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Biodiversity of marine planarians revisited (Platyhelminthes, Tricladida, Maricola)

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Biodiversity of marine planarians revisited (Platyhelminthes, Tricladida, Maricola)

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Abstract

An account is given of new distributional records and the taxonomy of nine species of marine triclad, including the description of two new species. After more than 100 years of uncertainty, the paper resolves the taxonomic status of the enigmatic nominal species *Procerodes solowetzkianus* Sabussow, 1900. The study concludes with a biogeographic analysis of all species of marine planarian by documenting patterns of species richness on an equal area grid map of the world.

Keywords: *Platyhelminthes, Tricladida, Maricola, taxonomy, biogeography, new species*

Introduction

Progress in our knowledge on the diversity, taxonomy and biogeography of the marine triclads is usually slow, due to the fact that the animals are relatively rare and generally receive little attention from marine biologists. Sluys (1989) provided the most recent and comprehensive review of the group and since then only a few papers have been devoted to this group of animals (cf. Sluys and Ball 1990; Sluys et al. 1990; Sluys and Kawakatsu 1995, 2000; Tekaya et al. 1996).

Over the years we have come across new information and materials of several species of marine planarian, including new species. In this paper we detail these new data, thus contributing to an up-to-date taxonomy, and we review the biodiversity and biogeography of the entire group of marine triclads.

Material and methods

Specimens that were collected and/or processed by the authors were fixed or post-fixed in Bouin's or Steinmann's fluid. Serial sections were made at intervals of 4–6 µm and were stained in Delafield's haematoxylin and erythrosin or in Mallory-Cason.

Material is deposited in the Queensland Museum, Brisbane (QM) and in the Zoological Museum, Amsterdam (ZMA).

The following abbreviations are used in the figures: bc, bursal canal; br, brain; ca, common atrium; cap, copulatory apparatus; cb, copulatory bursa; cod, common oviduct; cvd, common vas deferens; cx, cervix; ed, ejaculatory duct; e, eye; fgd, female genital duct; gid, genito-intestinal duct; go, gonopore; in, intestine; le, lens; lm, longitudinal muscles; ma, male atrium; mo, mouth; od, oviduct; ov, ovary; pg, penis gland; ph, pharynx; pp, penis papilla; rcd, receptacular duct; sg, shell gland; sv, seminal vesicle; te, testis; tm, transverse muscles; ug, unicellular gland; vd, vas deferens; vf, valve-like fold; vnc, ventral nerve cord.

Systematic account

Foviella affinis (Oersted, 1843)

(Figures 1–3)

Synonymy: *Procerodes solowetzkianus* Sabussow, 1900.

Material examined

ZMA V.Pl. 948.1, Chupa Bay, White Sea (1986, 1987 or 1988), sagittal sections on four slides; V.Pl. 948.2, *ibid.*, sagittal sections on four slides; V.Pl. 948.3, *ibid.*, sagittal sections on four slides.

Comparative discussion

Since no copy of Sabussow's (1900) paper was available at the time, Sluys (1989) had to rely on the summaries provided by Wilhelmi (1909) and Böhmig (1906), workers who both pointed to the incomplete and inadequate original description of the species *Procerodes solowetzkianus* Sabussow, 1900 from the Solovetskiye Islands in the White Sea. When R.S. obtained a personal copy of Sabussow's paper, no new light was thrown on the enigmatic

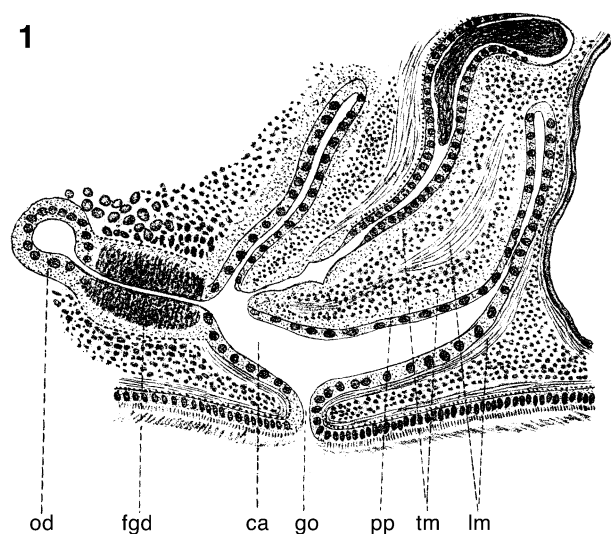
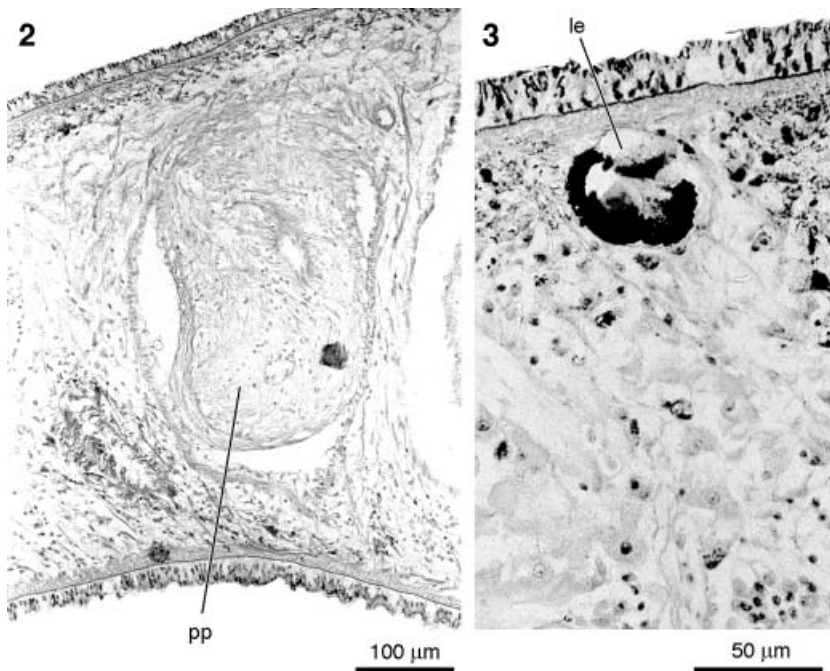


Figure 1. *Foviella affinis*, sagittal section through copulatory apparatus (from Sabussow 1900: pl. III, figure 34; labels adapted according to current terminology).



Figures 2, 3. *Foviella affinis*. (2) V.Pl. 948.3, sagittal section of the copulatory apparatus. (3) V.Pl. 948.3, sagittal section through eye cup with lens.

status of *P. solowetzkianus*, albeit that thus there was direct access to the drawing of a sagittal section of the copulatory apparatus (Figure 1).

Russian workers continued to report *P. solowetzkianus* from the White Sea (Timoshkin 1979; Poljakova 1991) and when finally new material became available it was immediately clear how Sabussow's account should be correctly interpreted. It turned out that a good deal of misunderstanding had been caused by the fact that Sabussow described as a small, ball-shaped 'Uterus' (i.e. copulatory bursa) a structure that actually is the very distal end of the female genital duct, in point of fact the precise point where the oviducts communicate with the genital duct. A copulatory bursa, as present in many maricolans, is actually missing in these animals from the White Sea. Examination of histological sections unequivocally revealed that the specimens are representatives of the species *Foviella affinis* (Oersted, 1843). This species is further characterized by: (1) a female genital duct receiving the secretion of penial glands; (2) a well-muscularized penial papilla with a distinct caudally directed bend or with the tip of the papilla curved towards the dorsal body surface; (3) vasa deferentia that expand within the penis bulb to form intrabulbar spermiducal vesicles before uniting to form the ejaculatory duct; and (4) a large lens in each eye cup. All of these features occur in our presumed *P. solowetzkianus* animals, a finding that we here substantiate by providing a photograph of a sagittal section of the copulatory apparatus (Figure 2) and of an eye cup with a lens (Figure 3).

Sabussow's (1900) description now turns out to be in close agreement with our findings based on examination of new material, since he depicted the curved nature of the penial papilla (his figures 32–34), the female genital duct receiving the secretion of shell glands (his figure 34) and the intrabulbar spermiducal vesicles (his figure 33).

