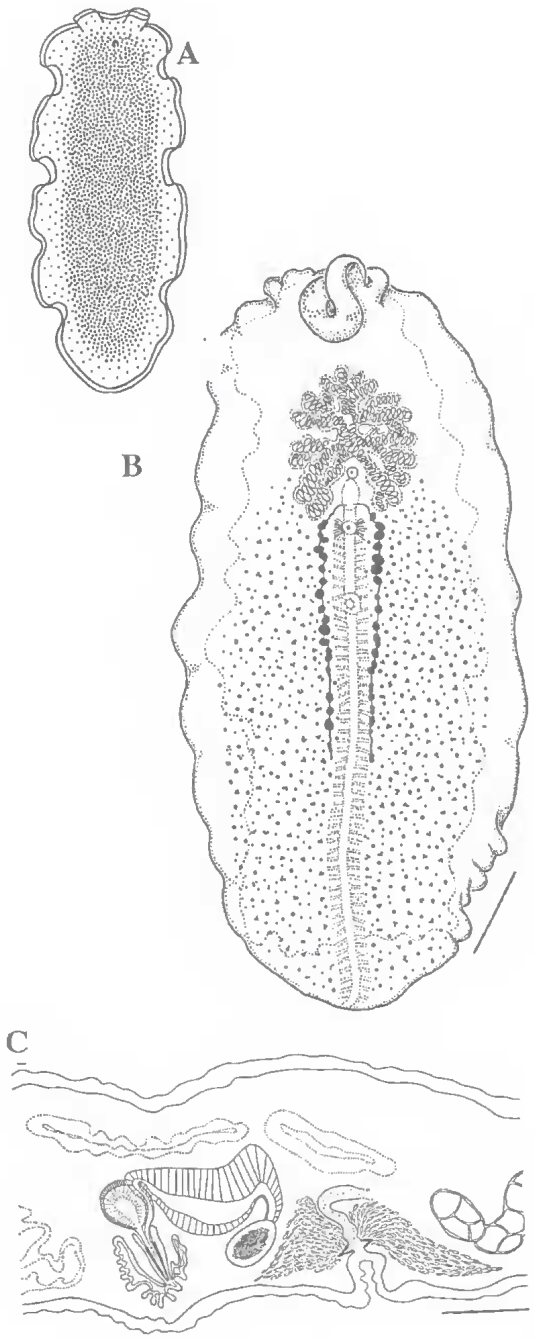


FIG. 28. *Pseudoceros prudhoei* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210398, wholemount showing the morphology from the ventral surface; C, QMG210402, reconstruction of the reproductive anatomy. Scales: B, 2.5mm; C, 500µm.

Pseudoceros sapphirinus sp. nov.
(Figs 29A - C; 49D)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef slope, 10m, night, 29.01.92, WM, QMG210444.

PARATYPES: Heron Is., reef slope, 12m, 25.02.92, LS, QMG210445; 10m, 04.09.92, LS, QMG210447.

OTHER MATERIAL: Heron Is., reef slope, 6 - 10m, 26.06.91, LS, QMG210443; 20.01.92, WM, QMG210488; night, 25.02.92, S, QMG210446; One Tree Is., reef slope, 15m, 17.08.93, QMG210522. Other Record: Philippines, 10 km S of Anilao, reef slope, 10m, night, , T. Gosliner, 26.06.93, CT.

DESCRIPTION

Colour & pattern. Background velvety black with a wide bright royal blue lateral band (near but not at the margin;), extremely narrow bright white (sometimes yellow or turquoise) line at rim. Ventral surface velvety black with white rim.

External Features. Margin not ruffled, body thick and fleshy. Pseudotentacles broad flaps. Cerebral eyespot with about 40 eyes. Pseudotentacular eyes not visible due to dark pigment. Size: mature 35 × 20mm to 58 × 30mm; juvenile from 16 × 8mm.

Reproductive anatomy. Seminal vesicle large (1.0mm long); ejaculatory duct long, coiled. Prostate round (315µm wide). Stylet small (130µm long). Male and female antra deep.

DIAGNOSIS

Black with vibrant blue lateral band and extremely narrow white rim.

ETYMOLOGY

From the Latin *sapphirinus* = sapphire, for its brilliant sapphire- blue lateral band.

REMARKS

This species belongs in Group 2 in which several species possess a black background and vibrantly coloured marginal bands but only in *P. sapphirinus* is the band located laterally, not at the margin. This species is similar in colour to *P. peripurpureus* which possesses marginal bands of purple and violet rather than a lateral blue band. *P. caeruleocinctus* Hyman, 1959a was also described as black with a blue margin (not a lateral band as in *P. sapphirinus*), however, the validity of the species remains uncertain.

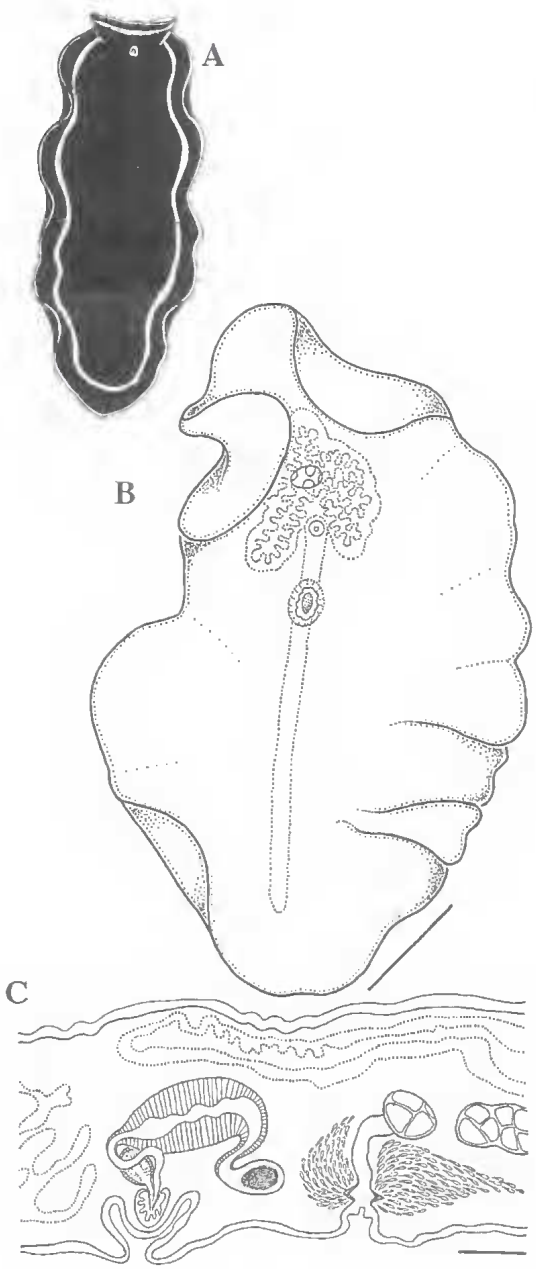


FIG. 29. *Pseudoceros sapphirinus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210444, wholemount showing the morphology from the ventral surface; C, QMG210447, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 500µm.

BIOLOGY

Often observed moving across live coral (*Acropora* sp.) during the day and night. This species extrudes a dark red mucus when disturbed.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope, especially at night. Common from Heron Is. Record: Philippines.

Pseudoceros scintillatus sp. nov.
(Figs 30A - C; 49E)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 15.08.92, WM, QMG210629.

PARATYPE: Heron Is., reef crest, 01.08.92, LS, QMG210628.

DESCRIPTION

Colour & pattern. Background velvety black with a bold pattern of large irregularly sized yellow-green maculae (393); maculae extend into the marginal band, each macula encircled by white. Marginal band distinct, wide orange (137).

External features. Small species. Pseudotentacles simple folds. Size: mature 9 × 4mm; juvenile 6 × 2mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle small, rounded oval (413µm long). Prostate rounded small, oval (143µm wide). Stylet relatively short (135µm long), slightly longer than the prostate. Male and female antra shallow.

DIAGNOSIS

Black with large irregular yellow-green maculae and orange marginal band.

ETYMOLOGY

From the Latin *scintillatus* = scintillating, for its dramatic colour pattern.

REMARKS

This species belongs in Group 5. Two other species are similar, *P. lindae* and *P. glaucus*. However, *P. scintillatus* is black with yellow-green maculae not burgundy with golden-yellow and blue maculae as in *P. lindae* or grey with black maculae as in *P. glaucus*. *P. scintillatus* also resembles *P. mossambicus* (Group 4) which possesses spots (not maculae).

HABITAT & DISTRIBUTION

Found on colonial ascidians under boulders at reef crest. Rare from Heron Is.

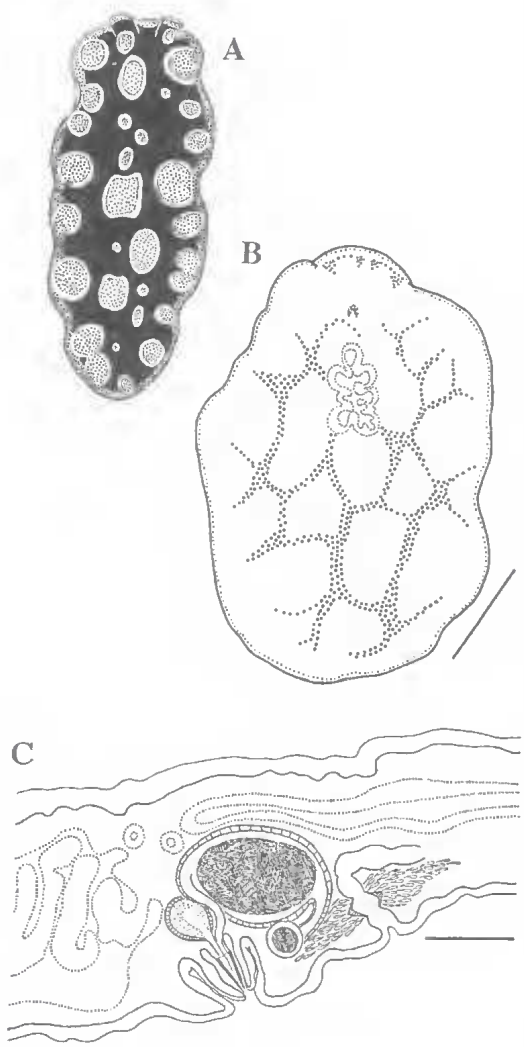


FIG. 30. *Pseudoceros scintillatus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210629, wholemount showing the morphology from the ventral surface; C, QMG210628, reconstruction of the reproductive anatomy. Scales: B, 1mm; C, 250µm.

Pseudoceros verecundus sp. nov.
(Figs 31A - C; 49F)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 08.09.92, WM, QMG210409.

PARATYPE: Heron Is., reef crest, 18.02.93, LS, QMG210410.

OTHER MATERIAL: Heron Is., reef crest, 15.09.89, S, QMG210404; 24.06.91, S, QMG210437; 30.07.92, WM, QMG210405; 01.08.92, WM, QMG210406; 02.08.92, WM, QMG210407;15.08.92, WM, QMG210408; One Tree Is., 19.08.93, WM, QMG210499.

DESCRIPTION

Colour & pattern. Background cream-white with orange microdots over the entire surface. Two discontinuous or interrupted narrow lateral bands (near but not at the margin): inner band narrow, black; outer wide, orange-brown (144). Margin cream-white with a narrow lemon yellow rim. Three distinct marginal bands across the pseudotentacles; inner band orange-brown, middle band black, yellow (102) at rim. Faint black triangle with one large median white spot anteriorly between pseudotentacles. Few animals found with light brown microdots forming faint blotches medially. Ventrally cream.

External features. Pseudotentacles simple folds. Cerebral eyespot with about 40 eyes. Size: mature from 20 × 8mm to 26 × 14mm; juvenile from 10 × 5mm.

Reproductive anatomy. Vas deferens unbranched. Seminal vesicle rounded oblong (645µm long), ejaculatory duct short, coiled. Prostate rounded oval (188µm wide). Stylet small (113µm long). Male and female antra deep.

DIAGNOSIS

Cream with interrupted orange and black lateral bands: pseudotentacles with three marginal bands; orange, black and yellow.

ETYMOLOGY

From the Latin *verecundus* = demure, for its cryptic colour pattern.

REMARKS

This species belongs in Group 2. Three other species possess a cream background, however, no other species has interrupted lateral bands. This species most resembles *P. bimarginatus* which has three marginal band around the entire margin, however, in *P. verecundus* the marginal bands cover only the pscudotentacles. This species is also similar to *P. heronensis* (Group 4) but *P. verecundus* is covered with microdots (not spots and blotches medially) and the tricoloured marginal bands cover only the pseudotentacles (not the pseudotentacles and posterior end).

HABITAT & DISTRIBUTION

Found feeding on cream-white colonial ascidians. Common from Heron Is. Rare from One Tree Is.

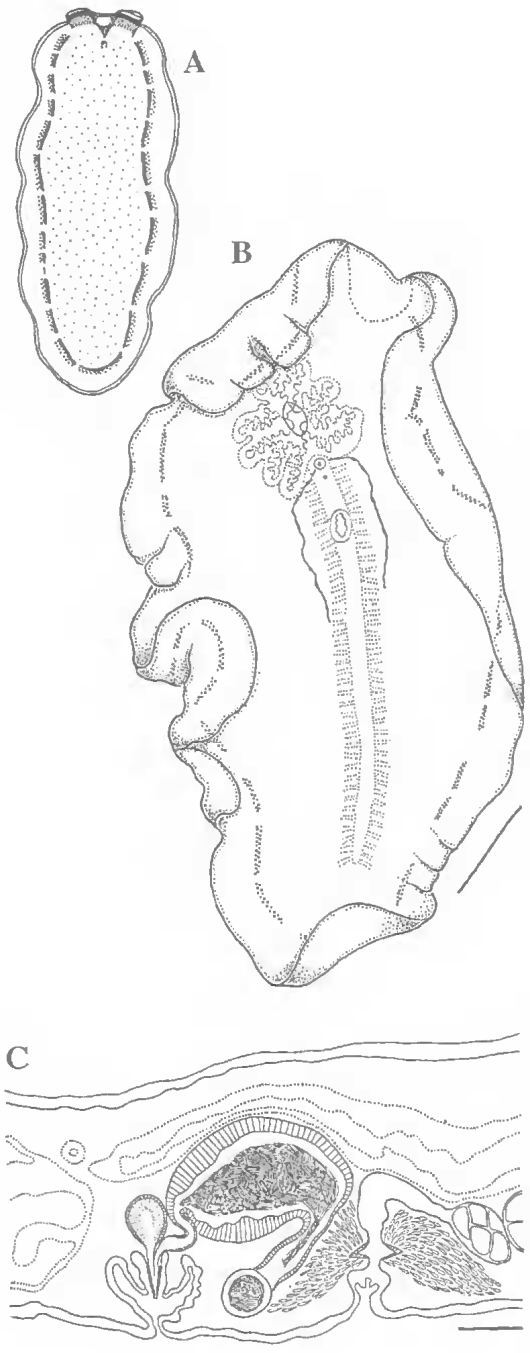


FIG. 31. *Pseudoceros verecundus* sp. nov.: A, diagram of the dorsal colour pattern; B, QMG210409, wholemount showing the morphology from the ventral surface; C, QMG210410, reconstruction of the reproductive anatomy. Scales: B, 2mm; C, 250µm.

