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CONTRIBUTION TO AN INVENTORY OF THE FRESHWATER PLANARIANS OF AUSTRALIA AND NEW ZEALAND (PLATYHELMINTHES, TRICLADIDA, DUGESIIDAE), WITH DISTRIBUTION MAPS OF THE SPECIES EXAMINED

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ABSTRACT

An account is given of 13 species of freshwater planarians from the family DugesIIDae, based on samples from new localities in New Zealand and Australia; these include four newly described and one problematic species. In the case of three species, the material described represents the second series of specimens available since the material used in the original descriptions of these species, as a result of which our understanding of the morphology of the animals can be expanded. In other cases, the new material also contributed to a more detailed understanding of the anatomy of the species. The study concludes with detailed distribution maps for the species examined, including not only the new distributional records described in the paper but also incorporating all earlier records.

Key words: Platyhelminthes, DugesIIDae, Australia, New Zealand, taxonomy, biogeography

INTRODUCTION

In a recent paper Sluys (1997) highlighted our limited knowledge on the freshwater planarians of Australia, counting a meagre 22 nominal species, recorded from only a few localities. The diversity of the freshwater planarians of New Zealand may seem relatively large, considering the six species that were then known from this much smaller landmass. However, it is obvious that there is much more to be learned about the morphologically and phylogenetically interesting planarian fauna of Australia and New Zealand.

Recent studies have started to contribute to an inventory of the paludicolans of these two countries, with Sluys et al. (1998) describing a new species of the genus *Dugesia* Girard, 1850 from Australia, St. Clair et al. (1999) presenting a survey of the Victorian Alps, and Allison (1997) reporting a new species of *Spathula* Nurse, 1950 from New Zealand.

Over the years we have accumulated samples of freshwater planarians collected from various parts of Australia and New Zealand. In the present paper we describe the material of these collections, thus contributing to, and hopefully stim-

ulating a future, more extensive inventory of these animals.

MATERIALS AND METHODS

Animals were fixed in Bouin's or Steinmann's fluid. Some of the material not fixed in Steinmann's was postfixed in this fluid before sectioning. Serial sections were made at intervals of 7-8 μm and were stained in Delafield's hematoxylin and erythrosin or in Mallory-Cason.

With respect to the samples originally contained in Kawakatsu's private collection, detailed descriptions of the collection data, including photographs of the specimens, can be found in Kawakatsu et al. (1995a, b). In order to facilitate correct cross reference, photographs in Kawakatsu et al. (1995b) are cited below with the plate and figure numbers concerned.

The material is deposited in the Queensland Museum, Brisbane (QM), the Zoological Museum of the University of Amsterdam (ZMA), the National Science Museum, Tokyo (NSMT), or the Museum of New Zealand Te Papa Tongarewa (MNZ).

Abbreviations used in the figures: bc, bursal canal; br, brain; ca, common atrium; cb, copulatory bursa; cc, clump of cells; cg¹, first type of cement gland; cg², second type of cement gland; cod, common oviduct; cp, ciliated pit; cpg, cyanophilic penial glands; di, diverticulum; du, duct; e, eye; ed, ejaculatory duct; eg, erythrophilic gland; epg, erythrophilic penial glands; fa, female atrium; gd, gonoduct; gic, genito-intestinal canal; gl, gland; go, gonopore; in, intestine; ma, male atrium; od, oviduct; ov, ovary; pb, penis bulb; pg, penial gland; pg¹, first type of penial gland; pg², second type of penial gland; pg³, third type of penial gland; ph, pharynx; pp, penis papilla; sf, sensory fossa; sg, shell gland; sp, spermatozoa; spe, spermatophore; sph, sphincter; sv, seminal vesicle; te, testis; vd, vas deferens.

SYSTEMATIC ACCOUNT

Suborder Tricladida Lang, 1884

Infraorder Paludicola Hallez, 1892

FAMILY DUGESIIDAE BALL, 1974

GENUS *DUGESIA* GIRARD, 1850

Dugesia notogaea Sluys & Kawakatsu, 1998
Figs. 1, 49

MATERIAL

AUSTRALIA. - ZMA: V.Pl. 915.1, Porcupine Gorge National Park, 70 km NE of Hughenden, north Queensland, Australia, 23-IX-1986, sagittal sections on 7 slides; V.Pl. 915.2, *ibid.*, sagittal sections on 5 slides.

DISCUSSION. - In all essential details these specimens correspond to the species *D. notogaea*. Since this species was recently described in detail (Sluys et al., 1998) we here only provide a reconstruction of the copulatory apparatus (Fig. 1), report differences between the present material and the material used for the first description of the species, and present a more detailed description of the various glands associated with the copulatory apparatus.

In the specimens examined the ovaries are much less developed than in the animals described by Sluys et al. (1998), which showed hyperplastic ovaries; in specimen V.Pl. 915.2 ovarian tissue seems to be completely absent. Furthermore, in each of the specimens only one oviduct could be discerned opening at the junction of bursal canal and common atrium. Vitellaria are well developed in both specimens.

There are three types of gland opening into the atrium and/or bursal canal. A coarse-grained, orange secretion is discharged into the gonopore and constitutes the product from what is usually described as cement gland. An equally coarse but red secretion is discharged into the atrium immediately dorsally to the openings of the orange glands and may involve a second type of cement gland. A third, slightly less coarse-grained, cyanophilic secretion is discharged through the epithelium directly adjacent to the opening of the oviduct. Most likely, this third type of gland concerns the shell glands, albeit that their secretion is usually of an erythrophilic nature.

Two kinds of gland are associated with the penis. A coarse-grained, orange secretion is discharged into the ejaculatory duct. A second type of gland produces an equally coarse, purplish-blue secretion and has its openings in the conus of the diaphragm and in the seminal vesicle. These

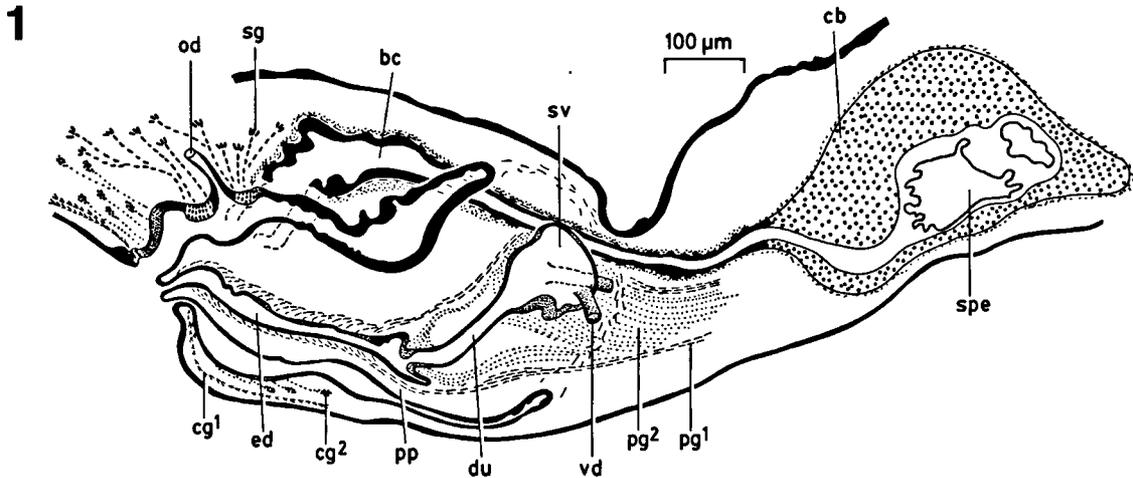


Fig. 1. *Dugesia notogaea*. V.Pl. 915.2, sagittal reconstruction of the copulatory apparatus.

two types of gland were characterized ultrastructurally by Vreys et al. (1999) for *Dugesia gonocephala* (Dugès, 1830).

The copulatory bursa contains remnants of a spermatophore.

GENUS *CURA* STRAND, 1942

Cura pinguis (Weiss, 1909)

Figs. 2, 3, 51

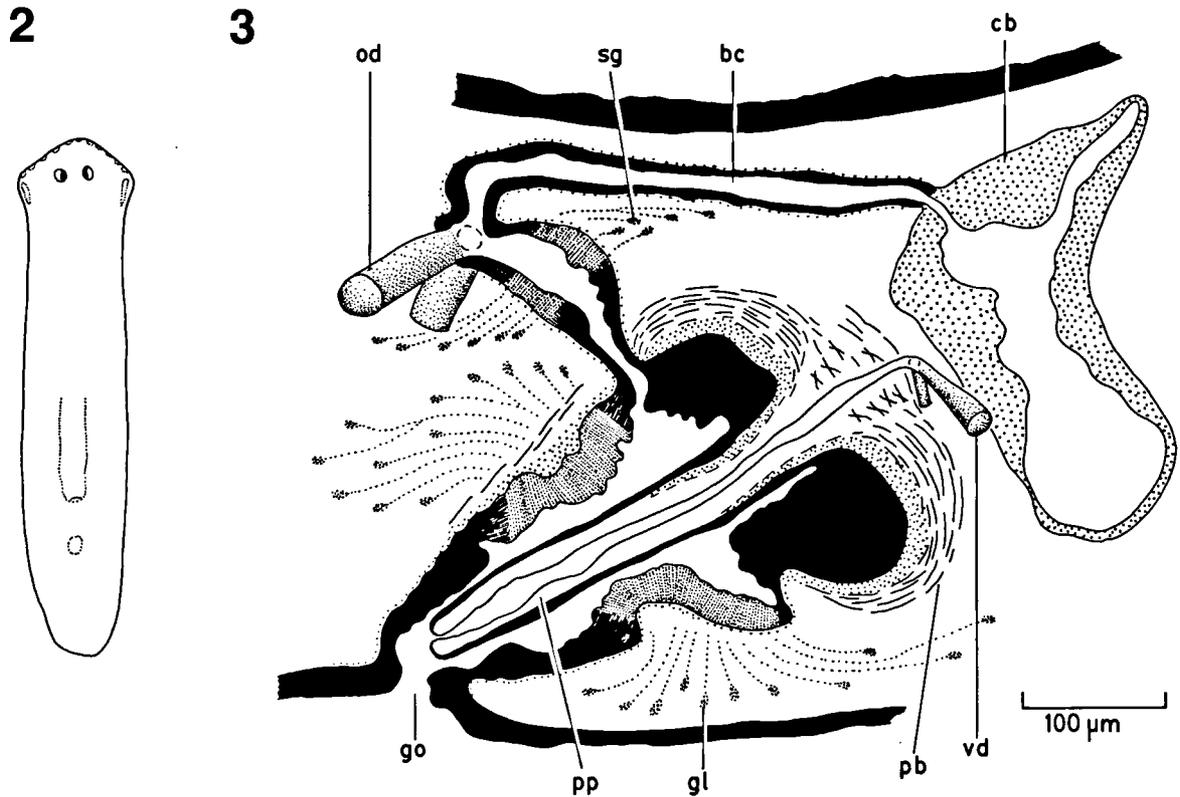
MATERIAL

AUSTRALIA. - ZMA: V. Pl. 770.1, Twin Creeks, Tasmania, sagittal sections on 2 slides; V. Pl. 772.1, near Brunswick Junction, Australia (33° 15'S 115° 45'E), sagittal sections on 2 slides; V. Pl. 772.2, sagittal sections on 1 slide; V. Pl. 772.3, horizontal sections on 2 slides; V. Pl. 772.4, horizontal sections on 1 slide; V. Pl. 772.5, transverse sections on 3 slides; V.Pl. 916.1, Murrumbidgee River, at Bredbo, 80 km S of Canberra, New South Wales, Australia, 26-XII-1974, sagittal sections on 5 slides; V.Pl. 916.2, sagittal sections on 3 slides; V.Pl. 916.3, sagittal sections on 4 slides; V.Pl. 916.4, sagittal sections on 4 slides; V.Pl. 916.5, sagittal sections on 3 slides; V.Pl. 916.6, sagittal sections on 3 slides; V.Pl. 916.7, sagittal sections on 3 slides; V.Pl. 916.8, sagittal sections on 3 slides; V.Pl. 916.9, sagittal sections on 3 slides; V.Pl. 916.10, sagittal sections on 4 slides; V.Pl. 916.11, sagittal sections on 4 slides; V.Pl. 916.12, sagittal sections on 5 slides; V.Pl. 917, preserved specimens (Kawakatsu et al. 1995b, PI. V, figs. P & Q), Mt Field National Park, SE Tasmania, Australia, 17-VIII-1978; V.Pl. 917.1, *ibid.*, sagittal sections on 2 slides; V.Pl. 917.2, horizontal sections on 3 slides; V.Pl. 917.3, sagittal sections on 3 slides; V.Pl. 917.4, sagittal sections on 2 slides; V.Pl. 918.1, Cotter River, 30 km W of Canberra, New South Wales, Australia, 22-VIII-1978, sagittal sections on 3

slides; V.Pl. 918.2, transverse sections on 6 slides; V.Pl. 918.3, horizontal sections on 2 slides; V.Pl. 918.4, sagittal sections on 2 slides; V.Pl. 918.5, horizontal sections on 1 slide (Kawakatsu et al. 1995b, PI. V, figs. C & D); V.Pl. 919.1, Alderley Creek, New South Wales, May - June 1996, sagittal sections on 2 slides; V.Pl. 919.2, *ibid.*, sagittal sections on 2 slides; V.Pl. 919.3, *ibid.*, sagittal sections on 3 slides; V.Pl. 920.1, Chichester River, New South Wales, January 1997, sagittal sections on 2 slides; V.Pl. 920.2, *ibid.*, sagittal sections on 2 slides; V.Pl. 920.3, *ibid.*, horizontal sections on 2 slides.

V.Pl. 921.1, William River, New South Wales, January 1997, sagittal sections on 3 slides; V.Pl. 921.2, *ibid.*, sagittal sections on 4 slides; V.Pl. 921.3, *ibid.*, sagittal sections on 4 slides; V.Pl. 922.1, Cootralantra Creek, 9 km NW of Berridale, New South Wales, 5-I-1985, sagittal sections on 6 slides.

NEW ZEALAND. - ZMA: V.Pl. 923.1, river Avon, Christchurch, South Island, New Zealand, 19-I-1975, sagittal sections on 4 slides; V.Pl. 923.2, *ibid.*, sagittal sections on 3 slides (Kawakatsu et al. 1995b, PI. VI, Fig. U); V.Pl. 924, preserved specimens (Kawakatsu et al. 1995b, PI. VI, figs. B & C), Waingarō Spring, Waingarō, 20 km W of Hamilton, North Island, New Zealand, 6-VIII-1978; V.Pl. 924.1, *ibid.*, sagittal sections on 2 slides; V.Pl. 924.2, transverse sections on 3 slides; V.Pl. 924.3, sagittal sections on 3 slides; V.Pl. 924.4, sagittal sections on 2 slides; V.Pl. 924.5, sagittal sections on 2 slides; V.Pl. 924.6, sagittal sections on 2 slides; V.Pl. 925.1, at Atiamuri, 25 km SW of Rotorua, North Island, New Zealand, 9-VIII-1978, sagittal sections on 2 slides; V.Pl. 925.2, sagittal sections on 2 slides (Kawakatsu et al., 1995b, PI. VI, figs. D & E); V.Pl. 926, preserved specimens (Kawakatsu et al., 1995b, PI. VI, figs. C & H, P & Q), at Mairoa, 15 km SW of Te Kuiti, near Waitomo, North Island, New Zealand, 10-VIII-1978; V.Pl. 926.1, *ibid.*, sagittal sections on 3 slides; V.Pl. 926.2, sagittal sections on 3 slides; V.Pl. 926.3, horizontal sections on 2 slides; V.Pl. 926.4, sagittal sections on 3 slides; V.Pl. 926.5, horizontal sections



Figs. 2, 3. *Cura pinguis*. 2, V.Pl. 918, free-hand sketch of living animal. 3, V.Pl. 927.1, sagittal reconstruction of the copulatory apparatus.

on 1 slide; V.Pl. 927, preserved specimens (Kawakatsu et al., 1995b, Pl. VI, figs. I & J, R), at Mairoa, 15 km SW of Te Kuiti, near Waitomo, North Island, New Zealand, 10-VIII-1978; V.Pl. 927.1, *ibid.*, sagittal sections on 4 slides; V.Pl. 927.2, transverse sections on 7 slides; V.Pl. 927.3, horizontal sections on 3 slides; V.Pl. 927.4, sagittal sections on 3 slides.

DISCUSSION. - Since this species has been adequately described in the literature (Weiss, 1910; Nurse, 1950; Kawakatsu, 1969a, b; Ball, 1974b) and can readily be recognized, it suffices to present here only an outline drawing of its habitus and reconstruction of the copulatory apparatus (Figs. 2, 3) and to discuss some minor differences between our observations and those of previous workers.

Some differences in external morphology could be observed between animals from Australia and New Zealand. The head of New Zealand specimens is of a lower triangular shape as compared with Australian animals, resembling

Ball's morphological type A (Ball, 1974b: fig. 5A). The Australian animals resemble Ball's morphological type B (Ball, 1974b: fig. 5B), albeit that the anterior margin may be less obtusely pointed.

Animals from the Australian samples (V.Pl. 916, V.Pl. 917, V.Pl. 918) showed large eyes set in large pigment-free patches (cf. Ball, 1974b: fig. 5B), whereas the New Zealand specimens (samples V.Pl. 924, V. Pl. 925, V. Pl. 926, V. Pl. 927) had small eyes surrounded by small white patches (cf. Ball, 1974b: fig. 5A). Ball (1974b) observed both morphological types from one locality, viz. New South Wales. He was not able to correlate the external features of the animals with any anatomical differences, which corresponds with our findings.

Nurse (1950) reported a wide common oviduct but Kawakatsu (1969b) reported a very short common oviduct. However, after examination of the material presented in the present study, we

find the situation more in agreement with the account of Weiss (1910), who described the two oviducts as separately opening into the bursal canal, close to the point where the canal sharply bends anteriorly.

***Cura fortis* n.sp.**

Figs. 4-6, 51

MATERIAL

Holotype: MNZ ZW 1495, near Wellington, North Island, NEW ZEALAND, 1-I-1975, sagittal sections on 12 slides.

DIAGNOSIS. - *Cura fortis* n.sp. can be distinguished from its congeners by its numerous dorsal testes that extend backwards to the level of the mouth, a relatively voluminous penial papilla, a gonopore located in the middle of the common atrium, and reversed bursal canal musculature.

ECOLOGY AND DISTRIBUTION. - Known only from the type locality, a narrow river near Wellington.

ETYMOLOGY. - The specific epithet is derived from the Latin adjective *fortis*, meaning 'firm', and alludes to the large penial papilla, as compared with other species of *Cura*.

DESCRIPTION. - Preserved up to 8 x 3.5 mm. Dorsal surface dark brown, in some specimens slightly reddish; ventral surface with dark greyish ground colour and many blackish spots. Sensory spots were not observed, neither in the intact animals nor in the sections (Fig. 4). Eyes set in pigment-free patches.

Pharynx located in the middle of the body; mouth opening at the posterior end of the pharyngeal pocket.

Relatively small testes located dorsally, extending from a considerable distance behind the brain to the level of the mouth (Fig. 5).

The vasa deferentia penetrate separately the penis bulb, within which they unite to form the ejaculatory duct. The latter is a rather wide duct, lined with a nucleate epithelium, opening at the tip of the penial papilla. The ejaculatory duct receives the openings of penis glands over its entire length, while there is a particularly dense accumulation of secretion at the distal part of the duct, near the tip of the penial papilla (Fig. 6).

