Winsor, Leigh (2003) ***Studies on the systematics and biogeography of terrestrial flatworms (Platyhelminthes: Tricladida: Terricola) of the Australian region.*** **PhD thesis, James Cook University.**

Chapter 5

Systematic Account and Phylogeny

...I don't care much about working with land planarians. There are just too many of them and the older descriptions based primarily on colour are very difficult to apply to pickled specimens.

Libbie Hyman *in litt* to Carl Pantin, early 1950
(letter in the Pantin Collection, Zoology Department, University of Cambridge, access courtesy of Dr Janet Moore)

It is curious that so few Australian zoologists have concerned themselves with the study of the Land-Planarians. This is the more to be regretted inasmuch as the opportunities for collecting these animals are rapidly passing away with the clearing of the bush. Moreover, much remains to be done in the investigation of these and other Cryptozoic animals. The Land-Planarians, in particular, still demand thorough comparative anatomical investigation with a view to revising the generic classification.

Dendy (1915)

5.1 INTRODUCTION TO THE FAMILIES, SUBFAMILIES & GENERA

The classification of the Terricola provided in the *Land Planarian Indices of the World* (Ogren, Kawakatsu and others), together with the provisional classification of the Australian Geoplanidae (Winsor 1991c), are taken as the starting points for the taxonomy and systematics of the Terricola of the Australian region in this thesis. A summary of the families, subfamilies, and genera of the Terricola worldwide is provided elsewhere (Table 1.4, Chapter 1)

Australia and New Zealand and their subantarctic islands share Terricola taxa at the levels of sub-family and genus, especially *Artioposthia sensu lato* and *Caenoplana.* They also share some species through the inadvertent introduction of flatworms such as *Parakontikia ventrolineata*. For these reasons, and for comparative anatomical purposes, New Zealand taxa are included in this study and accordingly *Arthurdendyus, Coleocephalus* and *Fyfea carnleyi* have been revised. The collective group genus *Australopacifica* Ogren & Kawakatsu, 1991 is not considered here as it is a repository for caenoplaninids about which insufficient internal details are known to permit reliable assignment of these species elsewhere. In order to provide a complete account, all genera present in the Australian region are included here (Table 5.1). Current diagnoses from the literature, emended only to harmonize the terminology used throughout this thesis, are provided for those genera that have not been considered in detail in this study. The following descriptions are accompanied by simple line drawings of a representative species, eye pattern, simple diagram of the copulatory organs, and a map showing the distribution of the genus (solid dots or lines) together sometimes with an indication of tracks connecting them (dashed lines). Detailed descriptions and anatomical illustrations of new and revised taxa are provided in Appendix 8.

In order to facilitate later phylogenetic analysis and comparisons between taxa, the format of descriptions adopted here accords with that also used by the team of Dr Ana Maria Leal-Zanchet, Instituto de Pesquisas de Planárias, UNISINOS, São Leopoldo, RS, Brazil. The descriptions consider external features, and internal anatomy of the head, pre-pharyngeal region, and reproductive organs. Abbreviations used in figures follow the glossary.

5.1.1 Nomenclature

The new taxa described in this thesis are *nomina nuda* as the provisions of Article 11 of the International Code of Zoological Nomenclature (ICZN 1999) are not met. It is intended to publish the descriptions of new taxa as soon as possible.

5.1.2 Etymology

The names of many genera in the Terricola have the suffix *–plana*, gender feminine, from the Latin *planus*, flat. The early workers, for example Diesing (1850), did not provide an explanation of the etymology of names in which this suffix was used. It possibly alluded to the common name, planarian, by which free-living triclad flatworms are generally known. It is in this context in which the suffix *-plana* is used for new taxa in this thesis.

5.1.3 Field Keys to the Terricola in Australia

Pictorial field keys, based upon external characters, are provided in Appendix 9, Keys A9.1– 9.5 for the families and genera of Terricola in Australia.

Table 5.1. List of Families and Genera of the Australian Region (*refer also to species description in Appendix 8)

FAMILY: Rhynchodemidae

Subfamily: Rhynchodeminae

Cotyloplana
Digonopyla
Dolichoplana
Platydemus
Rhynchodemus

FAMILY: Geoplanidae

Subfamily: Anzoplaninae sub.fam.nov.

Anzoplana gen.nov*
Fyfea gen.nov*

Subfamily: Caenoplaninae

Apogaioplana gen.nov.*
*Arthurdendyus**
Artioposthia s.l.
*Australoplana**
Barringtoplana gen.nov.*
Bassioplana gen.nov.*
Caenoplana
*Coleocephalus**
Danidoplana gen.nov.*
Fletchamia
Kontikia
Kynagoplana gen.nov.*
*Lenkunya**
Nelipoplana (Nelipoplana) gen. et sub.gen.nov.*
Nelipoplana (Peokrypta) gen. et sub.gen.nov.*
Newzealandia
Parakontikia
Reomkago
Sokoplana gen.nov.*
Tasmanoplana
Thosteelia gen.nov.*

FAMILY: Bipaliidae

Bipalium

SYSTEMATIC ACCOUNT

The present three families of the Terricola are insecurely based (Cannon 1986). None of the diagnoses for the families and subfamilies includes a comparable suite of characters at each level. Revision of these diagnoses is outside the scope of this thesis.

In my view inclusion of general characters concerning the presence and distribution of eyes are best included in the diagnoses for family, with detailed descriptors used in the diagnoses for genera. Eye distribution patterns provide useful diagnostic characters at the genus level. At the subfamily level the descriptors are broad and serve little diagnostic purpose; the family diagnoses adequately cover the subfamilies. The character for eye type, for which there is unfortunately a paucity of data, is likely to be important at the family or subfamily levels.

5.2. RHYNCHODEMIDAE

Diagnosis (Ogren & Kawakatsu1988a): Land planarians of elongate cylindroid form with two eyes near the simple, tapered anterior end; no tentacles or headplate; with well-defined creeping sole occupying part of the ventral surface. Anterior end may have a sucker organ on ventral surface (*Cotyloplana*).

5.2.1 Rhynchodeminae

Diagnosis (Ogren & Kawakatsu, 1988a): Rhynchodemidae with strong cortical musculature in which the subepithelial longitudinal muscle fibres are grouped into large, definite bundles; penis papilla absent or greatly reduced (*Platydemus* in part).

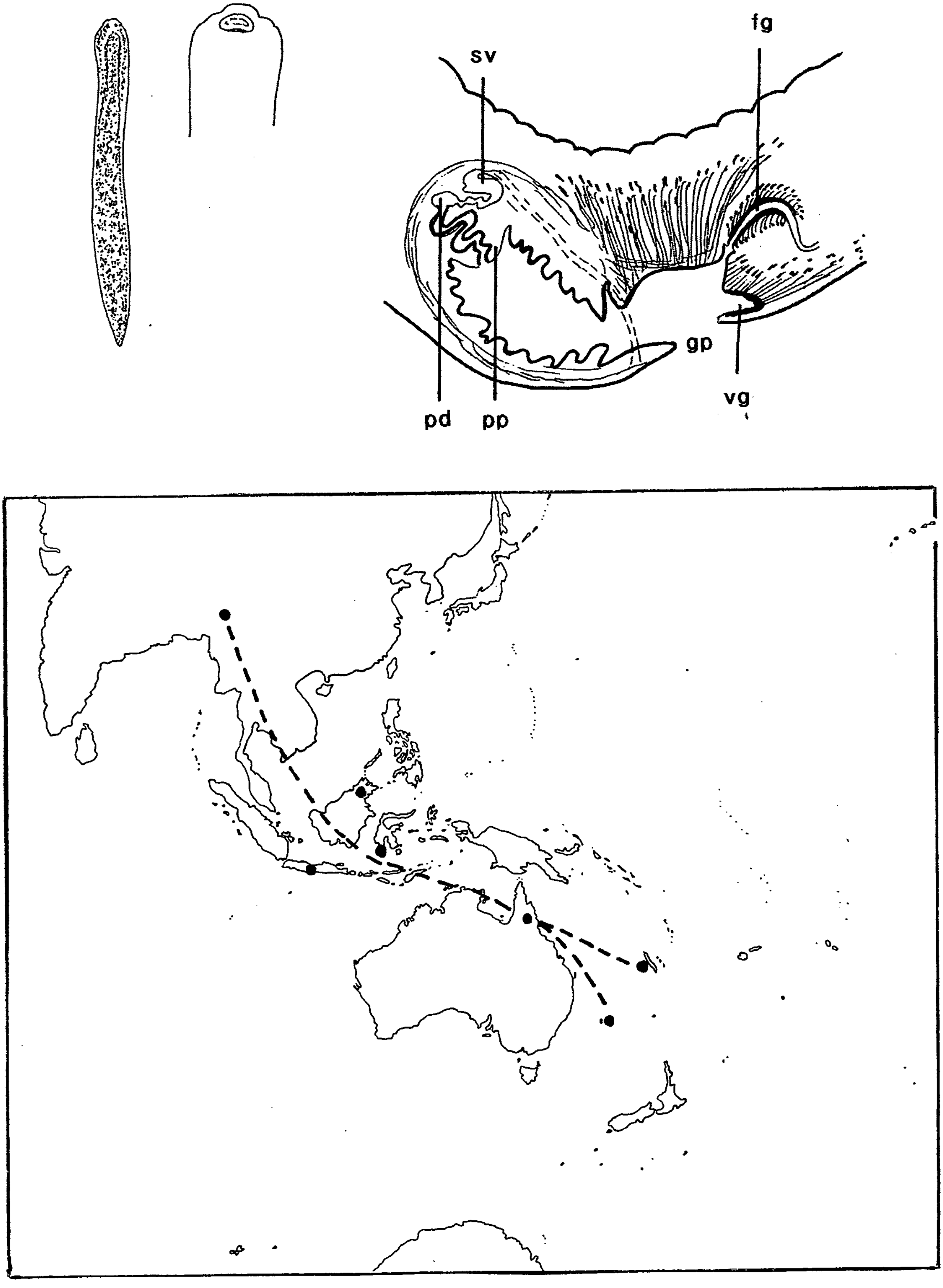
5.2.1.1 Genus *Cotyloplana* (Plate 5.1)

Cotyloplana Spencer, 1892

Cotyloplana Spencer, 1892; Graff, 1899; Ogren & Kawakatsu, 1988a; Winsor, 1997

Diagnosis (Ogren & Kawakatsu 1988a): Rhynchodeminae, flattened body, with wide creeping sole; one sucker, ventrally located, present at anterior of body in front of the creeping sole; copulatory organs similar to *Platydemus* with large,

Plate 5.1. The habitus, eye pattern, copulatory organs, and occurrence of *Cotyloplana* (Rhynchodemidae: Rhynchodeminae)



spacious male antrum having a small, obtuse, penis papilla at its base through which the ejaculatory duct empties; female organ simple, with narrow curved female genital duct, dorsally situated, reduced anteriorly where it opens into the dorsal part of the common antrum; viscid gland (posterior diverticulum) present.

Diagnosis (emended, this thesis): Rhynchodeminae with small robust body, flattened, mouth about mid body, with gonopore closer to posterior end than to mouth. Broad creeping sole 60-70% of body width. Anteroventral sucker present, single cup-type, in front of creeping sole. Eyes, large, paired, retina-type. Cutaneous musculature tripartite, with circular, decussate helical, and longitudinal muscles. Longitudinal muscles in strong bundles. CMI 11–14%. Insunk ventrally (in part the sucker retractor muscles). Parenchymal longitudinal musculature strong, concentrated in ventral plate. PMI 13-25%. Anteriorly very strong dorsal longitudinal parenchymal muscles. Supraintestinal transverse muscles, subneural transverse muscles, dorsoventral muscles strong. Pharynx bell-form. Pharyngeal musculature with inner epithelium, longitudinal, mixed circular-longitudinal, then longitudinal muscles; outer musculature with epithelium, longitudinal, circular, then longitudinal muscles; pharyngeal pouch diverticulum may be present. Testes ventral, lateral to nerve cords, uniserial, post-pharyngeal, extend from just anterior to mouth to just before copulatory organs; vasa deferentia ventral, rise, recurve anteriorly, separately enter penis bulb, unite in anterodorsal bulb, open mid anterior bulb into seminal, then prostatic vesicles, with muscular ejaculatory duct. Penis papilla poorly differentiated. Penis eversible-type. Penis bulb strongly muscular, with inner longitudinal, outer circular muscles. Male antrum large, capacious, with distal mucosal folds. Ovaries anterior; ovovitelline ducts unite, form common ovovitelline duct which enters female genital duct posteriorly. Female genital duct short, dorsally situated, in-line with small simple weakly muscularized female antrum with columnar sclerotin strand cell-epithelium. Common antrum with strongly muscular roof, with sclerotin globule-cell secretory epithelium. Vitellaria present between intestinal diverticula, not extensive. Adenodactyls absent. Viscid gland may be present.
Type species: *Cotyloplana whiteleggei* Spencer, 1892.

Etymology: *Cotyloplana* from the Greek *kotyle,* cup, cavity, and Latin *plana,* flat, alluding to the anterior adhesive sucker – the planarian with an adhesive sucker. Gender feminine.

Distribution: Sulawesi, Kalimantan, and Java, Indonesia;? New Caledonia (*Rhynchodemus lindsaysianus* Schröder, 1924). *Cotyloplana punctata* and *C. whiteleggei* are described from Lord Howe Island, and there are two undescribed species from far north Queensland in the Torresian zoogeographic sub-region (Winsor, 1997).

Systematic discussion: The emended diagnosis is based upon a re-examination of four of the seven described species, which together with new species, were excluded from detailed consideration in this thesis.

5.2.1.2 Genus *Digonopyla* (Plate 5.2)

Digonopyla Fischer, 1926

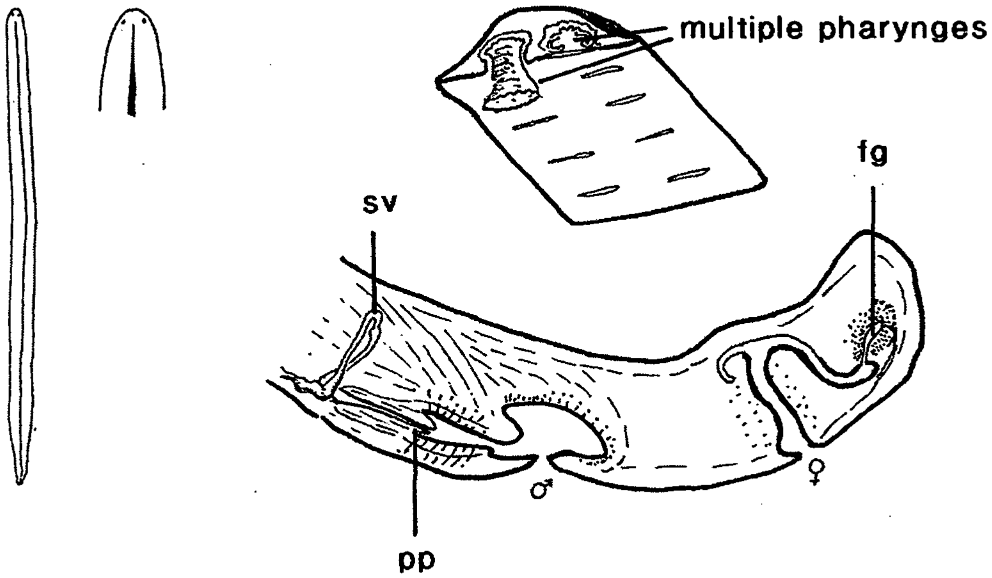
Digonopyla Fischer, 1926; Meixner 1928; Hyman 1938; Ogren & Kawakatsu 1988a; Winsor 1997.

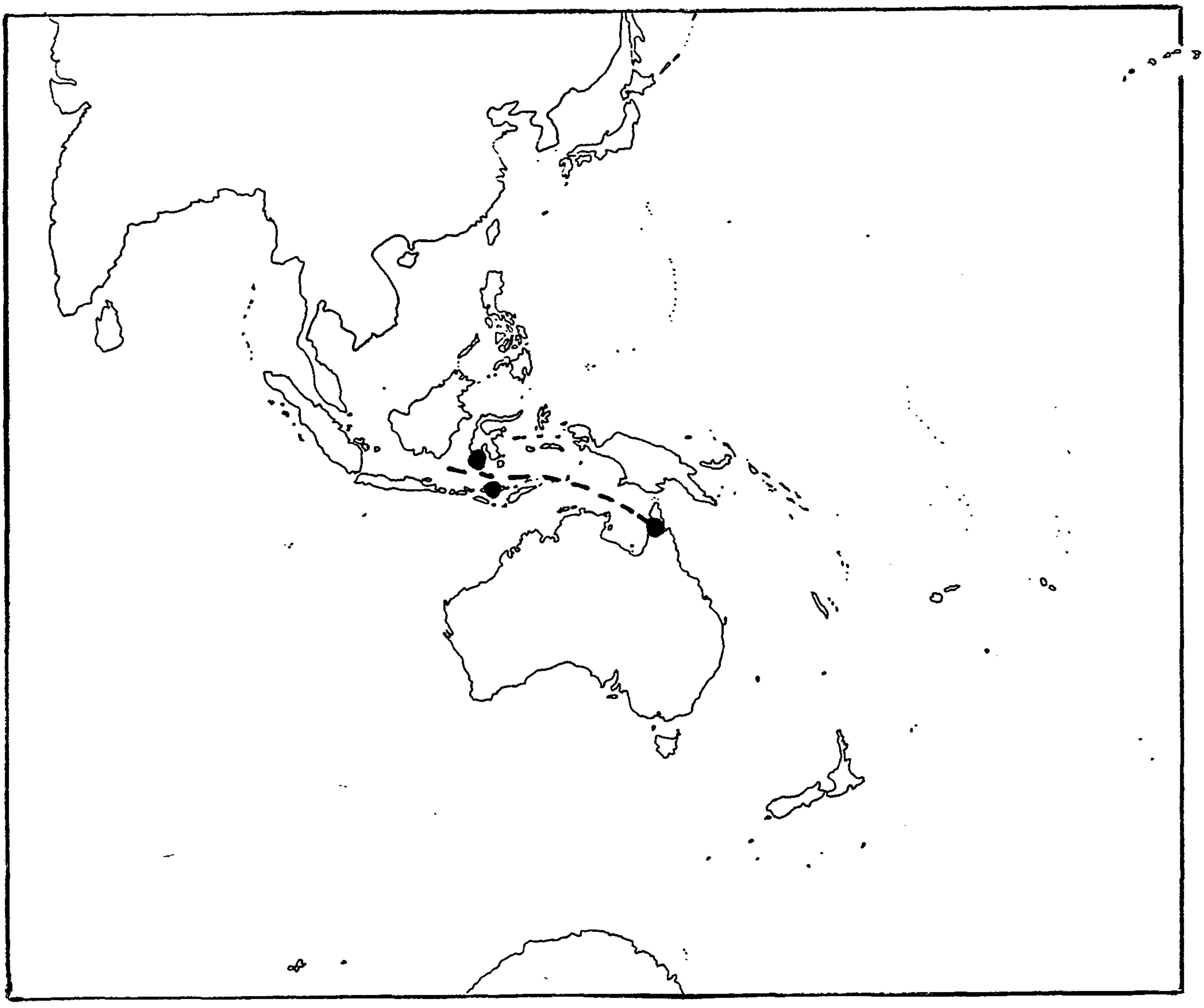
Original diagnoses (Fischer 1926): Familie: Landplanarien mit zwei Geschlechtsöffnungen, einer männlichen und einer weiblichen, zahlreichen Mundporen und Pharyngen. (Family diagnosis: Land planarians with two gonopores, one male and one female, with numerous mouths and pharynges).

Gattungsdiagnosis: Körper langgestreckt von ovalem Querschnitt mit schwach ausgebildeter Kriechsole, zwei Retinaaugen und Sinnesgrübchen am Vorende (Genus diagnosis: Body elongate, oval in cross section, with weakly developed creeping sole, two retinal eyes and sensory pits on the anterior end).

Diagnosis (Ogren & Kawakatsu 1988a): Rhynchodeminae with numerous pharynges and mouths; no suckers; usual condition of copulatory apparatus has a wall of tissue separating the gonopores, resulting in independent male and female openings; copulatory organs as in *Platydemus* with minute penis papilla and dorsal entrance of female genital canal; viscid gland (posterior diverticulum) absent in type species. Type species: *Digonopyla harmeri* (Graff, 1899).

Plate 5.2. The habitus, eye pattern, copulatory organs, and occurrence of *Digonopyla*
(Rhynchodemidae: Rhynchodeminae)





Etymology: *Digonopyla* from Greek *di*, two, and *gonos*, that which produces seed, and *pyl* = entrance. With two gonopores. Gender: masculine.

Distribution: South Sulawesi (Barabatuwa and Makassar Islands), Indonesia. There is one undescribed species from Iron Range, far north Queensland (Winsor 1997).

Systematic discussion: Fischer's new Family, the Digonopylidae, was not recognized; the taxon was regarded by Meixner (1928) as a highly differentiated descendent of his Type C rhynchodemids, and subsumed within the Rhynchodemidae (Ogren & Kawakatsu 1988a). A four-eyed species originally described from Flores, Indonesia, as *Myriopharynx tetracelis* Haslauer-Gamisch, 1981, has provisionally been included by Ogren & Kawakatsu (1988a) in *Digonopyla*. Terricola with multiple pharynges will be considered elsewhere outside this thesis.

5.2.1.3 Genus ***Dolichoplana*** (Plate 5.3)

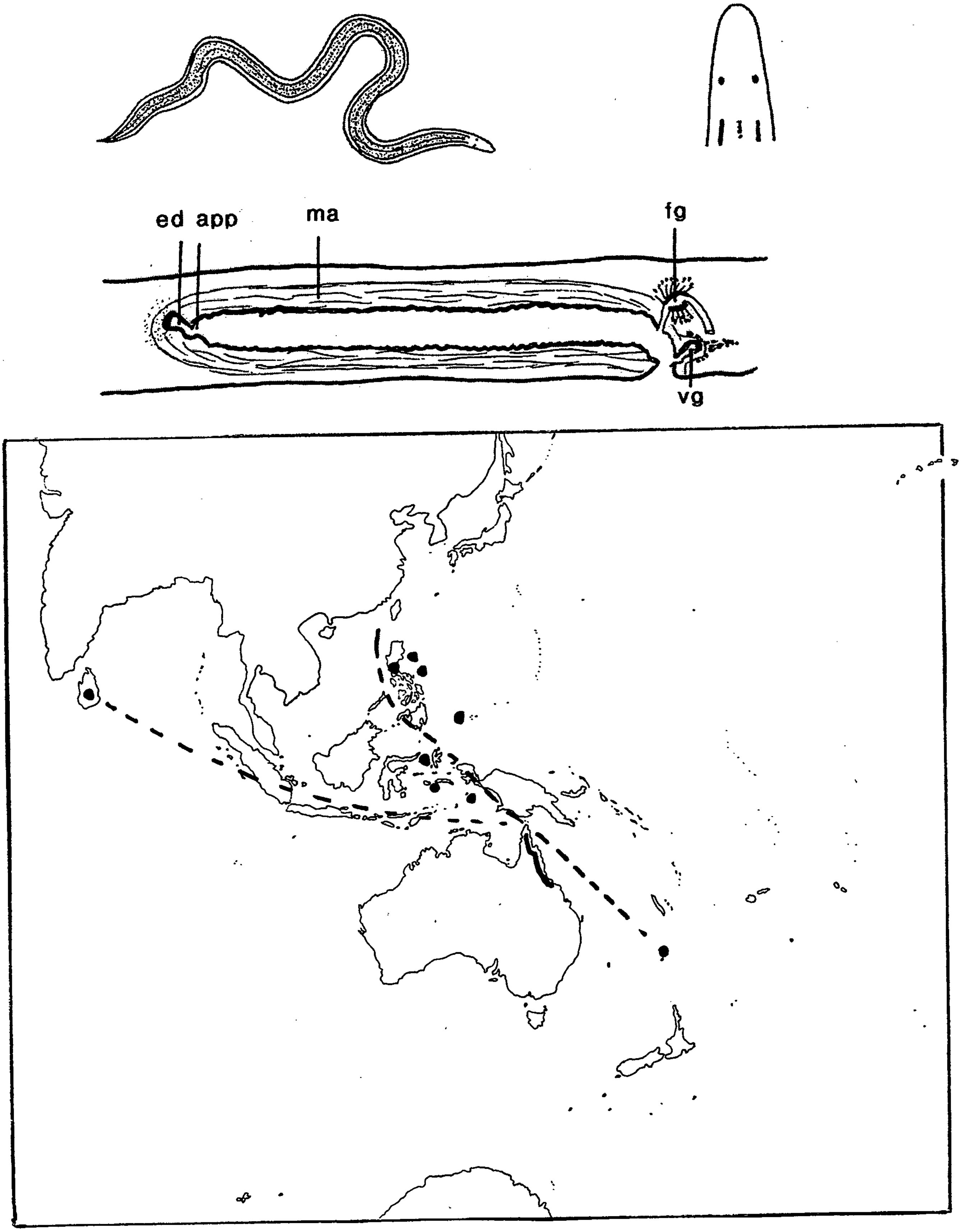
Dolichoplana Moseley, 1877

Dolichoplana Moseley, 1877; Graff 1899; Corrêa 1947; Ogren & Kawakatsu 1988a; Winsor 1997

Diagnosis (Ogren & Kawakatsu 1988a): Rhynchodeminae of very elongate flattened form, cross section broad and flattened with median dorsoventral indentation; creeping sole of moderate width; the rounded, slightly concave anterior end is bordered by glandular and sensory tracts; two large retinal eyes located a short distance behind the anterior tip; parenchymal longitudinal muscle fibres occur only ventral to the intestine; male copulatory organs without penis papilla, antrum very large, elongate with many folds, opens into large elongated common antrum; the short female genital duct opens dorsally into the common antrum; a prominent viscid gland (diverticulum) opens from the posterior wall of common antrum near the gonopore.

Etymology: *Dolichoplana* from the Greek *dolichos,* long, and Latin *plana*, flat. The Long planarian. Gender feminine.

Plate 5.3. The habitus, eye pattern, copulatory organs, and occurrence of *Dolichoplana* (Rhynchodemidae: Rhynchodeminae)



Distribution: Madagascar; Brazil; Peru; Togo; Java, Kai Islands, Moluccas Islands, Indonesia; Sri Lanka; Palau Islands. Some 9 – 10 undescribed species of *Dolichoplana* occur in north Queensland, Australia, in the Torresian zoogeographic subregion (Winsor 1997).

Systematic discussion: As noted by Ogren & Kawakatsu (1988a, page 44), the genus is functional and members are characterized by distinctive copulatory apparatus. Some species of *Dolichoplana* are adventives, having been transported to European countries and elsewhere. At least two of the nine *Dolichoplana* species in Australia are introductions. It is uncertain whether all dolichoplanids have retina-type eyes.

5.2.1.4 Genus *Platydemus* (Plate 5.4)

Platydemus Graff, 1896

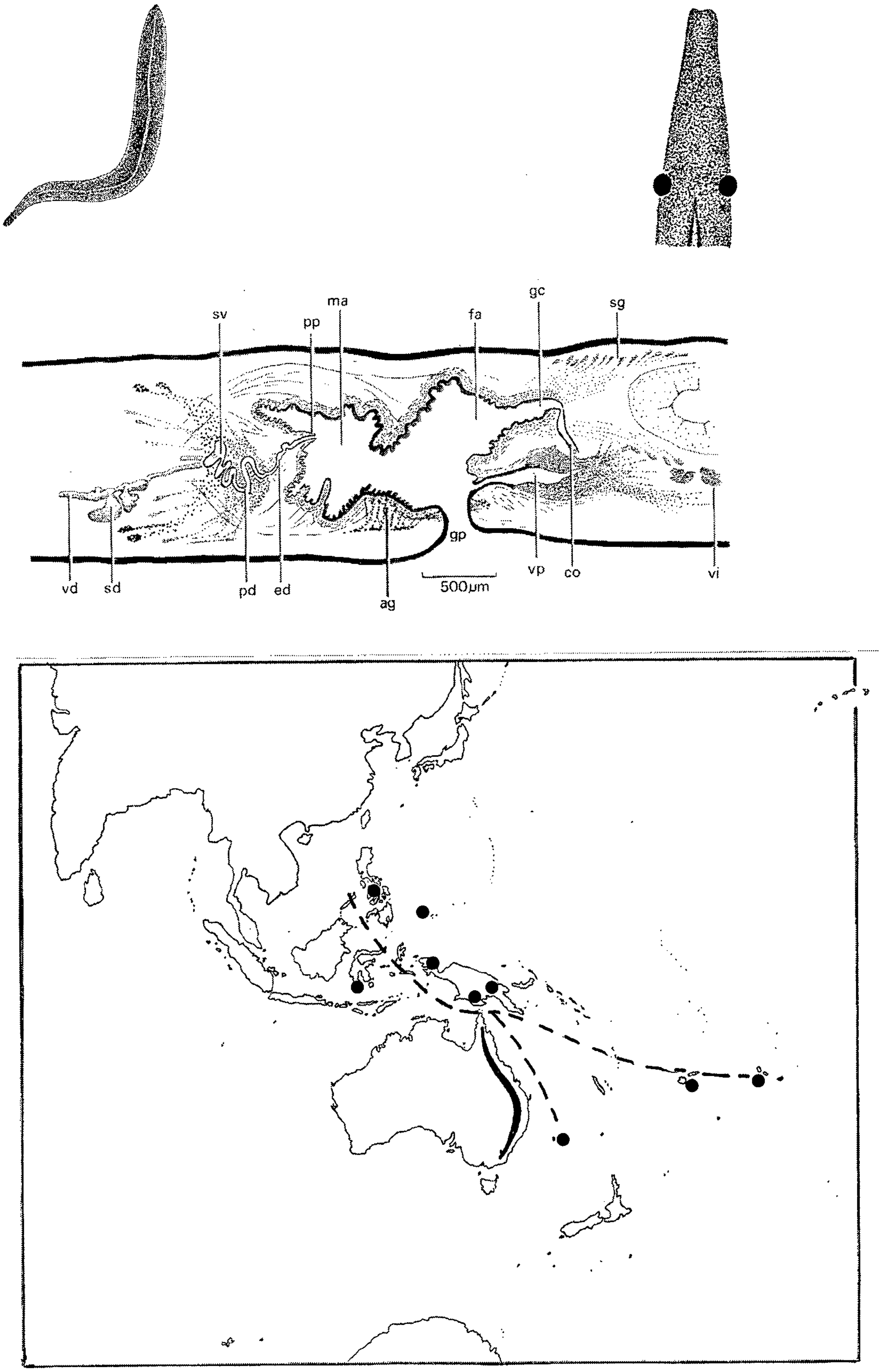
Platydemus Graff, 1896, 1899; Heinzel 1929; Hyman 1943; Beauchamp 1962.

Diagnosis (Ogren & Kawakatsu 1988a): Rhynchodeminae of massive, plano-convex body, both ends tapered, with broad creeping sole; with very large eyes; anterior secretory and sensory tracts; cross section broad, flattened, nerve cords plate-like; male copulatory organ consists of a large chamber with folded epithelium and in most cases a short penis papilla; female genital duct opens from the dorsal aspect into the large common antrum; ventrally a viscid gland (diverticulum) opens from the posterior wall of the common antrum. Type species: *Rhynchodemus grandis* Spencer, 1892.

Etymology: *Platydemus* from the Greek *platys,* broad, wide, flat, and *demas*, living body, frame. Alludes to the broad dorso-ventrally flattened body of these worms. Broad, flat bodied. Gender masculine.

Distribution: *Platydemus* is found in the Philippines; Comoro Islands, Sulawesi, Indonesia; Irian Jaya – Papua- New Guinea; Palau Islands; Caroline Islands; Fiji; Samoa; Tonga; Ethiopia. In Australia there are 5 species described from the mainland: *P. assimilis* Wood, 1926, *P. moseleyi* (Fletcher & Hamilton, 1888), *P. niger* (Fletcher & Hamilton, 1888), *P. trilineatus* (Fletcher & Hamilton, 1888), *P.*

Plate 5.4. The habitus, eye pattern, copulatory organs, and occurrence of *Platydemus* (Rhynchodemidae: Rhynchodeminae)



victoriae (Dendy, 1891) and six species from Lord Howe Island: *P. dubius* (Spencer, 1892), *P. fasciatus* (Spencer, 1892), *P. grandis* (Spencer, 1892), *P. laterolineatus* (Spencer, 1892), *P. mediolineatus* (Spencer, 1892). A further six undescribed species have been reported from north Queensland (Winsor 1997).

Systematic discussion: The genus is in need of revision, and presently accommodates taxa with, and apparently without, a penis papilla. Ogren & Kawakatsu (1988a) provided a current appreciation of the taxonomic problems within the genus. The type species *Platydemus grandis* has retina-type eyes. It is not known whether all described platydemids share this eye-type.

5.2.1.5 Genus *Rhynchodemus* (Plate 5.5)

Rhynchodemus Leidy, 1851

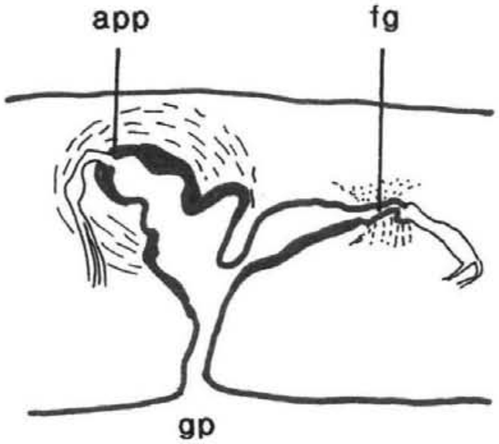
Rhynchodemus Leidy, 1851; Graff 1896b, 1899; Heinzel 1929; Hyman 1943; Pantin 1953

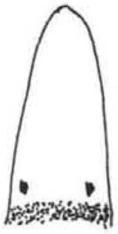
Diagnosis (Ogren & Kawakatsu 1988a): Rhynchodeminae with elongate body, attenuated at both ends, with oval to round cross section, without peculiarities of parenchymal musculature or nervous system; having a creeping sole, occupying most of ventral surface; anterior end has sensory tracts and a pair of medium to large eyes situated close to anterior tip; mature male copulatory apparatus lacks a penis papilla, but develops large folds in the antrum only; and the female copulatory apparatus is simple, consisting of antrum and female genital canal without bursa or genito-intestinal connection.

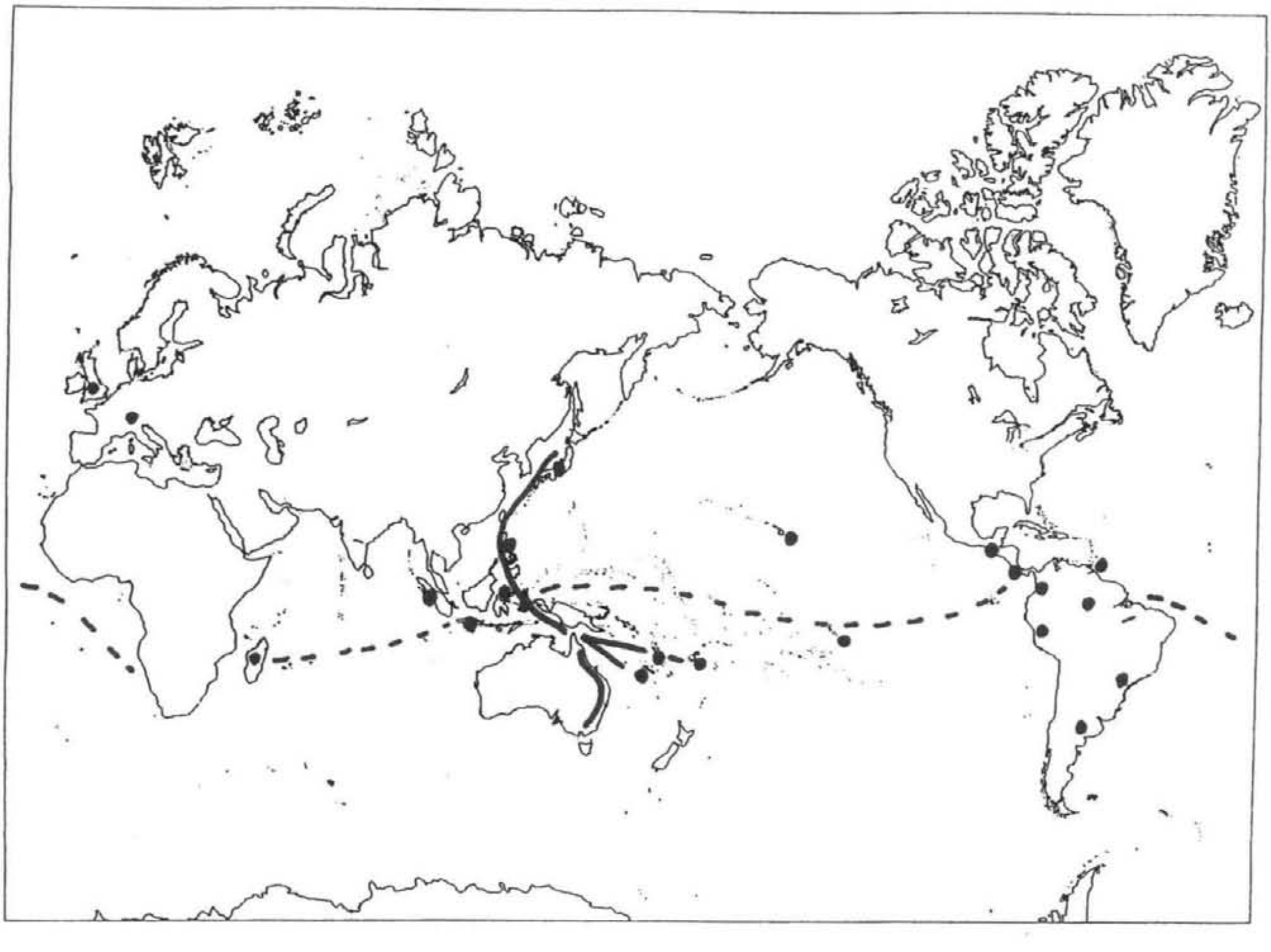
Etymology: *Rhynchodemus* from the Greek *rhynchos*, nose, snout, and *demas*, living body. Alludes to the snout-like extension of the anterior end in the living worm. Snout bodied. Gender masculine.

Distribution: *Rhynchodemus* is an old widespread genus with some 50 described species. The greatest species diversity is found in Indonesia, then states in South America, Central America, Philippines, with scattered records in Indo-Pacific countries. Four species are described from the Bassian zoogeographic sub-region in Australia, and there are a further eight undescribed species from the Torresian zoogeographic sub-region in north Queensland (Winsor 1997). The molluscivorous

Plate 5.5. The habitus, eye pattern, copulatory organs, and occurrence of *Rhynchodemus* (Rhynchodemidae: Rhynchodeminae)







species *Platydemus manokwari*, used as a biological control agent for the Giant African Snail, has been deliberately spread to various islands in the Pacific region (Winsor 1999).

Systematic discussion: Ogren & Kawakatsu (1988a) comment that *Rhynchodemus* is an old and valid genus. Problems arise when only the juvenile condition of the copulatory apparatus is known (Ogren 1986). It is uncertain whether all rhynchodemids share the retina-type eye.

5.3 GEOPLANIDAE

Diagnosis (Ogren & Kawakatsu 1990): Terricola with numerous small eyes concentrated around the anterior, and along the sides, sometimes located dorsally, or without eyes; without auricular or tentacular organs or semilunar headplate.

5.3.1 **Anzoplaninae** sub.fam.nov

Anzoplaninae sub.fam.nov

Diagnosis: Geoplanidae with tripartite cutaneous musculature, with cutaneous longitudinal muscles in well-defined bundles, with parenchymal longitudinal muscles present in a ventral plate or ring zone. With or without a ciliated creeping sole. Inner pharyngeal wall includes a layer with mixed musculature. With dorsoventral testes and ventral efferent ducts.

Systematic discussion: Within the Geoplanidae, the Anzoplaninae with dorsoventral testes and ventral efferent ducts are intermediate between the Caenoplaninae with ventral testes and ventral efferent ducts, and the Geoplaninae with dorsal testes and dorsal efferent ducts. The presence of cutaneous longitudinal muscles in well-defined bundles in the Anzoplaninae distinguishes them from the Pelmatoplaninae in which the cutaneous longitudinal muscles are weak and not in bundles.

Both dorsoventral and dorsal testes are considered to be apomorphic states of the character *dorsoventral extent of the testes*. Consistent with this is the recognition of this distinctive group with dorsoventral testes as a subfamily, with elements in Australia, New Zealand, and their subantarctic islands. The subfamily includes a number of known but as yet undescribed taxa.

5.3.1.1 Genus *Anzoplana* gen. nov (Plate 5.6)

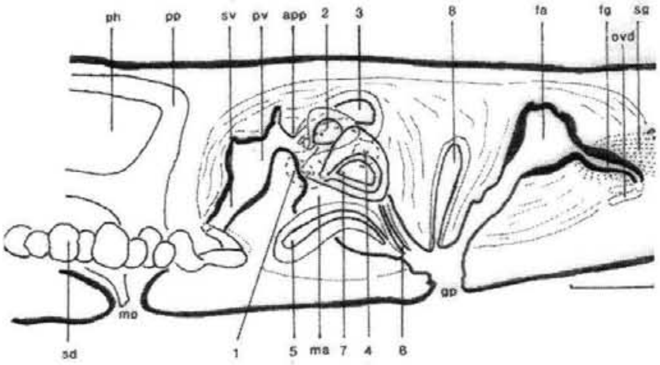
Anzoplana gen. nov

Diagnosis: Anzoplaninae with small, robust body, lanceolate, broader posteriorly than anteriorly, sub cylindrical in cross section. Mouth situated just behind mid body, gonopore closer to mouth than to posterior end. Eyes in single row around anterior tip, clustered for some distance laterally in uneven rows for anterior body quarter, then sparsely in single staggered submarginal row to posterior. Creeping sole 60% of body width. Cutaneous musculature tripartite, with circular, helical muscles, with cutaneous longitudinal muscles in well-defined bundles; ventral cutaneous musculature slightly thicker than that dorsally, CMI 9.4-10.6%. Parenchymal longitudinal muscles not clearly aggregated into bundles, present in well developed subneural plate PMI 9%, with isolated fibres in weak ring zone. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, longitudinal, then mixed longitudinal and circular muscles; outer musculature with epithelium, longitudinal, circular, then mixed longitudinal and circular muscles sparse ectally, slightly stronger entally. Testes dorso-ventral, extend almost entire length of body. Efferent ducts ventral. Penis eversible, without papilla. Ovaries in anterior body third. With lateral bursae. With resorptive vesicles surrounding ovovitelline ducts. Ovovitelline ducts separately enter female genital duct; genital duct enters female antrum posterioventrally. Adenodactyls and adenomuralia present. Type species of genus: *Anzoplana trilineata* sp. nov

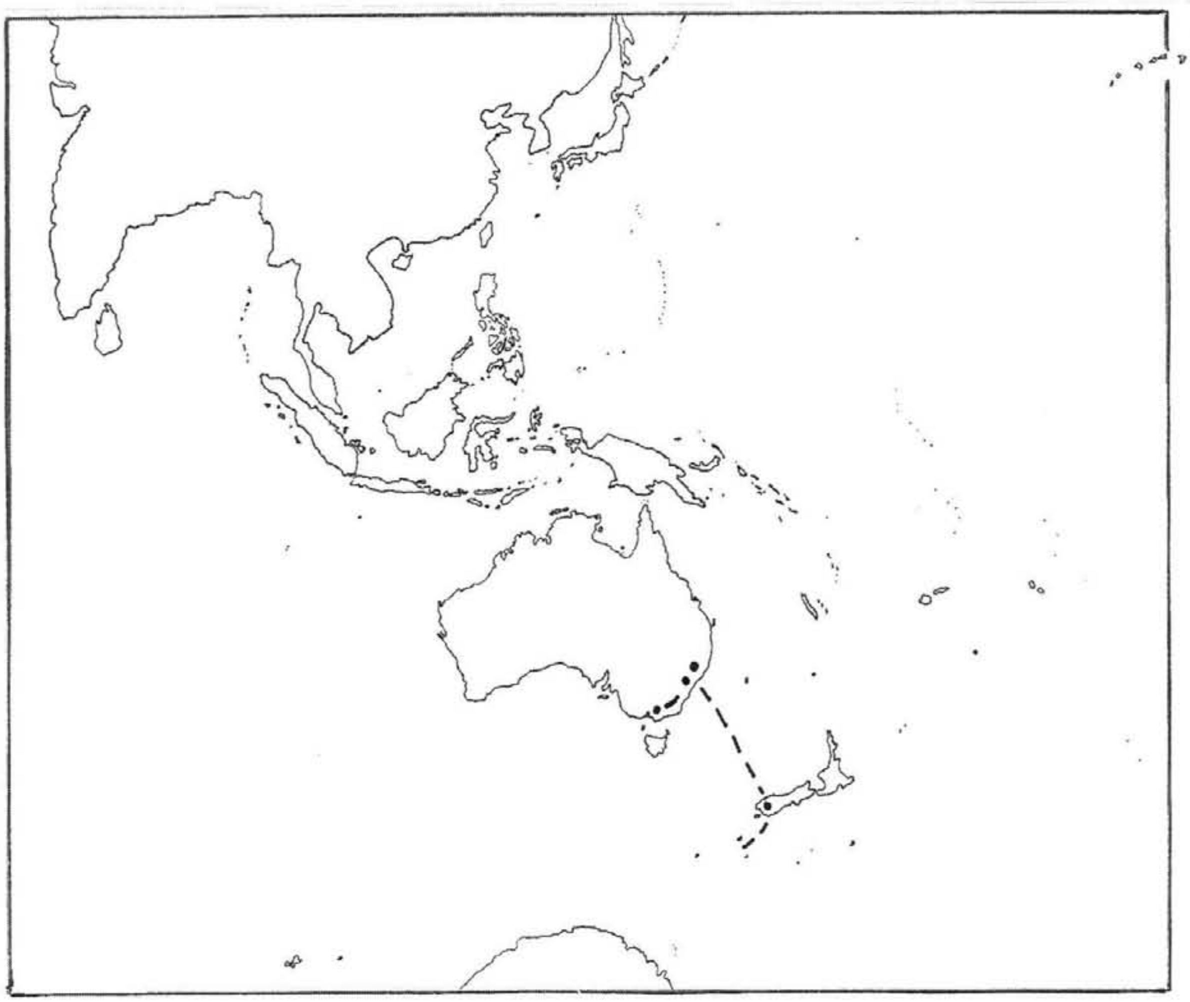
Etymology: *Anzoplana,* The Australian and New Zealand planarian is contrived from the traditional abbreviation ANZ for Australia and New Zealand and Latin *plana*, flat. Gender feminine.

Distribution: Bombala, NSW; Nimmitabel, NSW; Girraween, SEQld; Dalmorton, NSW; Research, Vic (introduction); Berridale, NSW; Cootralantra Creek

Plate 5.6. The habitus, eye pattern, copulatory organs, and occurrence of *Anzoplana* (Geoplanidae, Anzoplaninae).



(numbers refer to adenodactyls)



north of Berridale, NSW; Nr Tatangara dam, between Adaminaby and Kiandra, NSW; Mt Wilson, NSW (? introduction); Armidale, NSW.

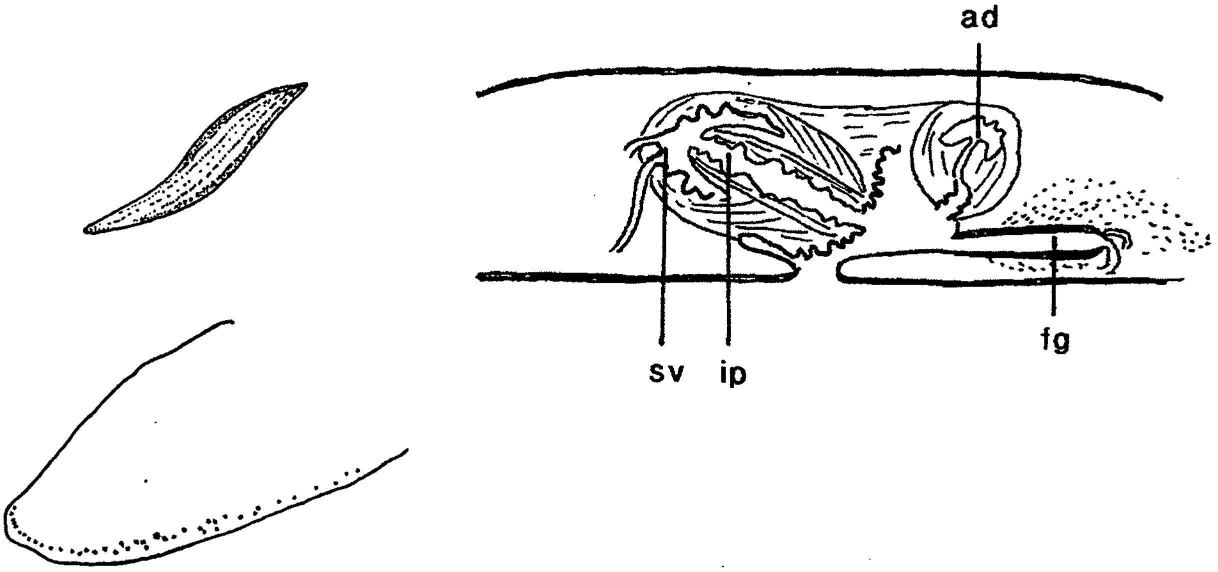
Systematic discussion: *Anzoplana* is chiefly differentiated from other adenodactylate anzoplaninids by the presence of the ovary between anterior tip and the pharyngeal root, eversible penis, resorptive bursae either side of the pharynx, resorptive vesicles surrounding the ovovitelline duct, and both adenomuralia and adenodactyls present. The presence of adenomuralia and an apapillate penis characterize the caenoplaninid *Newzealandia* (ventral testes).

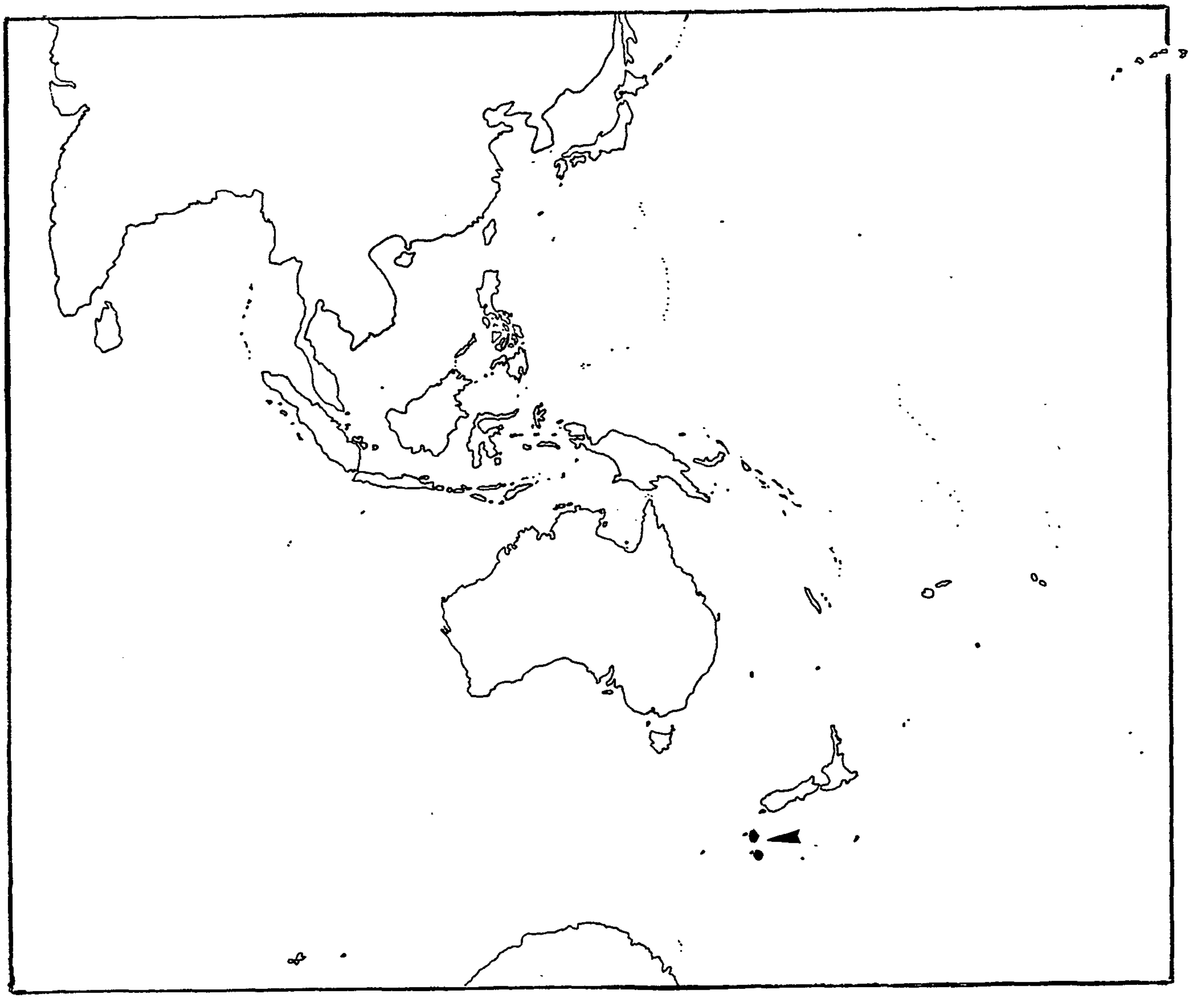
5.3.1.2 Genus *Fyfea* gen. nov. (Plate 5.7)

Fyfea gen. nov.
Artioposthia (part), Fyfe, 1956; Ogren & Kawakatsu 1991

Diagnosis: Anzoplaninae with small, elongate body, with mouth just behind mid body, gonopore closer to mouth than posterior end. Creeping sole more than 70% of body width. Anterior adhesive cup, sucker absent. Sensory papillae absent. Eyes? lens-type, in single row around anterior tip, in two to three rows antero-laterally, then in staggered single row to posterior. Cutaneous musculature tripartite; circular, helical muscles, with longitudinal muscles in bundles, stronger ventrally than dorsally. CMI 22%. Parenchymal musculature with mixed longitudinal-transverse muscles in small bundles in sub-neural plate, PMI 10.8%; with strong bundles of supraneural longitudinal muscles, small bundles and single fibres of longitudinal fibres sparsely scattered in ring zone; strong supra- and infra-intestinal transverse muscles regularly spaced along body; with strong dorsoventral muscles. Pharynx cylindrical with oesophagus. Pharyngeal musculature with inner epithelium, strong longitudinal, then mixed circular-longitudinal muscles, then longitudinal muscle layer; outer pharyngeal musculature with thick layer of longitudinal muscles, then evenly spaced circular muscles, then grades into region of mixed circular and longitudinal muscles. Testes dorsoventral, sperm ducts ventral. Testes loculate, extend from midway between anterior tip and root of pharynx, to posterior end. Vasa deferentia with spermiducal vesicles; sperm ducts separately enter dorsal wall of seminal vesicle; with prostatic vesicle; penis inverted-type. Ovaries with parovarian resorptive tissue, situated between mouth and copulatory organs. Ovovitelline ducts separately enter distal end

Plate 5.7. The habitus, eye pattern, copulatory organs, and occurrence of *Fyfea* (Geoplanidae: Anzoplaninae)





female genital canal; female genital canal enters antrum horizontally via ventro-posterior atrial wall. Vitellaria sparse. Adenodactyl present. Viscid gland absent. Type species: *Fyfea carnleyi* (Fyfe, 1956) comb.nov.

Etymology: *Fyfea* honours Marion Fyfe, 1894-1986, for her pioneering taxonomic anatomical work on the Terricola of New Zealand. Gender feminine.