Miroplana paulula Sluys, sp. nov.
(Figures 4–8)

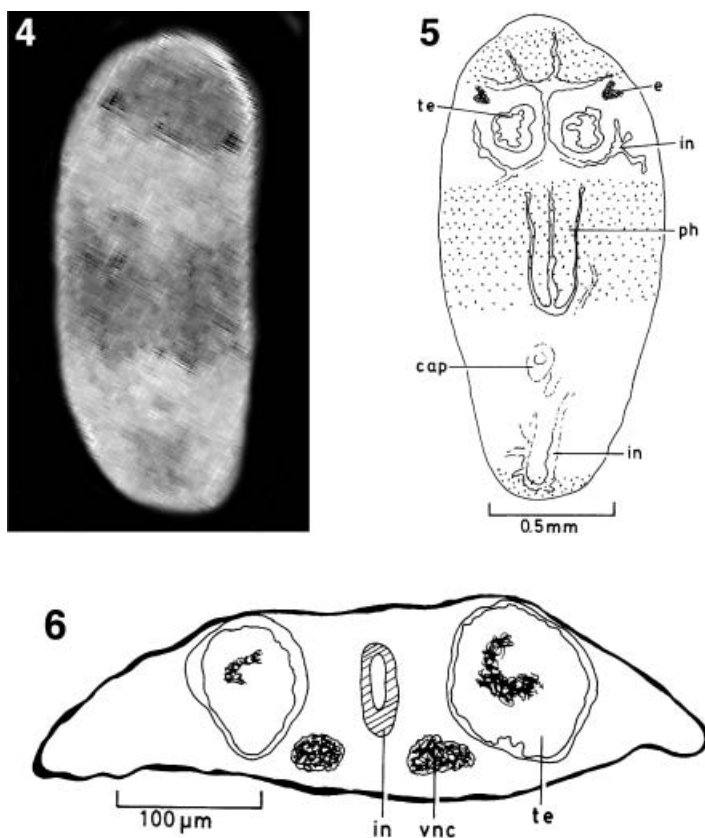
Material examined

HOLOTYPE: QM G222882, Coomera River, Coomera (27°51'00"S, 153°21'00"E), Queensland, Australia, 24 June 1998, sagittal sections on three slides.

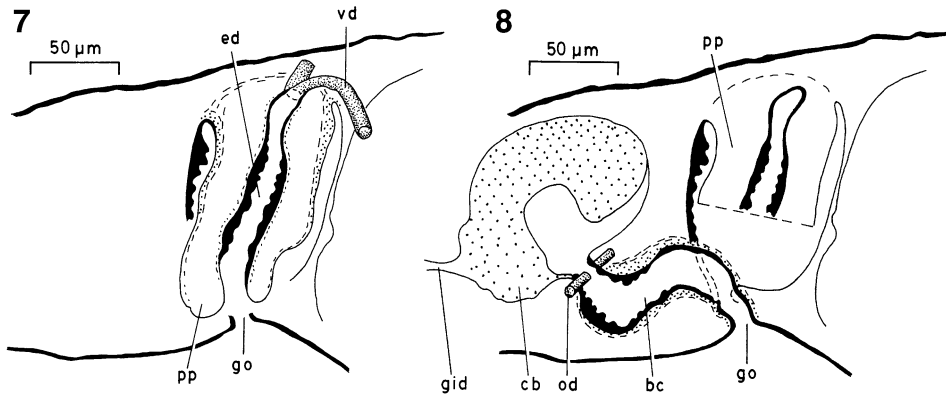
PARATYPES: ZMA V.Pl. 949.1, *ibid.*, whole mount on one slide; QM G 222883, *ibid.*, transverse sections on three slides; ZMA V.Pl. 949.2, *ibid.*, transverse sections on five slides; ZMA V.Pl. 949, preserved specimens.

Diagnosis

Miroplana paulula Sluys, sp. nov. is characterized by three pigmented transverse bands, with the anterior band located in front of the eyes, a genito-intestinal duct between copulatory bursa and the gut, and one pair of large testes located between the brain and the root of the pharynx. The species differs from its congener by the absence of spines in the ejaculatory duct and lack of a communication between bursal canal and male atrium.



Figures 4–6. *Miroplana paulula*. (4) Photograph of a live specimen. (5) V.Pl. 949.1, dorsal view of whole mount. (6) QM G 222883, transverse section.



Figures 7, 8. *Miropilana paulula*. (7) QM G 222882, sagittal reconstruction of the penis papilla. (8) QM G 222882, sagittal reconstruction of the female copulatory apparatus.

Ecology and distribution

The animals were found in brackish water (11‰) sediments of the Coomera River.

Etymology

The specific epithet is derived from the Latin adjective '*paululus*', few in number, and alludes to the small number of testes in this species.

Description

Living animals up to 1.5 mm in length; preserved specimens measuring up to 0.85×0.4 mm. Body lanceolate-oblong in shape, with broadly rounded anterior end and a somewhat narrower tail end that is rounded or obtusely pointed.

Dorsal surface with three dark brown, pigmented bands: an anterior band extending from the level of the eyes to the anterior body margin, a broad band lying over the region of the pharynx, and a posterior band at the very tail end of the body (Figure 4).

The eyes are well developed, the pigment cup measuring about 37 µm in diameter; the number of retinal cells present in each eye cup could not be determined. An eye lens is absent.

The pharynx is situated in the middle of the body and measures about one-quarter of the body length in preserved specimens. The mouth opening is located at the posterior end of the pharyngeal pocket.

The anterior ramus of the intestine extends forward anterior to the eyes and gives off pre-ocellar diverticula. The posterior intestinal gut trunks communicate in the very hind end of the body (Figure 5).

A pair of large testes is located between the brain and the root of the pharynx, the follicles occupying most of the dorso-ventral space (Figure 6). The vasa deferentia expand to form well-developed spermiducal vesicles in the pharynx region. At the posterior end of the pharyngeal pocket the sperm ducts curve dorso-medially and subsequently penetrate the penial bulb. Immediately after having penetrated the bulb, the vasa deferentia unite to form the ejaculatory duct. The latter is lined with a relatively tall, nucleated epithelium and is

surrounded by a well-developed coat of muscle; the ejaculatory duct opens at the tip of the penial papilla (Figure 7).

The penis bulb consists of a well-developed coat of muscle. The penial papilla is an obtusely pointed cone, covered with a flat, nucleated epithelium that is underlain with a subepithelial layer of circular muscle, followed by a thin layer of longitudinal muscle.

The male atrium communicates through a constriction with the common genital atrium, which is actually very small and immediately passes into the gonopore.

The paired ovaries are located medially to the testes and are also situated medially to the ventral nerve cords. The oviducts open separately into the bursal canal, close to the point of communication between the canal and the copulatory bursa. Distinct shell glands were not observed.

The bursal canal is lined with an infranucleate epithelium and is surrounded by a well-developed, subepithelial layer of circular muscle, followed by a layer of longitudinal muscle. The copulatory bursa of the specimens examined is filled with a finely granular substance. Through a genito-intestinal duct the bursa communicates with the intestine (Figure 8).

Comparative discussion

Although the present species differs in several respects from the type species of the genus, *Miroplana trifasciata* Kato, 1931 (cf. Kato 1931), we have nevertheless assigned it to *Miroplana* for several reasons. It should be recognized that the current diagnosis of the genus (cf. Sluys 1989) is based only on the type species and therefore may be highly biased. Furthermore, we are of the opinion that in cases of limited knowledge a conservative approach to taxonomy should be followed as much as possible and therefore we refrain from creating a new genus for the present species.

The three transverse bands of *M. paulula* immediately remind one of the similar bands reported for *M. trifasciata*. In *M. trifasciata*, however, the anterior band is positioned behind the eyes, whereas in *M. paulula* it occurs anterior to the eyes. Furthermore, the posterior band in *M. trifasciata* is located more anteriorly than in *M. paulula*.

In contrast to the type species, *M. paulula* does not have any spines in the ejaculatory duct, nor does it exhibit the communication between the male atrium and the bursal canal. Both species show a connection between the bursa and the intestine. *Miroplana trifasciata* has two pairs of testes, one pair situated in the same location as the testes of *M. paulula*, the other pair located at about the posterior quarter of the pharynx.