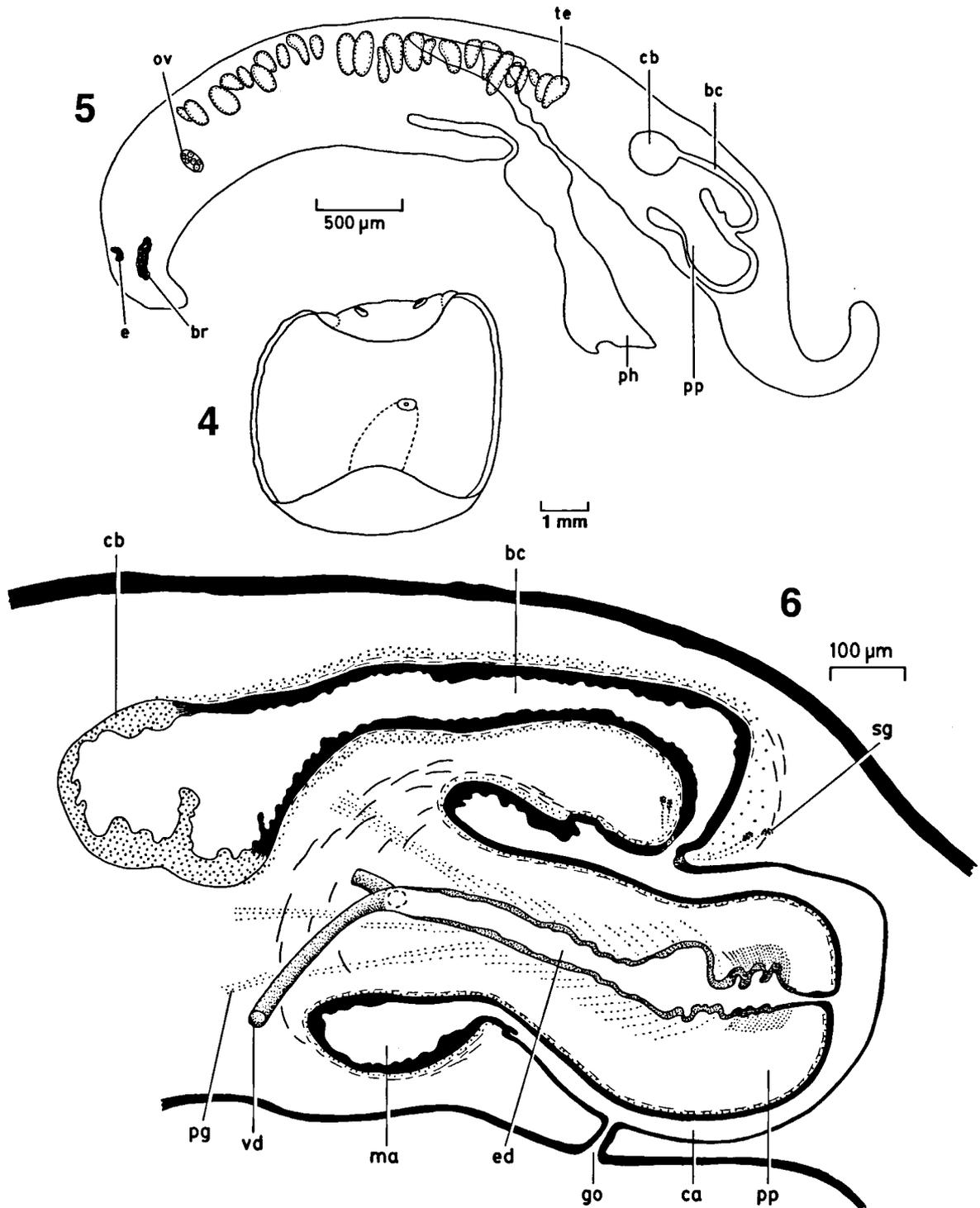
The penial papilla is a rather stout, cylindrical structure with a very blunt tip; it is covered with a cuboidal, nucleate epithelium that is underlain with a layer of circular and longitudinal muscle. The penis papilla projects into both the male and the common atrium, which are separated from each other by a constriction. The male atrium is lined with tall, nucleate cells, whereas the common atrium is lined with a very flat, nucleate epithelium. The gonopore is located at the mid-ventral portion of the common atrium.

The mid-dorsal section of the common atrium receives the opening of the bursal canal, which receives the erythrophilic secretion of shell glands near the opening. The bursal canal is lined with a nucleate epithelium and is provided with a subepithelial layer of longitudinal muscle and a well developed layer of circular muscle. The bursal canal communicates with a relatively small, rounded copulatory bursa.

The ovaries are poorly developed in the specimen examined, being located at about 700 µm behind the brain. Although oviducts could be discerned in the prepharyngeal part of the animal, no traces of the ducts are visible in the posterior section; consequently, there is no information on the openings of the oviducts into the bursal canal.

COMPARATIVE DISCUSSION. - Sluys (1997) restricted the genus *Cura* to the species *C. pinguis* (Weiss, 1909), *C. foremanii* (Girard, 1852), and *C. graffi* (Weiss, 1909). The last-mentioned species is known only from its original description, based on two not fully mature specimens, and was only tentatively assigned to the genus *Cura* since it could belong also to the genus *Girardia* Ball, 1974 (because of the absence of a double seminal vesicle, it is unlikely that *C. graffi* belongs to the genus *Schmidtea* Ball, 1974).

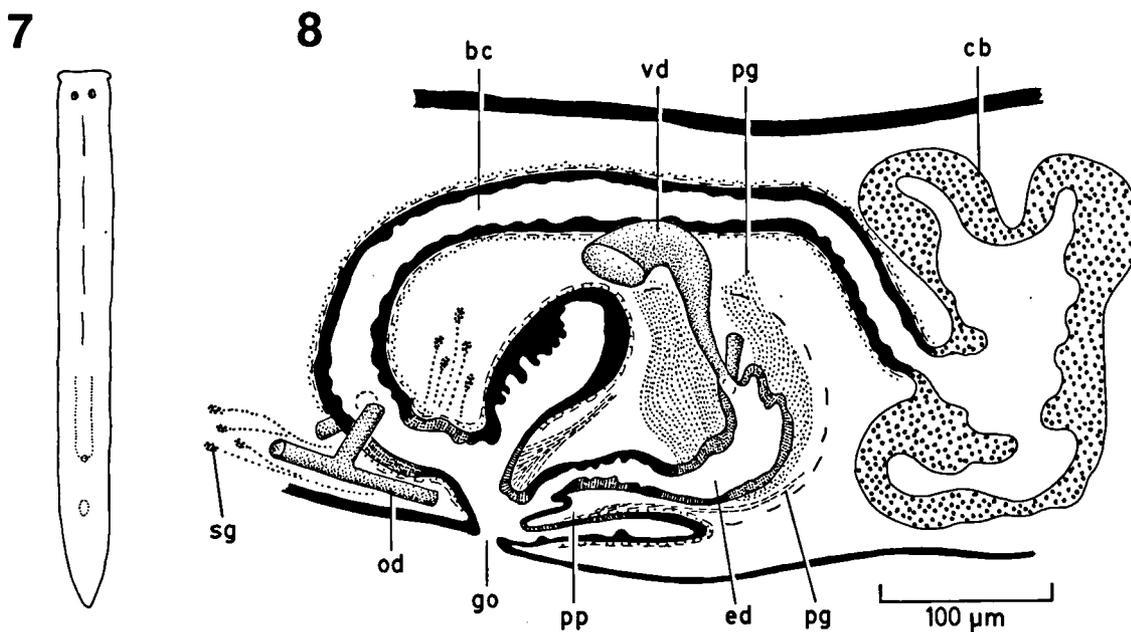
The gross morphology of the copulatory complex of *C. graffi* is rather different from that of *C. fortis* n.sp. and precludes any synonymy of the two species. The species *C. pinguis*, *C. foremanii*, and *C. fortis* n.sp., however, are very similar in the gross morphology of the copulatory apparatus. The most characteristic features, in this respect, are the finger- or thumb-shaped penial papilla, and the opening of the bursal canal into the mid-dorsal or even antero-dorsal section of the common atrium. As a result of the taxonomic restriction



Figs. 4-6. *Cura fortis* n.sp. 4, ZW 1495, sketch of preserved specimen. 5, ZW 1495, sagittal section. 6, ZW 1495, sagittal reconstruction of the copulatory apparatus.

mentioned above, for the first time in its complex history (cf. Ball, 1974b) the genus now has attained some morphological unity.

In *C. foremanii* and *C. pinguis* there are very few prepharyngeal testes, located dorsally in the former and ventrally in the latter, thus contrasting



Figs. 7, 8. *Spathula schauinslandi*. 7, free-hand sketch living animal. 8, V.Pl. 929.1, sagittal reconstruction of the copulatory apparatus.

with the situation in *C. fortis* n.sp. (with numerous dorsal testes between the ovaries and the mouth). Other differences concern the shape of the penial papilla, the location of the gonopore, and the musculature of the bursal canal. In *C. fortis* n.sp. the penial papilla is thumb-shaped, whereas the papillae of *C. pinguis* and *C. foremanii* are thinner and more finger-shaped. In *C. fortis* n.sp. the gonopore is located in the middle of the common atrium, whereas in *C. pinguis* and *C. foremanii* the gonopore occupies a more usual position at the posterior end of the atrium.

In recent phylogenetic analyses of the Dugesidae (Sluys, 1997, 2001) a reversed bursal canal musculature was postulated as an apomorphy for all genera of the family, except *Schmidtea*, *Girardia*, and *Cura*. The non-reversed condition is present in *C. pinguis* and *C. foremanii* and has been described also for *C. graffi*, although there remains some uncertainty about the correctness of Weiss' (1910) observations on the last-mentioned species (Sluys, 1997). The assignment of the species *C. fortis* n.sp. to the genus *Cura* introduces a case of parallelism for the reversed bursal canal musculature, a character that is now no longer confined to

the clade comprising all dugesiid genera, except *Cura*, *Girardia*, and *Schmidtea*. However, it should be noted that the character of the reversed bursal canal musculature is not a strict synapomorphy, since there are component species of the clade that have a non-reversed musculature (cf. Sluys, 2001).

GENUS *SPATHULA* NURSE, 1950

Spathula schauinslandi (Neppi, 1904)

Figs. 7, 8, 51

MATERIAL

NEW ZEALAND. - ZMA V.Pl. 929, preserved specimens (Kawakatsu et al. 1995b, Pl. VI, figs. N & O), Waioura, Kaimanawa mountains, North Island, New Zealand, 11-VIII-1978; V.Pl. 929.1, ibid., sagittal sections on 2 slides.

DESCRIPTION. - Live specimens 15-20 mm long and 1 mm wide (Fig. 7). Head truncated, with blunt auricles. Dorsal surface dark brown or blackish; ventral surface greyish.

The pharynx measures about one-fourth of the body length in preserved specimens; mouth opening located at the posterior end of the pharyngeal

cavity.

In the postpharyngeal region of the body the large testicular follicles are situated ventrally but in the prepharyngeal part of the body the follicles occupy most of the dorso-ventral space. The testes extend from directly behind the ovaries to the tail.

In the posterior part of the body, the vasa deferentia expand to form spermiducal vesicles, which narrow considerably before penetrating the penial bulb and separately opening into the proximal section of the ejaculatory duct. The latter is an irregularly shaped duct, lined with a nucleate epithelium, opening at the tip of the penial papilla (Fig. 8).

Very extensive glands discharge a finely granular, erythrophilic secretion into the proximal section of the ejaculatory duct. The cell bodies of these glands are located well outside and dorsally of the penis bulb. Another, more coarse-grained erythrophilic secretion is discharged into parts of the more distal section of the ejaculatory duct and through the covering, nucleate epithelium of the penial papilla.

The paired ovaries are located at some distance behind the brain. Posterior to the gonopore the oviducts give off a medially directed branch that opens laterally into the ventral, proximal section of the bursal canal; the oviducts extend towards the tail. Ectally to the openings of the oviducts, the bursal canal receives the erythrophilic secretion of shell glands.

The bursal canal is lined with a nucleate epithelium and is covered with a subepithelial layer of longitudinal muscle and a layer of circular muscle, consecutively; the canal communicates with a sac-shaped copulatory bursa.

DISCUSSION. - The anatomy of the specimen described above resembles closely the material described by Neppi (1904) and Ball (1977) and therefore there cannot be any doubt about the identity of this specimen. The external appearance of our animal, however, differs from the situation described by Ball (1977), who reported for living animals a bluntly triangular head with distinct auricles, more or less similar to the head shape of European *Ijimia felina* (Dalyell, 1814). Furthermore, according to Neppi (1904) and Ball (1977) the seminal vesicle receives the openings of

cyanophilic glands, whereas in our material these glands are of an erythrophilic nature.

***Spathula limicola* Nurse, 1950**

Figs. 9-12, 51

MATERIAL

NEW ZEALAND. - ZMA: V.Pl. 930, Omara Stream, Omarama, South Island, New Zealand, 22-II-1998, preserved specimens; V.Pl. 930.1, *ibid.*, sagittal sections on 3 slides; V.Pl. 930.2, *ibid.*, sagittal sections on 3 slides; V.Pl. 930.3, *ibid.*, sagittal sections on 3 slides; V.Pl. 930.4, sagittal sections on 3 slides.

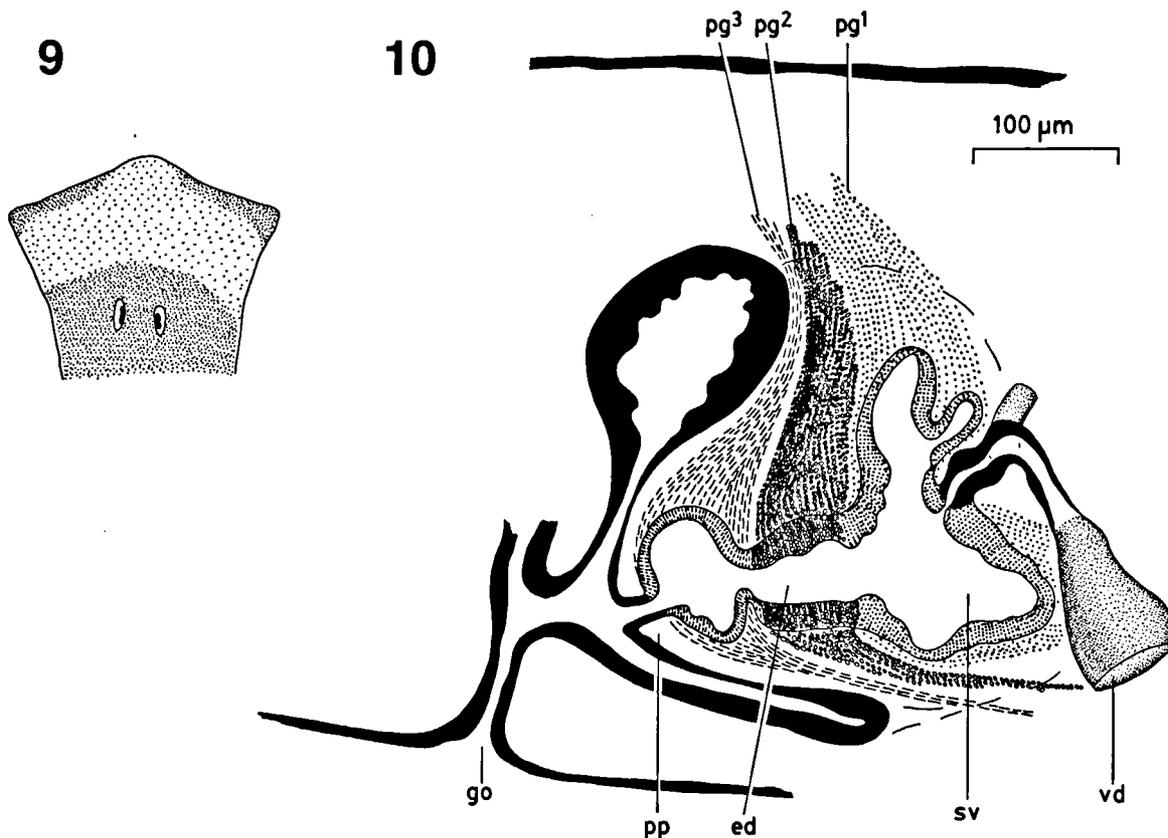
DESCRIPTION. - Maximum length of living animals 8 mm. Head spathulate. Dorsal surface light brown, with paler area on head (Fig. 9). Eyes in pigment-free patches. Small number of sensory fossae at anterior margin; ciliated pits absent.

Pharynx situated in the posterior half of the body; mouth opening at the posterior end of the pharyngeal pocket.

The rather small testes are situated ventrally and extend from directly behind the ovaries to the level of the mouth or, occasionally, to the level of the copulatory apparatus.

The vasa deferentia are expanded to spermiducal vesicles. Within the penial bulb the vasa deferentia unite to form a very short common duct that opens through the antero-dorsal wall of the intrabulbar seminal vesicle, the latter communicating with the ejaculatory duct, which opens at the tip of the short, conical penial papilla. Seminal vesicle and ejaculatory duct are lined with a rather tall, nucleate epithelium and are surrounded by a layer of circular muscle.

Three distinct regions can be distinguished in the penial lumen, i.e. the combined seminal vesicle and ejaculatory duct: an expanded proximal section (the vesicle), a narrow middle section, and a somewhat expanded distal section (Figs. 10-12). These parts are distinguishable on the basis of (1) different types of secretion that are discharged through their lining epithelium, and (2) more or less pronounced constrictions between the sections. The seminal vesicle and the distal section receive weakly staining erythrophilic secretions, probably originating from different types of gland. The middle section receives an equally faintly staining cyanophilic secretion.



Figs. 9-12. *Spathula limicola*. 9, V.Pl. 930, free-hand sketch of head of living animal. 10, V.Pl. 930.1, sagittal reconstruction of the male copulatory apparatus. 11 (page 172), V.Pl. 930.1, sagittal reconstruction of the female copulatory apparatus. 12 (page 172), V.Pl. 930.4, sagittal reconstruction of the copulatory apparatus.

The penial papilla, which is covered by a nucleate epithelium, almost entirely fills the male atrium. Through a narrow passage the male atrium communicates with the bursal canal and the gonoduct leading to the gonopore.