Distribution: St. Col Peak, elevation 300 metres above sea level, Campbell Island, 169°10'E 52°53', and Ocean Island, Auckland Islands, islands of New Zealand.

Systematic discussion: *Fyfea* presently has only one species *F. carnleyi*. Within the Anzoplaninae *Fyfea* is close to *Kontikia ashleyi* (Fyfe, 1953) (referred to in the thesis as "Parafyfea") with which it shares the ovary situated between mouth and copulatory organs, and an inverted penis. It is distinguished from "Parafyfea" chiefly by the presence of an adenodactyl, (absent in "Parafyfea"). In *Anzoplana* the ovaries are situated near the anterior end, and the penis is eversible.

The inverted penis *bauplan* is found in Plagiostomidae, Monocelididae, some Acoela, and the maricolan taxa *Nexilis epichitonius* and *Centriovarioplana tenuis* (Sluys, 1989). It is uncommon in the Terricola, found only in *Fyfea carnleyi*, "Parafyfea", in *Australopacifica aucklandica* sensu Fyfe 1953, (? = *Kontikia marrineri* (Dendy, 1901)), all three of which have pharyngeal -post oral ovaries, and eyes which appear to be lens-type – peripheral pigment with inner cyanophil generally featureless mass (though this may be a fixation artefact). Of particular interest are the parallels between the foregoing terricolan taxa from Auckland Islands, and the maricolan *Centriovarioplana tenuis* recorded from the subantarctic South Georgia Islands, at about the same latitude. *Centriovarioplana tenuis* has an inverted penis, ovaries located immediately anterior to the mouth on either side of the gut, and a musculoglandular organ external to the copulatory organs.

5.3.2 Caenoplaninae

Diagnosis (Ogren & Kawakatsu 1990): “Testes ventrally situated; subepithelial longitudinal musculature in large bundles; mouth in third quarter; eyes often in single row around anterior, continuing posteriorly but not usually extending dorsally.

Section 1: Broad ciliated creeping sole occupying entire width of ventral surface; parenchymal longitudinal musculature is strong, well-developed forming a prominent ring zone.

Section 2: Ciliated creeping sole occupies less than 50% or less (25% to 30%) of width of ventral surface; parenchymal longitudinal muscle weak or absent, not forming a ring zone.

Section 3: Creeping sole occupies most of ventral surface; often with weak subepithelial longitudinal musculature; parenchymal longitudinal muscle system weak or absent; ovaries near central body region; copulatory apparatus with adenodactyls; or with recessed accessory glands.

Section 4: A collective group for species lacking sufficient internal details but found in the Australian-Pacific regions.”

Diagnosis (emended, this thesis): Geoplanidae with bipartite or tripartite cutaneous musculature, with cutaneous longitudinal muscles in well defined bundles, with or without parenchymal longitudinal muscles present in a ventral plate or ring zone. With or without a ciliated creeping sole. Inner pharyngeal wall with or without a layer with mixed musculature. With ventral testes and ventral efferent ducts.

Systematic discussion: The original Diagnosis of the Caenoplaninae (Ogren & Kawakatsu 1990) was restrictive in that a large proportion of caenoplaninids have a mouth close to the mid body. Consequently Caenoplaninae is redefined. In the light of new taxa described in this thesis, the four sections designated by Ogren & Kawakatsu (1990) within the Caenoplaninae are considered here to be obsolete.

5.3.2.1 Genus *Apogaioplana* gen.nov. (Plate 5.8)

Apogaioplana gen.nov.

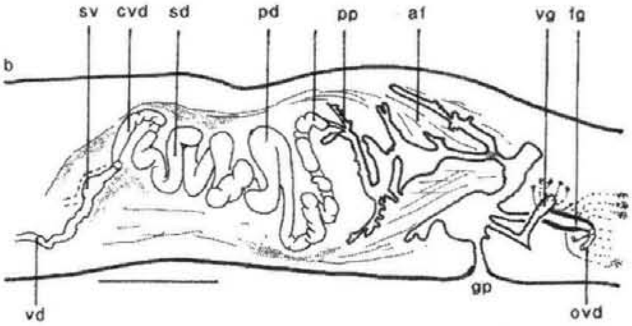
Diagnosis: Caenoplaninae with elongate body, convex dorsally, flat ventrally. Mouth and gonopore situated in third body quarter. Creeping sole absent. Eyes absent. Anterior adhesive pad or cup absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular, helical muscles, with strong longitudinal muscles in well defined bundles, with dorsal musculature weaker than ventrally, CMI 9%. Parenchymal musculature weak; longitudinal muscles absent. Pharynx cylindrical, folded. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; outer musculature with epithelium, longitudinal, circular, then mixed circular-longitudinal muscles. Testes ventral, lateral to nerve cords, extend to root of pharynx. Vasa deferentia enter penis bulb separately, unite, enter seminal – prostatic duct. Ejaculatory duct tubular, sinuous, strongly muscular, with intra-penial papilla. Ovovitelline ducts approach proximal end of female genital canal anteroventrally, unite, enter female genital canal via common opening. Female canal horizontal, enters ventro-posterior wall of common antrum; underlies female antrum. Musculature of copulatory organs with mixed circular-longitudinal muscles. Viscid gland present, to left of female canal, bent dorsad. Adenodactyls absent. Type species: *Apogaioplana paluma* gen et sp nov.

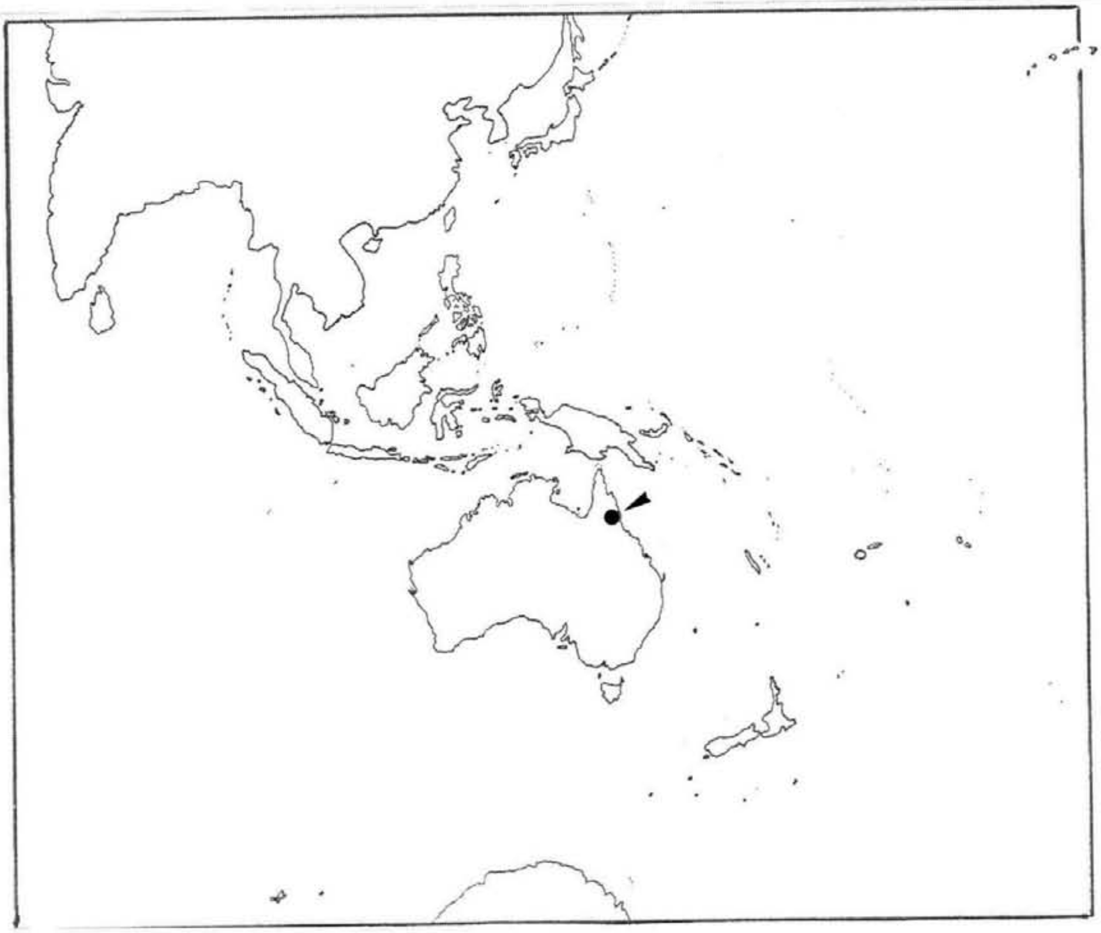
Etymology: The genus name is contrived from the Greek *apogaios*, from the earth, and Latin *plana* flat, and alludes to the presence of the species in the soil formed from well-rotted logs and litter. Gender feminine.

Distribution: Near Paluma dam, Paluma, north Queensland, in soil in decayed log, rainforest. Torresian zoogeographic sub-region.

Systematic discussion: *Apogaioplana paluma* (caenoplaninid – ventral testes) closely parallels *Geobia subterranea* (geoplaninid – dorsal testes) of Brazil in the following characters: absence of pigmentation, eyes, and creeping sole, presence of strong cutaneous musculature CMI 9% (*Geobia* CMI 8.5%), and absence of parenchymal longitudinal muscles. There are also similarities in the general conformation of the copulatory organs, and both have a penis papilla and muscular

Plate 5.8. The habitus, copulatory organs and occurrence of *Apogaioplana*
(Geoplanidae: Caenoplaninae)





tubular ejaculatory duct. They differ in that in *A. paluma* the vasa deferentia unite within the penis bulb (unite before entering the bulb in *Geobia*), ovovitelline ducts approach the genital canal antero-ventrally (anterodorsally in *Geobia*), and viscid gland present (absent in *Geobia*).

Of the externally similar taxa within *Australoplana sensu lato* (Appendix 8), Apogaioplana stands closest to *Sokoplana*. It is differentiated from this genus by the absence of eyes (present in *Sokoplana*), normal tripartite cutaneous musculature, stronger ventrally than dorsally (in *Sokoplana* dorsal and ventral cutaneous musculature are equal, plus presence of the unusual helical layer*)*, cylindrical pharynx (bell-form in *Sokoplana*), tubular ejaculatory duct (cavernous in *Sokoplana*), atrial muscular flaps (absent in *Sokoplana*) genital canal below female antrum (antrum and genital canal in-line in *Sokoplana),* mixed musculature in copulatory organs (differentiated in *Sokoplana*). Both have vasa deferentia uniting within the penis bulb, presence of a penis papilla, ovovitelline ducts entering the proximal canal through a common orifice, and viscid gland with dorsad bend, arising from inside the gonopore to the left of the genital canal. With respect to relative position and shape, the diverticulate viscid gland has some superficial similarity to the cutaneo-intestinal canal of the geoplaninid *Enterosyringia*; however they are neither homologous nor analogous structures.

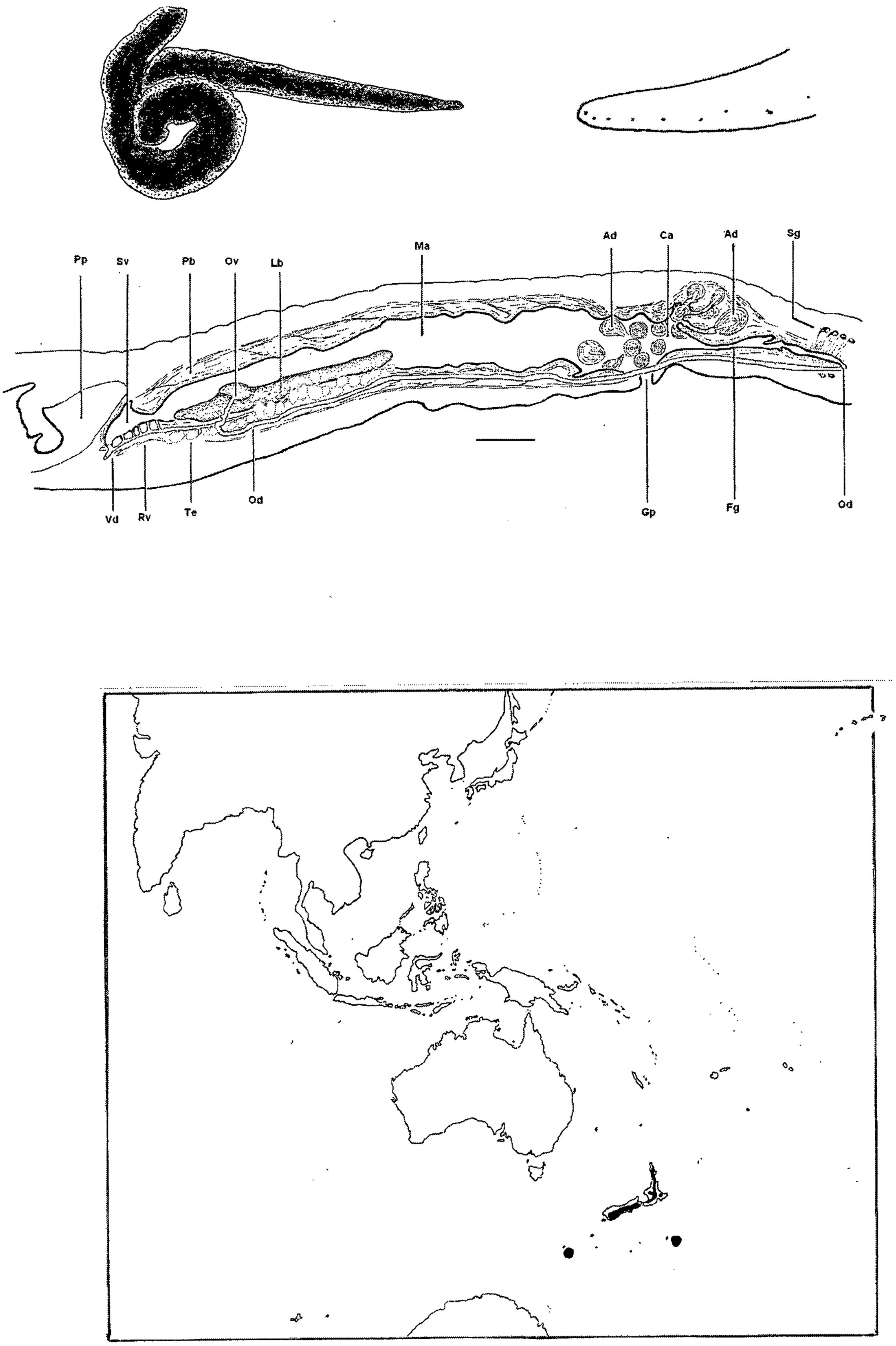
5.3.2.2 Genus *Arthurdendyus* (Plate 5.9)

Arthurdendyus Jones & Gerard, 1999 emend
Arthurdendyus Jones & Gerard, 1999
Arthurdendius Jones & Gerard, Ogren *et al* (1999)
Artioposthia (in part) Dendy, 1895a; Johns 1998

Original diagnosis (Jones & Gerard 1999): "Geoplanid land planarians with ovaries lateral to the male copulatory apparatus, adenodactyli (or accessory glands) present. Pharynx bell-shaped, not cylindrical".

Emended diagnosis (this thesis): Caenoplaninae with broad, elongate and strap-like body. With mouth situated posterior to mid body; gonopore closer to mouth than to posterior end. Ciliated creeping sole absent. Anterior adhesive pad or sucker

Plate 5.9. The habitus, eye pattern, copulatory organs, and occurrence of *Arthurdendyus* (Geoplanidae: Caenoplaninae)



absent. Sensory papillae absent. Eyes pigment cup-type, small, in single row around anterior end, and anterolaterally to posterior. Cutaneous musculature tripartite, strong, with circular, helical muscles, with longitudinal muscles in bundles. CMI 14%. Parenchymal musculature with strong dorsal and ventral transverse muscles, weak to absent longitudinal muscles. Pharynx plicate (collar-form). Pharyngeal musculature with inner epithelium, longitudinal, circular, thin inner layer longitudinal muscles; outer pharyngeal musculature with epithelium, circular, longitudinal, then strong circular muscles. Oesophagus present. Testes, sperm ducts ventral. Testes extend almost entire length of body. Vasa deferentia retiform distally, enter seminal vesicle horizontally, both sides, at multiple points. Penis eversible, without papilla. Male antrum capacious, elongate. Ovaries lateral to male copulatory apparatus, with lateral resorptive bursae situated behind mouth, before gonopore. Ovovitelline ducts unite, form short common duct which enters posterior female genital canal horizontally. Female genital canal horizontal, in-line with female antrum. Female antrum elongate, enters common antrum via ventroposterior atrial wall. Adenodactyls present. Type species: *Geoplana triangulata* Dendy, 1895.

Etymology: “Named in honour of Arthur Dendy for his great contributions to the study of land flatworms. Gender. Male”. (Jones & Gerard 1999). The alteration of the genus name to *Arthurdendius* by Ogren *et al* (1999) and subsequently used in their species lists (Kawakatsu *et al* 2000; 2001), is an “unjustified emendation” under Art. 33.2.3 (ICZN, 1999). The original spelling must be maintained under Art. 32.2 (ICZN, 1999).

Distribution: The genus occurs in New Zealand. Circumstantial evidence suggests that it may be adventive in the Australian and New Zealand subantarctic islands (this thesis). Two species are adventive in the United Kingdom, one of which is *A. triangulatus*, an agricultural pest and serious threat to earthworms in the U.K. and the Faeroe Islands.

Systematic discussion: Within the adenodacylate taxa of the Caenoplaninae, the combination of the presence of ovaries posterior to the pharynx at the level of the copulatory organs, the pharynx type, and absence of a creeping sole, chiefly differentiates *Arthurdendyus* from other similar taxa. *Artioposthia ventropunctata*, *A.*

lucasi, and *A. mariae* have no creeping sole, but have cylindrical pharynges, and pre-pharyngeal ovaries. The subantarctic species *Fyfea carnleyi* has post-pharyngeal ovaries anterior to the copulatory organs, has a creeping sole, cylindrical pharynx, and dorsoventral testes (see the Anzoplaninae).

Arthurdendyus species have a plicate collar-form pharynx, characterized by the location of the dorsal insertion of the pharynx in the posterior third of the pharyngeal pouch. In bell-form pharynges the dorsal insertion of the pharynx is located in the mid pouch region (Graff 1899).

5.3.3 Genus *Artioposthia* (complex) (Plate 5.10)

Artioposthia Graff, 1896b
Artioposthia Graff, 1896b; 1899; Fyfe 1937

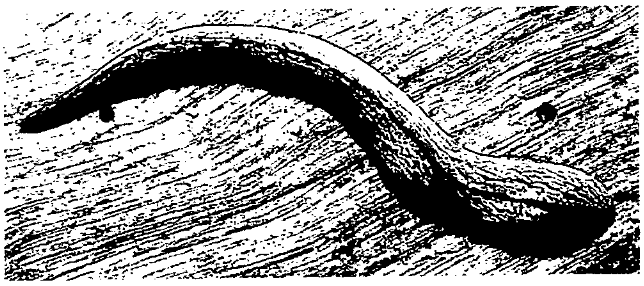
Original Diagnosis (translated from Graff 1896b): Geoplanidae without creeping ridge and glandular margin, of elongate form, with body apertures on the ventral surface, and with at least a pair of accessory auxiliary organs in addition to the male copulatory organ. Emended: testes and sperm ducts ventral.

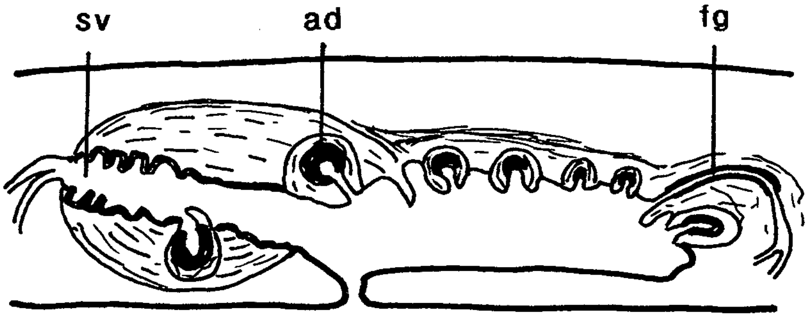
Etymology: *Artioposthia* form the Greek *artios,* complete, even (numbered), *posthe*, penis, and *–ia*, possession of. Possessing an even number of penes, an allusion to the presence of adenodactyls in the copulatory organs, the distinguishing character of the genus.

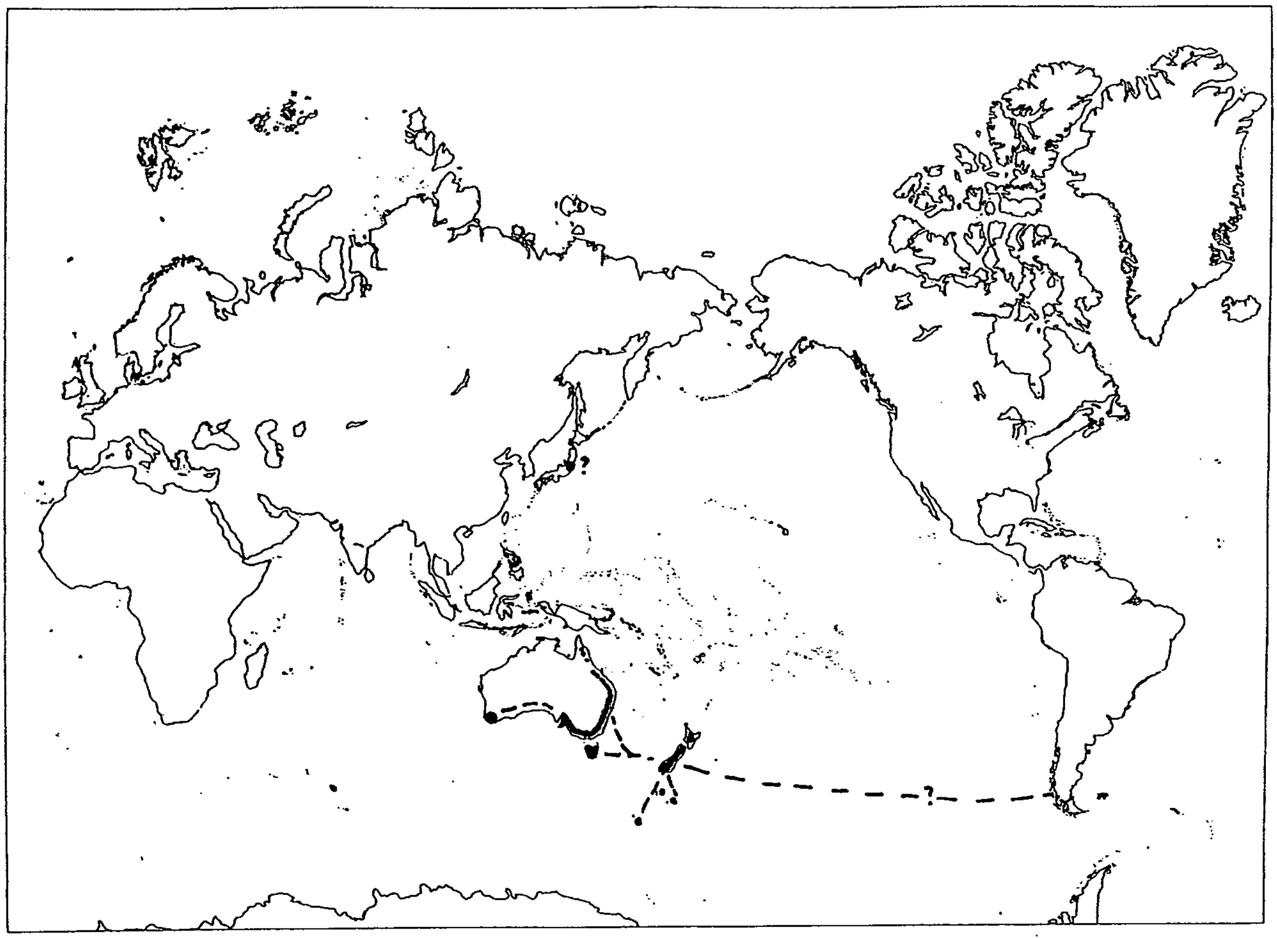
Distribution: Australia, New Zealand, and the subantarctic islands, with one spurious species in Japan. Within Australia, *Artioposthia* species are mainly found in the south eastern States: New South Wales, Victoria, and particularly in Tasmania.

Systematic discussion: Graff assigned six species to the genus. There are now some 30 species, sixteen of which are Australian taxa, and 14 species of New Zealand taxa investigated by Marion Fyfe during the period 1937-1956. Unfortunately the majority of descriptions are incomplete and lack details of body musculature and other data required for current taxonomy. Anatomical studies on several species reveal that the genus is heterogeneous. Winsor (1991c) identified

Plate 5.10. The habitus, eye pattern, copulatory organs, and occurrence of *Artioposthia* s.l. (Geoplanidae: Caenoplaninae)







five groups, based primarily upon body musculature. The position of the ovaries can also be used to identify some component taxa (Jones & Gerrard 1999). The genus is currently regarded as an inclusive group (Johns 1998) from which component taxa are relocated to new genera eg *Arthurdendyus, Fyfea, Barringtoplana* considered in detail, this thesis.

5.3.2.3 Genus *Australoplana* (Plate 5.11)

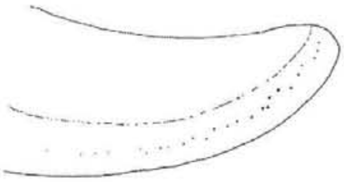
Australoplana Winsor, 1991c

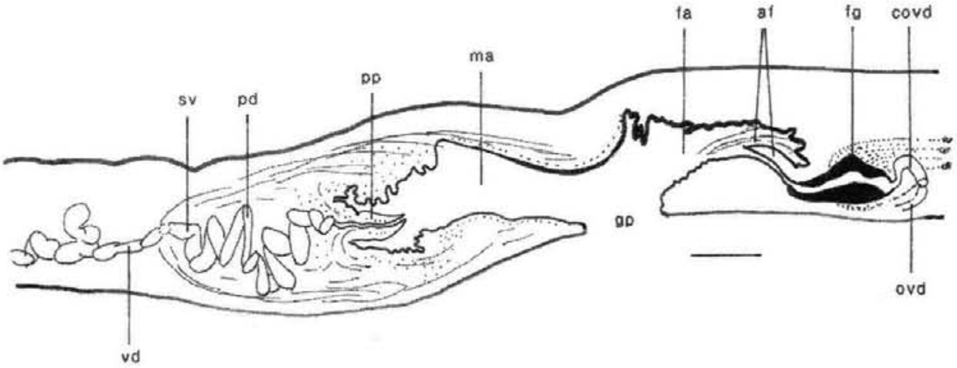
Australoplana Winsor, 1991c; Ogren *et al* 1993b

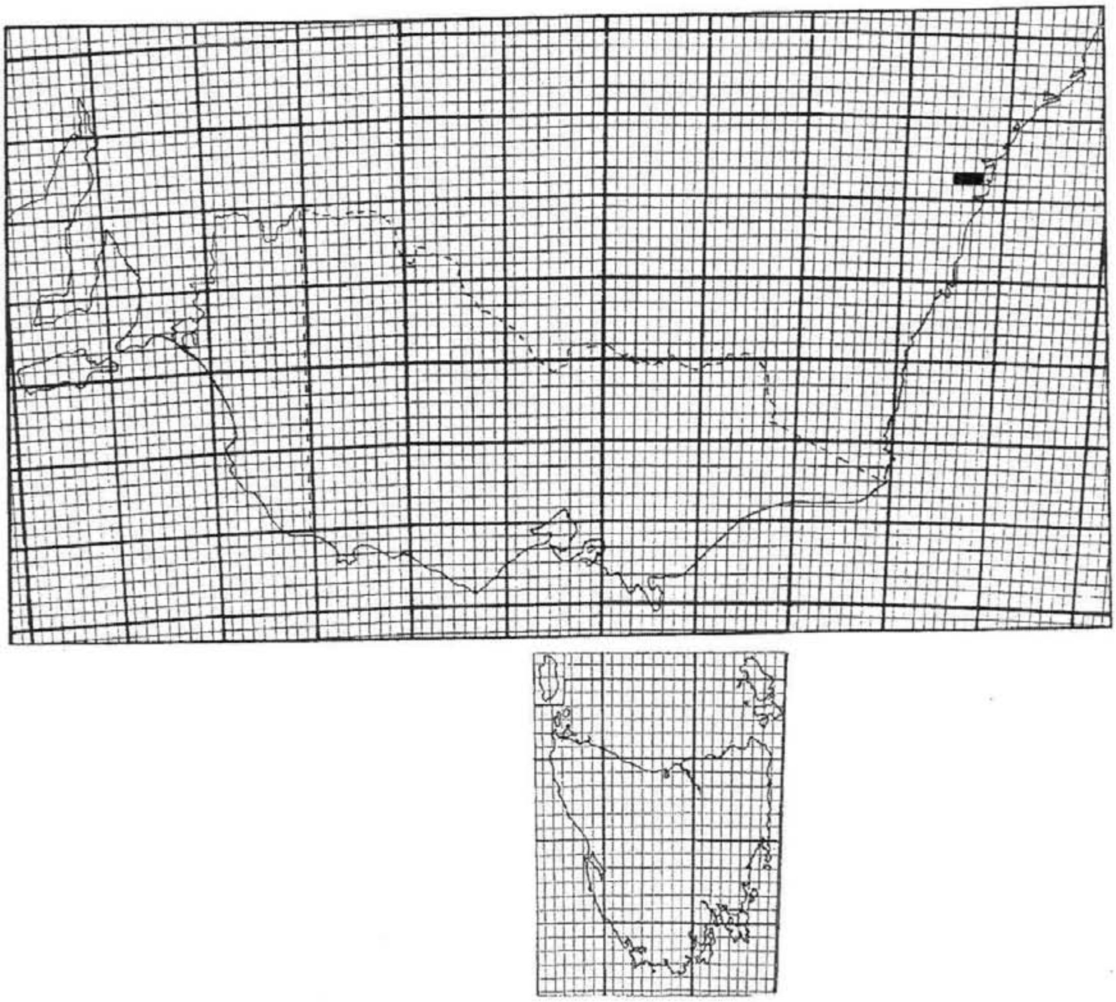
Diagnosis (emended from Winsor 1991c): Caenoplaninae with elongate, strap-like body, broadly convex dorsally, flat ventrally. Mouth situated in posterior third of body, gonopore closer to mouth than to posterior end. Creeping sole less than a third body width. Eyes pigment cup-type, very small (pin-point), in single row around anterior tip, then sparsely submarginally to posterior end. Anterior adhesive pad or cup absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular, helical muscles; with very strong cutaneous longitudinal muscles in bundles; dorsal musculature weaker than that ventrally, CMI 8.7 – 15.6%. Parenchymal longitudinal muscles very weak or absent. Pharynx cylindrical, folded, with oesophagus. Pharyngeal musculature with inner epithelium, circular, then longitudinal muscles; outer pharyngeal musculature with epithelium, longitudinal, then circular muscles. Testes ventral, lateral to nerve cords, extend from just behind ovaries to between pharynx and copulatory organs. Vasa deferentia enter penis bulb separately, unite, enter sinuous tubular, seminal duct, prostatic duct. Ejaculatory duct tubular, sinuous, strongly muscular, with intra-antral penis papilla. Ovaries in anterior third, with tuba. Ovovitelline ducts unite at posterior end of female genital canal. Female genital canal horizontal, enters ventro-posterior wall of common antrum; underlies elongate female antrum. Musculature of copulatory organs comprises mixed circular and longitudinal muscles. Viscid gland absent. Adenodactyls absent. Type species: *Australoplana sanguinea* (Moseley, 1877).

Etymology: The genus name *Australoplana* is derived from the Latin *austral*, southern, and *plana*, flat. Gender feminine. The Southern planarian.

Plate 5.11. The habitus, eye pattern, copulatory organs, and occurrence of *Australoplana* (Geoplanidae: Caenoplaninae)







Distribution: Found in restricted areas of the cool temperate moisture regions of the Bassian zoogeographic subregion in southeastern mainland Australia.

Systematic discussion: Three provisional groups were recognized by Winsor (1991c) in the genus *Australoplana sensu lato*:

- the *Australoplana sanguinea* group comprising the species *sanguinea, rubicunda; alba, alba roseolineata,* and *minor* (now *Australoplana sanguinea, A. minor* (provisionally), and *Nelipoplana (Nelipoplana) alba,* this thesis);
- the *Australoplana typhlops* group comprising *typhlops* and previously undescribed species (now *Bassioplana typhlops*, *Sokoplana kanangra,* and *Apogaioplana paluma* this thesis); and
- the New Zealand Group containing *Australoplana sanguinea alba sensu* Jones (1981), and undescribed species (now *Nelipoplana (Peokrypta) enigma*, this thesis) placed in a separate group because of the alleged presence of parenchymal longitudinal muscles which was a significant departure from the parenchymal musculature in the other taxa.

Comparison of *Australoplana* with these new genera is provided in Appendix 8. For each genus there is undescribed material, precluded from consideration in this thesis.

Australoplana is mainly differentiated from *Nelipoplana* and *Apogaioplana* by the presence of a creeping sole (absent in *Nelipoplana* and *Apogaioplana*), cylindrical pharynx (bell form in *Nelipoplana*), dugesiid-type pharyngeal musculature (non-dugesiid in *Nelipoplana* and *Apogaioplana*), and female genital canal underlying the female antrum (female genital canal and antrum in-line in *Nelipoplana* and *Apogaioplana*). *Australoplana* shares with *Nelipoplana (Peokrypta) enigma* a muscularised, tubular prostatic and ejaculatory duct. However the penis papilla in *Australoplana* appears to be fixed (as in *Nelipoplana (Nelipoplana) alba*), not erectile (as in *Nelipoplana (Peokrypta) enigma*). *Australoplana* is distinguished from *Bassioplana* by the presence of eyes (absent in *Bassioplana*), pharynx type and musculature (dendrocoelid musculature in *Bassioplana*), fixed penis papilla (erectile in *Bassioplana*) and details of the female copulatory organs.

5.3.2.4 Genus *Barringtoplana* gen.nov. (Plate 5.12)

Barringtoplana gen.nov.

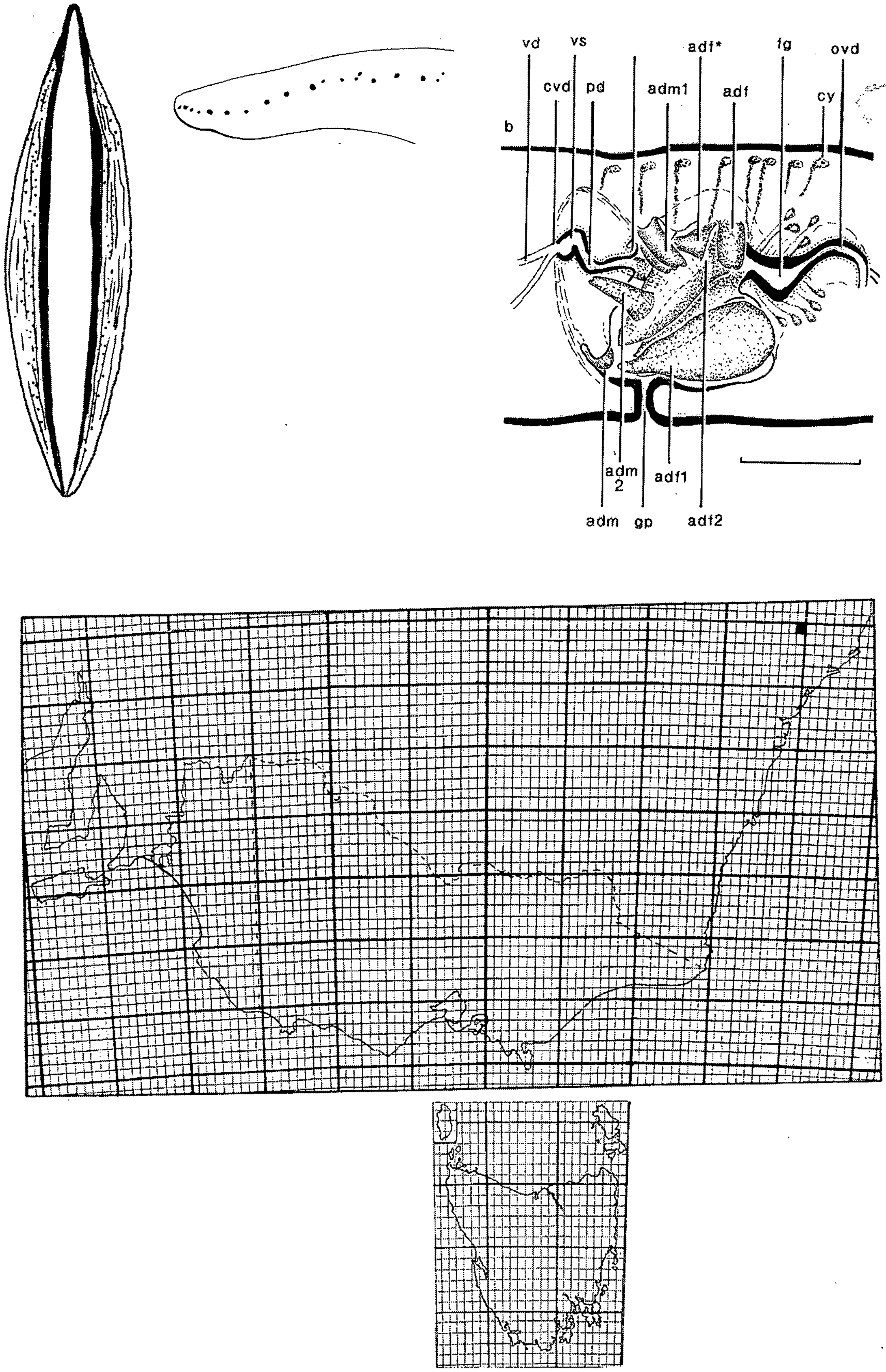
Diagnosis: Caenoplaninae with small, broad body, tapered slightly more anteriorly than posteriorly. With mouth just behind mid body, gonopore in last body quarter. Creeping sole almost entire width of body. Anterior adhesive pad or sucker absent. Sensory papillae absent. Eyes pigment cup-type, in single row around tip, submarginally along body. Cutaneous musculature bipartite, with layer of helicoid muscles underlain by well-developed sheath of cutaneous longitudinal muscles in bundles. Cutaneous musculature developed more strongly ventrally than dorsally. CMI 5.2-6.3%. Paranchymal musculature weak, with transverse-oblique muscles in ventral plate. Pharynx cylindrical, with distinct oesophagus. Pharyngeal musculature with inner epithelium, thin circular, then mixed circular-longitudinal muscles. Outer pharyngeal musculature with epithelium, longitudinal, then broadband of weak mixed circular-longitudinal muscles. Testes, sperm ducts ventral. Testes extend from just behind ovaries, to just beyond female copulatory organs. Vasa deferentia unite, then enter bulb, seminal duct, prostatic duct; with muscular ejaculatory duct, with partly sheathed penis papilla, with specialized secretory elements. Ovaries anterior, pre-pharyngeal. Ovovitelline ducts with tubae; unite, form common duct, enters female genital canal ventroposteriorly, female canal expanded, enters dorsoposterior female antrum. Adenodactyls present. Viscid gland absent.

Etymology: *Barringtoplana*, the Barrington Tops planarian, a name contrived from the name of the location where it was found, and the Latin *plana,* flat. Gender feminine. Type of genus: *Barringtoplana harrisoni* (Wood, 1926)

Locality: Barrington Tops, and Sharpes Creek, Barrington Tops National Park, NSW, Australia, 156°26' E 32°02'S; Point Lookout, New England National Park, NSW; Copeland Tops State Forest, north west of Gloucester, NSW, 151°51'E 32°01'S.

Ecology: Other species found in the area include *Caenoplana coerulea, Kynagoplana citrina,* and *Platydemus assimilis*. The specimen from Copeland Tops (elevation about 610 metres above sea level) was found in dry open forest on a ridge,

Plate 5.12. The habitus, eye pattern, copulatory organs, and occurrence of *Barringtoplana* (Geoplanidae: Caenoplaninae)



in association with *Caenoplana coerulea* and *Parakontikia atrata*, whilst at Sharpes Creek (elevation about 1,000 metres above sea level) the specimen was found in tall closed eucalypt forest together with *Caenoplana coerulea, C. variegata, Parakontikia atrata,* an *Australoplana* sp., and the nemertean Argonemertes *hillii.*

Systematic discussion: The presence of adenodactyls in the copulatory organs led Wood (1926) to assign the species *harrisoni* to the genus *Artioposthia.* Her succinct description of *A. harrisoni* did not include details of the eyes and eye pattern, or a description of the histology of the internal structures such as body musculature.

Artioposthia was later found to be heterogenous and was divided into five groups, chiefly on the basis of body musculature (Winsor 1991c). *A. harrisoni* was tentatively allocated to Group 5 characterized as "body robust, elongate; convex dorsally, slightly concave ventrally; with strong cutaneous longitudinal muscles, the ventral muscles developed slightly more developed than those dorsally; parenchymal longitudinal muscles weak or absent". Re-examination of the Type specimen of *A. harrisoni* revealed characters which excluded the species from *Artioposthia*, but required that it be accommodated in a new genus *Barringtoplana.*

Barringtoplana shares with the caenoplaninids *Caenoplana* and *Kynagoplana* (this thesis), the apomorphy of a bipartite cutaneous musculature, though stronger dorsally than ventrally. The parenchymal musculature in *Barringtoplana* is predominantly composed of helicoid muscles, reduced to a ventral plate; longitudinal parenchymal muscles are absent. *Barringtoplana* differs from *Caenoplana* and *Kynagoplana* in external morphology, the relative position of the body apertures, the extreme width of the creeping sole, single row of eyes, absence of parenchymal longitudinal muscles, presence of an oesophagus, and presence of adenodactyls and a penis papilla. *Barringtoplana* is differentiated from taxa within Artioposthia chiefly by its bipartite cutaneous musculature and unusual glandular sheathed penis papilla.

5.3.2.5 Genus *Bassioplana* gen.nov. (Plate 5.13)

Bassioplana gen.nov.

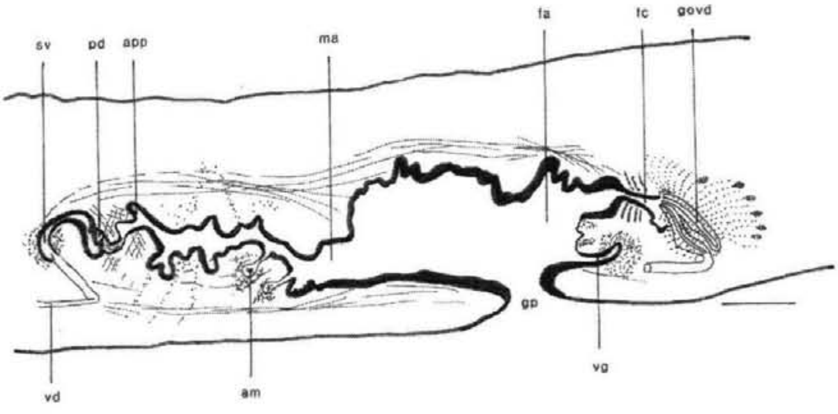
Diagnosis: Caenoplaninae with elongate, strap-like body, convex dorsally, flat ventrally. Mouth in hind third of body, gonopore about midway between mouth and posterior end. Creeping sole 15% body width, present almost to anterior tip. Eyes absent. Anterior adhesive cup or pad absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular muscles, with helical muscles almost longitudinally oriented ectally, almost circular entally; with strong longitudinal muscles in large bundles, dorsal musculature developed slightly more than ventrally, CMI 13%. Parenchymal musculature weak; longitudinal muscles sparse, very weak, single fibres. Pharynx bell-form. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; outer pharyngeal musculature with epithelium, circular, then longitudinal muscles. Testes ventral, dorsolateral to nerve cords, extending from behind ovaries to pharynx. Vasa deferentia enter penis bulb separately, unite, then pass into seminal vesicle anterodorsally. Ejaculatory duct tubular, weakly muscular; penis papilla present, poorly differentiated. Penis eversible type. Ovaries anterior. Ovovitelline ducts with shell glands distally (become paired genital (glandular) canals); paired genital canals enter dorsoposterior wall of female antrum separately. Female antrum almost horizontal, in ventro-posterior wall of common antrum. Atrial musculature differentiated. Viscid gland present. Male antrum with adenodactyls (adenomuralia). Type species: *Bassioplana typhlops* (Dendy, 1894).

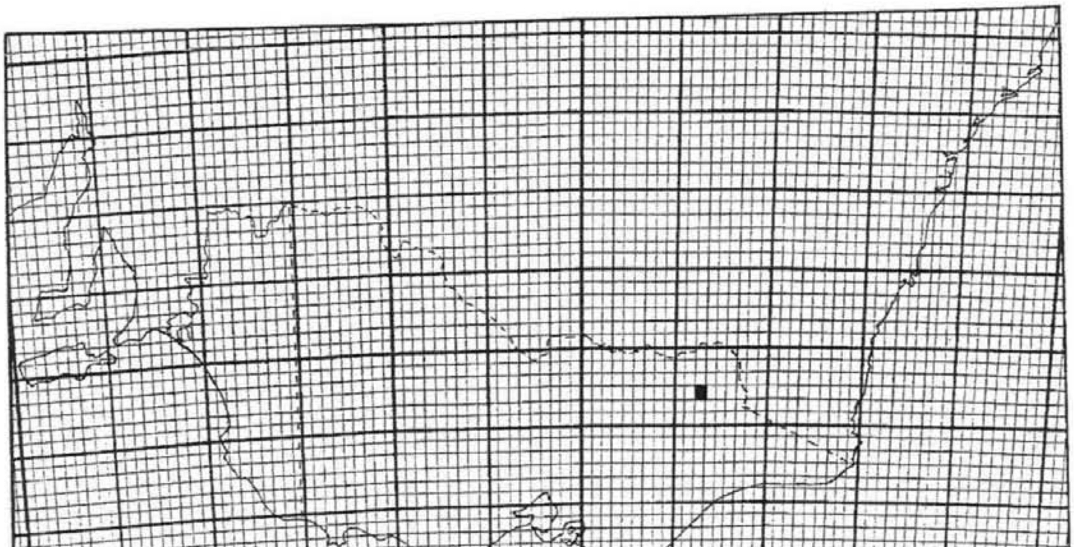
Etymology: The genus name *Bassioplana* is derived from the name of George Bass (1771-1803), explorer and naturalist, who explored the southeastern coastline of New South Wales and Victoria, and who, with Mathew Flinders circumnavigated Tasmania. Gender feminine. The name commemorates Bass, and alludes to distribution of the species in the Bassian zoogeographic sub-region – the Bassian planarian.

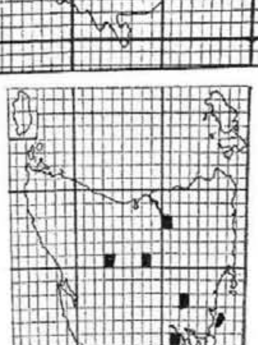
Distribution: Cool temperate zone of the Bassian zoogeographic sub-region, in northern, central, and southeastern Tasmania, and the north eastern highlands, Victoria.

Plate 5.13. The habitus, eye pattern, copulatory organs, and occurrence of *Bassioplana* (Geoplanidae: Caenoplaninae)

eyeless







Systematic discussion: Within the caenoplaninid genus *Australoplana sensu lato* in Winsor (1991c) a narrow creeping sole was found to be present in two groups: the *Australoplana typhlops* group, now *Bassioplana* gen.nov. and the *Australoplana sanguinea* group, now the restricted genus Australoplana. *Bassioplana* is differentiated from *Australoplana* chiefly by the absence of eyes (present in *Australoplana*), bell-form pharynx (cylindrical in *Australoplana*), mixed inner pharyngeal musculature (mixed musculature absent in *Australoplana*), poorly differentiated penis papilla (well differentiated in *Australoplana*), paired female genital canals separately entering the female antrum (single genital canal in *Australoplana*), presence of adenomuralia in male antrum (absent in *Australoplana*), and presence of a viscid gland (absent in *Australoplana*).

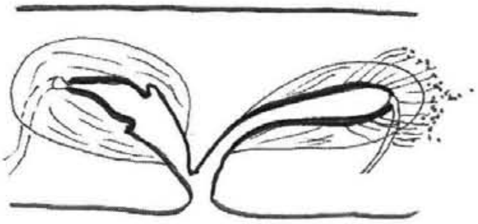
5.3.2.6 Genus *Caenoplana* (Plate 5.14)

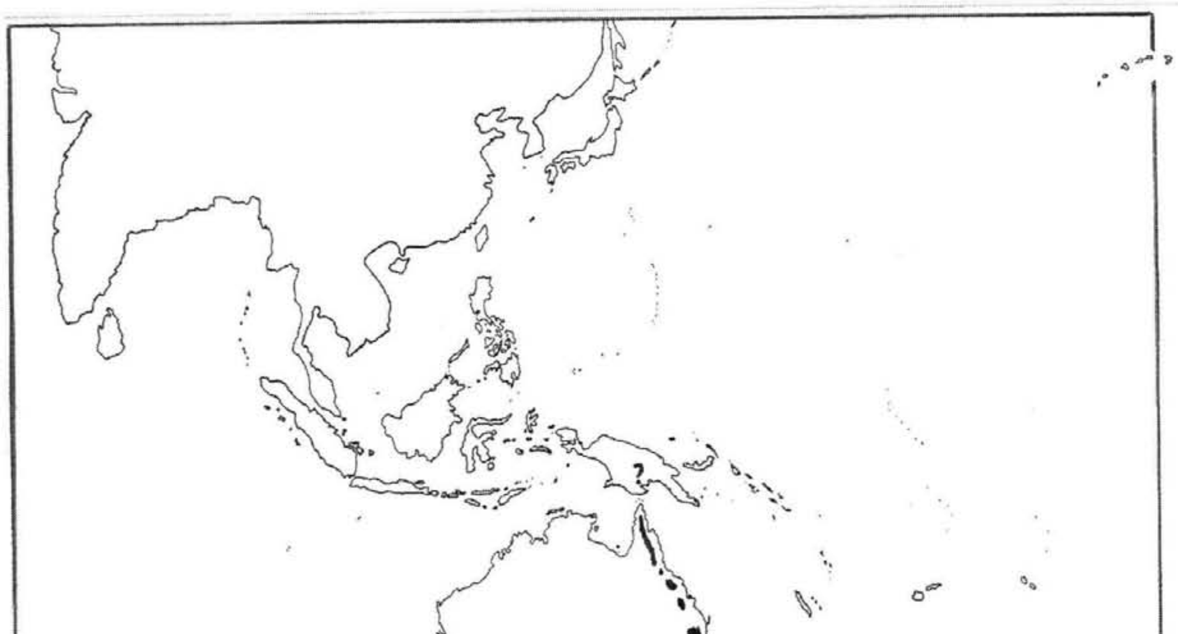
Caenoplana Moseley, 1877
Caenoplana Moseley, 1877; Ogren & Kawakatsu 1988a, 1991; Winsor 1991c
Geoplana, (part), Fletcher & Hamilton 1888; Graff 1899.

Original diagnosis (Moseley 1877): "Body long and wormlike, much rounded on the back, flattened on the under surface, without an ambulacral line. External longitudinal muscular bundles largely and evenly developed over both dorsal and ventral regions. Lateral organs distinct and isolated as in *Rhyncodemus,* and, as in it, connected by a transverse commissure. Eyes absent from the front of the anterior extremity, but present in two lateral elongate crowded patches placed just behind the anterior extremity and scattered sparsely on the lateral margins of the body for its entire extent. Mouth nearly central, pharynx cylindrical".

Diagnosis: Emended from Winsor, 1991c: Caenoplaninae with elongate, cylindrical to sub-cylindrical body. With mouth situated just posterior of mid body, with gonopore closer to mouth than to posterior end; creeping sole 60% or more body width. Anterior adhesive pad or sucker absent. Sensory papillae absent. Eyes pigment cup-type, mostly small in single row around the anterior tip, with irregular cluster antero-laterally, then extending posteriorly in staggered submarginal row.

Plate 5.14. The habitus, eye pattern, copulatory organs, and occurrence of *Caenoplana* (Geoplanidae: Caenoplaninae)





Cutaneous musculature bipartite or tripartite, with circular and paired helical muscle layers mostly poorly differentiated, presenting as circulo-helical layer; with longitudinal muscles very weak, in bundles, equally developed dorsally, ventrally. CMI 1.6 - 4.5%. Parenchymal musculature with circulo-helical muscle fibres, dense, arranged in distinct ring zone, with longitudinal muscles present as single fibres or small isolated bundles in circulo-helical muscle mass. PMI (ring zone) 20 - 28.5%. Pharynx cylindrical. Pharyngeal musculature with inner eithelium, then mixed circular – longitudinal muscles; outer pharyngeal musculature with epithelium, then longitudinal, circular, then mixed circular-longitudinal muscle layers. Testes, sperm ducts ventral; testes extend from behind ovaries to just before copulatory organs. Vasa deferentia separately enter seminal vesicle, with prostatic duct, penis of the eversible type, without papilla. Male antrum elongate. Ovaries anterior. Ovovitelline ducts enters female genital canal ventrally; female genital canal enters female antrum horizontally. Atrial musculature with mixed circular-longitudinal muscles. Adenodactyls absent. Type species: *Caenoplana coerulea* Moseley, 1877; designated by Ogren & Kawakatsu, 1988a.

Etymology: *Caenoplana* from the Greek *kainos*, new, recent and Latin *plana*, flat. The New planarian. Moseley (1877) wrote" I have been able to find no published description of these forms, for the reception of which I have made the new genus *Caenoplana*." Hitherto the only genus for flatworms with multiple eyes was *Geoplana*. Moseley erected *Caenoplana* with the key character distinguishing it from *Geoplana* being the absence of eyes around the anterior tip. In fact he was in error - the eyes do go around the tip - an unusual slip for the normally observant Moseley. Use of the diphthong *æ* in *Caenoplana* and misprinting as *œ* led to variations in spelling *Caenoplana*, are discussed by Ogren & Kawakatsu (1988b, pages 85-86).

Distribution: Caenoplana is present in south-western Western Australia, South Australia, northern Tasmania, Victoria, New South Wales, and Queensland, but predominantly in the eastern mainland Australian states (Bassian and Torresian zoogeographic sub-regions). The genus occurs in New Zealand (*C. purpurea* (Dendy, 1895b), *C. tenuis* (Dendy, 1895b), and five new species (Johns 1998). *Caenoplana coerulea* is a tramp species introduced into disturbed areas of New

Zealand, Norfolk Island, the United States of America, the United Kingdom, and Paris, France (new record, this thesis).

Systematic discussion: *Caenoplana* had earlier been suggested as a repository for chiefly Oriental and Australian taxa that belonged to Graff's muscle groups (a) and (b) with ventral testes, that could not remain in *Geoplana* (in C.G. Froehlich 1955, pages 200, 246), and exclusive of *Kontikia* (in Beauchamp 1961, page 121). The genus was re-instated by Ogren & Kawakatsu (1988a) to accommodate *Caenoplana coerulea vaga* (Hyman 1943), and re-defined by Winsor (1991c), and Ogren & Kawakatsu (1991).