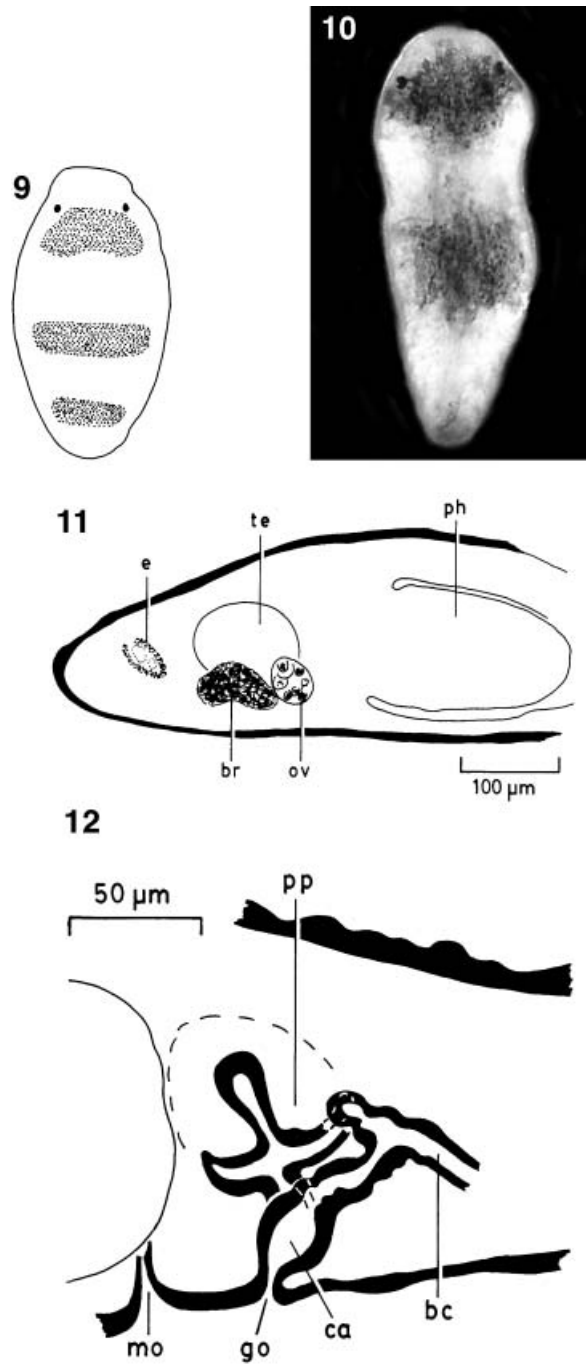
In *M. trifasciata* the posterior gut trunks give rise to about four medial diverticula, forming commissures between the two main branches. In *M. paulula* the posterior gut trunks are only connected at their most posterior ends.

Miroplana trifasciata was collected from a brackish habitat (see below) and also the biotope of *M. paulula* differs from that of a standard marine planarian in that it lives in brackish water.

***Miroplana trifasciata*? Kato, 1931** (Figures 9–13)

Material examined

ZMA V. Pl. 950.1, narrow stream near Kimpo Airport, Seoul, South Korea, 14 June 1975, sagittal sections on one slide.



Figures 9–12. *Miroplana trifasciata*? (9) Freehand sketch of preserved specimen. (10) Specimen from the Tamagawa River. (11) V.Pl. 950.1, sagittal section. (12) V.Pl. 950.1, sagittal reconstruction of the copulatory apparatus.

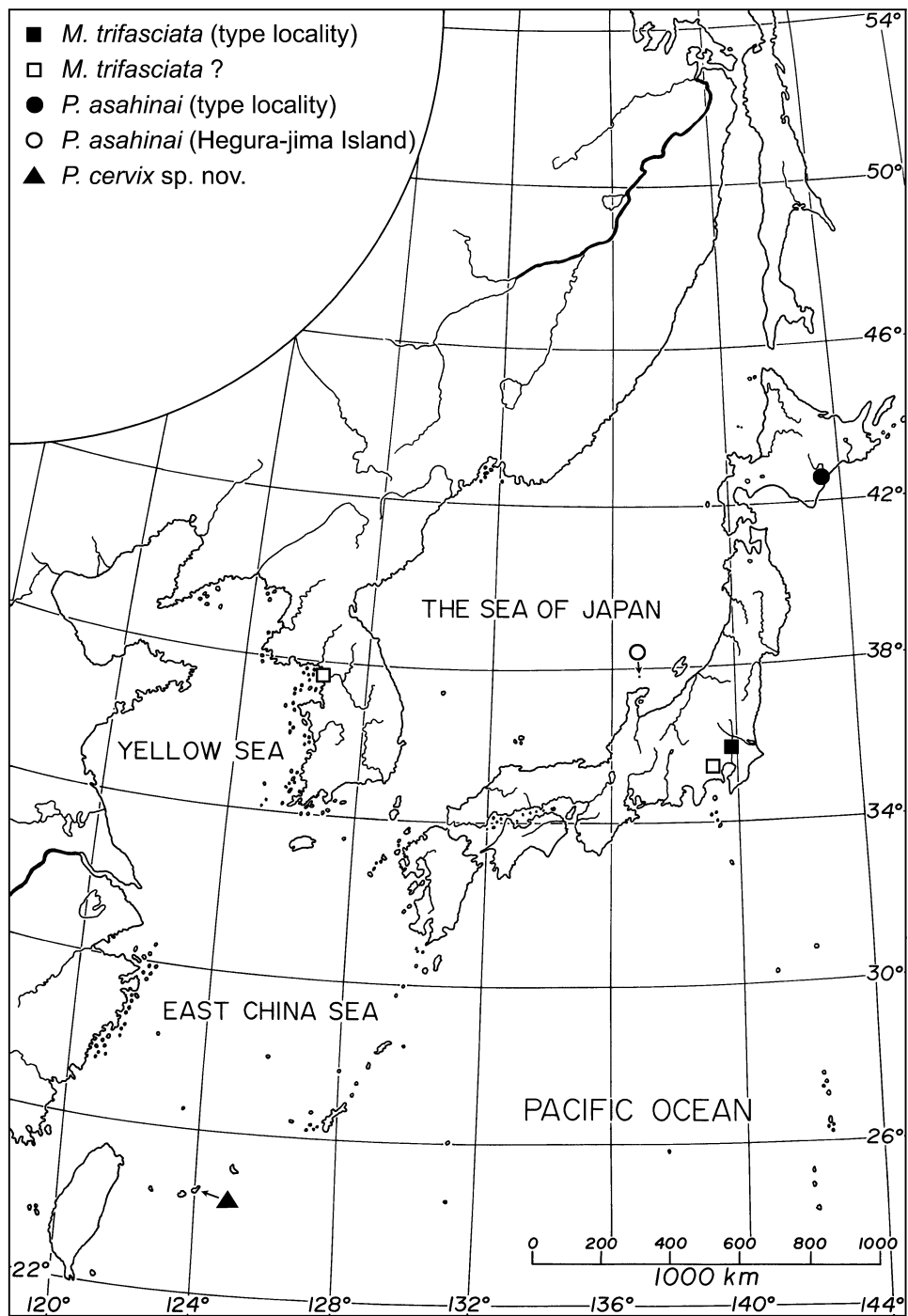


Figure 13. Geographic distribution of *M. trifasciata*, *M. trifasciata*?, *P. asahinai* and *P. cervix* in the Far East.

Description

Preserved specimens oblong, 3×1 mm, with truncated anterior body margin and slight constriction anterior to the eyes; posterior end rounded. Dorsal surface with three transverse bands, one directly behind the eyes, one over the pharynx region and a third band across the tail end (Figure 9).

With a pair of relatively large eyes (largest diameter of pigment cup $50\ \mu\text{m}$) that each houses three retinal cells and are devoid of a lens.

The pharynx is situated in the middle of the body and measures about one-quarter of the body length; the mouth opening is at the posterior end of the pharyngeal pocket.

The reproductive system is not yet fully developed. Two pairs of large, albeit not fully matured, testes could be distinguished, one pair located between the brain and the root of the pharynx and the other pair at the level of the posterior end of the pharyngeal pocket; the follicles occupy most of the dorso-ventral space. The paired ovaries are situated postero-medially to the anterior testis follicles (Figure 10).

The copulatory apparatus *in statu nascendi* consists of a penial papilla and penis bulb, a presumably female genital canal or bursal canal, provided with an anterior outgrowth (Figure 11).

Comparative discussion

Although the animal evidently is not fully mature there is much similarity with the type species, *M. trifasciata*. The transverse bands are precisely in the same position as those described for *M. trifasciata*, as holds true also for the two pairs of testes. Furthermore, the outgrowth of the presumed bursal canal suggests that this is the beginning of the communicating duct between bursal canal and male atrium, as present in *M. trifasciata*. It is also striking that the present specimen was collected from a narrow stream at approximately 5 km distance from the shore of the Yellow Sea and that consequently its habitat most likely corresponds with that of *M. trifasciata*.

The species *M. trifasciata* so far has been reported only from its type locality: Tokyo, on the border of the Arakawa River, 20 miles inland from its estuary, but still within the limits of tidal action (Kato 1931, 1965). The presumed present record from Seoul does not strike us as a remarkable range extension of this South-East Asian species (Figure 13).

Sasaki (2000) reported the finding of *M. trifasciata*? from a brackish pond located in the riverbed of the lower part of the Tamagawa River system, in the south-west of Tokyo (Figure 10). The animal was found relatively close to the type locality of *M. trifasciata* and also relatively close to the upper part of the Sumida-gawa River, from which Kato (1965) also reported *M. trifasciata* from the vicinities of Shimura and Akabane, these last-mentioned localities more or less coinciding with the type locality (Sudzuki 1981). Over land, the distance between Sasaki's sampling locality and the Shimura-Akabana area is approximately 22 km.