Pseudobiceros Faubel, 1984

Pseudobiceros strigosus (Marcus, 1950)[junior synonym of *P. gratus* (Kato, 1937)]: Unknown, painting only?

TYPE LOCALITY

Ceylon.

EMENDED DIAGNOSIS

Flamboyantly or cryptically coloured. Body soft and extremely delicate, raised medially, elongate oval, tapering posteriorly, margin with numerous deep ruffles (Fig. 2B). Pseudotentacles well developed, either pointed and ear-like or square with lateral ruffles (Fig. 3C, D). Cerebral eyespot small, horseshoe shaped, with 20 to 200 eyes in semi-circular rows, eyespot in a clear area which is pointed anteriorly and posteriorly. Dorsal pseudotentacular eyes in four elongate clusters (not along the anterior margin), ventral pseudotentacular eyes in four dense clusters extending medially over the pseudotentacles, with 100's of eyes (Fig. 3F). Pharynx anterior, oval, with 10 to 20 shallow simple pharyngeal folds (Figs, 4B, 5B). Intestine wide, extends to about 2/3 body length, numerous extremely narrow intestinal branches not extending to the posterior end of the intestine. Two symmetrical male pores are posterior to pharynx, male apparatus double, and identical. Female pore between and usually close to male pores. Sucker indistinct, three to five times the distance between the gonopores. Male copulatory apparatus double, each with seminal vesicle and armed penis papilla. Prostatic vesicle orientated to the male complex antero-dorsally.

TAXONOMIC REMARKS

Faubel (1984) erected *Pseudobiceros* on the basis of the double male apparatus and described the genus as: 'Pseudocerotidae with smooth dorsal surface and elongate oval outline. Tentacular and cerebral eyespots present. Male copulatory apparatus double, each with seminal vesicle and armed penis papilla. Prostatic vesicle orientated to the male complex antero-dorsally.' Although Faubel's name appears etymologically incorrect (these worms do not have paired pseudotentacles, but paired male systems), it is quite valid.

LIST OF RECOGNISED SPECIES

The following 14 known species we believe may be reliably placed in *Pseudobiceros* sensu

TABLE 2. Colour pattern groups for recognised and new species of *Pseudobiceros*

#	Colour Pattern	Recognised Species	New Species
1	Even Colour	none	none
2	Marginal Bands	***evelinae*** - red; orange & black margin ***hancockanus****- black; orange & white margin ***splendidus*** - black; orange & brown margin	***flavocanthus*** - black; white & yellow margin ***gloriosus*** - black; orange & pink & purple margin ***periculosus*** - black; orange margin ***uniarboretus*** - black; orange, grey & white margin
3	Longitudinal Stripes	**cincereus** - black; 2 grey stripes, grey margin ***gratus*** *- white; 3 or 4 black stripes ***nigromarginatus*** - black; 2 brown stripes, black margin ***philippinensis*** - black; 3 purple-grey stripes, orange margin	none
4	Spots, Dots & Mottling	***bajae*** - black; sometimes white irregular dots ***fulvogriseus*** - grey; mottled yellow & brown ***gardineri*** - grey; mottled black ***izuensis*** - white; black dots; interrupted margin	***apricus*** - orange; white dots, black margin ***damawan*** - grey & white; black spots, orange margin ***stellae*** - black; white regular dots
5	Maculae	none	none
6	Transverse Streaks & Stripes	***bedfordi****- black; yellow dots, pink streaks ***dendricticus*** - yellow; mottled brown, yellow stripes ***flavolineatus***- brown; yellow stripes, black margin	***fulgor*** - brown; yellow & white stipes, black margin

* collected during this study

stricto based on the morphology of the pharynx, eyes, pseudotentacles or reproductive anatomy (Table 2): *bajae* (Hyman, 1953) comb. nov.; *bedfordi* (Laidlaw, 1903)*; *cincereus* (Palombi, 1931); *dendricticus* (Prudhoe, 1989); *evelinae* (Marcus, 1950); *flavolineatus* (Prudhoe, 1989); *fulvogriseus* (Hyman, 1959); *gardineri* (Laidlaw, 1902); *gratus* (Kato, 1937)*; *hancockanus* (Collingwood, 1876) comb. nov.*; *izuensis* (Kato, 1944); *nigromarginatus* (Yeri & Kaburaki, 1918); *philippinensis* (Kaburaki, 1923); *splendidus* (Lang, 1884)(*collected during this study).

Species from eastern Australia & Papua New Guinea

Pseudobiceros apricus sp. nov.
(Figs 32A - D; 50A)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 02.02.92, WM, QMG210585.

PARATYPE: Heron Is., reef crest, 22.02.93, LS, QMG210577.

OTHER MATERIAL: Heron Island, reef crest, 28.12.90, WM, QMG210571; 30.12.90, WM, QMG210572; 02.01.91, WM, QMG210573; 18.01.92, WM, QMG210580; 23.01.92, WM, QMG210582; S, QMG210583; 31.01.92, S, QMG210584; 02.02.92, WM, QMG210586; 14.02.92, WM, QMG210587; 16.02.92, LS, QMG210588; 19.02.92, LS, QMG210589; S, QMG210590; 18.02.93, S, QMG210574; 20.02.93, S, QMG210576; 21.02.93, S, QMG210575; 22.02.93, LS, QMG210578; One Tree Is., reef crest, 16.08.93, WM, QMG210579.

DESCRIPTION

Colour & pattern. Background transparent orange (178); entire dorsal surface covered with raised white microdots and irregular scattered clusters of larger white dots, darker pigment medially. Marginal band narrow, black with white dots. Pseudotentacles grey-black with white tips. Gut diverticula sometimes bright orange.

External features. Pseudotentacles square with slight lateral ruffles. Cerebral eyespot with about 30 eyes in a clear round area. Two male pores close together. Size: mature from 24 × 10mm to 60 × 25mm; juvenile from 5 × 2mm.

Reproductive anatomy. Unbranched vas deferens. In one system: seminal vesicle oval (713µm long), ejaculatory duct short, coiled; prostate round (263µm wide); stylet long (368µm long). Male and female antra shallow.

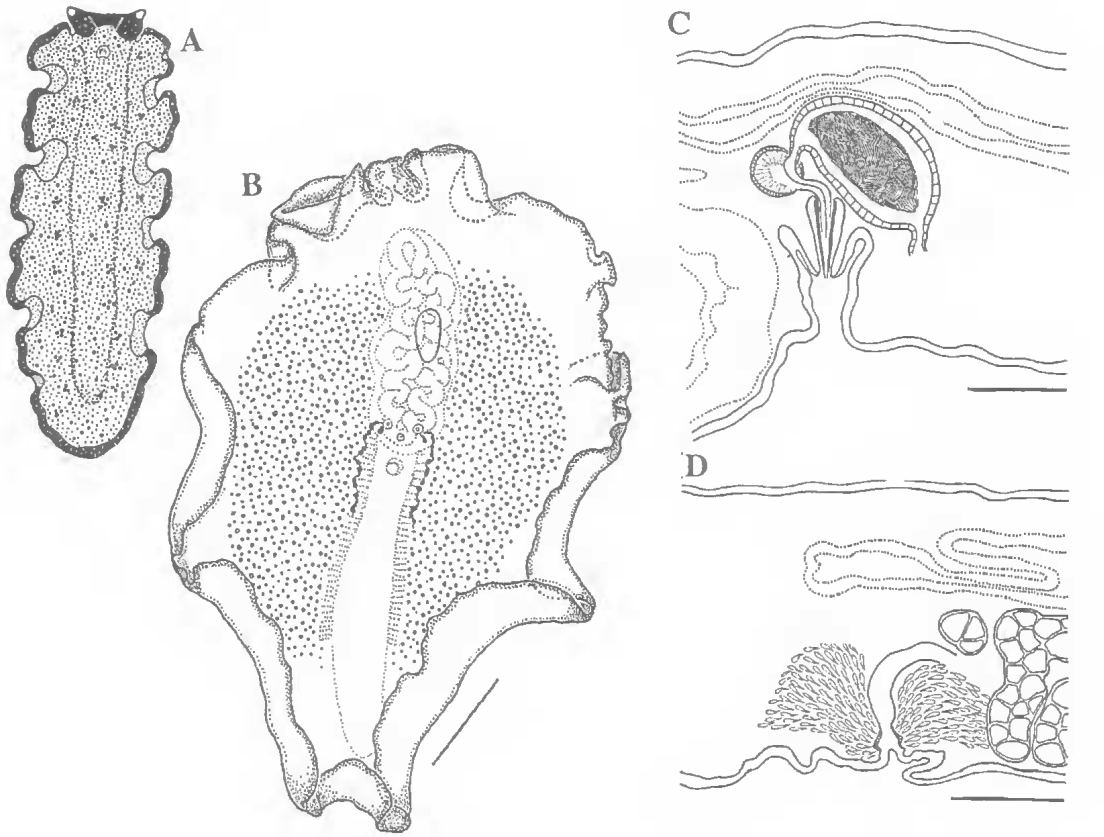


FIG. 32. *Pseudobiceros apricus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210585 wholemount showing the morphology from the ventral surface; C, D, QMG210577, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2mm; C, D, 500µm.

DIAGNOSIS

Transparent orange with raised white microdots, black marginal band with white dots.

ETYMOLOGY

From the Latin *apricus* = orange, for its apricot-like colour.

REMARKS

This species belongs in Group 4 where the majority of species are black or grey. No other species possesses an orange background and white microdots (Table 2).

HABITAT & DISTRIBUTION

Found on pink colonial ascidians under boulders at the reef crest. Common from Heron Is., rare from One Tree Is.

Pseudobiceros bedfordi (Laidlaw, 1903)
(Figs 33A - D; 50B)

Pseudoceros bedfordi Laidlaw, 1903: 302, 314, pl. 23, fig. 9; Bock, 1913: 254, pl. III, figs 2 - 4; Bresslau, 1933: 59; Kato, 1943, 87; 1944; 299; Marcus, 1950: 84; Dawydoff, 1952: 82; Hyman, 1954: 220; 1959: 566; Prudhoe, 1977: 586; George & George, 1979: 43, pl. 49, fig. 10.

Pseudoceros micronesianus Hyman, 1955: 66, fig. 5.

Pseudobiceros bedfordi (Laidlaw, 1903): Faubel, 1984: 216.

MATERIAL EXAMINED

HOLOTYPE: Unknown, painting only?, Singapore.

OTHER MATERIAL: Heron Is., reef slope, 7 - 10m, 28.04.89, S, QMG210513; 16.06.91, WM, QMG210509; 19.06.91, LS, QMG210510; 26.06.91, S, QMG210511; 22.01.92, LS, QMG210512; 27.01.92, S, QMG210514; 31.01.92, WM,

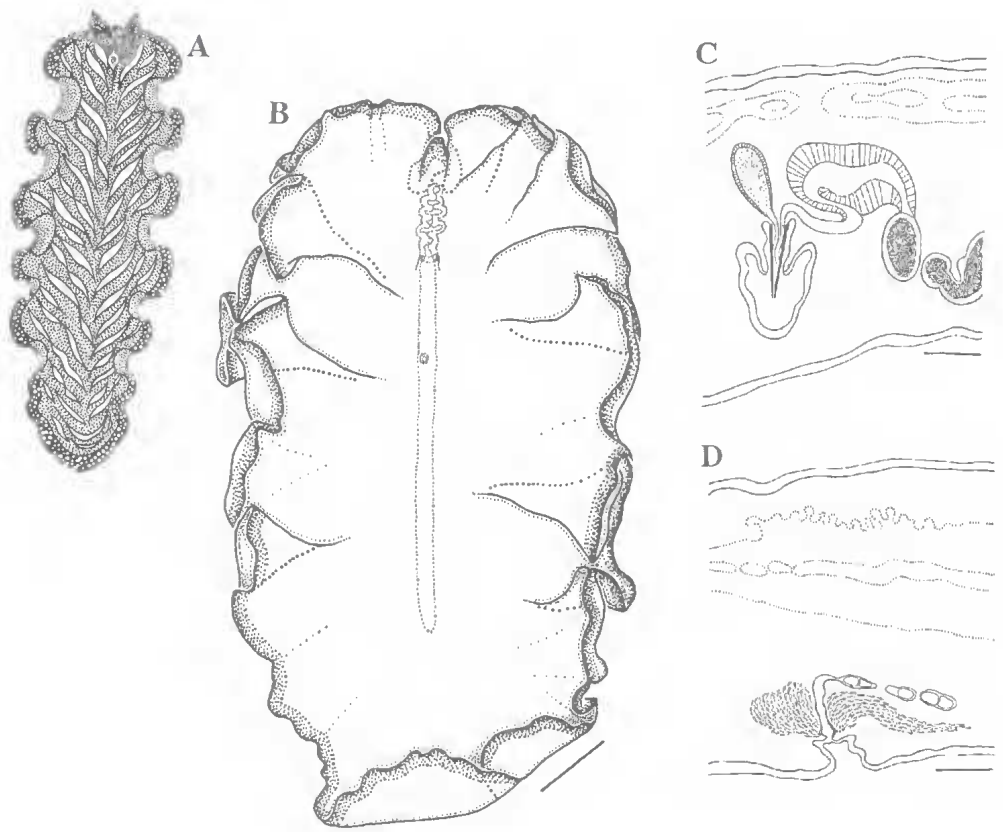


FIG. 33. *Pseudobiceros bedfordi* (Laidlaw, 1903). A, diagram of the dorsal colour pattern; B, QMG210509 wholemount showing the morphology from the ventral surface; C, D, QMG210519 reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 250µm.

QMG210515; 05.02.92, WM, QMG2105, WM; 08.08.92, LS, QMG210518; J. Tanner, 03.09.92, LS, QMG210519; 05.02.93, S, QMG210521; Madang, reef slope, 4m on rubble, night, 03.06.92, LS, QMG210517; Hansa Bay, Laing Is., reef flat, 1m, J.-M. Ouin, 09.06.92, WM, QMG210520.

DESCRIPTION

Colour & pattern. Background colour varies from brown to black with numerous compacted bright yellow dots; numerous transverse bilateral streaks of pink (190) outlined in black, variable in shape; yellow dots more concentrated between the streaks. Margin black with white dots. Ventrally deep pink (191) with black marginal band.