Two groups were recognized within *Caenoplana* (Winsor 1991c):

- The *Caenoplana coerulea* group, characterized by presence of blue-green rhabdoids in the cutaneous epithelium, and intermixed circular – longitudinal musculature of the pharynx and copulatory organs comprising *C. coerulea* Moseley, 1877; *C. spenceri* (Dendy, 1890); *C. walhallae* (Dendy, 1891), and *C. dendyi* (Spencer, 1891). The cutaneous musculature of *C. dendyi* was tripartite. This group was recognized by Ogren *et al* (1993b).
- The *Caenoplana sub-viridis* group, most members of which were characterized by yellow or brown colour, with green or dark brown stripes. The musculature of the pharynx and copulatory organs exhibit greater differentiation, and the copulatory organs are more complex than species within the *coerulea* group. Members of the group were *C. sub-viridis* Moseley, 1877; *C. variegata* (Fletcher & Hamilton, 1888); *C. sulphurea* (Fletcher & Hamilton, 1888); *C. hoggii* (Dendy, 1891); *C. dubia* (Dendy, 1892a); *C. bicolor* (Graff, 1899); *C. citrina* (Wood, 1926), and *C. barringtonensis* (Wood, 1926). This group was not recognized by Ogren *et al* (1993) who in the absence of published descriptions of copulatory organs, transferred the taxa to *Australopacifica;* the re-assignment is not accepted by this author.
- Species included within *Caenoplana* but not assigned to a group included *C. viridis* (Fletcher & Hamilton, 1888); C. *hillii* (Steel, 1897); *C. ponderosa*

(Steel, 1897); *C. albolineata* (Steel, 1897), and *C. daemeli* (Graff, 1899) in part.

Investigations on *Caenoplana* species within the context of this thesis are largely incomplete, but so far have revealed that:

- The blue-green pigmented rhabdoids present in *Caenoplana coerulea* appear to be an adaptation to cool closed forest habitats; some specimens found in dry open forest and isolated urban gardens have lost this pigmentation. Rhabdoid colour is not a reliable character.
- *Caenoplana coerulea* is one of a complex of species of similar external appearance, confirming an earlier opinion (Winsor 1979) based upon the examination of external characters of component taxa. The chiefly southern Australian complex includes an adenodactylate species. The complex may be partly resolved when types of all the described component taxa are examined.
- *C. citrina* and *C. barringtonensis* are synonymous, and are now transferred to a new genus *Kynagoplana* (this thesis).
- Taxa remaining in the *sub-viridis* groups are better considered with taxa in the *coerulea* group.
- Pharyngeal musculature in *Caenoplana* is not homogeneous. In *C. coerulea, C. bicolor*, and *C. hoggii* the pharyngeal musculature comprises inner mixed circular – longitudinal, with outer longitudinal, circular then mixed circular – longitudinal, whilst in *C. dendyi* and *C. spenceri* it comprises inner circular, then mixed circular – longitudinal, with outer longitudinal, then mixed circular – longitudinal muscles.

5.3.2.7 Genus *Coleocephalus* (Plate 5.15)

Genus ***Coleocephalus*** Fyfe, 1953 emend

Coleocephalus Fyfe, 1953

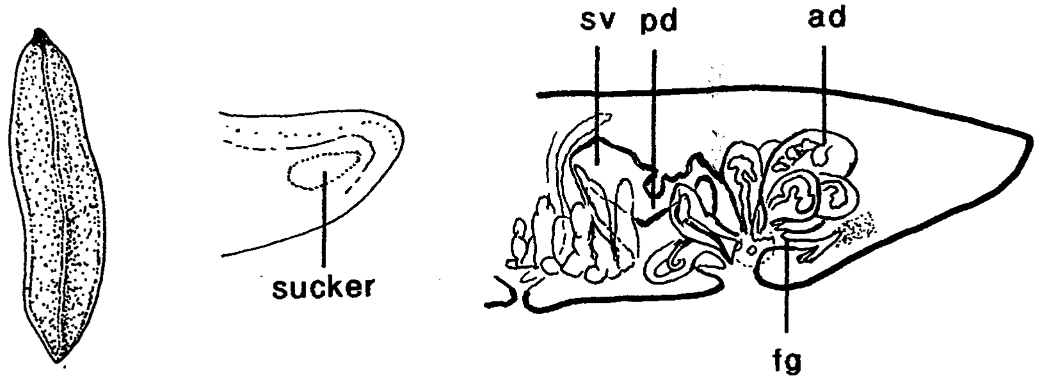
Coleocephalus Fyfe: Ogren and Kawakatsu, 1991; Johns 1998

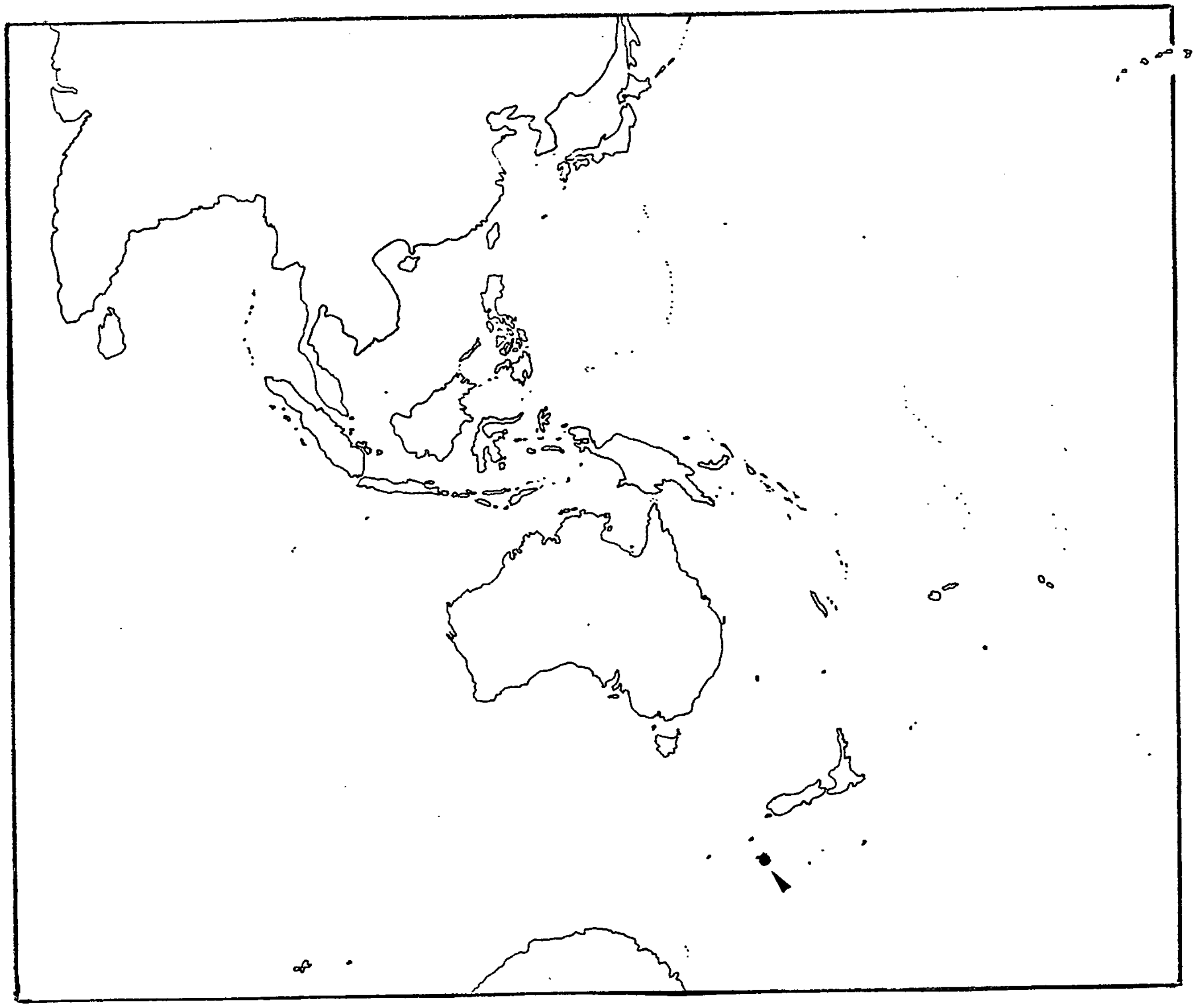
Original diagnosis (Fyfe 1953): "Geoplanidae with hooded anterior end partly covering an oval glandular area on the ventral surface". Emended (Ogren and Kawakatsu 1991) to include: "penis papilla present; adenodactyls present".

Diagnosis emended (this thesis): Caenoplaninae with small, robust body, broadest in posterior body third, tapering gradually to anterior tip; more abruptly to posterior end; flat to slightly concave dorsally, with sharply rounded margins, convex ventrally; with sucker antero-ventrally. Sensory papillae absent. Eyes pigment cup-type, in single row around anterior tip, continuing in submarginal row to posterior end. Mouth and gonopore situated in hind third of body. Creeping sole 70% or more of body width. Cutaneous musculature tripartite, very strong, with circular, helical muscles, with longitudinal muscles in bundles, developed equally dorsally and ventrally, CMI 22-24%. Parenchymal musculature with strong dorsal and ventral transverse muscles; longitudinal parenchymal muscles weak or absent. Pharynx plicate, collar-form. Pharyngeal musculature with inner epithelium, then mixed circular-longitudinal muscles; outer musculature with epithelium, longitudinal, then circular muscles. Testes ventral, extend from anterior body to posterior tip. Vasa deferentia ventral to nerve cords. Penis eversible, without papilla. Ovaries just forward of root of pharynx, with parovarian resorptive tissue. Ovovitelline ducts join, form common duct which enters female genital canal ventroposteriorly. Female genital canal enters female antrum through ventroposterior wall, below adenodactyls. Adenodactyls present. Viscid gland absent. Type species: *Coleocephalus fusca* Fyfe, 1953

Etymology: Fyfe (1953) did not indicate the etymology of the taxon names. *Coleocephalus* is derived from the Greek *koleus* – sheath, and kephale – head, and alludes to the hooded anterior end. Gender masculine.

Plate 5.15. The habitus, eye pattern, copulatory organs, and occurrence of *Coleocephalus* (Geoplanidae: Caenoplaninae)





Distribution: Auckland Islands: Horseshoe Lake, Ranui Cove, and Port Ross on Auckland Island, and from Enderby Island (Fyfe 1953).

Remarks: Although Fyfe (1953) was unable to find testes in her material, Ogren and Kawakatsu (1991) provisionally included the genus in the Caenoplaninae, confirmed here. The testes are ventral. Examination of the Type and other material has shown that the hooded anterior end, alluded to in the generic epithet, is an unreliable character. It is a fixation artefact. Ogren and Kawakatsu (1991) interpreted an adenodactyl papilla in Fyfe's figure as a penis papilla. The penis is apapillate. At present there is only one described species of *Coleocephalus*, though possibly more than three undescribed species are represented in collections (Johns 1998).

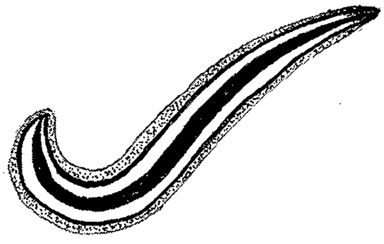
The differential diagnosis between the three caenoplaninid taxa with anterior adhesive suckers and pads, *Coleocephalus fuscus, Pimea monticola,* and *Thosteelia mesibovii,* is provided elsewhere in this thesis (Appendix 8)

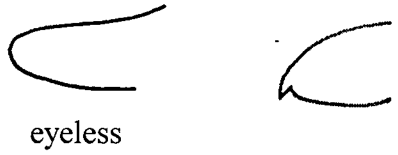
5.3.2.8 Genus *Danidoplana* gen. nov (Plate 5.16)

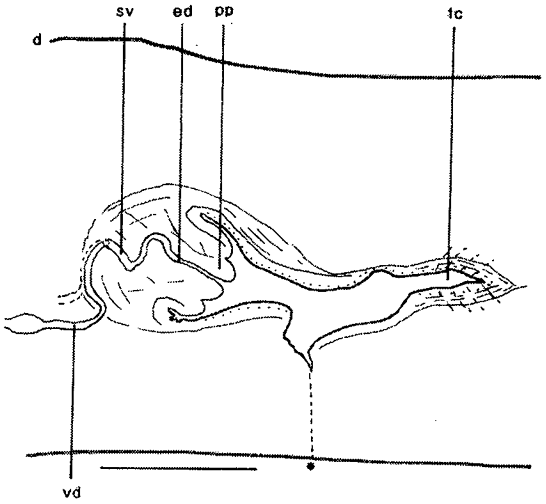
Danidoplana gen. nov

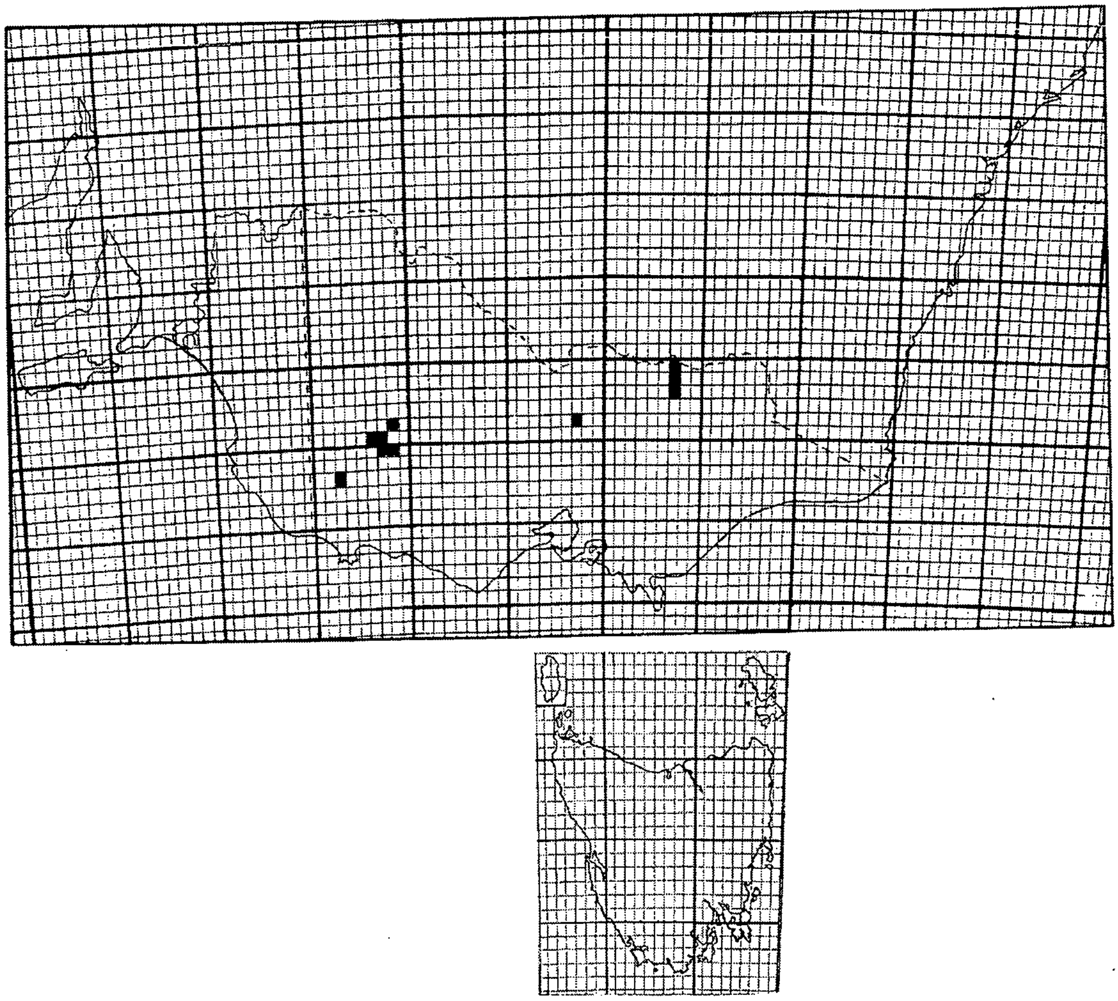
Diagnosis: Caenoplaninae with small elongate body, subcylindrical in cross section, mouth in first half close to mid body, gonopore closer to mouth than to posterior end. Creeping sole more than 60% body width. Anterior adhesive sucker, pad or cup absent. Sensory papillae absent. Eyeless. Cutaneous musculature tripartite, weak, with circular, helical muscles, longitudinal muscles in bundles, with ventral musculature stronger than that dorsally. CMI 4%. Parenchymal musculature weak, with subneural longitudinal muscles present as sparse single fibres, not organized in ring-zone or distinct plate. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; with outer epithelium, longitudinal, then circular muscles. Testes and sperm ducts ventral. Testes extend from ovaries to just anterior of copulatory organs. Vasa deferentia separately enter penis bulb, penis papilla present. Ovaries closer to anterior tip than to pharynx, female genital canal enters antrum horizontally. Adenodactyls. Viscid gland absent.
Type of genus: *Danidoplana palatris*

Plate 5.16. The habitus, eye pattern, posterior end, copulatory organs, and occurrence of *Danidoplana* (Geoplanidae: Caenoplanidae)









Etymology: *Danidoplana*, the dry forest planarian, a name contrived from the Greek *danos,* dry, parched, burnt, *ide, forest*, and Latin *plana* flat. Gender feminine. The name alludes to the open dry sclerophyll woodland where members of the genus occur.

Distribution: In the Eyrean zoogeographic sub-region. And warm temperate moisture zone of the Bassian zoogeographic sub-region, west, central, and northeastern Victoria.

Systematic discussion: In general habitus *Danidoplana* is similar to *Lenkunya, Tasmanoplana,* and *Parakontikia.* It is distinguished from these genera in being eyeless, lacking a ring zone or subneural plate of strong parenchymal longitudinal muscles, and differing in pharyngeal musculature. It shares with *Lenkunya* and *Tasmanoplana* a broad creeping sole and penis papilla, and relative positions of the body apertures.

5.3.2.9 Genus *Fletchamia* (Plate 5.17)

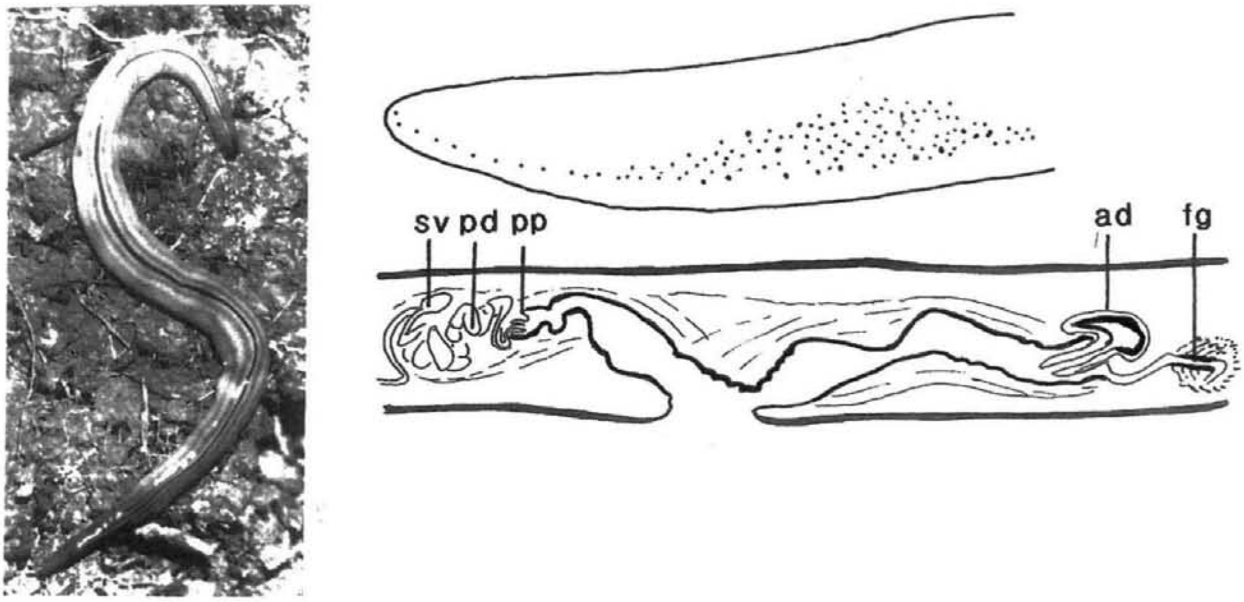
Fletchamia Winsor, 1991c

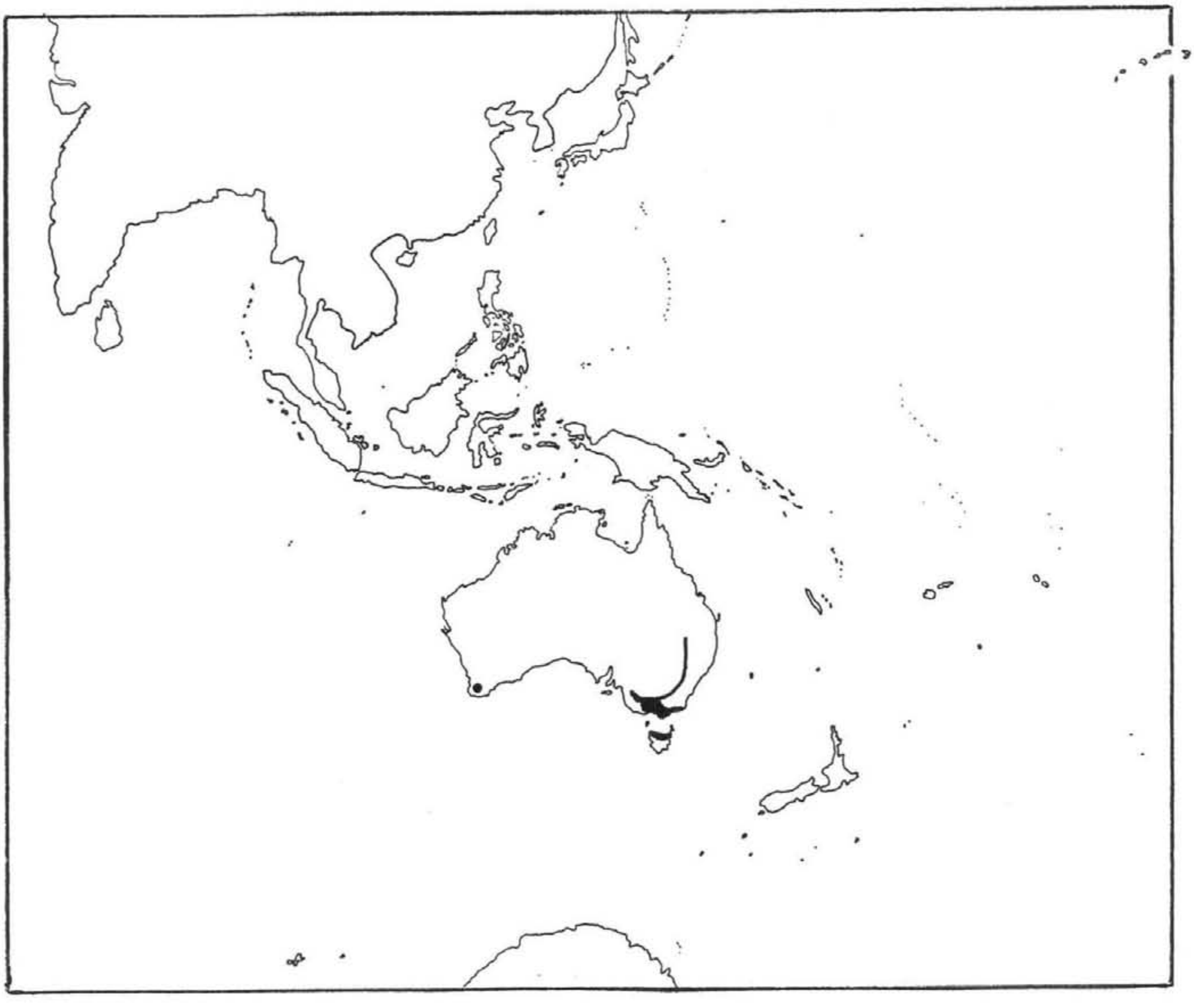
Fletchamia Winsor, 1991c; Ogren *et al* 1993b

Australopacifica (part) Ogren & Kawakatsu, 1991

Diagnosis: Caenoplaninae with elongate, sub-cylindrical body; mouth approximately central; gonopore generally nearer mouth than the posterior end; creeping sole 50-70% body width. Eyes pigment cup-type, in single row around anterior tip, crowded antero-laterally in lens-shaped patch, which extends to lateral region of the dorsal surface; eyes then continue posteriorly in two to three staggered submarginal rows. Anterior adhesive pad or sucker absent; sensory papillae absent. Cutaneous musculature tripartite, weak, with circular, helical and longitudinal muscles, with longitudinal muscles in bundles. CM1 2.3-6.2%. Parenchymal musculature weak, with loose ring zone of circulo-helical fibres, with parenchymal longitudinal muscles present as isolated fibres largely confined to weak ventral plate. PMI (plate) 2.3-4.3%. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, then circular, then mixed circular - longitudinal muscles; outer pharyngeal musculature with epithelium, then longitudinal, then mixed circular -

Plate 5.17. The habitus, eye pattern, copulatory organs, and occurrence of *Fletchamia* (Geoplanidae: Caenoplaninae)





longitudinal muscles. Pharyngeal pouch diverticulum absent. Main nephridial canals dorsal, dorsal and ventral, or ventral only (Type species ventral); bilateral; single, paired or in triads. Testes and sperm ducts ventral; testes pre-oral. Vasa deferentia enter seminal vesicle dorsally; with sinusoidal prostatic region, with strongly muscular ejaculatory duct, with small penis papilla, penis of eversible type. Ovary in anterior third; ovovitelline ducts separately enter female genital canal ventro-posteriorly; female genital canal elongate, horizontal, with shell glands opening into proximal third, enters floor of antrum below adenodactyl; female antrum in-line, elongate, deeply rugose, with sclerotin-producing epithelium and crypts. Adenodactyl, Type VII, present dorsoposterior end of antrum, with capacious reservoir, with elongate papilla. Viscid gland absent. Vitellaria extensive, surround gut diverticula. Type species: *Geoplana quinquelineata* Fletcher & Hamilton, 1888.

Etymology: The generic epithet is derived from the surnames of J.J. Fletcher and A.G. Hamilton. Gender masculine. It commemorates the valuable contributions to the knowledge of the Australian terrestrial flatworms by these two colonial naturalists.

Distribution: eastern and Western Australia; New Zealand. In southeastern Australia *Fletchamia* species mostly occur in the warm temperate moisture zone of the Bassian zoogeographic sub-region, with extension into the Eyrean (*F. quinquelineata*) and cool temperate moisture zone of the Bassian (*F. sugdeni*).

Systematic discussion: Included in this genus are *F. quinquelineata* (Fletcher & Hamilton, 1888); *F. mcmahoni* (Dendy, 1891); *F. sugdeni* (Dendy, 1891); *F. mediolineata* (Dendy, 1891); *F. quinquelineata accentuata* (Steel, 1897) and *Fletchamia* sp. (Winsor, 1993c). The species *F. fuscodorsalis* (Steel, 1901a); *F. mediolineata simularis* (Steel, 1901a): *F. dakini* (Dendy, 1915) and *F. flavilineata* (Dendy, 1915) may also be referred to the genus. Members of this genus have yet to be fully investigated anatomically. Given the variations in width of creeping sole, and in other characters, observed between species tentatively assigned to this genus, the genus may be heterogeneous.

Fletchamia quinquelineata shares with the New Zealand species *Artioposthia* *glandulosa* Fyfe, 1953 from the Dunedin region, similar colour and longitudinal striping, relative positions of the body apertures, similar conformation of the copulatory organs, in particular the terminal antral Type VII adenodactyl. Details of eye pattern, body musculature, pharynx type and musculature, and fine histology of the copulatory organs of *A. glandulosa* have yet to be determined.

5.3.2.10 Genus *Kontikia* (Plate 5.18)

Kontikia C.G. Froehlich, 1955

Kontikia C.G. Froehlich, 1955; 1967; Beauchamp 1956; 1961; E.M & C.G. Froehlich 1972; Ogren & Kawakatsu 1991; Ogren *et al* 1993b

Diagnosis (English abstract, in C.G. Froehlich 1955): "Geoplanidae of elongate body form. Creeping sole one or two thirds, or a little more, of body width. Strong cutaneous longitudinal muscles. Rather strong longitudinal parenchymal muscles, chiefly located in an annular zone. Ventral testes. Glandulo-muscular organs, sensory papillae, and adenodactyls absent". Type species: *Kontikia orana* C.G. Froehlich, 1955. Emended (Ogren & Kawakatsu 1991) to include: "Dorsal body often has dark longitudinal stripes; male copulatory apparatus of the type species has the penis papilla".

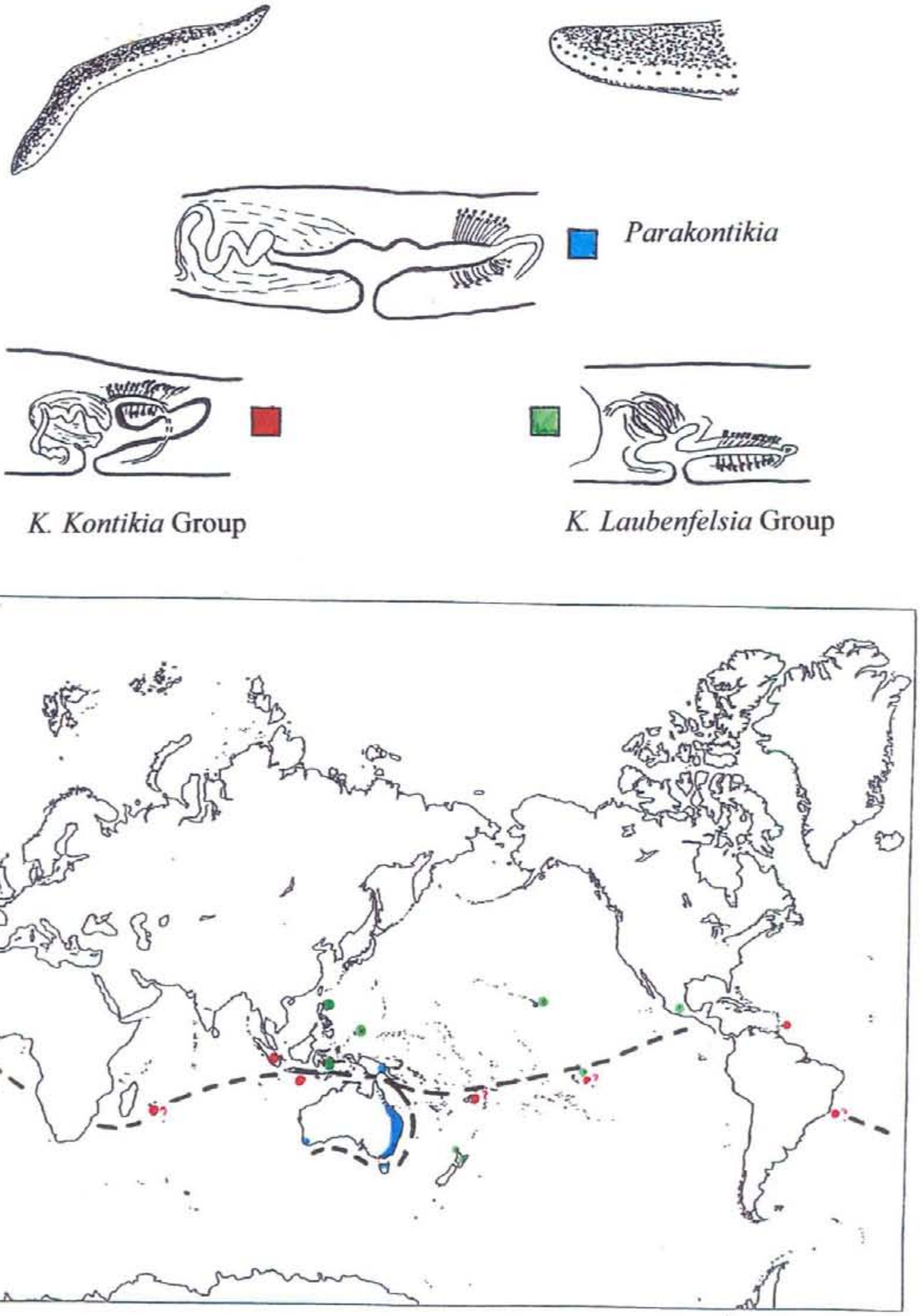
Etymology: *Kontikia* from the Thor Heyerdahl expedition 1969-70 by the balsa raft *Kon Tiki* travelling east to west, along the Humboldt current, from Peru to the Tuamoto Islands, to prove his migration theory about the colonization of the Pacific by South American Indians. The name is an allusion to the origins and spread of *Kontikia*, from the west Indo-Pacific west to South America.

Distribution: Indo-Pacific. *Kontikia orana* is a tramp species. It is adventive in Townsville, Queensland (Winsor 1986).

Systematic discussion: Ogren *et al* (1993b) established two sub-genera within *Kontikia*:

- *Kontikia Kontikia* to accommodate taxa with dorsal entrance of the female canal into the common genital antrum and having the posterior diverticulum

Plate 5.18. The habitus, eye pattern, copulatory organs, and occurrence of *Parakontikia* and the two groups of *Kontikia* (Geoplanidae: Caenoplaninae)



Key: *Parakontikia* blue; *K. Kontikia* Group – red; *K. Laubenfelsia* Group – green (antral bursa); often three dark stripes. Type species: *Kontikia orana* C.G. Froehlich, 1955.

- *Kontikia Laubenfelsia* to accommodate taxa with a female canal having a horizontal entrance into the common genital antrum; without ventro-posterior diverticulum; often more than three dark stripes. Type species: *Geoplana mexicana* Hyman, 1939.

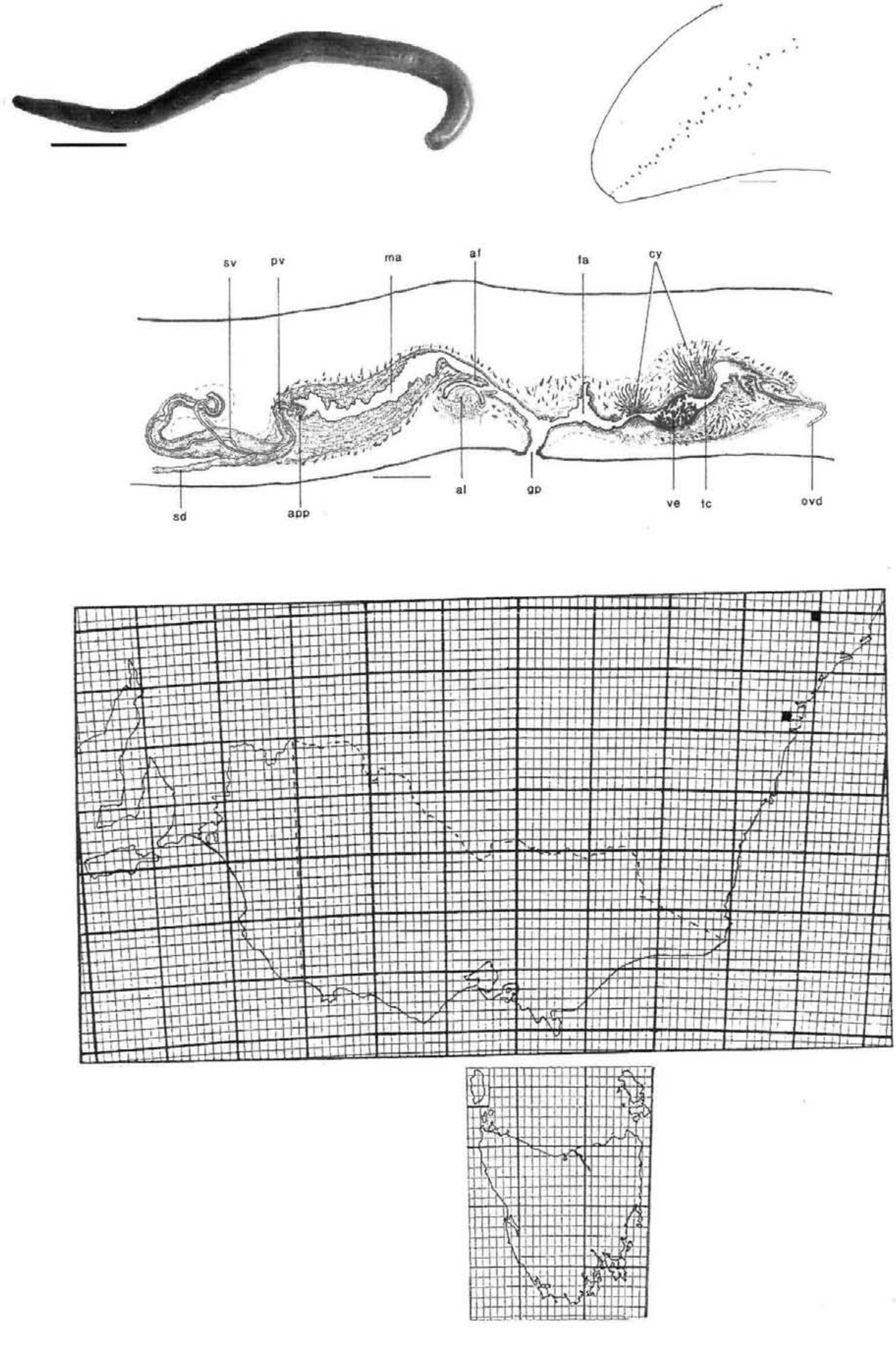
The Type species of the latter sub-genus has subsequently been synonymised under *Parakontikia ventrolineata*. There is presently uncertainty as to whether *Kontikia* and *Parakontikia* are synonymous (refer to discussion under *Parakontikia*, following). Recognition of the sub-genera of *Kontikia* by taxonomists is in abeyance pending further investigations.

5.3.2.11 Genus *Kynagoplana* gen.nov (Plate 5.19)

Kynagoplana gen.nov

Diagnosis: Caenoplaninae with elongate body, sub cylindrical in cross section, mouth just behind mid body, gonopore closer to mouth than to posterior end. Creeping sole more than 70% body width. Anterior adhesive pad or sucker absent. Sensory papillae absent. Eyes pigment cup-type, in single row around anterior tip, clustered anterolaterally, then in single staggered submarginal row posteriorly. Cutaneous musculature bipartite, weak, with helical, longitudinal muscles; longitudinal muscles in bundles. CMI 2.5 – 3.3. Parenchymal muscles strong, with predominantly mixed longitudinal and helical fibres in ring zone, PMI 38%. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; outer musculature with epithelium, longitudinal, then mixed circular-longitudinal muscles. Testes, sperm ducts ventral. Testes biserial, extend from just behind ovaries to level of mouth. Vasa deferentia unite dorsally to form common sperm duct; joins extra-bulbar seminal vesicle; penis eversible type, papilla or intra-antral papilla absent. Ovaries pre-oral, with multiple secondary ovaries. Ovovitelline ducts unite behind copulatory organs, form common duct that enters female genital canal almost horizontally, female genital canal in-line with female antrum. Female antrum elongate, complex, comprising secretory ridges separated by highly folded glandular mucosa. Adenodactyls absent. Type of genus:

Plate 5.19. The habitus, eye pattern, copulatory organs, and occurrence of *Kynagoplana* (Geoplanidae: Caenoplaninae)



Kynagoplana citrina (Wood), 1926

Etymology: *Kynagoplana*, the Hunter planarian, is a name contrived from the Greek *kynagos* hunter and Latin *plana* flat. Gender feminine. The name is an allusion to the presence of this genus in the Hunter Region of northern New South Wales, and also reflects the nature of these predators.

Distribution: Barrington Tops, 156°26' E 32°02'S, New South Wales. *Fagus* scrub.

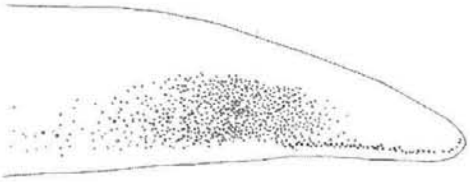
Systematic discussion: *Kynagoplana* shares with *Caenoplana* the apomorphy of a bipartite cutaneous musculature, and parenchymal musculature predominantly composed of mixed longitudinal and helical muscles in a ring zone. It is distinguished from *Caenoplana* by the extra-bulbar seminal vesicle, complex secretory structures in the female copulatory organs, and presence of multiple secondary ovaries.

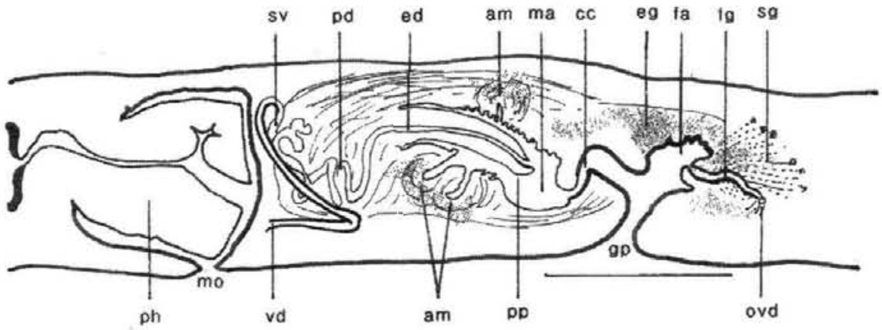
5.3.2.12 Genus *Lenkunya* (Plate 5.20)

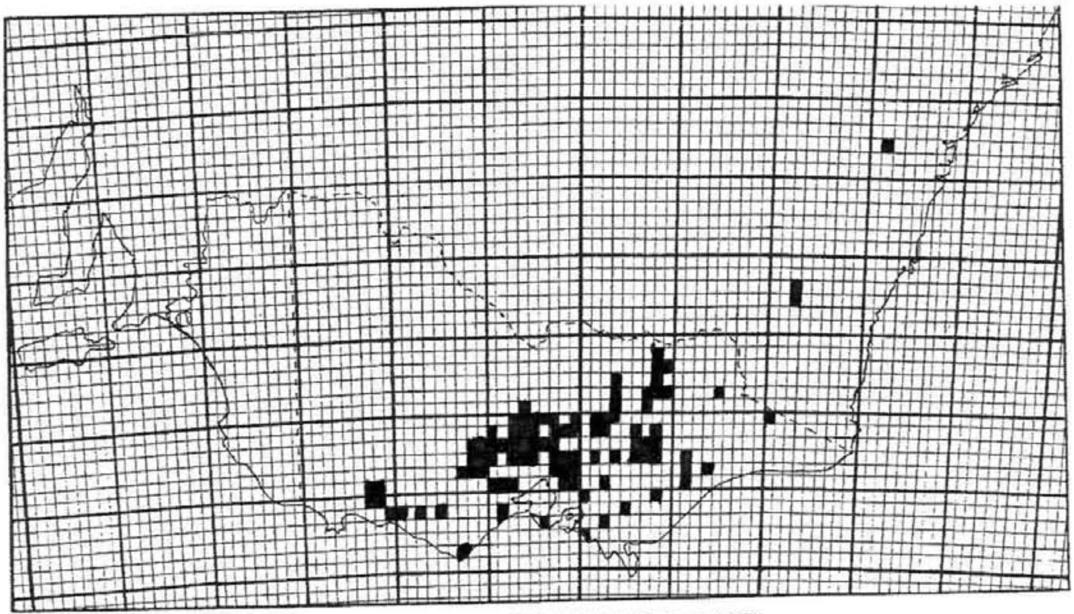
Lenkunya Winsor, 1991b
Lenkunya Winsor, 1991b; Ogren *et al* 1993
Caenoplana (part), Ogren & Kawakatsu 1991

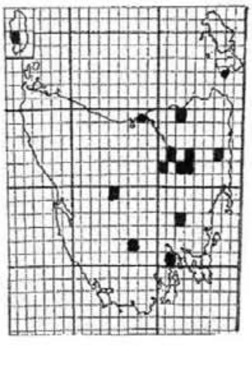
Diagnosis: Caenoplaninae with robust body, broadly convex dorsally, flat ventrally. Mouth just anterior to mid body, or central; gonopore closer to mouth than to posterior end. Creeping sole 70-80% of body width. Eyes pigment-cup type, in single row around anterior tip, crowded in characteristic lens-shape anterolaterally, extending to anterolateral region of dorsal surface; continue in staggered submarginal row to region of pharynx, very sparse thereafter. Cutaneous musculature tripartite, weak, with longitudinal muscles in small bundles. CMI 3.6 – 5.5%. Parenchymal musculature strong, with subneural ventral plate of longitudinal muscles, with ringzone of longitudinal muscles present as single fibres, with diagonal muscles, PMI 12 – 18%. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, longitudinal, then mixed longitudinal and circular muscles; outer epithelium, longitudinal, circular, then longitudinal muscles. Testes and sperm ducts ventral. Testes extend anterior to ovary, almost entire length of body. Ovary in anterior body

Plate 5.20. The habitus, eye pattern, copulatory organs, and occurrence of *Lenkunya* (Geoplanidae, Caenoplaninae)









third. Copulatory organs complex, with highly differentiated seminal vesicle – ejaculatory duct, with well developed penis papilla. An intra-penial papilla present in some species. Male and common atria highly glandular. Adenomuralia present. Ovovitelline ducts unite to form common ovovitelline duct which enters female genital canal ventrally. Female genital canal enters antrum horizontally. Type species: *Geoplana munda* Fletcher & Hamilton, 1888.

Etymology: *Lenkunya* is an aboriginal word meaning beautiful. The origin of the dialect and language group for the word is unknown. The name alludes to the attractively marked species in this genus. Gender feminine.

Distribution: Throughout the Warm and Cool temperate moisture regions of the Bassian zoogeographic sub-region in Tasmania, Bass Strait islands, south-eastern South Australia, Victoria, Australian Capital Territory, and central eastern New South Wales, and South Western zoogeographic sub-region, Western Australia.

Systematic discussion: In addition to *L. munda*, included in this genus (Winsor 1991c) are *L. adae* (Dendy 1891), *L. frosti* (Spencer 1891), *L. adae extralineata* (Dendy 1892d), *L. adae fusca* (Dendy 1894), *L. ornata* (Fletcher & Hamilton 1888), *L. virgata* (Fletcher & Hamilton 1888), *L. arenicola* (Steel 1901a). To these are added *L. pava* (Steel 1897) and *L. scaphoidea* (Steel 1901a) previously *Geoplana elegans* (renamed, Steel 1897). The Type specimens of *L. munda, L. ornata* and *L. virgata* are presumed lost. Preliminary investigations on non-Type material of the *L. adae – L. frosti* complex indicate that at least three or more species are present. Resolution of the complex must await analysis of the type and supplementary material. *Lenkunya* is differentiated from *Caenoplana* by the distinctive lens-shaped antero-lateral crowding of the eyes. It is distinguished from *Fletchamia* principally by its small robust body (elongate in *Fletchamia*), strong parenchymal musculature (weak in *Fletchamia*), pharyngeal musculature with mixed musculature only in inner pharyngeal wall (mixed musculature present in inner and outer walls in *Fletchamia*), and general morphology of the copulatory organs. *Lenkunya* is probably closely related to *Fletchamia*, and both have a similar distribution pattern. The innermost longitudinal muscle layer of the pharyngeal wall is absent in *Lenkunya adae.*

5.3.2.13 Genus *Nelipoplana* gen.nov. (Plate 5.21)

Nelipoplana gen.nov.

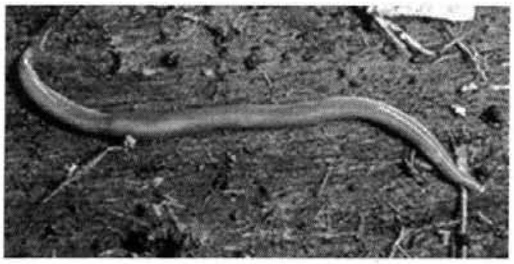
Australoplana (part), Winsor, 1991c

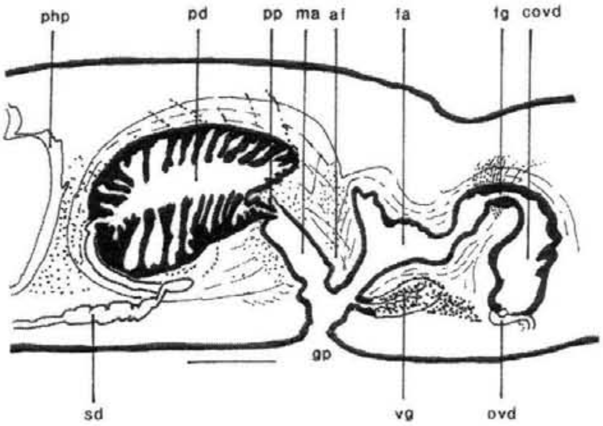
Diagnosis: Caenoplaninae with elongate, strap-like body, broadly convex dorsally, flat ventrally. Mouth situated in posterior third of body, gonopore closer to mouth than to posterior end. Creeping sole absent. Eyes pigment cup-type, very small, in single row around anterior tip, then sparsely laterally to posterior end. Anterior adhesive pad or cup absent. Cutaneous musculature tripartite, with circular, helical muscles; strong longitudinal muscles in bundles. CMI 9.4 – 18%. Parenchymal longitudinal muscles very weak or absent. Pharynx bell-form. Pharyngeal musculature inner, epithelium, longitudinal, circular, then longitudinal muscles; outer, epithelium, longitudinal, circular, then longitudinal muscles. Testes ventral, dorsal to dorso-lateral to nerve cords, extend from just behind ovaries to root of pharynx. Vasa deferentia enter penis bulb separately then unite before passing into seminal vesicle. Seminal vesicle, prostatic region ejaculatory duct tubular, sinuous, strongly muscular, or spermiducal vesicles with cavernous prostatic region. Penis papilla present. Ovaries in anterior third. Ovovitelline ducts unite, form common duct that enters ventroposterior end of female genital canal. Female genital canal with expanded proximal end, almost horizontal, enters terminal end of tubular female antrum. Musculature of copulatory organs mixed, with wickerwork circular and longitudinal muscles. Viscid gland absent. Adenodactyls absent. Type species: *Nelipoplana alba* (Dendy, 1891)

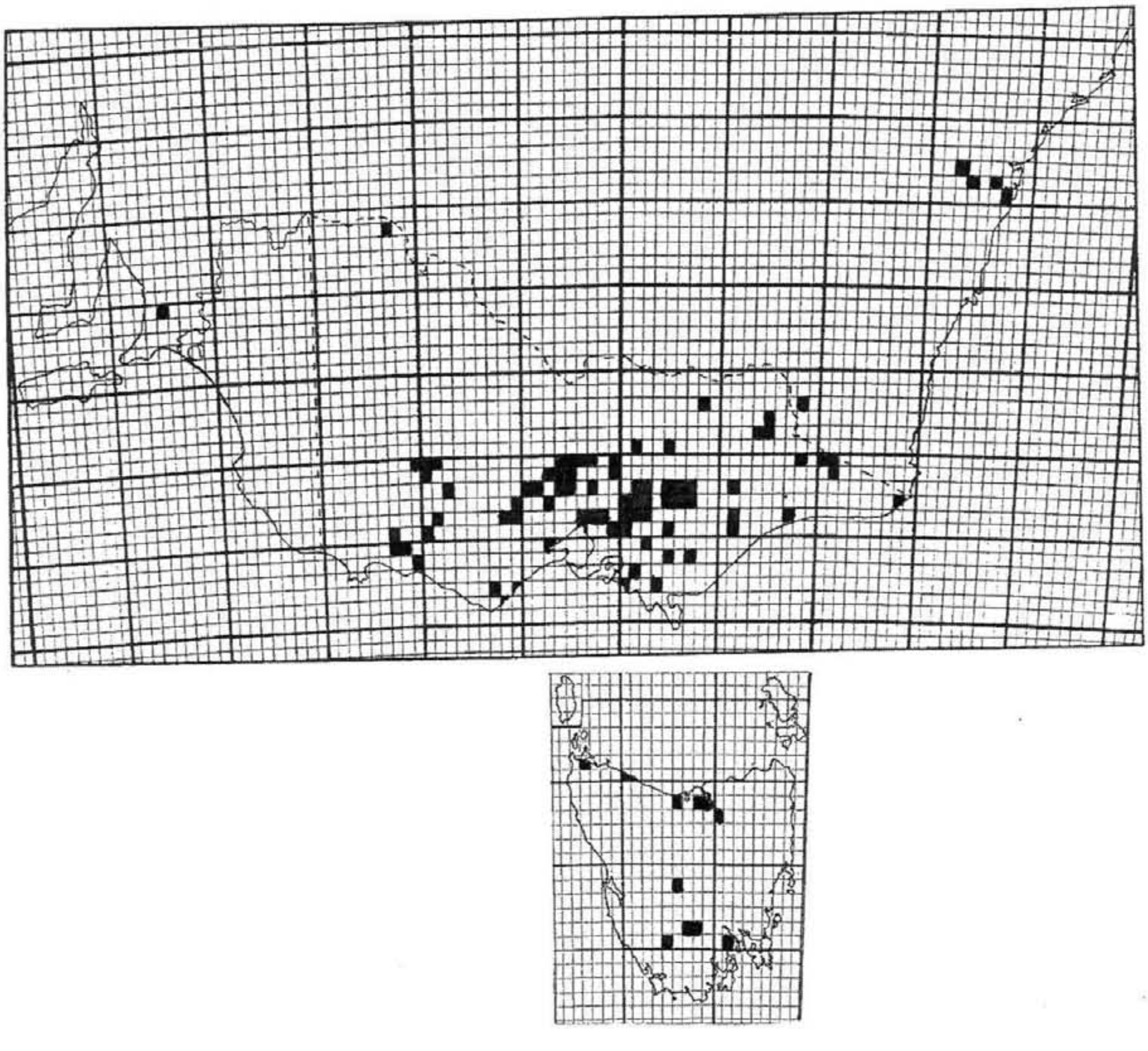
Etymology: The genus name *Nelipoplana* is derived from the Greek *nelipos* barefooted and Latin *plana* flat, and alludes to the absence of a ciliated creeping sole in this genus. Gender masculine. The Bare-footed planarian.

Distribution: Found in the cold, cool and warm moisture regions of the Bassian zoogeographic subregion of mainland of southeastern Australia, and Tasmania (Fig. 5.21). It possibly occurs in small pockets in cool upland sclerophyll forests in the Torresian zoogeographic subregion of southern and northern Queensland (material not yet examined anatomically). Adventive in New Zealand and

Plate 5.21. The habitus, eye pattern, copulatory organs, and occurrence of *Nelipoplana* sensu lato (Geoplanidae: Caenoplaninae)







the United Kingdom.

Nelipoplana sub.gen.nov.

Diagnosis: As previously defined, with seminal vesicle, prostatic region cavernous, small ejaculatory duct; penis papilla fixed type, encloses most of ejaculatory duct. Viscid gland present. Type species: *Nelipoplana (Nelipoplana) alba* (Dendy, 1891) gen. et sub. gen. nov.

Peokrypta sub.gen. nov.

Diagnosis: As previously defined, with seminal vesicle, prostatic region, ejaculatory duct tubular, sinuous, strongly muscular; penis papilla very small, enclosing little of the ejaculatory duct. Viscid gland absent. Type species: *Nelipoplana (Peokrypta) enigma* gen. et sub. gen. et sp. nov.

Etymology: *Peokrypta*, hidden penis, contrived from the Greek *peos* penis and kryptos hidden, alludes to the poorly differentiated penis papilla in species in this genus. Gender feminine.

Distribution: Southeastern Australia including Tasmania. Adventive in New Zealand and the U.K.

Systematic discussion: *Nelipoplana* is differentiated from *Australoplana* chiefly by the absence of a creeping sole (narrow sole present in species of Australoplana), presence of a bell-form pharynx (cylindrical in *Australoplana*), and in-line female antrum – genital canal (genital canal below female antrum in *Australoplana*). In both *Nelipoplana* and the more robust *Sokoplana* a ciliated creeping sole is absent. However *Nelipoplana* is differentiated from *Sokoplana* in having normal tripartite cutaneous musculature (additional layer of helical muscles present in *Sokoplana*), by the presence of mixed (wickerwork) musculature of the copulatory organs (well differentiated, not wickerwork in *Sokoplana*). However species of the subgenus *Nelipoplana (Nelipoplana)* share with *Sokoplana* a cavernous prostatic duct, and presence of a viscid gland, though in *Sokoplana* the bulb contains seminal vesicle and prostatic region, whilst in *Nelipoplana* the extra-bulbar spermiducal vesicles receive cyanophil secretions and appear to have the role of seminal vesicles; the prostatic region is intra-bulbar. The two genera may share a common lineage.