Sluys (1989) concluded that the type locality of *M. trifasciata* was a freshwater habitat. However, in the upper parts of the Arakawa River, at 20–25 km from Tokyo Bay, both freshwater and brackish water fishes are found. The salinity of the pond from which Sasaki (2000) reported *M. trifasciata*? was about one-quarter of usual seawater, and the pond houses animals such as bryozoans and the barnacle *Balanus improvisus*. Thus, we must conclude that the habitat of *M. trifasciata* is brackish water and not pure freshwater. Kimpo International Airport in Seoul is located at about 5 km from the sea; consequently, the locality from which *M. trifasciata*? was obtained may well be brackish.

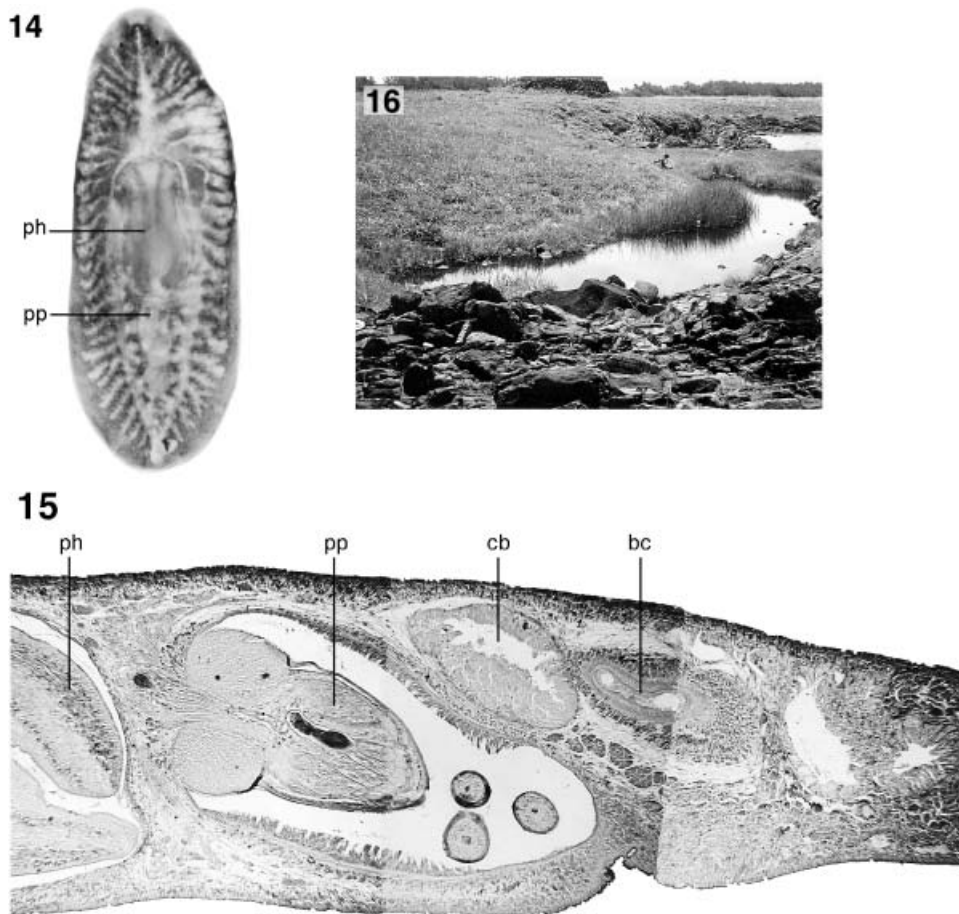
Obrimoposthia wandeli (Hallez, 1906)

(Figures 14–15)

Synonymy: *Procerodes sanderi* [Hauser, 1987].

Material examined

ZMA V.Pl. 951.1, King George Island, South Shetland Island, 1983, sagittal sections on 15 slides; V.Pl. 951.2, *ibid.*, whole mount on one slide; V.Pl. 951.3, *ibid.*, sagittal sections on 13 slides; V.Pl. 951.4, *ibid.*, sagittal sections on 13 slides; V.Pl. 951.5, *ibid.*, transverse sections on 19 slides; V.Pl. 951.6, *ibid.*, horizontal sections on eight slides.



Figures 14–16. *Obrimoposthia wandeli* and *Procerodella asahinai*. (14) *O. wandeli*, V.Pl. 951.2, photomicrograph of whole mount. (15) *O. wandeli*, V.Pl. 951.3, photomicrograph of sagittal section through the copulatory apparatus. (16) *P. asahinai*, photograph of the pond on Hegura-jima Island.

Comparative discussion

Without further comments, but after having studied relevant material, Sluys (1989) synonymized *P. sanderi* with *O. wandeli* (Hallez, 1906). Here we further substantiate this taxonomic conclusion through re-examination of material from the original samples of *P. sanderi* that was made available to us by Prof. Hauser.

In a Portuguese publication, Hauser (Anonymous 1987) described the finding of the presumed new species *Procerodes sanderi* [Hauser, 1987] (authorship in square brackets, according to Rec. 51D of the ICZN 1999) from King George Island of the South Shetland Islands. Specimens were collected and fixed in 1983 while live specimens were also brought back to the UNISINOS laboratory in Sao Leopoldo for further examination. Hauser (Anonymous 1987) described the external features of the animals and provided a clear photograph of living animals. It was stressed that the animals moved in a way different from that observed in congeneric species in that specimens of *P. sanderi* exhibit solely a looping type of locomotion and do not show the usual gliding movement of many other planarians. Further it was claimed that the anatomy of the copulatory apparatus of *P. sanderi* differs from congeneric species but, unfortunately, the paper did not give any illustrations to clarify these differences.

The external appearance of the preserved specimens and the dorsal view of a cleared whole mount, showing the copulatory apparatus (Figure 14), are in close agreement with the situation documented for *O. wandeli* (cf. Sluys 1989: figures 138, 140). Furthermore, reconstruction of the copulatory apparatus of the animals from King George Island clearly revealed the features that are characteristic for *O. wandeli*: T-shaped bursal canal and diverticulum, copulatory bursa situated latero-dorsally to the male atrium, tip of penial papilla folded within atrium, basal part of penial papilla with extremely thick, annular zone of circular muscle (Figure 15).

The exclusively looping type of locomotion of presumed *P. sanderi* (observed by R.S. when he visited Hauser's laboratory in 1994) can also be observed in other maricolans, with the difference that in these species this type of movement is usually observed more occasionally (cf. Sluys 1989).

That specimens of *O. wandeli* could be newly collected from King George Island during expeditions in 1983 is unsurprising in view of the fact that Hallez (1913) reported the species from the same locality.

***Oregoniplana opisthopora* Holmquist and Karling, 1972**

Comparative discussion

Thus far, this species has been reported in the scientific literature only from its type locality, Yaquina Head, Oregon, USA. However, in an unpublished student report Poljakova (1991) mentioned the species from Paramushir Island (Kuril Islands) and from the Komandorskiye Islands. Unfortunately, the report does not substantiate this finding and identification with drawings or photographs of the specimens from Kamchatka; the report merely reproduces figures of the external appearance and copulatory apparatus already published by Holmquist and Karling (1972). Furthermore, the material studied by Poljakova (1991) could not be retrieved for re-examination. Although this record of *O. opisthopora* from Kamchatka may well be correct, and very interesting from a biogeographical point of view, we feel that it requires more supporting evidence.