External features. Pseudotentacles pointed and ear-like. Cerebral eyespot with about 100 eyes. Pharynx small. Male pores close together. Sucker well separated from gonopores. Size: mature from 29 × 18mm to 100 × 45mm; juvenile from 25 × 12mm.

Reproductive anatomy. Vas deferens unbranching. In one system: seminal vesicle short (1.0mm long), ejaculatory duct long, coiled; prostate large, oval (796µm wide); stylet extremely long, narrow (592µm long). Male and female antra shallow.

REMARKS

This species belongs in Group 6 and is similar to *P. dendrictus* and *P. flavolineatus*. *P. bedfordi* is black, yellow and pink not yellow and brown

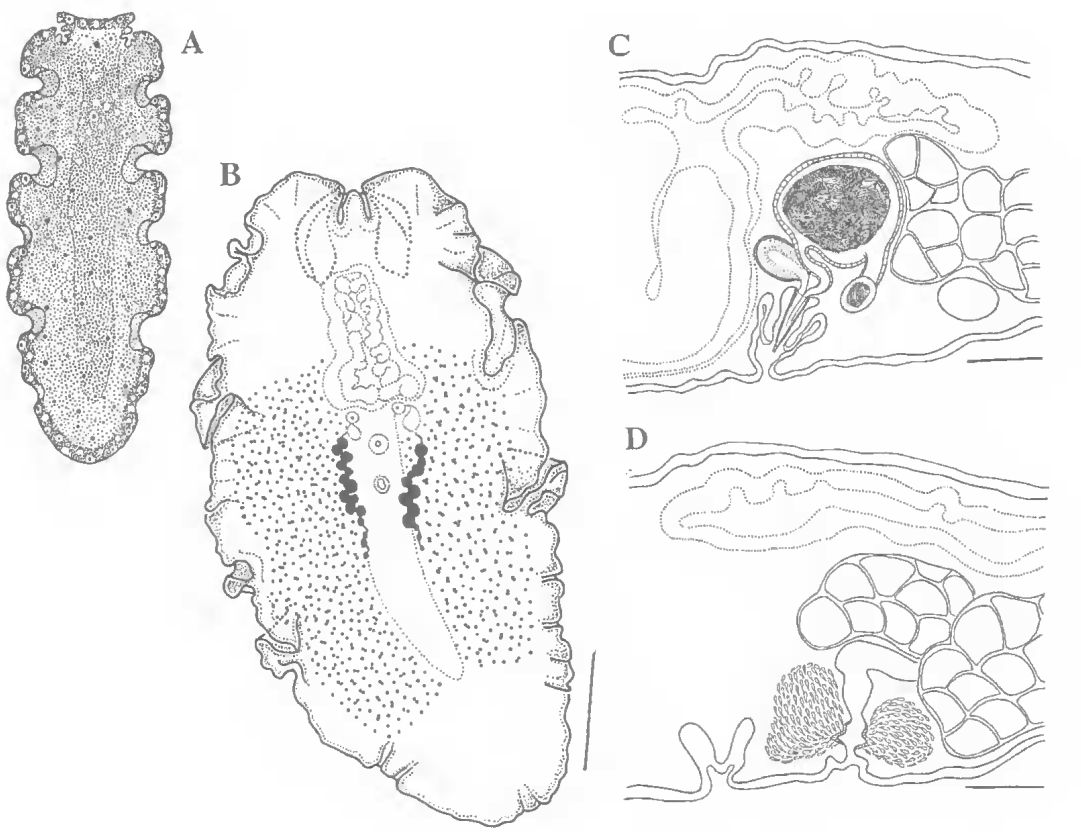


FIG. 34. *Pseudobiceros damawan* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210613, wholemount showing the morphology from the ventral surface; C,D, QMG210607, reconstruction of the reproductive anatomy. C, one male system; D, the female system. Scales: B, 2.5mm; C, D, 250μm.

as in *P. dendrictus* and has wide streaks not narrow lines as in *P. flavolineatus*.

Pseudoceros micronesianus Hyman, 1955 (Holotype, USNM25947 was examined) is considered a synonym of this species since the pattern as described by Hyman (based on a damaged preserved specimen) clearly resembles the pattern after fixation in *P. bedfordi*.

BIOLOGY

Eggmasses were laid on the side of an ice cream container. Müller's larvae hatched within 10 days.

HABITAT & DISTRIBUTION

Found under boulders at the reef crest and under ledges on the reef slope. Common from Heron Is.; rare from Madang and Laing Is. Records: GBR, Singapore, Philippines, Micronesia.

Pseudobiceros damawan sp. nov.
(Figs 34A - D; 50C)

MATERIAL EXAMINED

HOLOTYPE: Laing Is., reef crest, J.-M. Ouin, 15.09.92, LS, QMG210613.

PARATYPE: Laing Is., reef crest, J.-M. Ouin, 15.09.92, WM, QMG210612.

OTHER MATERIAL: Madang, reef crest, 3 - 5m, 27.05.92, WM, QMG210603; WM, QMG210604; S, QMG210605; 11.06.92, WM, QMG210606; S, QMG210608; S, QMG210609; The Quarry, 40 km N Madang, reef slope, 10m, 13.06.92, WM, QMG210610; Heron Is., reef slope, 10m, 09.09.92, LS, QMG210611.

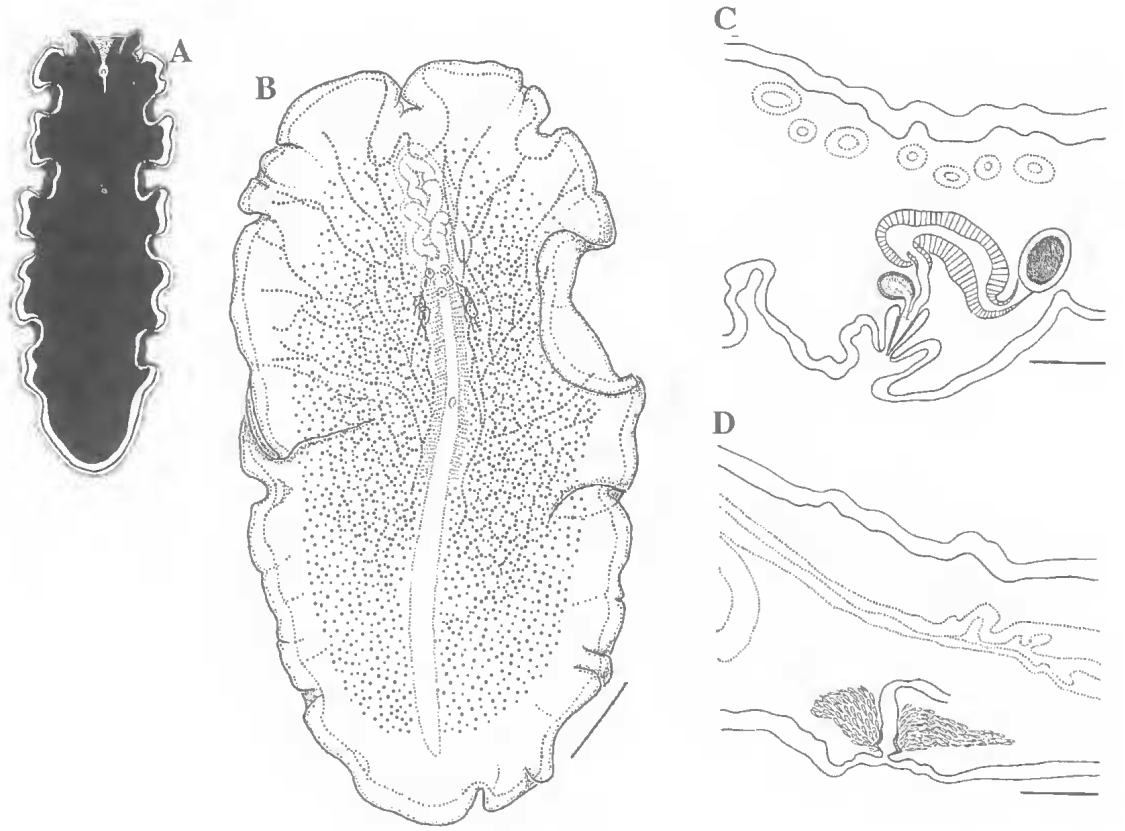


FIG. 35. *Pseudobiceros flavocanthus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210470, wholemount showing the morphology from the ventral surface; C,D, QMG210471, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 5mm; C, D, 500µm.

DESCRIPTION

Colour & pattern. Background mottled, transparent grey and opaque white with widely spaced black spots over the entire surface. Light orange (163) medially, marginal band orange (163) interrupted with white spots; extremely narrow black rim. Ventral surface cream with a mottled orange marginal band and black rim.

External features. Pseudotentacles square and ruffled. Cerebral eyespot small, round with about 50 eyes. Male pores well separated. Size: mature from 10 × 5mm to 18 × 8mm; juvenile from 1.5 × 0.5mm.

Reproductive anatomy. Vas deferens unbranched. In one system: seminal vesicle round, short (413µm long); ejaculatory duct short, coiled; prostate small, oval (203µm wide); stylet small (135µm long), larger than the prostate. Male and female antra shallow.

DIAGNOSIS

Mottled grey and white, orange medially and laterally, covered in sparse black spots.

ETYMOLOGY

From the Rewo Village language (Madang, PNG) name of the reef where it was collected.

REMARKS

This species belongs in Group 4. Two other species are mottled grey, *P. fulvogriseus* and *P. gardineri*, however, only *P. damawan* possesses an orange margin and black spots. Cryptic especially when found on colonial ascidians.

HABITAT & DISTRIBUTION

Found on colonial ascidians under boulders at reef crest and on reef slope. Common from Madang. Rare from Laing and Heron Islands.

Pseudobiceros flavocanthus sp. nov.
(Figs 35A - D; 50D)

MATERIAL EXAMINED

HOLOTYPE: Madang, reef crest, 3m, 29.06.92, WM, QMG210616.

PARATYPE: Madang, reef crest, 3m, 16.06.92, LS, QMG210615.

DESCRIPTION

Colour & pattern. Background velvety black with two narrow marginal bands of equal width; inner band white, outer band narrow, bright yellow. White-grey triangle between the pseudotentacles extending into the cerebral eyespot. Ventrally grey with same marginal bands.

External features. Pseudotentacles small, square and slightly ruffled. Cerebral eyespot round with about 30 eyes. Male pores extremely close together. Sucker well separated from gonopores. Size: mature from 35 × 15mm to 50 × 16mm.

Reproductive anatomy. Vas deferens branched, testes forming network throughout the body. In one system: seminal vesicle elongate, small (465µm long); ejaculatory duct short, not coiled; prostate round, extremely small (135µm wide). Male and female antra shallow.

DIAGNOSIS

Black with two narrow marginal bands; inner white and outer yellow.

ETYMOLOGY

From the Latin *flavo* = yellow, *canthus* = ribbon, for its conspicuous yellow marginal band.

REMARKS

This species belongs in Group 2 in which the majority of species possess a black background, however, only *P. uniarborensis* sp. nov. and *P. hancockanus* have similar coloured marginal bands.

HABITAT & DISTRIBUTION

Found under rubble at reef crest. Rare from Madang.

Pseudobiceros fulgor sp. nov.
(Figs 36A - D; 50E)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 24.02.93, S, QMG210559.

PARATYPES: Heron Is., reef crest, 10.08.92, LS, QMG210556; reef slope, 20m, 05.09.92, LS, QMG210557.

OTHER MATERIAL: 28.09.89, S, QMG210552; 19.01.92, S, QMG210553; 02.02.92, WM, QMG210554; 14.02.92, WM, QMG210555; 20.02.93, S, QMG210558. Records: 10 km S. Anilao, Philippines, 10m, night, T. Gosliner, 26.03.93, CT.

DESCRIPTION

Colour & pattern. Background orange-brown (143) or deep pink (184), intensifying toward the margin; numerous fine broken irregular longitudinal and transverse, short white stripes; yellow or cream blotches dispersed evenly over the entire surface. Margin black with numerous white streaks, parallel to the rim. Ventral surface light orange-brown (141) with a black marginal band

External features. Extremely fragile species. Pseudotentacles pointed and ear-like. Cerebral eyespot relatively small, elongate with about 60 eyes. Pharynx relatively small. Size: mature from 38 × 20mm to 70 × 38mm; juvenile from 5 × 2mm.

Reproductive anatomy. Vas deferens unbranched. In one system: seminal vesicle rounded (740mm long); ejaculatory duct extremely short, not coiled; prostate oval (370µm wide); stylet short (158µm long). Male and female antra extremely shallow.

DIAGNOSIS

Light brown background and black margin with fine white broken stripes.

ETYMOLOGY

From the Latin *fulgor* = lightning, for its fine white and yellow broken stripes.

REMARKS

This species belongs in Group 6. Only *P. flavolineatus* also possesses a brown background, however, *P. fulgor* possesses broken streaks not concentric stripes as in *P. flavolineatus*. *P. fulgor* is similar to *Pseudoceros cerebralis* (Kelaart, 1858) which is described as

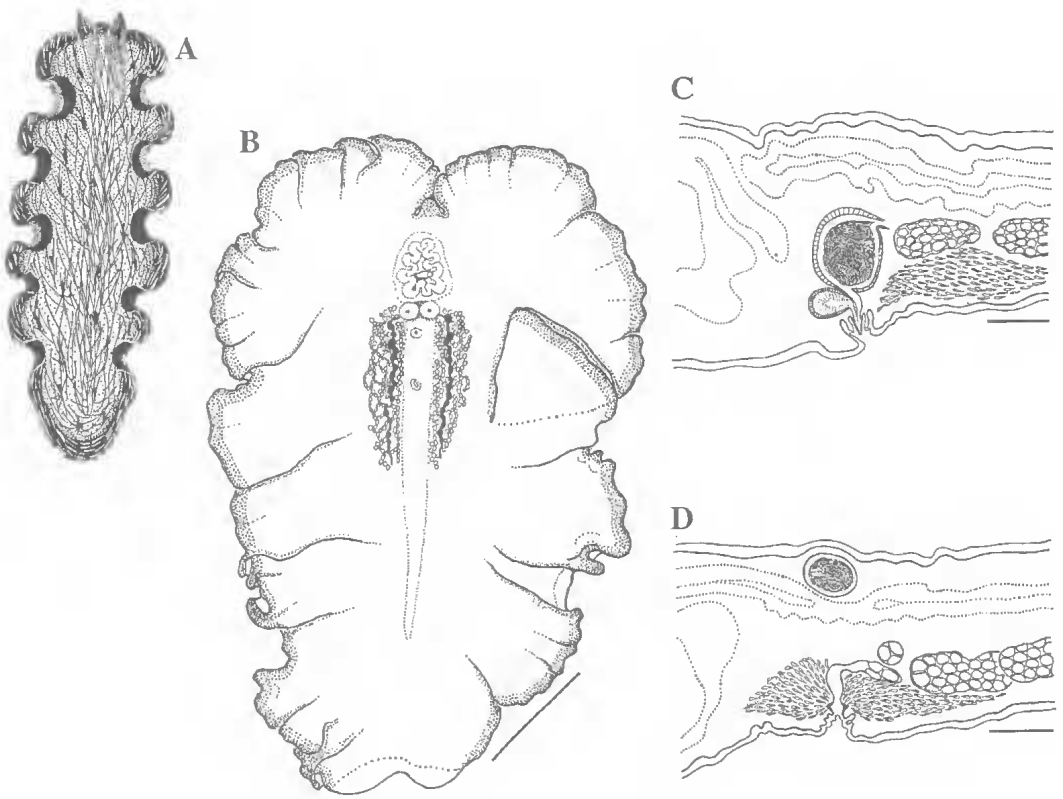


FIG. 36. *Pseudobiceros fulgor* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210559, wholemount showing the morphology from the ventral surface; C, D, QMG210556, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 5mm; C, D, 500µm

having broken brown stripes (not yellow or white), but the validity of *P. cerebralis* is uncertain as the number of male pores and morphology of the pharynx was not given.