There are two distinct groups within *Nelipoplana*, mainly distinguished by major differences in the structure of the male copulatory organs (tubular, sinuous, strongly muscular seminal vesicle, prostatic region and ejaculatory duct, with poorly differentiated penis papilla *versus* spermiducal vesicles with cyanophil secretions (acting as seminal vesicles), with cavernous prostatic region and ejaculatory duct, with well differentiated penis papilla) and presence or absence of a viscid gland in gonad-mature specimens. These groups appear to be closely related and have in common their general external morphology and internal anatomy, with the exceptions previously noted. For this reason they are presently accommodated within the same genus. However given the quite disparate structures of the male copulatory organs, and pending the examination of other species in the genus, they are regarded here as the subgenera *Nelipoplana (Nelipoplana)* and *Nelipoplana (Peokrypta),* rather than species groups, best reflecting a possible dichotomy in a common lineage.

5.3.2.14 Genus *Newzealandia* (Plate 5.22)

Newzealandia Ogren & Kawakatsu, 1991
Newzealandia Ogren & Kawakatsu, 1991; Johns 1998

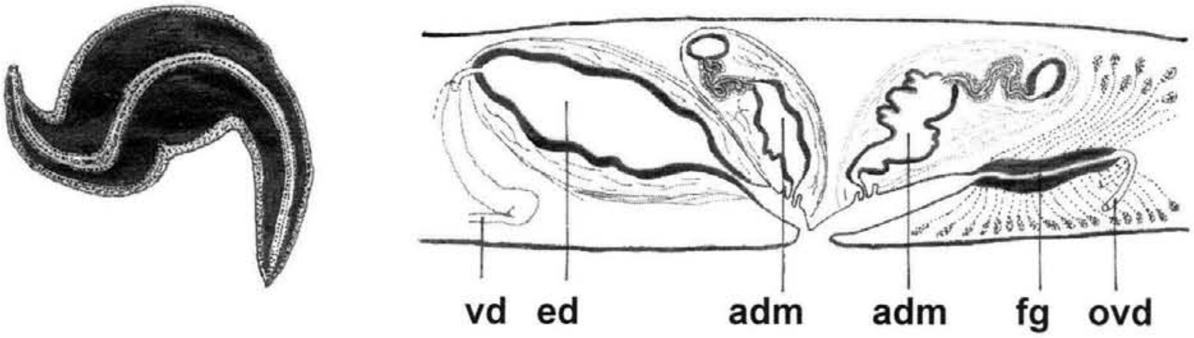
Diagnosis: Caenoplaninae with ventral testes; penis papilla absent; recessed accessory glands present in copulatory organ, but without adenodactyls.

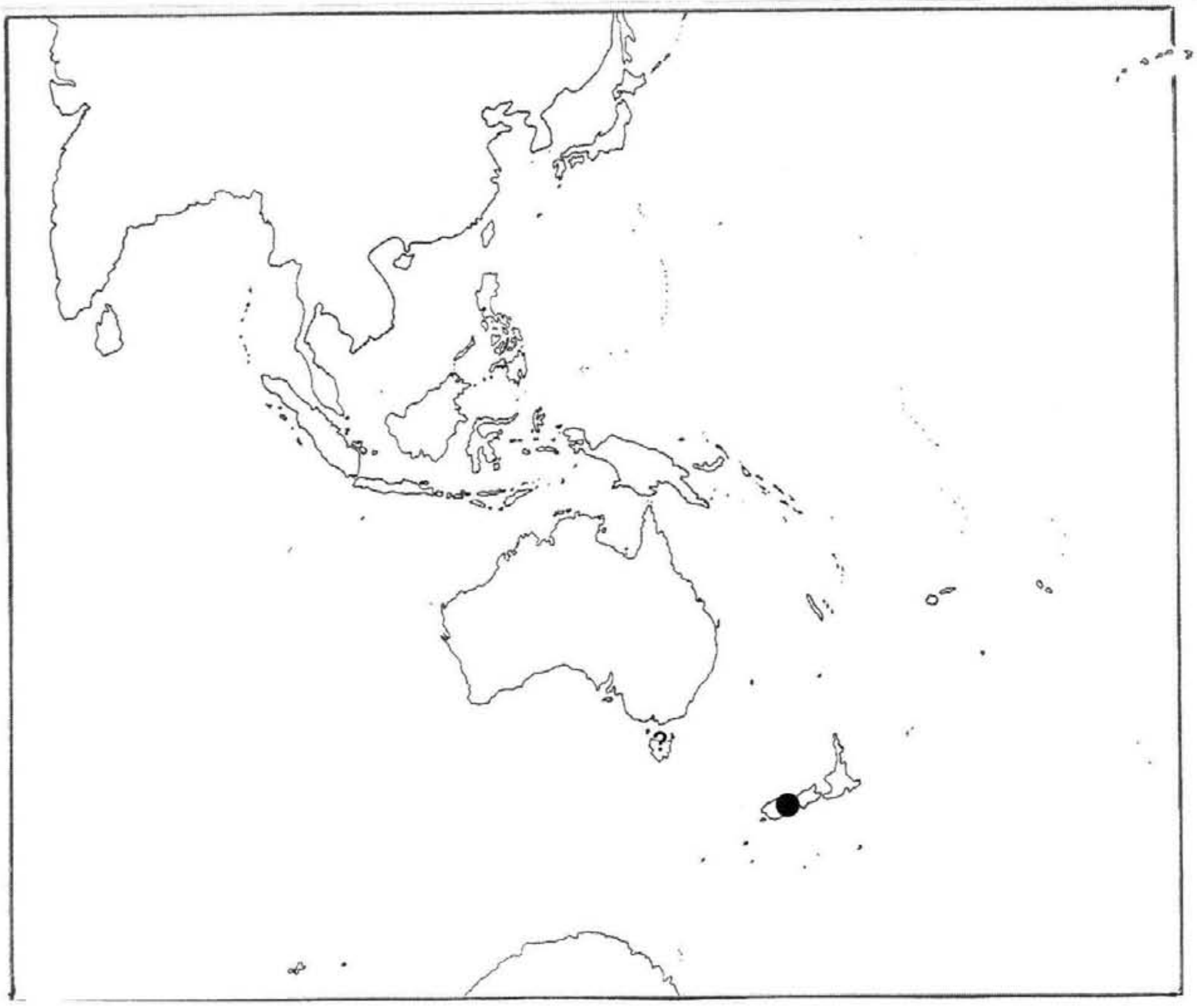
Etymology: Named after New Zealand where the genus occurs.

Distribution: Localities throughout New Zealand. Possibly also in Tasmania.

Systematic discussion: This genus is reluctantly accepted by austral taxonomists (Johns pers. comm) as it is another poorly defined collective genus, incorporating some 17 species and more than ten undescribed species (Johns 1998). The accessory glands in this genus are adenomuralia, Type VII musculoglandular organs. Undescribed material in the author's (LW) collection suggests that the genus

Plate 5.22. The habitus, copulatory organs and occurence of *Newzealandia* (Geoplanidae: Caenoplaninae)





may also be present in Tasmania.

5.3.2.15 Genus *Parakontikia* (See Plate 5.18)

Parakontikia Winsor, 1991b

Parakontikia Winsor, 1991b; Ogren *et al* 1993; Jones *et al* 1998

Kontikia (part), Ogren & Kawakatsu, 1991

Laubenfelsia Ogren *et al*, 1993

Diagnosis: Caenoplaninae with elongate, cylindrical to subcylindrical body. With mouth situated just posterior to mid venter; gonopore closer to mouth than to the posterior end. Anterior sucker pad or cup absent, sensory papillae absent. Creeping sole 54-84% body width. Eyes pigment cup-type, generally large, in single row around anterior lip, in submarginal row posteriorly without antero-lateral crowding. Cutaneous musculature tripartite, with circular, helical and longitudinal muscles; with longitudinal muscles strong in bundles, generally equally developed bundles dorsally and ventrally. CM1 6.7-13.%. Parenchymal longitudinal muscles present in a ventral plate or ring-zone; PMI (ring zone or plate) 5.5-13.8%. Pharynx cylindrical, with pharyngeal musculature with inner epithelium, then mixed circular – longitudinal muscles; with outer epithelium, then longidudinal, circular, then longitudinal muscle layers. Testes and sperm ducts ventral; testes extend from just behind ovaries to the copulatory organs; efferent ducts generally complex. Penis of the eversible type without a papilla, with elongate bulb. Male antrum strongly invested with circular muscles. Ovaries anterior. Ovovitelline ducts unite, form long common ovovitelline duct, enters ventroposterior female genitalcanal. Female genital canal generally gently sloping dorsally, enters female antrum dorsoposteriorly. Ovovitelline, common ovovitelline ducts may divide and loop posteriorly. Adenodactyls absent. Viscid gland absent. Type species: *Geoplana ventrolineata* Dendy, 1892a.

Etymology: *Parakontikia* from the Greek *para*, beside, and *Kontikia*, alludes to the similarities between this genus and the Indo-Pacific genus *Kontikia.*

Distribution: Western Australia, Papua-New Guinea.

Systematic discussion: The genus includes *P. ventrolineata* (Dendy, 1892a); *P. atrata* (Steel, 1897); *P coxii* (Fletcher & Hamilton, 1888); and *P. melanochroa* (Steel, 1901a). The Papua-New Guinea species *Caenoplana chapmani* Ogren & Kawakatsu, 1988b has only 16 large eyes around the anterior tip and for a short distance laterally; other characters accord with this genus to which the species is transferred.

Parakontikia ventrolineata, originally from southern Queensland, is a tramp species, adventive in southern Australian states, Norfolk Island, New Zealand, Hawaii, United States, and United Kingdom, often in association with *Caenoplana coerulea.*

Parakontikia is principally differentiated from *Kontikia* by the absence of a penis papilla (*Kontikia* has a permanent blunt penis papilla), the penis being formed by eversion of the antrum (*Kontikia* protrusible penis). This is a constant and pronounced feature of the type species and undescribed taxa in *Parakontikia* and has parallels with the apappillate penis and copulatory organs present on *Dolichoplana,* just as have the copulatory organs of *Kontikia* species general similarities with *Cotyloplana.* All four genera also share similar pharyngeal musculature, but not eye type (rhynchodeminids with lens-type eyes, caenoplaninids with pigment-cup eyes). Sluys (1995) has drawn attention to the pan-Pacific tracks of *Kontikia, Dolichoplana,* and *Rhynchodemus.* Synonymy of *Parakontikia* with *Kontikia* (in Jones *et al* 1998) has been proposed, but a final decision must await the anatomical examination of described and undescribed taxa in the author's (LW) collection.

5.3.2.16 Genus *Reomkago* (Plate 5.23)

Reomkago Winsor, 1991c
Reomkago Winsor, 1991c; Ogren *et al* 1993b
Australopacifica (part), Ogren & Kawakatsu 1991

Diagnosis: Caenoplaninae with elongate body, quadrangular in cross section with rounded corners; dorsal and ventral surfaces flat; with lateral surfaces inwards sloping in both living, preserved specimens. Mouth posterior of mid- venter; with gonopore half way between mouth and posterior end. Creeping sole almost 50%

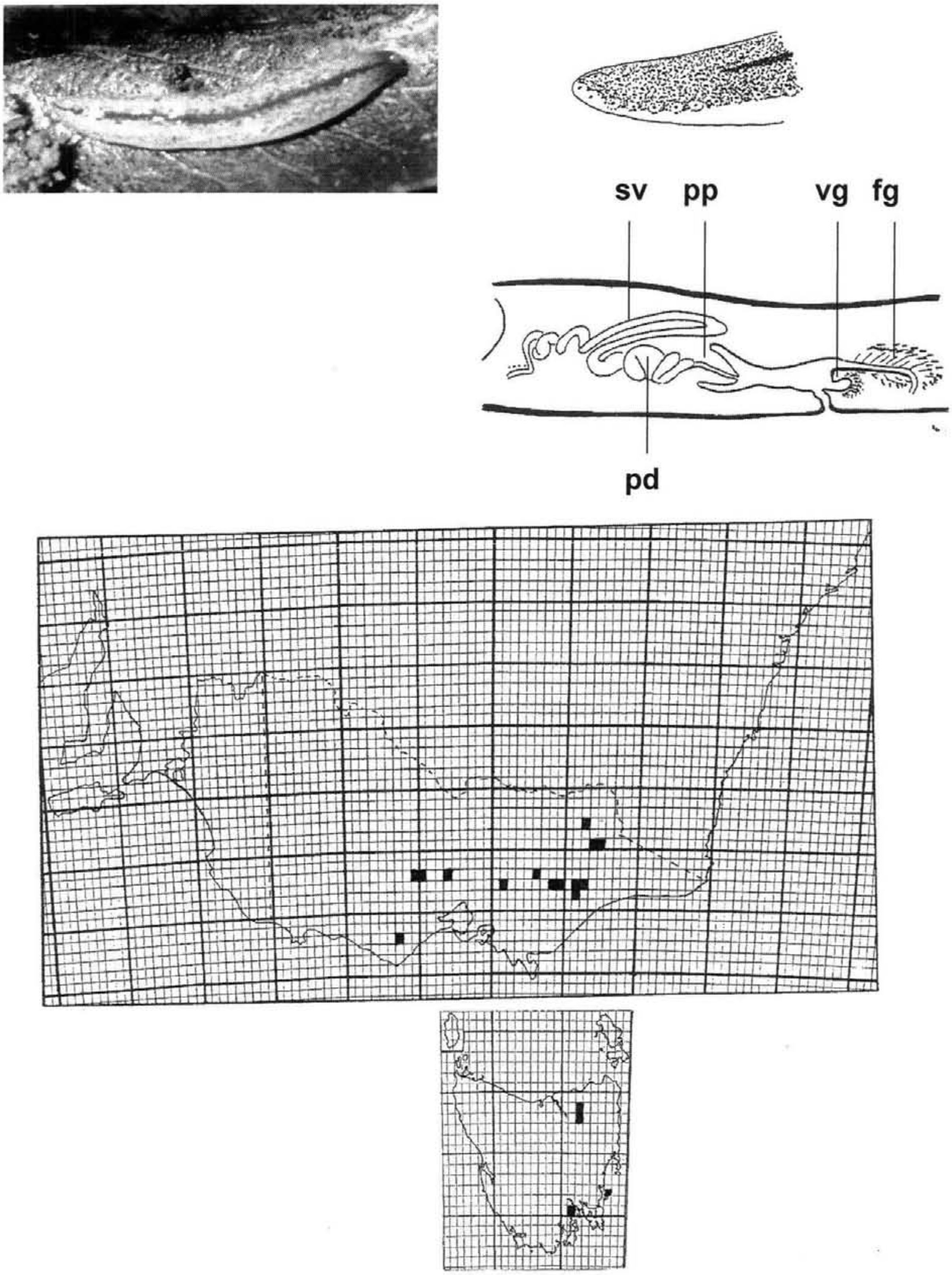
body width. Eyes pigment cup-type, small, in single row around anterior tip, in a staggered sub-marginal row postediorly without anterolateral crowding. Anterior adhesive sucker pad or cup absent. Sensory papillae absent. Cutaneous musculature tripartite, strong, comprising circular, helical, longitudinal muscles; with longitudinal muscles in bundles, ventral layer thicker than that dorsally. CMI 9-18%. Longitudinal parenchymal musculature weak to absent, with strong periintestinal muscles. Mixed oblique parenchymal muscles form strong ventral plate. PMI 8.5-15% (plate); with very strong laterally situated dorso-ventral muscles, largely responsible for quadrangulate shape. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, mixed circular – longitudinal muscles; outer musculature with epithelium, longitudinal, circular muscles, then loose longitudinal muscle layer. Copulatory organs complex. Testes, ventral, dorsal to nerve cords, below and between gut diverticula, extend from ovaries to just before pharynx. Efferent ducts simple.Vasa deferentia ventral to nerve cords, rise at pharynx, separately enter seminal vesicle which skirts anterior end of copulatory organs; unite mid anterior bulb, form common sperm duct, enters seminal vesicle dorsoanteriorly; with prostatic vesicle. Ejaculatory duct strongly muscular, with fixed-type penis papilla. Male antrum strongly muscular. Ovaries anterior; ovovitelline ducts separately enter posterior end of female genitalcanal; female genital canal opens dorsoposteriorly into female antrum. Female antrum lined by strand, globule sclerotin-forming epithelium.Vitellaria extensive, surround gut. Adenodactyls absent. Resorptive bursa may be present. Viscid gland may be present. Type species: *Geoplana quadrangulata* Dendy, 1891

Etymology: The generic epithet is a combination of the initials of R. E. Ogren and M. Kawakatsu with the Greek suffix *-ago*, to lead, guide, stimulate, promote. Gender masculine. It honours the industry and magnificent achievement of these two compilers in indexing the species of the Terricola, thus greatly facilitating future taxonomic studies.

Distribution: Present in the Cool to Cold temperate moisture zones of the Bassian zoogeographic region of Tasmania, Victoria, and New South Wales.

Systematic discussion: The genus includes *R. quadrangulatus* (Dendy,

Plate 5.23. The habitus, eye pattern, copulatory organs, and occurrence of *Reomkago* (Geoplanidae: Caenoplaninae)



1891); *R. wellingtoni* (Dendy, 1892c) and *R. flynni* (Dendy, 1915). These small agile species are distinguished from other small flatworm taxa by their pale ground colour with distinctive brown mottling, and distinctive cross-sectional shape. The eyes are generally haloed. The diagnosis is based upon material collected at Creswick, some 60 km from the type locality at Macedon, central Victoria. The Syntypes have not yet been examined.

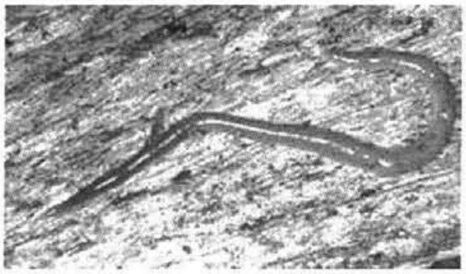
5.3.2.17 Genus *Sokoplana* gen.nov. (Plate 5.24)

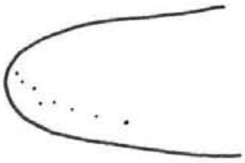
Sokoplana gen.nov.

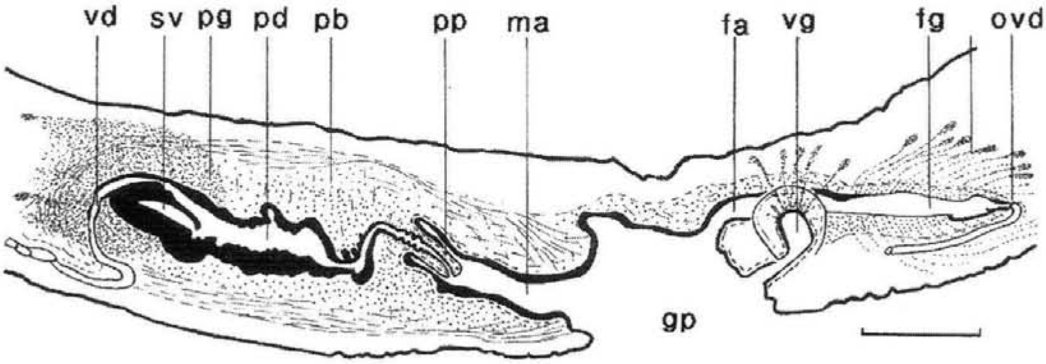
Diagnosis: Caenoplaninae with elongate body, convex dorsally, flat ventrally. Mouth and gonopore situated in third body quarter. Creeping sole absent. Eyes pigment cup-type, very small, in single row around anterior tip, then sparsely laterally to posterior end. Anterior adhesive pad or cup absent. Cutaneous musculature tripartite, with circular, decussating helical - helico-circular, and longitudinal layers; dorsal and ventral cutaneous musculature equal; with strong longitudinal muscles in well defined bundles. CMI 11%. Parenchymal musculature weak; longitudinal muscles absent. Pharynx bell-form. Pharyngeal musculature with inner epithelium, thin longitudinal, thick circular, then thin longitudinal muscle layers; outer epithelium, longitudinal, strong circular, then loose longitudinal muscle layers. Testes ventral, lateral to nerve cords, extend from just behind ovaries to root of pharynx. Vasa deferentia enter penis bulb separately then unite before passing into anterior – antero-dorsal wall of seminal vesicle. Bulb lumen cavernous, with seminal vesicle, prostatic region, ejaculatory duct. Penis papilla fixed-type; papilla without glandular ducts. Ovaries anterior, with tuba. Ovovitelline ducts unite at posterior end of female genital canal. Female genital canal horizontal, enters terminal end of elongate female antrum. Musculature of copulatory organs differentiated, with outer longitudinal and inner helical muscle layers. Viscid gland present. Adenodactyls absent. Type species: *Sokoplana kanangra* gen. et sp. nov.

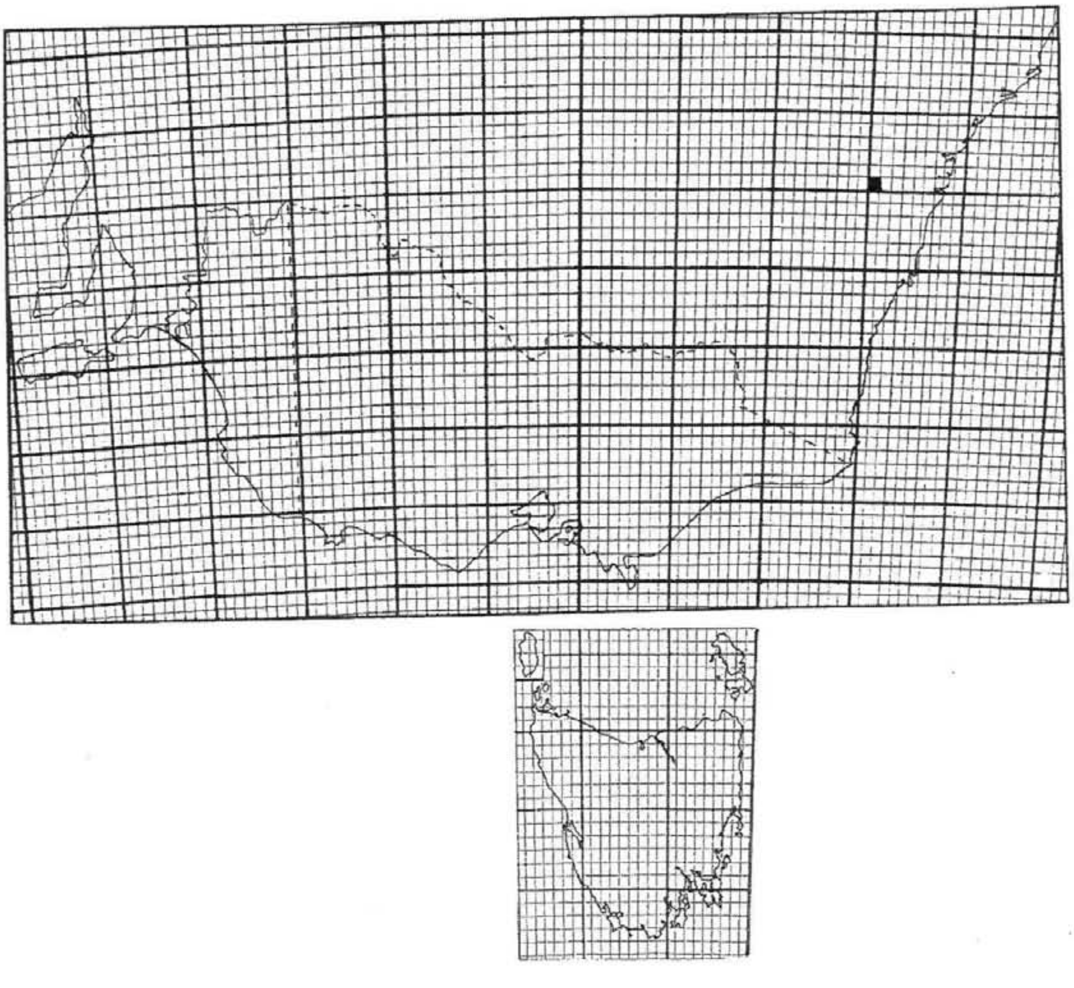
Etymology: The genus name *Sokoplana* is derived from the Greek *sokos* strong, and Latin *plana* flat, and alludes to the physical attributes of species of the genus, in particular the strong cutaneous musculature with the unusual additional helical muscles. The Strong planarian. Gender feminine.

Plate 5.24. The habitus, eye pattern, copulatory organs, and occurrence of *Sokoplana* (Geoplanidae: Caenoplaninae)









Distribution: The genus occurs in the Cool temperate moisture region of the Bassian zoogeographic sub-region of New South Wales.

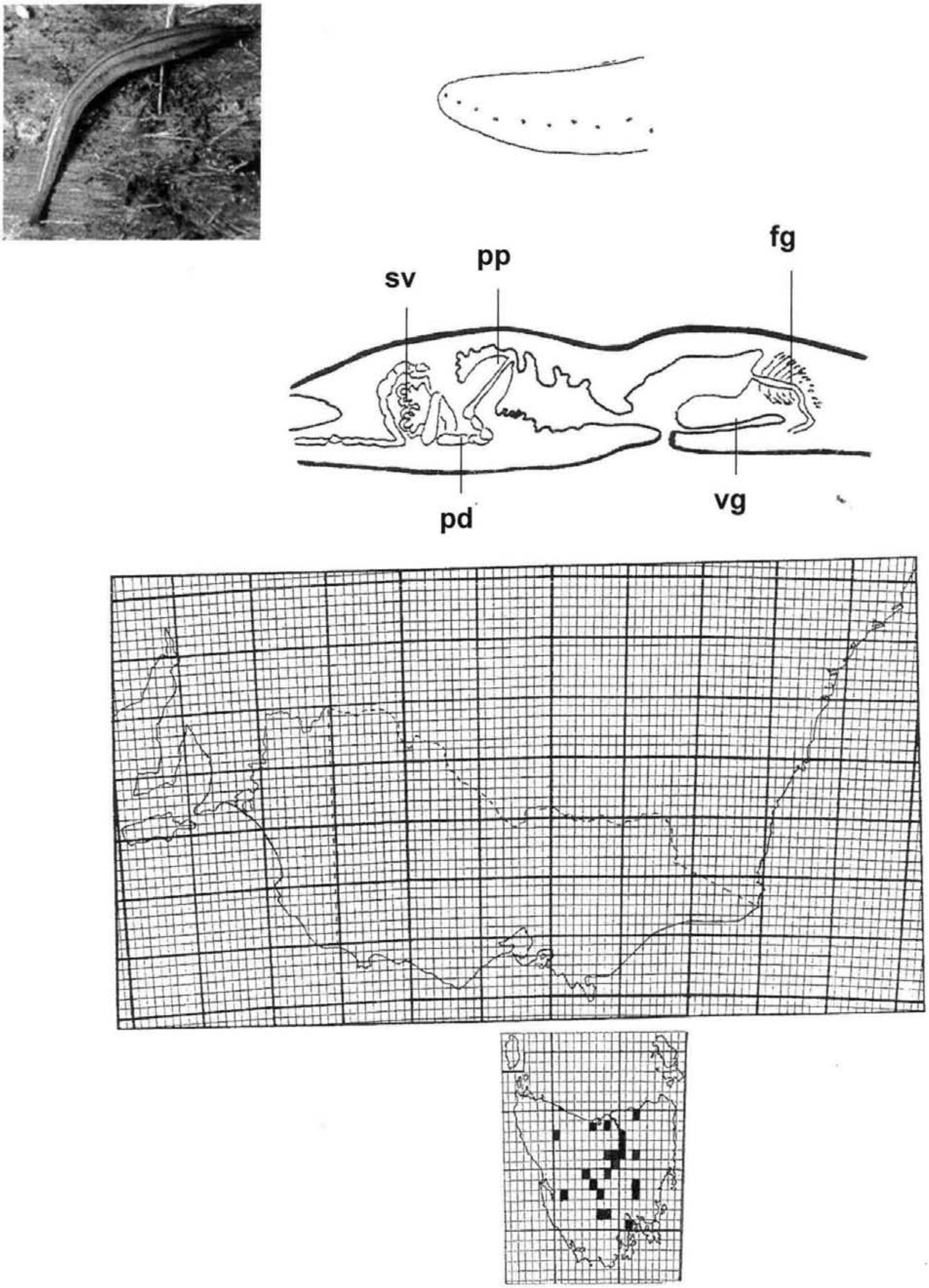
Systematic discussion: A comparison of taxa, including *Sokoplana*, of similar external appearance in the old *Australoplana sensu lato* group is provided in Appendix 8. *Sokoplana* is unique amongst these taxa in having an unusual helical muscle sheath within the cutaneous musculature, also reflected in the musculature of the pharynx and copulatory organs. *Sokoplana* stands closest to *Apogaioplana*, and a differential diagnosis for these two taxa has been provided previously within the discussion for the latter genus. There is presently only one species, *Sokoplana kanangra*.

5.3.2.18 Genus *Tasmanoplana* (Plate 5.25)

Tasmanoplana Winsor, 1991c
Tasmanoplana Winsor, 1991c; Ogren *et al* 1993b
Australopacifica (part), Ogren & Kawakatsu 1991

Diagnosis: Caenoplaninae with elongate, sub-cylindrical body, flat ventrally, with mouth just posterior of mid body, with gonopore nearer to mouth than to posterior end. Creeping sole over 60% body width. Eyes pigment cup-type, small, in single row around anterior tip, extending posteriorly in single staggered submarginal row without antero-lateral crowding. Anterior adhesive sucker or cup absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular, decussate helical and longitudinal muscles, with longitudinal muscles in bundles. CMI 7%. Parenchymal musculature with very strong, compact longitudinal muscle fibres in ring zone. PMI (ring zone) 11.5-20%. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then mixed circular and longitudinal muscles; outer musculature with epithelium, longitudinal, circular, then mixed circular-longitudinal muscles. Testes and sperm ducts ventral; testes extend from just behind ovary to well before pharyngeal root. Efferent ducts simple. Copulatory organs simple. Vasa deferentia unite mid anterior of penis bulb, form common sperm duct, enters dorsal end of seminal vesicle, with well differentiated prostatic duct, ejaculatory duct, with small well formed penis papilla; male antrum elongate, with deeply folded walls, sclerotin

Plate 5.25. The habitus, eye pattern, copulatory organs, and occurrence of *Tasmanoplana* (Geoplanidae: Caenoplaninae)



strand secretory epithelium. Ovaries anterior. Ovovitelline ducts duct enter female genital canal ventrally; female genital canal enters female atrial mid posterior wall horizontally; female antrum capacious, with sclerotin globule-secreting epithelium. Viscid gland present. Vitellaria between gut diverticula. Adenodactyls absent. Type species: *Planaria tasmaniana* Darwin, 1844.

Distribution: *Tasmanoplana* occurs in the Cool temperate moisture zone of the Bassian zoogeographic sub-region of Tasmania. The genus may occur in southwestern Australia.

Etymology: *Tasmanoplana* is derived from Tasmania, and Latin *plana* flat, Tasmanian planarian. It alludes to the first record of terrestrial flatworms in Australia. Charles Darwin collected the type species during the visit of H.M.S. Beagle to Hobart, Tasmania, 2nd-17th February 1836.

Systematic discussion: The genus includes: *T. tasmaniana* (Darwin, 1844), *T tasmaniana* var *flavicincta* (Steel, 1901b), and *T. lyra* (Steel, 1901b). The species *T. bafflouri* (Graff, 1899) and *T. comitalis* (Dendy, 1915) may also be referred to the genus.

The very strong parenchymal longitudinal musculature and general morphology is reminiscent of a subantarctic terricolan (undescribed, Macquarie Island). *Tasmanoplana* is differentiated from *Reomkago* principally by strong parenchymal longitudinal musculature (very weak to absent in *Reomkago*), flattened oval cross-sectional shape (quadrangulate in *Reomkago*), and pharyngeal musculature (mixed in both inner and outer musculature in *Reomkago*). Both share similar general conformation of the copulatory organs. *Tasmanoplana* is distinguished from *Kontikia* and *Parakontikia* chiefly by pharyngeal musculature, with layers of mixed circular-longitudinal muscles in both inner and outer pharynx (*Kontikia* and *Parakontikia* with mixed musculature only in inner pharynx), and greater differentiation of copulatory organs, especially seminal vesicle and prostatic duct, and well formed penis papilla (simple seminal and prostatic duct; blunt penis papilla in *Kontikia*, *Parakontikia* penis apapillate).

5.3.2.19 Genus *Thosteelia* gen.nov. (Plate 5.26)

Thosteelia gen.nov.

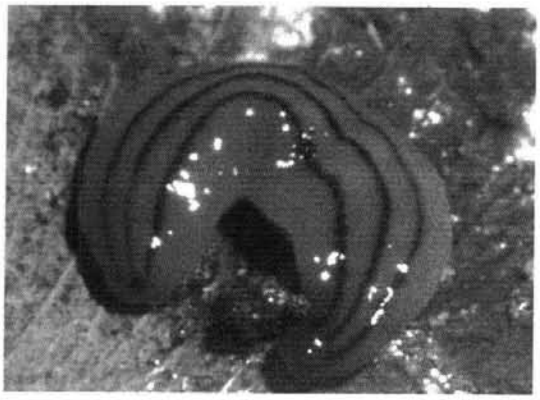
Diagnosis: Caenoplaninae with small, robust, elongate body. Creeping sole two thirds of body width. Anterior end slightly expanded, with single antero-ventral adhesive pad, incompletely bipartite. Eyes pigment cup–type, in single row around anterior tip, with slight crowding laterally, and in a single row submarginally to posterior extremity. Sensory pits simple, on either side of but not continuous around anterior tip. Cutaneous musculature tripartite, weak, unevenly developed, dorsal musculature stronger than ventral musculature. CMI 2.7 %. Ventral cutaneous longitudinal muscles insunk entally to cutaneous nerve net. Mediad dorsal cutaneous longitudinal muscles almost dorsoventral. Parenchymal musculature strong comprising strong transverse and dorsoventral muscles, and subneural plate and ringzone of longitudinal muscles. Insunk cutaneous longitudinal muscles and ventral plate acts as retractor for adhesive pad. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then longitudinal muscles; outer epithelium, longitudinal, then circular muscles. With oesophagus. Penis papilla fixed-type. Female genital canal horizontal. Testes and ovaries pre-pharyngeal, half way between anterior tip and mouth. Vitellaria surround gut diverticula. Type and only species: *Thosteelia mesibovii*

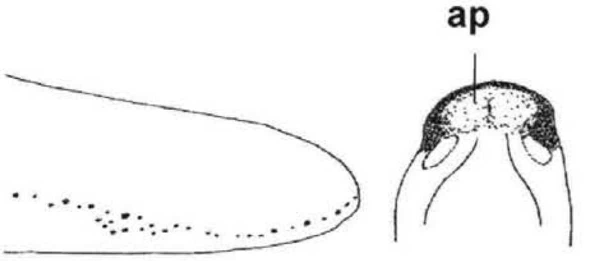
Etymology: *Thosteelia* honours Thomas Steel (1858-1925) for his research on the austral Terricola and the legacy of his specimens, library and literature. Gender feminine. The specific epithet *mesibovii* is for Dr Bob Mesibov in appreciation of a long friendship, welcome help and enthusiasm in collecting Tasmanian flatworms, and a common interest in the austral cryptofauna.

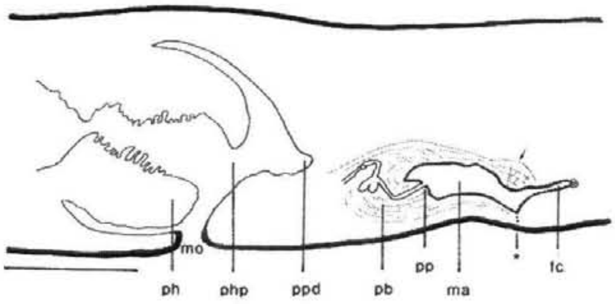
Distribution: Table Cape, N.W. Tasmania, 145°44'E 40°57'S. Coastal, cool temperate Bassian. Known only from this site.

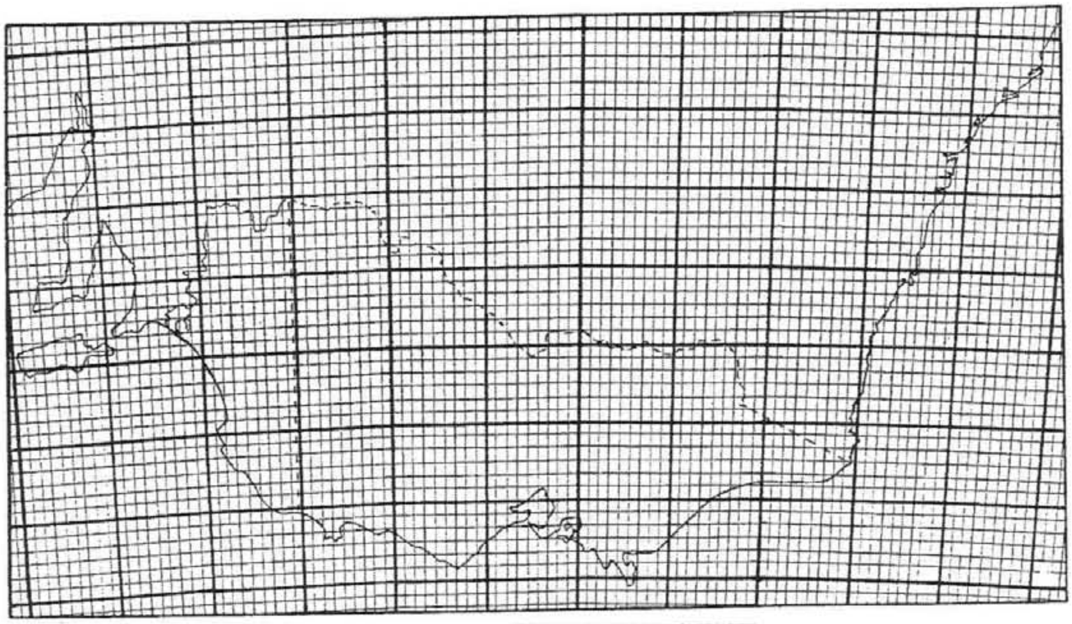
Systematic discussion: The differential diagnosis between the three caenoplaninid taxa with anterior suckers and pads: *Coleocephalus fuscus, Pimea monticola,* and *Thosteelia mesibovii,* is provided elsewhere (Appendix 8).

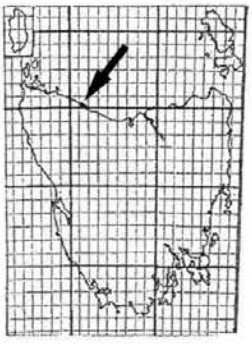
Plate 5.26. The habitus, eye pattern, anterior ventral surface showing adhesive pad (ap), copulatory organs, and occurrence of *Thosteelia* (Geoplanidae: Caenoplaninae)











5.4 BIPALIIDAE

Diagnosis (Kawakatsu *at al* 2002): Body elongate and flattened, with a semilunate head; with numerous small marginal eyes, and sensory groove around head; creeping sole begins at the base of the headplate.

5.4.1 Genus *Bipalium* (Plate 5.27)

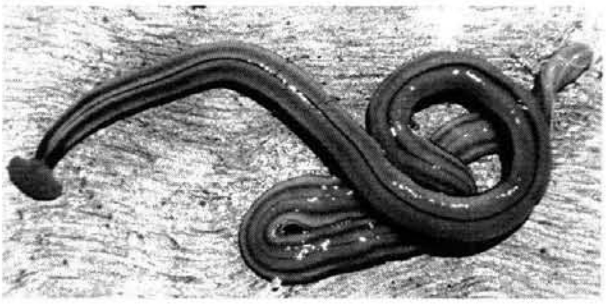
Bipalium Stimpson, 1858
Sphyrocephalus Schmarda, 1859
Dunlopea Wright, 1860
Bipaliuria Stimpson, 1861
Perocephalus Graff, 1896b
Placocephalus Graff, 1896b

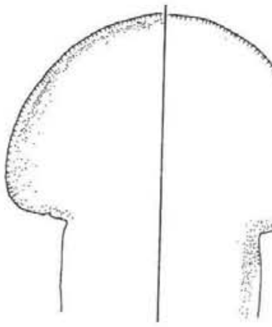
Diagnosis (Kawakatsu *et al* 2002): Bipaliidae with simple copulatory organs and without accessory ducts, or copulatory bursa; male and female exit ducts are separated by a fold of tissue before they enter the common genital antrum.

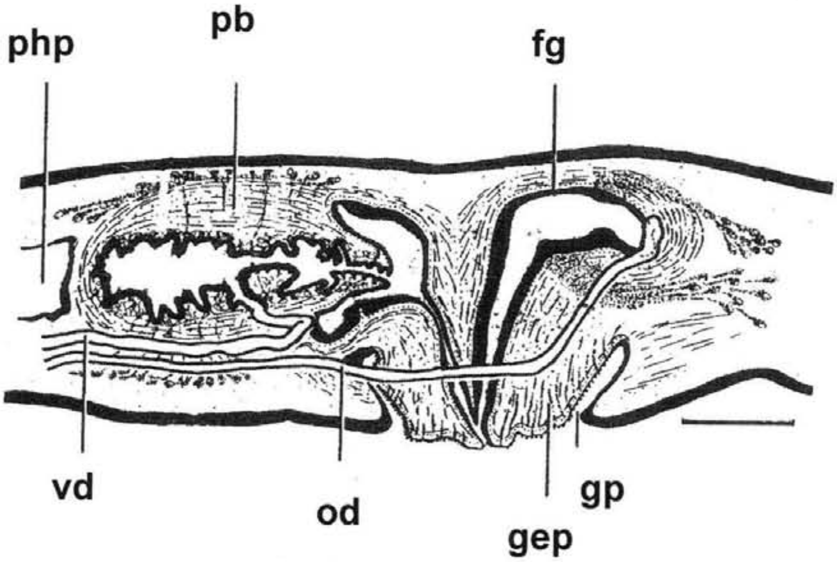
Etymology: *Bipalium* from the Latin *bi,* two and *pala* shovel, alludes to the shovel-like shape of the head, characteristic of the genus. The Shovel-headed flatworm. Gender feminine.

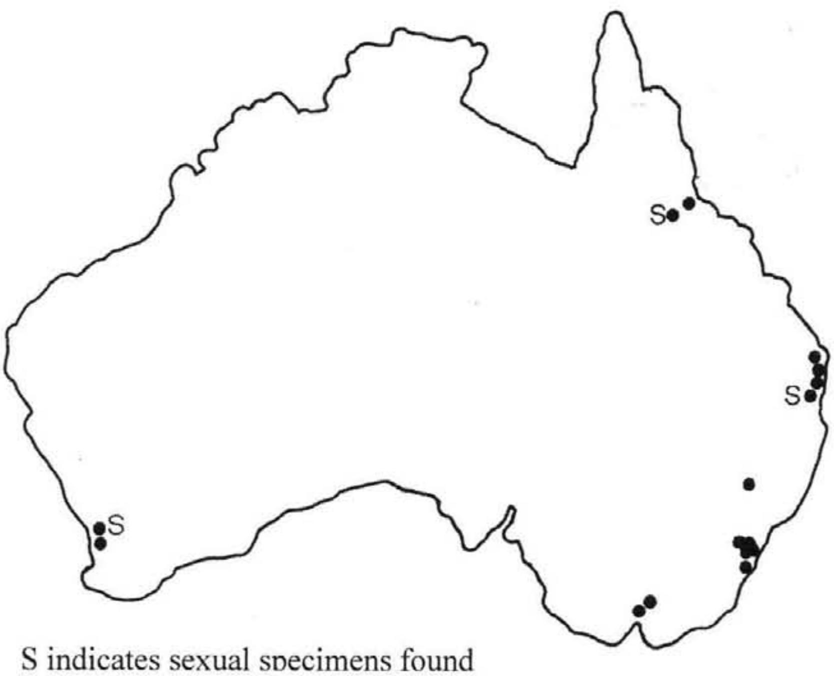
Distribution: With the exception of *Bipalium kewense* Moseley, 1878, the Bipaliidae predominantly occur in the Oriental zoogeographic region, with elements in the Madagascan, Wallacean, and adjacent Palaearctic regions. Originally from Vietnam, *Bipalium kewense* is an adventive cosmopolitan species elsewhere (Winsor 1983), and the sole representative of the genus in Australia (Winsor 1985). *Bipalium kewense* is included here because records of the species in Australia pre-dated by some years the discovery and description of the species in the U.K., leading to erroneous speculation that the species originated in Australia (Anon 1968; Pope 1974).

Plate 5.27. The habitus, eye pattern, copulatory organs, and Australian occurrence of *Bipalium kewense* (Bipaliidae)









S indicates sexual specimens found

5.5 PHYLOGENY

The focus of this thesis was initially to gather data to facilitate cladistic analysis of the Terricola of the Australasian region, rather than to undertake phylogenetic analyses. Furthermore, time and circumstances have precluded such analysis of this data using available cladistic analytical software. Nevertheless some broad observations on possible relationships between taxa are possible.

The taxonomy of the Terricola is in a state of flux, with current taxonomic revisions of the Bipaliidae (Kawakatsu *et al* 2002), studies on the Geoplaninae (Carabayo & Leal-Zanchet 2001), and studies on the austral taxa (this thesis) in progress. More importantly the findings of recent molecular studies have significant implications for the taxonomy of the Terricola.

Early phylogenetic analysis of triclads using morphological characters supported the monophyly of the four infraorders of the suborder Tricladida – the Maricola, the Cavernicola, the Paludicola, and the Terricola (Ball 1981; Sluys 1989a), although the status of the Terricola was problematic (Ball 1981). Monophyly of the Terricola is not strongly supported by recent investigations using 18S rRNA sequences (Carranza *et al.* 1998a,b; Baguñà *et al* 2001) and its position within the Tricladida needs to be reassessed. These recent analyses support the monophyly of the Maricola, and paraphyly of the Paludicola and Terricola + Dugesiidae. They do not support the monophyly of the Terricola, and Dugesiidae. On the basis of their molecular studies Carranza *et al* (1998) suggest that the Infraorder Terricola seems redundant and would be better considered, like the Dugesiidae, a family. However these authors underline the need for denser sampling to better test the monophyly or polyphyly of the Terricola, a view with which I fully concur.

In the cytochrome oxidase 1 (CO1) analyses, the Terricola and Dugesiidae cluster together though the low support does not permit firm conclusions to be drawn regarding the monophyly of each of these clades (Baguñà *et al* 2001). However within the Terricola the family Bipaliidae, and the rhynchodemid subfamily Microplaninae appear highly supported (Baguñà *et al* 2001).

Carranza *et al* (1997, 1998) and Baguñà *et al* (2001) have also shown the monophyly of the Geoplanidae, but polyphyly of the Rhynchodemidae where the Microplaninae and Rhynchodeminae form separate clades, agreeing with the view, based upon morphological characters (L. Winsor and P.M. Johns, pers. comm. to Baguñà), which considers the Rhynchodemidae an artificial clade. Molecular analyses of representatives of the Geoplanidae have so far included only members of the Caenoplaninae. Molecular analyses of geoplaninids, anzoplaninids, and especially the pelmatoplaninids are required before a firm view of the apparent monophyly of the Geoplanidae emerges.

Bipalium, Arthurdendyus (= *Artioposthia triangulata in* the molecular studies), *Nelipoplana* (= *Australoplana* in the molecular studies), and *Caenoplana* cluster in the molecular analyses (Carranza *et al* 1998; Baguñà *et al* 2001). All share the same or a derived form of the pharyngeal musculature seen in the Planariidae, Dugesiidae and Maricola (Chapter 4, Table 4.5). The rhynchodeminid *Platydemus manokwari* and microplanids, which have derived dendrocoelid-type pharyngeal musculature, cluster in the molecular studies with the dugesiids rather than with the dendrocoelids as would be expected if the pharyngeal musculature character was a good predictor of lineage. Again greater sampling of a variety of terricolans is required for both molecular and morphological analyses in order to assess the application and taxonomic usefulness of paludicolan pharyngeal muscular characters and states to the Terricola.

Carranza *et al* (1998) considered that the strong links between the Terricola and freshwater dugesiids, indicated by the molecular evidence, suggests that invasion and colonization of land by terricolans occurred from freshwater ancestors and not from marine triclads as previously hypothesized (Marcus 1953, Ball 1981, Sluys 1989a), although the Maricola are not represented in their data set. In other animal groups, colonization of land has usually passed through some freshwater intermediaries (Carranza *et al* 1998).

However support for the earlier view of a maricolan ancestor for the Terricola comes from morphological characters examined in the course of this study. The presence of lensed eyes, position of the testes and ovaries, and inverted penis in some caenoplaninid and anzoplaninid taxa, is strong support for a maricolan ancestor for some subantarctic geoplanid lineages, rather than for the rhynchodemid ancestors proposed earlier (Marcus 1953). The criterion of Carranza and others (1998) for a freshwater ancestor may be met, as on several southern hemisphere islands maricolan planarians are known from freshwaters. Whether a similar situation exists on the New Zealand subantarctic islands is not known. Molecular analyses have been undertaken on only a few boreal Maricola, and apparently on no austral maricolans and the subantarctic geoplanids. In my view it is too early to dismiss the Maricola as possible ancestors of at least some lineages in the Terricola.

At a morphological level parallel themes in caenoplaninid and geoplaninid taxa are identified here. Whether these parallels are examples of homology, other relationships, or convergence remains to be tested. For example, there are parallels in the morphology between the geoplaninid *Geobia* and the caenoplaninid *Apogaioplana*. Both occupy a similar subterranean niche. Beauchamp (1939) observed similar anatomical convergence between the boreal Rhynchodemidae, and Pelmatoplaninae which in Asia fill the niche normally occupied by rhynchodemids elsewhere.

Another frequent theme and problem in caenoplaninid taxa is a common ground plan of internal anatomy, with pairs of taxa differing from one another only by the presence of a musculoglandular organ (MGO), as in the *Caenoplana* complex, and in *Fyfea* and “Parafyfea” (this thesis). Under current practice the adenodactylate specimen would be transferred to a new genus, as the presence of the MGO is regarded as a new acquisition (apomorphy). Only after the examination of the numerous species of *Artioposthia,* together with presently undescribed austral taxa, will it be possible to consider whether the presence of adenodactyls is part of an evolutionary transition series within a particular taxon.

At this early stage of unravelling the systematics of austral terricolan taxa, the further I investigate the taxa, often the more blurred the picture becomes. In concluding this chapter on systematics and phylogeny, Beauchamp's observations have a certain resonance:

> *"One has the impression that each species varies itself without reason of a functional adaptation, but according to certain determined directions and that all kinds of combinations of characters are possible and one cannot deduce from it a phylogenetic group; they are reproduced also in other Turbellaria or Platodes in general about which the same thing may be said."* (Translation from Beauchamp 1939 page 336)

Chapter 6

Biogeography and Conservation of Terricola of the Australian Region

The origins and composition of the Australian fauna are rendered easier of explanation by the adoption of Wegener's hypothesis. Harrison (1928)

The terrestrial planarians are of relatively little interest to the historical biogeographer in that their distribution has been heavily influenced by man. Moreover, their taxonomic relationships are poorly known. Ball (1983)

It is highly likely that an evolutionarily old group as flatworms still indicate in their present-day distributional record geographic situations of old. Sluys (1995)

6.1 INTRODUCTION

The Terricola exhibit low vagility making them particularly useful for biogeographical studies (Sluys 1995). Historical biogeography must await a phylogeny of the Terricola. Unfortunately the following commentary on the biogeography of the Terricola worldwide and in the Australian region is a narrative account based on distribution patterns.

6.2 BIOGEOGRAPHY AT A SUBFAMILY LEVEL

Orders and families of macro soil fauna (size greater than 10 mm), the size group to which the flatworms belong, are cosmopolitan; at the subfamily, genus and species levels, endemism is high (Anderson 1977). Most of this group are sedentary, with low vagility. The Terricola accord with this pattern. Harrison (1928) provided a detailed explanation of the distribution of the Terricola with reference to both Wegener's theory of continental drift and the phylogeny of the Terricola proposed by

Graff (1899). Marcus (1953) noted that Graff's phylogeny of the Terricola was obsolete, and nearly in inverse order to the natural system proposed by Meixner (1928). Dispersal events were invoked in Marcus' account of the zoogeography of the Rhynchodemidae, though he also observed that the distribution maps of the Terricola were made more intelligible by Wegener's theory. The vicariance events of plate tectonics at present provide the best explanation for the continental distribution of terrestrial flatworms, especially at subfamily level.

The Terricola comprises 815 species in three principal families (Ogren *et al* 1997; Kawakatsu *et al* 2002). The oldest family (Meixner 1928) is the widely spread Rhynchodemidae (206 named species) which has 12 genera in two subfamilies. The Rhynchodeminae (5 genera) that occur principally in the Oriental and Notogaeic (Australia, New Zealand and Pacific) zoogeographic regions, and Microplaninae (7 genera) mostly centred in the Ethiopian, Madagascan and Palaearctic regions. A few microplanids are present in the Nearctic, Oriental and Neotropical regions. It is uncertain whether the presence of the rhynchodemid genera *Cotyloplana* in Indonesia, Australia and Lord Howe Island, and *Platydemus* in these regions as well as New Guinea, and possibly New Zealand (Johns 1998) is due to large-scale vicariance events, or more recent dispersion events accompanying lowered sea levels during the Quaternary.

The Geoplanidae (442 species) has 31 genera in three subfamilies. The older Caenoplaninae (15 genera), chiefly in Australia, New Zealand, the Pacific (Notogaeic region), and in southern Chile (Neotropical region), probably arose before the separation of New Zealand from Gondwana in the late Cretaceous. The Geoplaninae (14 genera and two sub-genera) is a relatively young group that has successfully radiated throughout South America (Neotropical region) (Froehlich 1967) after the separation of New Zealand and Australia from Gondwana. The Pelmatoplaninae (2 genera) occur in the Oriental region. The Bipaliidae (169 species) with 4 genera occurs throughout the Madagascan and Oriental regions. They possibly arose on the adjoined Madagascan and Indian plates, but did not reach Africa before its separation from Madagascar in the late Cretaceous (sequence of break up of Pangea taken from Dietz & Holden 1976).

6.3 BIOGEOGRAPHY OF THE AUSTRALIAN TERRICOLA

The Australian terrestrial flatworm fauna is an interesting assemblage of taxa. It is probably derived in part from an ancient Pangean lineage and Gondwanan elements, together with possibly more recent fauna of southeastern Asian origin, similarly to various other terrestrial invertebrates (York-Main 1981). On the basis of current investigations, and considering areas that are likely to contain terrestrial flatworms but which have not yet been surveyed, it is estimated that the flatworm fauna may be in excess of 300 species (Winsor 1997a). However the majority of these new species are likely to be very small and strongly seasonal.

Despite the imperfections of the current taxonomy of Australian taxa, absence of a clear phylogeny of Australian Terricola, and poor knowledge of western and northern Australian taxa, two broad flatworm faunal elements can be recognised: a southern element, and a northern element (Winsor, 1997a; 1998c).

6.3.1 Southern Element

The southern element includes taxa largely present in southeastern and southwestern Australia and southern Queensland, with disjunct elements in north Queensland. This correlates with the Southwestern, Tasmanian, and Kosciuskan (Bassian) zoogeographic subregions of a generally accepted biogeographic model of Australia (Heatwole 1987) (Fig. 6.1). Included in this group are species in the anzoplaninid genus *Anzoplana*, and the caenoplaninid genera Apogaioplana, *Artioposthia, Australoplana, Barringtoplana, Bassioplana, Caenoplana, Danidoplana, Fletchamia, Kynagoplana, Lenkunya, Nelipoplana, Reomkago, Tasmanoplana* and *Thosteelia.*

Within this southern element are as yet poorly defined Gondwanan relict taxa that probably include *Anzoplana, Caenoplana, Nelipoplana, Reomkago* and genera presently accommodated within the heterogeneous *Artioposthia.* Members of the relict group, particularly the numerous adenodactylate taxa, have affinities with flatworm taxa of New Zealand, the subantarctic islands and Chile (Fig. 6.2).