***Procerodella asahinai* (Kato, 1943)**
(Figures 13, 16–21)

Material examined

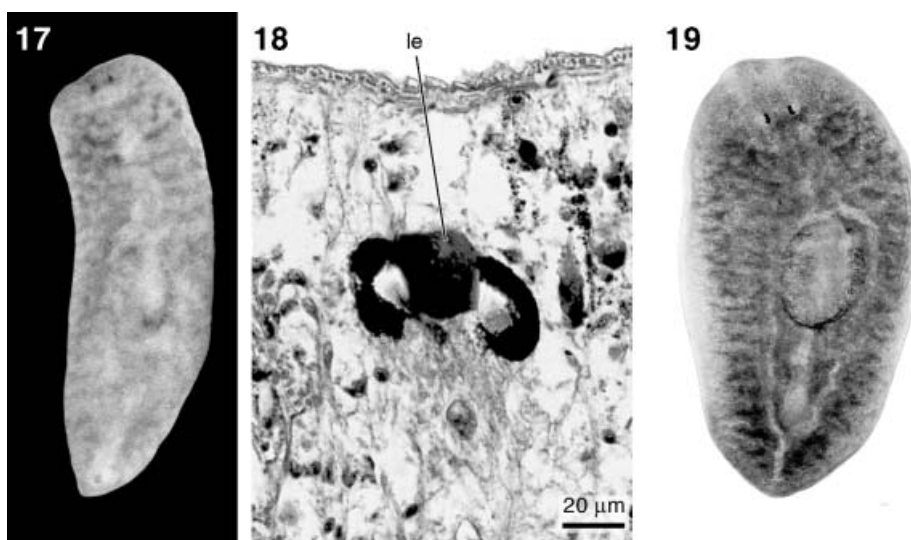
ZMA V.PL. 952.1, Ryûjin-ike Pond, Hegura-jima Island (37°52'N, 136°56'E), Wajima City, Ishikawa Prefecture, Chûbu Region, Honshû, Japan, sagittal sections on two slides; V.Pl. 952.2, *ibid.*, sagittal sections on three slides; ZMA V.PL. 952.3, *ibid.*, sagittal sections on one slide; V.Pl. 952.4, *ibid.*, sagittal sections on two slides; V.Pl. 952.5, *ibid.*, sagittal sections on two slides; V.Pl. 952.6–16, *ibid.*, sagittal sections of 11 specimens, each on one slide; V.Pl. 952.17, *ibid.*, sagittal sections on one slide; V.Pl. 952.18, *ibid.*, one whole mount on one slide; V.Pl. 952.19, *ibid.*, one whole mount on one slide; V.Pl. 952.20, *ibid.*, one whole mount on one slide; V.Pl. 952, *ibid.*, preserved specimens.

Ecology and distribution

The specimens examined were collected from a pond on Hegura-jima (also spelled as Hekura-jima) Island, a small island approximately 48 km NW of the Suzu-zaki Cape of the Noto Peninsula, Japan (Figure 9). The pond measured about 26.4 × 5.6 m, with a maximum depth of 0.5 m; sandy bottom; salinity 1556.5 mg l⁻¹ (Figure 13).

Description

Preserved specimens about 2.8 × 1.0 mm; front end rounded, posterior end pointed (Figure 17). Dorsal body surface yellowish; ventrally pale. Each eye cup contains three retinal cells and is provided with a lens (Figure 18). Behind the copulatory apparatus the two posterior gut trunks fuse to form a common branch (Figure 19). The pharynx measures



Figures 17–19. *Procerodella asahinai*. (17) Photograph of preserved specimen. (18) V.Pl. 952.2, photomicrograph of eye cup with lens. (19) V.Pl. 952.17, photomicrograph of whole mounted specimen.

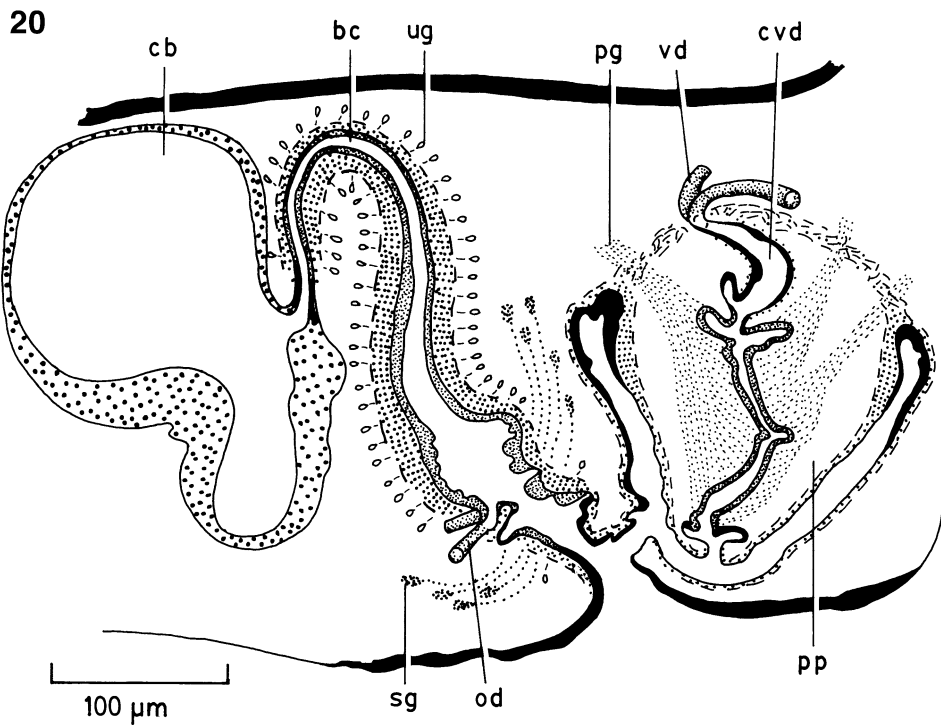


Figure 20. *Procerodella asahinai*, V.Pl. 952.5, sagittal reconstruction of the copulatory apparatus.

between one-quarter and one-fifth of the body length. The mouth opening is located at the posterior end of the pharyngeal pocket.

The rounded testes are situated ventrally between the ovaries and the root of the pharynx. Ovaries well developed, located at a short distance behind the brain.

The vasa deferentia separately penetrate the dorsal section of the penis bulb, but thereafter immediately fuse to form a common vas deferens; the point of fusion of the two ducts may also be located within the well-developed coat of intermingled muscles that make up the penis bulb. The common vas deferens is lined with a nucleate epithelium and is surrounded by a thin layer of mostly circular muscle fibres; the duct makes a characteristic anteriorly directed bend before communicating with the broad proximal section of the penial lumen. In general, the penial lumen is wide and of an elongate triangular shape; it is lined with an infranucleate epithelium that receives the numerous openings of erythrophilic penial glands. The lumen opens at the tip of the broadly cone-shaped penial papilla. The distal end of the penial lumen forms a constriction, after which it widens again and subsequently opens to the exterior at the tip of the papilla (Figure 20). This transition between penial lumen and tip of the papilla is such that the very tip appears as a club-shaped structure, at least in histological sections. It may well be the case that in much more extended penial papillae this club-shaped appearance can no longer be traced.

Posterior to the male copulatory apparatus lies a sac-shaped copulatory bursa, connected with the common atrium through a highly muscularized bursal canal. The canal is lined with an infranucleated epithelium and is surrounded by a thick, subepithelial layer of circular muscle, followed by a much thinner layer of longitudinal muscle fibres. Numerous unicellular glands are located just outside of the muscle coat, discharging their secretion

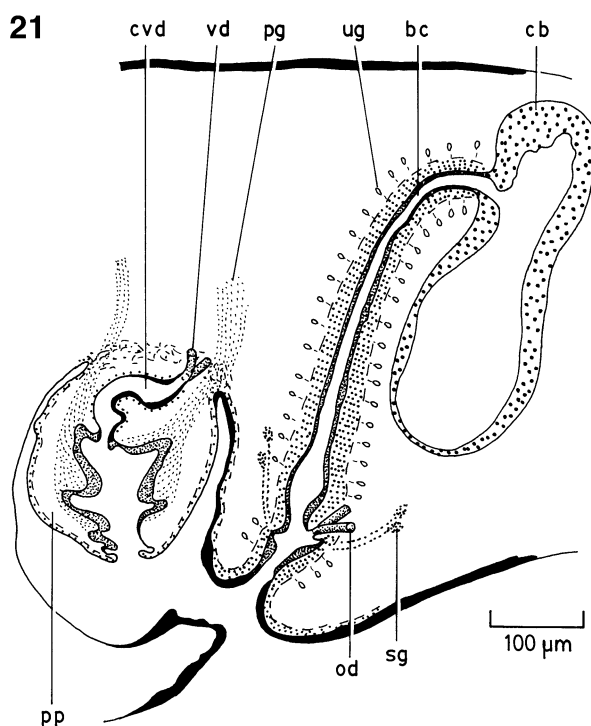


Figure 21. *Procerodella asahinai*, V.Pl. 952.2, sagittal reconstruction of the copulatory apparatus.

into the bursal canal. The distal, or ventral, portion of the bursal canal shows an expanded section that narrows again slightly before communicating with the common atrium. Just ventrally to this expansion the bursal canal receives the openings of the oviducts. The ducts separately penetrate the posterior wall of the bursal canal but in some specimens (e.g. V.Pl. 952.2; Figure 21) the openings are so closely together that there is a suggestion of a very short common oviduct. The bursal canal receives the openings of shell glands, just ectally to the openings of the oviducts.

Discussion

The gross morphology of the reproductive system immediately suggested that the specimens examined are representatives of the species *P. asahinai*, albeit that in anatomical details there are differences between the material examined and Kato's (1943) account of the species, collected from Lake Yūdō-numa, the estuary of the Tokachi River, near Tokachi, Hokkaidō (Figure 13).