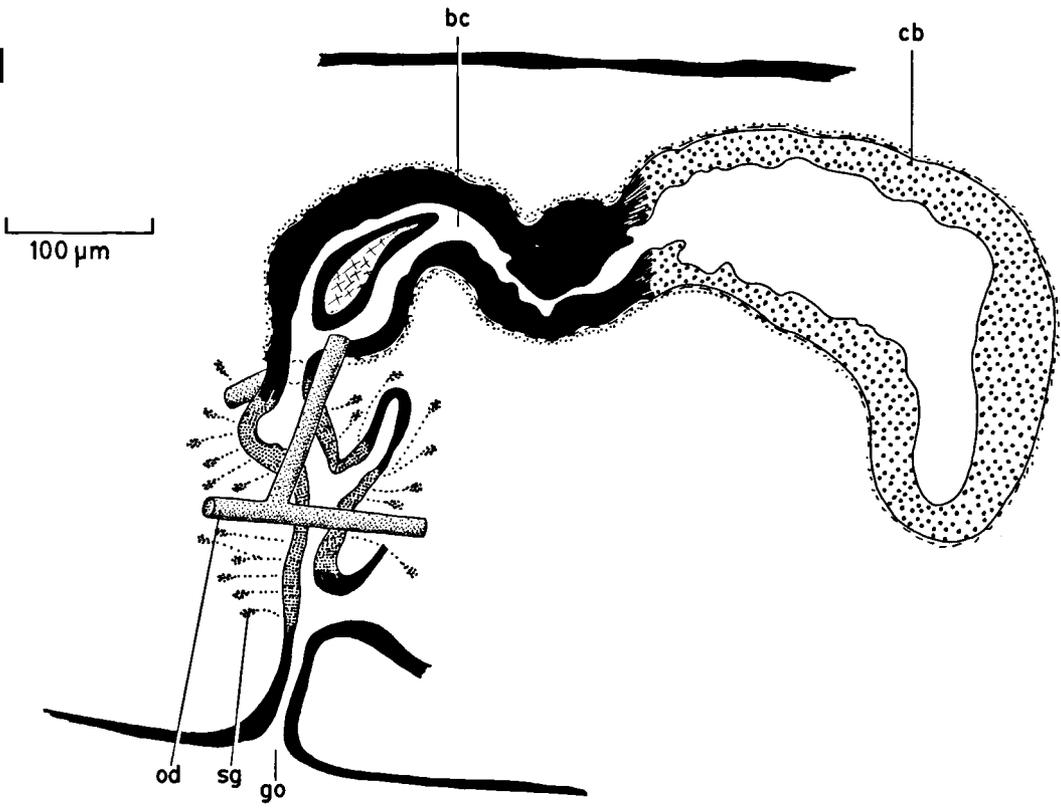
The paired ovaries are situated directly behind the brain. The oviducts run far into the posterior end of the body, giving off a medially directed branch just posterior to the level of the gonopore. These medially running oviducal branches open separately into the bursal canal.

The bursal canal is lined with a well developed nucleate epithelium with prominent cilia and is surrounded by a subepithelial layer of longitudinal muscle, followed by a layer of circular muscle. Ectally or ventrally to the openings of the oviducts, the bursal canal receives the openings of the abundant erythrophilic shell glands. The bursal canal communicates with a sac-shaped copulatory bursa. In specimen V.Pl. 930.1 (Fig. 11) the

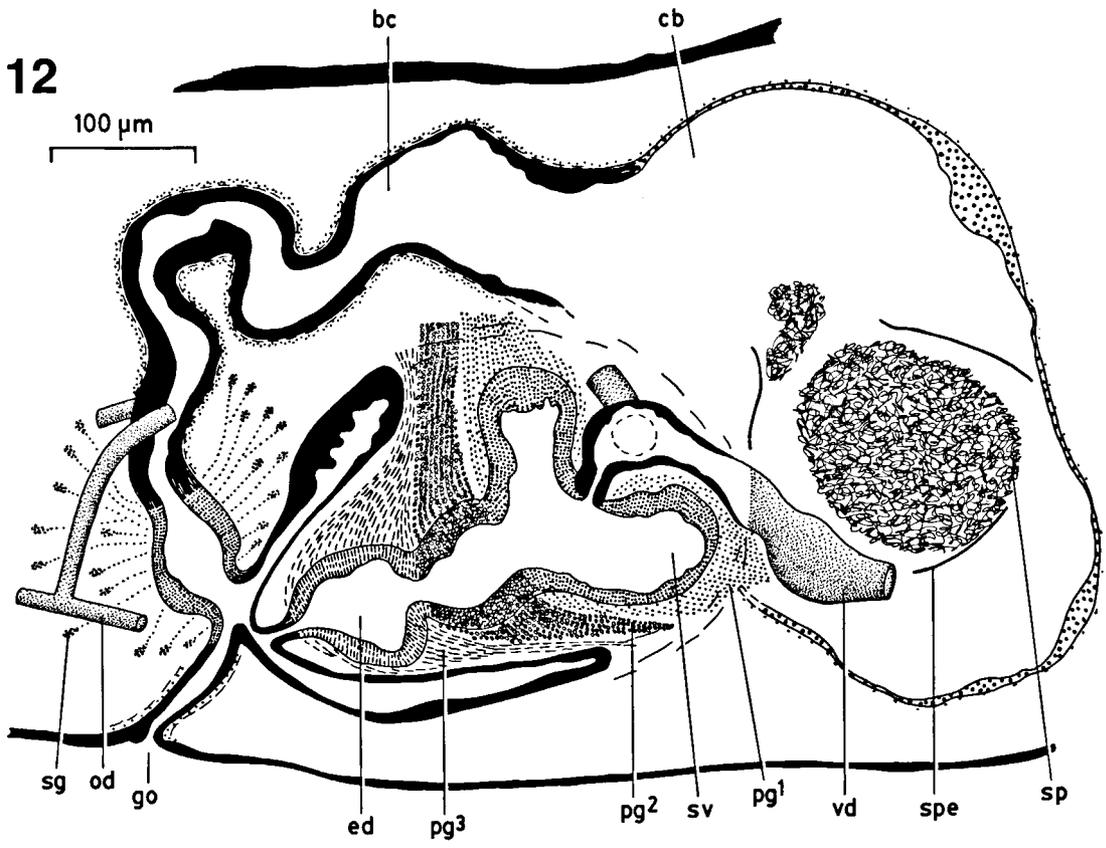
bursa is rather small and lined with a rather tall epithelium. However, in other specimens (e.g. specimen V.Pl. 930.4 ; Fig. 12) the bursa is greatly expanded and has a highly reduced epithelium; in these specimens the bursa contains clumps of sperm and remnants of a spermatophore.

DISCUSSION. - The specimens are assigned to the genus *Spathula* mainly on the basis of their spathulate head and possession of branched oviducts. In addition to branched oviducts, most species of *Spathula* are characterized also by the presence of ciliated pits. *S. limicola* was described with ciliated pits (Ball, 1977) but these structures appeared to be absent in the Omara stream specimens. Ball (1977) argued that the apparent absence of sensory fossae in *S. limicola* might be the result of the poor histological condition of the type material that he examined; Dr F. R. Allison (née Nurse) (in litt.) recently confirmed that the

11



12



Figs. 11,12. For legends, see page 171.

sections have somewhat faded in the anterior region of the animals. The present specimens confirm that *S. limicola* also possesses sensory fossae.

S. limicola was described with the testes arranged in two zones, viz. one anterior zone from just behind the ovaries to the root of the pharynx and a second posterior zone, extending from just behind the copulatory apparatus to the tail, testis follicles being absent from the pharyngeal region. This differs from the situation in the present specimens, in which the testes extend to about the mouth and are absent from the tail region. After re-examination of the type material, Dr Allison (in litt.) concluded that the testes do not extend to the tail but extend to just behind the genital pore.

Other differences between previous accounts of *S. limicola* and the specimens from the Omara stream concern the communication between vasa deferentia and penial lumen and the shape of the latter. *S. limicola* was described with the vasa deferentia opening separately into the proximal section of the penial lumen or ejaculatory duct, that is not expanded to form a seminal vesicle. However, upon re-examination of the type material Dr Allison agreed that a seminal vesicle is present (see also Nurse, 1950: Pl. 49, fig. 2). Furthermore, no distinct penial glands were reported for *S. limicola*, but Dr Allison informed us that penial glands are present in the type material but are not well stained.

Another species with well developed glands associated with the penial complex is *S. schauinslandi*. In this species two types of gland open into the penial lumen. Although *S. schauinslandi* may show a well developed intrabulbar seminal vesicle, it differs from *S. limicola* in the fact that the recurved vasa deferentia open separately into this vesicle or proximal section of the ejaculatory duct.

Specimens with similar external appearance as the ones collected from the Omara stream were found near Maryborn and Lindis Pass on South Island, but these animals could not be examined anatomically.

Spathula fontinalis Nurse, 1950
Figs. 13-18, 51

MATERIAL

NEW ZEALAND. - ZMA:V.Pl. 931, preserved specimens, Kowai River, Porters Pass, South Island, New Zealand, 14-VIII-1978; V.Pl. 931.1, *ibid.*, sagittal sections on 3 slides; V.Pl. 931.2, *ibid.*, horizontal sections on 3 slides; V.Pl. 931.3, *ibid.*, sagittal sections on 5 slides; V.Pl. 931.4, *ibid.*, sagittal sections on 5 slides.

DESCRIPTION. - Live specimens upto 25 mm long and 2-4 mm wide. Head of low triangular form, with very short auricles (Fig. 13). Dorsal surface grey-brown to blackish brown; frequently with a dark stripe on either side of the mid-line, fusing to a single stripe on the posterior part of the body.

The eyes are set in pigment-free patches; a distinct ciliated pit is present on either side of the head.

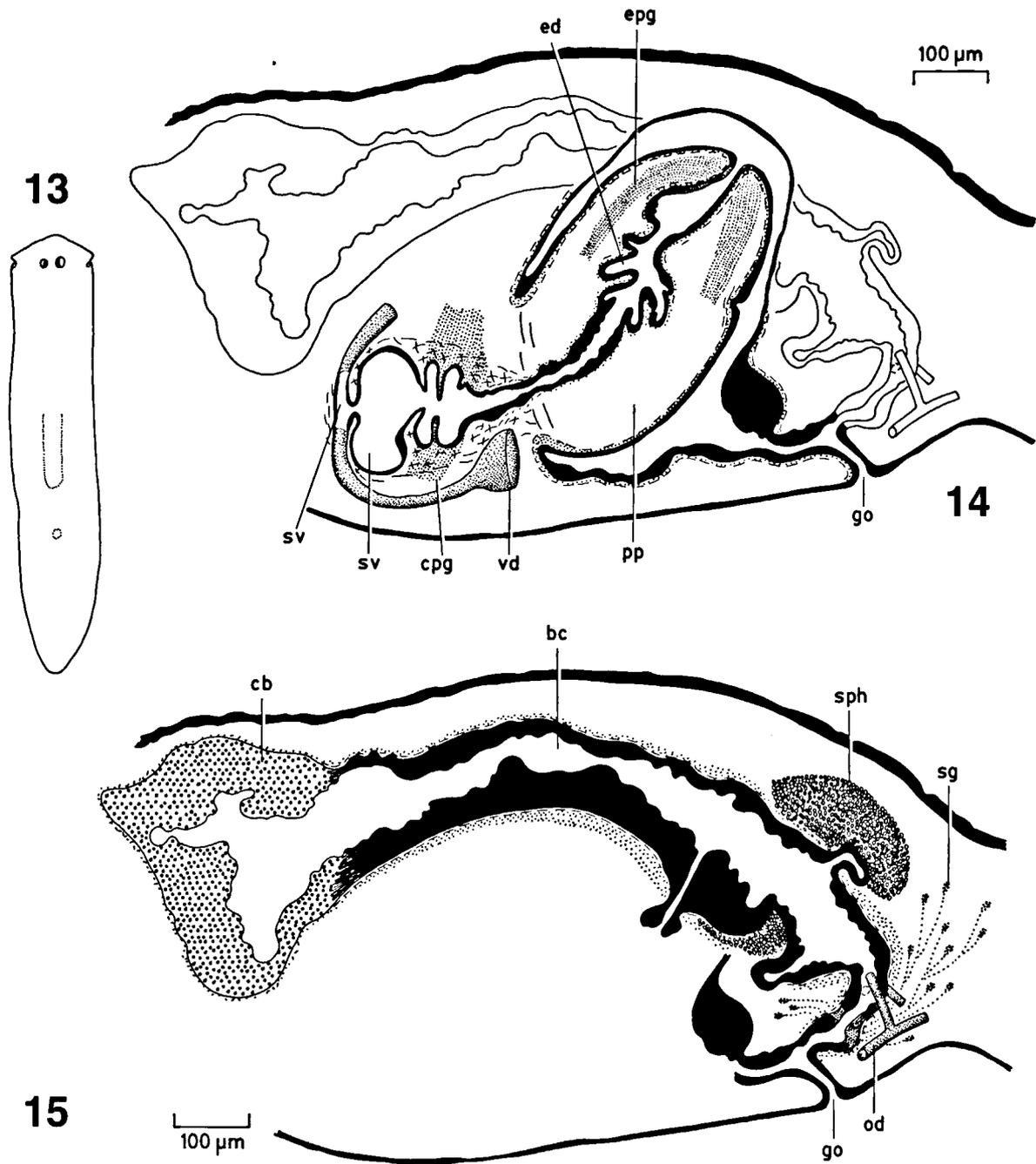
The pharynx is situated in the middle of the body, measuring between one-fourth and one-fifth of the body length in preserved specimens; the mouth opening is located at the posterior end of the pharyngeal pocket.

Numerous testes principally dorsal but frequently occupying almost the entire dorso-ventral space; the follicles extend from a short distance behind the ovaries to the posterior end of the body.

The vasa deferentia, which are expanded to form very large spermiducal vesicles, recurve anteriorly at the level of the penis bulb. Subsequently, the ducts narrow and open separately into a small intrabulbar seminal vesicle that communicates with a second, much larger seminal vesicle. A duct with pleated walls, forming 2-4 diaphragmatic constrictions, connects this second seminal vesicle with the ejaculatory duct (Figs. 14, 16, 18). Seminal vesicles, diaphragms and ejaculatory duct are lined with a nucleate epithelium. The ejaculatory duct is surrounded by mostly circular muscles.

The pleated section of the duct intercalated between the second, large seminal vesicle and the ejaculatory duct receives the secretion of cyanophilic penial glands.

The seminal vesicles and the diaphragms are situated within the penis bulb, consisting of a longitudinal and intermingled musculature. The penial papilla is a relatively large, cylindrical structure, covered with a flat, nucleate epithelium. Erythrophilic penis glands open at the tip of

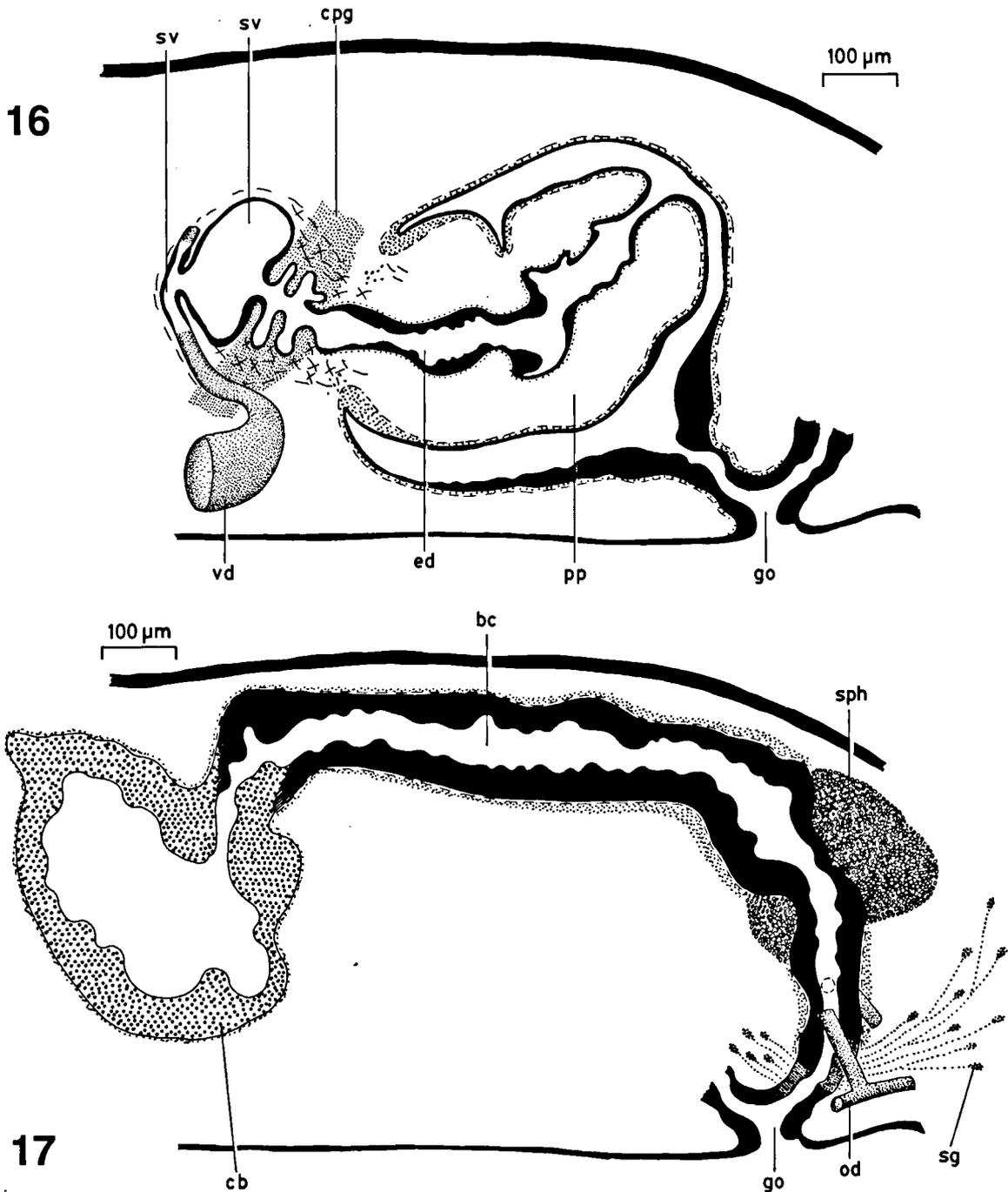


Figs. 13-15. *Spathula fontinalis*. 13, V.Pl. 931, free-hand sketch of living animal. 14, V. Pl. 931.1, sagittal reconstruction of the male copulatory apparatus. 15, V.Pl. 931.1, sagittal reconstruction of the female copulatory apparatus.

the penial papilla. The postero-ventral section of the male atrium narrows to form a kind of duct that communicates with the common atrium and the gonopore.

The paired ovaries are situated almost directly behind the brain. The oviducts extend from the

ovaries far into the posterior end of the body, giving off a medial branch just posterior to the gonopore. These medially directed oviducal branches open into the ventral, proximal section of the bursal canal. Erythrophilic shell glands open into the bursal canal, ventrally to the open-



Figs. 16, 17. *Spathula fontinalis*. 16, V.Pl. 931.3, sagittal reconstruction of the male copulatory apparatus. 17, V.Pl. 931.3, sagittal reconstruction of the female copulatory apparatus.

ings of the oviducts.

The bursal canal is a duct with a variable diameter that is lined with a tall, nucleate epithelium; the duct communicates with a large sac-shaped copulatory bursa that may contain the remnants

of a spermatophore.