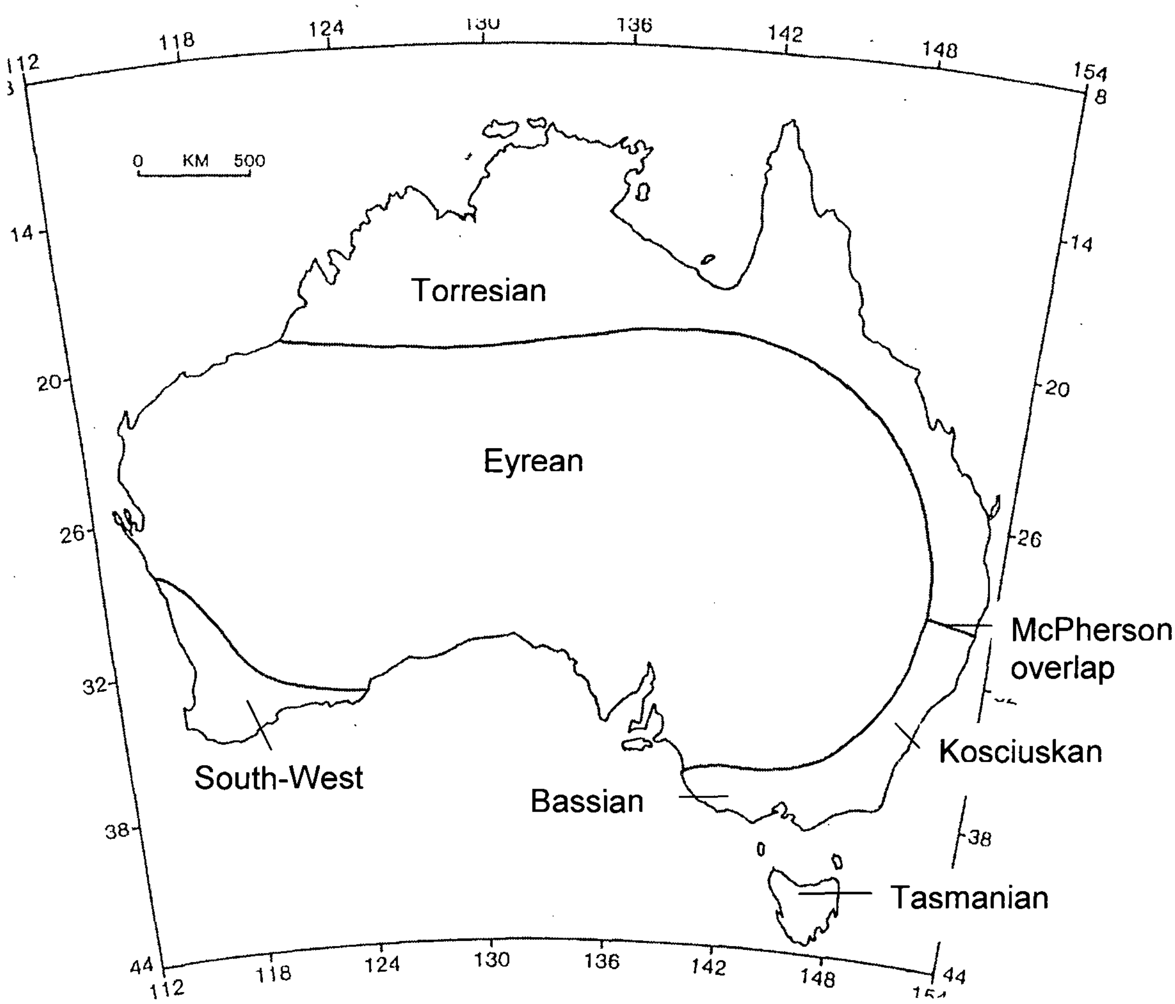


Figure 6.1 Australia – Zoogeographic Sub-regions (after Heatwole 1987)

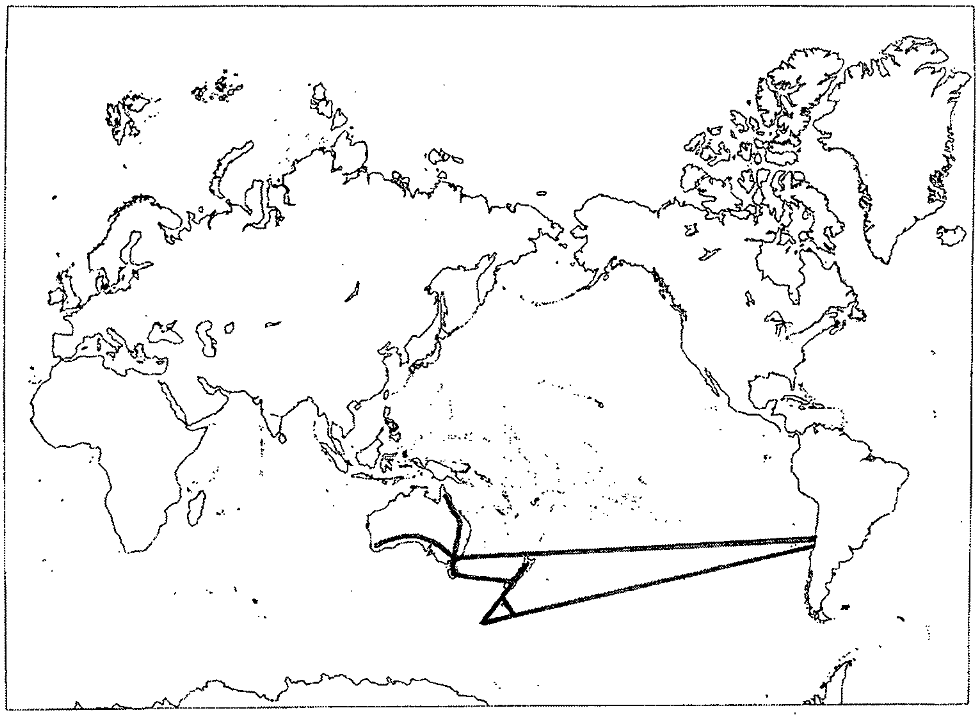


Figure 6.2 Southern element flatworms - tracks
The tracks connect south Western Australia and eastern Australia with New Zealand, the subantarctic islands, and Chile.

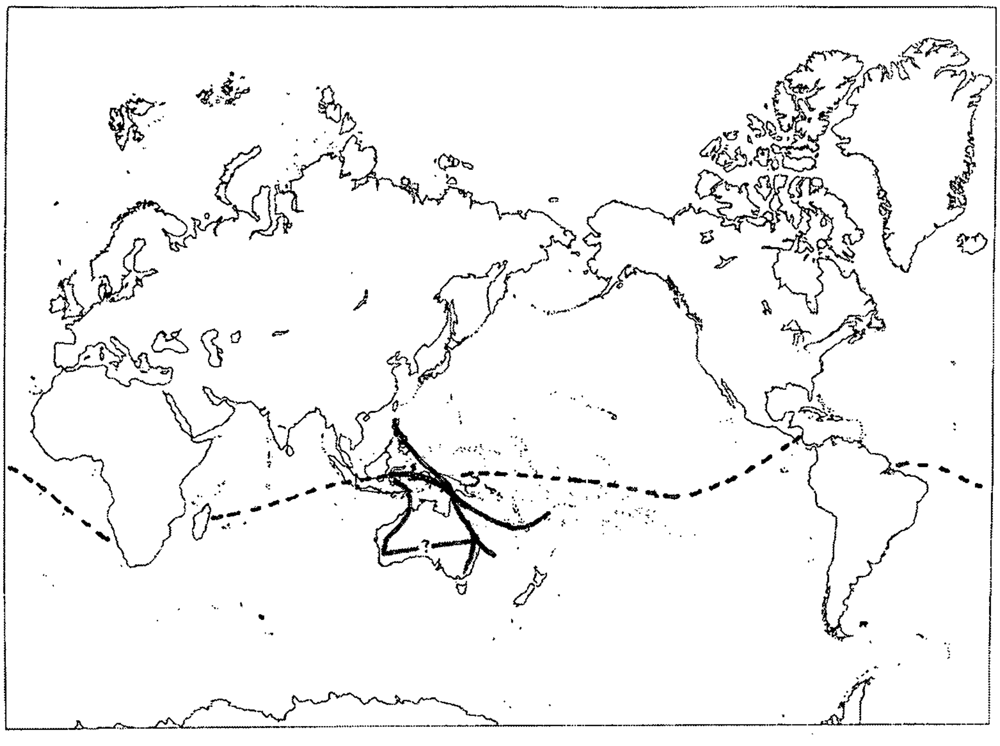


Figure 6.3 Northern element flatworms - tracks
The tracks connect the Philippines, Indonesia, New Guinea, Australia, Lord Howe Island, New Caledonia, and Fiji. The trans-Pacific track of *Dolichoplana, Kontiki* and *Rhynchodemus* (Sluys 1995) is indicated by a dashed line.

A number of different species of flatworms of this southern element are frequently found associated together in the same microhabitat. This raises interesting ecological questions regarding food partitioning and species interactions. Typical species associations found in the cool wet eastern highlands are *Artioposthia howitti, A. lucasi, Nelipoplana (N) alba, Caenoplana spenceri, Lenkunya adae, Reomkago quadrangulatus* and the terrestrial nemertean *Argonemertes australiensis*. Commonly four to five species are associated together, though up to nine species have been found under the same log. In the warm drier woodlands and plains a different association of species is encountered. It commonly includes *Caenoplana hoggii, Fletchamia quinquelineata, F. mediolineata, F. sugdeni,* and *Lenkunya munda*.

6.3.2 Northern Element

The northern element includes taxa that also occur in Papua New-Guinea, Irian Jaya, Indonesia, Philippines, New Caledonia and small Indo-Pacific oceanic islands (Fig. 6.3). They occur chiefly in the uplands and rainforests of the Torresian zoogeographic subregion of Australia, and exhibit disjunct distribution throughout their range. Taxa of the northern element include the rhynchodeminids *Cotyloplana, Digonopyla, Dolichoplana, Platydemus, Rhynchodemus*, four undescribed genera of the Rhynchodemidae (Winsor 1997c), and possibly four undescribed geoplanid genera (Winsor 1997a).

Cotyloplana has a very disjunct distribution (Indonesia, New Caledonia, northern Queensland and Lord Howe Island). *Platydemus* and *Rhynchodemus* occur in the uplands of Queensland, New South Wales, Victoria, and *Platydemus* also occurs on Lord Howe Island. *Dolichoplana* occurs from far north Queensland to southeastern Queensland. There is presently only one Australian specimen and record of *Digonopyla*, from Iron Range, Cape York, Queensland.

Australia was connected to New Guinea via Cape York Peninsula during the Pleistocene glacial period (Walker 1972). The terricolans of the northern element may have dispersed from Indonesia via New Guinea to Australia. This cannot be discounted. An alternative explanation, especially given the natural low vagility of terricolans, is that the taxa of the northern element are possibly Pangean cosmopolites. Sluys (1995) identified trans-Pacific biogeographical tracks for *Dolichoplana, Rhynchodemus*, and *Kontikia.* The Gondwanan *Kontikia* taxa included by Sluys belong in other genera (investigations by LW) thus strengthening Sluys' argument for a trans-Pacific track for *Kontikia. Cotyloplana, Digonopyla,* and *Platydemus* also share a generalized track in the Pacific basin (coinciding with the solid line track, Fig. 2, Sluys 1994). These trans-Pacific tracks, also exhibited by other organisms including maricolans (Sluys 1995), cannot be explained under the vicariance model of the pre-drift reconstruction of Pangea (Sluys 1994; 1995) – the Pacific Ocean has been present since Pangean times. Debate continues on alternative biogeographical theories (reviewed by Sluys 1994) advanced to explain the biogeography of the Pacific basin.

Although *Parakontikia* has a mid to southeastern Australian distribution, it appears to have closer affinities with the terricolans of the northern rather than the southern element. Its southern occurrence is similar to those of *Rhynchodemus* and *Platydemus*. The genus is closely related to *Kontikia,* which has a trans-Pacific track. *Parakontikia* exhibits a trans-Australian track (Fig. 6.3) to the region of the McPherson overlap where the Torresian and Bassian zoogeographic subregions meet Fig. 6.1). Similar tracks are exhibited by many plants and animals (Croizat 1962). This suggests a possible link between *Kontikia* in the northwest and *Parakontikia* in western Australia. Unfortunately there are no detailed terricolan distribution data for north Western Australia except that it is known that Terricola occur in the Kimberley region.

Unlike many taxa of the southern element, most of the species in the northern element are solitary, and associations of more than one or two species of flatworms are uncommon. There is also a perception that the flatworms of the northern element are not as numerically abundant as those of the southern element (Winsor 1997a).

6.3.3 Distribution patterns of flatworms in Australia

Examination of the distribution of the more common terricolan genera and species in Australia reveals a number of patterns, also shared by other Australian forest animals. These patterns, as yet not fully analysed, are briefly considered here.

6.3.3.1 Disjunctions in north-south distributions

Southern element caenoplaninids e.g. *Caenoplana* and Northern element rhychodeminids e.g. *Platydemus* exhibit disjunctions throughout their range. A major coastal disjunction occurs in the arid central Queensland region, and in the dry tropics in the Townsville region. These disjunctions are generally attributed to the contraction in dry periods, of once extensive cooler wetter forests (Heatwole 1987). It is not yet known whether this vicariance event has resulted in allopatric speciation in any terricolans. *Caenoplana coerulea* exhibits a cline variation in size, with northern specimens generally of smaller size than those in the south. The internal anatomy is the same throughout the species range.

6.3.3.2 Disjunctions in east-west distributions

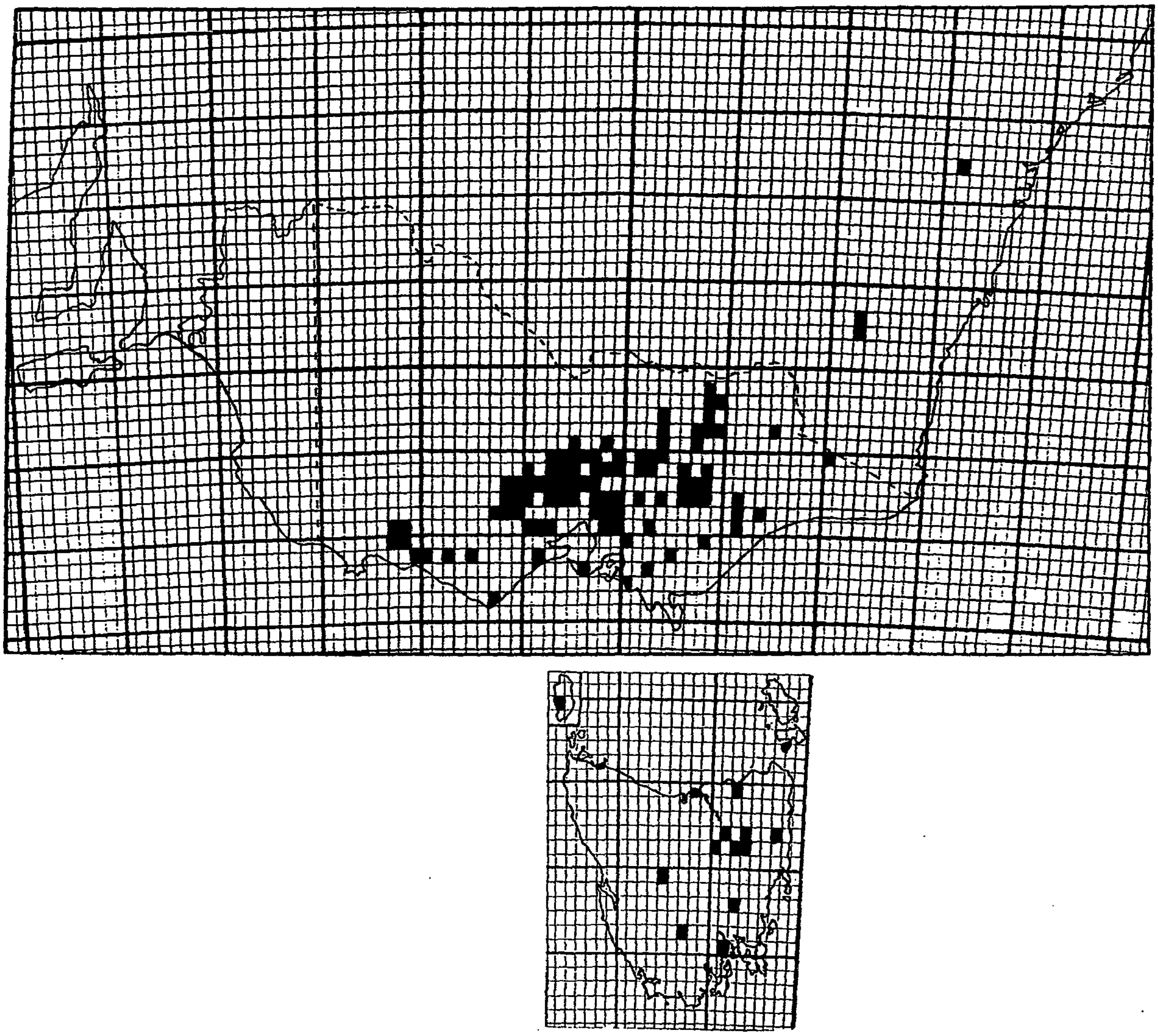
Preliminary investigations of terricolans from southwestern Western Australia by the author indicate the presence of the southeastern Australian taxa *Artioposthia, Caenoplana, Fletchamia* and? *Nelipoplana*. Similar explanations to those previously indicated for north-south disjunctions may also apply here. However east-west dispersal of taxa is invoked for many species e.g. reptiles (Heatwole 1987), most of which are far more vagile than terricolans.

6.3.3.2 Disjunctions over Bass Strait

In the glacials of the late Tertiary and in the Pleistocene, there were marked eustatic changes. During these periods when the sea levels dropped, land connections existed between the Australian mainland and Tasmania (and in the north between Australia and New Guinea). The land bridge between the mainland and Tasmania

Figure 6.4 *Lenkunya* – disjunct distribution over Bass Strait.

Lenkunya species are present in the Otway ranges (Victoria) and King Island which separated 14,750 ybp, in Tasmania isolated from the mainland 12,750 ybp, and on Flinders Island isolated from the mainland 12000-13000 ybp. Distribution of *Lenkunya* in Tasmania is immature, confined to coastal and relatively warm eastern regions. It is considered here that *Lenkunya* species dispersed from Victoria to Tasmania before the separation of the Otway Ranges from King Island. Estimated times of isolation, in years before present (ybp) are from Rawlinson 1974.



allowed faunal interchange including terricolans. Evidence for this is provided by the presence of *Lenkunya* species on Bass Strait islands (Fig. 6.4). It is also suggested by the coastal distribution in Tasmania of some species with principally mainland occurrence, and species present in both Tasmania and the mainland (Winsor 1977).

6.3.3.3 Flatworm distribution and moisture regions

Terrestrial flatworms are primarily restricted in their environment by the availability of moisture, and their distribution in Australia may best be explained in terms of moisture regions (Winsor 1977). Using the hydroxeric index, the mathematical expression of moisture budget, which takes into account evaporation, ground storage and run-off, Gentilli (1972) defined moisture regions for Australia (Fig. 6.5). Terrestrial flatworms are largely confined to areas with hyper humid, per humid, humid, and sub arid climate types, with a few species around the margins of the semi arid climate regions in southeastern Australia. Distributional studies undertaken on some southern element species (e.g. *Caenoplana spenceri* and *Fletchamia quinquelineata* Fig. 6.6) show that there is a strong correlation between their distribution and the thermal zones of the Bassian (Kosciuskan) and Eyrean zoogeographic subregions, which can also be regarded as moisture zones (Winsor 1977). Soil moisture status has been advanced as a contributing factor in the success in Europe of *Arthurdendyus triangulatus*, a New Zealand vermivorous species, regarded as a serious agricultural pest (Fraser & Boag 1998). Comparison of the distribution of flatworms to areas of differing soil moisture deficits may be worthy of further investigation (Fraser & Boag 1998).

6.3.3.4 Endemics and rare taxa

Given the large number of Australian terricolan specimens yet to be examined and identified, large gaps in the distribution record, and the continuing investigations into the Terricola of New Zealand (Johns 1998) caution must be exercised in identifying taxa as endemic. Genera endemic to Australia appear to include *Apogaioplana, Australoplana, Barringtoplana, Bassioplana, Danidoplana,*

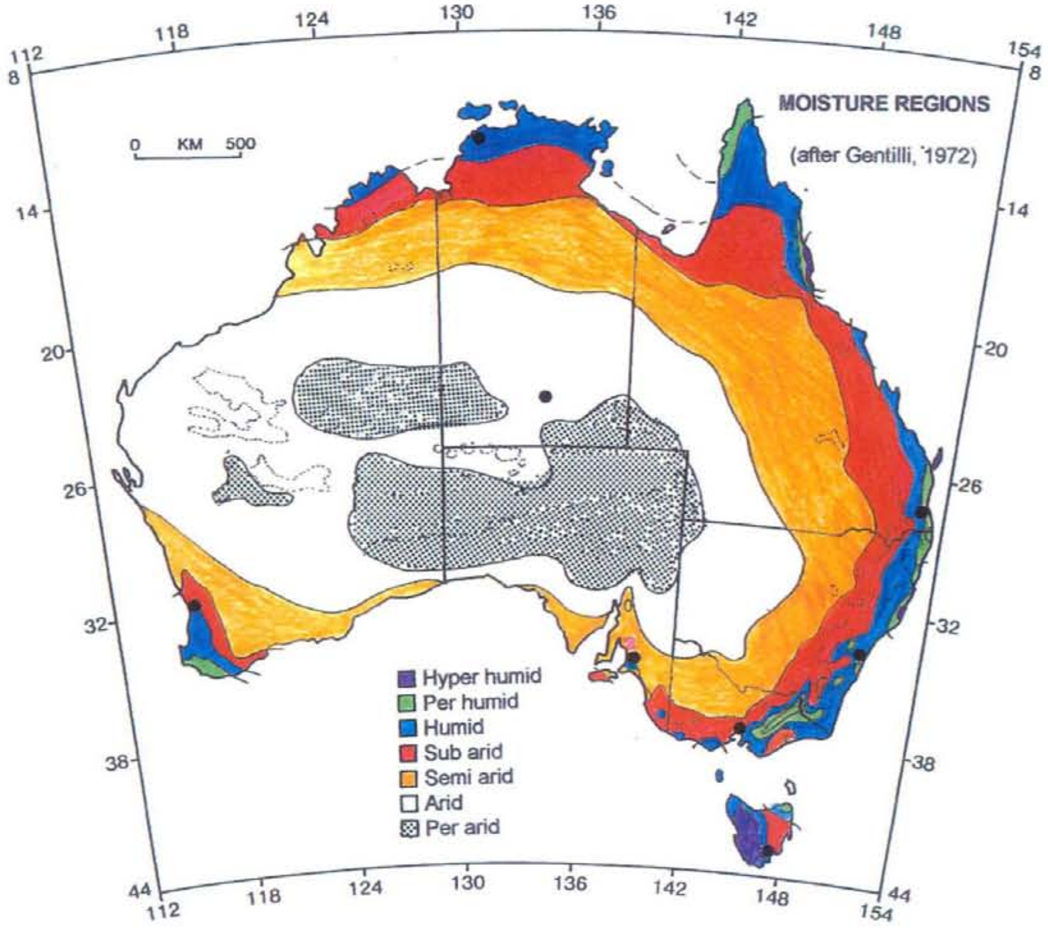


Figure 6.5 Australia – Moisture Regions
Terrestrial flatworms are largely confined to areas with hyper humid, per humid, humid, and sub arid climate types, with a few species around the margins of the semi arid climate regions in south eastern Australia.

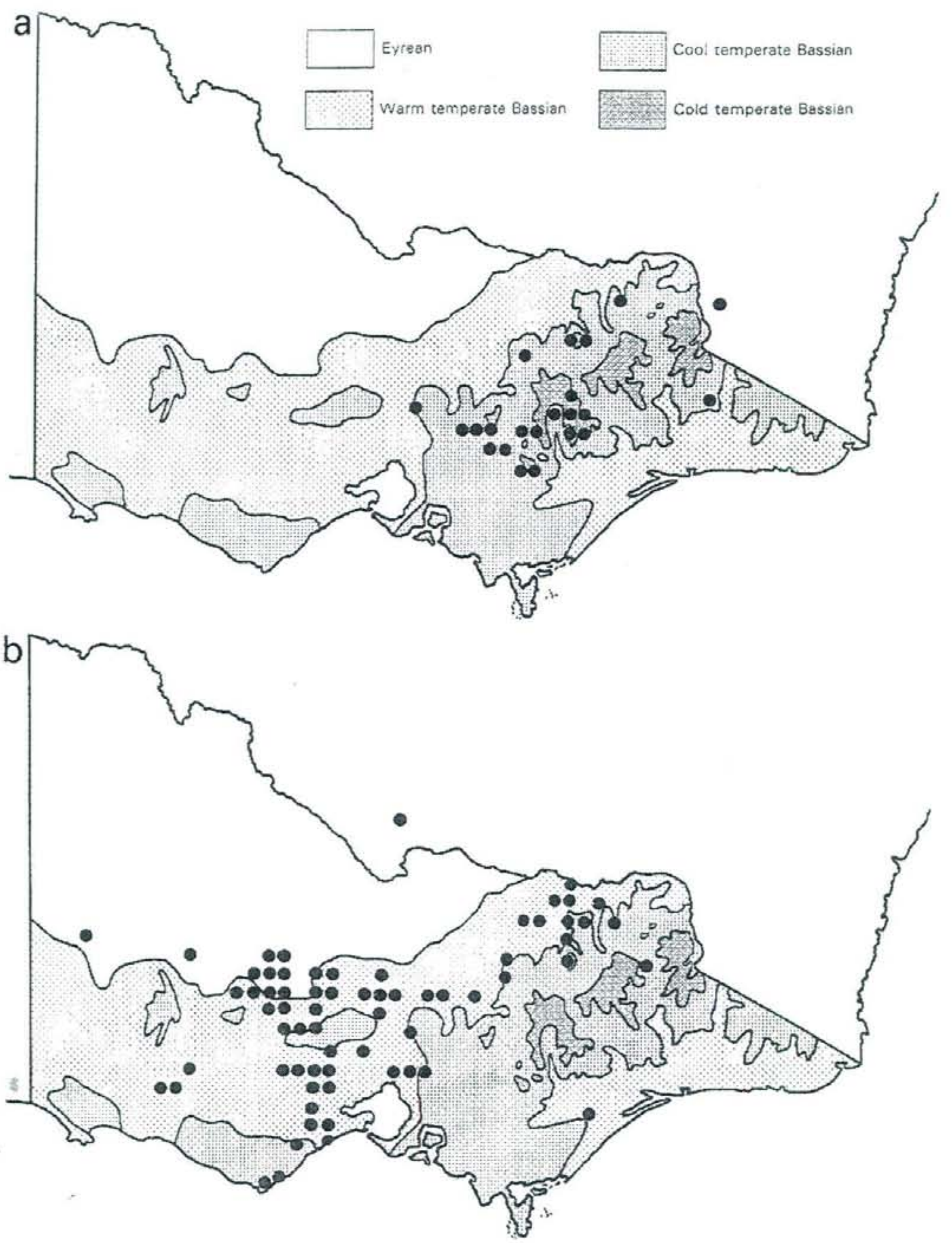


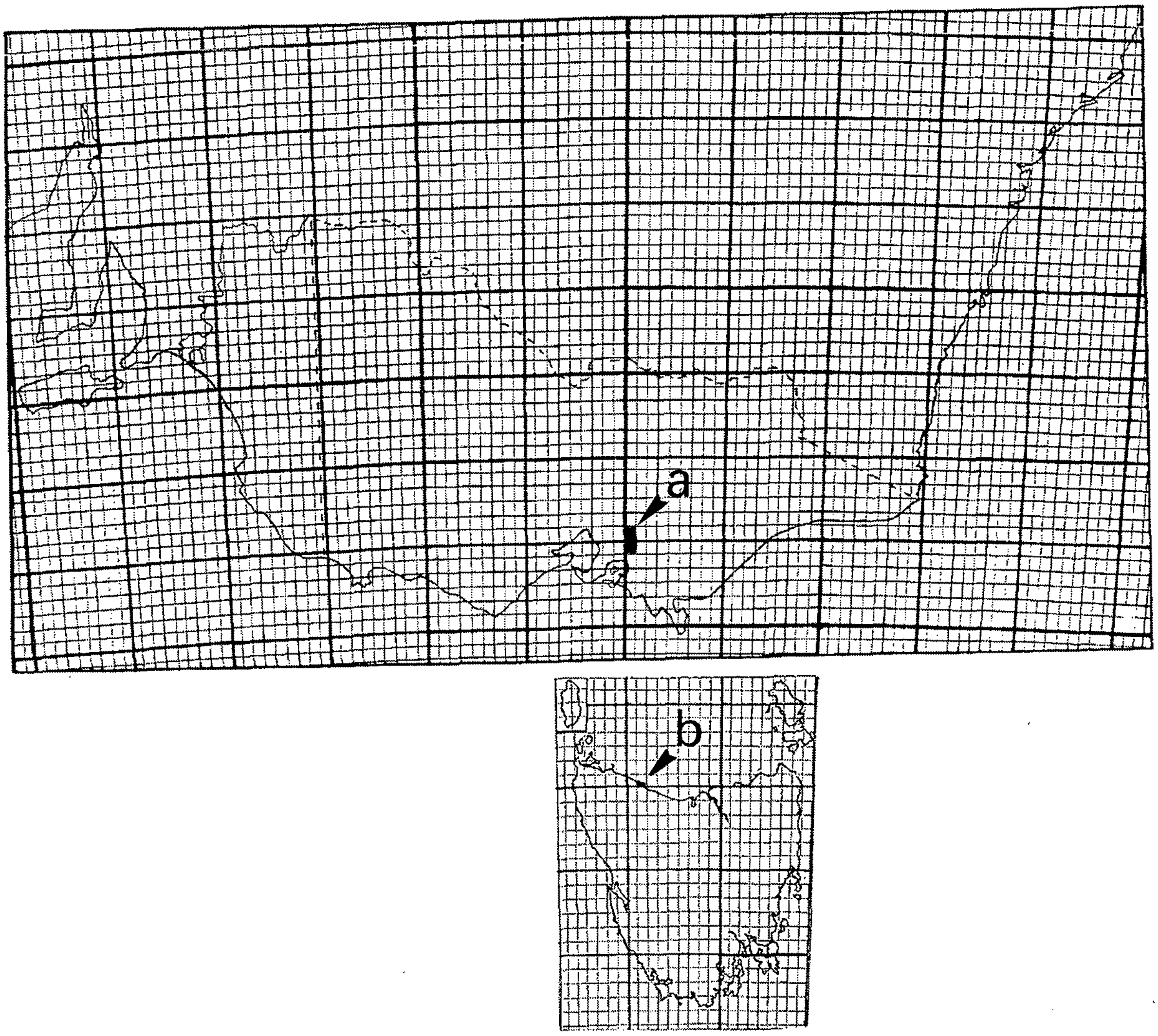
Figure 6.6 Correlations between the distributions of two species of caenoplaninid flatworms in Victoria, Australia and the thermal - moisture zones of the Bassian (Kosciuskan) and Eyrean zoogeographic subregions. Flatworm distributional data by the author (unpublished). Zoogeographic maps after Rawlinson, P. A. 1971. Amphibians and reptiles of Victoria. *Victorian Year Book No. 85* 1-36.

a. Distribution of *Caenoplana spenceri* (Dendy, 1890), a species restricted to the south eastern cool temperate and cold temperate Bassian zones (humid - per humid / hyper humid moisture regions).

b. Distribution of *Fletchamia quinquelineata* (Fletcher & Hamilton, 1888), a species largely present in the warm temperate Bassian zone and adjacent Eyrean subregion (sub humid to semi arid moisture regions) of eastern Australia. The species extends northwards into southern Queensland.

Figure 6.7 Rare, possibly endangered endemic species

Examples of rare endemic species are *Caenoplana dubia* (a) and *Thosteelia mesibovii* (b). Both are known only from restricted areas, despite intensive searches in the regions where they occur. The species may be endangered, given the increasing urban and agricultural pressures on the country where these two species occur.



Fletchamia, Kynagoplana, Lenkunya, Parakontikia, Reomkago, Tasmanoplana, and *Thosteelia.*

Endemic and rare species include *Thosteelia mesibovii*, which despite exhaustive searching is known only from a single site (Fig. 6.7). Similarly *Australoplana sanguinea Caenoplana dubia, Artioposthia ventropunctata,* and Australoplana *sanguinea* are known only from restricted areas, although there are numerous records of other terricolans from adjacent districts.

6.3.4 Introduced, Threatening and Vagrant Species

The passive dispersal of terricolans by humans is well documented (summarized by Sluys 1995; Alford *et al* 1998). In my opinion, the major factor in the worldwide dispersal of these flatworms was the invention, in 1833 by Dr Nathaniel Bagshaw Ward of East London, of portable terrariums – Wardian cases - for the transportation of plants (Ward 1834). Terrariums are also the perfect way to transport flatworms. Thus was mediated the initial intercontinental dispersal of flatworms, present in the soil or vegetation accompanying the collected plants. Hitherto the intercontinental transportation by sea of live plants was fraught with difficulties, and only the hardiest plants survived. The first test of the Wardian case was the transportation of ferns and grasses from the United Kingdom to Sydney in 1833, on the return trip stocked with native Australian ferns– the ferns arrived in perfect condition (Honigsbaum 2001). Wealthy orchid collectors were the first to use the Wardian case to bring orchids from India. In the 1840s these cases were used to bring plants from China, which included orchids (Honigsbaum 2001). It is no surprise then that Moseley's *Bipalium kewense* was collected in 1878 from the orchid house, Kew Gardens. Secondary dispersal of flatworms occurs with the purchase and exchange of plants between nurseries, botanical institutes, and domestic gardeners (Alford *et al* 1998).

Nine introduced terrestrial flatworm species are reported from Australia. Records from Sydney of the cosmopolitan species *Bipalium kewense* predate by four years the description of the species from Kew gardens by Moseley in 1878. This flatworm is now reported from major urban areas in eastern Australia and Western Australia (Winsor 1979; 1983b; 1985) where it is a minor pest in small-scale earthworm farms. In Queensland a *Pelmatoplana* species was found in disturbed scrub in the Brisbane suburb of Robertson. *Kontikia circularis* originally reported from New Zealand by Fyfe (1956) is recorded from central Queensland in the Rockhampton Botanic Gardens (Winsor 1997a) though it is likely that this specimen is in fact *Parakontikia ventrolineata* (Johns pers. comm.).

Five introduced species are found in tropical north Queensland. All appear to have been introduced with plants such as ferns, banana rhizomes and orchids, probably from New Guinea and countries in the Pacific region. Included are *Kontikia orana*, first found in Brazil (Froehlich 1955) and more recently in Townsville (Winsor 1986), and two species of *Dolichoplana* found sporadically in urban and public gardens. The New Guinea planarian *Platydemus manokwari*, used in an ill-considered attempt control the Giant African snail *Achatina fulica* in Guam and other Pacific islands, occurs sporadically in urban and agricultural areas from far northern to south eastern Queensland. Whilst the species is considered a grave threat to native molluscs in Pacific islands (Pearce-Kelly *et al* 1997), it has not yet been encountered outside human modified habitat in Queensland. *Nelipoplana (Peokrypta) enigma* (previously *Australoplana alba sanguinea*), a southern Australian species implicated in predation on earthworms in Britain, is also found in urban Adelaide (Terrace & Baker 1996). My view is that the species, together with other Australian flatworms, was probably transported from Tasmania to New Zealand, and thence to the United Kingdom.

A *Caenoplana* (?) species of unknown origin, now common in Townsville and Cairns, was recently implicated in a case of pseudoparasitism (Winsor 1995). The phenomenon of pseudoparasitism is where terrestrial flatworms are mistakenly considered to be parasitic. This arises because of the often unusual circumstances of accidental contact by humans and animals, especially where the flatworms are found around the anus or genitalia. Other cases of pseudoparasitism in Australian have been reported by Winsor (1980).

Two Australian species, *Parakontikia ventrolineata* and *Caenoplana coerulea,* are vagrants, having been spread overseas by human agency, probably first to New

Zealand and from there to Norfolk Island during the Second World War; also to Hawaii, the United States of America, and South Africa. These two species are also commonly encountered in Australian gardens. Terrace & Baker (1994) report on the predation by *C.* coerulea on the introduced pest black Portuguese millipede *Ommatoiulus moreleti* in southern Australia.

6.4 CONSERVATION

The biggest threat to the conservation of terrestrial flatworms is loss of habitat from land clearing - increasing urbanisation, agricultural expansion, deforestation and monoculture. Land management practices such as burning and not windrowing fallen and cleared timber, and the public gathering of fallen timber for firewood further reduce habitat. Australia has long sad history of deforestation, habitat destruction and degradation, as well as an equally long history of environmental conservation (Bonyhady 2000). Concerns about land clearing practices were raised in the first paper written in 1888 by resident zoologists on the Australian flatworms:

> *Such large tracts of country have now been, and are yearly being cleared and burnt over, a procedure which means extermination to animals of feeble locomotive powers, like planarians, that unless residents in the country help in this matter it is almost certain that some of the more local species will never otherwise be rescued from oblivion.*
>
> (Fletcher & Hamilton 1888 page 360).

Some of the species described in their paper have never been found, nor any of the new taxa briefly described in Hamilton's note book (refer Chapter 2, this thesis). Some 115 years later, despite intervention by Governments and despite an overwhelming body of evidence demonstrating the serious effects of land clearing, deforestation seemingly continues unabated in parts of Australia (Plate 6.1).

Terricolans can serve as ecological and biological indicators of pristine or disturbed habitat. In Australian native forest frequent rotational fuel reduction burning leads to simplification of the flatworm fauna (Springett 1976). In the wake of severe

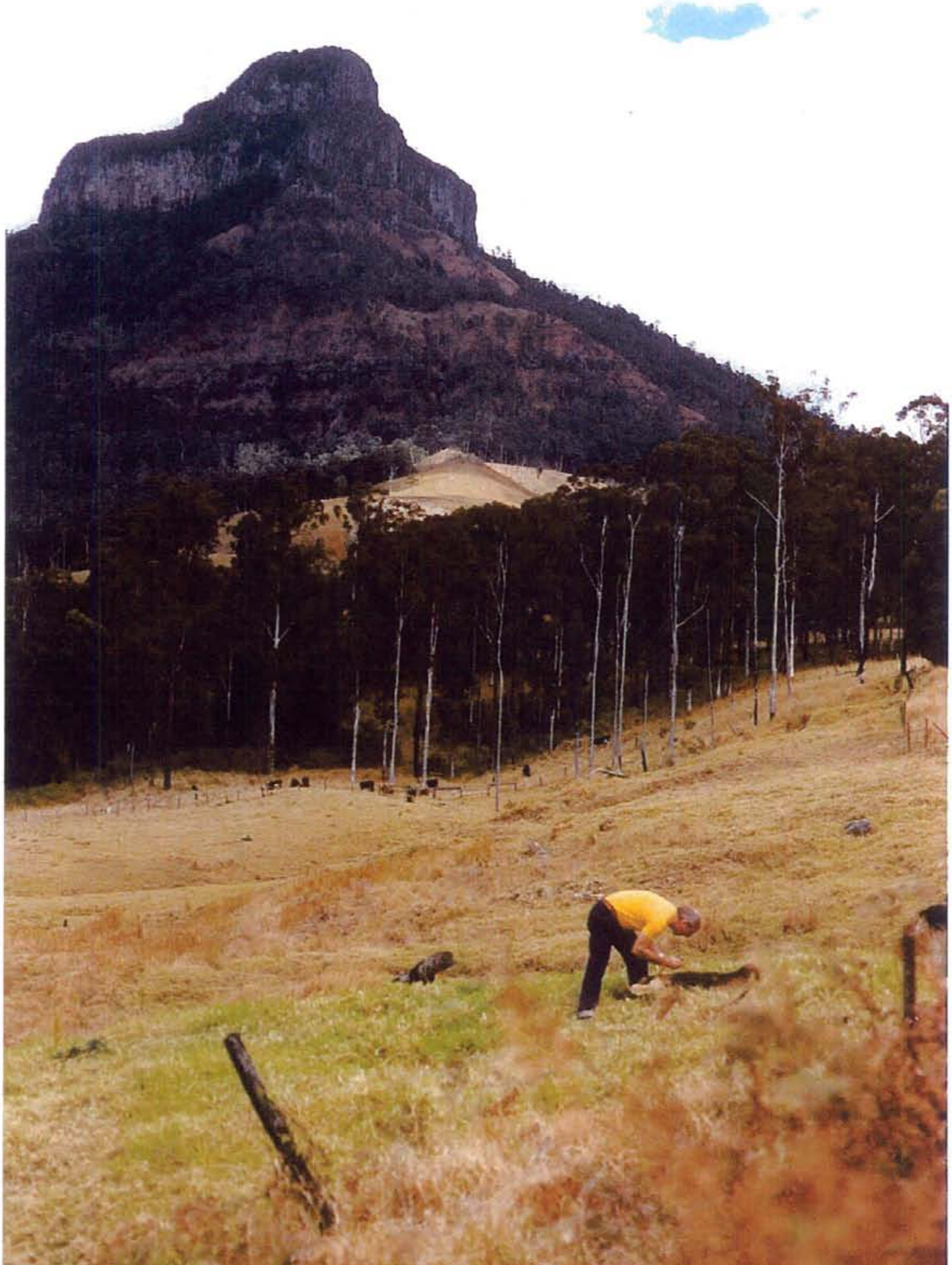


Plate 6.1. Threats to conservation: land clearing in an area being "developed" as part of the urban sprawl on the Mt Lindsay Highway, Jimboomba area, south-eastern Queensland (the author in the field).

forest fires over the past few years in Australia, there is public pressure for increasing the frequency of fuel reduction burning in National Parks. Terricolans could serve as bio-indicator species to monitor the post-fire recovery of habitat and also the long-term effects of fuel reduction burning. Studies on the flatworm diversity *versus* human disturbance of Brazilian rainforest (Carabayo *et al* 2002) showed that (a) the diversity of terricolans is inversely related to the degree of habitat disturbance (b) some species prefer well preserved, natural habitats, and can be regarded as indicators of such habitat, and (c) another suite of species prefers more disturbed habitats, and may act as biological indicators of such disturbance.

Terricolans have been promoted by Sluys (1998; 1999) as indicator taxa in biodiversity and conservation studies in identifying hotspots of species richness, and identifying areas of richness in endemic taxa. Using an equal-area grid map (WORLDMAP) with species counts per grid cell, he demonstrated 15 global hotspots which included Tasmania, New South Wales, and Sydney, also noting the possible influence of the distribution of collection effort. My own view is that whilst the published Australian biodiversity data for Sydney largely reflects urban collector effort, eastern Australia, and probably also southwestern Western Australia are hotspots of terricolan species richness and are also rich in endemic taxa. The systematic surveying of flatworms using a biogeographic grid system (Winsor 1977) is one way in which the influence of collection effort can be minimized. The resulting species distribution maps (this thesis) allow an improved assessment of species richness, richness in endemic species, rare and endangered species, and the identification of possible adventive taxa. At a later stage it is hoped to integrate distributional data on the Terricola into existing national or state faunal databases such as that used by the Queensland Museum to produce an atlas of Queensland's frogs, reptiles, birds and mammals (Ingram & Raven 1991).

What then is the best strategy for the conservation of cryptofauna, and in particular terrestrial flatworms? In a western Tasmanian study, Mesibov (1993) demonstrated the occurrence of similar assemblages of litter invertebrates including flatworms in three floristically different vegetation types. On the basis of this and other data he considered that the traditional approach of conserving habitat on the basis of vegetation type was a weak strategy for conserving litter invertebrates. Physiography, microclimate and the presence of hot spots - areas with the co-occurrence of geographically restricted species - were better bases for selection of sites for conservation. Degraded woodland, and stands of remnant forest along roadsides and in small reserves are valuable refugia for a variety of cryptofauna, in particular terrestrial flatworms. The final word should go to Arthur Dendy, as valid now as when it was written:

> *But one fact must be not lost sight of, and that is the opportunities which we now enjoy will not be always with us. Not only will the agency of man result in greatly confusing the problems of geographical distribution, but our cryptozoic fauna must be largely exterminated in the near future by the wholesale destruction of forests which is now going on. At present this clearing process is to a large extent an advantage to the collector, for experience has shown me that it is far easier to find cryptozoic animals in partially-cleared localities, where they are collected together under remaining fallen logs, than in virgin forest, where there is so much cover that the animals are widely scattered, and the search becomes very laborious. When the clearing process is complete, however, and the last logs have disappeared from the ground in any district, then we may expect to lose sight for ever of many peculiar forms which formerly dwelt there.*

Arthur Dendy
Presidential address
6th Meeting AAAS
Brisbane, Queensland, January (1895d)

Chapter 7

General conclusion

While I have argued that DNA sequence data may be better suited for phylogenetic analysis, I do not at all think that they will supplant morphology-based systematics and evolutionary studies.

Reinhard M. Rieger 1998

What is needed in the future is more phylogenetically centred descriptive work.

Littlewood *et al* 1998.

To further support the conclusion here obtained, and to resolve the contradictions posed, further studies will be needed, including denser sampling of Tricladida taxa for molecular data, complementary sequences from independent genes, and the broad and thorough morphological database already available for the Tricladida, used together in a combined "total evidence" approach.

Baguñà *et al* 2001

When this study began, the most poorly known groups of the Terricola were those of Australia and New Zealand (Ogren *et al* 1997b). It was estimated that published anatomical data were available for only some 12% of the 90 named Australian Terricola in 15 genera (Winsor 1991c) within a fauna estimated in excess of 300 species (Winsor 1997a).

The purpose of this study was to develop the alpha and beta taxonomy of some key taxa of the Terricola fauna in the Australian region. It is the only comprehensive morphological study of the Australian Terricola since 1899. Through the identification of reliable taxonomic characters, and provision of data on the distribution of taxa, this study provides the foundations for subsequent cladistic and biogeographical analysis of the Terricola of the region. Ten new genera and a new record (*Digonopyla*) are described here, almost doubling the number of genera in Australia to a total of 25, for which anatomical data are now available. Two new genera of New Zealand terricolans are described bringing the total number of genera for New Zealand to 18, at least four genera of which are shared with Australia.

7.1 OBJECTIVES OF THIS STUDY FULFILLED

1. Type and other specimens of terrestrial flatworms of the Australian region held in museums worldwide have been located. Some of these types and supplementary material were examined in the course of this study and form the basis for taxonomic descriptions provided here.

2. Aspects of the functional anatomy of Terricola with particular reference to Australian taxa were reviewed.

    a. Identified fixation and parasite-induced artifacts that can cause misinterpretation of anatomical characters.
    b. Investigated the histology and functional anatomy of colour and pattern of markings, body wall and its components, the pharyngeal diverticulum, the nephridial ducts, penis type, resorptive organs, musculoglandular organs (adenodactyls), and cocoon wall.
        i. Identified seven types of the hitherto enigmatic adenodactyls.
        ii. Determined the function of adenodactyls in some taxa, found to be the secretion of sclerotins that form the cocoon wall.
    c. Provided extensive comparative data sets for various characters and states.
    d. Developed a suite of taxonomic characters and states and used them to provide standardized diagnoses for taxa. Attempted to address identified problems in morphology-based systematics (Littlewood *et al* 1998) in providing presence / absence characters, and discrete characters which lend themselves to placement in transformation series. Characters assessed for their application in taxonomy included colour and pattern of markings, pharyngeal musculature, pharyngeal

diverticulum, configuration of the nephridial ducts, dorsoventral distribution of testes, penis type, resorptive organs, and musculoglandular organs (adenodactyls).

e. Elucidated the mechanism of cocoon formation in the Terricola. It involves the deposition of sclerotins, derived from antral secretions or adenodactyls, on the outer pre-cocoon membrane. This mechanism differs from the generally accepted Triclad model based upon the Paludicola, in which the cocoon is formed from within the pre-cocoon membrane by shell-globule components of the vitellocytes.

3. Identified reliable taxonomic characters and states, and attempted to determine which of the latter are plesiomorphic, and which are apomorphic conditions. These characters and states will be subsequently used in the cladistic analysis of austral terricolan taxa.

4. Erected a new sub-family of the Geoplanidae to accommodate taxa with testes that are continuous in the dorsoventral plane. This taxon provides a link between the Neotropical geoplaninids with dorsal testes, and the austral caenoplaninids, Rhynchodemidae, and Bipaliidae with ventral testes.

5. Undertaken taxonomic revisions of some Caenoplaninid taxa.

    a) Considered a total of twenty-six genera in three families.
    b) Erected ten new genera.
    c) Resolved the problematic *Australoplana* complex into five genera and two sub-genera.
    d) Re-described *Coleocephalus fuscus*
    e) Re-defined *Caenoplana* and *Arthurdendyus*.

6. Determined a possible phylogenetic relationship between some austral caenoplaninid and maricolan taxa based upon shared anatomical characters. Other anatomical findings support the view that the Terricola are polyphyletic, and in part closely related to the Paludicola.

7. Developed simple keys, and aids such as the Infosheets to make knowledge of the austral Terricola accessible to the scientific and lay communities

8. Determined the distribution of key taxa of the Australian region.

    a) Determined that the Australian flatworms mostly occur within hyper-humid to sub-humid moisture regions,
    b) Assigned the genera to two principal families. In the Rhynchodemidae: Rhynchodeminae 45 species are accommodated within *Cotyloplana, Digonopyla, Dolichoplana, Platydemus* and *Rhynchodemus*, and in new genera not considered in this study. In the Geoplanidae: Caenoplaninae, 80 species are assigned to *Artioposthia, Australoplana, Caenoplana, Fletchamia, Lenkunya, Parakontikia, Reomkago, Tasmanoplana* and an additional 10 new genera considered here.
    c) Assigned four species to two new genera in a new subfamily of the Geoplanidae.

9. Identified and described the biogeographical components of the Terricola fauna of the Australian region. Two major flatworm faunal units are recognized in Australia.

    a) A northern element dominated by rhynchodemid genera including taxa that also occur in Papua-New Guinea – Irian Jaya and Indonesia.
    b) The southern element is dominated by geoplanid genera including some with presently poorly defined Gondwanan affinities.
    c) These faunal units broadly accord with the Torresian (northern) and with the Tasmanian, South-western, and Bassian or Kosciuskan (southern) zoogeographic sub-region

10. Discussed examples of distribution patterns of some species of Australian terricolans, such as the disjunctions in range between the Australian mainland

and Tasmania, between southern and northern, and eastern and western Australia.

11. Identified some endemic and rare taxa.

12. Determined the identity and occurrence of introduced, threatening and vagrant taxa. There are nine introduced species, including the sole representative of the Bipaliidae, *Bipalium kewense*, none of which presently poses an ecological or commercial threat in the Australian region.

13. Provided a preliminary report on the biodiversity of Terricola in Queensland (Winsor 1997): a result of this study the known flatworm fauna was increased over six fold, now with some 8 genera, and 62 species of which 80% are new.

7.2 FUTURE RESEARCH

There remain large collections of specimens of terricolan taxa from the Australian region yet to be examined and described. The phylogenetic analyses of taxa are a priority. Future research should include parallel morphological and molecular studies as part of the total evidence approach advocated by Littlewood *et al* (1998), and Baguñà *et al* 2001. Cooperative research is in progress on saproxylic fauna (Sunnucks Group, Monash University), and cryptofaunal organisms (Tait Group, Macquarie University), and includes both molecular and morphological investigations on the representative terricolan taxa.

The primary private and museum collections of formaldehyde-preserved specimens, which largely form the basis for this study, presently preclude molecular analyses. However I subscribe to the view (Carter 2002) that the DNA in formaldehyde specimens is just difficult to extract, rather than being highly degraded. The development of improved extraction techniques may make it possible to utilize formaldehyde fixed material more widely (Carter 2002) as part of the denser sampling of Tricladida for molecular analyses.

There are considerable gaps in the distribution records for Australian terricolans that require targeted field work in the right seasons. Whilst there are good collections from north Queensland (Winsor 1977), records from south and far northern Queensland are sparse. Both areas are important biogeographically, with the McPherson overlap in the south, and Cape York adjacent to the bridge and barrier of Torres Strait. There are now a few records of terricolans from the Northern Territory, all of them introductions; nothing is known of the native terrestrial flatworms there. To date the only record of flatworms in the north of Western Australia is a sighting of a specimen in the Kimberley region (B. York-Main, pers. comm.).

Morphological studies place heavy reliance upon the use of histological preparations, and time-consuming reconstruction of the anatomy from serial sections. These, together with the taxonomic impediment (Winsor *et al* 1998) act as constraints to rapidly progressing revisionary studies, especially in complex adenodactylate taxa. The use of dental X-radiography on flatworms, especially following secondary fixation in heavy metal salts, has been considered by me but not yet undertaken. In my experience confocal microscopy is presently of little use to examine unsectioned terricolan material. Non-invasive high resolution X-ray microtomography, coupled with integrated 3-D reconstruction software, used to examine both living vertebrate and invertebrate animals, is now available (De Clerk *et al* 2003). If this technique is able to resolve dense muscular structures, subject to its availability and if used in conjunction with standard anatomical methods, it offers one means of overcoming some of the present obstacles to reconstruction of the copulatory organs in terricolan taxonomy.

References

Anderson, J.M. 1977. The organization of soil communities. *In:* Lohm, U., Persson, T. (Eds) Soil organisms as components of ecosystems. *Proc. 6th International College of Soil Zoologists Ecological Bulletin 25:* 15-23.

Annon. 1968. The shovel-headed garden worm. *Leaflet No 15, The Australian Museum, Sydney.*

Alford, D.V., Boag, B., Johns, P.M., and Yeates, G.W. 1998. Report on the OECD Workshop on Terrestrial Flatworms held at the Zoology Department, University of Canterbury, Christchurch, New Zealand, 16-20 February 1998. *Pedobiologia 42:* 385-388.

Arndt, W. 1925. Über die Gifte der Plattwürmer. *Verhandlungen der Deutschen zoologischen Gesellschaft 30*: 135-145.

Ax, P. 1984. Multicellular animals. A new approach to the phylogenetic order in nature. Volume 1. Springer: Berlin.

Baguñà, J., Carranza, S., Paps, J., Ruiz-Trillo, I., and Riutort, M. 2001. Molecular taxonomy and phylogeny of the Tricladida. *In:* Littlewood, D.T. and Bray, R.A. (Eds) Interrelationships of the Platyhelminthes. London: Taylor and Francis. Chapter 6. 49-56.

Bailey, A.M., Sorensen, J.H. 1962. Subantarctic Campbell Island. Denver Museum of Natural History: Denver.

Ball, I.R. 1974. A contribution to the phylogeny and biogeography of the freshwater triclads (Platyhelminthes: Turbellaria). Chapter 15, pages 339-401. In: Riser, N.W. and Morse, N.P. (Eds) Biology of the Turbellaria. Mc Graw Hill: New York.

Ball, I.R. 1981. The phyletic status of the Paludicola. *Hydrobiologia 84:* 7-12.

Ball, I.R. 1983. Planarians, plurality and biogeographic explanations. *In:* Sims, R.W., Price, J.H., Whalley, P.E.S. *eds*. Evolution, Time and Space. Systematics Association Special Volume *23:* 409-430. London. Academic Press.