Kato (1943) described a broad, cone-shaped penial papilla with a sinuous common vas deferens communicating with a wide, funnel-shaped penis lumen, the latter receiving the abundant secretion of numerous glands (cf. Sluys 1989). Furthermore, he described the fusion of the two vasa deferentia at the dorsal side of the penis bulb. The only differences between Kato's account of the male copulatory apparatus and our observations are that we did not observe cyanophilic glands opening into the common vas deferens and that Kato did not report the club-shaped tip of the penial papilla.

According to Kato (1943), the oviducts unite to form a very short common oviduct that opens through the posterior wall of the widened ventral section of the bursal canal, the vestibulum. The latter receives the secretion of shell glands ectally to the opening of the common oviduct. In our specimens there is an expanded section in the bursal canal just dorsally to the separate openings of the oviducts. On the other hand, it is also the case that in our specimens the ventral section of the bursal canal, receiving the openings of the oviducts and the secretion of shell glands, is wider than the more dorsal section of the bursal canal and therefore may be considered to represent the vestibulum. That Kato (1943) reported a very short common oviduct agrees with our observations that certain specimens indeed give the impression that the oviducts unite very shortly before opening into the bursal canal. In all, we consider the differences between our observations on the female copulatory apparatus and Kato's account to result from differences in preservation artifacts. Kato (1943) did not report histological details on eye structure, but the presence of eye lenses in the species is not unexpected since it belongs to a clade for which lenses are postulated as an apomorphy (Sluys 1989).

The material examined represents the first series of specimens that has become available to science since the destruction of the type specimens.

Procerodella cervix Sluys and Kawakatsu, sp. nov.
(Figures 13, 22–27)

Material examined

HOLOTYPE: ZMA V.Pl. 953.1, Ishigaki-jima Island (24°20'–24°37'N, 124°20'–124°40'E), Yaeyama Islands, Southwest Islands, Japan, 11 March 1986, sagittal sections on one slide.

PARATYPES: ZMA V.Pl. 953.2–12, *ibid.*, sagittal sections of 11 specimens, each on one slide; V.Pl. 953.13–21, *ibid.*, sagittal sections of nine specimens, each on one slide; V.Pl. 953.22, *ibid.*, one whole mount on one slide.

Diagnosis

Procerodella cervix differs from its congeners by having a strongly muscularized male atrium, provided with a short neck projecting into the common atrium, and a knob-shaped tip at the penis papilla.

Ecology and distribution

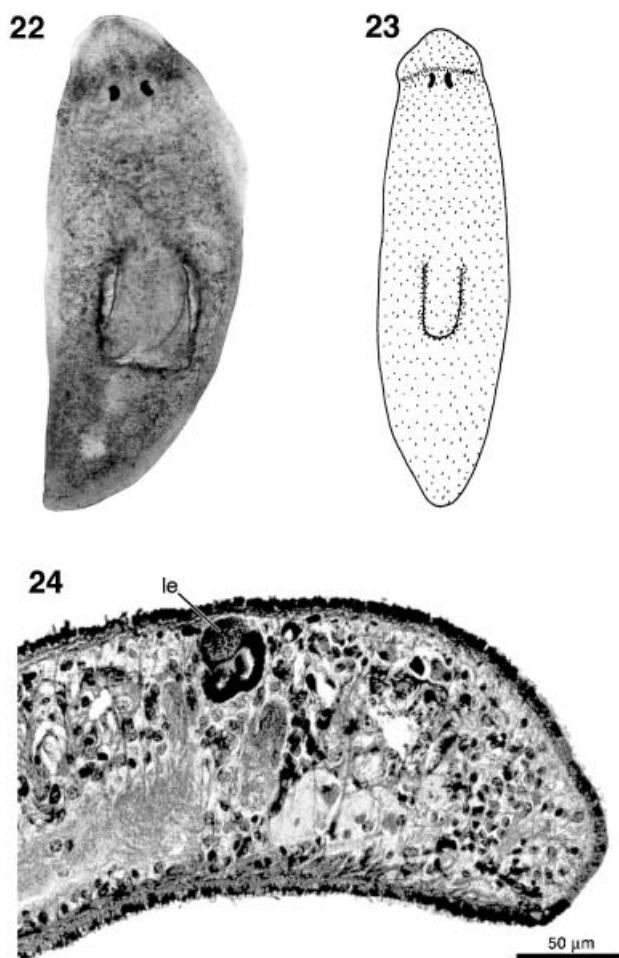
The animals were collected from a brackish culture pond of the crab *Scylla serrata* (Forskål, 1775) in Ishigaki-jima Island, one of the Yaeyama Islands in the Southwest Islands of Japan (Figure 13). In the winter of 1986 a very large population of planarians was present in the pond.

Etymology

The specific epithet is based on the Latin noun '*cervix*', neck. It refers to the muscular nozzle of the male atrium pointing into the common atrium, reminding one of the cervix uteri of the female human.

Description

Preserved specimens approximately 2 × 1 mm, with obtusely pointed body ends (Figures 22, 23). Dorsal surface uniformly pale brown with a somewhat darker transverse band

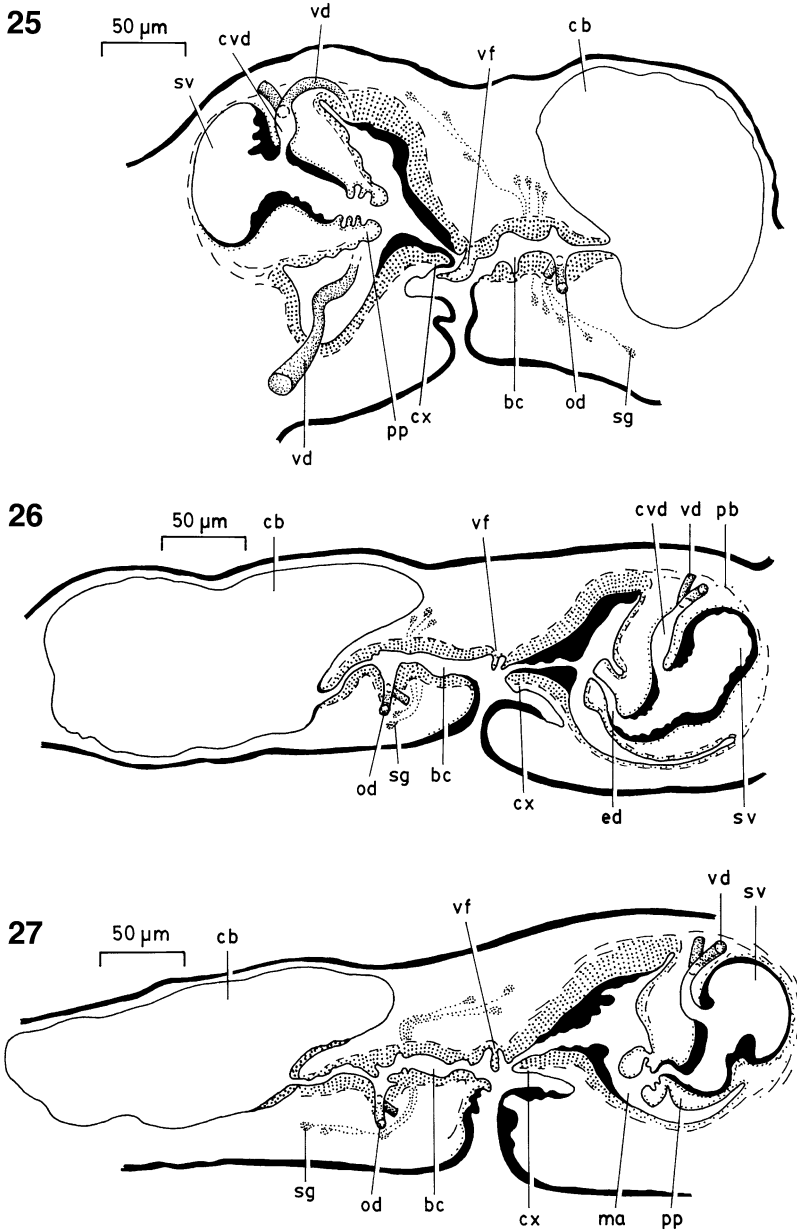


Figures 22–24. *Procerodella cervix*. (22) V.Pl. 953.22, photomicrograph of whole mounted specimen. (23) Freehand sketch of preserved specimen. (24) V.Pl. 953.18, photomicrograph of eye lens.

directly anterior to the eyes. The eye cups contain three retinal cells; there is a rounded, relatively large, granular structure to the eyes that probably represents a lens (Figure 24). The pharynx measures between one-quarter and one-fifth of the body length; mouth opening at the posterior of the pharyngeal pocket.