BIOLOGY

This species extrudes copious amounts of transparent mucus and animals readily disintegrated during collection.

HABITAT & DISTRIBUTION

Found under boulders at reef crest. Common from Heron Is. Record: Philippines.

Pseudobiceros gloriosus sp. nov.
(Figs 37A - D; 50F)

MATERIAL EXAMINED

HOLOTYPE: Bagabag Is., 62 km NE Madang, reef slope, 30.06.92, WM, QMG210549.

OTHER MATERIAL: Heron Is., reef slope, 6 -15m, M. McCarthy, 20.09.89, WM, QMG210546; 19.01.92, LS, QMG210547; 05.02.92, LS, QMG210548; 10.09.92, LS, QMG210550; 17.02.93, S, QMG210551. Record: Namalata Reef, Kadavu, Fiji, reef slope, 12m, J. Marshall, 07.07.93, CT.

DESCRIPTION

Colour & pattern. Background velvety black with three marginal bands: inner band wide,

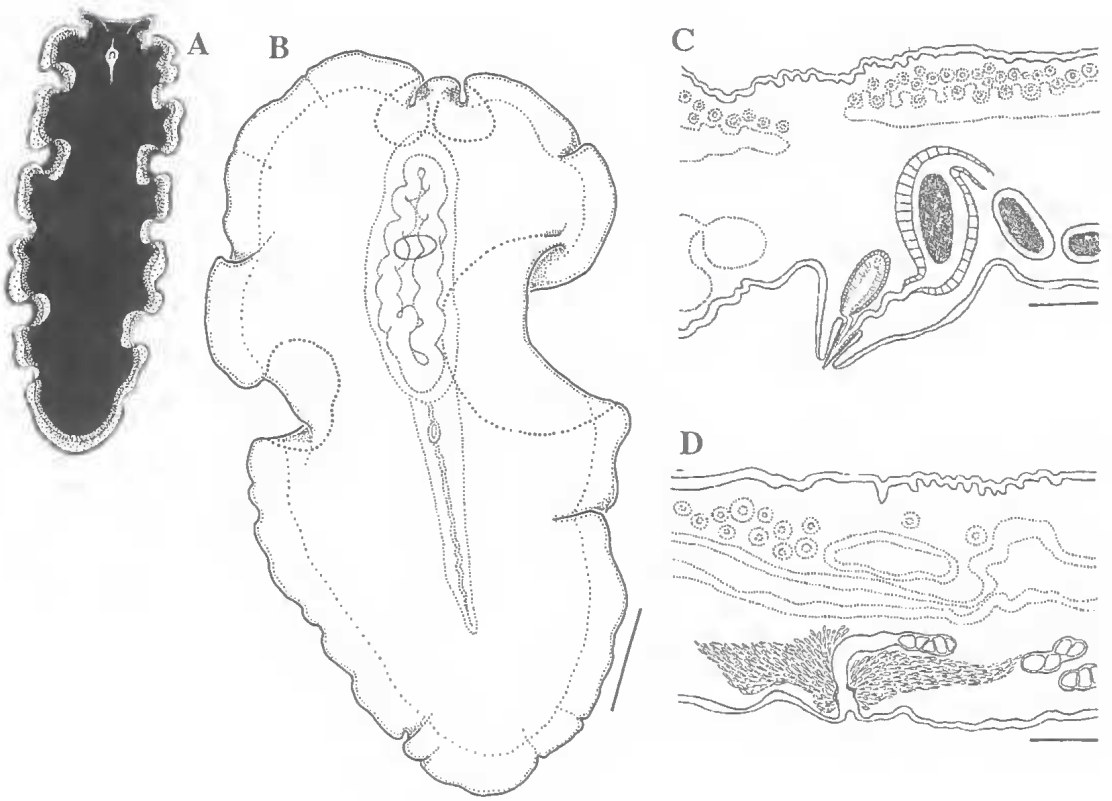


FIG. 37. *Pseudobiceros gloriosus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210549, wholemount showing the morphology from the ventral surface; C,D, QMG210548, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 500μm.

orange (165); middle band narrow, pink (223); outer band extremely narrow, dark burgundy (214). Largest specimen with a thin, pink median line beginning at the cerebral eyespot and extending posteriorly to about 3/4 body length. Pseudotentacles with orange and burgundy marginal bands (no pink). Ventrally deep burgundy (214) medially with same marginal bands.

External features. Large species. Pseudotentacles square and slightly ruffled. Cerebral eyespot with about 200 eyes. Two male pores extremely close together. Size: mature from 70 × 25 to 90 × 50mm; juvenile from 28 × 12mm.

Reproductive anatomy. Vas deferens branching. In one system: seminal vesicle oval, large (1.1μm long); ejaculatory duct long, coiled; prostate elongate, oval (537μm wide); stylet long (463μm). Male and female antra shallow.

DIAGNOSIS

Black with three marginal bands; inner orange, middle pink and burgundy at rim.

ETYMOLOGY

From the Latin *gloriosus* = glorious, for its flamboyant colour pattern.

REMARKS

This species belongs in Group 2 in which the majority of species are black with vibrantly coloured

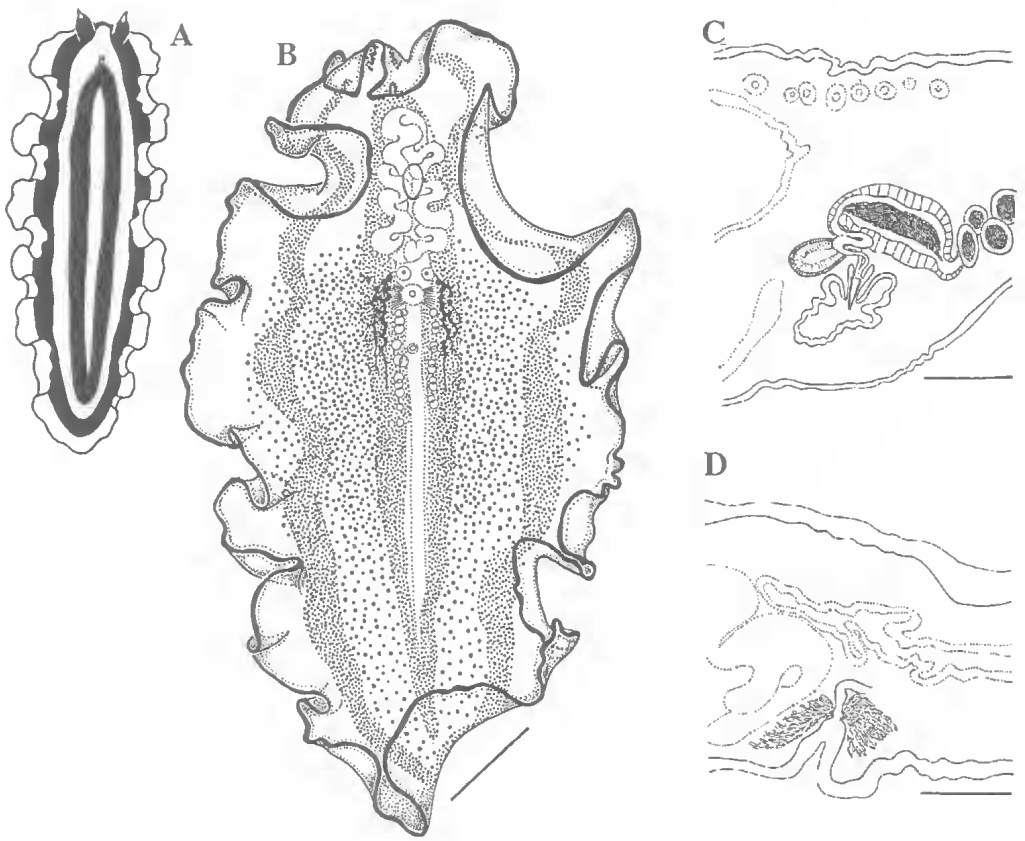


FIG. 38. *Pseudobiceros gratus* (Kato, 1937). A, diagram of the dorsal colour pattern; B, QMG210361, wholemount showing the morphology from the ventral surface; C, D, QMG210566, reconstruction of the reproductive anatomy. C, male system; D, female system. Scales: B, 2.5mm; C, D, 500µm.

marginal bands. *P. gloriosus* has three distinct marginal bands rather than two as found in all other species, except *P. uniarborensis* sp. nov. However, in *P. gloriosus* the marginal bands are orange, purple and violet not orange, grey and white.

HABITAT & DISTRIBUTION

Found under ledges on the reef slope. Common from Heron Is. Rare from Bagabag Is., N Madang. Record: Fiji.

Pseudobiceros gratus (Kato, 1937)
(Figs 38 A - D; 51A, B)

Eurylepta striata Schmarda, 1859: 27-28, fig. 62.
Pseudoceros striatus (Schmarda, 1859): Stummer-Traunfels, 1933: 3487, 3540, 3544, figs. 95, 96.
Pseudoceros gratus Kato, 1937: 227-229; Kato, 1944: 300; Hyman, 1959a: 566; Prudhoe, 1977: 593-594.
P. strigosus Marcus, 1950: 88.
P. habroptilus Hyman, 1959a, fig. 8.

Pseudobiceros strigosus (Marcus, 1950): Faubel, 1984: 216.
Pseudobiceros gratus (Kato, 1937): Poulter, 1987: 46, pl. 2.I.2.d.

MATERIAL EXAMINED
HOLOTYPE: Unknown, Korôru, Japan [according to Poulter (1975) all Kato's types were lost during World War II].
OTHER MATERIAL: Heron Is., reef slope, 6 - 10m, 27.04.89, S, QMG210562; 30.09.89, WM, QMG210561; 09.09.92, S, QMG210567; 28.01.93, LS, QMG210566; 02.02.93, S, QMG210568; 17.02.93, S, QMG2105569; 25.02.93, Müller's larvae, 10 days old, S, QMG210627; One Tree Is., reef crest, 17.08.93, S, QMG210570; Madang, reef crest, 2 - 3m, 08.06.92, LS, QMG210565; WM, QMG210563; 12.06.92, QMG210564.

DESCRIPTION
Colour & pattern. Background varies from transparent white to light brown with three or four parallel thick black (can vary from brown to grey with black borders) lateral stripes, joining posteriorly, extremely narrow black rim. Pseudotentacles black with white tips. Ventral surface transparent white with a narrow black rim.

External features. Body fragile, with deep crenulated marginal ruffles. Pseudotentacles pointed and ear-like. Cerebral eyespot small with about 60 eyes. Size: mature from 40 × 12mm to 50 × 15mm; juveniles from 8 × 6mm.

Reproductive anatomy. Vas deferens branched. In one system: seminal vesicle rounded, oblong (700µm long); ejaculatory duct long, coiled; prostate oval (354µm long); stylet small (158µm long). Male and female antra deep.

REMARKS
This species belongs in Group 3. *P. gratus* is the only species with a white background and appears be the opposite to *P. philippinensis* which is black with purple-grey stripes.

Confusion has arisen over the synonymy of this species. Schmarda (1859) first named it *Pseudoceros striatus,* a name already occupied by Kelaart, 1858. Kato (1937) named a new species *P. gratus* which proved to be a synonym. Marcus (1950), however, did not recognise the similarities between *P. gratus* and *P. striatus* but renamed Schmarda's species *P. strigosus.* Hyman (1959a) added yet another synonym, *P. habroptilus,* although in the same paper she comments on the previous synonymy of *P. gratus.* However, Poulter (1987) clearly states Hyman's position on the priority of the name *P. gratus.* We accept this here and thus *P. strigosus* becomes a junior synonym of *P. gratus,* although it remains the type of the genus as designated by Faubel (1984).

Kato (1937) figures the male apparatus of this species which conforms to our specimens whereby the ejaculatory duct is long and coiled, prostate oval, and the seminal vesicle oblong. Details of the female system were not sufficient to compare to our specimens.

BIOLOGY
Eggmasses were laid in containers in the laboratory and Müller's larvae hatched after 10 days.

HABITAT & DISTRIBUTION
Found under boulders from the reef slope and crest. Common from Heron Is. and Madang; rare from One Tree Is. Records: Western Australia, Ceylon, Japan, Micronesia, Hawaii.

Pseudobiceros hancockanus (Collingwood, 1876) comb. nov.
(Figs 39A - D; 51C)

Proceros hancockanus Collingwood, 1876: 91, pl. XVII, fig. 5.
Stylochopsis malayensis Collingwood, 1876: 94, pl. XVIII, fig. 12.
Pseudoceros hancockanus Collingwood, 1876: Laidlaw, 1903: 301, 302, 315; Kaburaki, 1923: 635, 639; Marcus, 1950: 86.
Pseudoceros malayensis (Collingwood, 1876): Bock, 1913: 258, 259.
Pseudoceros hancockanus (Collingwood, 1876): George & George, 1979: 43, pl. 49.

MATERIAL EXAMINED
HOLOTYPE: Not known, painting only?, Singapore.
OTHER MATERIAL: Heron Is., reef slope, 3 - 15m, 21.09.89, WM, QMG210500; 12.90, LS, QMG210501; 02.01.91, S, QMG210502; 21.06.91, WM, QMG210504; 05.09.92, WM, QMG210503; LS, QMG210505; S, QMG210506; 24.02.93, S, QMG210507; One Tree Is., reef slope, 15m, S, 17.08.93, QMG210508.

DESCRIPTION
Colour & pattern. Background velvety black with two distinct marginal bands; inner band wide, orange (151), outer band narrow, white. Pseudotentacles with same marginal bands. Ventral surface grey intensifying to purple medially, marginal bands same.