In some specimens, notably V.Pl. 931.1 (Fig. 15), the bursal canal is provided with a number of blob-like perforations, similar to the ones observed in some specimens of *Spathula ochyra* Ball

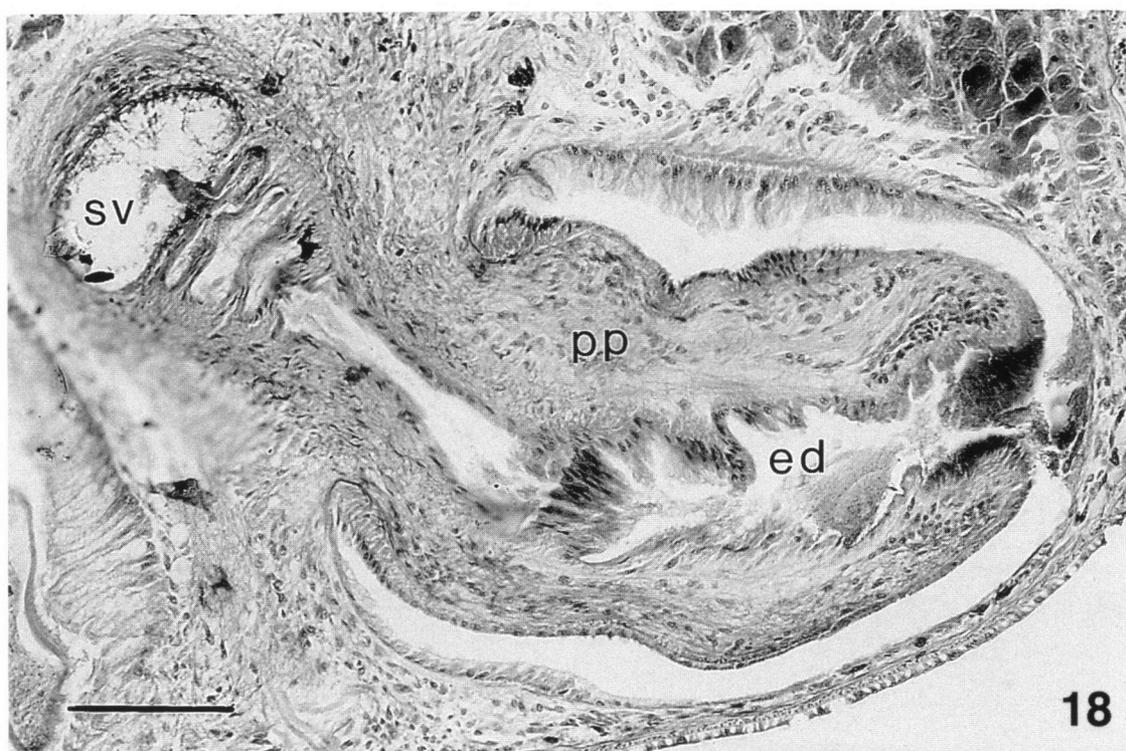


Fig. 18. *Spathula fontinalis*. V.Pl. 931.4, microphotograph of penial papilla (scale bar = 100 μ m).

& Tran, 1979.

The section of the bursal canal dorsal to the openings of the oviducts is surrounded by a relatively huge muscular sphincter, consisting of strong circular fibres (Figs. 15, 17). Other sections of the bursal canal are surrounded by a thin, subepithelial layer of longitudinal muscle and a well-developed layer of circular muscle.

DISCUSSION. - The specimens described are essentially similar to the ones described by Nurse (1950) and Ball (1977), albeit that in our animals the diaphragms are more distinct.

The species has been reported only from the Canterbury Plains region and therefore the present record from Porters Pass represents the first finding from a distinctly higher altitude.

Spathula ochyra Ball & Tran, 1979

Figs. 19-23, 50

MATERIAL

AUSTRALIA. - ZMA: V.Pl. 932, Preserved specimens, Mt.

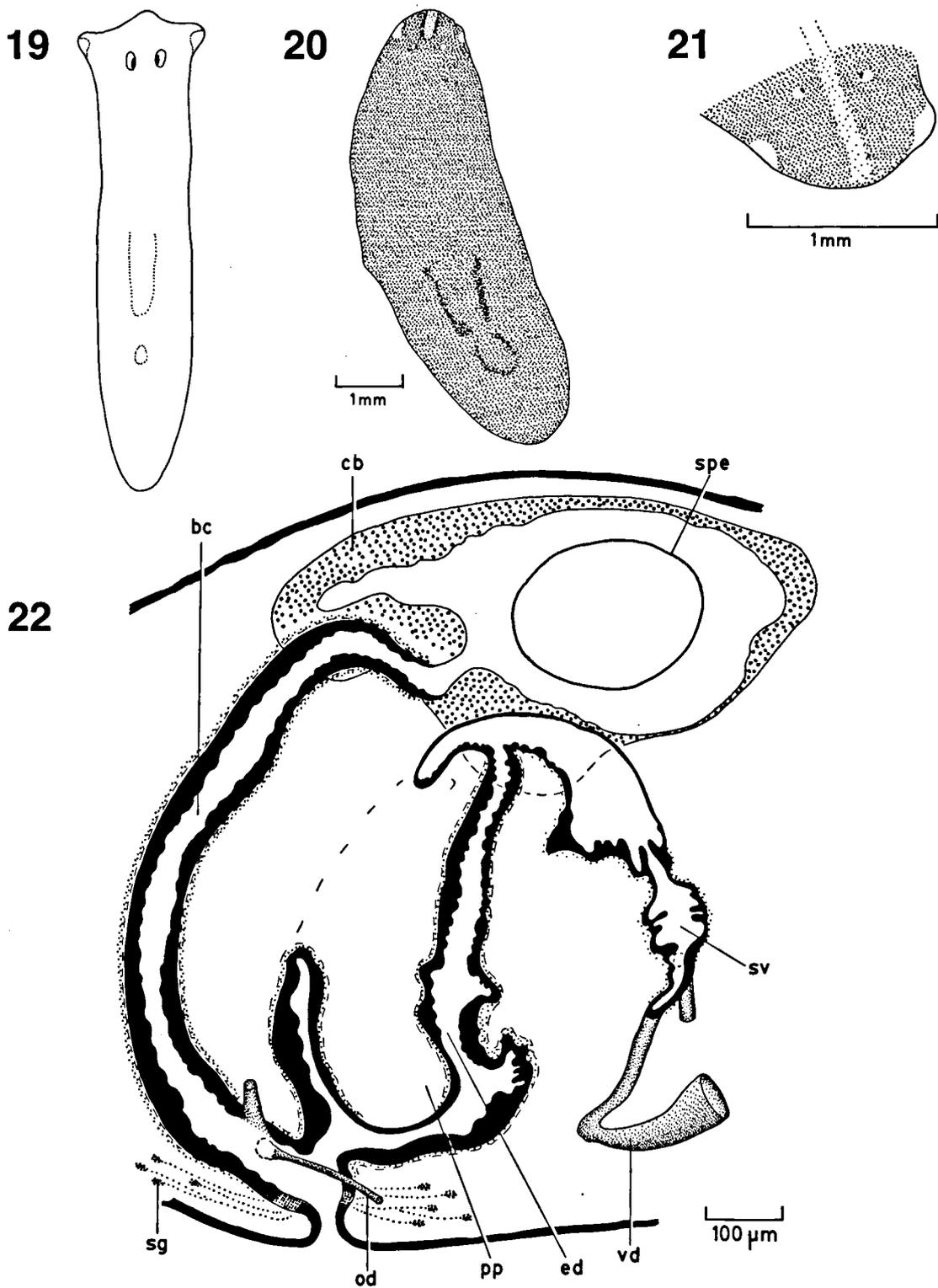
Wellington, Hobart, Tasmania, Australia, 17-VIII-1978; V.Pl. 932.1, *ibid.*, sagittal sections on 3 slides; V.Pl. 932.2, *ibid.*, horizontal sections on 2 slides; V.Pl. 932.3, *ibid.*, horizontal sections on 2 slides; V.Pl. 932.4, *ibid.*, sagittal sections on 3 slides; V.Pl. 932.5, *ibid.*, sagittal sections on 2 slides; V.Pl. 932.6, *ibid.*, sagittal sections on 3 slides; V.Pl. 932.7, *ibid.*, sagittal sections on 2 slides.

DESCRIPTION. - Live animals 12-15 mm long and 2-3 mm wide. Head spathulate, bluntly triangular, with small auricles (Fig. 19). Dorsal surface dark brown; ventral surface pigmented but paler than dorsal surface. Auricles unpigmented; eyes situated in unpigmented patches. A somewhat paler middorsal stripe may be present anterior to the eyes (Figs. 20, 21)

A distinct ciliated pit is present on either side of the head and several sensory fossae are located at the anterior body margin.

Testes ventral, extending from some distance behind the brain into the posterior end of the body.

In the posterior part of the body the vasa deferentia expand to form well developed spermidu-



Figs. 19-22. *Spathula ochyra*. 19, V.Pl. 932, free-hand sketch of living animal. 20, V.Pl. 932, dorsal view of preserved specimen. 21, V.Pl. 932, preserved specimen; dorsal view of head. 22, V.Pl. 932.4, sagittal reconstruction of the copulatory apparatus.

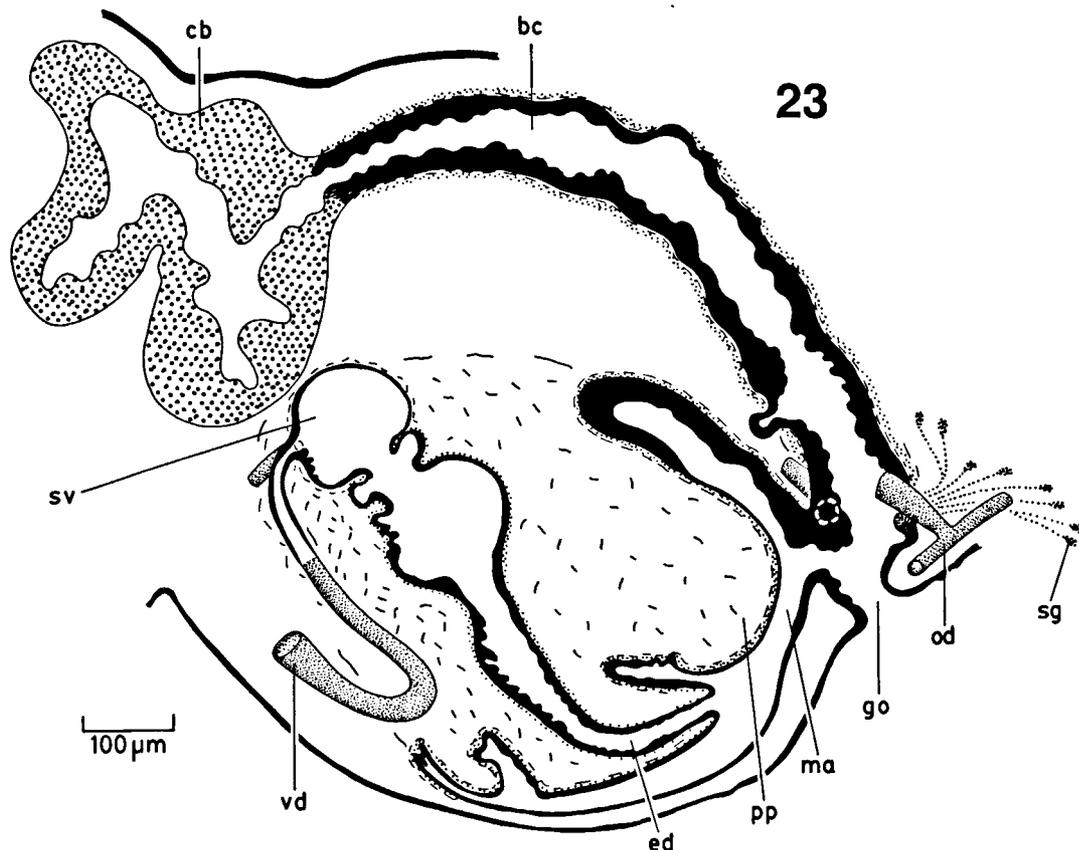


Fig. 23. *Spathula ochyra*. V.Pl. 932.1, sagittal reconstruction of the copulatory apparatus.

cal vesicles. At the level of the penis bulb the vasa deferentia recurve and subsequently open separately, albeit in close proximity, into a large, globular intrabulbar seminal vesicle. A constriction separates this seminal vesicle from the proximal section of the ejaculatory duct, which may be expanded to form a sort of additional seminal vesicle. Seminal vesicle and ejaculatory duct are lined with a nucleate epithelium.

The shape of the penial papilla is variable as a result of the apparently eversible nature of the papilla. In a strongly contracted condition (V.Pl. 932.5; Fig. 22) the tip of the papilla becomes very blunt, whereas in a more extended condition (V.Pl. 932.1; Fig. 23) the penis may show a distinctly pointed tip. In all cases the penial papilla is highly asymmetrical in that it shows a large dorsal lip and a much less developed ventral lip. The penial papilla is lined with a nucleate epithelium. A constriction separates the male atrium from the common atrium, a separate female atrium being

absent.

The paired ovaries are located at a short distance behind the brain. At the level of the gonopore the oviducts give off a medially directed branch, after which the ducts extend for a short distance into the posterior end of the body. The medially directed oviducal branches open into the ventral, proximal section of the bursal canal, close to the opening of the canal into the common atrium. Erythrophilic shell glands discharge their secretion into the same ventral section of the bursal canal, albeit ventrally to the openings of the oviducts.

The bursal canal is lined with a tall, nucleate epithelium and is covered with a thin subepithelial layer of longitudinal muscle and a well developed layer of circular muscle. In the specimens V.Pl. 932.1 and V.Pl. 932.2 the bursal canal shows a few blob-like perforations that seem to communicate with the gut. The histology and morphology of these perforations does not suggest that

they result from preservation artefacts. The relatively large copulatory bursa contains remnants of a spermatophore in specimens V.Pl. 932.4 and V.Pl. 932.7.

DISCUSSION. - Thus far, the species *S. ochyra* has been known only from its type material, collected from Arthurs Lake, Tasmania. The present material is assigned to *S. ochyra* since it exhibits the same variability in penis shape and the presumed eversibility of the papilla as described for this species. Furthermore, the specimens examined also have (1) very deep ciliated pits, (2) oviducts that open into the very ventral, or proximal, section of the bursal canal, and (3) asymmetrical penial papilla with a more strongly developed dorsal lip, all being features that were described also for the type specimens.

Spathula (?) sp.
Figs. 24, 25, 50

MATERIAL

AUSTRALIA. - ZMA: V.Pl. 933.1, stream at Mt. Wellington, SE Tasmania, Australia, 20-XII-1974, sagittal sections on 2 slides.

DESCRIPTION. - Preserved specimens up to 3-4 mm long and 0.5 mm wide. Dorsal surface dark brown, ventrally blackish; head rounded, with distinct unpigmented auricular sense organs. Ciliated pit on either side of the head, located between the eyes and the anterior margin of the body.

Pharynx located in the middle of the body, measuring about one-sixth of the body length. Mouth at the posterior end of the pharyngeal pocket.

Testes located ventrally, extending from some distance behind the brain into the posterior part of the body.

Immediately after having reached the muscular wall of the penis bulb, the vasa deferentia unite and open into a spacious intrabulbar seminal vesicle. The ventral section of the latter tapers to form a short duct that communicates with another seminal vesicle that distally narrows to form a wide ejaculatory duct that opens at the blunt tip of a stubby and short penis papilla (Fig. 24). The penis bulb is well developed, its musculature

being dominated by longitudinal fibres. The penis papilla points into a spacious male atrium that ventrally tapers to form a gonoduct that communicates with the gonopore. All epithelia of the male copulatory complex are nucleate.

The paired ovaries are situated directly behind the brain. Well developed vitellaria are located between the intestinal branches, extending throughout the body and occupying most of the dorso-ventral space.

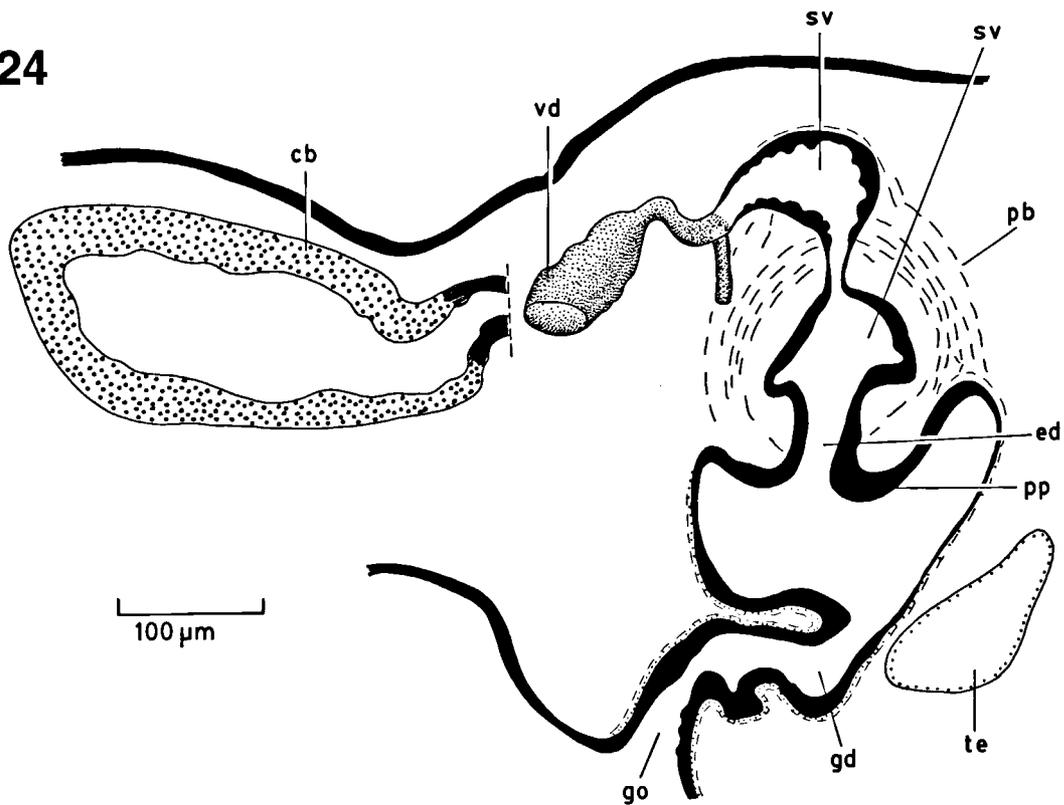
The oviducts arise from the ventral surface of the ovaries. Unfortunately, there were only few traces of oviducts in the post-pharyngeal part of the body, thus making it impossible to determine the connection between the oviducts and the female copulatory apparatus. The position of a section of an oviduct near the gonopore (Fig. 25) suggests that each oviduct gives rise to a branch that extends into the posterior part of the animal.

From the posterior wall of the sac-shaped copulatory bursa arises a short bursal canal that is lined with relatively tall, nucleate cells. The bursal canal is covered with a well developed subepithelial layer of longitudinal muscle, followed by an equally developed layer of circular muscle. The proximal, ventral section of the bursal canal expands to form a spacious chamber, lined with short, nucleate cells, that ventrally narrows and communicates with the gonoduct. The chamber receives the secretion of shell glands. The most ventral, proximal lining of the bursal canal, at its opening into the chamber, gives rise to a clump of cells that points into the chamber. This clump of cells does not obstruct the opening of the bursal canal into the chamber since its main mass is located on one side.