Ball, I.R. and Reynoldson, T.B. 1981. British Planarians. (Synopses of British fauna 19) Linnean Society of London / Cambridge University Press: Cambridge. 141pp.

Ball, I.R. and Sluys, R. 1990. Turbellaria. Tricladida: Terricola. In: D.L. Dindal (Ed) *Soil Biology Guide*. Wiley: New York. 1349 pp.

Bautz, A. 1977: Structure fine de l'épiderme chez des Planaires Triclades terrestres et paludicoles. *Archives de Zoologie Expérimentale & Générale 118*: 155-172.

Baylis, H.A. and Munro, C.C.A. 1941. *British Museum (Natural History) Instructions for collectors. No 9A. Invertebrate animals other than insects.* British Museum: London.73pp.

Beauchamp, P. de. 1912. Planaires terrestris des Broméliacées de Costa-Rica Recueilles par M.C. Picado. *Archives de Zoologie Expérimentale et Générale 10:* 1-10.

Beauchamp, P. de 1926. Planaires Terrestres de Sarawak. Sarawak Museum Journal No. 10 328-358.

Beauchamp, P. de. 1939. Planaires terrestres de L'Indochine française récoltées par M. C. Dawydoff. *Memoires du Museum National D'Histoire Naturelle 10*: 300-337.

Beauchamp, P. de. 1956. A propos de *Kontikia whartoni* (Gulliver) planaire terrestre des Madagascareignes. *Bulletin de la Sociétié zoologique de France 80:* 307-313.

Beauchamp, P. de. 1961. Classes de Turbellaires. In: Grasse, P.P. (Ed) *Traité de Zoologie Anatomie-Systématique Biologie 4:*113-123.

Beauchamp, P. de. 1962. *Platydemus manokwari* n.sp. Planaire terrestre de la Nouvelle-Guinée Hollandaise. *Bulletin de la Sociétié zoologique de France 87:* 609-616.

Bendl, W.E. 1909. Europaische Rhynchodemiden. I. *Zeitschrift für Wissenschaftliche Zoologie 92*: 51-74.

Birch, L.C.; Clarke, D.P. 1953. Forest soil as an ecological community with special reference to the fauna. *Quarterly Review of Biology. 28:* 13-36.

Blackshaw, R.P. 1990. Studies on *Artioposthia triangulata* (Dendy) (Tricladida: Terricola), a predator of earthworms. *Annals of Applied Biology 116:* 169-176.

Blackshaw, R.P., Stewart, V.I. 1992. *Artioposthia triangulata* (Dendy, 1894), a predatory terrestrial planarian and its potential impact on lumbricid earthworms. *Agricultural Zoology Reviews 5*: 201-219.

Bloomer, J.R., Straka, J.G. 1990. Disorders of porphyrin metabolism. *In*: Stein, J.H. ed. Internal Medicine. 3rd ed Boston: Little, Brown & Co.

Bonyhady, T. 2000. *The Colonial Earth.* Miegunyah Press: Melbourne

Branagan, D.L. and Packham, G.H. 1967. Field geology of New South Wales. Sydney: Science Press.

Bresslau, E. 1928-1933. Turbellaria, pages 52-320. In: Kukenthal, W., Krumbach, T. (Eds) *Handbuch der Zoologie.* W. De Gruyter: Berlin.

Brook, A.J. 1976. A biogeographic grid system for Australia. *Search 7*: 191-195.

Brook, A. 1977. Australian Biogeographical Integrated Grid System Technical Manual. Department of Zoology, University of Melbourne.

Brown, P.A. 1997. A review of techniques used in the preparation, curation and conservation of microscope slides at the Natural History Museum, London. *The Biology Curator. Issue 10. Special Supplement*: 1-33.

Bryant, C., Janssens, P.A. 1969. Intermediary metabolism in a terrestrial planarian, *Geoplana caerulea* (Moseley). *Comparative Biochemistry and Physiology 30:*841-856

Burr, A. 1912. Zur Fortpflanzungsgeschichte der Süsswassertricladen. *Zoologische Jahrbücher (Systematik) 33*: 595-636.

Busson, H. 1903. Über einige Landplanarien. *Situngsberichte Osterreichische Akadamie der Wissenschaften, Wein 122:*375-429.

Campbell, J.W. 1965. Arginine and urea biosynthesis in the land planarian: its significance in biochemical evolution. *Nature208:* 1299-1301.

Cannon, L.R.G. 1986. Turbellaria of the world. A guide to families and genera. Queensland Museum.

Carabayo, F., Leal-Zanchet, A.M. 2001. A new species of terrestrial planarian (Platyhelminthes: Tricladida: Terricola) from South Brazil. *Brazilian Journal of Zoology 61*: 437-447.

Carabayo, F., Leal-Zanchet, A.M., Vieira, E.M. 2002. Terrestrial flatworm (Platyhelminthes: Tricladida: Terricola) diversity *versus* man-induced disturbance in an ombrophilous forest in southern Brazil. *Biodiversity and Conservation 11:* 1091-1104.

Carranza, S., Baguñà, J., Riutort, M. 1997. Are the Platyhelminthes a monophyletic primitive group? An assessment using 18S rDNA sequences. *Molecular Biology and Evolution 14:* 485-497.

Carranza, S., Ruiz, I, Littlewood, D.T.J., Riutort, M., Baguñà, J. 1998. A reappraisal of the phylogenetic and taxonomic position of land planarians (Platyhelminthes, Turbellaria, Tricladida) inferred from 18SrDNA sequences. *Pedobiologia* (this volume).

Carter, J. 2002. DNA preservation in fluid preserved collections. *Society for the Preservation of Natural History Specimens, Newsletter 16:* 14-15.

Cernosvitov, L. 1931. Studien über die Spermaresorption. III Die Samenresorption bei den Tricladen. *Zoologische Jahrbuch 54* 295-332.

Cernosvitov, L. 1932. Studien über die Spermaresorption. IV Verbreitung der Samenresorption bei den Turbellarien. *Zoologische Jahrbuch 55* 137-172..

Clark, R.B., Cowey, J.B. 1958. Factors controlling the change of shape of certain Nemertean and Turbellarian worms. *Journal of experimental biology 35:* 731-748.

Cloudsley-Thompson, J.L. 1945. Pigments and chromatophore reactions of *Polycelis nigra* and *Planaria lugubris*. *Nature 156:* 294-295.

Cook, H.C. 1974. Manual of histological demonstration techniques. Butterworths: London.

Cooper, D. 1988. The preparation of serial sections of platyhelminth parasites, with details of the materials and facilities required. *Systematic Parasitology 12*: 211-229.

Corrêa, D.D. 1947. A primeira *Dolichoplana* (Tricladida Terricola) do *Brasil. Boletim da Faculdade de filosofia, ciéncias e letras, Universidade de São Paulo 12:*57-81.

Croizat, L. 1962. *Space, Time, Form: The Biological Synthesis.* Published by the author: Caracas.

Culling, C.F.A. 1974. *Handbook of histopathological and histochemical techniques.* 3rd ed. Butterworths: London.

Curini-Galletti, M., Cannon, L.R.G. 1997. A polypharyngeal marine flatworm (Platyhelminthes, Proseriata, Archimonocelididae) from eastern Australia. *Zoological Journal of the Linnaean Society 121:* 485-494.

Curry, W.W., Shaw, C., Johnston, C.F., Thim, L., Buchanan, K.D. 1991. Isolation and characterisation of neuropeptide F from the turbellarian *Artioposthia triangulata. Regulatory Peptides 35*: 231.

Curtis, F. 1905. Nos méthodes de coloration élective du tissu conjonctif. *Achives de medicine expérimentale et d'anatomie pathologique. 17*: 603-636.

Curtis, S.K., Cowden, J.D., Moore, J.D., Robertson, J.L. 1983. Histochemical and ultrastructural features of the epidermis of the land planarian *Bipalium adventitium. Journal of Morphology 175*: 171-194.

Danielli, J.F, Pantin, C.F.A. 1950. Alkaline phosphatase in protonephridia of terrestrial nemerteines and planarians. *Quarterly Journal of Microscopical Science 91:* 209-213.

Darwin, C. 1844. Brief description of several terrestrial planariae, and of some remarkable marine species, with an account of their habits. *Annals and Magazine of Natural History. 14*: 241-256

Darwin, C. 1845. *Journal of Researches.* (The Voyage of the "Beagle", facsimile edition, 1968 Heron Books).

De Clerck, N.M., Van Dyck, D., Postnov, A.A. 2003. Non-invasive high resolution µCT of the inner structure of living animals. *Asia Pacific Microscopy and Analysis January:* 17-19.

Dendy, A. 1890a. The anatomy of an Australian land planarian. *Transactions of the Royal Society of Victoria 1* (for 1889): 50-59.

Dendy, A. 1890b. Zoological Notes on a trip to Walhalla, Victoria. *Victorian Naturalist 6:* 128-136 (for 1889).

Dendy, A. 1891. On the Victorian land planarians.. *Transactions of the Royal Society of Victoria 2* (for 1890): 65-80.

Dendy, A. 1892a. Short descriptions of new land planarians. *Proceedings of the Royal Society of Victoria* 4 (for 1891): 35-38.

Dendy, A. 1892b. On the presence of ciliated pits in Australian land planarians. *Proceedings of the Royal Society of Victoria 4*: 39-46 (for 1891).

Dendy, A. 1892c. Descriptions of some land planarians from Queensland. *Proceedings of the Royal Society of Victoria 4*: 123-129 (for 1891).

Dendy, A. 1892d. Notes on the planarian worms obtained on the Upper Wellington. *Victorian Naturalist 8*: 43-44 (for 1891).

Dendy, A. 1892e. Additional observations on the Victorian land planarians. *Transactions of the Royal Society of Victoria* 2: 25-41 (for 1891).

Dendy, A. 1892f. Notes on some land planarians from Tasmania and South Australia. *Report of the Australasian Association for the Advancement of Science 4*: 369-374 (for 1892).

Dendy, A. 1894a. Notes on some new or little-known land planarians from Tasmania and South Australia. *Proceeding of the Royal Society of Victoria 6*: 175-188.

Dendy, A. 1894b. Further notes on the land planarians of Tasmania and South Australia. *Report of the Australasian Association for the Advancement of Science 5:* 420-423.

Dendy, A. 1895a. Additions to the cryptozoic fauna of New Zealand. *Annals and Magazine of Natural History 14*: 393-401.

Dendy, A. 1895b. Notes on some land planarians collected by Thos. Steel, Esq. F.L.S., in the Blue Mountains, N.S.W. *Proceedings of the Linnean Society of New South Wales 9*: 729-734.

Dendy, A. 1895c. Notes on New Zealand land planarians. Part I. *Transactions of the New Zealand Institute 27*: 177-189.

Dendy, A. 1895d. The cryptozoic fauna of Australasia. *Australian Association for the Advancement of Science 6:* 99-119.

Dendy, A. 1896. Notes on New Zealand land planarians. Part II. *Transactions of the New Zealand Institute 28:* 210-214.

Dendy, A. 1897. Notes on New Zealand land planarians. Part III. *Transactions of the New Zealand Institute 29:* 258-264.

Dendy, A. 1901. Notes on New Zealand land planarians. Part IV. *Transactions of the New Zealand Institute 33:* 222-240.

Dendy, A. 1904. Platyhelminthes. In: Hutton, F.W. (Ed). *Index Faunae Novae Zealandiae* pp306-308. Dulau & Co: London.

Dendy, A. 1909. On land planarians from Auckland and Enderby Islands. In: Chilton, C. *The Subantarctic Islands of New Zealand 2:* 672-673. Philosophical Institute of Canterbury. John Mackay: Government Printer.

Dendy, A. 1911. *Geoplana aucklandica* and *Geoplana marrineri*: a correction in nomenclature. *Proceedings of the New Zealand Institute 43:* 100.

Dendy, A. 1915. On land planarians collected from Western Australia and Tasmania by members of the British Association for the Advancement of Science. *Proceedings of the Zoological Society of London 48*: 693-703.

Diesing, C.M. 1850. Systema Helminthum, I. Vindobonae. W. Braumüller.

Diesing, C.M. 1861. Revision der Turbellarien. Abtheilung: Dendrocoelen. *Sitzungsbeichte der Akademie der Wissenschaften in Wien. 44*: 485-578.

Dietz, R.S., Holden, J.C. 1970. The breakup of Pangea. In: Wilson, J.T. (Ed) *Continents adrift and continents aground.* Freeman & Co.: New York.

Dixon, R.M.W. 1991. *Words of our country: stories, place names and vocabulary in Yidniy, the Aboriginal language of the Cairns-Yarrabah region.* Queensland University Press: St Lucia.

Drury, R.A.B., Wallington, E.A. 1980. *Carleton's histological technique*. 5 ed. Oxford, Oxford University Press.

Du Bois-Reymond Marcus, E. 1951. Turbellaria Brasilieros (9). Boletim da Faculdade de filosophia, ciências e letras, Universidade de São Paulo. 19: 5-215.

Ehlers, U. 1985. Phylogenetic relationships within the Platyhelminthes. Chapter 9, pages 143-158. In: Conway Morris, S, George, J.D., Gibson, R., Platt, H.M. (Eds) *The origins and relationships of lower invertebrates.* The Systematics Association Special Volume No 28. Clarendon Press: Oxford.

Ehlers, U. 1986. Comments on a phylogenetic system of the Plathelminthes. *Hydrobiologia 132:* 1-12.

Ethridge, R. 1889. Lord Howe Island. *Annelida page 36. Memoirs No. 2. The Australian Museum, Sydney.*

Farnesi, R.M., Marinelli, M., Tei, S., Vagnetti, D. 1979. Localization de la phosphatase acide dans les cellules parietals de la bourse copulatrix chez *Dugesia lugubris* s.l. etude ultrastructurale. *Acta Embryologiae Experimentalis 1*: 69-78.

Fernandes, M.C., Alvares, E.P., Gama, P., Silveira, M. 2001. The sensory border of the land planarian *Bipalium kewense* (Tricladida, Terricola). *Belgian Journal of Zoology 131 (Supplement 1):* 173-178.

Fischer, O. 1926. *Digonopyla (Dolichoplana) harmeri* (Graff), eine Landtriclade aus Celebes mit vollkommen getrenten Geschlechtsapparaten. *Zoologische Anzeiger66*: 257-261.

Fletcher, J.J. 1887. Remarks on an introduced species of land planarian apparently *Bipalium kewense* Moseley. *Proceedings of the Linnaean Society of New South Wales 2:* 244-249.

Fletcher, J.J. 1901. On the rise and early progress of our knowledge of the Australian fauna. *Australasian Association for the Advancement of Science 8:* 69-104.

Fletcher, J.J., Hamilton, A.G. 1888. Notes on Australian Land Planarians with descriptions of some new species. Part 1. *Proceedings of the Linnaean Society of New South Wales 2:* 349-374.

Fox, H.M., Veevers, H.G. 1960. *The nature of animal colours.* Sidgwick & Jackson: London.

Fox, D.L. 1976. *Animal Biochromes and structural colours.* University of California Press: Los Angeles & London.

Fraser, C. 1986. *Beyond the roaring forties – New Zealand's Subantarctic Islands.* GPO Publishing: Wellington.

Fraser, P.M., Boag, B. 1998. The distribution of lumbricid earthworm communities in relation to flatworms: a comparison between New Zealand and Europe. *Pedobiologia 42:* 542-553.

Froehlich, C.G. 1955. Sôbre morphologia e taxonomia das Geoplanidae. *Boletim da Faculdade de filosofia, ciências e letras, Universidade de São Paulo 19*: 197-251.

Froehlich, C.G. 1956. On the biology of land planarians *Boletim da Faculdade de filosofia, ciências e letras, Universidade de São Paulo 20:* 263-272.

Froehlich, C.G. 1967. A contribution to the zoogeography of Neotropical land planarians. *De Acta Zoológica Lilloana 23:* 153-162.

Froehlich, E.M. 1955. Sôbre espécies Brasileiras do Gênero Geoplana. *Boletim da Faculdade de filosofia, ciências e letras, Universidade de São Paulo 19*: 289-329.

Froehlich, E.M. 1978. On a collection of Chilean landplanarians. *Boletim de Zoologia, Universidade de São Paulo 3*: 7-80.

Froehlich, E.M., Froehlich, C.G. 1972. Land planarians from the Amazonian region. *Papéis Avulsos de Zoologia 26:* 29-45.

Fuhrmann, O. 1914. Planaires terrestris de Colombie. In: O. Furhman & E. Mayor (Eds) Voyage d'Exploration Scientifique en Colombie. *Mémoires de la Sociétie Neuchâtel des Sciences Naturelle 5:* 748-792.

Fuhrmann, O. 1916. Eine in *Geoplana* parasitierende Gregarine. *Centralblatt für Bakteriologie, Parasiten Kunde, und Infectionskrankherten 77:* 482-485.

Fyfe, L.M. 1937: The reproductive system of the planarian *Artioposthia triangulata.* Quarterly Journal of the Microscopical Society. 80: 99-126.

Fyfe, L.M. 1944. The classification and reproductive organs of New Zealand land planarians. Part I. *Transactions of the Royal Society of New Zealand 74*: 288-293.

Fyfe, M.L. 1946: The classification and reproductive organs of New Zealand land planarians. Part II. *Trans. Roy. Soc. N.Z. 76:* 135-138.

Fyfe, M.L. 1947. The classification and reproductive organs of New Zealand land planarians. Part III. *Transactions of the Royal Society of New Zealand 76*: 517-523.

Fyfe, M.L. 1948. The reproductive organs of *Geoplana sanguinea* Moseley. *Records of the Australian Museum 22*: 64-66.

Fyfe, M.L. 1953. Land planarians from Auckland and Campbell Islands. *Cape Expedition Series. Bulletin No. 12*: 5-20.

Fyfe, L.M. 1956. The classification and reproductive organs of New Zealand land planarians. Part IV. *Transactions of the Royal Society of New Zealand 83*: 505-514.

Gabe, M. 1976. *Histological techniques*. Masson, Paris.1106pp.

Gaunt, W.A. 1971. *Microreconstruction.* Pitman: London.108pp.

Gelei, J. von 1929. Untersuchungsmethoden für Turbellarien. *Zeitschrift für wissesnschaftliche mikroskopie und mikroskopische technik 46*: 45-88.

Gentilli, J. 1972. *Australian Climate Patterns.* Nelson: Melbourne.

Gibson, R. 1972. *Nemerteans*. London: Hutchinson University Library.

Graff, L. von. 1896a. Über die morphologie des Geschlecht-sepparates der Landplanarien. *Verhandlungen Deutsche Zoologische Gesellschaft 6:* 61-75.

Graff, L. von. 1896b. Über das System und die geographische Verbreitung der Landplanarien. *Verhandlungen Deutsche Zoologische Gesellschaft 6:* 75-93.

Graff, L. von. 1899. Monographie der Turbellaria. II Tricladida Terricola (Landplanarien). Text & Atlas. Wilhelm Engelmann: Leipzig.

Graff, L. von. 1912-1917. Turbellaria. In: H.G. Bronn (Ed). *Klassen und ordnung des Tier-Reichs.* Bd 4 Academie Verlagsgesellschaft.

Gremigni, V. 1983. Platyhelminthes – Turbellaria. In: K.G. & R.G. Adiyodi (Eds) Reproductive Biology of Invertebrates. Volume 1, Oogenesis, Oviposition, and Oosorption. Chapter 3: 67-107. Wiley: New York.

Gremigni, V. 1992. Features of sex evolution in Platyhelminthes-Turbellaria. In: R. Dallai (ed) Selected Symposia and Monographs U.Z.I. *6*: 69-86.

Grimmett, R.E.R. 1926: Forest-floor covering and its life. *Trans. Proc. N.Z. Inst. 56:* 423-440.

Guraya, S.S., Parshad, V.R. 1988. Accessory Sex Glands: I. Platyhelminthes. In: Adiyodi, K.G. & R.G. (Eds) *Reproductive Biology of the Invertebrate 3:* 1-49. Wiley & Sons: New York.

Hackman, R.H. 1953. Chemistry of insect cuticle. 3 - hardening and darkening of the cuticle. *Biochemical Journal 54*: 371-377.

Hallez, P. 1892. Classification des Triclades (Note préliminaire). *Bulletin de la Société zoologique de France 17:* 106-109.

Hallez, P. 1893. Catalogue des Turbellariés (Rhabdocoelides, Triclades et Polyclades) du Nord de la France et de la Cote Boulonnaise. *Revue Bioiologique du Nord du France, Lille. 5:* 92-107.

Hamilton, A.G. 1937. *Bush Rambles*. Sydney: Angus & Robertson.

Harrison, L. 1928. The composition and origins of the Australian fauna, with special reference to the Wegener hypothesis. *Reports of the Australasian Association for the Advancement of Science 18:*332-396.

Hauslauer-Gamisch, L. 1981. Die Terricolan Planarien- Ausbeute der Sunda-Expedition Rensch. I. *Myriopharynx tetracelis* nov. spec. *Acta Biologia Leoplodensia 3*: 23-54.

Hauser, J. 1966. Beiträge zur Turbellarienhistologie. Der struktur der Kriechliche von *Bipalium kewense. Pesquisas Zoologia 19*: 1-23.

Heatwole, H. 1987. Major components and distributions of terrestrial fauna. *In*: Dyne, G.R. *ed.* Fauna of Australia. 1A General articles. Canberra, Australian Government Publishing Service.

Heidenhain, M. 1916. Über die Mallorysche Bindegewebesfärbung mit Karmin und Azocarmin als Vorfarben. *Zeitschrift für wissenschaftliche Mikroskopie und für mikroskopische Technik 32*: 361-372.

Heinzel, L. 1929. Zur kenntnis der Rhynchodemiden. *Zoologische Jahrbücher (Systematik) 56*: 425-462.

Hendelberg, J. 1983. Platyhelminthes – Turbellaria. In: K.G. & R.G. Adiyodi (Eds) Reproductive Biology of Invertebrates. Volume 2, Spermiogenesis and sperm function. Chapter 3: 67-107. Wiley: New York.

Hermans, C.O. 1983. The duo-gland adhesive system. *Oceanography and Marine Biology Annual Review 21:*283-339.

Hickman, V.V. 1964. On *Planarivora insignis* Gen. et sp.n. (Diptera; Mycetophilidae), whose larval stages are parasitic in land planarians. *Papers and Proceedings of the Royal Society of Tasmania 99:* 1-8.

Hollander, D.H. and Frost, J.K. 1971. Antioxidant inhibition of stain fading and mounting medium crazing. *Acta cytologica 15*: 419.

Honigsbaum, M. 2001. The fever trail – the hunt for the cure of malaria. Macmillan: London.

Hori, I. 1978: Possible role of rhabdite-forming cells in cellular succession of the planarian epidermis. *Journal of electron microscopy 27*: 89-102.

Humason, G.L. 1972. *Animal tissue techniques.* 3rd ed. San Francisco, W.H. Freeman.641pp.

Hyman, L.H. 1938. Landplanarians from Yucatan. *Carnegie Institution of Washington, Publications 491*: 23-32.

Hyman, L.H. 1940. Land planarians from the Palau and Caroline Islands, Micronesia. *Annals and Magazine of Natural History 5*: 345-362.

Hyman, L.H. 1943. Endemic and exotic land planarians in the United States with a discussion of necessary changes of names in the Rhynchodemidae. *American Museum Novitates No.1241*: 1-21.

Hyman, L.H. 1951. The Invertebrates: Platyhelminthes and Rhynchocoela. The acoelomate Bilateria. Vol 2. New York, McGraw-Hill.

International Commission on Zoological Nomenclature (ICZN). 1999. *International Code of Zoological Nomenclature* 4th ed. International Trust for Zoological Nomenclature: Natural History Museum, London. 306pp.

Ingram, G.J., Raven, R.J. 1991. *An atlas of Queensland's Frogs, Reptiles, Birds & Mammals.* Board of Trustees, Queensland Museum: Brisbane.

Ishii, S. 1980a. The ultrastructure of the protonephridial tubules of the freshwater planarian *Bdellocephala brunnea. Cell and Tissue Research 206:* 441-449.

Ishii, S. 1980b. The ultrastructure of the protonephridial flame cell of the freshwater planarian *Bdellocephala brunnea. Cell and Tissue Research 206:* 451-458.

Jameson, H.L. 1907. On some Natal land planarians. *South African Association for the Advancement of Science. Papers 3:* 27-39.

Jenkins, M.M., Brown, H.P. 1963. Cocoon-production in *Dugesia dorotocephala* (Woodworth) 1897. *Transactions of the American Microscopical Society 82*: 167-177.

Jennings, J.B. 1959. Observations on the nutrition of the land planarian *Orthodemus terrestris* (O.F. Müller). *Biological Bulletin 117*: 119-124.

Jennings, J.B. 1968. Feeding, digestion and food storage in two species of temnocephalid flatworms (Turbellaria: Rhabdocoela). *Journal of Zoology, London 156*: 1-8.

Jennings, J.B., Gibson, R. 1968. The structure and life history of *Haplosporidium malacobdellae* sp. Nov., a new sporozoan from the entocommensal rhynchocoelan *Malacobdella grossa* (O.F. Müller). *Archives of Protistenk. 111:* 31-37.

Jennings, J.B., Cannon, L.R.G. 1987. The occurrence, spectral properties and probable rôle of haemoglobins in four species of entosymbiotic turbellarians (Rhabdocoela: Umagillidae). *Ophelia 27*: 143-154.

Johns, P.M. 1993. A short checklist and bibliography of New Zealand terrestrial flatworms (Platyhelminthes: Turbellaria). *Entomological Society of New Zealand. Proceedings of the 42nd annual conference*:17-31.

Johns, P.M. 1998. The New Zealand terrestrial flatworms: a 1997-98 perspective. *Pedobiologia 42:* 464-468.

Johns, P., Boag, B., Yeates, G.W. 1998. Observations on the geographic distribution of flatworms (Turbellaria: Rhynchodemidae, Bipaliidae, Geoplanidae) in New Zealand. *Pedobiologia 42:* 469-476.

Johri, L.N. 1952. Report on a turbellaria *Placocephalus kewense*, from Delhi State and its feeding behaviour on the live earthworm, *Pheretima posthuma. Science and Culture Calcutta 18*: 291.

Jones, H.D. 1978a. Fluid skeletons in aquatic and terrestrial animals. In: *Comparative physiology: 267-281.* Schmidt-Nielson, K (Ed). Cambridge: University Press.

Jones, H.D. 1978b: Observations on the locomotion of two British terrestrial planarians (Platyhelminthes, Tricladida). *Journal of Zoology, London 186:* 407-416.

Jones, H.D. 1981. A specimen of the Australian land planarian *Geoplana sanguinea* (Moseley) var. *alba* (Dendy) from the Isles of Scilly. *Journal of Natural History, London 15:* 837-843.

Jones, H.D., Cumming M.S. 1998. Feeding behaviour of the termite-eating planarian *Microplana termitophaga* (Platyhelminthes: Turbellaria: Tricladida: Terricola) in Zimbabwe. *Journal of Zoology London 245:* 53-64.

Jones, H.D., Cumming, M.S., Kennaugh, J.H. 1995: The anatomy of *Microplana termitophaga* from Zimbabwe and Kenya: confirmation of the subfamily and genus. *Hydrobiologia 305*: 121-126.

Jones, H.D. and Gerard, B.M. 1999. A new species of terrestrial planarian (Platyhelminthes; Tricladida; Terricola) from Scotland, and an emendation of the genus *Artioposthia*. *Journal of Natural History 33*: 387-394.

Jones, H.D., Johns, P.M., and Winsor, L. 1998. The proposed synonymy of *Parakontikia ventrolineata* (Dendy, 1892) and *Kontikia mexicana* (Hyman, 1939): what is a penis papilla. *Hydrobiologia* **383**: 91-96.

Kawakatsu, M. 1986. Land planarians from West Malaysia. *Bulletin of the Biogeographical Society of Japan 41*: 1-15.

Kawakatsu, Ogren, R.E., M., Froehlich, E.M. 2000. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world – 8 (2). *Bulletin of the Fuji Womens' College 38*: 83-103.

Kawakatsu, M., Ogren, R.E., Froehlich, E.M., Sasaki, G-Y. 2001. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world – 9. *Bulletin of the Fuji Womens' College 39:* 111-120.

Kawakatsu, M., Ogren, R.E., Froehlich, E.M., Sasaki, G-Y. 2002. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world – 10. *Bulletin of the Fuji Womens' College 40:* 162-177.

Kier, W.M., Smith, K.K. 1985. Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats. *Zoological Journal of the Linnean Society of London 83:* 307-324.

Lawrence, R.F. 1953. The biology of the cryptic fauna of forests. Cape Town: Balkema.

Leal-Zanchet, A.M., Carabayo, F. 2001. Two new species of Geoplanidae (Platyhelminthes, Tricladida, Terricola) of south Brazil. *Journal of Zoology, London 253*: 433-446.

Leal-Zanchet, A.M., Hauser, J. 1999. Penis glands of the dugesiid planarian *Girardia schubarti* (Platyhelminthes, Tricladida, Paludicola). *Invertebrate Biology 118:* 35-41.

Leidy, J. 1851. Helminthological contribution No. 3. *Proceedings of the Academy of Natural Sciences of Philadelphia 5*: 239-244.

Lillie, R.D. 1997. H.J. *Conn's Biological Stains.* 9th ed. Williams & Wilkins: Baltimore. 692pp.

Littlewood, D.T.J., Bray, R.A., Clough, K.A. 1998. A phylogeny of the Platyhelminthes: towards a total-evidence approach. *Hydrobiologia 383*: 155-160.

Littlewood, D.T.J., Rohde, K., Clough, K.A. 1999. The interrelationships of all major groups of Platyhelminthes: phylogenetic evidence from morphology and molecules. *Biological Journal of the Linnean Society 66:* 75-114.

Mann, T. 1954:. The biochemistry of semen. London, Methuen.

Mann, T., Lutwak-Mann, C. 1981. Male reproductive function and semen. Springer-Verlag: New York.

Marcus, E. 1951. Turbellaria Brasileros (9). Boletim da Faculdade de filosofia, ciéncias e letras, Universidade de São Paulo *16*:5-215.

Marcus, E. 1953. Turbellaria Tricladida. In: Exploration du Parc National de l'Upemba. 1. Mission G.F. de Witte. Fascicule 21: 3-61. Institut des Parcs Nationaux du Congo Belge: Bruxelles.

Mather, J.G., Christensen, O.M. 1998. Behavioural aspects of the "New Zealand flatworm", *Artioposthia triangulata*, in relation to species spread. *Pedobiologia 42:* 520-531.

Mayr, E. and Ashlock, P.D. 1991. *Principles of Systematic Zoology* 2nd ed. McGraw-Hill: New York. 475pp.

McCarthy, G. 1991. *Guide to the archives of science in Australia.* Thorpe: Port Melbourne.

McGee, C., Fairweather, I., Blackshaw, R.P., McIlroy, J., Walker, B., Wisdom, B. 1995. Ultrastructural features of the epidermis and partial characterisation of the various proteinases present in the mucus of *Artioposthia triangulata. The Microscopical Society of Ireland, 19th Annual Symposium Communications. Supplement to Proceedings of the Royal Microscopical Society 30*: 6.

McKanna, J.A. 1968a. Fine structure of the protonephridial system in planaria. I. The flame cells. *Zeitschrift für Zellforschung 92:* 509-523.

McKanna, J.A. 1968b. Fine structure of the protonephridial system in planaria. II. The Ductules, collecting ducts, and osmoregulatory cells. *Zeitschrift für Zellforschung 92:* 524-535.

McLachlan, H. 1935. *Records of a family 1800-1933. Pioneers in education, social service and liberal religion.* Manchester University Press: Manchester.

McRae, E.K. 1961. Localization of porphyrin fluorescence in planarians. *Science 134:* 331-332.

Mecznikow, E. 1866. Über *Geodesmus bilineatus* Nob. (*Fasciola terrestris* O.Fr. Müller?), eine europäische Land-planarie. *Bulletin of the Imperial Academy of Science of St Petersbourg 9:* 433-447.

Meixner, J. 1928. Der Genital apparat der Tricladen und seine Beziehungen zu ihrer allgemeinen Morphologie, Phylogenie, Ökologie und Verbreitung. *Zeitschrift für Morphologie und Ökologie der Tiere 11*: 570-612.

Mesibov, B. 1993. Species-level comparison of litter invertebrates from three vegetation types in Northwest Tasmania. *Tasmanian National Rainforest Conservation Program Report No. 13.*

Minelli, A. 1981. Of locomotion in terrestrial planarians. *Bollettino di Zoologia 48:* 41-50.

Minelli, A. 1993. *Biological Systematics – the state of the art.* Chapman & Hall: London.

MinMin, L., Watson, N.A., Rohde, K. 1992. Ultrastructure of sperm and spermiogenesis of *Artioposthia* sp. (Platyhelminthes: Tricladida: Terricola). *Australian Journal of Zoology 40:* 667-674.

Mombrum de Carvalho, I., Hauser, J., Friedrich, S.M.G. 1975. Preparation methods for the light microscopy of the basal membrane in *Geoplana carinata* Reister (Turbellaria, Tricladida). *Mikroskopie 31:* 323-332.

Moore, S. 1989. Conservation of spirit specimens. In: Howie, C.V. ed. Conservation of natural history specimens spirit collections. Manchester, Manchester Museum and Department of Environmental Biology, University of Manchester.

Moretto, H.J.A. 2001. The resorptive vesicle of *Temnocephala jheringi* (Temnocephalida). *Belgian Journal of Zoology 131* (Supplement 1): 179-182.

Moseley, H.N. 1875. On the anatomy and histology of the land planarians of Ceylon, with some accounts of their habits, and a description of two new species, and with notes on the anatomy of some European aquatic species. *Philosophical Transactions of the Royal Society, London 4:*105-171.

Moseley, H.N. 1877a. On the colouring matters of various animals, and especially on deep-sea forms dredged by H.M.S. *Challenger. Quarterly Journal of Microscopical Science. 17:* 9-11.

Moseley, H.N. 1877b. Notes on the structure of several forms of land planarian with a description of two new genera and several new species, and a list of all species at present known. *Quarterly Journal of microscopical Science. 17*: 273-292.

Moseley, H.N. 1878. Description of a new species of landplanarian from the hothouses at Kew Gardens. *Annals and Magazine of Natural History1*: 237-239.

Müller, J. 1907. Weitere Beiträge zur Kenntnis der Bipaliiden. *Zeitschrift für wissenschaftliche zoologie 86*: 75-114.

Müller, O.F. 1774. Vermium terrestrium et fluviatilium, seu Animalium infusoriorum, helminthicorum, et testaceorum, non marinorum, succincta historia. I. Pars altera, Helminthica. pp 1-72 and Index. Havniae et Lipsiae.

Mulvaney, D.J., Calaby, J.H. 1985. *"So much that is new "Baldwin Spencer, 1860-1929. A biography.* Melbourne University Press: Melbourne.

Neville, A.C. 1993. Biology of fibrous composites: development beyond the cell membrane. Cambridge University Press.

Nicholas, F.W., Nicholas, J.M. 1989. *Charles Darwin in Australia.* Cambridge University Press: Cambridge.

Nurse, F.R. 1950. Quinnone tanning in the cocoon-shell of *Dendrocoelum lacteum. Nature 165*: 570.

Ogren, R.E. 1955. Ecological observations on the occurrence of *Rhynchodemus*, a terrestrial turbellarian. *Transactions of the American Microscopical Society 74*: 54-60.

Ogren, R.E. 1981. Land planarians in Pennsylvania. *Proceedings of the Pennsylvania Academy of Science 55:* 52-56.

Ogren, R.E. 1984. The land planarian *Microplana terrestris* (Platyhelminthes: Turbellaria) from the United Sates. *Transactions of the American Microscopical Society 103:* 130-136.

Ogren, R.E. 1986. The development of the reproductive apparatus of the land planarian *Rhynchodemus sylvaticus* and its significance for classification in the genus. *Hydrobiologia 132:* 175-180.

Ogren, R.E. 1989. Redescription and a new name for the blue land planarian *Geoplana vaga* now considered conspecific with *Caenoplana coerulea* Moseley from Australia (Turbellaria: Tricladida: Geoplanidae). *Journal of the Pennsylvanian Academy of Science 63:* 135-142.

Ogren, R.E. 1991. Developmental sequence for the copulatory organs of *Kontikia mexicana* with remarks on taxonomic significance (Turbellaria: Tricladida: Geoplanidae). *Hydrobiologia 227*: 139-144.

Ogren, R.E. 1998. Selected characters of the copulatory organs of the land planarian family Bipaliidae and their significance (Tricladida, Terricola). *Hydrobiologia*

Ogren, R.E. and Kawakatsu, M. 1988a. Index to the species of the family Rhynchodemidae (Turbellaria, Tricladida, Terricola). Part I: Rhynchodeminae. *Bulletin of the Fuji Womens' College 26*: 39-91.

Ogren, R.E. and Kawakatsu, M. 1988b. A juvenile land planarian of the genus *Caenoplana* Moseley, 1877, from Papua New Guinea (Turbellaria, Terricola, Geoplanidae). *Bulletin of the Fuji Womens' College 26*: 93-103.

Ogren, R.E. and Kawakatsu, M. 1989. Index to the species of the family Rhynchodemidae (Turbellaria, Tricladida, Terricola). Part II: Microplaninae. *Bulletin of the Fuji Womens' College 27*: 53-111.

Ogren, R.E. and Kawakatsu, M. 1990. Index to the species of the family Geoplanidae (Turbellaria, Tricladida, Terricola). Part I: Geoplaninae. *Bulletin of the Fuji Womens' College 28*: 79-166.

Ogren, R.E. and Kawakatsu, M. 1991. Index to the species of the family Geoplanidae (Turbellaria, Tricladida, Terricola). Part II: Caenoplaninae and Pelmatoplaninae. *Bulletin of the Fuji Womens' College 29*: 25-102.

Ogren, R.E. and Kawakatsu, M. 1992a. Index to the species of the family Geoplanidae (Turbellaria, Tricladida, Terricola). Part II: Caenoplaninae and Pelmatoplaninae (a continuation). *Bulletin of the Fuji Womens' College 30*: 35-58.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1992b. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Tricladida, Terricola). *Bulletin of the Fuji Womens' College 30*: 59-103.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1993a. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Tricladida, Terricola). Addendum I. Combined taxonomic index: Bipaliidae; Rhynchodemidae (Rhynchodeminae; Microplaninae); Geoplanidae (Geoplaninae; Caenoplaninae; Pelmatoplaninae) Exclusive of Winsor's Second 1991 paper. *Bulletin of the Fuji Womens' College 31*: 33-60.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1993b. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Tricladida, Terricola). Addendum II. Hallez's (1890-1893, 1894) classif9icatuion system of land planarians. Addendum III. Winsor's (1991b) provisional classification of Australian and New Zealand caenoplanid land planarians. *Bulletin of the Fuji Womens' College 31*: 61-86.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1994. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world - 3. *Bulletin of the Fuji Womens' College 32*: 73-86.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1995. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world - 4. *Bulletin of the Fuji Womens' College 33*: 79-85.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1996. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world - 5. *Bulletin of the Fuji Womens' College 34:* 87-93.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1997a. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world - 6. *Bulletin of the Fuji Womens' College 35:* 55-61.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1997b. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Addendum IV. Geographic locus index: Bipaliidae; Rhynchodemidae (Rhynchodeminae; Microplaninae); Geoplanidae (Geoplaninae; Caenoplaninae; Pelmatoplaninae). *Bulletin of the Fuji Womens' College 35*: 63-103.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1998. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Additions and corrections of the previous land planarian indices of the world – 7. *Bulletin of the Fuji Womens' College 36*: 75-82.

Ogren, R.E., Kawakatsu, M., Froehlich, E.M. 1999. Additions and corrections of the previous land planarian indices of the world (Turbellaria, Seriata, Tricladida, Terricola). Addendum V. The taxonomic change of land planarians reported in recent publications (1998-1999). Additions and corrections of the previous land planarian indices of the world – 8 (1). *Bulletin of the Fuji Womens' College 37*: 93-103.

Ogren, R.E., Sluys, R. 1998. Selected characters of the copulatory organs in the land planarian family Bipaliidae and their taxonomic significance (Tricladida: Terricola). *Hydrobiologia 383*: 77-82.

Ogren, R.E., Sluys, R. 2001. The genus *Humbertea* gen. nov., a new taxon of the land planarian family Bipaliidae (Tricladida: Terricola). *Belgian Journal of Zoology 131*(Supplement 1): 201-204.

Palladini, G., Medolago-Albani, L., Margotta, V., Conforti, A., Carolei, A. 1979. The pigmentary system of planarai. *Cell and Tissue Research 199:* 197-202.

Pantin, C.F.A. 1950. Locomotion in British terrestrial nemertines and planarians: with a discussion on the identity of *Rhynchodemus bilineatus* (Mecznikow) in Britain, and on the name of *Fasciola terrestris,* O.F.Müller. *Proceedings of the Linnaean Society of London 162:* 23-37.

Pantin, C.F.A. 1953. On the name of the ground fluke *Fasciola terrestris* O.F. Müller, on *Othelosoma symondsi* Gray, and on the genus *Amblyplana* von Graff. *Zoological Journal of the Linnean Society 42*: 207-218.

Papps, E.H. 1965. Aboriginal words of Australia. Terry Hills N.S.W.: Reed.

Pasey, W. and Edwards, C.A. 1978. A modification of the Martius Yellow - Scarlet Red - Aniline Blue method for fibrin. *Stain Technology 53*: 58-59.

Pearce-Kelly, P., Clarke, D., Walker, C., Atkin, P. 1997. A conservation programme for the Partulid tree snails of the Pacific region. *Memoirs of the Museum of Victoria 56*: 431-433.

Pedersen, K.J. 1961a. Studies on the nature of planarian connective tissue. *Zeitschrift für Zellforschung 53:*569-608.

Pedersen, K.J. 1961b. Some observations on the fine structure of planarian protonephridia and gastrodermal phagocytes. *Zeitschrift für Zellforschung 53:*609-628.

Pedersen, K.J. 1965. Slime secreting cells of planarians. *New York Academy of Science 118:*424-443.

Percival, E. 1925. *Rhynchodemus britannicus*, n.sp. A new British terrestrial triclad, with a note on the excretion of Calcium Carbonate. *Quarterly Journal of Microscopical Science 69:* 343-355.

Pfitzner, I. 1958. Die Belingungen der Fortbewegung bei den deutschen Landplanarien. *Zoologische Beiträge 3:* 235-311

Platnick, N.I. 1991. Patterns of biodiversity: tropical vs temperate. *Journal of Natural History, London 25:* 1083-1088.

Pope, E. C. 1974. More animals of the leaf litter. *Australia's Wildlife Heritage 2:*890-893.

Prudhoe, S. 1949a. Some roundworms and flatworms from the West Indies and Surinam. IV. Land planarians. *Zoological Journal of the Linnean Society 41*: 420-433.

Prudhoe, S. 1949b. Some land planarians from the Marquesas Islands. *Occasional Papers of the Bishop Museum 19:* 248-255.

Puchler, H., McGowan, L. and Meloan, S.N. 1989. Why do some stains fade? Part II. Effects of dye structure, molecular orbital systems, metals, substrates, moisture and chemical reactions. *Journal of Histotechnology 12*: 1225-1226.

Raw, F. 1959. Estimating earthworm populations by using formalin. *Nature 184*:257.

Rawlinson, P.A. 1974. XI. Biogeography and ecology of the reptiles of Tasmania and Bass Strait area. In: Williams, W.D. (Ed) *Biogeography and Ecology of Tasmania.* Junk: The Hague.

Rieger, R.M. 1998. 100 years of research on "Turbellaria". *Hydrobiologia 383:* 1-27.

Riester, A. 1938. Beiträge zur Geoplaniden-Fauna Brasiliens. *Abhandlungen der Senckenbergischen Naturforschended Gesellschaft 441:*3-88 + Plate 1.

Rohde, K., Watson, N.A. 1992. Ultrastructure of flame bulbs and protonephridial capillaries of *Artioposthia* sp. (Platyhelminthes, Tricladida, Geoplanidae). *Acta zoologica 73*: 231-236.

Rohde, K., Johnson, A.M., Baverstock, P.R. Watson, N.A. 1995: Aspects of the phylogeny of Platyhelminthes based on 18S ribosomal DNA and protonephridial ultrastructure. *Hydrobiologia 305*: 27-35.

Romeis, B. 1968. *Mikroscopische Technik.* Wein, R. Oldenbourg Verlag.

Sanderson, J.B. 1994. *Biological Microtechnique.* Microscopy Handbooks 28. Royal Microscopical Society & Bios: Oxford.

Schmarda, L.K. 1859. Neue Wirbellose Thiere beobachtet und gesammelt auf einer Reise um die erde 1853 bis 1857. I. Turbellarien, Rotatorien und Anneliden. Leipzig. Wilhelm Engelmann.

Schröder, O. 1924. Landplanarien von Neu-Caledonien und den Loyalty-Inseln. In: F. Sarasin & J. Roux (Eds) Nova Caledonia.Forschungen in Neu-Caledonien und auf den Loyalty-Inseln. A. Zoologie. Vol III. C.W. Kreidel: Berlin.

Schultze, M.; Müller, F. 1857. Beiträge zur Kenntniss der Landplanarien nach Mittheilungen des Dr. Fritz Müller in Brasilien und nach einegen Untersuchungen von Dr. Max Schultze. *Abhandlungen Naturforschung Gesellschaft. zu. Halle. 4:* 19-38.

Schoobridge, M.P.K. 1983. A new principle in polychrome staining: a system of automated staining, complementary to haematoxylin and eosin, and usable as a research tool. *Stain Technology 58:* 245-258.

Selkirk, P.M., Seppelt, R.D., Selkirk, D.R. 1990. Subantarctic Macquarie Island: environment and biology. Cambridge University Press: Cambridge.

Silveira, M. 1970. Microscopia electrônica do sistema nefridial de planárias. *Sociedade Brasiliera Papa o Progresso* Ciencia: 309.

Silveira, M. 1998. Ultrastructure of muscle cells from a few selected turbellarians: possible correlations between form and function. *Hydrobiologia 383:* 191-196.

Silveira, M. Corinna, A. 1976. Fine structural observations on the protonephridium of the terrestrial Triclad *Geoplana pasipha. Cell & Tissue Research 168:* 455-463.

Sluys, R. 1988. Structural and functional morphology within the genus *Synsiphonium* (Tricladida, Maricola). *Forschritte der Zoologie 36:* 413-417.

Sluys, R. 1989a. Phylogenetic relationships of the triclads (Platyhelminthes, Seriata, Tricladida). *Bijdragen tot de Dierkunde 59*: 3-25.

Sluys, R. 1989b. A Monograph of the Marine Triclads. Rotterdam, Balkema.

Sluys, R. 1989c. Sperm resorption in triclads (Platyhelminthes, Tricladida). *Invertebrate Reproduction and Development 15:* 89-95.

Sluys, R. 1990. On *Bdellasimilis barwicki* (Platyhelminthes: Tricladida) and its Phyletic position. *Invertebrate Taxonomy 4:* 149-158.

Sluys, R. 1994. Explanations for biogeographic tracks across the Pacific Ocean: a challenge for palaeogeography and historical biogeography. *Progress in Physical Geography 18:* 42-58.

Sluys, R. 1995. Platyhelminthes as paleogeographical indicators. *Hydrobiologia 305:* 49-53.

Sluys, R. 1998. Land planarians (Platyhelminthes, Tricladida, Terricola) in biodiversity and conservation studies. *Pedobiologia 42:* 490-494.

Sluys, R. 1999. Global diversity of land planarians (Platyhelminthes, Tricladida, Terricola): a new indicator-taxon in biodiversity and conservation studies. *Biodiversity and Conservation 8:* 1663-1681.

Sluys, R. 2001. Towards a phylogenetic classification and characterization of dugesiid genera (Platyhelminthes, Tricladida, Dugesiidae): a morphological perspective. In D.T.J. Littlewood & R.A. Bray (Eds). Interrelationships of the Platyhelminthes. Systematics Association Special Volume Series 60. Taylor & Francis, London & New York: 57-73.

Sluys, R., Toimoshkin, Q.A., Kawakatsu, M. 1998. A new species of giant planarian from Lake Baikal, with some remarks on character states in the Dendrocoelidae (Platyhelminthes, Tricladida, Paludicola). *Hydrobiologia 383:* 69-75.

Smith, B.J., Stone, S, Ayling, A., and Winsor, L. 1991. Arthur Dendy: Biography, Bibliography and list of new taxa. *Unpublished manuscript.*

Soppot-Ehlers, B. 1985. The phylogenetic relationships within the Seriata (Platyhelminthes). Chapter 10, pages 159-167. In: Conway Morris, S, George, J.D., Gibson, R., Platt, H.M. (Eds) *The origins and relationships of lower invertebrates.* The Systematics Association Special Volume No 28. Clarendon Press: Oxford.

Southwood, T.R.E. 1996. *Ecological Methods.* Chapman & Hall: London.391.

Souza, S.T., Leal-Zanchet, A.M. 2002. Histological and histochemical aspects of the penial glands of *Girardia biapertura* Sluys, 1997 (Platyhelminthes, Tricladida, Paludicola). *Brazilian Journal of Biology 62*:547-555.

Spencer, W.B. 1891:. Notes on some Victorian land planarians. *Proceedings of the Royal Society of Victoria.* 3 (for 1890): 84-92.

Spencer, W.B. 1892. Land planarians from Lord Howe Island. *Transactions of the Royal Society of Victoria 2* (for 1891): 42-51.

Springett, J.A. 1976. The effects of prescribed burning on the soil fauna and litter decomposition in Western Australian forests. *Australian Journal of Ecology 1*: 77-82.

Stanbury, P. J. 1987. The discovery of the Australian Fauna and the establishment of collections. In: Dyne, G.R. and Walton, D.W. (Eds) *Fauna of Australia* General Articles. Chapter 9. Canberra: Australian Government Publishing Service Vol 1A.

Steedman, H. F. 1960. *Section cutting in microscopy* Blackwell: Oxford.

Steedman, H.F. 1970. A one-solution triacid general stain which differentiates oxygenated from non-oxygenated red blood corpuscles. *Stain Technology 45:* 247-253.

Steedman, H.F. (Ed). 1976. *Zooplankton fixation and preservation* .UNESCO Press: Paris.

Steel, T. 1897. Australian land planarians: descriptions of new species and notes on collecting and preserving. *Proceedings of the Linnean Society of New South Wales. 22*: 104-119

Steel, T. 1901a. Australian land planarians: descriptions of new species and notes on collecting and preserving. No. 2. *Proceedings of the Linnean Society of New South Wales 25* (for 1900): 563-580.

Steel, T. 1901b. Tasmanian land planarians. *Proceedings of the Linnean Society of New South Wales 25* (for 1900): 6t8-631.

Steel, T. 1901c. Land planarians from Fiji with descriptions of new species. *Proceedings of the Linnean Society of New South Wales 22:* 120-122.

Steigerwald, M., Laframboise, S. 1996. Tape application: a jar sealing method for reducing ethanol evaporation in fluid-preserved collections. *Collection Forum 12*: 45-54.

Stimpson, W. 1857. Prodromus descriptiones animalium evertebratorum quae in Experitione ad Oceanum, Pacificum Septemtrionalem a Republica Federata missa, Johnne Rodgers Duce, observavit et descripsit. *Proceedings of the Academy of Natural Sciences, Philadelphia 9:* 19-31.

Stimpson, W. 1861. On the genus *Bipalium. American Journal of Science and the Arts 31*: 134-135.

Storch, V., Abraham, R. 1972. Elektronenmikroskopische untersuchungen über die Sinneskante des Terricolen Turbellars *Bipalium kewense* Moseley (Tricladida). *Zeitschrift für Zellforschung und mikroskopische Anatomie 133*: 267-275.

Storch, V., Welsch, U. 1977. Septate junctions in the cephalic epidermis of Turbellarians (*Bipalium*). *Cell and Tissue Research 184*: 423-425.

Sun, C.N., Cheng Chew, S.B., White, H.J. 1979. The fine structure of smooth muscle in *Bipalium kewense* Moseley, its possible relation to evolution of skeletal muscle. *Cytologia 44*: 181-190.

Tekaya, S., Sluys, R., Zghal, F. 1997. Sperm transfer and fertilization in the marine planarian *Sabussowia dioica* (Platyhelminthes, Tricladida, Maricola). *Invertebrate Reproduction and Development 32*: 143-147.

Terrace, T.E., Baker, G.H. 1994. The blue planarian, *Caenoplana coerulea* Moseley (Tricladida: Geoplanidae), a predator of *Ommatoiulus moreleti* (Lucas) (Diplopoda: Julidae) in South Australia. *Journal of the Australian Entomological Society 33*: 371-372.

Terrace, T.E., Baker, G.H. 1996. Predation of earthworms by the land planarian, *Australoplana sanguinea* (Moseley) var. *alba* (Dendy) *sensu* Jones, 1981 (Tricladida: Geoplanidae). *Transactions of the Royal Society of Australia 120*: 177-178.

Toedtmann, W. 1913. Die Schalenbildung der Eicocons bei Turbellarien. *Archiv für Hydrobiologie 8*: 529-552.

Tyler, M.J. 1962. On the preservation of anuran tadpoles. *Australian Journal of Science 25:* 222.

Tyler, S. 1976. Comparative ultrastructure of adhesive systems in the Turbellaria. *Zoomorphologie 84*: 1-76.

Tyler, S. 1984. Turbellarian Platyhelminthes. *In*: Bereiter-Hahn, J., Matolsky, A.G., Richards, K.S. *eds*. Biology of the integument. 1. Invertebrates. Berlin: Springer-Verlag.

Tyler, S. 1988. The role of function in determination of homology and convergence – examples from invertebrate adhesive systems. *Fortschritte der Zoologie 36:* 331-347.

Veevers, G. 1982. *The colours of animals.* Edward Arnold: Bristol.

Waite, J.H. 1983. Quinone-tanned scleroproteins. *In*: Fretter, J., Peake, J *eds.* The Mollusca 1. New York, Academic Press.

Walker, D. 1972. *Bridge and barrier: The natural and cultural history of Torres Strait.* ANU: Canberra.

Wallwork, J.A. 1970. Ecology of Soil Animals. New York. McGraw-Hill.

Wallwork, J.A. 1976. The distribution and diversity of soil fauna. London. Academic Press.

Ward, N.B. 1834. On growing fern and other plants in glass cases, in the midst of the smoke of London; and on transporting plants from one country to another by similar means. *Gardener's Magazine 10:* 207-208.

Williams, E.C. 1941. An ecological study of the floor fauna of the Panama rain forest. *Chicago Academy of Science Bulletin 6:*63-124.

Williams, J.B. 1981. The protonephridial system of *Temnocephala novaezealandiae:* structure of the flame cells and main vessels. *Australian Journal of Zoology29:* 131-145.

Wilson, R.A., Webster, L.A. 1974. Protonephridia. *Biological Review 49:* 127-160.

Winsor, L. 1973a. *Geoplana atrata* Steel, 1897 – a new planarian record for Victoria. *Victorian Naturalist 90:* 101-102.

Winsor, L. 1973b. *Geoplana virgata* Fletcher and Hamilton 1887 – a new planarian record for Victoria. *Victorian Naturalist 90:* 264-265.

Winsor, L. 1973c. Land planarians. In: *Report on the Melbourne Study Area.* Land Conservation Council: Melbourne.

Winsor, L. 1977. Terrestrial planarians and nemerteans of the Otway Region. *Proceedings of the Royal Society of Victoria. 89*: 137-146.

Winsor, L. 1978. Oblique illumination and interference phase contrast microscopy: aids in the taxonomic histology of land planarians. *Mikroskopie 34:* 319-321.

Winsor, L. 1979. Land planarians (Tricladida: Terricola) of the Royal Botanic Gardens, Melbourne, Victoria. *Victorian Naturalist 96*: 155-161.

Winsor, L. 1980. Pseudoparasitism of domestic and native animals by geoplanid land planarians. *Australian Veterinary Journal 56*: 194-196.