External features. Largest pseudocerotid recorded. Pseudotentacles square and slightly

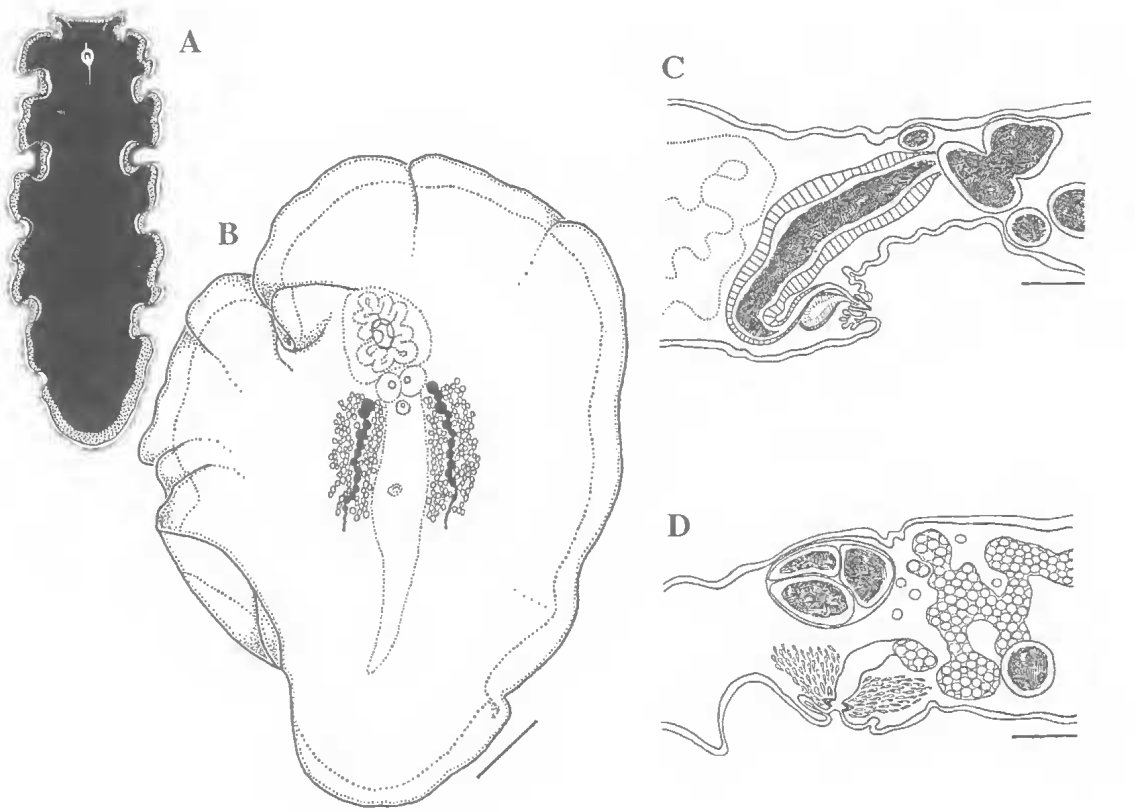


FIG. 39. *Pseudobiceros hancockanus* (Collingwood, 1876) comb. nov. A, diagram of the dorsal colour pattern; B, QMG210507, wholemount showing the morphology from the ventral surface; C,D, QMG210501, reconstruction of the reproductive anatomy. C, one male system, D, female system. Scales: B, 5mm; C, D, 250μm.

ruffled. Cerebral eyespot with 100's of eyes. Two male pores well separated. Size: mature from 55 ×32mm to 140 ×80mm; juvenile from 4 ×2mm.

Reproductive anatomy. Vas deferens unbranching. In one system: seminal vesicle elongate, large (1.1mm long), ejaculatory duct short, not coiled; prostate extremely small (175μm wide); stylet extremely small (128μm long). Male and female antra shallow.

Remarks

This species belongs in Group 2 where the majority of species possess a black background and vibrantly coloured marginal bands. Only one other species also possesses orange and white marginal bands, *P. uniarborensis* sp. nov.

Proceros hancockanus Collingwood, 1876 was originally described as deep velvety brown with a double marginal band of equal widths; inner deep orange, outer opaque white. Our specimens clearly possess marginal bands of unequal width. Although no other morphological data were given, we assume that the colour pattern is characteristic for this widespread and common species.

Biology

One animal was found on an orange sponge and appeared to be feeding.

Habitat & Distribution

Found under ledges on the reef slope. Common from Heron Is. Records: GBR to Laccadives, Japan, Singapore, Philippines.

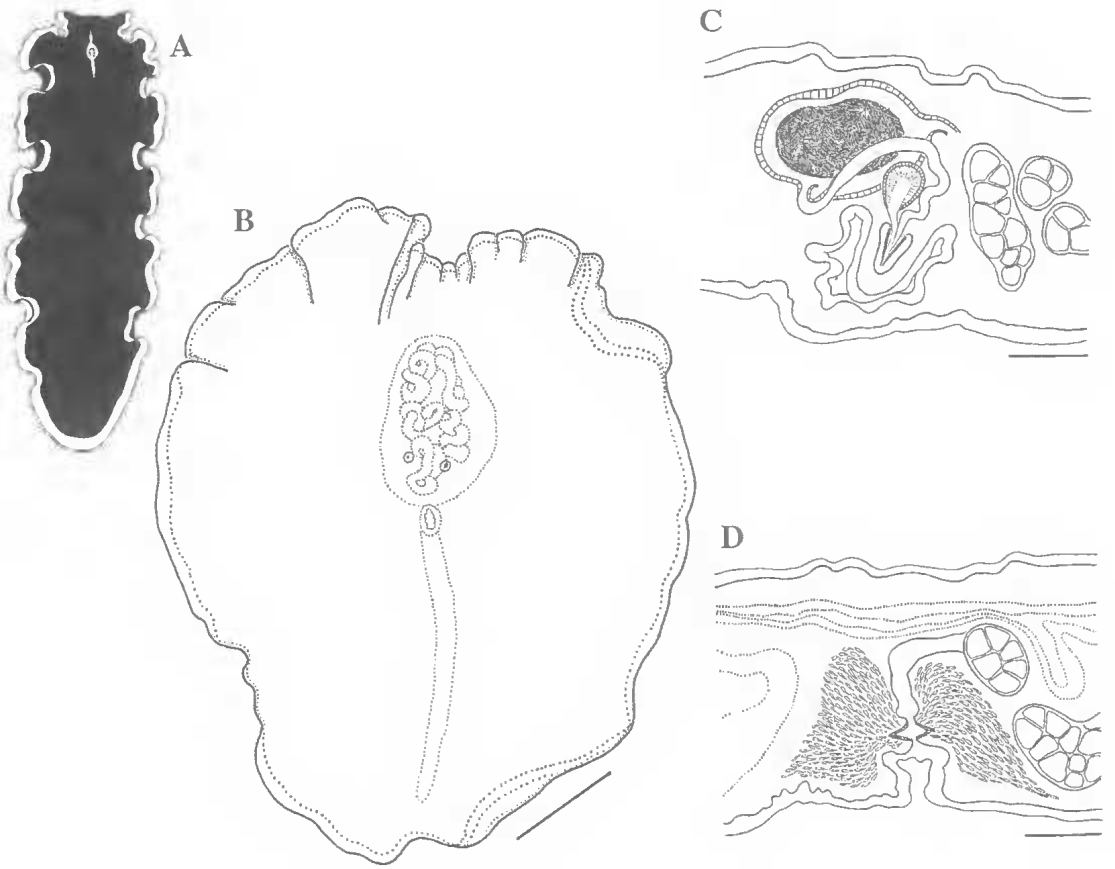


FIG. 40. *Pseudobiceros periculosus* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210532, wholemount showing the morphology from the ventral surface; C,D, QMG210535, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 250µm.

Pseudobiceros periculosus sp. nov.
(Figs 40A - D; 51D)

? Pseudocerotid Poulter, 1987: 49, pl. 2.I.4 c.

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 12.08.92, WM, QMG210532.

PARATYPES: Heron Is., reef crest, 03.02.92, WM, QMG210526; 20.02.93, LS, QMG210535.

OTHER MATERIAL: Heron Is., reef crest, 17.01.92, WM, QMG210523; 23.01.92, WM, QMG210524; S, QMG210525; 03.02.92, S, QMG210528; 04.02.92, WM, QMG210527; 05.02.92, WM, QMG210529; 07.02.92, WM, QMG210626; 02.08.92, WM, QMG210530; WM, QMG210531; 04.02.93, S, QMG210534; 17.02.93, S, QMG210533.

DESCRIPTION

Colour & pattern. Background velvety black with a wide, distinct, brilliant orange (021) marginal band; extremely narrow colourless transparent rim. Pseudotentacles black without the marginal band. Ventrally grey.

External features. Relatively small species, body with shallow marginal ruffles. Pseudotentacles square and distinctly ruffled. Cerebral eyespot with about 60 eyes. Two male pores well separated. Size: mature from 25 ×10mm to 30 ×12mm; juvenile from to 5 ×2mm.

Reproductive anatomy. In one system: seminal vesicle small, round (570µm long); ejaculatory duct extremely long, coiled; prostate small, oval (175µm wide); stylet small (135µm long), slightly larger than the prostate. Male and female antra deep.

DIAGNOSIS

Black with wide orange marginal band.

ETYMOLOGY

From the Latin *periculosus* = danger, for its black and orange warning colouration.

REMARKS

This species belongs in Group 2 in which the majority of species are black with vibrantly coloured marginal bands, however, only *P. periculosus* possesses a single coloured margin. This species closely resembles *Pseudoceros periaurantius* (see above) which is also black with a brilliant orange margin but can be differentiated by its gross morphology. Newman and Cannon (1994) first recognised the similarity of colour pattern between *Pseudoceros* and *Pseudobiceros*. It is assumed that this colour pattern is aposematic.

Laidlaw (1902) originally described *P. flavomarginatus* as velvety-black with an orange margin about 1.5mm wide. No other details were given regarding the shape of the pharynx, eyes or the number of male pores. Therefore, *P. flavomarginatus* is considered incerta sedis as its generic determination is unclear.

DISTRIBUTION

Found on colonial ascidians under boulders at the reef crest. Common from Heron Is. Rare from One Tree Is. Record: Hawaii.

Pseudobiceros stellae sp. nov.
(Figs 41A - D; 51E)

Pseudobiceros sp. Poulter, 1987: pl. 2.I.2 e.

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, on algae, WM, 28.08.89, QMG210633.

PARATYPE: Heron Is., reef crest, on algae, LS, QMG210634.

OTHER MATERIAL: Heron Is., reef crest, 28.12.90, WM, QMG210536; 19.01.92, WM, QMG210537; reef slope, 3m, night, 29.01.92, WM, QMG210538; 29.07.92, WM, QMG210541; WM, QMG210542; night, 30.01.93, S, QMG210540; night, off jetty, P. Lawn, 02.02.93, S, QMG210543; reef crest, 08.02.93, S, QMG210544. One Tree Is., reef crest, 16.08.93, LS, QMG210545; Madang, reef crest, 3m, 16.06.92, S, QMG210539.

DESCRIPTION

Colour & pattern. Background velvety black or chocolate brown with raised white microdots evenly distributed over the entire surface; larger dots regularly distributed and arranged in 'flower-like' clusters. Pseudotentacles with white tips. Ventral surface blue-black or dark grey.

External features. Pseudotentacles highly developed, square, inflated with deep lateral ruffles. Cerebral eyespot with about 40 eyes in clear oval area. Male pores large, conspicuous and well separated. Size: mature from 50 × 18mm to 60 × 25mm; juveniles from 7 × 4mm.

Reproductive anatomy. Vas deferens unbranched. In one system: seminal vesicle extremely narrow, elongate (667µm long); ejaculatory duct long, coiled; prostate oval (367µm wide); stylet long (244µm long). Male and female antra deep.

DIAGNOSIS

Black with evenly distributed white dots; highly developed, square, ruffled pseudotentacles; extremely narrow and elongate seminal vesicle.

ETYMOLOGY

In honour of the late Mrs Stella Laycock.

REMARKS

This species belongs in Group 4 and only one other species possess a black background colour, *P. bajae.* However, *P. stellae* has regular white dots that form a 'flower-like' arrangement not irregular white dots and highly developed ruffled pseudotentacles. One animal found with two suckers of unequal sizes.

P. stellae is sometimes found under the same boulder as the common nudibranch *Dendrodoris nigra.* Both animals have the same colour pattern, size range and are possibly mimics.

DISTRIBUTION

Found under boulders and out on the rubble at night on the reef crest. Common from Heron Is., rare from One Tree Is. and Madang. Record: Hawaii.

Pseudobiceros uniarborensis sp. nov.
(Figs 42A - D; 51F)

MATERIAL EXAMINED

HOLOTYPE: Heron Is., reef crest, 14.08.92, WM, QMG210599.

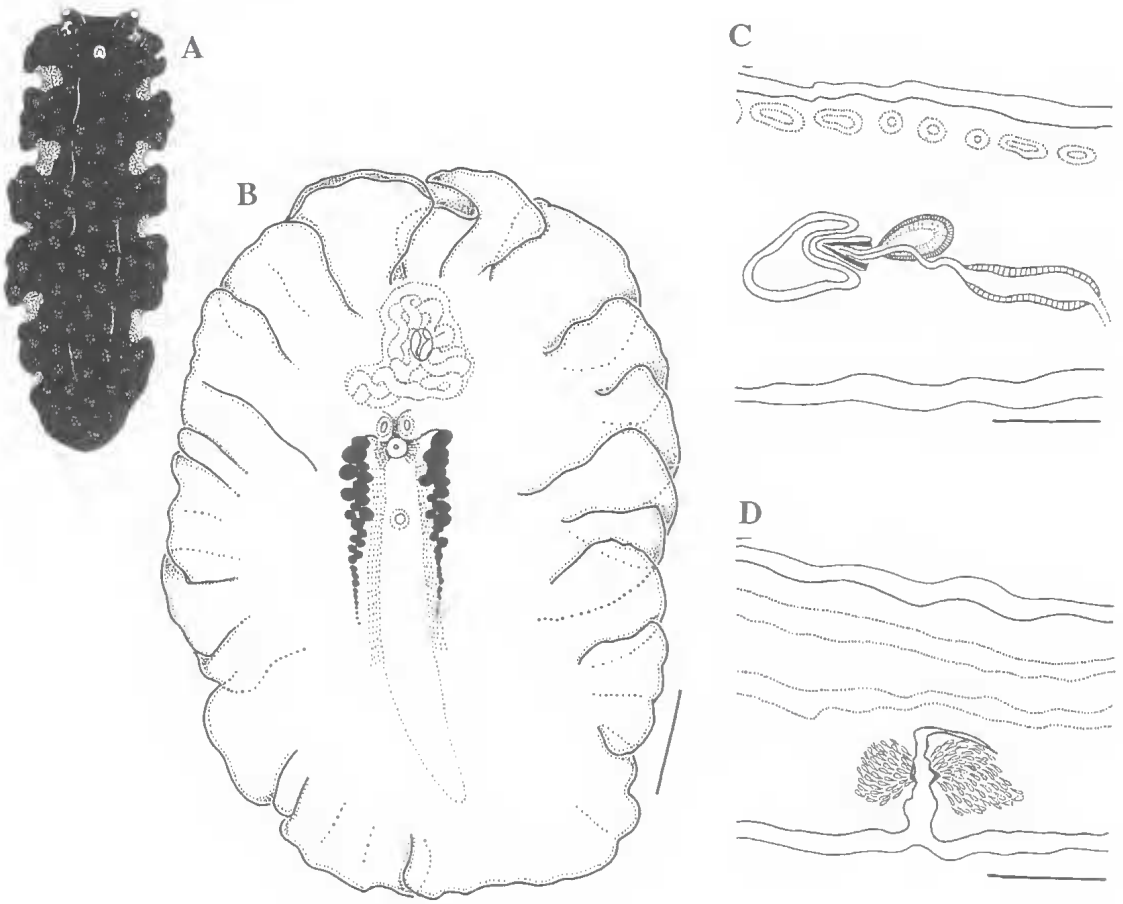


FIG. 41. *Pseudobiceros stellae* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210532, wholemount showing the morphology from the ventral surface; C,D, QMG210535, reconstruction of the reproductive anatomy. C, male system; D, female system. Scales: B, 5mm; C, D, 500μm.