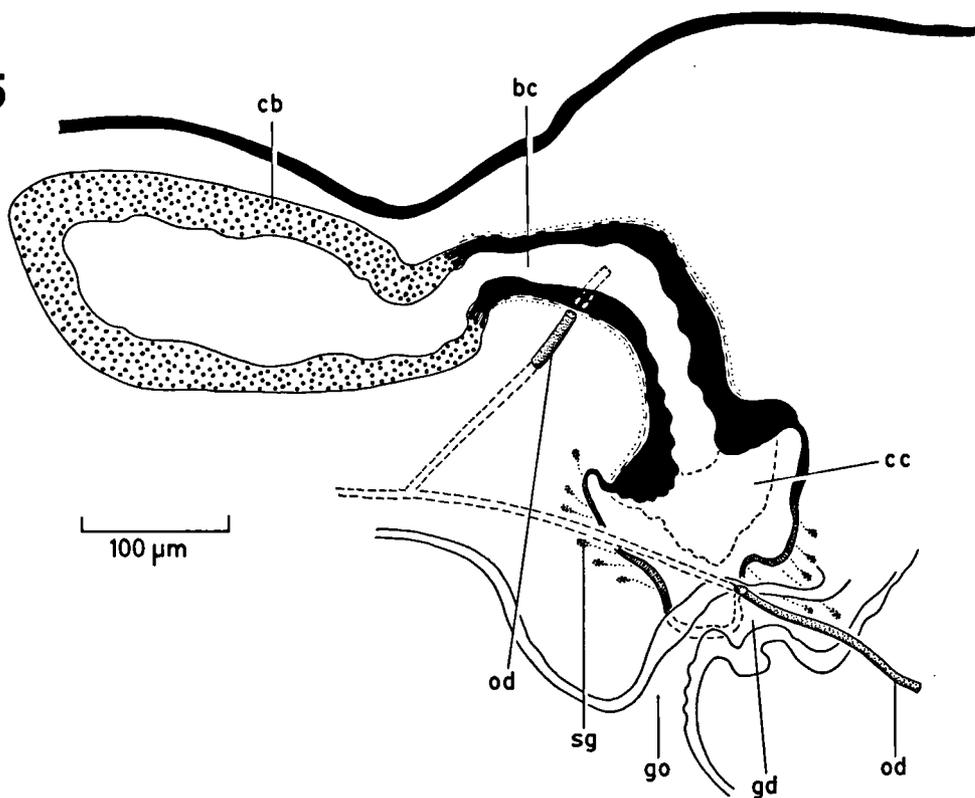
DISCUSSION. - Present information is inconclusive on the precise communication between oviducts and female copulatory apparatus, but to our mind it suggests that the oviducts branch, one branch continuing towards the hind end of the body and the other ascending towards the bursal canal (Fig. 25).

This animal combines a number of features that usually occur separately in various genera. For example, the genus *Schmidtea* is characterized by (1) the presence of a double seminal vesicle, (2) a widening of the distal part of the bursal canal before it communicates with the atrium, and (3)

24



25



Figs. 24, 25. *Spathula* (?) sp. 24, V.Pl. 933.1, sagittal reconstruction of the male copulatory apparatus. 25, *Spathula* (?) sp. V.Pl. 933.1, sagittal reconstruction of the female copulatory apparatus.

shell glands that open into this expanded portion of the bursal canal, all being features that apply also to *Spathula* (?) sp. However, *Schmidtea* does not have oviducts that extend into the posterior part of the body, while the bursal canal musculature is non-reversed, in contrast to *Spathula* (?) sp.

Branched oviducts in combination with a reversed bursal canal musculature are found in the genera *Spathula* and *Romankenkius* Ball, 1974. Caudally branched oviducts occur also in the monotypic genus *Eviella* Ball, 1974, but here the bursal canal musculature is non-reversed or intermingled. *Spathula* (?) sp. cannot be assigned to *Romankenkius* because it lacks the characteristic apomorphy of the latter, viz. the common oviduct or diverticulum of the bursal canal, receiving the secretion of shell glands (cf. Sluys, 1997).

Ciliated pits, like the ones in *Spathula* (?) sp., are found in the genera *Spathula*, *Romankenkius*, and *Eviella* Ball, 1977, and also in *Neppia magnibursalis*, a new species that will be described below.

The overall shape of penial papilla and distal-most seminal vesicle in *Spathula* (?) sp. reminds one of the situation in *Eviella hynesae* Ball, 1977. However, *Spathula* (?) sp. cannot be equated with *Eviella* since it lacks the fused testes of the latter and *E. hynesae* is devoid of eyes and a copulatory bursa.

A stubby, vertically oriented penial papilla and a very spacious intrabulbar seminal vesicle were described also for *Spathula schauinslandi* (Neppi, 1904) by Neppi (1904). However, it has been noted that Neppi's specimens were probably not fully mature (Ball, 1977), which may be reflected also in the small size and the orientation of the penial papilla in these specimens.

GENUS *NEPPIA* BALL, 1974

Neppia montana (Nurse, 1950)

Figs. 26-29, 52

MATERIAL

NEW ZEALAND. - NSMT: NSMT-pl-5049, Wylies Cave, NW of Nelson, South Island, New Zealand, 24-I-1975, sagittal sections on 2 slides; NSMT-pl-5050, *ibid.*, sagittal sections on 40 slides (Kawakatsu et al. 1995b: Pl. VH, fig. G); ZMA: VPl. 934.1, brook running into Lake Wanaka, Otago, South Island, New Zealand, 25-I-1975, sagittal sections on 11 slides (Kawakatsu et al., 1995b: Pl. VII, figs. E & F); VPl.

935 (Kawakatsu et al., 1995b: Pl. VI, figs. L & M), preserved specimens, Waikaka stream, 25 km NW of Taumarunui, North Island, New Zealand, 10-VIII-1978; VPl. 935.1, *ibid.*, sagittal sections on 10 slides; VPl. 935.2, *ibid.*, sagittal sections on 12 slides; VPl. 935.3, *ibid.*, sagittal sections on 9 slides; VPl. 936 (Kawakatsu et al., 1995b: Pl. VI, fig. S, Pl. VII, figs. A & B), preserved specimens, Waioura, Kaimanawa mountains, North Island, New Zealand, 11-VIII-1978; VPl. 936.1, *ibid.*, sagittal sections on 11 slides; VPl. 937 (Kawakatsu et al., 1995b: Pl. VII, figs. C & D), preserved specimens, Akatarawa, 15 km NW of Upper Hutt, North Island, New Zealand, 12-VIII-1978; VPl. 937.1, *ibid.*, sagittal sections on 10 slides; VPl. 937.2, *ibid.*, sagittal sections on 8 slides; VPl. 937.3, *ibid.*, horizontal sections on 5 slides; VPl. 938 (Kawakatsu et al., 1995b: Pl. VI, fig. W, Pl. VII, figs. J-L), preserved specimens, stream near Lake Lyndon, 85 km of Christchurch, South Island, New Zealand, 14-VIII-1978; VPl. 938.1, *ibid.*, sagittal sections on 2 slides; VPl. 938.2, *ibid.*, sagittal sections on 5 slides; VPl. 939.1, Porters Pass, South Island, New Zealand, 17-II-1998, sagittal sections on 23 slides; VPl. 940.1, Cass, South Island, New Zealand, 17-II-1998, sagittal sections on 47 slides; VPl. 940.2, *ibid.*, sagittal sections on 41 slides; VPl. 940.3, *ibid.*, horizontal sections on 43 slides; VPl. 941, preserved specimens, Banks Peninsula, New Zealand, 19-II-1998; VPl. 941.1, *ibid.*, sagittal sections on 8 slides; VPl. 941.2, *ibid.*, sagittal sections on 8 slides; VPl. 941.3, *ibid.*, horizontal sections on 4 slides; VPl. 941.4, *ibid.*, sagittal sections on 12 slides; VPl. 941.5, *ibid.*, sagittal sections on 10 slides.

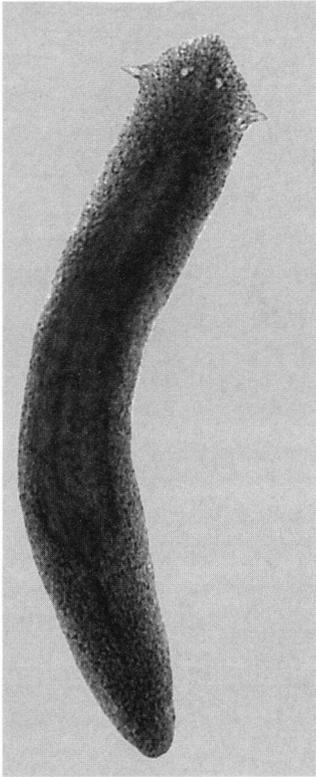
DESCRIPTION. - Head of low triangular form and provided with distinct auricles. Dorsal surface mottled brown, with paler mid-dorsal stripe and sometimes a dark stripe on either side of the mid-line running from behind the eyes to the level of the copulatory apparatus (Figs. 26, 27). Auricles whitish. Ventral surface pale. Live specimens up to 20-30 mm long and 4-5 mm wide. The eyes are set in pigment-free patches.

Pharynx situated in the middle of the body, measuring between one-fourth and one-fifth of the body length; the mouth opening is at the hind end of the pharyngeal pocket.

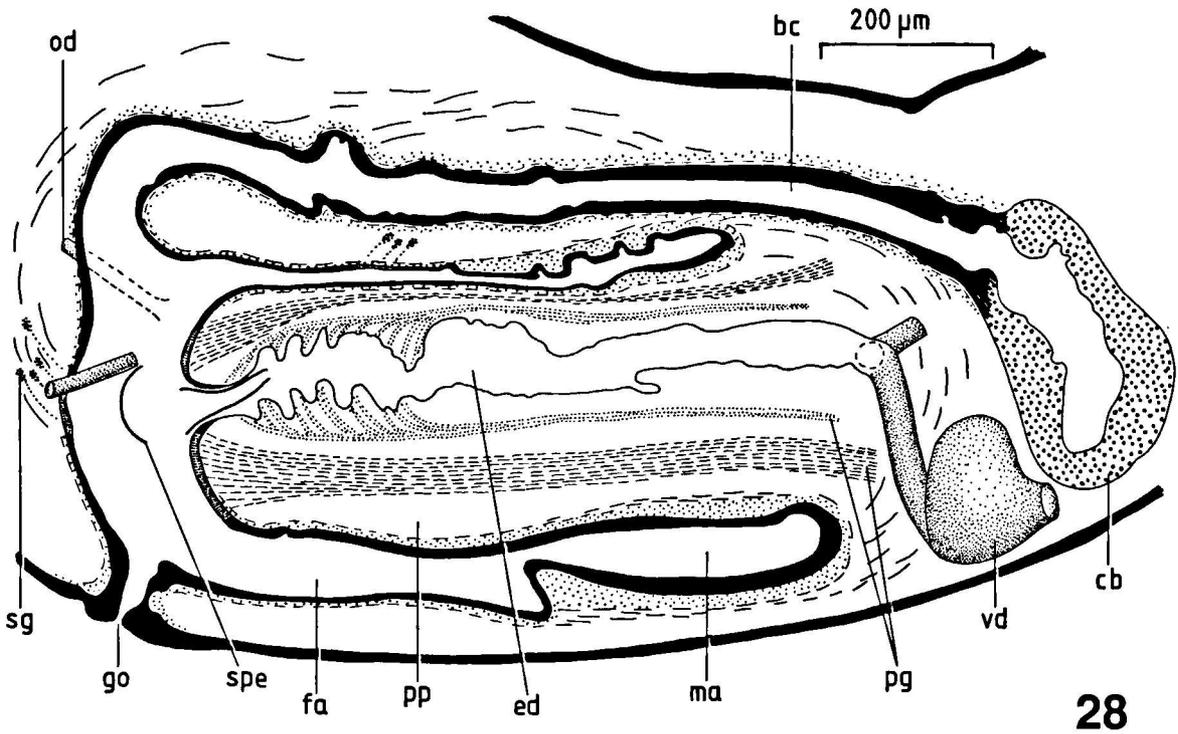
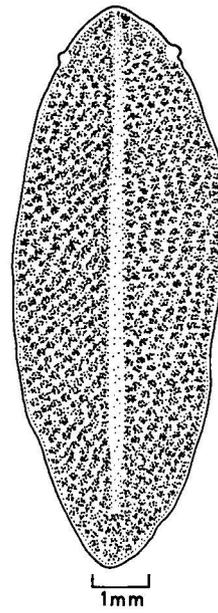
Testes situated dorsally and extending from directly behind the ovaries to almost the posterior end of the pharyngeal pocket.

The vasa deferentia separately enter the well-muscularized penial bulb and open into the proximal section of the ejaculatory duct; this proximal section may be enlarged, thus forming a seminal vesicle. The ejaculatory duct is a broad, somewhat irregularly shaped and slightly convoluted duct with the wall of its distal section arranged into folds (Fig. 28). This particular, folded section of the ejaculatory duct receives the secretion of

26



27



28

Figs. 26-28. *Nephia montana*. 26, V.Pl. 938, photograph of living animal. 27, V.Pl. 937, dorsal view of preserved specimen. 28, V.Pl. 934.1, sagittal reconstruction of the copulatory apparatus.

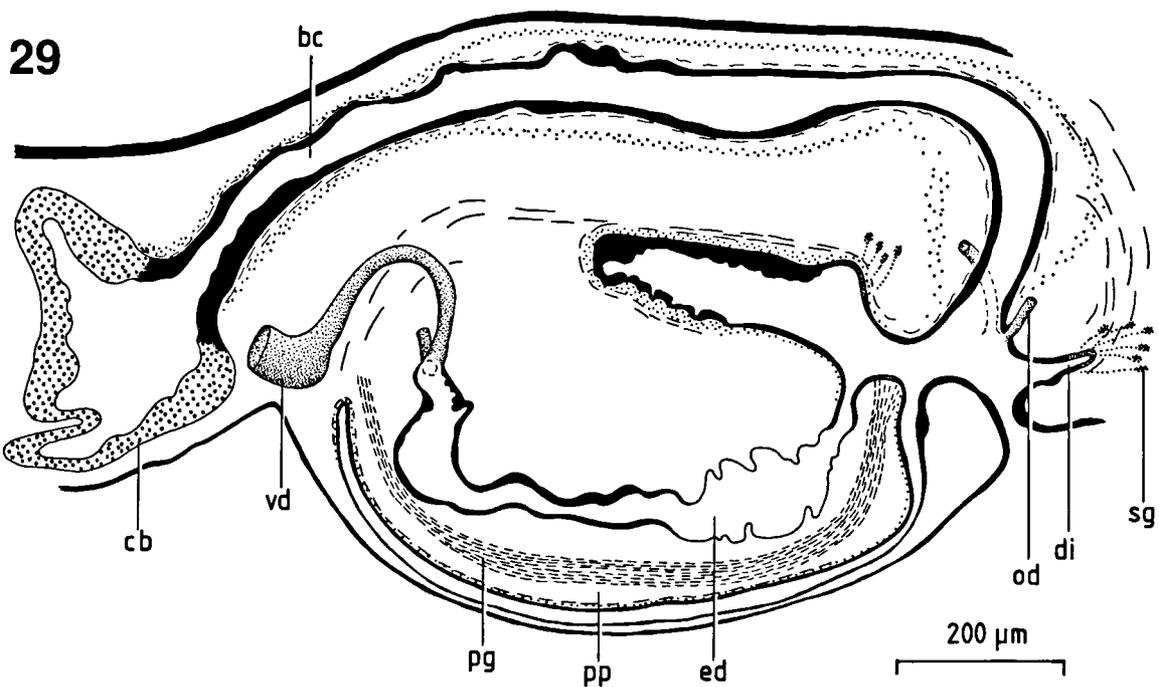


Fig. 29. *Neppia montana*. V.Pl. 937.1, sagittal reconstruction of the copulatory apparatus.

one group of cyanophilic penial glands. Another type of erythrophilic penial gland discharges through the covering epithelium at the tip of the papilla.

In many of the specimens examined the penis papilla is asymmetrical, in that the ejaculatory duct opens on the dorsal surface near the tip (Fig. 29). However, in other specimens this asymmetry was much less pronounced. The penis papilla is covered with a nucleate epithelium.

The paired ovaries are situated at a considerable distance behind the brain (ranging from 600-1200 μm , depending on the specimen examined). A sac-shaped copulatory bursa lies immediately anterior to the penis bulb. The bursa communicates with a bursal canal that runs dorsally to the male atrium and, subsequently, curves ventrad to communicate with the male and common atria. The bursal canal is well-developed, lined with a nucleate epithelium, and at places forms irregular expansions or outbulgings. The canal is surrounded by a subepithelial layer of longitudinal muscle and a thick, but usually loosely arranged, layer of circular muscle. Very close to its point of communication with the atrium the bursal canal

receives the separate openings of the oviducts. The openings of these ducts may be located at the lateral sides or at the postero-lateral sides of the bursal canal.

The female atrium may show a posterior diverticulum, receiving the secretion of shell glands. These glands also open into the frontal section of the female atrium, close to the point where it communicates with the male atrium. The change from female to male atrium is indicated by a change in histology, the male atrium being lined with a taller epithelium and being surrounded by a more developed muscle coat (Figs. 28, 29).

The gross morphology of the region around the opening of the bursal canal into the atrium is rather variable, due to differences in contraction. There are well developed muscles attached to the posterior wall of the bursal canal, i.e. where it gives rise to the diverticulum; the muscles extend dorsally over a part of the bursal canal. The situation can be interpreted in such a way that contraction of these muscles apparently results in the formation of the diverticulum, whereas relaxation only leaves a shallow outbulging of the bursal canal. It is not only the diverticulum that

changes shape but also the locations of the oviducal openings into the bursal canal seem to alter. However, careful reconstruction reveals that the oviducts always open laterally and at the very point of communication between bursal canal and atrium.

DISCUSSION. - In the above, a description of the material has been presented since the present collection represents only the second series of specimens that has become available since the material used in the original description of the species.

Ball (1974a, b) re-examined paratypes of *N. montana* and concluded that the oviducts penetrate separately the frontal wall of the bursal canal, his reconstruction in point of fact suggesting that the ducts open through the roof of the frontal part of the female atrium (Ball 1974a, fig. 9). Now that new material has become available, it can be concluded that generally the oviducal openings are neither associated with the frontal face of the bursal canal, nor with the roof of the female atrium.

Ball (1974a, b) noted that the paratypes possess a diverticulum of the bursal canal, not described by Nurse (1950), that might be the result of a fixation artefact resulting from deformations caused by the very strong ectal musculature of the bursal canal. However, the presence of this diverticulum in most of the new specimens examined precludes its artefactual status.

***Neppia magnibursalis* n.sp.**

Figs. 30-37, 49

MATERIAL

Holotype: QM G 217904, pool at Mt Barrow, northeastern Tasmania, AUSTRALIA, 26-XII-1974, sagittal sections on 5 slides. Paratypes: ZMA: V.Pl. 944.1, *ibid.*, sagittal sections on 4 slides; V. Pl. 944.2, *ibid.*, sagittal sections on 4 slides; V.Pl.944.3, *ibid.*, sagittal sections on 4 slides; V.Pl. 944.4, *ibid.*, sagittal sections on 4 slides; V.Pl. 944.5, *ibid.*, sagittal sections on 4 slides; V. Pl. 944.6, *ibid.*, sagittal sections on four slides; V. Pl. 944.7, *ibid.*, sagittal sections on 4 slides (Kawakatsu et al., 1995b: Pl. V, fig. I (not L!)).

DIAGNOSIS. - *Neppia magnibursalis* n.sp. can be distinguished from its congeners by having ventral testes extending throughout the body length, and oviducts that open asymmetrically into the bursal canal.

ECOLOGY AND DISTRIBUTION. - The species is known only from its type locality.

ETYMOLOGY. - The specific epithet is derived from the Latin *magnus*, 'large', and alludes to the relatively large size of the copulatory bursa.

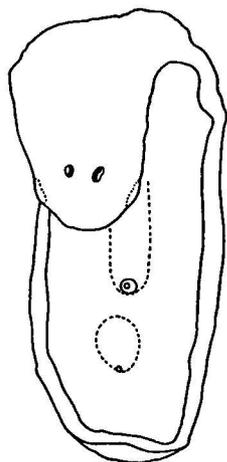
DESCRIPTION. - Preserved specimens 10-12 mm long and 1.5 mm wide (Fig. 30). Dorsal surface deeply dark brown; ventral surface with dark brown ground colour and numerous black spots. A mid-dorsal swelling of the body was present anterior to the eyes, corresponding with a narrow, antero-ventral slit, resembling the slit present in *Phagocata vivida* (Ijima & Kaburaki, 1916) from the Far East (cf. Kawakatsu et al., 1994: fig. 1C). Sensory organs were not observed in the intact specimens, but the sections revealed several shallow sensory fossae at the anterior body margin and a deep ciliated sensory pit on either side of the body, situated between the eyes and the anterior margin (Fig. 31).