Winsor, L. 1981. The taxonomy, zoogeography and biology of *Bipalium kewense* Moseley, 1878 (Tricladida: Terricola). *Hydrobiologia 84*: 17.

Winsor, L. 1983a. Vomiting of land planarians (Turbellaria: Tricladida: Terricola) ingested by cats. *Australian Veterinary Journal 60:* 282-283.

Winsor, L. 1983b. A revision of the cosmopolitan land planarian *Bipalium kewense* Moseley, 1878 (Turbellaria: Tricladida: Terricola). *Zoological Journal of the Linnaean Society 79*: 61-100.

Winsor, L. 1984a. Manual of Basic Zoological Microtechniques for light microscopy. 2nd. Ed. James Cook University: Townsville.

Winsor, L. 1984b. Land planarians. In: Thornton, I.W.B. (Ed) *Zoological Expedition to the Krakataus – Preliminary Report.* Biological Sciences: La Trobe University.

Winsor, L. 1985. Land planarians (Turbellaria: Tricladida: Terricola) Introduced into Australia - 1.*Bipalium kewense* Moseley, 1878. *Victorian Naturalist 103*: 102-105.

Winsor, L. 1986. Land planarians (Turbellaria: Tricladida: Terricola) Introduced into Australia - 2. *Kontikia orana* Froehlich, 1955. *Victorian Naturalist 103*: 9-11.

Winsor, L. 1990. Taxonomic studies on free-living flatworms (Turbellaria: Platyhelminthes) of the Australian zoogeographic region. M.Sc thesis. James Cook University.

Winsor, L. 1991a. Methods for taxonomic and distributional studies of terrestrial flatworms (Tricladida: Terricola). *Hydrobiologia 227*: 349-352.

Winsor, L. 1991b. A new genus and species of terrestrial flatworm from the central highlands of New Caledonia (Tricladida: Terricola). *Mémoirs du Muséum nationale D'Histoire Naturelle*. Series A, *149*: 19-30.

Winsor, L. 1991c. A provisional classification of Australian terrestrial geoplanid flatworms (Tricladida: Terricola: Geoplanidae). *Victorian Naturalist 108*: 42-49.

Winsor, L. 1994. Tissue processing. In: Woods, A.E., Ellis, R.C. eds. *Laboratory Histopathology - a complete reference*. Volume 1. Edinburgh, Churchill Livingstone.

Winsor, L. 1995. Human pseudo-parasitism by terrestrial flatworms. *Abstracts of papers presented at the 10th annual conference of the Australian Institute of Medical Scientists and the Australian Association of Clinical Biochemists, Townsville, 9-11 June 1995.*

Winsor, L. 1976. Platyhelminthes. p15, 61.In: B.J. Smith, H.E. Malcolm & P. Morison. Dartmouth Dam Environment Study. Report on the survey of the invertebrate fauna of the Mitta Mitta valley. National Museum of Victoria.

Winsor, L. 1997a. The biodiversity of terrestrial flatworms (Tricladida: Terricola) in Queensland: a preliminary report. *Memoirs of the Museum of Victoria 56*: 575-579.

Winsor, L. 1997b. Terrestrial Flatworms Infosheet No. 1. The collection, handling and preservation of specimens for general identification. James Cook University: Townsville.

Winsor, L. 1997c. Terrestrial Flatworms Infosheet No. 2. The collection, handling and fixation of specimens in the field for taxonomic purposes. James Cook University: Townsville.

Winsor, L. 1997d. Terrestrial Flatworms Infosheet No 3. Prevention and control of flatworm infestation of earthworm beds. James Cook University: Townsville.

Winsor L. 1997e. Terrestrial Flatworms Infosheet No 4. The Long Wanderers – *Dolichoplana* species: earthworm predators. James Cook University: Townsville.

Winsor, L. 1998a. Collection, handling, fixation, histological and storage procedures for taxonomic studies of terrestrial flatworms (Tricladida: Terricola). *Pedobiologia 42*: 405-411.

Winsor, L. 1998b. Aspects of taxonomy and functional histology in terrestrial flatworms (Tricladida: Terricola). *Pedobiologia 42:* 412-432.

Winsor, L. 1998c The Australian terrestrial flatworm fauna (Tricladida: Terricola). *Pedobiologia 42:* 457-463.

Winsor, L. 1998d. The role of the atrial diverticulum in the copulatory apparatus of *Platydemus manokwari* de Beauchamp (Tricladida: Terricola). *Hydrobiologia 383*: 83-89.

Winsor, L. 1998e. Flatworm infestation of commercial earthworm farms in Australia (abstract). *Pedobiologia* **42**: 573.

Winsor, L. 1998f. Terrestrial Flatworm Infosheet No 5. Predators in earthworm beds – flatworms or leeches? James Cook University: Townsville.

Winsor, L., Johns, P.M., and Yeates, G.W. 1998. Introduction, and ecological and systematic background, to the Terricola (Tricladida). *Pedobiologia* **42:** 457-463.

Winsor, L. 1999. Terrestrial Flatworm Infosheet No 6. The New Guinea Flatworm – *Platydemus manokwari*: predator of land snails. James Cook University: Townsville.

Winsor, L. 2003. Terrestrial Flatworms – Facts Sheet. James Cook University: Townsville.

Wood. L.M. (1926). On some land planarians from Barrington Tops, N.S.W, with descriptions of some new species. *Proceedings of the Linnean Society of New South Wales 51*: 608-613.

Wright, E.P. 1860. Notes on *Dunlopea. Annals and Magazine of Natural History6*: 54-56.

Yanagita, Y., Yamamoto, T.S. 1981. Formation of chemical property of the cocoon in a freshwater planarian, *Dendrocoelopsis ezensis* Ichikawa et Okugawa (Turbellaria, Tricladida). *Zoologischer Anzeiger 207*: 130-142.

Yeates, G.W., Boag, B., Johns, P.M. 1998. Field and laboratory observations on terrestrial planarians from modified habitats in New Zealand. *Pedobiologia 42:* 554-562.

York-Main, B. A comparative account of the biogeography of terrestrial invertebrates in Australia: some generalizations. In: Keast, A. (Ed). *Ecological Biogeography of Australia.* Chapter 37. Junk: The Hague.

Glossary of Terms

General agreement and consistency in the terminology for morphological characters and character states required for morphological and phylogenetic analysis of the Terricola is tacitly assumed by taxonomists. Often this is not the case. Inconsitencies abound in the literature. A glossary is an effective means of addressing this issue. Ball & Reynoldson (1981) provide a glossary for Triclad planarians, and Cannon (1986) and Stachowitz (1992) provide glossaries for the Turbellaria. This glossary is based upon that of Cannon (1986). Some terms have been altered, and additional terms, definitions, explanations and examples have been included which may often relate generally to the Tricladida, but specifically to the Terricola studied in this thesis. An illustrated glossary was contemplated, but constraints of space and time precluded this option.

ACIDOPHIL - (acid loving) is a generic term which refers to the preferential uptake of acid dyes by certain tissue elements. In many, but not all trichrome and polychrome staining methods these are red coloured dyes. From this is derived the terms erythrophil and erythrophilous (red loving) which refer specifically to the uptake of these red dyes. Histochemically these substances are often acidic proteins. Acidophil elements also include those that have an affinity for yellow or orange coloured acid dyes incorpoprated in some trichrome and polychrome staining methods. For these elements the term xanthophil and xanthophilous (yellow loving) has been coined. Histochemical studies on these secretions indicate that they often have a high arginine content and are basic proteins. Refer to BASIPHIL for notes on spelling. In the descriptors acidophil, basiphil, cyanophil, erythrophil and xanthophil there is no need for adding **-ic** at the end of the word eg. acidophil is correct, acidophili**c** is incorrect. The -ophilous termination is common in the European literature.

ADENAL: pertaining to a glandular pocket.

ADENOCHIRE: Comb-like structures, the "teeth" of which are ADENODACTYLS in the copulatory apparatus of certain taxa e.g. *Artioposthia diemenensis* and *A. lucasi.* These structures are involved in COCOON formation.

ADENODACTYL: Finger-like musculoglandular organs which protrude into the atria and ducts of the copulatory organs in taxa of the inclusive genus *Artioposthia* and other recently erected genera. Some seven types are recognized. These structures are involved in COCOON formation. Plural *adenodactyli,* or *adenodactyls* as adopted in this thesis.

ADENOMURALIA: Musculoglandular organs embedded in the walls of the copulatory apparatus, generally with little or none of the distal duct protruding finger-like into the atria or ducts. These structures are involved in COCOON formation..

ADHESIVE PAD / SUCKER: musculoglandular structures with an adhesive function (Drüsenpolster) for capture of prey or during copulation e.g. the anterior musculoglandular organ in *Choeradoplana, Cotyloplana, Pimea, Thosteelia* and *Xerapoa*.

ANTRUM: terminal cavity of male or female systems when opening separately, or the space into which both the male and female systems open before expulsion of sex products via a common gonopore. The term antrum in this thesis refers to both antrum and atrium. Histological criteria such as cell types should be used to define antral functions.

APOCRINE SECRETION: where secretions accumulate below the free margin of a cell, but can only be released by the breaking away of the distal part of the cell with some loss of cytoplasm, e.g. sclerotin globule cells in the atria of copulatory organs.

ATRIUM: see ANTRUM. The space into which both the male and female systems open before expulsion of sex products via a common gonopore (Cannon 1986).

ATHROCYTE: see FIXED PARENCHYMAL CELLS

BASIPHIL - (base loving) is a generic term which refers to the preferential uptake of basic dyes by certain tissue elements such as basement membranes and collagen. In many, but not all trichrome and polychrome staining methods these are blue coloured dyes (in some polychrome methods, as a matter of personal preference - a green dye is frequently substituted for the blue dye). From this is derived the terms cyanophil and cyanophilous (blue loving) which refer specifically to the uptake of these blue dyes e.g. aniline blue. Some basiphil substances are carbohydrates - glycoproteins and other mucins. The correct spelling of this term is as here ie. basiphil. Basophil is commonly encountered but is not correct (refer to Baker, J.R. 1958. *Principles of biological microtechnique.* Methuen. Page 329). However acidophil is correct as it derives from a Latin noun with a different declension.

BEAUCHAMP'S CANAL: a duct which links the resorptive bursa with the female glandular canal (or anonymous canal), present in certain rhynchodemid taxa of India and Africa. It is essentially an overflow system to ensure fertilization of oocytes and at the same time the retention and resorption of excess donor sperm.

BIPARTITE CUTANEOUS MUSCULATURE: Cutaneous (subepidermal) musculature consisting of an outer layer of circulo-helicoid (oblique) muscles, and an inner layer of longitudinal muscles. Considered to be an apomorphic condition.

BRAIN: anterior nerve complex, sometimes enclosed in a connective tissue capsule.

BURSA part of the female system into which donor sperm are deposited and resorbed: very variable in development. See COPULATORY BURSA and LATERAL BURSA.

CANAL: see BEAUCHAMP'S CANAL, GENITO-INTESTINAL CANAL

CEMENT GLANDS: glands near gonopore, which secrete material to assist fixation of the egg capsules to a substrate. Term mainly used for freshwater and marine triclads. See also VISCID GLAND.

CEPHALIC GANGLION: see BRAIN.

CEREBRAL: pertaining to brain or head.

CERVICAL: pertaining to the 'neck' region, as in the Bipaliidae, just behind the headplate.

CHONDROCYST: see RHABDOID.

CILIUM (CILIA): locomotory hair-like organelles found over the surface of Terricola, especially the creeping sole, and in many ducts e.g. in protonephridia, in the ovovitelline duct, and vas deferens. Although not yet demonstrated in the Terricola, it is suspected by this author that some cilia in the copulatory organs will, on ultrstructural examination, be found to be stereocila which have an absorptive function, concentrating sperm or removing nutrients. Other "cilia" have been fond to be sclerotin strands.

COCOON: a structure formed by species to enclose and protect fertilized eggs. The cocoon is made from sclerotin secretions in the copulatory apparatus, and laid onto the substratum to which it may be adhered by cement or viscid gland secretions, or it may be expelled through rupture of the dorsum in some taxa e.g. *Lenkunya.*

COMPRESSION TISSUE: Sponge-like areas of tissue found in the musculature penis bulb or adjacent musculature of the male atrium in species with eversible penes. It is postulated that the low tissue density in these areas facilitates eversion by allowing the musculature supporting the pseudophallus to crease and lock. It is often associated with an atrial lip.

COPULATORY APPARATUS / ORGANS: generally comprise the penis and female glandular canal, together with auxiliary structures such as adenodactyls, bursa, and viscid gland opening into antra or atrium accessible via the gonopore or other external duct.

COPULATORY (SEMINAL) BURSA: tubiform or sacculate structure(s) in the immediate vicinity of the copulatory organs which receive and resorbs donor sperm. May be bilateral.

COPULATORY PORE / CANAL: ventral pore(s) and canal(s), separate from the gonopore, through which donor sperm is deposited into the gut and which, via a genito-intestinal canal can enter the copulatory organs, as in *Incapora*; alternatively may be a pressure-relief pore for excess donor sperm in the copulatory bursa, or copulatory pore for the deposition of donor sperm as in *Diporodemus*. The pore may facilitate mutual copulation.

CORSET; CORSETING: a tubular or bracing (elastic stocking, corset) structure formed from interwoven muscle which maintains a constant body diameter during flexion, retraction or protraction. For example in the head of taxa with adhesive suckers, where the parenchymal dorso-ventral and dorsal transverse muscles intermesh to provide internal bracing – corseting - for the anterior end, thus facilitating the action of retractor muscles for the sucker. Also termed "Muskelgeflecht".

CREEPING SOLE: generally flattened ventral region of body. May be ridged, ciliated or non-ciliated

CYANOPHIL - is a generic term which refers to the preferential uptake of blue dyes in trichrome and polychrome methods by certain tissue elements. Refer to BASIPHIL.

DIVERTICULUM, DIVERTICULA: out-pouching from lumen of a hollow organ, especially gut, pharyngeal pouch, and genital structures.

DRÜSENPOLSTER: glandular pads. Refer to ADHESIVE PAD / SUCKER.

ECTOLECITHAL: pertains to those systems in the more advanced Platyhelminthes in which the yolk incorporated into the oocyte via secretions from the vitelline glands. See

VITELLARIA: cells and organs which produce nutrient material which is incorporated within the egg capsule with one or more oocytes. The vitelline granules have been found to contain polyphenol oxidase, basic protein, tryptophane, di- and polyphenols, aromatic amines, carbohydrates including glycogen, neutral and phospholipids. Typically the vitellaria lie below and between gut diverticula and just above the ovovitelline duct Secretions pass into the ovovitelline duct via short funnels. The latter may be modified to form resorptive vesicles as in *Anzoplana.*

EJACULATORY DUCT: terminal part of the male duct, sometimes eversible, which carries sperm and usually seminal and prostatic secretions through the copulatory organ. Also defined as the duct within the penis papilla by which the sperm is discharged during copulation (Ball & Reynoldson 1981).

EGG (EGG CAPSULE): one or more oocytes (ova) and sperm (and yolk) or zygotes or young developing from them combined into a capsule. The terms are often used synonymously. One or more young may hatch.

EPITHELIOSOMES: microrhabdites, found in areas of mechanical stress, such as the creeping sole, where they may provide a strengthening element in the cell web. They contain basic protein.

EPITHELIUM (EPIDERMIS): the superficial cellular layer; on the surface of structures and lining cavities, nuclei in the epithelium may be above the muscle layers, or sunk below into the parenchyma (infranucleate epithelium).

ERYTHROPHIL - tissue elements with an affinity for red dyes. Refer to ACIDOPHIL.

EVERSIBLE PENIS: Refer to PENIS.

EXCRETOPHORE: large vacuolated cells of the gut epithelium.

EXCRETORY PORE: exterior opening to NEPHRIDIAL SYSTEM, also termed nephridiopore.

EYES: ocelli; usually pigmented, light sensitive structures mostly near the brain. There are types of eyes found in the Terricola: unicellular pigment cup e.g. in *Bipalium*; lensed eye restricted to the Maricola but possibly present in *Fyfea*; multicellular pigment cup (*Microplana terrestris* Type); and the multicellular pigment cup (*Platydemus grandis* Type – Graff's 1899 Retinaaugen). Refer to Sluys 1989 for a detailed consideration of eyes in the Terricola.

FEMALE GENITAL CANAL: this term is now used (Sluys & Winsor *in litt*) to refer to the whole of the female canal which includes what was termed the vagina, vaginal duct or ductus vaginalis (distal canal) and glandular (proximal) canal. The proximal glandular portion of the canal distal to the entrance of the oviducts, receives shell gland secretions responsible for producing the inner cocoon membrane.

FEMALE GLANDULAR CANAL: See FEMALE GENITAL CANAL

FIXED PARENCHYMAL CELLS: (Athrocytes, paranephrocytes) – resorptive cells in the protonephridium (Pedersen 1961a,b).

FLAGELLUM (FLAGELLA): long and/or prominent cilium (cilia).

FLAME CELL: terminal cell with tuft of cilia in a nephridial duct system used to push fluid along.

FOLLICULAR: organ arranged in several small compartments (follicles), i.e. neither diffuse nor compact.

GENITO-INTESTINAL CANAL: a duct or canal from the female system or bursa to the intestine, to facilitate the passage of excess sperm for digestion in the gut.

GERM CENTRE: A group of small undifferentiated cells found in the ovary - also termed *Keimlager,* (or germarium by Fyfe).

GLOBULE CELLS: cells of the secretory epithelium of the antra and atrium of the copulatory organs which generally secrete, in an apocrine manner, fine erythrophil granules within membrane-bound globules. Histochemically, the globules contain a sclerotin which forms part of the cocoon.

GLUE GLAND: see VISCID GLAND

GONOPORE: exterior opening to genital system of male or female; or when both may be called a common gonopore.

GUT: since Terricola lack an alimentary system with an anus, the gut is a space which holds captured food. It is lined by the gastrodermis (which commonly contains food vacuoles). Leading from the pharyngo-intestinal junction, the gut divides into an anterior ramus and two posterior rami. The rami then further divide into intestinal branches (= diverticular roots of Graff, lateral caecae of Jennings). These branches then further divide e.g. bifurcate, trifurcate, into diverticula (=terminal branches, Graff) which may anastomose, particularly anteriorly. The pattern of branches and diverticula can be simple (few branches) or complex (extensively divided), though is rarely described in detail.

HAFTPAPILLEN: Specialized adhesive papillae found in the Maricola, and in the adhesive pad of the caenoplaninid *Pimea.* The papillae resemble small brushes attached to muscle fibres. In *Pimea* fine granular cyanophil and erythrophil secretions, histochemically neutral mucins or glycoproteins, pass to the surface via long ducts which spiral up the muscular columns to the haftpapillen. Other secretions pass between the papilla. see also PAPILLA.

HEAD: anterior of flatworm containing the brain.

HEAD PLATE: the broadened cephalic end of a flatworm, a term generally restricted to the Bipaliidae.

HELICOID MUSCLES: There are two forms of helicoid (oblique)muscles: helical and circulo-helical cutaneous muscles. Helical muscles are always found in flatworms with **tripartite cutaneous musculature**, and always in two opposing sets - decussate pairs - left and right spiralling muscles around the of the long axis of the outer body. Circulo-helical muscles are found in flatworms with a **bipartite cutaneous musculature**, where the circular muscles assume a shallow helicoid path in apparently only one direction; the true helical muscle layers appear to be absent. In some taxa there may be an additional helical layer intimately associated with the cutaneous longitudinal muscles e.g. *Sokoplana.*

HERMAPHRODITIC: having both male and female organs.

HOLOCRINE SECRETION: the secretion is released by the complete breakdown of the cell.

INFRA-NUCLEATE EPITHELIUM: where nuclei of epithelial cells are situated in cytoplasm below the basement membrane e.g. in pharyngeal epithelium, creeping sole.

INSERTIONS: pharyngeal insertions where the pharynx is inserted into the parenchyma – see PHARYNX

INSUNK EPITHELIUM: see INFRA-NUCLEATE EPITHELIUM

INSUNK MUSCLES: term generally applied to cutaneous longitudinal muscles which traverse the cutaneous nerve net to merge with adjacent parenchymal longitudinal muscles. They are generally found in taxa which bear an anterior adhesive structure, for which the insunk muscles form part of the retractor muscle e.g. *Thosteelia.*

INTRA-ANTRAL PAPILLA: an term sometimes incorrectly applied to the INTRA-PENIAL PAPILLA.

INTRA-PENIAL PAPILLA: a generally small papilla through which the ejaculatory duct opens within the penis or penis papilla as in *Pimea,* and a number of genera in the Maricola (see Sluys 1989).

INTESTINAL-CUTANEOUS DUCT: ducts which connect the gut to pores in the ventral epidermis, as in the terricolan *Incapora weyrauchi.*

INTESTINE: see GUT.

INTRAEPITHELIAL GLAND: secretory cells embedded in an epithelial surface, as in the atria of some taxa.

KEIMLAGER: see GERM CENTRE

LATERAL BURSA (BURSAE): sacculate resorptive structure(s) generally connected via a small duct from the oviduct (PAROVARIAN), or ovovitelline duct that receive and resorb excess donor sperm. May be bilateral e.g. *Anzoplana.*

LUMEN: inner space of a hollow organ, e.g. gut, seminal vesicle, antrum.

LYSOCYTES: lysozyme-secreting cells found in resorptive bursae. Lysozyme and acid phosphatase are present in erythrophil granules which are secreted in a merocrine manner into the bursal lumen where they participate in intraluminal digestion of sperm and other copulatory products.

MEROCRINE SECRETION: where secretions accumulate below the free surface of a cell, and are released without loss of cytoplasm, e.g. lysocytes in copulatory bursae, and the secretory cells of viscid glands.

MUSCULO-GLANDULAR ORGAN: a generic term which covers discrete structures with a glandular secretory element together with a discrete musculature, such as adhesive structures - suckers and pads, and also adenodactyls, adenochiren and adenomuralia. These structures are not homologous.

MUSKELGEFLECHT: term coined by Graff 1899 for a structure formed from interwoven muscle. See CORSET.

NEPHRIDIAL (CANALS, SYSTEM): a system of main (dorsal and ventral) and secondary (dorsoventral and transverse) excretory canals interconnected with convoluted canals, end canals, PROTONEPHRIDIA, and EXCRETORY PORES responsible for osmoregulation.

OCELLI, OCELLUS: see EYES.

OESOPHAGUS: part of gut immediately inward from the pharynx, generally with specialized musculature and epithelium different than the oesophagus e.g. as in *Barringtoplana.*

OOCYTE: the cell which undergoes meiosis to form an ovum and which then may be fertilized by a sperm to produce a zygote. Often used synonymously for ovum or even egg.

OSMOREGULATION: control of body fluid salt concentration by means of expelling (or not) excess water.

OVARY: female gonad containing oogonia and oocytes.

OVIDUCT: that proximal portion of the duct which communicates between the ovary and female copulatory organs which does not receive yolk secretions.

OVOVITELLINE DUCT: continuous with the oviduct and which receives yolk secretions from the vitellaria via vitelline or yolk funnels.

OVUM (OVA): the female germinal cell. Strictly speaking the oocyte after reduction division to a haploid state, but before fertilization to become a zygote. Often used synonymously for oocyte and sometimes for egg.

PAPILLA: a soft protuberance from the external body often sensory e.g. *Xerapoa,* or glandular such as the prominent adhesive papillae called 'Haftpapillen, e.g. as occur in the adhesive pad of *Pimea.* Internally the distal element of secretory structures such as adenodactyls may have a papilla. The penis papilla is the free intromittent part of the penis (Ball & Reynoldson 1981).

PARANEPHROCYTE: See FIXED PARENCHYMAL CELLS

PARENCHYMA: tissue of body in which the organs are embedded. Also termed mesenchyme.

PAROVARIUM / PAROVARIAN: literally, beside the ovary. Tissue structures attached to the ovary which may be clumps of cells or sac of unknown functions, RESORPTIVE VESICLES, or LATERAL BURSA(E).

PENIS (& PENIS BULB, PAPILLA, SHEATH; PENIAL -): that terminal part of the male system which delivers sperm into a partner at copulation, i.e. an intromittent organ. It is often bulbous (penial or penis bulb) containing the elements of the seminal vesicle, prostatic duct, and ejaculatory duct which may terminate in a prominent or poorly differentiated penis papilla. A permanent large penis papilla appears capable of elongatation to protrude through the gonopore (protrusible type penis). In taxa with poorly differentiated penis papilla, or a small INTRA-PENIAL PAPILLA, the male antrum constricts, everts and extends to form an intromittent organ (eversible-type of penis or pseudophallus) e.g. *Parakontikia, Nelipoplana, Pimea.* In some taxa the distal male antrum is equipped with lips suggestive of a papilla, but more correctly interpreted as the penis sheath e.g. *Parakontikia, Reomkago.* This portion of the atrium is not intromittent, but probably forms a supporting collar (reduced sheath) for the pseudophallus. A more developed penis sheath is present in some species of bipaliid flatworms.

PHAGOCYTES: cells present in copulatory bursae and other resorptive structures which engulf sperm or products of intraluminal digestion. They are vacuolate and contain acid phosphatase.

PHARYNX: the glandulo-muscular structure between mouth and gut, inwards of which may be found an OESOPHAGUS. The pharynx is protrusible and used to feed upon prey. The form and musculature are of taxonomic value. The main terms, based upon the appearance of the protruded organ, irrespective of histological structure are: cylindrical, as in the Rhynchodeminae, cylindrical and folded as in *Australoplana*, bell-form (Glockenförmig) as in *Nelipoplana*, and collar-form (Kragenförmig) – plicate, folded curtain like, as in *Arthurdendyus*. Some taxa have two or more pharynges (polypharyngia) e.g. *Digonopyla*. The root of the pharynx is where it is inserted into the parenchyma, and the relative position of the dorsal and ventral INSERTIONS is of taxonomic importance.

PHARYNGEAL POUCH: the chamber in which the pharynx and mouth (peripharyngeal aperture) are situated. It may have a PHARYNGEAL POUCH DIVERTICULUM.

PHARYNGEAL POUCH DIVERTICULUM: the diverticulum leading from the posterior wall of the PHARYNGEAL POUCH in some taxa acts as an excretory sinus for the NEPHRIDIAL SYSTEM e.g. in *Nelipoplana*. It is surrounded by cyanophil glands, and terminal EXCRETORY PORES which together discharge into the lumen of the diverticulum.

PLATE: see VENTRAL PLATE.

PLICATE (PLICATUS): see PHARYNX.

PROSTATE (PROSTATIC - CELLS, DUCT, GLANDS, REGION, SECRETION, TISSUE, VESICLE): that part of the male copulatory system, generally located immediately before and in line with the ejaculatory duct in the penis in the Terricola. Sometimes the mucosa of the prostatic region may be thrown into folds forming chambers. Prostate secretion is combined with sperm on release. The prostatic region receives erythrophil granular secretions and has been shown to contain acid phosphatase, lipids, tryptophane and basic proteins.

PROTANDROUS (PROTANDRY): when male reproductive systems mature before female ones. Male mature.

PROTOGYNOUS (PROTOGYNY): when female reproductive systems mature before male ones. Female mature.

PROTONEPHRIDIA: organs containing one or more flame cells and connecting ducts which function in an osmoregulatory fashion. See also NEPHRIDIAL.

PROTRACTOR MUSCLES: those muscles, perpendicular to the long axis of the body, which extend a part or draw it out of the body, generally applied in the context of adhesive suckers and copulatory organs.

PROTRUSIBLE PENIS: Refer to PENIS.

RECEPTACULUM SEMINIS: see seminal receptacle

RESORBTIVE VESICLE: an organ absorbing donor sperm sometimes identical with all or part of the seminal receptacle and often in communication with the gut via a genito-intestinal canal.

RETRACTOR MUSCLES: those muscles, parallel to the long axis of the body, which withdraw or contract a part into the body, generally applied in the context of adhesive suckers and copulatory organs.

RHABDITE: see rhabdoid.

RHABDOID: epidermal inclusions secreted as short rods (rhabdites), long rods or spindles (rhammites) or thick oblong - ellipsoidal rods (chrondrocysts - ?fixation artefact). See also EPITHELIOSOMES.

RHAMMITE: see RHABDOID.

RING ZONE: the annulate distribution of parenchymal longitudinal or circulo-helical muscles present in mesenchyme between the cutaneous nerve net and the gut, and underlying the nerve cords.

SHELL GLANDS: glands of the female system, generally the female genital (glandular) canal, which discharge after the sperm, oocyte and vitelline cells have combined, but before the egg capsule moves into the female antrum. The secretion coats the egg capsule, and includes basic protein, polysaccharides, phenols and phenol oxidase.

SEMINAL RECEPTACLE: part of the female system in which recipient sperm are stored and subsequently released for fertilization. See TUBA.

SEMINAL VESICLE: expanded part of the proximal ejaculatory duct which receives the vas deferens or common sperm duct, and holds sperm prior to release. It receives generally cyanophil secretions which contain proteins with disulphide groups e.g. cysteine, acid phosphatase, and lipids.

SOLE: see CREEPING SOLE.

SPERM: male sex cells.

SPERM DUCT: vas deferens - main collecting ducts from testes leading to male copulatory structures. In its simplest form this may be a sperm ductule (vas efferens or testicular funnel) passing directly into the vas deferens. In more complex arrangements the sperm ductule may open into an inter-testicular duct, then collecting duct and finally the vas deferens; these three longitudinal ducts are linked transversely by intermediary ducts. The vasa deferentia may join before entering the penis bulb, separately enter the penis bulb, or may form a rete sperm duct where the sperm ducts divide into a network of fine ducts which separately pierce the penis bulb.

SPERMIDUCAL VESICLES: generally thin-walled expansions, for sperm storage, of the distal sperm ducts before the latter combine to form a common sperm duct or ejaculatory duct. Muscular spermiducal vesicles may be termed spermiducal bulbs. Spermiducal vesicles which receive cyanophil secretions may be better regarded as seminal vesicles (generally found in taxa without evident seminal vesicle).

STRAND CELLS: cells of the secretory epithelium of the antra and atrium of the copulatory organs which generally secrete, in an merocrine manner, fine cyanophil granules as strands with the appearance of cilia. Histochemically, the strands contain a phenolic proteins which form part of the cocoon.

STEREOCILIA: not true cilia, but long thin, sometimes branched microvilli. They increase the surface area of cells involved in absorption. Suspected by the author of being present in the reproductive organs of Terricola.

SUCKER: an anterior glandulo-muscular adhesive organ usually clearly elevated above or depressed below the ventral surface.

SULCUS (SULCI; SULCIFORM): a groove or furrow, as in the atria of some taxa.

SULCIFORM GLANDS: Glands which discharge secretions into the base of a sulcus.

TACTILE: pertaining to sense of touch, especially proprioreceptors.

TESTIS (TESTES): male gonad in which sperm develop.

TRIPARTITE CUTANEOUS MUSCULATURE: cutaneous (subepidermal) musculature comprising an outer layer of circular muscles, a mid layer of opposing (decussate) helicoid muscles, and an inner layer of longitudinal muscles.

TUBA: pronounced expansions of the oviducts, close to their point of communication with the ovaries. They serve as a receptacle for sperm, and in some taxa have a sperm resorptive function. Non-resorptive tubae are lined by a non-ciliated columnar epithelium with basal nuclei and pale cyanophil cytoplasm. Resorptive tubae are lined by a thick layer of irregularly arranged phagocytic granular cells which may contain clumps of sperm. Tubae usually communicate with the ovaries via a pronounced and generally muscularised constriction or through a short and narrow duct.

TUNICA: connective tissue sheath about an organ, i.e. it contains an organ (e.g. gonad), discrete from the surrounding parenchyma.

UTERUS (UTERI, UTERINE VESICLE): a generally obsolete term for a spacious region in the female system which stores one or more egg capsules prior to release. What were formerly termed uteri have subsequently been shown to be bursae.

VAGINA: see FEMALE GLANDULAR CANAL

VAGINAL DUCT: also termed ductus vaginalis, which passes from the female antrum to the seminal / copulatory bursa, and which is separate from the female glandular canal. Present in some rhynchodemid taxa especially those of India and Africa.

VAGINAL PORE: small (usually ventral) pore, separate from gonopore, through which a vaginal duct may open.

VASA DEFERENTIA (EFFERENTIA): see sperm duct.

VENTRAL PLATE: A distinct concentration of parenchymal muscles underlying the nerve cords and commissure.

VESICULA RESORBIENS: see resorbtive vesicle.

VISCID GLAND: generally a ventro-posterior diverticulum located with the copulatory organs just inside the gonopore, which receives both erythrophil and cyanophil granular secretions, and produces a sticky collagen-like fibrous glyco-protein which cement the cocoon to the substratum. Present in taxa within all families of the Terricola, e.g. *Platydemus, Nelipoplana.*

VITELLARIA/VITELLINE: cells, glands, granules, funnels, ducts, secretions - yolk and cocoon precursor-producing tissue elements. Secretions contain phenols, phenol oxidase, carbohydrates, and lipids. The role of vitelline secretions in cocoon production in Terricola is unclear.

XANTHOPHIL - is a generic term which refers to the preferential uptake by cytoplasmic tissue elements of yellow or orange cytoplasmic dyes in trichrome and polychrome staining methods, such as the dyes Orange G, Picric Acid, Martius Yellow or Naphthol Yellow. Certain tissue elements, especially secretory granules in some terrestrial flatworms, take up these dyes and for them the term xanthophil and xanthophilous (yellow loving) has been coined. Histochemical studies on these secretions indicate that they often have a high arginine content and are basic proteins. Martius Yellow and Naphthol Yellow are closely related to Flavianic acid, an arginine precipitant, which may explain the affinity of these dyes for arginine.

YOLK: nutrient material which is incorporated within the female germinal cell (oocyte) produced by separate vitelline glands or vitellaria and which is included within an egg capsule with one or more oocytes, i.e. ectolecithal systems. See also VITELLARIA.

Abbreviations used in figures

ab	antral bursa
ad	adenodactyl
adm	adenomuralium
af	antral flap
al	antral lip
am	ampulla
ap	adhesive pad
app	apapillate penis
as	adhesive sucker
ba	battery of adenodactyls
bm	basketwork musculature
br	brain
ca	common antrum
cc	copulatory canal
cd	collecting duct
co	corseting muscle
covd	common ovovitelline duct
cvd	common vas deferens
cy	cyanophil glands
clm	cutaneous longitudinal muscles
cm	cutaneous musculature
cn	cutaneous nerve
cs	ciliated creeping sole
ct	compression tissue
cy	cyanophil secretion
du	duct
ed	ejaculatory duct
eg	erythrophil glands
el	eye lens
ep	epidermis
ey	eye
fa	female antrum
fe	flattened epithelium
fg	female genital canal
govd	glandular ovovitelline duct
gp	gonopore
hm	helical muscles
im	insunk muscles
ieg	intraepithelial gland
ip	inverted papilla
in	intestine
lb	lateral bursa
lm	longitudinal muscle
ln	lens
ma	male antrum
mg	marginal glands
mo	mouth
nc	nerve cord
oe	oesophagus
ov	ovary
ovd	ovovitelline duct
pb	penis bulb
pd	prostatic duct
pg	penial glands
pgc	paired genital canals
ph	pharynx
php	pharyngeal pouch
pi	pigment
plm	parenchymal longitudinal muscles
pne	papillate nucleate epithelium
ppd	pharyngeal pouch diverticulum
pp	penis papilla
rt	resorptive tissue
rv	resorptive vesicles
rvd	rete vas deferens
sa	sheathed adenodactyl
scl	sclerotin strands
sd	spermiducal vesicle
sg	shell glands
sm	secretory margin
ss	sulcus
sv	seminal vesicle
te	testis
tm	transverse parenchymal muscle
vd	vas deferens
ve	villiform epithelium
vg	viscid gland
vi	vitellaria
vp	ventral plate

Appendices

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

ID No.	Family	Genus	species	authority	year	Repository	Registration Numbe	pecimen statu	Specimen	Slides	Locality
1	Geoplanidae	Geoplana	agricola	Dendy	1895	MNH	1924.8.15.25-30	Syntypes	x		Agricultural
2	Geoplanidae	Geoplana	agricola var. maori	Dendy	1901	MNH	1924.8.15.25-30	Syntypes	x		St Martins
3	Geoplanidae	Geoplana	alba	Dendy	1891		LOST				Creek,
4	Geoplanidae	Geoplana	alba var. roseolineata	Dendy	1892	AM	W 2256	Syntype	x		Loch
5	Geoplanidae	Geoplana	alba var. roseolineata	Dendy	1892	MV	G 1458	Syntype	x		Loch
6	Geoplanidae	Geoplana	alba var. roseolineata	Dendy	1892	MNH	1924.8.15.1-10	Syntypes	x		Loch
7	Geoplanidae	Geoplana	albolineata	Steel	1897	AM	G 1513	Holotype	x		Bundanoon
8	Geoplanidae	Geoplana	alfordensis	Dendy	1896	AM	W 2004	Syntype		x	Springburn
9	Geoplanidae	Geoplana	alfordensis	Dendy	1896	MNH	1924.8.15.11-13	Syntype	x		Springburn
10	Geoplanidae	Geoplana	antarctica	Dendy	1909		LOST				
11	Geoplanidae	Geoplana	arenicola	Steel	1901	AM	G 3177	Holotype	x		near Perth
12	Geoplanidae	Geoplana	ashleyi	Fyfe	1953	NMNZ	ZW 101	Holotype	x	x	and summit, Mt
13	Geoplanidae	Geoplana	atrata	Steel	1897	AM	G 1509	Holotype	x		River
14	Cotyloplanidae	Cotyloplana	punctata	Spencer	1892	AM	G 11093	Syntype	x		Island
15	Cotyloplanidae	Cotyloplana	punctata	Spencer	1892	MV	G1462	Syntype	x		Island
16	Cotyloplanidae	Cotyloplana	punctata	Spencer	1892	NHMW		Syntype	x		Island
17	Cotyloplanidae	Cotyloplana	whiteleggei	Spencer	1892	AM	G11094	Syntype	x		Island
18	Cotyloplanidae	Cotyloplana	whiteleggei	Spencer	1892	MV	G1452	Syntype	x		island
19	Cotyloplanidae	Cotyloplana	whiteleggei	Spencer	1892	NHMW		Syntype (2)		x	Island
20	Geoplanidae	Artioposthia	carnleyi	Fyfe	1953	NMNZ	ZW102	Syntype (2)	x	x	Colonel Peak
21	Geoplanidae	Artioposthia	civis	Cardale	1941		LOST				Kelburn
22	Geoplanidae	Artioposthia	harrisoni	Wood	1926	AM	W2351; W2363	Syntypes?	x?	x	River
23	Geoplanidae	Artioposthia	glandulosa	Fyfe	1956	OM	A74-9	Holotype		x	Dunedin
24	Geoplanidae	Artioposthia	grubei	Graff	1899	ZIUH	2661	Syntypes	x		
25	Geoplanidae	Artioposthia	grubei	Graff	1899	ZIUB	MPW 412	Syntype	x		
26	Geoplanidae	Artioposthia	polyadoides	Fyfe	1956	OM	A74-16	Holotype		x	Pipikaretu
27	Geoplanidae	Caenoplana	coerulea	Moseley	1877	MNH	77.11.2.12	Holotype		x	Paramatta
28	Geoplanidae	Caenoplana	sanguinea	Moseley	1877	MNH	77.11.2.10	Holotype		x	Paramatta
29	Geoplanidae	Caenoplana	subviridis	Moseley	1877	MNH	77.11.2.9	Syntypes	x		Paramatta
30	Geoplanidae	Caenoplana	sp.	Moseley	1877	MNH	77.11.2.11	Syntypes	x		Paramatta
31	Geoplanidae	Caenoplana	fusca	Fyfe	1953	NMNZ	ZW 104	Holotype		x	Lake, Ranuii
32	Geoplanidae	Geoplana	adae	Dendy	1891	MNH	91.9.28.19	Syntype	x		Warburton
33	Geoplanidae	Geoplana	adae	Dendy	1891	MNH	1924.8.15.15-24	Syntypes	x		Warburton
34	Geoplanidae	Geoplana	adae var. extralineata	Dendy	1892	MV	G 1456	Syntype	x		Narrewarren
35	Geoplanidae	Geoplana	adae var. extralineata	Dendy	1892	MNH	1924.8.15.15-24	Syntypes	x		Narrewarren
36	Geoplaniade	Geoplana	adae var. fusca	Dendy	1892	MV	G 1457	Syntype	x		southern end
37	Geoplanidae	Geoplana	adae var. fusca	Dendy	1892	MNH	1924.8.15.15-24	Syntypes	x		souther end

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

District / State	Country	Notes
	New Zealand	A series of 10 microslides - ? Ex Christchurch, not type locality.
	New Zealand	Both agricola and varity in this lot.
Victoria	Australia	Microslides 1-6, carmine stained, incomplete, ex MUZD; status uncertain. Species complex.
Victoria	Australia	Collected Spencer, July 1891
Victoria	Australia	Collected Spencer, July 1891
Victoria	Australia	Collected Spencer, July 1891; specimen lot collected "between Kurumburra and Loch".
Wales	Australia	
	New Zealand	Serial sections H&E
	New Zealand	
Enderby Island	New Zealand	
Australia	Australia	Collected by A.G. Hamilton
Auckland Island	New Zealand	originally two specimens found
Wales	Australia	Collected by J.P. Hill; specimen non-sexual
	Australia	Collected E.T & W.
	Australia	Collected T. Whitelegge 1887. Labelled "figured specimen".
	Australia	See letter 9/5/1978
	Australia	Collected E.T & W
	Australia	Collected T. Whitelegge, 1887. ? Label error - Reg No G1453. Labelled "figured specimen"
	Australia	See letter 9/5/1978. Slide with TS anterior & posterior; one slide LVS anterior, mid, posterior.
Campbell Island	New Zealand	Collected by J. H. Sorensen; other specimens ex Auckland Island coll. Dawbin. Refer corresp. With Dell, Palma.
Wellington	New Zealand	Incertae sedis. Extensive search - nil refer to letters ex Dell etc.
Tops, NSW	Australia	Uncertain whether sections belong to specimen, or whether one specimen divided in two. Refer to notes.
	New Zealand	Paratype A63-44, slides 1-19 anterior, 1,3,4,6,7 posterior incomplete series; Fyfe's Nos 492, 492A
	Australia	Refer to letter from G. Hartmann-Schroder 12 Sept 1978;
	Australia	Refer to letter from W. Rydzewski 29 Nov 1978
	New Zealand	Paratype A63-47, slides 1-15; No. 13 missing
Wales	Australia	Slides stained with Masson's trichrome. Non-sexual
Wales	Australia	Slides stained with Mayer's Haemalum and Young's eosin-erythrosin
Wales	Australia	Slides stained with
Wales	Australia	subviridis var?; Graff considers this is G. variegata F&H
Enderby Islands	New Zealand	Originally Syntypes; whole specimens mising. See correspondence with Drs. Dell and Palma.
Victoria	Australia	Microslides 1-10, carmine stained, ex MUZD; status uncertain.
Victoria	Australia	All varieties of G. adae in this lot.
Victoria	Australia	Collected by Spencer and French. All varieties of G. adae in this lot.
Victoria	Australia	Collected by Spencer and French. All varieties of G. adae in this lot.
Tasmania	Australia	Collected by Spencer, January 1893
Tasmania	Australia	Collected by Spencer, January 1893; all varieties of adae in this lot.

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

38	Geoplanidae	Geoplana	aucklandica	Dendy	1901	MNH	1924.8.15.14	Holotype	x		gully
39	Geoplanidae	Geoplana	balfouri	Graff	1899	ZMB	3505	Syntype	x		Wellington;
40	Geoplanidae	Geoplana	balfouri	Graff	1899	MNH	1924.8.15.513-538	Syntypes	x		Wellington,
41	Geoplanidae	Geoplana	barringtonensis	Wood	1926	AM	W 2352	Holotype		x	Barrington Tops
42	Geoplanidae	Geoplana	bicolor	Graff	1899	ZMB	3506	Syntype		x	near Gympie
43	Geoplanidae	Geoplana	bicolor	Graff	1899	MNH	1924.8.15.486-495	Syntypes	x		near Gympie
44	Geoplanidae	Geoplana	challengeri	Graff	1899	MNH	1877.11.2.6	? Mislaid	x		Wellington
45	Geoplanidae	Geoplana	circularis	Fyfe	1956	OM	A74-12	Lectotype		x	Kohukohu
46	Geoplanidae	Geoplana	citrina	Wood	1926	AM	W 2353	Holotype		x	Barrington Tops
47	Geoplanidae	Geoplana	comitatis	Dendy	1915	MNH	1924.8.15.46-50	Syntypes	x		Mundaring Weir
48	Geoplanidae	Geoplana	cooperi	Dendy	1901	AM	W 2002	Syntype		x	Omaha
49	Geoplanidae	Geoplana	cooperi	Dendy	1901	MNH	1924.8.15.51	Syntype	x		Omaha
50	Geoplanidae	Geoplana	cucullata	Dendy	1897	AM	W 2003	Syntypes	x		Mahinapua
51	Geoplanidae	Geoplana	cucullata	Dendy	1897	MNH	1924.8.15.54-56	Syntypes	x	x	Mahinapua
52	Geoplanidae	Geoplana	cyanea	Fyfe	1956	OM	A74-04	Lectotype		x	Napier
53	Geoplanidae	Geoplana	daemeli	Graff	1899	ZMB	3438	Syntypes	x		
54	Geoplanidae	Geoplana	daemeli	Graff	1899	ZMB	3441	Syntype	x		Adelaide
55	Geoplanidae	Geoplana	daemeli	Graff	1899	ZMB	3464	Syntype	x		
56	Geoplanidae	Geoplana	dakini	Dendy	1915	MNH	1924.8.15.64-68	Syntypes	x		near Perth
57	Geoplanidae	Geoplana	dendyi	Spencer	1891	AM	W 1956	Syntype	x		road - Tanjil
58	Geoplanidae	Geoplana	dendyi	Spencer	1891	MV	G 1459	Syntype		x	road - Tanjil
59	Geoplanidae	Geoplana	dendyi	Spencer	1891	MNH	1924.8.15.60-63	Syntypes	x		road - Tanjil
60	Geoplanidae	Geoplana	diemenensis	Dendy	1894	AM	W 1840	Syntype	x		Parattah
61	Geoplanidae	Geoplana	diemenensis	Dendy	1894	MV	G 1460	Syntype	x		Mt Wellington
62	Geoplanidae	Geoplana	diemenensis	Dendy	1894	MNH	1924.8.15.57-59	Syntypes	x		localities
63	Geoplanidae	Geoplana	dovei	Steel	1901	AM	G 3181	Holotype	x		Table Cape
64	Geoplanidae	Geoplana	dubia	Dendy	1892	MNH	1924.8.15.84-85	Syntype	x		South
65	Geoplanidae	Geoplana	exulans	Dendy	1901	AM	W 2000	Syntype	x		Wharekauri
66	Geoplanidae	Geoplana	fagicola	Dendy	1901	MNH	1924.8.15.94	Holotype	x		Garvey's,
67	Geoplanidae	Geoplana	flavilineata	Dendy	1915	MNH	1924.8.15.69-70	Syntypes	x		Mundaring Weir
68	Geoplanidae	Geoplana	flavimarginata	Dendy	1897	AM	W 1998	Syntypes	x		Wellington
69	Geoplanidae	Geoplana	flavimarginata	Dendy	1897	MNH	1924.8.15.95-100	Syntypes	x		Wellington
70	Geoplanidae	Geoplana	fletcheri	Dendy	1891	NMW	2778	Syntype		x	Macedon
71	Geoplanidae	Geoplana	fletcheri	Dendy	1891	MNH	1891.9.28.22	Syntype	x		Macedon
72	Geoplanidae	Geoplana	fletcheri	Dendy	1891	MNH	1924.8.15.71-80	Syntypes	x		Macedon
73	Geoplanidae	Geoplana	fletcheri	Dendy	1891	AM	W 1951	Syntype ?	x		Macedon
74	Geoplanidae	Geoplana	flatcheri var adelidensis	Dendy	1893	NMW	2779	Syntype		x	Summit, nr
75	Geoplanidae	Geoplana	fletcheri var adelaidensis	Dendy	1893	NMW	13035	Syntype	x		nr Adelaide
76	Geoplanidae	Geoplana	fletcheri var borealis	Dendy	1895	AM	W 2271	Syntype	x		Blackheath

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

Auckland	New Zealand	Collected H. Suter
Tasmania	Australia	Six specimens sent to Graff;
Tasmania	Australia	
Wales	Australia	A series of 212 microslides prepared by Winsor
Queensland	Australia	is unknown.
Queensland	Australia	Specimens included in a mixed lot of Geoplana variegat
	New Zealand	Specimen in Geoplana traversii lot; no record of G. challengeri identified s such in BM collection
North Island	New Zealand	Microslides 1-3, Anterior 4-6; Paralectotype OM A63-56. Fyfe's Nos 541, 542, 546; Fyfe dsignated Syntypes
Wales	Australia	A series of 214 microslides, prepared by Winsor
Australia	Australia	
Province	New Zealand	A series of 60 microslides, prepared by Winsor
Province	New Zealand	
	New Zealand	
	New Zealand	A series of 18 microslides, prepared by Fyfe
	New Zealand	A series of microslides 1-3, anterior 1-10. Fyfe designated syntypes - a whole specimen and series of slides.
	Australia	Formerly F87, cited by Graff as F97
South Australia	Australia	Formerly F92 Collected by Schomburgk; non-sexual
Queensland	Australia	Formerly F 658; Collected by Rolle
Australia	Australia	
Victoria	Australia	Collected Spencer, November 1890
Victoria	Australia	Collected Spencer November 1890
Victoria	Australia	Collected Spencer November 1890
Tasmania	Australia	February 1893
Tasmania	Australia	Collected L.J. Balfour; sexual
Tasmania	Australia	Multiple localities
Tasmania	Australia	Collected H. Stuart-Dove
Victoria	Australia	Collected Spencer & French July 1891; other specimen not Syntype; ? Another specimen missing - ? Fwd to Graff
Chatham Island	New Zealand	Fyfe designated a Lectotype, 8 slides; uncertain as to which of the two specimens/localities was designated.
Te Anau	New Zealand	
Australia	Australia	
	New Zealand	labelled "Co-type, Wellington, NZ"
	New Zealand	A series of 18 microslides prepared by Fyfe 1946.
Victoria	Australia	Graff 1899 " ..specimen drawn by Dendy. This last was sent me by Dendy together with two others .."
Victoria	Australia	Specimen sent by Dendy 1891.
Victoria	Australia	Specimen lot includes material from Macedon that are Syntypes.
Victoria	Australia	Ex Dendy collection given to Steel. Uncertain whether part of original series or collected later on. Cf MV 1461 / MUZD 544.
South Australia	Australia	Given by Dendy to Graff; Ex Graff Collection
South Australia	Australia	Steel at a later date than the Syntypes.
Wales	Australia	Collected by Steel, Jan 1894. Ex Dendy Collection.

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

77	Geoplanidae	Geoplana	fletcheri var borealis	Dendy	1895	AM	W 2133	Syntype	x		Blackheath
78	Geoplanidae	Geoplana	flynni	Dendy	1915	MNH	1924.8.15.102-103	Syntypes	x		Maria Island
79	Geoplanidae	Geoplana	frosti	Spencer	1891	AM	W 2274	Syntype	x		Tanjil Track
80	Geoplanidae	Geoplana	frosti	Spencer	1891	MV	G 1463	Syntype	x		Tanjil Track
81	Geoplanidae	Geoplana	frosti	Spenceri	1891	MNH	1924.8.15.101	Syntype	x		Tanjil Track
82	Geoplanidae	Geoplana	fuscodorsalis	Steel	1901	AM	G 3176	Holotype	x		Near Perth
83	Geoplanidae	Geoplana	garveyi	Dendy	1901	MNH	1924.8.15.111-112	Syntypes	x	x	Garvey's,
84	Geoplanidae	Geoplana	gelatinosa	Dendy	1895	MNH	1924.8.15.178	Holotype	x		the Teremakau
85	Geoplanidae	Geoplana	graffii	Dendy	1895	AM	W 1976	Syntype	x		Ashburton
86	Geoplanidae	Geoplana	graffii	Dendy	1895	MNH	1924.8.15.133-141	Syntypes	x		various
87	Geoplanidae	Geoplana	graffii var angusta	Dendy	1901	AM	W 1982	Syntypes		x	Toi Toi
88	Geoplanidae	Geoplana	graffii var angusta	Dendy	1901	MNH	1924.8.15.133-141	Syntypes		x	Invercargill
89	Geoplanidae	Geoplana	graffii var castanea	Dendy	1901	AM	W 1985	Syntype	x		Invercargill
90	Geoplanidae	Geoplana	graffii var castanea	Dendy	1901	MNH	1924.8.15.142-172	Syntype	x		Invercargill
91	Geoplanidae	Geoplana	graffii var clintonensis	Dendy	1901	MNH	1924.8.15.133-141	Syntypes	x	x	house, Clinton
92	Geoplanidae	Geoplana	graffii var dorsomarmorata	Dendy	1901	MNH	1924.8.15.142-172	Holotype	x		The Nuggets
93	Geoplanidae	Geoplana	graffi var nigrescens	Dendy	1901	AM	W 2009	Syntype	x		near Jackson's
94	Geoplanidae	Geoplana	graffii var nodusa	Dendy	1901	AM	W 1984	Syntype	x		Invercargill
95	Geoplanidae	Geoplana	graffii var nodusa	Dendy	1901	MNH	1924.8.15.133-141	Syntypes		x	Invercargill
96	Geoplanidae	Geoplana	graffii var occidentalis	Dendy	1897	AM	W 1977	Syntype	x		Mahinapua
97	Geoplanidae	Geoplana	graffii var occidentalis	Dendy	1897	AM	W 1978	Syntype	x		Mahinapua
98	Geoplanidae	Geoplana	graffii var occidentalis	Dendy	1897	MNH	1924.8.15.142-172	Syntype			Mahinapua
99	Geoplanidae	Geoplana	graffii var ocellata	Dendy	1901	MNH	1924.8.15.142-172	Syntype			Paradise
100	Geoplanidae	Geoplana	graffii var otiraensis	Dendy	1897	AM	W 1980	Syntype	x		Otira
101	Geoplanidae	Geoplana	graffii var otiraensis	Dendy	1897	MNH	1924.8.15.142-172	Syntypes		x	mahinapua
102	Geoplanidae	Geoplana	graffii var somersii	Dendy	1896	AM	W 1983	Syntype	x		Springburn
103	Geoplanidae	Geoplana	graffii var somersii	Dendy	1896	MNH	1924.8.15.142-172	Syntypes		x	Springburn
104	Geoplanidae	Geoplana	graffii var wharekauriensis	Dendy	1901	AM	W 1979	Syntypes	x		Estate,
105	Geoplanidae	Geoplana	wharekauriensis	Dendy	1901	MNH	1924.8.15.133-141	Syntypes	x		Estate,
106	Geoplanidae	Geoplana	gramnicola	Steel	1901	AM	G 3179	Holotype		x	Petersham
107	Geoplanidae	Geoplana	hamiltoni	Dendy	1895	AM	W 2006	Syntype		x	Hawke's Bay
108	Geoplanidae	Geoplana	hamiltoni	Dendy	1895	MNH	1924.8.15.117	Syntype		x	Hawke's Bay
109	Geoplanidae	Geoplana	hillii	Steel	1897	AM	G 1510	Holotype	x		Bundanoon
110	Geoplanidae	Geoplana	hoggii	Dendy	1891	MNH	1891.9.28.8-11	Syntypes	x		Macedon
111	Geoplanidae	Geoplana	hoggii	Dendy	1891	MNH	1924.8.15.190-200	Syntypes	x		Macedon
112	Geoplanidae	Geoplana	howesi	Dendy	1901	MNH	1924.8.15.188-189	Syntypes	x		Invercargill
113	Geoplanidae	Geoplana	howitti	Dendy	1891	NMW	13040	Holotype	x		Wellington
114	Geoplanidae	Geoplana	howitti var obsoleta	Dendy	1892	MV	G 1465	Syntype	x		Narrewarren
115	Geoplanidae	Geoplana	howitti var obsoleta	Dendy	1892	MNH	1924.8.15.126-132	Syntypes	x		Narrewarren

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

Wales	Australia	Ex Dendy Collection; twisted
Tasmania	Australia	Collected by Nicholls
Victoria	Australia	Collected by Spencer, Nov 1890; brown variety; Ex Dendy Coll.
Victoria	Australia	green variety
Victoria	Australia	
Australia	Australia	non-sexual
Te Anau	New Zealand	Jan 1900; Series of 14 microslides prepared by Fyfe 1946
Gorge	New Zealand	Collected Miss Dendy
	New Zealand	Labelled: Aug '94 (co-type)
	New Zealand	Mixed lot includes syntypes.
Southland	New Zealand	Collected by Miss J.C. RichBoth specimens sectioned by LW. A - G. iris, 95 microslides; B.- G. angusta, 41 slides
	New Zealand	? 9 microslides prepared by Fyfe 1946; other localities include the Nuggets (Benham 19 Apr 1899); Toi Toi, Southland.
	New Zealand	Collected G. Howes April 20/98
	New Zealand	Syntype in mixed lot
Te Anau	New Zealand	Collected January 1900; Series of 3 microslides prepred by Fyfe 1946
and the Bluff	New Zealand	Collected Benham; Holotype in mixed lot.
road	New Zealand	
	New Zealand	Colleced G. Howes. Specimen damaged
	New Zealand	Collected G. Howes; 17 microslides prepared by Fyfe 1946
	New Zealand	Labelled "Co-type"
	New Zealand	
	New Zealand	Syntypes within specimen lot.
Wakatipau	New Zealand	Collected Mrs Mason
	New Zealand	Sexual
	New Zealand	including material labelled by Dendy; no such species / variety has been described; some sectioned by Fyfe (13 and 16
	New Zealand	labelled "Co-type"
	New Zealand	5 microslides prepared by Fyfe 1946
Chatham Island	New Zealand	Jan 1901
Chatham Island	New Zealand	Jan 1901
Wales	Australia	sectioned LW
near Napier	New Zealand	Collected by A. Hamilton 1894; 40 microslides prepared by LW
near Napier	New Zealand	Collected by A. Hamilton
Wales	Australia	
Victoria	Australia	"thrown away(dried up) Oct 1914"
Victoria	Australia	Syntypes in specimen lot.
	New Zealand	Collected by G. Howes, in bush.
Victoria	Australia	Graff 1899 "...I am in posession, through Mr Dendy's kindness of the original specimen.."
Victoria	Australia	Collected by Spencer & French, July 1891
Victoria	Australia	Syntype within this specimen lot.