PARATYPE: Heron Is., reef crest, night, 30.01.93, LS, QMG210602.

OTHER MATERIAL: Heron Is., reef crest, 05.02.92, LS, S, QMG210581; 07.02.92, LS, QMG210591; 19.02.92, WM, QMG210592; S, QMG210617; 29.07.92, S, 2 spec., QMG210594; 02.08.92, WM, QMG210595; 07.08.92, S, 2 spec., QMG210596; 11.08.92, S, QMG210597; WM, QMG210598; One Tree Is., reef crest, 13.09.92, S, QMG210600; 11.09.92, LS, QMG210601; 30.01.93, LS, QMG210602; 13.09.92, S, QMG210600; 13.08.93, S, QMG210618. Madang, reef slope, 3m, T. Gosliner, 12.06.92, S, QMG210593.

DESCRIPTION

Colour & pattern. Background velvety black or dark brown: margin with three extremely narrow bands; inner band bright orange (150 or 137), middle band wide, transparent grey and outer rim opaque white. Pseudotentacles black with white tips but without marginal bands; white-grey triangle between pseudotentacles extending into the cerebral eyespot. Ventrally brown with a white marginal band.

External features. Extremely delicate species. Pseudotentacles pointed and ear-like. Cerebral eyespot with about 60 eyes. Two male pores close together. Size: mature from 55 × 22mm to 60 × 35mm; juvenile from 8 × 3mm.

Reproductive anatomy. Vas deferens branched. In one system: seminal vesicle large rounded oblong (1.39mm long); ejaculatory duct short,

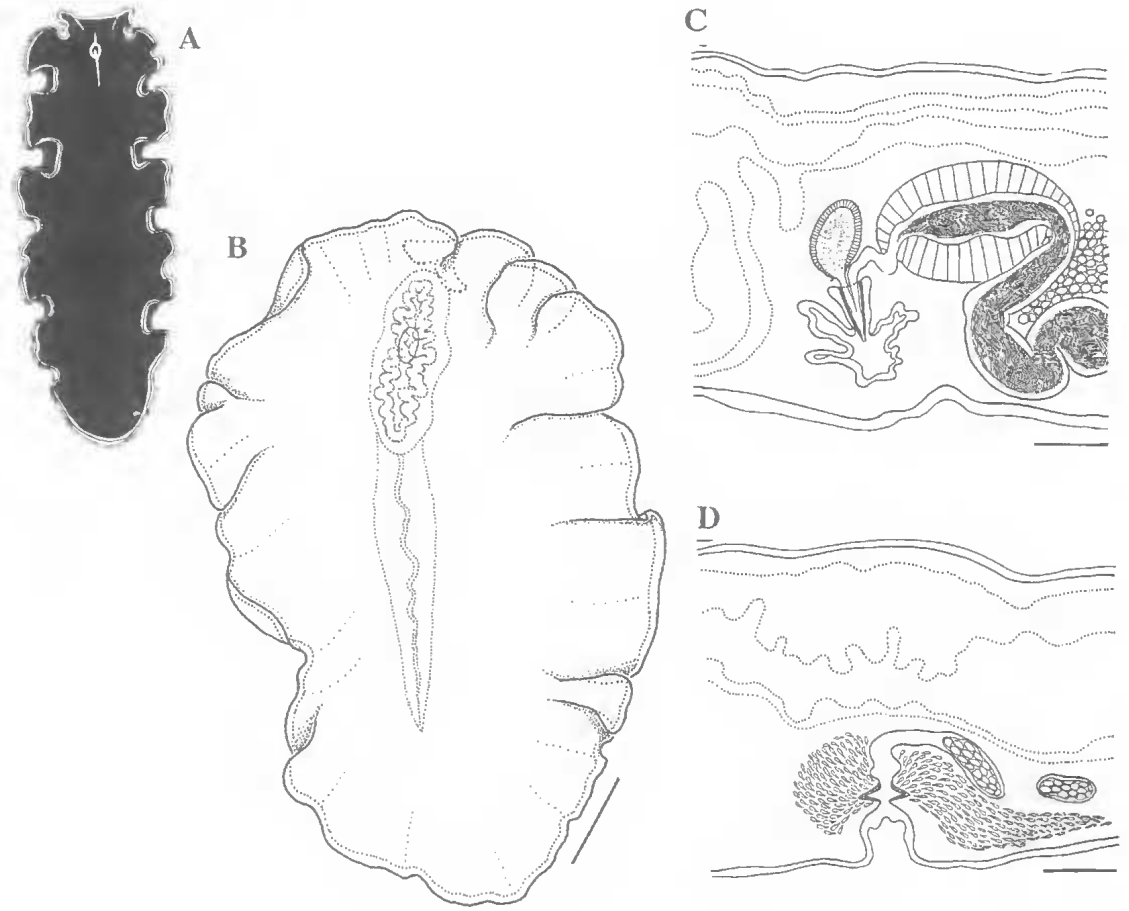


FIG. 42. *Pseudobiceros uniarborensis* sp. nov. A, diagram of the dorsal colour pattern; B, QMG210600, wholemount showing the morphology from the ventral surface; C, D, QMG210602, reconstruction of the reproductive anatomy. C, one male system; D, female system. Scales: B, 2.5mm; C, D, 500µm.

coiled; prostate large, oval (592µm long); stylet long (389µm long). Male and female antra deep.

DIAGNOSIS

Black with three extremely narrow marginal bands; inner orange, middle grey and white at rim.

ETYMOLOGY

From the Latin *uni* = one, *arborensis* = place of the tree, for the One Tree Island Research Station.

REMARKS

This species belongs in Group 2 and the majority of species are black with vibrantly coloured marginal bands. Only one other species is similar in colour, *P. hancockanus*. However, *P. uniarborensis* has three narrow marginal bands not two relatively wide bands and pointed ear-like pseudotentacles not square and ruffled pseudotentacles. One animal was found with two suckers.

HABITAT & DISTRIBUTION

Found under boulders at the reef crest and slope. Abundant from Heron and One Tree Is; rare from Madang.

BIOLOGY

FEEDING

Although pseudocerotids are thought to feed on sessile invertebrates, i.e. sponges and ascidians,

there are few reports in the literature. During our study a few feeding observations were made and these indicated that the majority of *Pseudoceros* fed on a variety ascidians species. One species (*P. bifurcus*) was often observed feeding on a several species of ascidians indicating non-specificity in diet. No other prey was observed being consumed (extended pharynx or feeding scars) although many species were often found crawling or resting on sponges and coralline algae. Crozier (1917) also observed one species (which he called *Pseudoceros* undescribed species, although it appears to be an euryleptid) feeding on three different species of ascidians.

During feeding, animals were often seen in situ with their highly ruffled pharynx expanded into white 'stringlike' projections extended into individual zooids of the colonial ascidians (Fig. 43). Prudhoe (1985) described this feeding behaviour and suggested that when the pharynx is extended a discharge of proteolytic secretions is used to macerate the zooids for digestion. The softened tissue is then supposedly drawn into the intestine which acts as a reservoir while further digestion takes place in the intestinal branches.

Although *Pseudobiceros* were not observed feeding during this study, several animals were collected with large 'lumps' in their intestine. It appears that the feeding behaviour is unlike that found in *Pseudoceros* as described by Prudhoe (1985). Our observations suggest that *Pseudobiceros* engulf prey with the pharynx which can expand to the same size as the animal, secretions from the pharynx may then induce digestion outside the body allowing the pharyngeal muscles to break up the prey which is then sucked, whole, into the intestine.

George & George (1979) reported that a specimen of *Pseudobiceros hancockanus* was found on a sponge and surmised that it was probably searching for small crustaceans inhabiting the sponge's water canals. The same species was also found during this study on an orange sponge and orange granules were found in its intestine suggesting that it was feeding on the sponge itself.

Morphological differences between the pharynx and intestine in the two genera clearly indicate distinct feeding behaviours. Unfortunately, feeding observations were rare and pseudocerotids did not feed in aquaria, possibly due to problems in retaining healthy prey for several days. For most species their prey is unknown.

Predation

We do not have direct observations of predation on polyclads. Nevertheless, worms have been seen on several occasions bearing rents and tears in their flesh. Minor tears may be the results of copulatory behaviour (see below), but large tears (presumedly bite marks) are thought to be from aborted feeding attempts - we assume by fish. To test this assumption worms were fed to fish in situ and in the laboratory. Although the pieces were readily accepted they were quickly spat out, however, other prey items (i.e. fish, molluscs) were consumed by the fish. These observations suggest worms are distasteful and that their visual predators, fish, would quickly learn to avoid them by recognition of their distinct and bright colour patterns.

Copulation

Copulatory behaviour in *Pseudoceros* and *Pseudobiceros* was observed for the first time (in situ and in the laboratory) and was recorded on video. During copulation animals were observed to move towards each other, touch, then roll around together, simultaneously everting their penis papillae and stylet(s) outward. They would then try to stab each other anywhere, sometimes causing considerable damage to their partner (Figs 44A, B; 48C, lower animal). On several occasions, both animals reared up and fell towards each other with stylets extended (Fig. 44B). When one animal was successful in penetrating the other, it often held on with its stylet embedded in the epidermis of its partner for up to five minutes and in situ animals often would not let go even if disturbed.

During copulation, loose bundles of white spermatozoa were seen injected in the partner. The sperm could be observed as it moved into the parenchyma in white lines, presumably towards the oviducts. This copulatory behaviour was observed in the laboratory for up to three days with each animal receiving multiple stab wounds. Animals with wounds were able to heal within 24 hours.

Larval Development

When *Pseudoceros* were removed from colonial ascidians under boulders, eggmasses were often observed adhering to the dorsal test of the ascidian. Each irregular shaped eggmass contained a few hundred eggs, tightly packed in a single layer. Eggmasses collected from the field did not hatch in the laboratory.

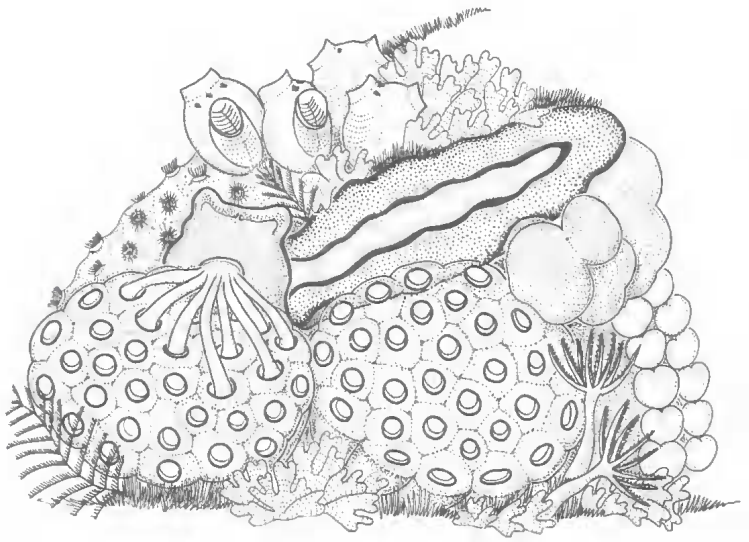


FIG. 43. *Pseudoceros bifurcus* feeding on colonial ascidians by extending sting-like projections of its large ruffled pharynx into individual zooids of the colony .

Pseudobiceros (*P. bedfordi* and *P. gratus*) egg-masses were laid on the side of ice cream containers in the laboratory. These eggmasses were transparent beige becoming darker and more opaque towards hatching, then the developing larvae could be seen moving in the egg cases. Each egg is approximately 75µm maximum diameter. Müller's larvae with their eight lobes (see Hyman, 1951: 174, fig. 67) all hatched on the tenth day of development (Fig. 45) and each measured between 53 - 70µm long. Larvae, although tiny, could clearly be seen swimming in the water column. Larvae from both species were identical; transparent with dark red spots (yolk cells). After six days of development, brown particles could be seen in the digestive gland. Larvae became more streamlined as the lobes were absorbed, swimming in a rolling ciliary motion. During development the lobes continued to be absorbed and the digestive gland grew larger. Larvae tended to cluster together in the surface of the water column only surviving for two weeks after hatching and not settling in this time.

HABITAT & DISTRIBUTION

Members of *Pseudoceros* were the most common polyclads found in the southern GBR (Newman & Cannon, 1994) and displayed the most diverse colour patterns. The majority of species were found on colonial ascidians under boulders at the reef crest. Many species, although colourful, were actually cryptic when found in situ on their ascidian prey. Some of the most flamboyantly patterned species of both genera (*Pseudoceros ferrugineus*, *P. lindae* and *P. sapphirinus*; *Pseudobiceros gloriosus*, *P. gratus* and *P. hancockanus*) were more often found out and about on or under ledges along the reef slope during the day.

The relatively large size, flamboyant colour pattern and fluid motion of the ruffled undulating margin of *Pseudobiceros* makes them the more conspicuous and easily observed of the genera. Animals were generally found to be active both during the day and at night. Occasionally, both *P. bedfordi* and *P. hancockanus* were found swimming off the reef crest during the day. Generally *Pseudoceros* were not observed swimming.

Three species were found to be abundant (*Pseudoceros bifurcus*, *P. bolool* and *P. uniarborensis*) from Heron Island. Few species were found to be abundant or even common at One Tree Island and Madang, but this may be due to the less frequent (and shorter) collecting trips to these locations.