The pharynx is located in the middle of the body, measuring between one-fourth and one-seventh of the body length; the mouth opening is located at the rear end of the pharyngeal pocket.

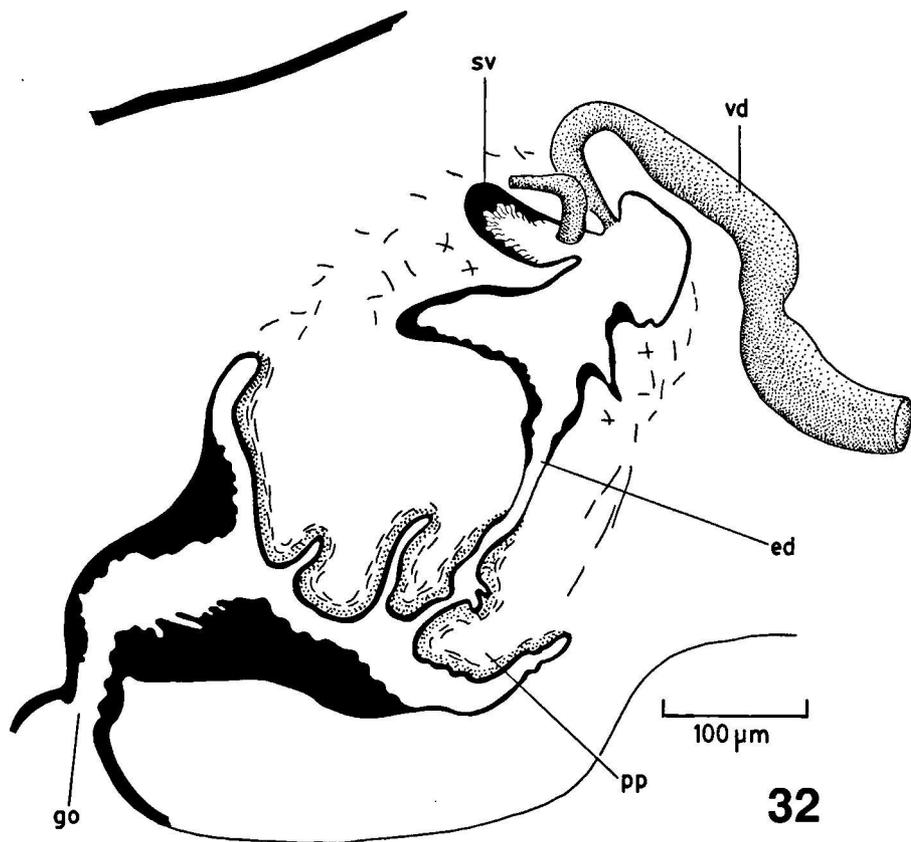
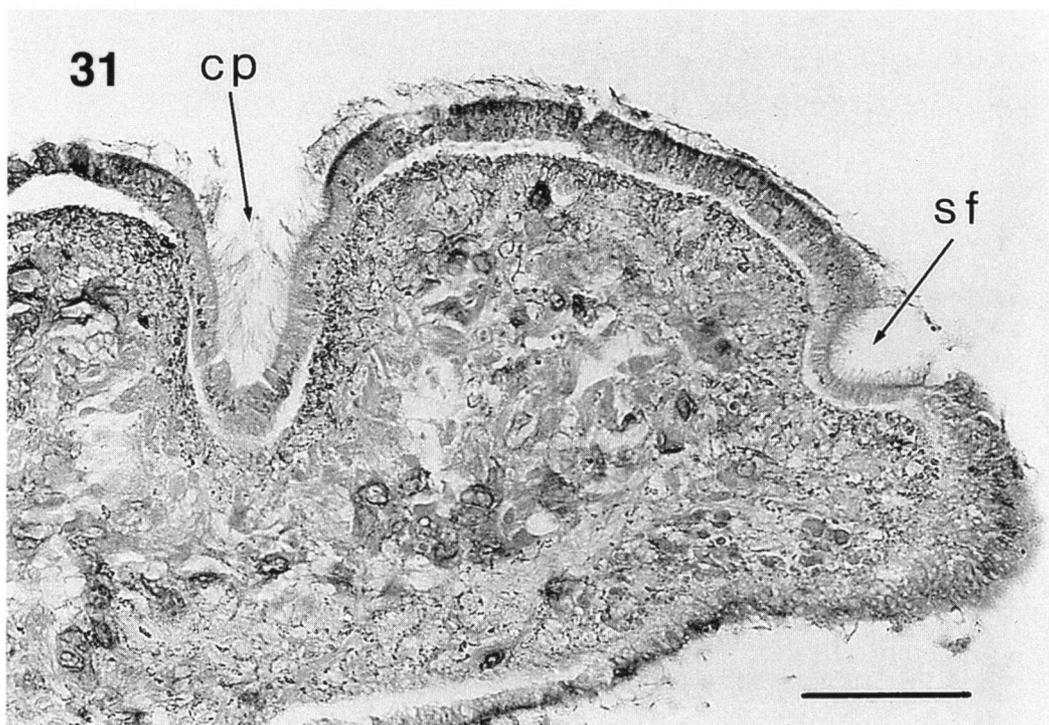
Small testicular follicles not numerous, situated ventrally, and extending from a short distance behind the ovaries to behind the copulatory apparatus.

Shape of the penial papilla variable, due to different states of contraction and preservation. When more or less extended, the penial papilla is a conical structure with a more pronounced upper lip and a smaller ventral section. This asymmetry results from the acentral, ventral course of the ejaculatory duct, which opens subterminally at the tip of the penial papilla.

Reconstruction of the communication between vasa deferentia and ejaculatory duct proved complex because of contractional distortions. One of the specimens examined (V.Pl. 944.5; Fig. 32) suggested that the vasa deferentia open separately, albeit in close proximity, into an intrabulbar, ciliated seminal vesicle, representing the proximal section of the ejaculatory duct. A second specimen (G 217904; Fig. 34) suggested fusion of the vasa deferentia, but the opening of the possible common duct into the seminal vesicle was not clear. As a result of contortion, the situation in a

30

1 mm

**32**

Figs. 30-32. *Neppia magnibursalis* n.sp. 30, V.Pl. 944, preserved specimen. 31, V.Pl. 944.4, microphotograph of ciliated pit and sensory fossa; scale bar: 50 μ m. 32, V.Pl. 944.5, sagittal reconstruction of male copulatory apparatus.

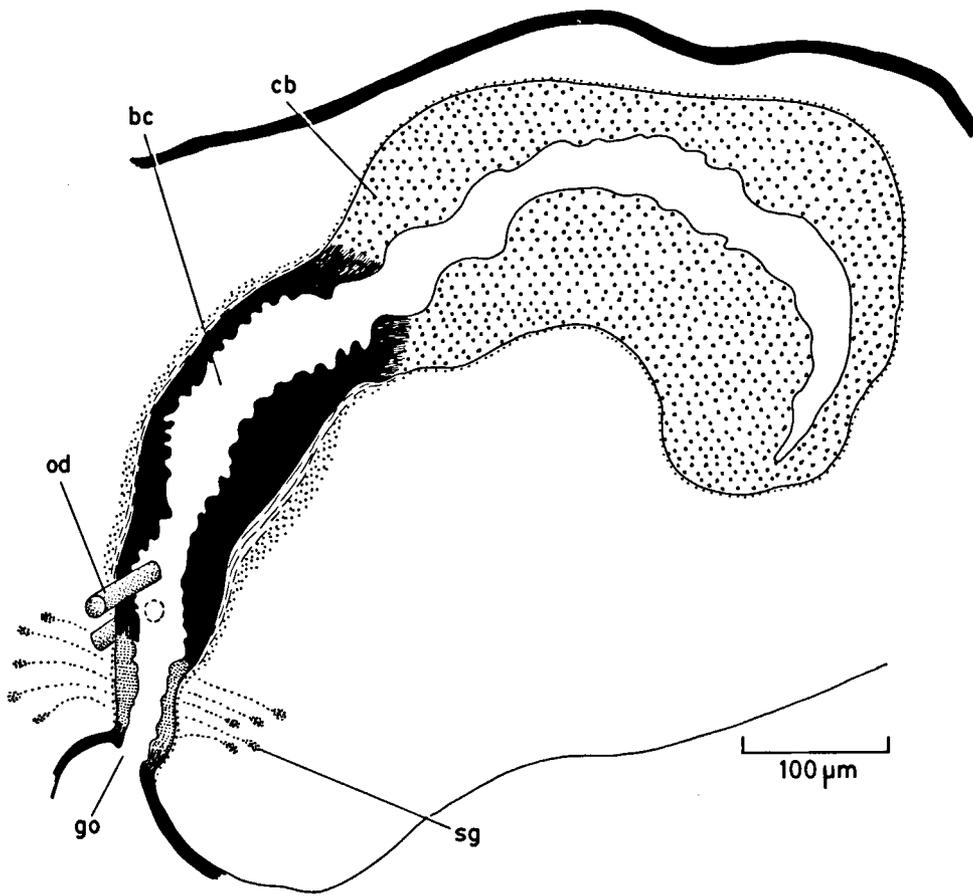


Fig. 33. *Neppia magnibursalis* n.sp. V.Pl. 944.5, sagittal reconstruction of female copulatory apparatus.

third specimen (V.Pl. 944.1; Fig. 36) is also difficult to interpret, seemingly suggesting both fusion and separate openings of the vasa deferentia. In all specimens the seminal vesicle communicates with a broad ejaculatory duct that is lined with a tall, nucleate epithelium.

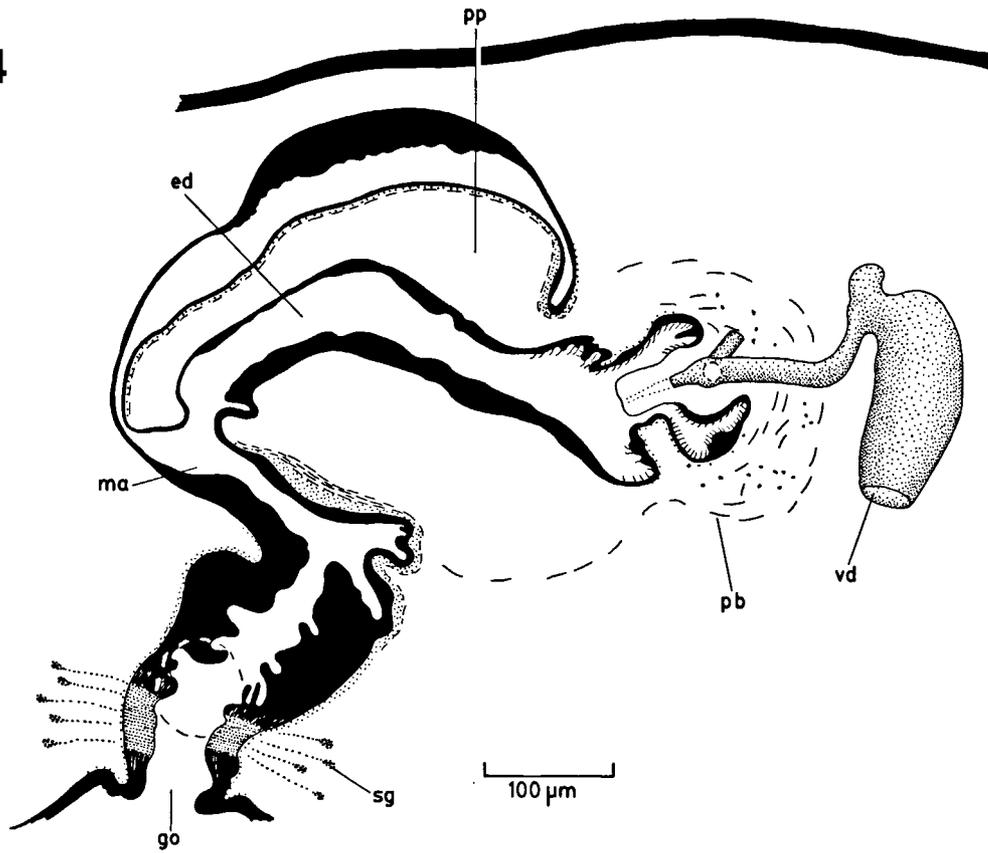
The male atrium constricts considerably before communicating with the bursal canal.

The paired ovaries are situated at a short distance behind the brain. The oviducts open separately into the distal, ventral section of the bursal canal, directly above the openings of the shell glands into the canal. The oviducts open asymmetrically into the bursal canal in that (a) one duct may have its opening more dorsally located than the other, or (b) one duct opens through the dorso-posterior wall and the other through the ventro-anterior wall of the bursal canal (Figs. 33, 35, 37).

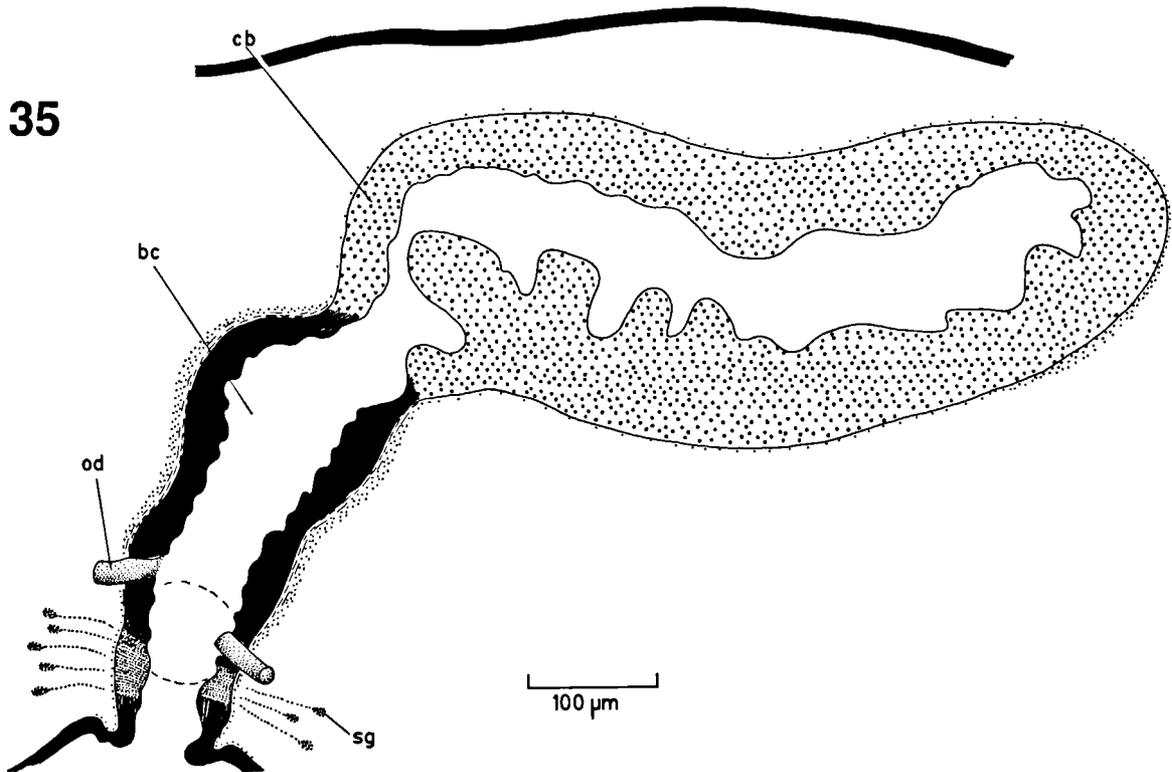
The most proximal or ventral section of the bursal canal communicates with the male atrium as well as with the gonopore, a common atrium virtually being absent. The bursal canal is a wide duct lined with tall, nucleate cells that is surrounded by a subepithelial layer of longitudinal muscle and a thick layer of circular muscles. The canal communicates with a large copulatory bursa that is covered with a weak muscle coat. The bursa of specimen V.Pl. 944.1 (Fig. 37) contained the remnants of a spermatophore.

COMPARATIVE DISCUSSION. - Generic assignment of southern hemisphere dugesiids is hampered by the fact that some of the relevant genera are poorly defined from a phylogenetic perspective, notably *Neppia*, *Cura*, and *Spathula* (Sluys, 2001). However, after considering the morphological Bauplans of the dugesiid genera as well as their

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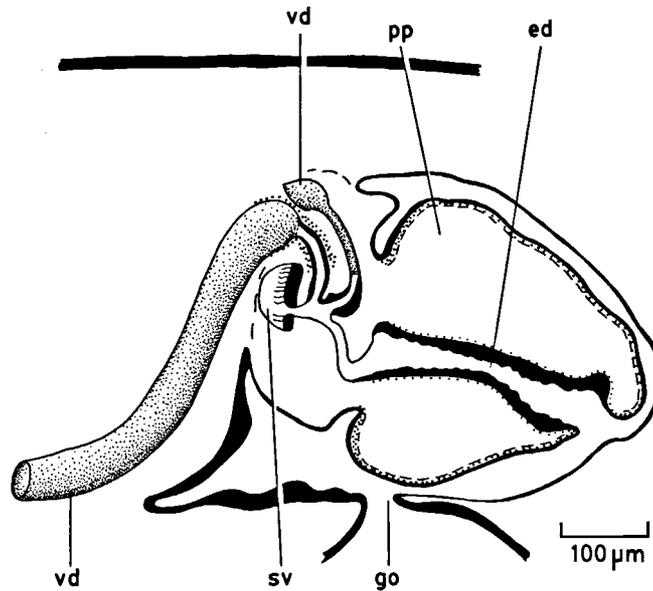


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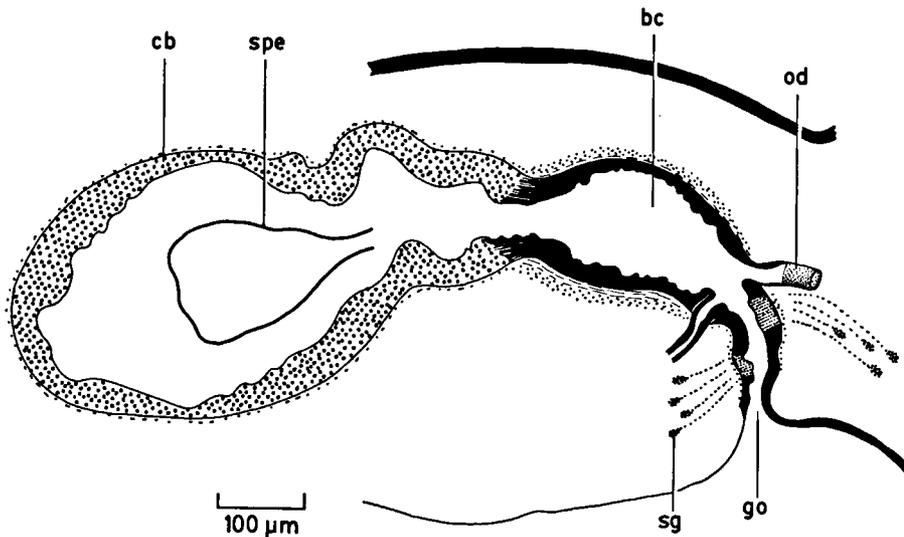


Figs. 34, 35. *Neppia magnibursalis* n.sp. 34, QM G 217904, holotype, sagittal reconstruction of male copulatory apparatus. 35 QM G 217904, holotype, sagittal reconstruction of female copulatory apparatus.