Relatively few and large testes situated between the ovaries and the root of the pharynx; there are about six follicles on either side of the body. The testis follicles occupy most of the dorso-ventral space. Ovaries located directly behind the brain.

The vasa deferentia form well-developed spermiducal vesicles; at the level of the male copulatory apparatus the ducts curve dorso-medially, decrease in diameter and penetrate the dorsal section of the penis bulb. Within the penial bulb the vasa deferentia fuse to form a common vas deferens, with a slightly larger diameter than the separate ducts, that communicates with the mid-dorsal section of the penis lumen. This penial lumen consists of a spacious vesicle in the penis bulb that gradually narrows to form a broad ejaculatory duct, opening at the knob-shaped tip of the broadly conical penial papilla. The penial lumen is provided with a layer of mostly circular muscle fibres. The nucleated epithelium of



Figures 25–27. *Procerodella cervix*. (25) V.Pl. 953.3, sagittal reconstruction of the copulatory apparatus. (26) V.Pl. 953.6, sagittal reconstruction of the copulatory apparatus. (27) V.Pl. 953.1, sagittal reconstruction of the copulatory apparatus.

the penis papilla is underlain with a subepithelial layer of circular muscle, followed by longitudinal muscle fibres (Figure 25).

The male atrium is of a very peculiar nature since it is provided with a thick layer of subepithelial circular muscle, followed by a much thinner layer of longitudinal muscle. But the most characteristic feature is that the distal, posterior section of the atrium forms a short

neck pointing into the common atrium. This neck, short blunt nozzle, or cervix is also provided with the well-developed muscle layers that surround the rest of the male atrium (Figure 26).

The female copulatory apparatus consists of a relatively large copulatory bursa, communicating with the common atrium through a bursal canal that runs more or less parallel to the body surface. The very distal end of the bursal canal (i.e. at the point of opening into the common atrium) is provided with more or less developed valve-like folds (Figure 27). The oviducts unite to form a very short common oviduct that opens into the ventral section of the bursal canal. The latter receives the secretion of shell glands just ectally to the opening of the common oviduct. The bursal canal is lined with an infranucleate epithelium and is surrounded by a thick, subepithelial layer of circular muscle and a much thinner layer of longitudinal muscle fibres. Distinct unicellular glands opening into the bursal canal were not clearly observed. However, it is not excluded that the presence of such glands is obscured by the numerous nuclei of the infranucleated epithelium of the canal that are located just outside the muscle coat.

Comparative discussion

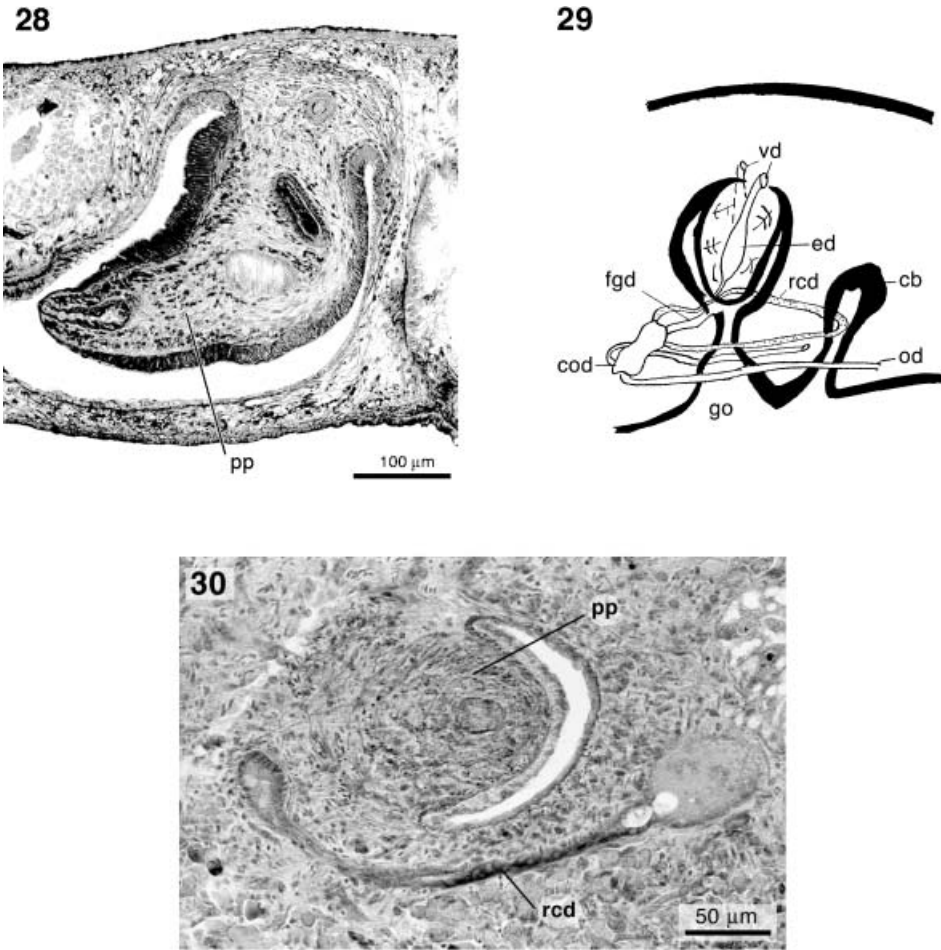
The genus *Procerodella* Sluys, 1989 was erected for two Japanese species and one from Chile: *P. japonica* (Kato, 1955), *P. asahinai* (Kato, 1943) and *P. macrostoma* (Darwin, 1844), respectively (Sluys 1989). Characteristic features for the genus were considered to be (1) a common oviduct; (2) a thick zone of circular muscle around the bursal canal; (3) bursal canal with vestibulum ectally to the opening of the common oviduct and receiving the secretion of shell glands; and (4) numerous unicellular glands discharging their secretion into the bursal canal. Not all of these features are present in *P. cervix*. In particular, *P. cervix* may lack the unicellular glands opening into the bursal canal and a vestibulum appears to be absent. On the other hand, the morphology of the female copulatory apparatus of *P. cervix* much resembles the situation in *P. japonica*, notably the well-muscularized common oviduct. It is evident that with the discovery of new species generic diagnoses may have to be adapted. Furthermore, it is also because we wish to follow a conservative approach to taxonomy and to refrain from coining unnecessary monotypic genera that we have decided to assign the new species to the genus *Procerodella*.

The presence of an eye lens in *P. cervix* is not unexpected since it belongs to a group of species, the superfamily Bdellouroidea Diesing, 1862, for which the presence of a lens is presumed to be an apomorphic feature (Sluys 1989). However, it should be noted that in histological preparations eye lenses usually appear as densely and brightly staining structures, in contrast to the faintly staining and granular lenses in *P. cervix*.

***Procerodes plebeius* (Schmidt, 1861)** (Figure 28)

Material examined

ZMA V.Pl. 954.1, Sandgerdhi (64°03'N, 22°43'W), Reykjanes Peninsula, Iceland, August 1999, sagittal sections on one slide; V.Pl. 954.2, *ibid.*, sagittal sections on three slides; V.Pl. 954.3, *ibid.*, sagittal sections on one slide.



Figures 28–30. *Procerodes plebeius* and *Uteriporus pacificus*? (28) *P. plebeius*, V.Pl. 954.2, photomicrograph of penial papilla. (29) *U. pacificus*?, sagittal reconstruction of the copulatory apparatus (from Poljakova, 1991: figure 15B; labels adapted according to current terminology). (30) *U. pacificus*, specimen BC 7-5 (ZMA), photomicrograph of horizontal section of the receptacular duct; anterior to the left.

Comparative discussion

In particular, this species of *Procerodes* is characterized by a well-developed penial papilla provided with a thick zone of circular muscle (Figure 28). The species *P. plebeius* differs from *P. dohrni* Wilhelmi, 1909, which also exhibits a thick zone of circular muscle on the penial papilla, by the presence of a copulatory bursa that is absent in the latter.

The present record for Iceland considerably extends the known range of the species since thus far it had been reported from Cephalonia, Crete, Black Sea and southern England, where it was found in brackish habitats. In Iceland, *P. plebeius* was collected from the extreme upper littoral, in coarse sand. At the same locality *P. littoralis* (Ström, 1768) was present, albeit on *Fucus* sp., a species of marine triclad that is also known to occur in brackish localities and that was already known from Iceland (cf. Sluys 1989).