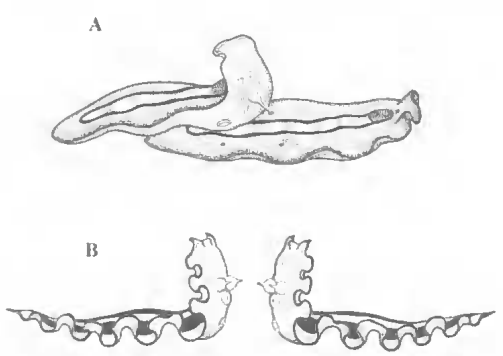


FIG. 44. Copulatory behaviour. A, *Pseudoceros*; B, *Pseudobiceros*.

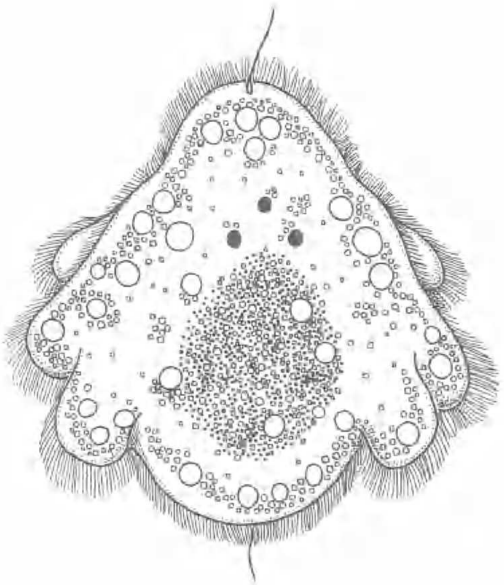


FIG. 45. Müller's larvae of *Pseudobiceros*.

Mimicry between pseudocerotids and toxic phyllidiid nudibranchs has been reported by Gosliner & Behrens (1991) and Newman et al. (1994). During this study two species (*P. bolool* and *P. stellae*) were found to be of similar pattern to the polymorphic nudibranch *Dendrodoris nigra*. This is presumedly a further case of mimicry but which animal is the mimic and which the model is not clear as the toxicity of pseudocerotids is yet to be examined.

CONCLUSIONS

We believe that we have demonstrated that the diversity of tropical polyclads belonging to the genera *Pseudoceros* and *Pseudobiceros* is considerable within tropical reefs of eastern Australia and Papua New Guinea. Undoubtedly we have been greatly aided in this research by the development of a reliable fixation procedure for these delicate worms (Newman & Cannon, in press). This aside, we have also shown how vital to the study of these worms is live observation, photography and videography. Criteria of considerable importance which are evident in live study are too often unobserved or totally lost in fixation.

Our observations demonstrate clearly that Prudhoe (1985) was incorrect when he argued for polymorphism in *Pseudoceros* with regard to the number of reproductive systems. We have shown that a suite of characters (easily seen in live animals) including size, shape, eye arrangement, pseudotentacles, pharynx and topography of the gonopores and sucker all uphold Faubel's (1984) recognition of *Pseudoceros* and *Pseudobiceros* as distinct genera.

We are convinced nevertheless that Prudhoe (1985, 1989) was correct in claiming relative homogeneity within *Pseudoceros* of both the male and female reproductive systems and musculature making determination of species possible on the basis of colour pattern. In this Prudhoe followed Hyman (1954, 1959a) who had also claimed colour patterns were adequate to determine species. Taxonomic problems due to inadequate generic determinations has meant that the number of species belonging to *Pseudoceros* s.s. has been greatly inflated in the past.

We have made a determined effort to provide evidence of homogeneity of the reproductive anatomy by illustrating the sectioned reproductive systems (both male and female) of nearly all species treated, and in so doing have shown camera lucida drawings of the actual sections with, as far as practical, a minium of interpretative distortion. Our observations, in situ and in the laboratory, of copulatory behaviour provides a convincing explanation for relative reproductive homogeneity. A crude, even savage, intradermal insemination strategy is unlikely to generate elaborate morphological copulatory isolating mechanisms.

Observations did reveal, however, that animals of like patterns copulated simultaneously, mitigating against any argument for polymorphism of colour pattern within species. Further support for species distinctiveness is seen in differences between size at maturity and habitat which indicates that species separated on colour pattern are reliable biological entities. Of course similar or virtually identical patterns have been detected in species in separate genera (cf. *Pseudoceros periaurantius* and *Pseudoceros periculosus*) and even separate families (Newman & Cannon, 1994). This reinforces the assertion that though species determination within a genus can rely on colour pattern alone; generic determinations rely on careful morphological analyses. We maintain at this time that serial sectioning of the reproductive structures will be necessary until the limit of criteria needed to determine genera within the family are understood.

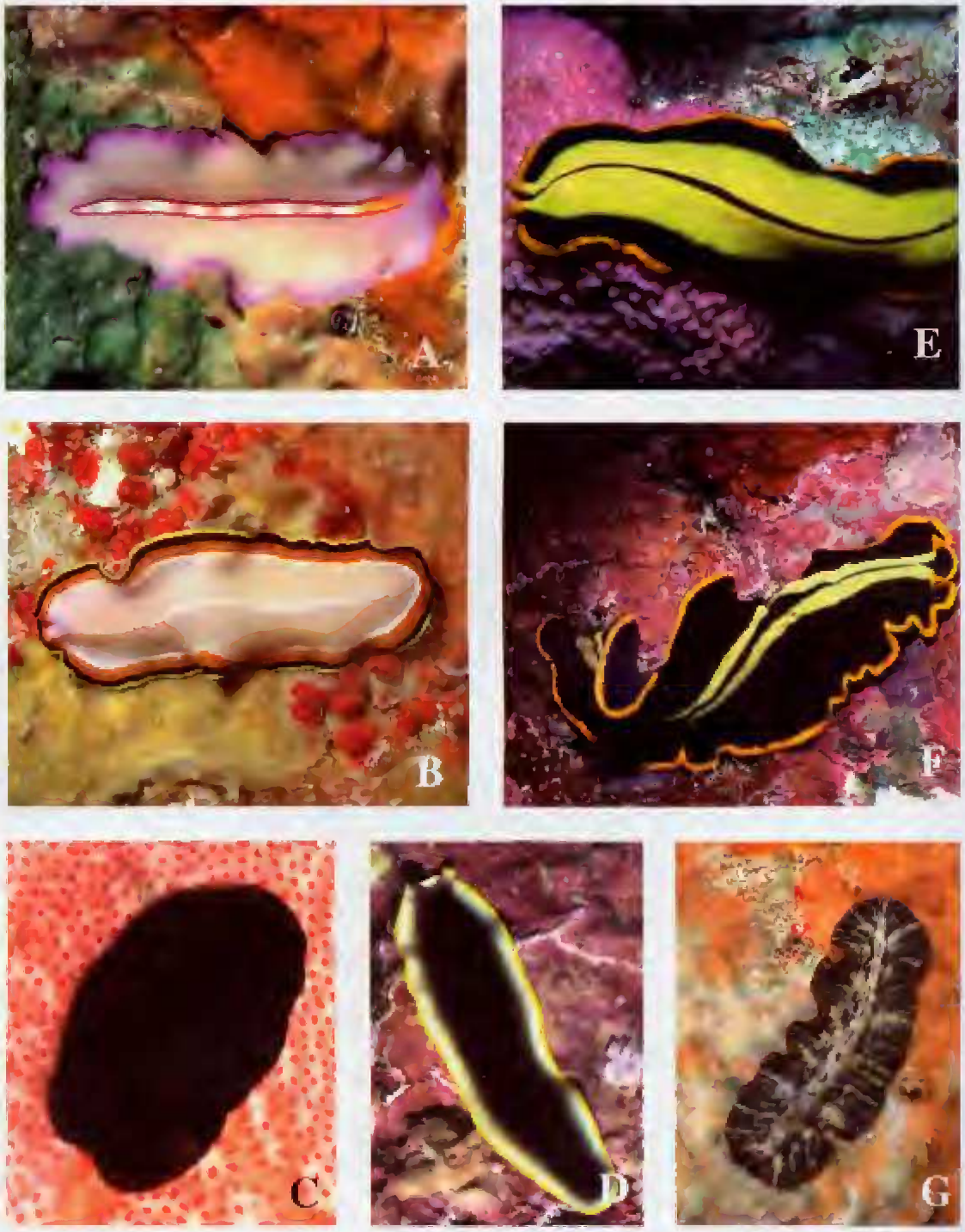


FIG. 46. A, *Pseudoceros bifurcus*, QMG210335, Heron Is.; B, *Pseudoceros bimarginatus*, QMG210381, Heron Is.; C, *Pseudoceros bolool*, QMG210630, One Tree Is.; D, *Pseudoceros depiliktabub*, holotype, Madang; E, *Pseudoceros dimidiatus*, QMG210489, Madang; F, *Pseudoceros dimidiatus*, record only, Madang; G, *Pseudoceros felis*, holotype, Heron Is.

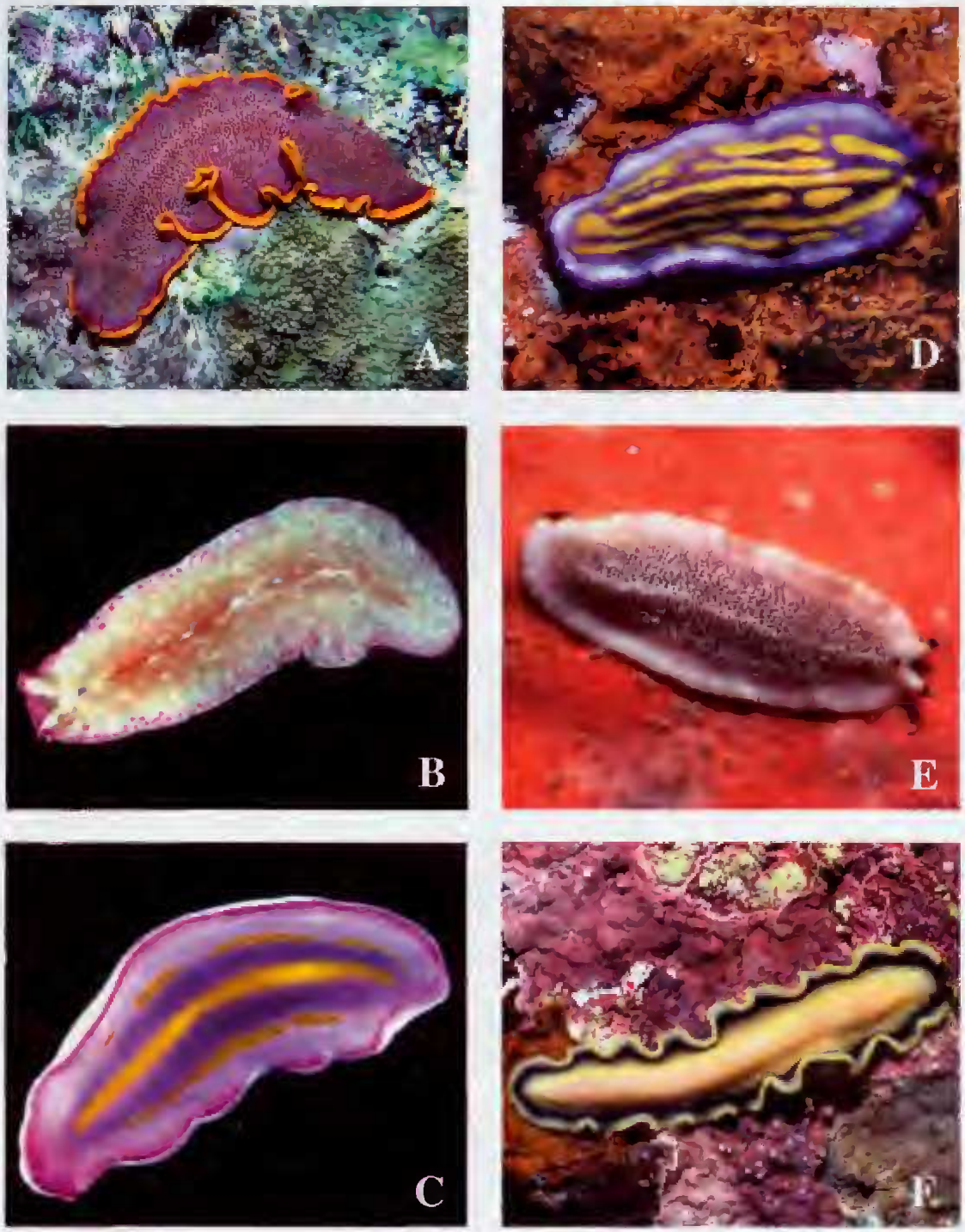


FIG. 47. A, *Pseudoceros ferrugineus*, QMG210368, Heron Is.; B, *Pseudoceros goslineri*, QMG210452, *Heron Is.*; C, *Pseudoceros gravieri* juvenile, QMG210345, Heron Is.; D, *Pseudoceros gravieri* adult, GBR (photo only G. Allen); E, *Pseudoceros heronensis*, QMG210461, Heron Is.; F, *Pseudoceros jebborum*, QMG210469, Madang.