36



37



Figs. 36-37. *Neppia magnibursalis* n.sp. 36, V.Pl. 944.1, sagittal reconstruction of male copulatory apparatus. 37, V.Pl. 944.1, sagittal reconstruction of female copulatory apparatus.

defining features, there is only one genus left, after successive elimination, to which the present species can justifiably be assigned, viz. *Neppia*. The present species does not fit within *Cura* since it lacks the characteristic penial papilla and the anterior opening of the bursal canal into the male atrium of this genus. It does not belong to *Spathula*, *Eviella* or *Reynoldsonia* Ball, 1974 because it lacks the branched oviducts of these genera.

A presumed autapomorphic feature of *Neppia* is a convoluted ejaculatory duct (cf. Sluys, 1997). However, this is a character that can be rather

variable and is subject to preservation artefacts, and therefore difficult to interpret. Furthermore, *N. evelinae* Marcus, 1955 and *N. wimbimba* Marcus, 1970 were described with rather straight ejaculatory ducts. Therefore, we feel that the rather non-convoluted ejaculatory duct in the present species should not prevent its assignment to the genus *Neppia* (see also Sluys, 2001).

Comparison with described species of the current genus *Neppia* [*N. evelinae*, *N. falklandica* (Westblad, 1952), *N. jeanneli* (de Beauchamp, 1913), *N. montana*, *N. paeta* (Marcus, 1955), *N. tinga*

(Marcus, 1955), *N. wimbimba*] reveals that the present species shares a number of noteworthy similarities with its congeners. For example, in several other species of *Neppia* the proximal section of the ejaculatory duct is developed into a seminal vesicle that receives the openings of the vasa deferentia (e.g., *N. montana*, *N. tinga*, *N. paeta*, *N. wimbimba*). Furthermore, all described species have a highly developed coat of circular muscle on the bursal canal. One species, *N. wimbimba*, was described with oviducts opening asymmetrically into the bursal canal.

Despite these similarities with its congeners, *N. magnibursalis* n.sp. is different from every species of *Neppia* already described. Most species have dorsal testes, apart from *N. tinga* and *N. magnibursalis* n.sp., which have ventral testes. In *N. tinga*, however, the testes are prepharyngeal, whereas in *N. magnibursalis* n.sp. the follicles extend throughout most of the body. Like *N. magnibursalis* n.sp., also *N. wimbimba* shows asymmetrical openings of the oviducts into the bursal canal. However, *N. wimbimba* has very few, prepharyngeal and dorsal testes and a long bursal canal, in contrast to the situation in *N. magnibursalis* n.sp.

It is noteworthy that we have examined dark brown specimens from another locality in northern Tasmania (ZMA: V.Pl. 945: Gun Lagoon Creek, alt. 1140 m.; preserved specimens up to 20 x 6 mm; cf. Kawakatsu et al., 1995b: Pl. V, figs. E-H) which also showed a distinct slit or sucker at the anterior margin, as in *N. magnibursalis* n.sp. Unfortunately, the sectioned material revealed that the animals are not fully mature, showing only traces of the copulatory apparatus. Only new collections from this locality may be able to ascertain whether these animals belong to *N. magnibursalis* n.sp. or to another species.

GENUS *GIRARDIA* BALL, 1974

Girardia sphincter n.sp.

Figs. 38-42, 49

MATERIAL

Holotype: QM: G 217905, pool at Mt Barrow, northeastern Tasmania, AUSTRALIA, 26-XII-1974, sagittal sections on 2 slides. Paratypes: ZMA: V.Pl. 942.1, pool at Mt Barrow, northeastern Tasmania, Australia, 26-XII-1974, sagittal sections on 3 slides; V.Pl. 942.2, *ibid.*, sagittal sections on 2 slides; V.Pl. 942.3, sagittal sections on 2 slides; V.Pl. 942.4,

ibid., sagittal sections on 2 slides (Kawakatsu et al., 1995b: Pl. V, Figs. J & K).

DIAGNOSIS. - *G. sphincter* n.sp. differs from all of its congeners by the presence of a sphincter at the base of the bursal canal.

ECOLOGY AND DISTRIBUTION. - Known only from the type locality, a pool.

ETYMOLOGY. - The word 'sphincter' is originally Greek, but is here used in its latinized form; the specific epithet refers to the muscular sphincter at the base of the bursal canal.

DESCRIPTION. - Preserved specimens 7-10 mm long and 1 mm wide (Figs. 38-40). Dorsally pale yellowish brown, ventrally whitish. Eyes set closely to the midline of the body; auricular sense organs hardly visible.

Pharynx situated in the middle of the body, measuring between one-fifth and one-sixth of the body length. Mouth opening at the rear end of the pharyngeal pocket.

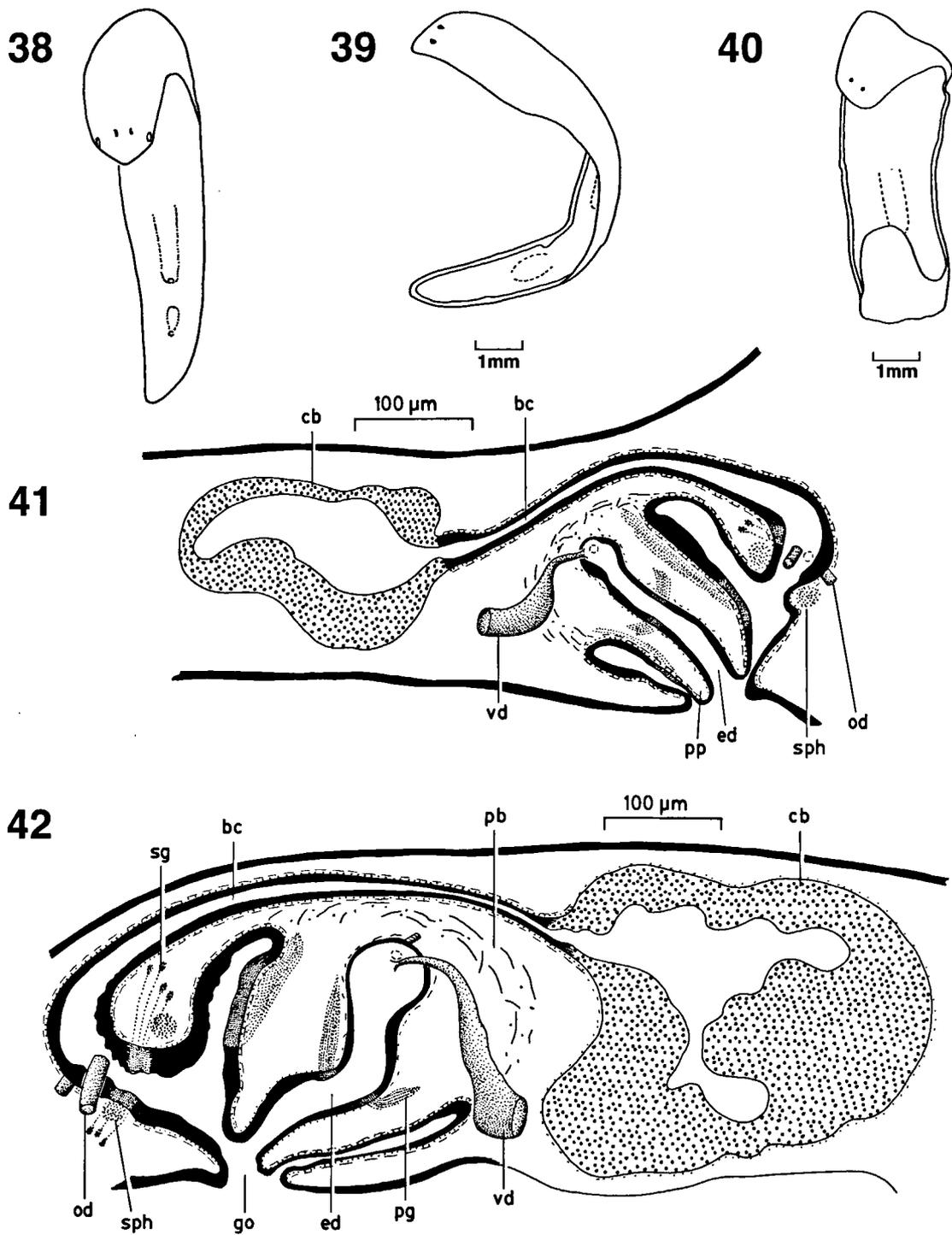
The testes are situated ventrally; the small follicles extend from some distance behind the ovaries to well posterior of the copulatory apparatus.

The vasa deferentia expand to form spermiducal vesicles, which narrow considerably before penetrating the penis bulb and opening separately into the spacious proximal section of the ejaculatory duct. The latter is a wide duct that opens at the tip of the conical penis papilla; at about halfway along its length, the ejaculatory duct receives the openings of penis glands (Figs. 41, 42). Another type of penial gland discharges its secretion through the covering epithelium of the penial papilla.

The penis bulb is well developed, consisting of interwoven muscle fibres.

The paired ovaries are located at some distance behind the brain. The oviducts open separately into the proximal, ventral section of the bursal canal, immediately dorsal to or almost at the point where the canal receives the openings of shell glands.

From its point of communication with the male atrium, a female or common atrium virtually being absent, the bursal canal smoothly curves



Figs. 38-42. *Girardia sphincter* n.sp. 38, G 217905/V.Pl. 942, free-hand sketch of preserved specimen. 39, G 217905/V.Pl. 942, free-hand sketch of preserved specimen. 40, G 217905/V.Pl. 942, free-hand sketch of preserved specimen. 41, QM G 217905, holotype, sagittal reconstruction of the copulatory apparatus. 42, V.Pl. 942.3, sagittal reconstruction of the copulatory apparatus.

anteriad towards a large copulatory bursa. The canal is lined with a nucleate epithelium and surrounded by a subepithelial layer of circular muscle and a layer of longitudinal muscle. At its point of communication with the male atrium the bursal canal is provided with a sphincter, consisting of a bundle of circular muscle.

COMPARATIVE DISCUSSION. - Previous records of species of *Girardia* in Australia concerned either presumably introduced animals (cf. Sluys et al., 1995) or indigenous species that were incorrectly assigned to this genus (e.g. *Romankenkius hoernesii* (Weiss, 1909) (cf. Sluys, 1997). Therefore, finding a notogaeon species of *Girardia*, well outside of the known natural range of the genus (North, Central, and South America), is very interesting. However, it should be born in mind that the genus *Girardia* is phylogenetically poorly defined, its presumed apomorphies being a high triangular head with pointed auricles, and a pigmented pharynx (cf. Sluys, 2001). But we do already know of exceptions, i.e. *Girardia*'s that do not show the high triangular head with the pointed auricles and/or lack the pigmented pharynx. Unfortunately, the head shape in living specimens of *G. sphincter* n.sp. is not known; in the sections of the material no pigment underneath the pharynx epithelium could be observed.

Nevertheless, the non-reversed bursal canal musculature suggests that the species phylogenetically belongs to the clade made up of the genera *Cura*, *Schmidtea*, and *Girardia* (cf. Sluys, 1997, 2001). However, the gross morphology of the copulatory apparatus precludes inclusion in either *Cura* or *Schmidtea*, leaving *Girardia* as the most likely genus. The present attribution of *G. sphincter* n.sp. to the genus *Girardia* is only tentative since another possibility is that the species represents a new evolutionary line within the clade *Cura*, *Schmidtea*, *Girardia* (cf. Sluys, 2001).

Species delimitation in *Girardia* is difficult (Sluys et al., 1997) and therefore it is fortunate that the present species distinguishes itself by an autapomorphy from its congeners, viz. the sphincter at the base of the bursal canal. Such a sphincter has not been reported for any other species of *Girardia* but is reminiscent of the situation described for *Spathula fontinalis* Nurse, 1950, and *S. alba* Allison, 1997. It is interesting to note that similar sphinc-

ters have been described for planarians from the family Planariidae, notably *Phagocata kawakatsui* Okugawa, 1956 and *Ph. myadai* Okugawa, 1939, the latter species probably being a junior synonym of *Ph. vivida* (Ijima & Kaburaki, 1916).

However, *G. sphincter* n.sp. cannot be considered identical with one of these species of *Spathula*. First, *G. sphincter* n.sp. does not belong to *Spathula* since it lacks the branched oviducts and the reversed bursal canal musculature of the genus *Spathula*. Second, *S. fontinalis* and *S. alba* both possess distinct sensory, ciliated pits, structures that are absent in *G. sphincter* n.sp.

In *G. sphincter* n.sp. there are penial glands that open through the covering epithelium of the penis papilla, a situation that is shared with its congeners *G. arimana*, *G. biapertura*, *G. festae*, *G. rincona*, and *G. schubarti*, and also with *Neppia paeta* and *Romankenkius patagonicus*.

GENUS *ROMANKENKIUS* BALL, 1974

Romankenkius kenki Ball, 1974

Figs. 43-46, 50

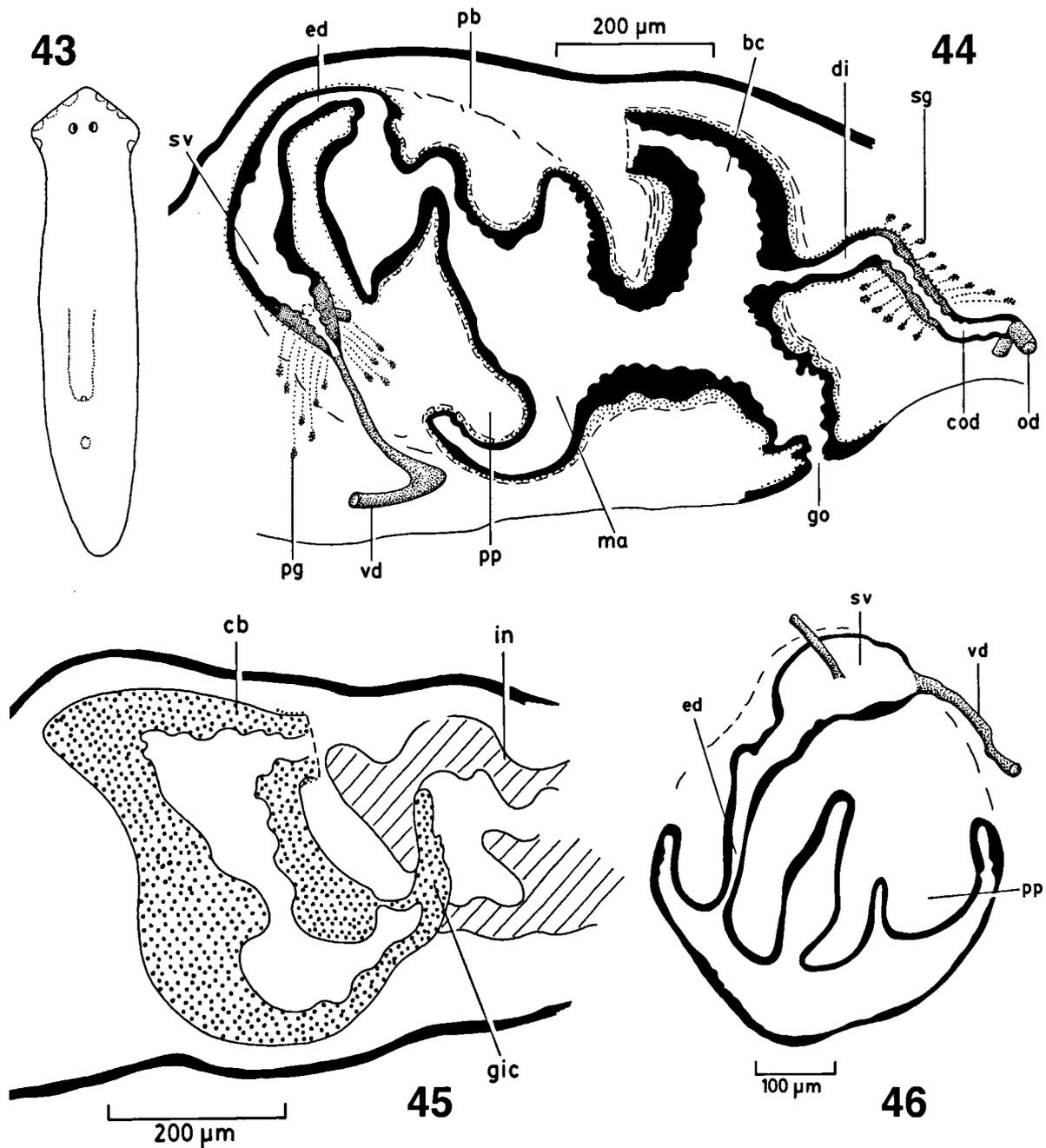
MATERIAL

AUSTRALIA. - ZMA: V.Pl. 943 (Kawakatsu et al., 1995b: Pl. VI, fig. A), preserved specimens, stream at top of pass, near dam of Lake Gordon, Tasmania, 18-VIII-1978; V.Pl. 943.1, *ibid.*, sagittal sections on 5 slides; V.Pl. 943.2, *ibid.*, transverse sections on 9 slides; V.Pl. 943.3, *ibid.*, sagittal sections on 6 slides; V.Pl. 943.4, *ibid.*, sagittal sections on 4 slides; V.Pl. 943.5, *ibid.*, sagittal sections on 7 slides; V.Pl. 943.6, *ibid.*, horizontal sections on 4 slides.

DESCRIPTION. - Living animals up to 20 x 3 mm; dorsal surface dark brown, ventrally pale. Head triangular, with blunt auricles and a number of sensory spots along the anterior margin; auricular sense organs in the form of sensory pits also present (Fig. 43).

Pharynx between one-sixth and one-fifth of the body length in preserved specimens; mouth opening located at the posterior end of the pharyngeal pocket.

The relatively small ovaries are situated at a short distance (approx. 400 μ m) behind the brain. The testes extend from a short distance behind the ovaries to about halfway the pharyngeal pocket; the follicles are rather small and located dorsally.



Figs. 43-46. *Romankenkius kenki*. 43, V.Pl. 943, free-hand sketch of living animal. 44, V.Pl. 943.3, sagittal reconstruction of the copulatory apparatus. 45, V.Pl. 943.3, sagittal reconstruction of communication between copulatory bursa and gut. 46, V.Pl. 943.6, horizontal reconstruction of the male copulatory apparatus.

The penis consists of a large and blunt, folded papilla and a large bulb consisting of interwoven muscle fibres. The papilla is covered with a nucleated epithelium.

The vasa deferentia are expanded to spermiducal vesicles that narrow before penetrating the penis bulb. Inside the bulb, the ducts open asym-

metrically into a seminal vesicle, one duct opening into the most proximal section of the vesicle, the other duct opening at a more distal and lateral section of the seminal vesicle (Figs. 44, 46). At its proximal section, the seminal vesicle receives a fine-grained orange secretion; it is surrounded by a coat of circular muscle. The seminal vesicle

tapers to form the ejaculatory duct that opens acentrally at the tip of the penial papilla. However, it would be equally valid to say that the seminal vesicle opens into a fold of the penis papilla, since histologically there seemed to be no difference between folds and presumed ejaculatory duct.

Via a constriction the male atrium communicates with the common atrium.