***Uteriporus pacificus*?** Sluys, 1989
(Figures 29, 30)

Comparative discussion

Poljakova (1991) mentioned a presumably new species of *Uteriporus* from the Avachinska Bay and the Gulf of Kronotski, on the east coast of Kamchatka, and from the Komandorskiy Archipelago, namely *Uteriporus* sp. n. The preserved specimens measured $5\text{--}9 \times 4$ mm, with rounded front and hind end. Dorsal surface red-brown, ventral surface pale. The posterior gut trunks fuse in the hind end of the body. Testes numerous, distributed between the gut diverticula and occurring throughout the body length. According to Poljakova (1991), the oviducts fuse posterior to the male copulatory apparatus to form a common oviduct, which subsequently gives rise to three ducts (Figure 29): two receptacular ducts, opening into the anterior copulatory bursa, and the female genital duct that communicates with the atrium. According to Poljakova (1991), common oviduct and female genital duct are penetrated by shell glands.

In our opinion, Poljakova's reconstruction of the female copulatory apparatus most likely is not fully correct. In the two species of the genus *Uteriporus* Bergendal, 1890 that have been described up to the present, the posterior, expanded portions of the receptacular ducts do not communicate directly with the female genital duct. The swollen portions of the receptacular ducts only receive a short, narrow branch of the oviduct before the latter communicates with the female genital duct (cf. Bergendal 1896: pl. 1, figure 4; Sluys 1989: figures 101–104). In her reconstruction, Poljakova (1991) may have been misled by Tomkiewicz and Ball's (1973) description of the copulatory apparatus of *U. vulgaris* Bergendal, 1890, since she bases her description of this species on the account of these workers and reproduces their reconstruction figure of the copulatory complex (incorrectly, Poljakova refers to Ball, 1973). However, Tomkiewicz and Ball's reconstruction is incorrect in that it describes a direct connection between the expanded portions of the receptacular ducts and the female genital duct, as already noted by Sluys and Ball (1983).

On the basis of Poljakova's (1991) description it is difficult to decide whether her specimens from the Far East represent *U. vulgaris*, *U. pacificus* or a third, new species. For *U. pacificus* a light brown or reddish brown dorsal surface was reported, which is in agreement with the Kamchatkan specimens, while the dorsal body surface of *U. vulgaris* varies from milky white to pale brown. In *U. vulgaris* the posterior sections of the receptacular ducts may be expanded to greater or lesser extent and thus may approach the generally smaller expansions in *U. pacificus* as well as those reported by Poljakova (1991) for the Russian animals. According to Sluys (1989), diagnostic features for *U. pacificus* are the testes occupying the entire dorso-ventral space (contrasting with the ventral follicles in *U. vulgaris*), and the absence of an anterior copulatory bursa (contrasting with the well-developed bursa in *U. vulgaris*). Unfortunately, Poljakova (1991) does not describe the vertical dimension of the testes, but a photomicrograph of a histological section (her figure 16A) seems to suggest that a testis follicle extends considerably towards the dorsal body surface. In *U. pacificus* the receptacular ducts fuse to form a common duct that opens to the exterior, whereas in *U. vulgaris* they open into an anterior bursa that subsequently opens to the outside. It must be noted that re-examination of the type material of *U. pacificus* revealed that the receptacular ducts do not merely fuse to form a common duct but expand before uniting and/or open into a small expansion (Figure 30). In the Russian specimens there seems to be an anterior bursa, which is suggested in Poljakova's reconstruction

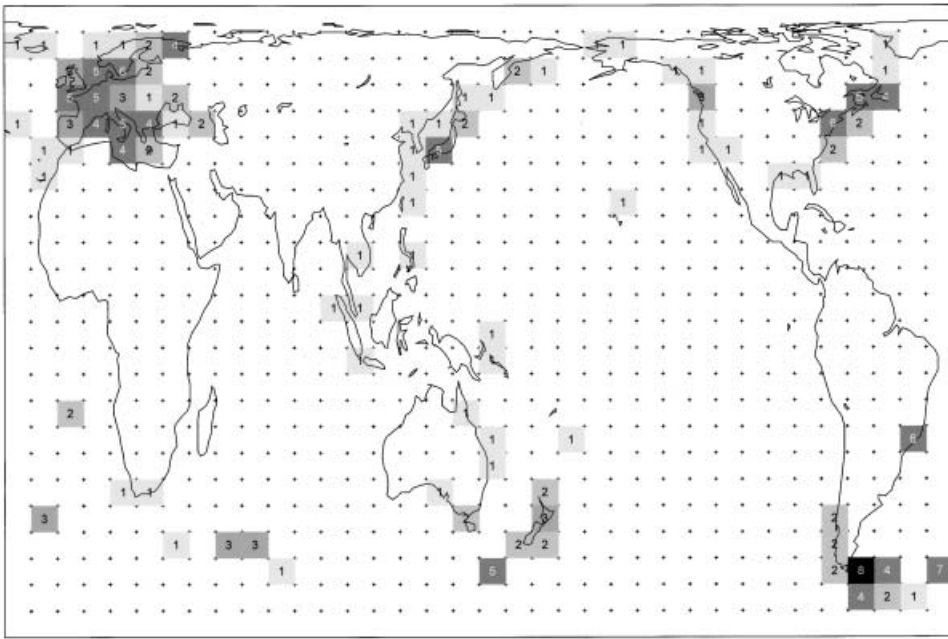


Figure 31. Map of species richness on an equal area grid map from the Worldmap program. Maximum richness shown in black and minimum in light grey, with intermediate scores grouped into grey-scale classes of approximately equal numbers of grid cells. Numbers within cells denote number of species recorded within that grid cell.

drawing (Figure 29) but also in a series of photomicrographs of serial sections (her figure 17). However, it must be noted that her reconstruction is not drawn to scale and that the photomicrographs show a distinct duct leading to the second, anterior gonopore. Such a duct is present in *U. pacificus*, whereas in *U. vulgaris* there is only a short and shallow opening of the anterior bursa to the exterior (cf. Bergendal 1896: pl. 4, figure 32; Sluys 1989: pl. 4, figure F).

Although we do not consider it to be impossible that an Atlantic species, like *U. vulgaris*, also occurs on the coasts of the Bering Sea, we do here attribute Poljakova's animals to the species *U. pacificus*, albeit with some reservations in view of the absence of more detailed anatomical information. This record considerably extends the range of *U. pacificus* since the species was originally recorded for the coast of British Columbia, Canada (Sluys 1989).

Biogeography

Records detailed in another paper (Sluys and Kawakatsu 2000) considerably enlarged the known range of the monotypic genus *Paucumara* Sluys, 1989. The present paper documents range extensions for the genera *Foviella* Bock, 1925, *Uteriporus* Bergendal, 1890, *Procerodella* Sluys, 1989 and *Miroplana* Kato, 1931. The most noteworthy changes in known geographical distribution concern: (1) the record of *M. paulula* from the east coast of Australia; (2) the presumed findings of *U. pacificus* and *O. opisthopora* in the western Bering Sea; (3) the finding of *P. plebeius* in Iceland; and (4) the occurrence of *F. affinis* in the White Sea.

Earlier, Sluys (1989: figure 30) gave a generalized distribution map for the Maricola. Here we provide a more detailed analysis of the biodiversity of marine triclads by documenting species richness with the help of a database that was created for an equal area grid map of the world (grid cell area approximately 611 000 km², based on intervals of 10° longitude). It is evident that the results of this study (Figure 31) should be interpreted with caution, since the known biogeography of the poorly studied Maricola is certainly influenced by the considerable differences in sampling effort deployed within the various areas.

A hotspot of diversity is located at the tip of South America, near Tierra del Fuego, with eight species having been reported for that particular grid cell. Other regions with relatively high numbers of species are the following: the (1) South Georgia and (2) São Paulo grid cells; (3) the eastern North Atlantic and Mediterranean region; and (4) the coast of eastern North America. The relatively high number of species reported from the coasts of the western and eastern North Atlantic as well as the Mediterranean Sea most likely result from the fact that marine biologists have studied these areas for a long period of time.

The subantarctic region has been the subject of several large expeditions that were launched at the end of the 19th and the beginning of the 20th century. During later parts of the 20th century there were also several much smaller expeditions, organized by institutions from various countries, which yielded subantarctic marine triclads.

The Worldmap program also enables the calculation of a range size rarity score for each occupied grid cell. The rarity score for a grid cell is the sum of each species' inverse frequency of occupancy among all grid cells. This index refers to species of restricted range size, or narrowly endemic species. For some datasets there is little difference between the scores for species richness and range size rarity, both showing a similar geographic pattern (cf. Sluys 1999 for land planarians). However, when examined for marine triclads, the Tierra del Fuego hotspot of species richness shifts to a São Paulo hotspot on the index of narrow endemism (with all other grid cells having rather low range size rarity scores).

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