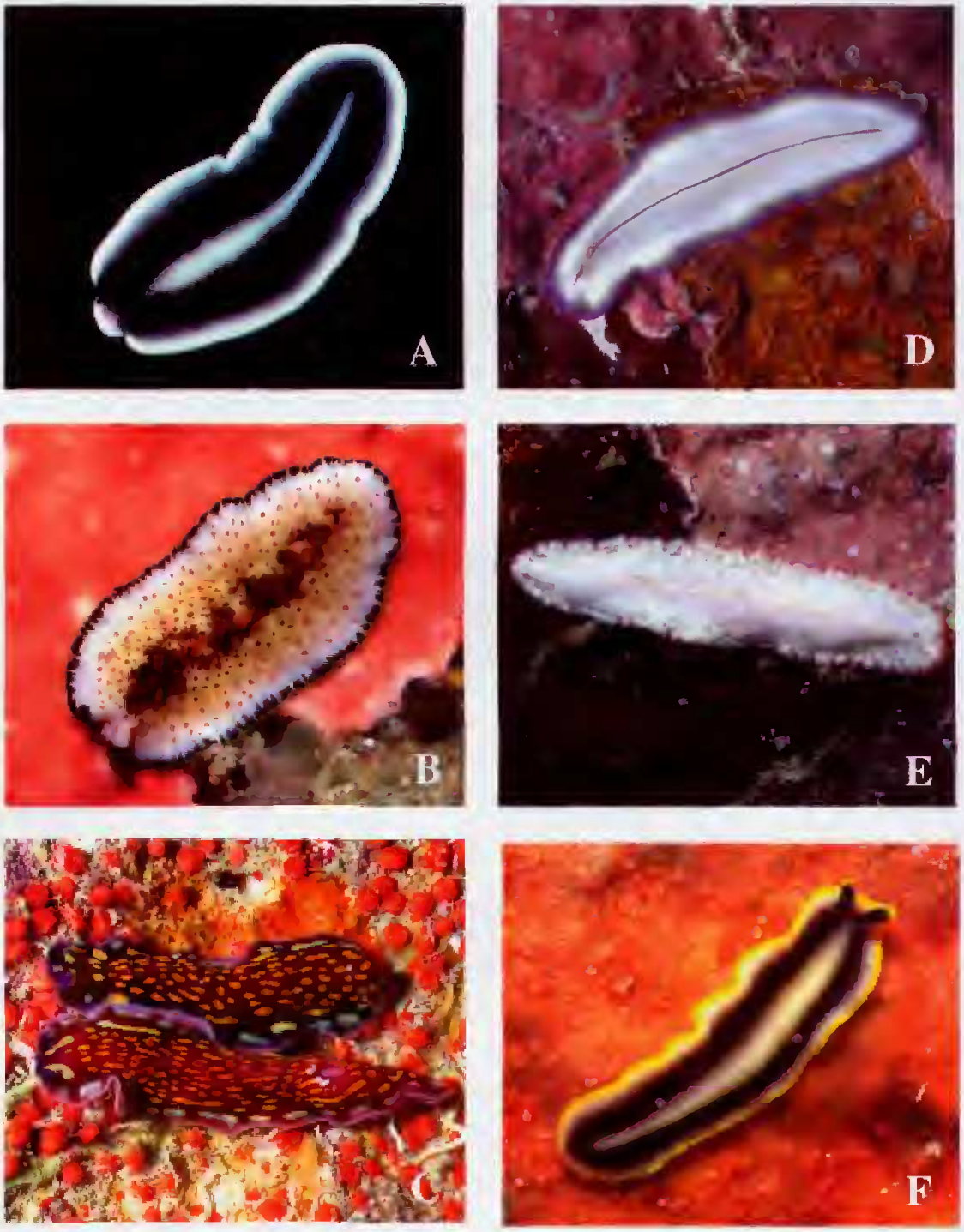


FIG. 48. A, *Pseudoceros laticlavus* (record only), Heron Is.; B, *Pseudoceros leptostictus*, QMG210341, Heron Is.; C, *Pseudoceros lindae*, holotype, Heron Is.; D, *Pseudoceros monostichos*, holotype, Heron Is.; E, *Pseudoceros ouini*, holotype, Madang; F, *Pseudoceros paralaticlavus*, paratype, QMG210428, Heron Is.

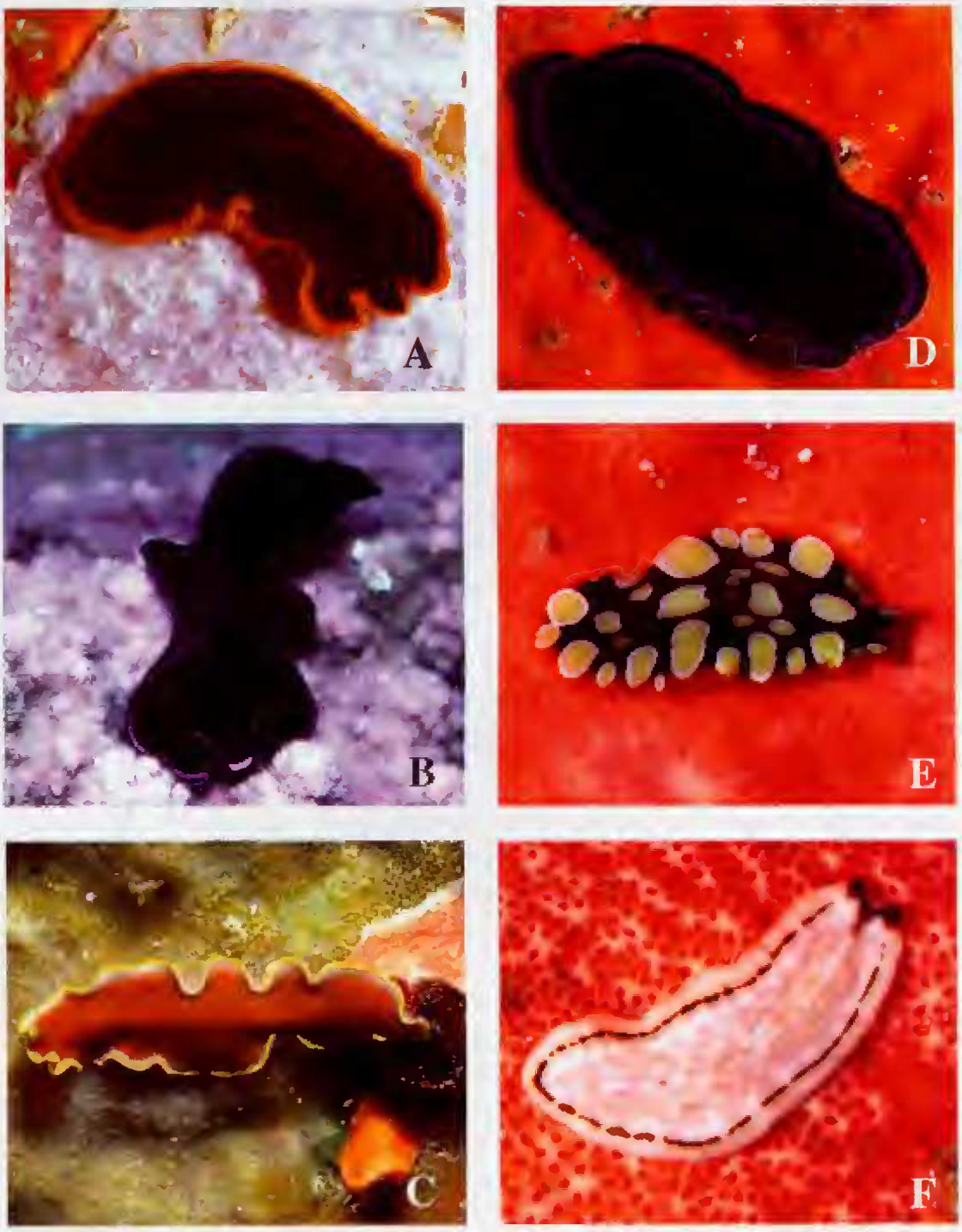


FIG. 49. A, *Pseudoceros periaurantius*, paratype, Heron Is.; B, *Pseudoceros peripurpureus*, holotype, Heron Is.; C, *Pseudoceros prudhoei*, paratype, QMG210402, Heron Is.; D, *Pseudoceros sapphirinus*, QMG210522, One Tree Is.; E, *Pseudoceros scintillatus*, holotype, Heron Is.; F, *Pseudoceros verecundus*, QMG210499, One Tree Is.

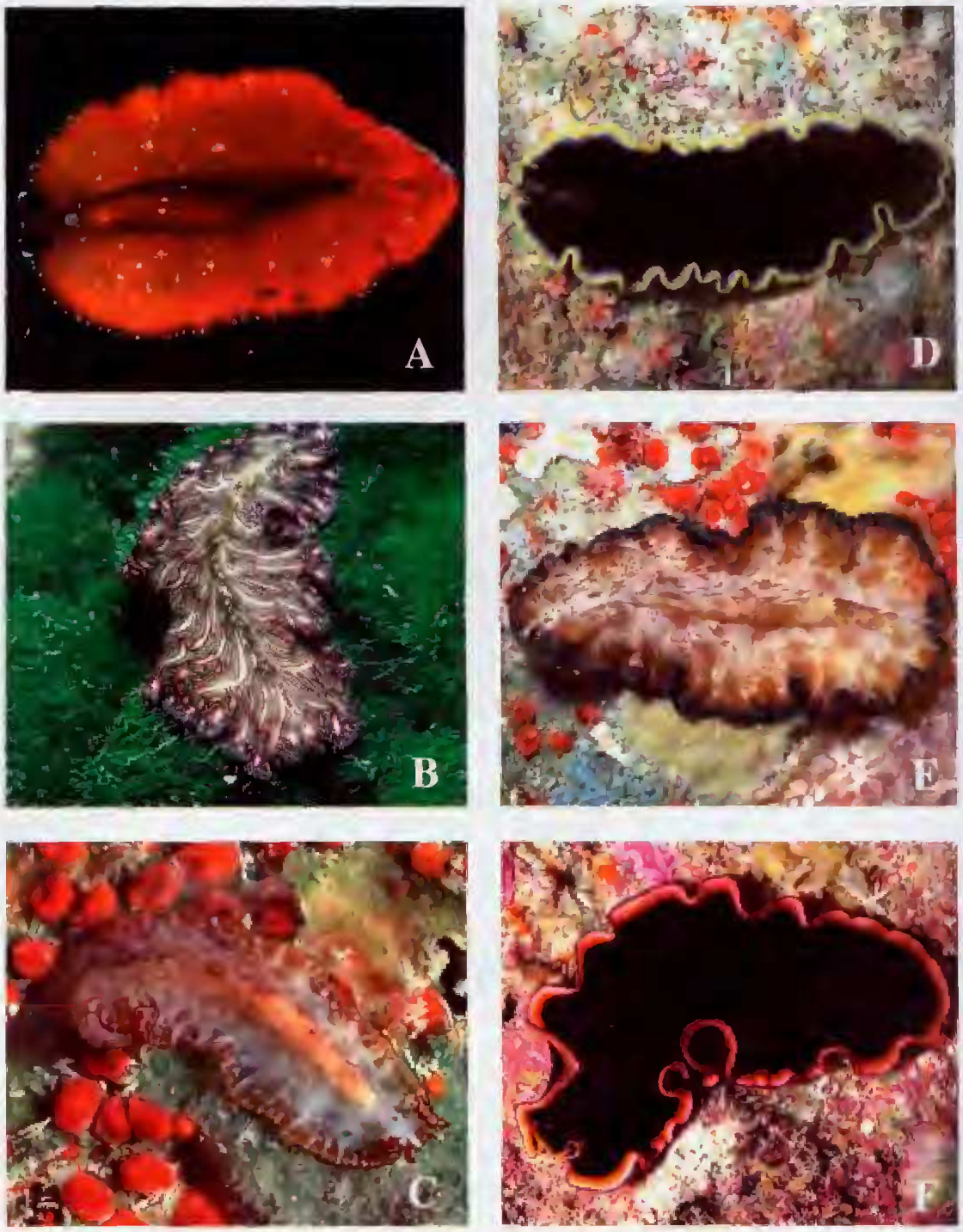


FIG. 50. A, *Pseudobiceros apricus,* QMG210571, Heron Is.; B, *Pseudobiceros bedfordi* (record only), Heron Is.; C, *Pseudobiceros damawan,* QMG210611, Heron Is.; D, *Pseudobiceros flavocanthus,* paratype, Madang; E, *Pseudobiceros fulgor,* paratype, QMG210556, Heron Is.; F, *Pseudobiceros gloriosus,* QMG210551, Heron

FIG. 51. A, *Pseudobiceros gratus*, QMG210570, One Tree Is.; B, *Pseudobiceros gratus*, QMG210564, Madang; C, *Pseudobiceros hancockanus*, QMG210508, One Tree Is.; D, *Pseudobiceros periculosus*, paratype, QMG210535, Heron Is.; E, *Pseudobiceros stellae*, holotype, Heron Is.; F, *Pseudobiceros uniarborensis*, paratype, Heron Is.

The taxonomic implications of our study are that without critical morphological details which allow a generic determination, many species in *Pseudoceros* sensu lato simply cannot be placed. By confirming the validity of *Pseudobiceros* and by examining descriptions of *Pseudoceros* s. l. in the light of our emended diagnoses we can reliably place only a limited number of species in these two genera. Other species may be placed within these genera following re-examination and careful recollection at their type localities.

We have attempted to standardise the description of colour patterns in pseudocerotids. First, we have adopted the Pantone standard for reliable colour recording. Secondly we have provided a vocabulary to describe colour patterns and finally we have erected six pattern groups to contain species. We are conscious that this is a first attempt and anticipate further refinement as more species are found and described.

We cannot believe the colours patterns are meaningful to the species in any intraspecific visual sense. Some are clearly warning colours, some serve to mimic other species (Newman et al., 1994) and some are clearly cryptic. Therefore colour pattern appears to be a specialiscd antipredation strategy. In the reef environment we must assume the primary visual predators of polyclads are fish. Our observations clearly suggest that scarred worms are tasted but not consumed by fish (wounds usually heal within 24 hours). Evidence from trials of worms fed to reef fish, in situ, and in the laboratory (Newman & Flowers, unpub. obs.) indicated that fish readily accept, but immediately reject, polyclad flesh. These observations strongly suggest an antipredatory nature to the chemistry of these worms.

Flamboyant colour patterns (aposematism) would serve to warn fish of the flatworm's distastefulness (toxicity) and dull colour patterns would provide camouflage (Newman et al., 1994). It should be noted that our perception on the quality of a colour pattern depends entirely on the habitat of the flatworm. A brilliantly coloured animal may be cryptic on a similarly coloured background (e.g. colonial ascidian) and hence there is a need to study these animals live and in situ.

The presence of aposematic colour patterns suggests that chemical defences are significant deterrents to predation. Chemicals must also be significant in precopulatory behaviour. Copulatory mechanisms are crude so presumably recognition must rely on chemical means since visual cues are discounted. The elaboration of the anterior margin into large pseudotentacles is further evidence that these worms rely substantially on chemosensory mechanisms to determine their behaviour. We believe these flatworms offer a rich field of research for marine chemists and fish ethnologists.

ACKNOWLEDGEMENTS

We wish to thank all the people who helped with the delicate task of hand collecting tropical polyclads. Special thanks are given to; Dr A. Flowers, Dr T. Gosliner, Dr M. Jebb, Mr J.-M. Ouin, Ms M. Preker, Mrs J. Marshall, Dr M Ghiselin, Dr D.J. Brunckhorst, Mr M. McCarthy, Mr H. Peterken and Mr. J. Tanner. Histological preparations were expertly provided by Ms Z. Khalil and Mrs C. Lee. Specimens were curated by Mr K. Sewell. Mr B. Cowell kindly helped with the colour plates, and we thank Clarity Photographics for image manipulation and production of the colour layouts. Mr L. Winsor and Mr J.-M. Ouin kindly gave invaluable advise on polyclad fixation. Dr A. Flowers greatly assisted with the underwater and laboratory photography. We are indebted to Mr I. Loch, Dr R. Bray and the late Mr S. Prudhoe for providing colour transparencies, specimens and advice. Thanks also to Dr A. Faubel for his advice. Special thanks are given to the Director and staff of the Heron Island Research Station and Christensen Research Station and to the Managers of the One Tree Island Research Station. Thanks are extended to Dr P. Mather for ascidian identifications and to the various photographers who provided further records. The anonymous reviewers are thanked for their helpful comments. Financial support was provided by ARC Grant AD# 9031806 (L.R.G.C.), P & O Pty. Ltd. & Heron Island Research Station Reef Fellowship (L.J.N.) and The Christensen Fund, Palto Alto, California (L.J.N.). This is Contribution No. 106 from the Christensen Research Institutc, Madang, Papua New Guinea.

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