The bursal canal is lined with a tall, nucleate epithelium and is surrounded by a well-developed, subepithelial layer of circular muscle and a thick, but diffuse, layer of longitudinal muscle. The bursal canal communicates with a sac-shaped copulatory bursa that, in turn, is connected with a branch of the intestine (Fig. 45). At its proximal, ventral section, the posterior wall of the bursal canal forms a diverticulum that receives the opening of the nucleate common oviduct. Shell glands discharge their secretion into the diverticulum, that is lined with a nucleate epithelium and is surrounded by a layer of circular muscle.

DISCUSSION. - Since the material used in the type description in 1974 by Ball, the present material represents only the second series of specimens of this species that has become available. Therefore, it is useful to note some differences between our material and the type description.

In the present material the bursal canal is surrounded by layers of circular and longitudinal muscle, consecutively, contrasting with the type specimens, in which the musculature of the bursal canal was described as being reversed (which agrees with our observations on the type material). Furthermore, Ball (1974b) described the testes as extending to, or just beyond the root of the pharynx, whereas in our material the follicles extend farther backwards (up to halfway the pharyngeal pocket).

The new material confirms earlier conclusions (Sluys, 1997) based on re-examination of type material, that (1) the diverticulum arises from the very proximal section of the bursal canal, (2) the diverticulum is surrounded by a layer of circular muscle, and that (3) the oviducts unite to form a common oviduct that opens into the diverticulum.

On the basis of the differences between the

type material and the present specimens a case could be made for assigning the new material to a new species. For example, it seems unlikely that within one species both reversed and non-reversed bursal canal musculature do occur. However, we have refrained from describing a new species until more material becomes available for detailed comparative study.

Romankenkius sinuosus n.sp.

Figs. 47-49

MATERIAL

Holotype: QM: G 217906, Mt. Wellington, Hobart, Tasmania, AUSTRALIA, 17-VIII-1978, sagittal sections on 5 slides.

DIAGNOSIS. - *Romankenkius sinuosus* n.sp. differs from its congeners by having an asymmetrical penial papilla, an elongated and winding seminal vesicle, a sinuous bursal canal, and a mouth opening located at a more anterior position than usual.

ECOLOGY AND DISTRIBUTION. - Collected from a stream at the foot of Mt. Wellington; known only from the type locality.

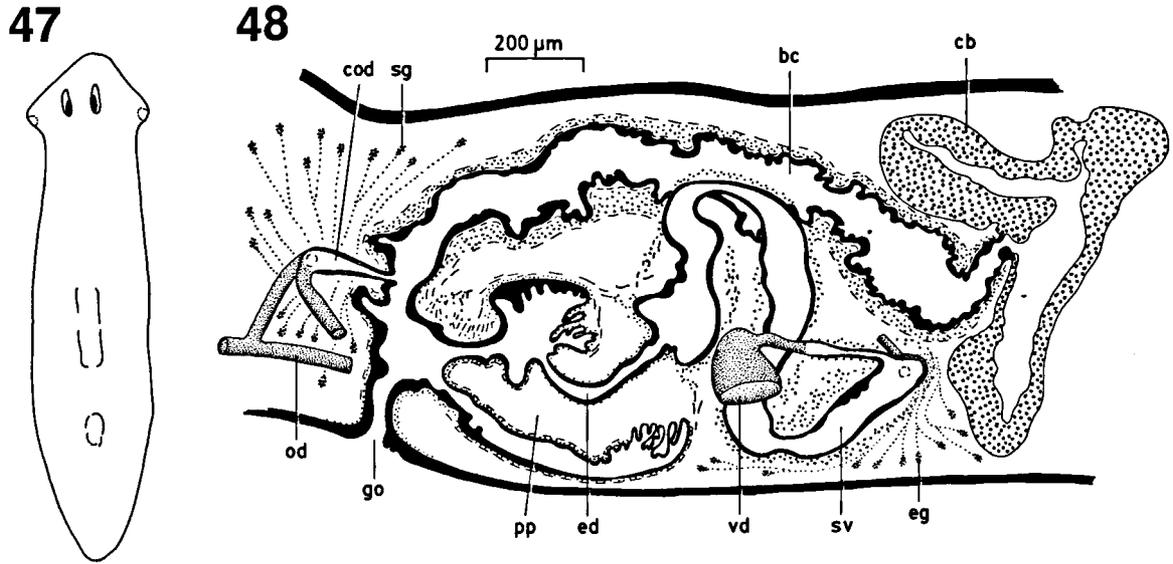
ETYMOLOGY. - The specific epithet is derived from the Latin adjective *sinuosus*, 'undulated', 'curved', and alludes to the sinuous appearance of the bursal canal.

DESCRIPTION. - Live specimens 20-25 mm long and 2-2.5 mm wide. Dorsal surface dark brown; ventrally pale. Head triangular, with short auricles; eyes set in pigment-free patches (Fig. 47). Several sensory fossae are present at the anterior body margin; ciliated pits are absent.

Pharynx situated in the middle of the body, measuring about one-seventh of the body length in the sectioned specimen; mouth opening slightly posterior to the middle of the pharyngeal pocket.

The paired ovaries are situated almost directly behind the brain. Vitellaria are well developed and provided with distinct resorptive vesicles, communicating with the oviducts.

Although the spermiducal vesicles are well developed and filled with sperm, no testicular fol-



Figs. 47-48. *Romankenkius sinuosus* n.sp. 47, G 217906, free-hand sketch of living animal. 48, G 217906, holotype, sagittal reconstruction of the copulatory apparatus.

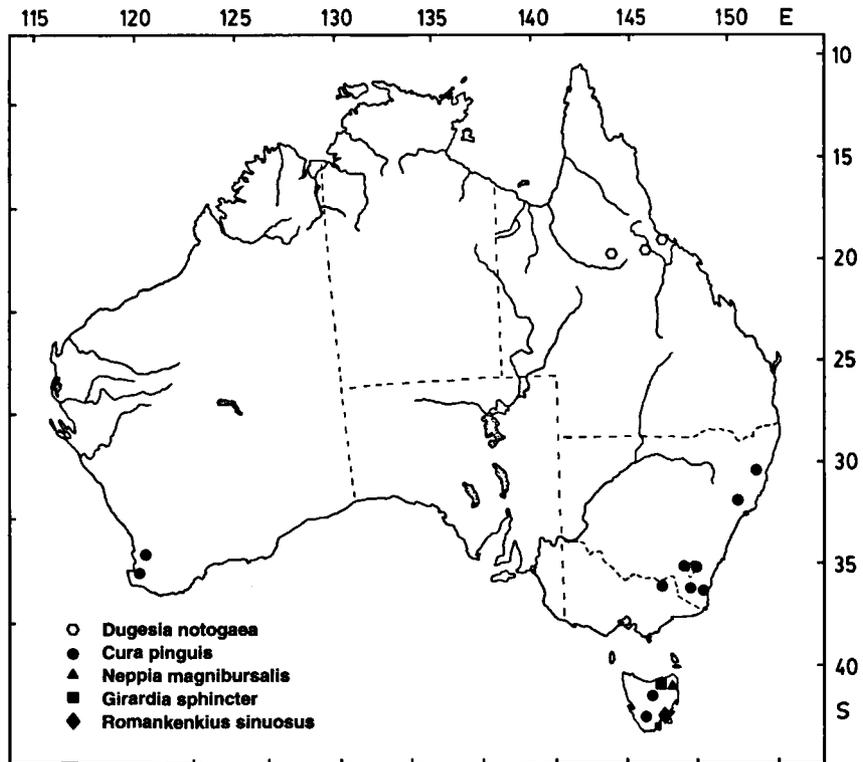


Fig. 49. Geographical distribution in Australia of *D. notogaea*, *C. pinguis*, *N. magnibursalis* n.sp., *G. sphincter* n.sp., and *R. sinuosus* n.sp.

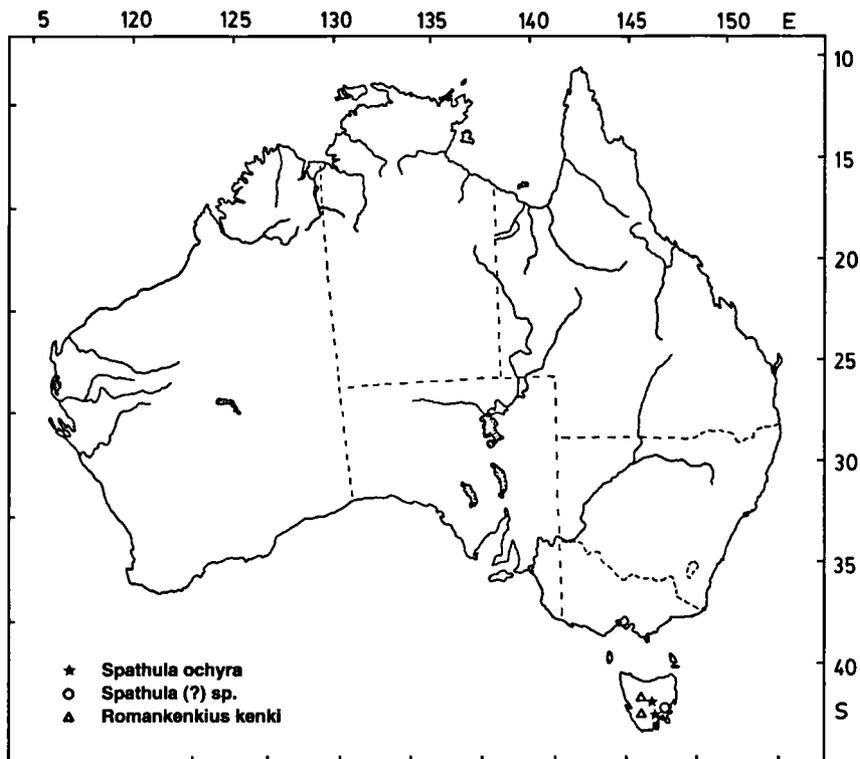


Fig. 50. Geographical distribution of *S. ochyra*, *S. (?) sp.*, and *R. kenki*.

lices could be discerned in the specimen examined.

At the level of the copulatory apparatus the spermiducal vesicles narrow considerably and make a pronounced anteriad bend before opening into the proximal section of a long and winding seminal vesicle (Fig. 48). Erythrophilic glands open into this section of the vesicle. At its distal section, this seminal vesicle communicates with the ejaculatory duct. Seminal vesicle and ejaculatory duct are lined with a nucleate epithelium. Seminal vesicle and ejaculatory duct are surrounded by a well developed layer and a weak layer of circular muscle, respectively.

The penial papilla is an irregular, asymmetrical structure with a small dorsal lip and a much larger ventral part; it is covered with a thin, nucleate epithelium.

At the level of the gonopore, the oviducts give off medially directed branches that unite to form a common oviduct, which opens into the ventral, proximal section of the bursal canal. The other branches of the oviducts extend well into the pos-

terior end of the body. The common oviduct and the sections of the separate oviducts just prior to opening into the common oviduct, receive the secretion of erythrophilic shell glands.

The bursal canal is a duct with a folded wall and a variable diameter; it is lined with a nucleate epithelium. The entire canal is surrounded by a thin, subepithelial layer of longitudinal muscle, a thick layer of circular muscle, and a thin outer layer of longitudinal muscle, the latter constituting the ectal reinforcement layer. The bursal canal communicates with a rather large, sac-shaped copulatory bursa.

COMPARATIVE DISCUSSION. - Although only two specimens were available, of which only one appeared to be mature, we feel, nevertheless, that description of a new species is warranted since the anatomy of the animal is rather distinct.

The common duct opening into the postero-ventral portion of the bursal canal places the species in the genus *Romankenkius* (cf. Sluys, 1997). The species *R. sinuosus* n.sp. is diagnosably distinct

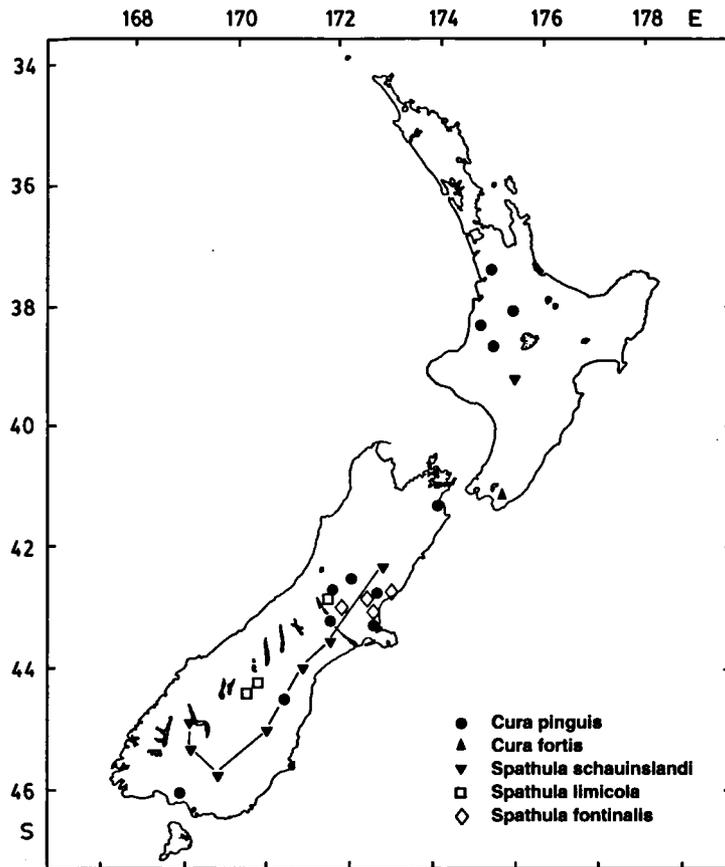


Fig. 51. Geographical distribution in New Zealand of *C. pinguis*, *C. fortis* n.sp., *S. schauinslandi*, *S. limicola*, and *S. fontinalis*. Interconnected localities of *S. schauinslandi* are meant to indicate that the species occurs in streams in Otago, Southland, and Canterbury.

from its known congeners in the possession of (1) an elongated and winding seminal vesicle, (2) a sinuous bursal canal, and (3) a mouth opening that is not located at the posterior end of the pharyngeal pocket but occupies a more anterior position. Furthermore, the irregular, asymmetrical penial papilla of *R. sinuosus* n.sp. is unlike that of any other species of *Romankenkius*. The penial papillae of *R. kenki* and *R. pedderensis* are also rather asymmetrical, but different from the papilla in *R. sinuosus* n.sp.

BIOGEOGRAPHY

The maps (Figs. 49-52) summarize the known distributional records of the species discussed in the present paper, i.e. the records concern not only information presented here but also those that have been published earlier. Additional data for

New Zealand were provided by F. R. Allison (in litt.).

The maps are confined to Australia and New Zealand but there is one species, *Cura pinguis*, for which there are also extralimital records since this species has been reported from New Caledonia (Beauchamp, 1968; Kawakatsu, 1969b) and Java (Beauchamp, 1929). However, the last-mentioned record is based solely on external features of asexual specimens and is therefore best considered as requiring more supporting evidence.

According to current taxonomy, the species *C. pinguis* is widely distributed across the Australian biogeographic region. Means of natural dispersal of this freshwater species must be ineffective to maintain a substantial gene flow among the allopatric populations. The existence of differences in details of external morphology among Australian and New Zealand specimens suggest

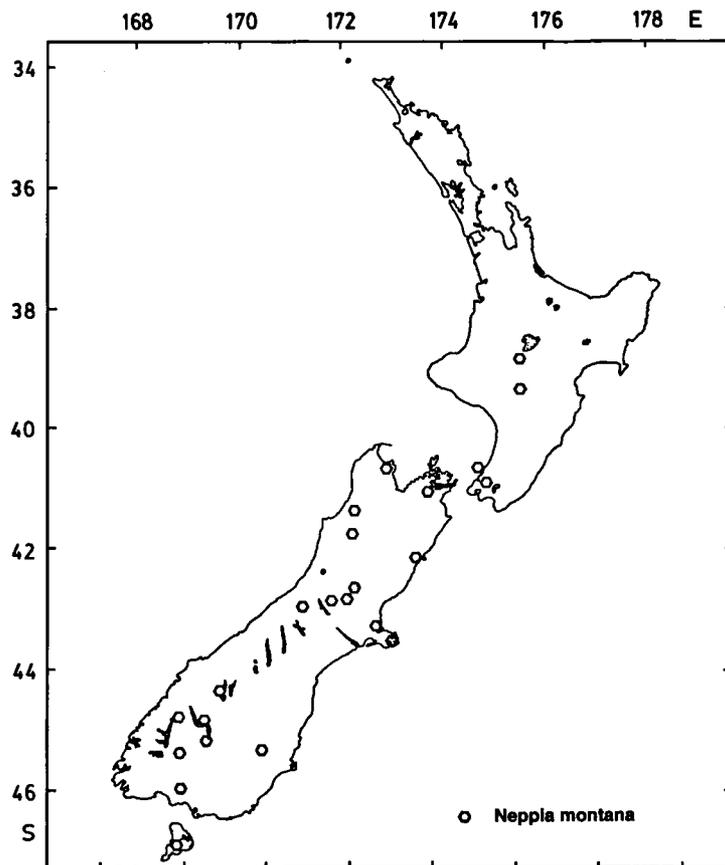


Fig. 52. Geographical distribution of *Neppia montana*.

that some differentiation has occurred, albeit that we consider it to be too faint and conflictual to form a basis for taxonomic distinction. Nevertheless, the chances are small that a single species will be present on these land masses as a result of historic events, excepting passive, human-induced introduction.

The finding of *G. sphincter* n.sp. in Tasmania has considerable biogeographic significance since the genus *Girardia* is mostly restricted to North, Central and South America. However, it should be noted that *G. sphincter* n.sp. is not known to possess the two main, albeit weak, defining apomorphies of its genus (high triangular head with pointed auricles, pigmented pharynx) and that its attribution to the genus *Girardia* is only tentative.

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Tokyo) and Dr Taiji Imamura (Mito, Japan) are thanked for putting at our disposal their collections of planarians from Tasmania and New Zealand. Their survey trip (1974-1975) to Australia and New Zealand was supported by a Grant-in-Aid for Scientific Research from the Ministry of Education of Japan. We are also indebted to the former members of Kawakatsu's 1978 collecting trip to Australia (including Tasmania) and New Zealand for their kind assistance in the field: Messrs. Hitoshi Murayama (Nagaoka, Japan), Genchû Ogawara (Kyôto, Japan), and the late Dr Minoru Hirano (Kyôto). We are grateful to Drs. B. Herbert (Department of Primary Industries, Walkamin), A. Colville (University of Technology, Sydney), and L. Winsor (James Cook University, Townsville) for making available to us their collections of Australian freshwater planarians. Dr F. R. Allison (Christchurch) kindly shared with us her knowl-

edge of New Zealand paludicolans and pointed out to RS possible sampling localities on South Island during his short fieldtrip in February 1998. The Organization for Economic Co-operation and Development - Directorate for Food, Agriculture and Fisheries, is thanked for inviting the authors to participate in the workshop on 'Terrestrial Flatworms' (Christchurch, 16-20 February 1998), which enabled us to study both the terrestrial and the freshwater planarian fauna of South Island. Prof. Dr Teiji Kifuna (Fukuoka, Japan) is thanked for his expert advice on Greek and Latin grammatical problems. We thank the following institutions for loans of material relevant to the present study: Royal Ontario Museum, Toronto; Natural History Museum, London; Museum für Naturkunde, Berlin; Western Australian Museum, Perth; Tasmanian Museum and Art Gallery, Hobart. Jan van Arkel is thanked for executing of the digitalized processing of the figures.

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