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

116	Geoplanidae	Geoplana	huttoni	Graff	1899	NMW	4069	Syntypes	x		
117	Geoplanidae	Geoplana	inaequalistriata	Dendy	1895	MNH	1924.8.15.119-122	Syntypes		x	Christchurch
118	Geoplanidae	Geoplana	inaequiabilis	Fyfe	1956	OM	A 74.03	Holotype		x	Kohukohu
119	Geoplanidae	Geoplana	iris	Dendy	1896	MNH	1924.8.15.113-118	Syntypes		x	Springburn
120	Geoplanidae	Geoplana	langii	Dendy	1895	AM	W 1995	Syntype		x	Taupo
121	Geoplanidae	Geoplana	laingii	Dendy	1895	MNH	1924.8.15.207	Syntype	x		Taupo
122	Geoplanidae	Geoplana	lateropunctata	Dendy	1901	AM	W 1996	Syntype	x		Whangamarino
123	Geoplanidae	Geoplana	lateropunctata	Dendy	1901	MNH	1924.8.15.206	Syntype	x		Whangamarino
124	Geoplanidae	Geoplana	latissima	Dendy	1895	AM	W 2001	Syntype	x		Springburn
125	Geoplanidae	Geoplana	latissima	Dendy	1895	MNH	1924.8.15.202-204	Syntypes		x	Springburn
126	Geoplanidae	Geoplana	lucasi	Dendy	1891	AM	W 2273	Syntype	x		Croajingolong
127	Geoplanidae	Geoplana	lucasi	Dendy	1891	MNH	1924.8.15.205	Syntype	x		Croajingolong
128	Geoplanidae	Geoplana	lyra	Steel	1901	AM	G 3182	Holotype		x	Table Cape
129	Geoplanidae	Geoplana	mariae	Dendy	1895	MNH	1924.8.15.213-218	Syntypes		x	of Otira Gorge
130	Geoplanidae	Geoplana	marrineri	Dendy	1911		LOST				
131	Geoplanidae	Geoplana	mediolineata	Dendy	1891	MNH	1891.9.28.20-21	Syntypes	x		Macedon
132	Geoplanidae	Geoplana	mediolineata var simularis	Steel	1901	AM	G 3180	Holotype	x		nr Adelaide
133	Geoplanidae	Geoplana	melanochroa	Steel	1901	AM	G 6178	Holotype	x		Darling Ranges
134	Geoplanidae	Geoplana	meridionalis	Graff	1899	MNH	371	Syntypes ?	x		The Bluff
135	Geoplanidae	Geoplana	minor	Dendy	1892	MV	G 1467	Syntype	x		Cooran
136	Geoplanidae	Geoplana	minor	Dendy	1892	MNH	1924.8.15.240-241	Syntypes	x		Cooran
137	Geolanaidae	Geoplana	m'mahoni	Dendy	1891		LOST				Creek, Upper
138	Geoplanidae	Geoplana	moebiusi	Dendy	1899	NMW	13262	Syntype	x		
139	Geoplanidae	Geoplana	mortoni	Dendy	1894	NMW	13043	Syntype	x		Parratah
140	Geoplanidae	Geoplana	mortoni	Dendy	1894	MNH	1924.8.15.236-239	Syntypes	x		Parattah
141	Geoplanidae	Geoplana	moseleyi	Hutton	1880		LOST				Dunedin
142	Geoplanidae	Geoplana	munda	F&H	1887		LOST				Hartley Vale
143	Geoplanidae	Geoplana	nichollsi	Dendy	1915	MNH	1924.8.15.273-283	Syntypes	x		Maria Island
144	Geoplanidae	Geoplana	ornata	F&H	1887		LOST				Hartley Vale
145	Geoplanidae	Geoplana	parva	Steel	1897	AM	G 1516	Holotype	x		Nerang River
146	Geoplanidae	Geoplana	ponderosa	Steel	1897	AM	G 1151	Holotype	x		Bundanoon
147	Geoplanidae	Geoplana	purpurea	Dendy	1895	MNH	1924.8.15.301-303	Syntypes	x		Ashburton
148	Geoplanidae	Geoplana	quadrangulata	Dendy	1891	MNH	1891.9.28.28-29	Syntypes	x		Macedon
149	Geoplanidae	Geoplana	quadrangulata	Dendy	1891	MNH	1924.8.15.325-335	Syntypes	x		Macedon
150	Geoplanidae	Geoplana	wellingtoni	Dendy	1892	MV	G 1470	Syntype	x		Wellington
151	Geoplanidae	Geoplana	wellingtoni	Dendy	1892	AM	W 2259	Syntype	x		Wellington
152	Geoplanidae	Geoplana	wellingtoni	Dendy	1892	MNH	1891.9.28.30-32	Syntypes	x		Wellington
153	Geoplanidae	Geoplana	wellingtoni	Dendy	1892	MNH	1924.8.15.325-335	Syntypes	x		Wellington
154	Geoplanidae	Geoplana	quinquelineata	F&H	1887	AM	W 2420	Syntype	x		Capertee

Appendix 1.
A Catalogue of Types of Australian New Zealand Terricola

	New Zealand	Acquisition No. 13779 cited by Graff 1899 is correct.
	New Zealand	18 microslides prepared by Fyfe 1946
nr Auckland	New Zealand	13 microslides, trichrome stained, prepared by Fyfe; Paratypes A74.33 A; A74.33B figured specimen
	New Zealand	14 microslides prepared by Fyfe 1946.
North Island	New Zealand	Collected by R.M. Laing; 88 microslides prepared by LW 1976.
North Island	New Zealand	Collected by R.M. Laing; only two specimens collected
Chatham Island	New Zealand	Collected 20 January 1901
Charham Island	New Zealand	Collected 20 January 1901
	New Zealand	sexual; coiled
	New Zealand	37 microslides prepared by Fyfe 1946
Victoria	Australia	one of the three original specimens collected by Spencer in 1889; one specimens given to Graff
Victoria	Australia	Collected by Spencer 1889
Tasmania	Australia	microslides prepared by LW
South Island	New Zealand	20 microslides prepared by Fyfe 1946
Auckland Island	New Zealand	Collected by Benham; previously G. aucklandica, junior homonym.
Victoria	Australia	Six specimens sent to Graff.
South Australia	Australia	
Australia	Australia	microslides prepared by LW; AM unregistered: one slide of serial sections, faded.
South Island	New Zealand	Syntypes within specimen lot
Queensland	Australia	
Queensland	Australia	
Victoria	Australia	Graff 1899: "A specimen from McMahon's Creek (U.Yarra) lies before me.."; preseumed lost in Graz.
Auckland Island	New Zealand	Dr G. Hartwich advised ZMB Nr 3445 (F107) specimen lost.
Tasmania	Australia	Collected Spencer
Tasmania	Australia	Collected Spencer; Syntypes in specimen lot.
	New Zealand	Fyfe's 1946 synonomies are not based on Hutton's specimens, rather on specimens identified by Dendy as G. moseleyi.
Wales	Australia	Numerous specimens are available but none near the Type locality
Tasmania	Australia	Syntypes within specimen lot
Wales	Australia	
Queensland	Australia	Collected Mr J. S. Steel
Wales	Australia	
	New Zealand	Syntypes within specimen lot
Victoria	Australia	
Victoria	Australia	Syntypes with specimen lot.
Victoria	Australia	Collected December 1890
Victoria	Australia	all twisted
Victoria	Australia	
Victoria	Australia	Syntypes within specimen lot.
Wales	Australia	Label: Geoplana-5-lineata Capertee June/86; mutiple locations for this species.

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

155	Geoplanidae	Geoplana	quinquelineata	F&H	1887	AM	W 2415	Syntype	x		Sandhurst
156	Geoplanidae	Geoplana	accentuata	Steel	1897	AM	G 1514	Holotype	x		Nerang River
157	Geoplanidae	Geoplana	ranuii	Fyfe	1953	NMNZ	ZW 103	Holotype		x	
158	Geoplanidae	Geoplana	regina	Dendy	1892	MV	G 1471	Syntype	x		River
159	Geoplanidae	Geoplana	robusta	Steel	1897	AM	G 1512	Holotype	x		Bundanoon
160	Geoplanidae	Geoplana	rubicunda	F&H	1888	AM		Holotype		x	Springwood
161	Geoplanidae	Geoplana	scaphoidea	Steel	1901	AM	G 1515	Holotype	x		Nerang River
162	Geoplanidae	Geoplana	spectabilis	Dendy	1894	MNH	1924.8.15.341	Holotype	x		near Wellington
163	Geoplanidae	Geoplana	spenceri	Dendy	1889	MV	G 1472 - 1475	Syntypes		x	Creek, Upper
164	Geoplanidae	Geoplana	splendens	Dendy	1895	MNH	1924.8.15.396	Holotype	x		the Teremaku
165	Geoplanidae	Geoplana	subquadrangulata	Dendy	1895	AM	W 2017	Syntypes	x		Ashburton
166	Geoplanidae	Geoplana	subquadrangulata	Dendy	1895	MNH	358, 3	Syntypes		x	The Bluff,
167	Geoplanidae	Geoplana	enderbyensis		1909		LOST				
168	Geoplanidae	Geoplana	sugdeni	Dendy	1891	MV	G 684	Syntypes	x		Macedon
169	Geoplanidae	Geoplana	sugdeni	Dendy	1891	MNH	1891.9.28.13-14	Syntypes			Macedon
170	Geoplanidae	Geoplana	sugdeni	Dendy	1891	MNH	1924.8.15.375-387	Syntypes	x		Macedon
171	Geplanidae	Geoplana	sulphureus	F&H	1888		LOST				Hartley Vale
172	Geoplanidae	Geoplana	suteri	Dendy	1897	AM	W1968	Syntype	x		Dunedin
173	Geoplanidae	Geoplana	suteri	Dendy	1897	MNH	1924.8.15.449-454	Syntypes		x	Dunedin
174	Geoplanidae	Geoplana	traversii	Moseley	1877	MNH	1877.11.26 (part)	Syntypes			Wellington
175	Geoplanidae	Geoplana	tasmaniana var flavicincta	Steel	1901	AM	G3183	Holotype	x		Launceston
176	Geoplanidae	Geoplana	tenuis	Dendy	1894	MNH	1924.8.15.455	Holotype	x		Nelson
177	Geoplanidae	Geoplana	ventrolineata	Dendy	1892	AM	W1954	Syntypes	x		Nursery Garden,
178	Geoplanidae	Geoplana	ventrolineata	Dendy	1892	AM	W2278	Syntypes	x		Nursery, St kilda
179	Geoplanidae	Geoplana	ventrolineata	Dendy	1892	MV	G1477	Syntypes	x	x	Nursery, St
180	Geoplanidae	Geoplana	ventropunctata	Dendy	1892	MV	G1478	Syntype	x		Ferntree Gully
181	Geoplanidae	Geoplana	ventropunctata	Dendy	1892	MNH	1891.9.28.44-46	Syntypes	x		Ferntree Gully
182	Geoplanidae	Geoplana	triangulata	Dendy	1895	MNH	1924.8.15.467-477	Syntypes	x		Christchurch
183	Geoplanidae	Geoplana	triangulata var australis	Dendy	1895	MNH	477; 4	Syntypes		x	Dunedin
184	Geoplanidae	Geoplana	typhlops	Dendy	1894	MNH	1924.8.15.456-466	Syntypes	x		Mt Wellington
185	Geoplanidae	Geoplana	variegata	F&H	1888		LOST	lost			Cumberland
186	Geoplanidae	Geoplana	ventrolineata	Dendy	1892	MNH	1924.8.15.496-499	Syntypes	x		Nursery, St
187	Geoplanidae	Geoplana	viridis	F&H	1888		LOST				Guntawang
188	Geoplanidae	Geoplana	virgata	F&H	1888		LOST				Hartley Vale
189	Geoplanidae	Geoplana	walhallae	Dendy	1891	MNH	1891.9.28.7	Syntype	x		Walhalla
190	Geoplanidae	Geoplana	warragulensis	Graff	1899	AM	no number	Syntype	x		Warragul
191	Geoplanidae	Geoplana	warragulensis	Graff	1899	MNH	1924.8.15.208-212	Syntype	x		Warragul
192	Geoplanidae	Geoplana	wellingtoni	Graff	1899			Syntypes	x		Mt Wellington
193	Geoplanidae	Planaria	tasmaniana	Darwin	1844		autolysed				

Appendix 1.
A Catalogue of Types of Australian New Zealand Terricola

Victoria	Australia	specimen twisted
Queensland	Australia	
Campbell sland	New Zealand	Collected by J.H. Sorenson.
Queensland	Australia	Collected by Spencer 1891; Dendy provided Graff with a single specimen, now presumed lost.
Wales	Australia	
Wales	Australia	Microslides prepared by LW
Queensland	Australia	Qld, 6 specimens "typical".
	New Zealand	Collected by R.M. Laing.
Victoria	Australia	Incomplete series of microslides; unable to determine whether slides are from a single or multiple specimens.
	New Zealand	Collected by Miss Dendy.
	New Zealand	Ex. Steel, ex. Dendy collection
	New Zealand	unknown (19 microslides); MNH 37 microslides prep Fyfe 1946
Enderby Island	New Zealand	Collected by Benham (?); all of Chiltern Exped flatworms lost.
Victoria	Australia	Donated by Dendy 27 April 1891; 4 specimens were sent to Graff.
Victoria	Australia	Donated by Dendy
Victoria	Australia	Syntypes within specimen lot.
Wales	Australia	
	New Zealand	Collected by H. Suter;labelled "Co-type"
	New Zealand	originally four specimens found;17 microslides prepared by Fyfe 1946
	New Zealand	Specimens missing from collection.
Tasmania	Australia	Collected by H. Stuart Dove.
	New Zealand	Collected by R.I. Kingsley.
Victoria	Australia	Collected by Grayson, July 1891
Victoria	Australia	Collected by Grayson, July 1891; mis-labelled as G. ventropunctata - checked by LW.
Victoria	Australia	Collected by Grayson, July 1891; 5 specimens were given by Dendy to von Graff, ? ZMB 2410.
Victoria	Australia	Collected by the Field Naturalists' Club excursion in 1891 near Sassafrass Gully, Nairn, Victoria (Ferntree Gully)
Victoria	Australia	Also lot 1924.8.15.500-510 - syntypes in this specimen lot.
	New Zealand	for antomical description for species.
	New Zealand	Collected by A. Hamilton; Fyfe designated a lectotype from non-type materiual - 11 microslides prepared by Fyfe 1946
Tasmania	Australia	forwarded to von Graff.
Wales	Australia	Multiple localities
Victoria	Australia	Collected by Grayson, July 1891
Wales	Australia	From the banks of an anabranch of the Cudgegong River
Wales	Australia	
Victoria	Australia	Originally two specimens found; Dendy gave one specimen from Walhalla to Graff - presumed lost.
Victoria	Australia	presumed lost
Victoria	Australia	In G. m'mahoni specimen lot.
Victoria	Australia	Refer to G. quadrangulata var wellingtoni.
Tasmania	Australia	Collected by Darwin in Van Diemen's land, February. All Darwin's specimens died, autolysed, and were not preserved.

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

194	Rhynchodemidae	Platydemus	assimilis	Wood	1926	AM	W2354	Holotype	x		Barrington Tops
195	Rhynchodemidae	Rhynchodemus	coxii	F&H	1888		autolysed				Mt Wilson
196	Rhynchodemidae	Rhynchodemus	dubius	Spencer	1892	AM	G60; G11088	Syntypes	x		Island
197	Rhynchodemidae	Rhynchodemus	dubius	Spencer	1892	MV	G1479	Syntypes	x		Island
198	Rhynchodemidae	Rhynchodemus	fasciatus	Spencer	1892	AM	G11087;G11091	Syntypes	x		Island
199	Rhynchodemidae	Rhynchodemus	fasciatus	Spencer	1892	MV	G1480	Syntypes	x		Island
200	Rhynchodemidae	Rhynchodemus	fasciatus	Spencer	1892	NMW	13272	Syntypes	x		Island
201	Rhynchodemidae	Rhynchodemus	fletcheri	Spencer	1892	MV	G706	Syntype?	x		Island
202	Rhynchodemidae	Rhynchodemus	grandis	Spencer	1892	AM	G11092	Syntypes	x		Island
203	Rhynchodemidae	Rhynchodemus	grandis	Spencer	1892	MV	G1481	Syntype	x		Island
204	Rhynchodemidae	Rhynchodemus	guttatus	F&H	1887	AM	W2422	Holotype	x		Springwood
205	Rhynchodemidae	Rhynchodemus	laterolineatus	Spencer	1892	AM	G11090	Syntypes	x		Island
206	Rhynchodemidae	Rhynchodemus	laterolineatus	Spencer	1892	MV	G1482	Syntypes	x		Island
207	Rhynchodemidae	Rhynchodemus	laterolineatus	Spencer	1892	MV	G704	Syntype	x		Island
208	Rhynchodemidae	Rhynchodemus	mediolineatus	Spencer	1892	AM	G11089	Syntypes	x		Island
209	Rhynchodemidae	Rhynchodemus	mediolineatus	Spencer	1892	MV	G1483	Syntype	x		Island
210	Rhynchodemidae	Rhynchodemus	mediolineatus	Spencer	1892	MV	G704	Syntype	x		Island
211	Rhynchodemidae	Rhynchodemus	moseleyi	F&H	1887		LOST				Hills,
212	Rhynchodemidae	Rhynchodemus	niger	F&H	1887		LOST				Guntawang
213	Rhynchodemidae	Rhynchodemus	putzei	Graff	1899	ZMB	1300	Syntypes	x		
214	Rhynchodemidae	Rhynchodemus	obscurus	F&H	1887	AM	W2423	Holotype	x		Ryde
215	Rhynchodemidae	Rhynchodemus	simulans	Dendy	1892	MV	G1484	Syntype	x		Bacchus Marsh
216	Rhynchodemidae	Rhynchodemus	simulans	Dendy	1892	AM	W1958	Syntype	x		Bacchus Marsh
217	Rhynchodemidae	Rhynchodemus	simulans	Dendy	1892	MNH	1924.8.15.557-564	Syntype	x		Bacchus Marsh
218	Rhynchodemidae	Rhynchodemus	testacea	Hutton	0						
219	Rhynchodemidae	Rhynchodemus	trilineatus	F&H	1887		LOST				Guntawang
220	Rhynchodemidae	Rhynchodemus	victoriae	Dendy	1891	NMW	2868	Holotype		x	Croajingalong
221	Rhynchodemidae	Rhynchodemus	victoriae var steelii	Dendy	1895	AM	W2177	Syntype	x		Wentworth Falls

Appendix 1.
A Catalogue of Types of
Australian New Zealand Terricola

Wales	Australia	Collected by the University of Sydney Part, February 1925
Wales	Australia	Subsequently found to be a geoplanid (now Parakontikia coxii)
Wales	Australia	Collected T. Whitelegge, 1887
Wales	Australia	Collected T. Whitelegge, 1887. Five specimens, ex Spencer collection.
Wales	Australia	Collected T. Whitelegge, 1887. Also some unregistered specimens in AM collection.
Wales	Australia	Collected T. Whitelegge, 1887. Two specimens ex Spencer
Wales	Australia	2 specimens Ex Graff Collection. Presumabley given to Graff by Spencer along with other material from Lord Howe Island.
Wales	Australia	Presumed lost by Smith & Convey 1970; LW discovered it in the collection, donated to the museum in Jan 1903 (ex Spencer).
Wales	Australia	Collected by E.T. & W. Also G60, 14 specimens Ex Lord Howe Is. purchased from E.H. Saunders, 1888.
Wales	Australia	Ex Spencer donation of 1903; agrees closely with the original description; Label states "figured". Sexual.
Wales	Australia	Ex J.J. Fletcher Estate. Label: "R. guttatus ..... Springwood 21.6.87 ...type" pencil, in Fletcher's hand (.... = indistinct)
Wales	Australia	Collected T. Whitelegge 1887.
Wales	Australia	Two specimens: 15 mm immature; 24mm ? Immature. Both brittle and coiled.
Wales	Australia	Ex. Spencer collection donated anuary 1903. There are two species in G704 - laterolineatus is given here as G704b.
Wales	Australia	Collected T. Whitelegge 1887.
Wales	Australia	Single specimen. ? Immature, broken, coiled.
Wales	Australia	Ex Spencer collection donated January 1903. There are two species in G704 -mediolineatus is given here as G704a.
Wales	Australia	Condobolin, NSW; NHM: 1924.8.15.553 Ex Dendy Collection.
Wales	Australia	
	Islands	record of this specimen at the Hamburg Museum (Hartmann-Schroder letter 12.9.78)
Wales	Australia	1892, 1894), though whether same species is uncertain.
Victoria	Australia	Collected by C.C. Brittlebank, July 1891.
Victoria	Australia	Collected by C.C. Brittlebank, July 1891
Victoria	Australia	NZare in this specimen lot.
	New Zealand	
Wales	Australia	Transferred to Platydemus by Graff (1899).
Victoria	Australia	Collected by Spencer. Sectioned and described by Heinzel
Wales	Australia	R. guttatus.

Appendix 2. Representative narcotizing and killing agents used on terrestrial flatworms.

Agent	Strength	Reference	Comments
Methylated spirit	6% aqueous	Steel (1897, 1901)	Specimens narcotized in 10-15 min without coagulation of mucus, maceration, or autolysis; slight swelling of rhabdoids; a highly variable product with additives.
Acidified ethanol used as a killing agent prior to fixation in Tyler's fixative.	0.4% nitric acid in 80% ethanol	Winsor, 1979	Rapidly kills species of *Australoplana, Parakontikia, Lenkunya*, and *Rhynchodemus*; slow acting causing severe contortion and contraction in *Fletchamia* and *Artioposthia* spp.
Ethanol	5 - 10% aqueous	Winsor (1991)	Rapid induction, usually within 5 min; preferred to methylated spirits for reagent consistency
Steinmann's fluid	Undiluted	Fyfe (1937)	Kills worms rapidly with little muscular contraction; tissues rendered brittle; markings may be obscured
Cobaltous nitrate/ cobaltous chloride	0.9 - 1.8% aqueous 150 - 300mM Co^{II}	Sakharov (1972)	Rapid narcotization; strong contraction; acts as primary fixative, producing poor preservation
Nitric acid	1% aqueous	Mahoney (1973)	Rapid killing; strong contraction; maceration of epidermis and parenchyma
Boiling water		Lincon & Sheals (1979)	Rapid killing when worm extended; some pigment loss; fixation by heat coagulation; histology fair; external markings may be obscured by coagulated mucus; inconvenient in the field
Microwave irradiation		Winsor (1991)	Rapid killing; fixation by heat coagulation, unsuited to field use

Appendix 3 Assessment of representative traditional and new fixatives used on terrestrial flatworms.
See Lillie & Fullmer (1976) for formulae for fixatives 2 - 9 ; see Appendix 4 for formula and methods for fixatives 10-13.

Fixative	**Comments**
1. Ethanol, 70-80%	Fixative may cause agonal contortion, loss of soluble pigments; melanin pigments retained; long-term 'alcohol-browning' (Winsor, 1983); good specimen flexibility; specimens can be stored indefinitely in fixative; poor histological fixation though sections will respond well to pre-staining mordanting; stain receptiveness otherwise poor; high evaporation rate; flammable; suitable for field use. Fair to good for molecular studies*
2. Carnoy's fixative	Reisinger, in Gelei (1929) " *glänzende Resultate gibt* "; uncertain whether the Carnoy referred to is the alcohol-acetic acid fixative (= Clarke's fixative), or that with alcohol, acetic acid and chloroform, unsuited to field use; satisfactory for small specimens for general histology. DNA preservation good.
3. Alcohol - formaldehyde - acetic acid (AFA)	Used for small rhynchodemids by Ogren 1955; unless used hot, or on narcotized specimens causes strong contractions and contortions in larger species of Terricola. Strongly acidic; AFA fixed specimens must be stored in 70% ethanol.
4. Bouin's fixative: aceto - formaldehyde - picric acid	Fixative stains specimens yellow; specimens cannot be stored in fixative without loss of nuclear staining (Thompson & Luna, 1978); fixative must be washed out of specimen before storage; retained picric acid affects sectioning (Pantin, 1969); fair histological fixation - strongly acidophilic image; picric acid explosive when dry; not recommended for field use
5. Mercuric chloride - acetic acid (Graff, 1899) 6. Gilson - Perenyi fluid (Reisinger in Gelei, 1929)	Fixatives render specimens grey-white in colour and brittle; specimens cannot remain in fixative (require transfer to strong alcohol); mercuric pigment must be removed; good histological fixation; excellent stain receptiveness.
7. Heidenhain's SUSA (Froehlich, 1955)	Recommended for Terricola by Bresslau (in Gelei, 1929). Fixative kills specimens with minimal contortion; external markings obscured; leaves tissues hard and brittle (Fyfe, 1936); prolonged fixation destroys rhabdites (Ball & Reynoldson,1981).

8. Steinmann's fixative (Steinmann & Bresslau's solution) mercuric chloride - nitric acid	Fixative discolours specimen; fixation time critical; specimens cannot be stored in fixative; fixative must be washed out; histological fixation fair; stain receptiveness average.
9. Zenker's fixative: dichromate - acetic - mercuric chloride	$HgCl_2$ is metal-corrosive, toxic and a cumulative environmental pollutant; $ZnCl_2$ substitution for $HgCl_2$ is not recommended for similar reasons. None of the mercuric chloride-based fixatives are recommended for field use. Saturated aqueous mercuric chloride is approximately 5.6% $HgCl_2$. DNA is poorly or not preserved in mercury-based fixatives.*
10. Formaldehyde 4% unbuffered or phosphate - buffered	Good colour retention; mucus not rendered opaque; specimen can be stored in fixative for months; buffered for years; fixation time not critical; poor fixation of epidermal structures with sloughing and abrasion; histological fixation good; stain receptiveness poor (for polychromes); not recommended for taxonomic purposes.
11. Formaldehyde 4% + 2% calcium acetate buffered	Good colour retention; mucus rendered slightly opaque; fixation time not critical; good fixation of epidermal structures; histological fixation good; stain receptiveness poor (for polychromes); specimens can be stored in fixative for years; highly recommended for taxonomic purposes - field use and for long-term storage. Non-cumulative in environment; can be legally disposed of by diluting 1:40 with water and flushing to sewerage. Poor to no preservation of DNA in formaldehyde-based fixatives (DNA is bound).*
12. Formaldehyde 4%/ calcium acetate/ cobalt nitrate (FCC ; modified Tyler's fixative)	Very good colour retention; mucus not rendered opaque; specimen can-be stored in fixative for years; fixation time not critical; epithelia well-fixed; histological fixation good; stain receptiveness good to fair for trichromes; highly recommended for taxonomic purposes - field use.
13. FCC fixative with Steedman's preservative	As for FCC fixative. In addition, specimen flexibility good; long-term storage good (years); suitable for field use.

---

* Carter, J. 2002. DNA preservation in fluid preserved collections.

Appendix 4

Formulae for fixatives and fixation methods suitable for Terricola

4.1 FORMALDEHYDE-BASED FIXATIVES

Formaldehyde-based preservatives best retain the external features essential for identification. They are presently unsuitable for molecular studies.

> Confusion often arises over formaldehyde and formalin terminology. A 37-40% aqueous solution of formaldehyde gas is generally known as a 100% formalin solution. Thus a simple fixative is 10% aqueous formalin solution which consists of 1part full strength (40%) formaldehyde solution + 9 parts tap water. This fixative is more correctly stated as a 4% aqueous formaldehyde solution.

4.1.1 *Formol-Calcium*

formaldehyde solution (37-40% - full strength commercial solution)	10 ml
calcium chloride (anhydrous) *	1 gm
tap water	90 ml

(***OR** calcium chloride dihydrate 1.3gm, **OR** calcium acetate anhydrous 2 gm)

This fixative is stable, and specimens can remain in it for a week to months. If calcium acetate is used, then specimens can remain in the fixative for years. For long term storage transfer specimens to 80% ethanol.

4.1.2 *Formol - cobalt - calcium fixative (modified Tyler's fixative)*

Add 0.2 gm cobaltous chloride or cobaltous nitrate to 100 ml of formal calcium fixative. This fixative is quite satisfactory and gives good colour retention, particularly for lipid-based pigments.

4.1.3 *Formol - cobalt - calcium - propylene glycol - propylene phenoxetol fixative (Tyler-Steedman fixative).*

To 95 ml of Tyler's fixative, add 0.5 ml of propylene phenoxetol and 4.5 ml propylene glycol (dissolve the phenoxetol in the glycol first). Specimens can remain in this fixative indefinitely.

4.1.4 *Ethanol - 80% special methylated spirits alcohol (museum alcohol)*

This traditional fixative is adequate provided that the specimen to fixative ratio is at least 1:20. Hot alcohol is better than cold reagent, as there is then an element of protein heat coagulation and rapid fixation. The disadvantage of alcohol is that colours and patterns may be lost. Great care should be taken when heating alcohol. Heat a container of alcohol in very hot water well away from naked flames and ignition sources.

4.2 MICROANATOMICAL FIXATIVES.

Traditional fixatives such as Bouin's picro-acetic formaldehyde, Zenker's fixative, and Heidenhain's SUSA may be used. However careful notes must be made of the colour and stripe pattern. Period in fixative should not exceed 12 hours (or less). These fixatives are unsatisfactory for large (> 30mm long) species. Zinc chloride can be substituted for mercuric chloride in the Zenker and SUSA fixatives. Specimens fixed in 80% ethanol or formaldehyde-based fixative can be secondarily fixed for up to 6 hours in one of these microanatomical fixatives. Fixative formulae are provided in Romeis (1968), Drury & Wallington (1980), and Lillie & Fullmer (1976), and post fixation procedures by Winsor (1994).

4.3 EMERGENCY PRESERVATIVES

Any of the following substances can be used if properly formulated fixatives are unavailable: rubbing alcohol (60% isopropyl alcohol) used full strength, uncoloured methylated spirits diluted 9 parts methylated spirits + 1 part tap water, strong alcoholic beverage e.g. brandy, whisky; aftershave or cologne may also be used in an emergency to preserve the specimen, nail hardener solution - check the label to see that it contains formaldehyde and use full strength. Specimens fixed in these substances should be transferred to a histological fixative as soon as possible.

4.4 FIXATION METHODS FOR TERRESTRIAL FLATWORMS

4.4.1 Basic rapid preservation method:

Flatworms can be preserved by simply dropping them into at least 10 - 20 times their volume of fixative solution. The specimen should be fully immersed. This method is satisfactory for identification of flatworms by their external features. Flatworms fixed in this manner are frequently contorted and this fixation method is not ideal for specimens intended for anatomical investigations.

4.4.2 Anaesthesia and fixation of small (30 - 40mm long) and long thin (1 - 2mm thick) species:

1. In a clean container of 10% ethanol (1 part 100% ethanol + 9 parts tap water) allow the flatworm to fully extend and crawl about.

2. Mucus and adherent soil will be shed from the worm. Clear debris from around the worm - a fine brush is useful for this. Leave the specimen in the ethanol to narcotise.

3. Whilst the worm is being narcotised, prepare the specimen label. Also prepare a piece of label or blank filing card cut to fit the specimen vial.

4. The vial should be large enough to contain 10 - 25 ml or more of fixative, and be long enough to accommodate the extended specimen.

5. When the worm is insensitive to touch (up to 5 minutes for small thin worms, longer for larger thicker species), using forceps carefully remove the worm from the solution and place on a wet facial tissue, wet sponge or wet finger - great care is necessary as the specimen will be very sticky.

6. With fine forceps or a damp twist of facial tissue carefully remove any remaining adherent soil and mucus from the specimen. If you experience any difficulties with this procedure, immediately cease and fix the specimen as is.
7. Using moistened forceps lay the flatworm belly-down and straight on the label reverse or file card. If two specimens are available, place one specimen belly uppermost, the other belly down on the card.
8. Place the specimen mounted on the card or label in a vial full of fixative - the specimen should be fully immersed, and the fixative volume should be at least 10 - 20 times that of the specimens.
9. If possible keep different species of flatworms in separate vials.
10. Ensure that labels are inside the vial together with the specimen.

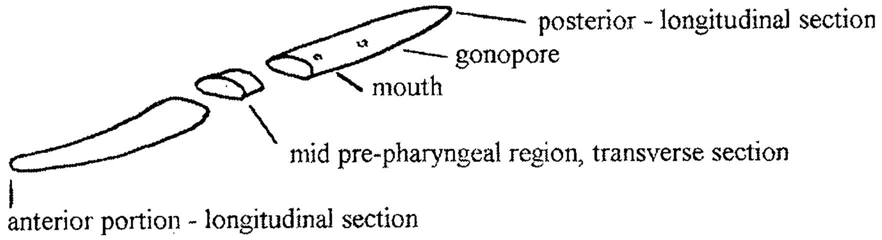
4.4.3 Hot fixative method for large, thick, long and robust specimens:

1. In a clean container of water allow the flatworm to fully extend and crawl about..
2. Mucus and adherent soil will be shed from the worm.
3. Carefully drain the water and soil from the container.
4. When the worm is fully extended and straight, rapidly flood with very hot (80+ degrees centigrade) or preferably boiling water or best - hot fixative.
5. Immediately carefully pour off the hot water and pour fixative carefully over the specimen. The flatworm should be fully immersed.
6. Leave the flatworm in the fixative for about 30 minutes before moving - until the preservative has had time to act the specimen will be extremely delicate. Cover the container so that fixative will not evaporate.
7. Specimens can safely be left in formaldehyde-based fixatives for weeks to months.
8. If it necessary to divide a specimen so it will fit within the container, cut it about 10mm in front of the mouth.

Appendix 5

Histological procedures for Terricola - Tissue processing

1. Subdivision of specimens



2. Representative tissue processing schedules

Schedule for manual processing

Processing solution	**2 mm thick**	**3-4 mm thick specimen**
70% ethanol	hold	hold
90% ethanol	½ hour	1 hour
ethanol 100%	½ hour	1 hour
ethanol 100%	½ hour	1 hour
ethanol 100%	½ hour	1 hour
methyl salicylate*[1]		overnight
toluene	½ hour	
toluene	½ hour	½ hour
paraffin wax mp 56°C	½ hour	1 hour
paraffin wax mp 56°C	½ hour	1 hour
paraffin wax mp 56°C	½ hour	1 hour
paraffin wax mp 56°C	½ hour	
@ 25 mm Hg vacuum	½ hour	½ hour
embed		

Schedule for overnight processing on a Shandon Duplex automatic tissue processor

70% ethanol		hold
90% ethanol		1 hour
ethanol 100%*[2]	1 hour	
ethanol 100%		1 hour
ethanol 100% - chloroform 1:1	1 hour	
toluene or chloroform *[3]		1 hour
toluene or chloroform		1 hour
paraffin wax mp 56°C *[4]		1 hour
paraffin wax mp 56°C		1 hour
paraffin wax mp 56°C		1 hour
paraffin wax mp 56°C @ 25 mm Hg vacuum*[5]	½ hour	
embed in paraffin wax*[6]		

Notes:

1. Methyl benzoate or methyl salicylate; for muscular species or old museum specimens, at this step process through a series of 0.25%, 0.5% and 1% low viscosity nitrocellulose in methyl benzoate or salicylate, ½ - 2 hour in each. An alternative strategy for muscular species is to precede this step by passing tissues through 90% ethanol, 5% phenol in 100% isopropanol (x 2 changes), then continue through the LVN-salicylate series. Absolute dehydration is avoided and the phenol keeps tissues relatively soft. For further information on processing tissues, refer to Winsor (1994).

2. high grade absolute ethanol; F3 grade ethanol is quite satisfactory.

3. antemedia: toluene was mostly used; chloroform for muscular species.

4. Plastic-polymer paraffin waxes, melting point 56°C: Paraplast, Tissue Prep or Pangalark wax.

5. Tissues placed under vacuum to improve wax infiltration.

6. Tissues embedded using a Shandon Histocentre, and Tissue-Tek moulds and cassettes, metal embedding boats, or Dimmock embedding irons and wooden object holders (thick blocks).

7. Duration at each step will depend upon the thickness and porosity of the tissue blocks. Care must be taken not to overprocess small specimens.

2. Clearing techniques for examination of eyes and internal structures

Eye pattern and internal structures of terrestrial flatworms were best observed with the aid of a stereo microscope on cleared specimens before processing the specimen to paraffin wax. The flatworms were dehydrated in increasing strengths of alcohol then transferred to a clearing agent (clearant) with a high refractive index (R.I). Of the reagents available, Terpineol (R.I. 1.48) is the most safe and pleasant to use. Specimens can be transferred to it from 80-90% ethanol, thus preventing excessive tissue hardening in absolute ethanol. Other excellent clearants include methyl benzoate (R.I. 1.52), methyl salicylate (R.I. 1.54), cedarwood oil (R.I. 1.50); all have strong odours and should be used in a fume cupboard.

Some of these reagents have a higher viscosity than alcohol and delicate specimens may collapse is transferred directly from alcohol to clearant (Winsor 1994). Transfer to the full strength clearant is best accomplished in a series of steps with ethanol:clearant 3:1, 1:1, 1:3, then pure clearant. Three or more changes of wax may be required to remove traces of clearant from the tissue. First transfer the specimen from clearant to wax in a series of steps as previously indicated (3:1, 1:1, 1:3, pure wax). A more effective method is to remove the clearant by one or two half hour changes of an antemedium such as toluene, chloroform, xylene or xylene substitute before proceeding to paraffin wax.

Appendix 6

Microtomy

Microtomy is best learned from one experienced in the art rather than from written instructions. For this reason, and because of the variety of microtomes and procedures, detailed instructions for microtomy are difficult to codify. The following overview encompass the main elements of sectioning cassette embedded blocks using a rotary microtome, and section flotation and mounting using the waterbath method.

When staining methods that use heat e.g. AZAN polychrome method, or alkaline solutions e.g. silver stains, a section adhesive should be used as sections are prone to detach during staining. Suitable adhesives include Mayer's glycerine-albumen, poly-l-lysine and aminoalkyl silane.

Mayer's egg albumen

egg albumen	100 ml (approximately 30 ml white from a middle sized egg),
glycerine	100 ml
sodium salicylate or thymol crystals	2 gm

Mix. Shake well. Allow to stand in closed vessel several hours. Filter thorough course cheese cloth if necessary. Store in a refrigerator. Very stable under these conditions.

Equipment required

- blocks of paraffin wax embedded tissue
- rotary microtome (Leitz, Jung)
- microtome knife, or disposable microtome blade and holder
- plain glass or frosted ended microslides, grease-free, previously cleaned with ethanol
- camel hair brush #3
- pair of 10 cm straight fine forceps
- etcher or HB pencil
- squeeze bottle of 10% ethanol
- glycerine-albumen
- water bath
- slide rack

All equipment must be clean and wax-free

Overview

Using one end of a microtome knife the wax blocks were faced (trimmed) on the microtome to almost expose the tissue. Using a safety razor blade the upper and lower margins of the block were cut so as to be parallel with the edge of the knife; the sides of the block were cut so as to give the block face a very slight pyramidal shape. These steps were taken so that straight ribbons would form (parallel faces), with each section clearly distinguished from another (sides off square, slightly pyramidal). The blocks were cooled in ice water, then serially sectioned with a fresh area of the knife at 8μm (thicker or less, depending upon requirements) to obtain a continuous ribbon of sections. These ribbons were "wound" onto a long-haired artists brush or small paint brush, then unwound back onto black corduroy (within a wooden lidded tray) with the last sections at the back, the earliest sections nearest the front. Using a scalpel, the ribbons were divided into groups of sections. These were then placed shiny-side down on dilute ethanol or distilled water, on serially labelled microslides. The sections were then floated on a water bath to allow them to expand and to facilitate transfer to the microslides. Slides with attached sections were placed in a stainless steel rack and were dried at 60° C overnight after which the sections were stained. Good accounts of serial sectioning technique are provided by Steedman (1960) and Cooper (1988).

Appendix 7

Histochemical staining methods for Terricola

Dyes may have a number of synonyms. In order to obtain comparable results obtained using the following staining methods, it is essential that dyes used have the same Colour Index numbers (C.I. numbers) as those cited here. Information on biological dyes is provided in *H.J. Conn's Biological Stains* (Lillie, 1997). Wherever possible use *Certified, Certistain* or other standardised dyes for histochemical purposes. In histological methods, the weight or concentration of dyes specified in staining solutions refers to the whole dye sample i.e. as it comes out of the bottle - the powdered "dye" (actually pigment + filler) is considered to be "100 % dye". Thus a 1 % dye solution 1 gram of powdered dye dissolved in 100 millilitre of water.

Sections may lift from slides during staining with hot reagent. For this reason it is strongly recommended that sections to be stained using the following methods are mounted on slides treated with Mayer's egg albumen or similar section adhesive.

Fixative, fixation, section thickness, and pH of the tapwater may influence the fidelity of staining. Effects of the former two can be compensated for by the use of pre-staining mordants. The following techniques work well for sections up to 8µm. Reduced staining times may be necessary for thicker sections; section thickness should not exceed 10µm as details may otherwise be obscured. Alkaline tap water may affect stain retention; if in doubt, use distilled water rinses.

7.1 Mayer's Haemalum and Young's Eosin-Erythrosin (Winsor, 1984)

Reagents:

Mayer's Haemalum

haematoxylin (C.I.75290)	0.1 g
sodium iodate	0.02 g
ammonium aluminium sulphate*	5 g
citric acid	0.1 g
chloral hydrate	5 g
distilled water to	100 ml

Dissolve the ammonium aluminium sulphate (*"alum"; potassium aluminium sulphate may also be used) in the distilled water. Dissolve the haematoxylin an a few mls of absolute ethanol, then add to the alum solution. Add and dissolve the chloral hydrate, citric acid and sodium iodate and bring to the boil. Continue boiling for five minutes. Cool, filter, and store in the fridge. The solution is ready for immediate use.

Scott's Tapwater Substitute

sodium hydrogen carbonate	0.35g
magnesium sulphate	2 g
distilled water	100 ml

Dissolve the salts in the water. Add a crystal of thymol to prevent mould. When in use containers should be tightly sealed to prevent absorption of carbon dioxide and minimise formation of a magnesium carbonate precipitate, the crystals of which can contaminate tissue sections.

Young's Eosin-Erythrosin Stain

eosin Y (Cl 45380)	0.75 g
erythrosin B (Cl 45430)	0.25 g
calcium chloride dihydrate	0.25 g
distilled water	100 ml

Dissolve the dyes and the calcium chloride separately in the water, then combine. Filter the solution and add a crystal of thymol to prevent mould. If a precipitate forms on storage, filter before use.

Method

1. Dewax and take sections to water.
2. Stain in Mayer's haemalum for 5 minutes. The nuclei stain red. The haematoxylin is used progressively, i.e. staining continued so the nuclei are stained to the desired intensity, but not the cytoplasm.
3. Rinse sections in running tap water.
4. Immerse in Scott's tapwater substitute for 2 minutes. The nuclei are "blued" - the amphoteric aluminium-haematein complex is converted to blue-black colour in this alkaline solution so as to contrast with the red counterstain.
5. Rinse sections in running tap water.
6. Examine sections microscopically to check nuclei have stained and are blue.

This is an important step; haematoxylin solutions oxidise over time and loose their staining capability, thus the nuclei may not be properly stained. Alternatively prolonged storage of tissues in an acidic fixative may have resulted in loss of chromatin; "pink disease" artefact (see Dury & Wallington, 1980).

7. Stain sections with Young's eosin-erythrosin for 2 minutes. This stains cytoplasmic structures shades of red and pink.
8. Differentiate the stain by rapidly rinsing sections in running tap water, then rapidly and thoroughly dehydrating through an ascending series of alcohols (70%; 90%, 100% x3 baths). Differentiation is controlled de-staining. The stain is removed by the water and alcohol, prolonged treatment with which will remove all the stain from the section.
9. Clear in xylene (x3 baths), and mount in D.P.X. or similar synthetic mountant.

Results

nuclei	blue to blue black
basiphil (cyanophil) secretions	blue-purple
rhabdoids	blue-purple
cytoplasm	shades of pink
muscle fibres	deep pink
acidophil (erythrophil) secretions	red
collagen fibres	pale pink

Mechanism

Haematoxylin and eosin staining are examples of charge-based affinity reactions. The positively charged haematoxylin (a metal coordination compound) has a high affinity for those tissue structures having a negative charge (anionic) e.g. nucleic acids, carboxylated and sulphated mucosubstances; but a low affinity for positively charged (cationic) substances. The opposite holds for the negatively charged acid dyes in the eosin and erythrosin dyes which have a high affinity for positively charged tissue components e.g. proteins under acid conditions - cytoplasm.

7.2 M.S.B. (Martius, Scarlet, Blue) polychrome method

(after Lendrum *et al* 1962 in Drury & Wallington, 1980)

Reagents:

Acid dichromate mordant

potassium dichromate	2.5 g
acetic acid, glacial	5 ml
distilled water to	100 ml

Add the acetic acid to the water and mix, then dissolve the potassium dichromate. Best made and used fresh. Discard when the solution darkens appreciably.

Celestine blue stain

Celestine blue B (C.I. 51050)	0.5 g
ferric ammonium sulphate	5 g
glycerol	14 ml
sulphuric acid, concentrated	0.5 ml
distilled water to	100 ml

Dissolve the iron alum in the water without heat. Add the celestine blue and boil for three minutes. Filter when cool and add the glycerol and sulphuric acid. The stain should keep for at least six months.

Mayer's Haemalum (formula previously provided)

Acid alcohol

hydrochloric acid, concentrated	0.25 ml
ethanol, 70% to	100 ml

Martius Yellow

Martius Yellow (C.I. 10315)	0.25 gm
ethanol, 95% to	100 ml
dodeca tungstophosphoric acid	2 gm

Using a hotplate stirrer, heat (but not to boiling) the ethanol and dissolve the phosphotungstic acid, then add and dissolve the Martius Yellow. The dye may take some time to dissolve as the solution is close to saturation. Cool and filter. The lower concentration of the dye (recommended by Pasey & Edwards 1978) given here is half that of the original method. Variations in the ease of solubility of this dye can be probably attributed to the different solubilities of the two different salts of the dye: sodium salt solubility in alcohol 0.16%, and calcium salt 1.90% in alcohol. The identity of the salt is rarely indicated by manufacturers.

Brilliant Crystal Scarlet

Brilliant Crystal Scarlet 2R (C.I.16250)*	
acetic acid, glacial	2.5 ml
distilled water to	100 ml

Add the acetic acid to the water. Mix. Dissolve the Brilliant Crystal Scarlet in the diluted acetic acid. Filter. The solution is stable at room temperature.
*Synonym: Crystal Ponceau 6R, available through SIGMA chemicals.

Soluble Blue

Soluble Blue (C.I. 42755)*	0.5 gm
acetic acid, glacial	1 ml
distilled water to	100 ml

Add the acetic acid to the water. Mix. Dissolve the Soluble blue in the diluted acetic acid. Filter. The solution is stable at room temperature.
*Synonym: Aniline Blue WS. Methyl Blue (C.I. 42780) may be substituted for the Soluble Blue.

1% phosphotungstic acid

dodeca tungstophosphoric acid	1 gm
distilled water to	100 ml

Dissolve the tungstophosphoric acid in water. The solution is stable and keeps indefinitely at room temperature.

2% acetic acid

acetic acid, glacial	2 ml
distilled water to	100 ml

Add the acid to the water. Mix. The solution is stable and keeps indefinitely at room temperature.

Method

1. Dewax and take sections to water.
2. Immerse in the pre-warmed acid dichromate mordant at 60°C for 30 minutes.
3. Wash in running water for 5 minutes.
4. Stain in celestine blue for five minutes.
5. Rinse in water.
6. Stain in Mayer's haematoxylin for five minutes.
7. Wash sections well in running tap water.
8. If there is background staining present, differentiate in acid alcohol solution.
9. Wash sections well in running tap water.
10. Rinse in 95% ethanol, and stain in Martius Yellow for 2 minutes.
11. Rinse sections in distilled water to remove excess Martius Yellow stain.
12. Stain in Brilliant Crystal Scarlet stain for 10 minutes.
13. Rinse sections in distilled water to remove excess stain.
14. Immerse sections in 1% phosphotungstic acid to fix and differentiate the red stain, for up to 5 minutes.
15. Rinse sections in distilled water.
16. Stain in Soluble Blue stain for 2½ - 5 minutes* (check staining after 2½ minutes).
17. Rinse sections in 2% acetic acid to remove excess dye (I find it best to have 2-3 baths of the acetic acid and swiftly dip the slides 10 times in each bath before passing to the dehydrating alcohols).
18. Dehydrate in an ascending ethanol series (70%; 90%, 100% x3 baths), clear in xylene (x3 baths), and mount in D.P.X. or similar synthetic mountant.

Results

Nuclei	black
Muscle	red - orange-red
Acidophil (= erythrophil, erythrophilous) granules	red
Xanthophil (= xanthophilous) granules	yellow
Nerves	pale violet
Collagen, reticulum, basement membrane, duct walls	deep blue
Basiphil (= cyanophil, cyanophilous) granules	deep blue
Mucin	blue - pale blue
Rhabdoids	black

Comments

Original method stated 10 minutes - this was found to be generally too long for Terricola. Collagen fibres and walls of secretory ducts, especially protonephridial ducts, are delicately demonstrated by this method.

Mechanism

Polyacid polychrome methods are all rate-controlled (Baker, 1958; Horobin, 1988) in which the crucial factor is the ease of dye diffusion through tissue components: dye size and tissue permeability. Thus timing of each step in the technique is crucial as too long in a particular reagent or dye may cause displacement of other dyes from tissues resulting in a monochromic section. Phosphotungstic acid acts as a colourless dye (Baker, 1958) selectively differentiating or blocking staining of collagen fibres. An alternative view of polychrome staining is that dye selectivity is based upon affinity reactions (Lillie, 1977) e.g. affinity of Martius yellow and related dyes for arginine.

7.3 Heidenhain's AZAN Trichrome

(after Heidenhain, 1916 in Culling,1974).

Reagents:

Acid dichromate mordant

potassium dichromate	2.5 g
acetic acid, glacial	5 ml
distilled water to	100 ml

Add the acetic acid to the water and mix, then dissolve the potassium dichromate. Best made and used fresh. Discard when the solution darkens appreciably.

Azocarmine stain

Azocarmine GX (C.I.50085)	0.1 g
acetic acid (glacial)	1 ml
distilled water to	100 ml

Mix the Azocarmine dye in the distilled water; bring to the boil; cool. When cool filter and add the acetic acid. Azocarmine GX was found to be superior to the more water soluble Azocarmine B which eluted from sections too rapidly during differentiation.

5% phosphotungstic acid

dodeca tungstophosphoric acid	5 gm

distilled water to	100 ml

Dissolve the tungstophosphoric acid in water. The solution is stable at room temperature.

Aniline Blue- Orange G stain

Aniline Blue (C.I. 42755)	0.5 g
Orange G (C.I.16230)	2 g
acetic acid (glacial)	8 ml
distilled water to	100 ml

Using a hotplate-stirrer separately dissolve each dye in warmed distilled water, combine and mix, then add the acetic acid. Filter before use. Use full strength. Stable at room temperature.

Method

1. Dewax and take sections to water.
2. Immerse in the pre-warmed acid dichromate mordant at 60°C for 30 minutes.
3. Wash in running water for 5 minutes.
4. Stain in prewarmed Azocarmine stain at 60°C for 30 minutes (sections may lift off; 15 minutes at 40 °C is generally satisfactory).
5. Wash in gently running tapwater until only the nuclei and erythrophil secretions are red and background is a pale pink. Sections should be under-differentiated as dye continues to elute in the next step. This step may take 1 - 5 minutes or longer.
6. Mordant in 5% phosphotungstic acid for 30 minutes.
7. Rinse sections in running water.
8. Stain in the full strength Aniline Blue-Orange G stain for 30 minutes.
9. Wash quickly in running water.
10. Dehydrate in an ascending ethanol series (70%; 90%, 100%x3 baths), clear in xylene(x3 baths), and mount in D.P.X. or similar synthetic mountant.

Results

Nuclei	red
Muscle	red - orange-red
Acidophil (= erythrophil, erythrophilous) granules	red
Xanthophil (= xanthophilous) granules	orange
Nerves	violet
Collagen, reticulum, basement membrane	deep blue
Basiphil (= cyanophil, cyanophilous) granules	deep blue
Mucin	blue - pale blue
Rhabdoids	red

Comment

Culling (1974) provides long (> 8 hours) and short (2 hours) variants of the AZAN technique. In the foregoing variant (2¼ hours), equal periods in the mordant, Azocarmine, phosphotungstic acid, and Aniline Blue - Orange G stain give consistent results, to the point where the technique is largely progressively staining and "automatic" requiring little microscopical control of differentiation. By controlling staining in Azocarmine, differentiation is readily accomplished in tap water instead of toxic alcoholic aniline solution. The Aniline Blue - Orange G stain is used full strength to provide optimal staining of secretions. Gabe (1976) provides the most detailed and useful account of this staining method.

Mechanism

Rate-controlled and affinity-based, as previously discussed for the MSB stain.

Appendix 8: Descriptions of selected genera and species.

Family: Geoplanidae

Subfamily: Anzoplaninae sub.fam.nov.

Subfamily: Caenoplaninae

A8.1 Genus *Anzoplana* gen. nov.

Anzoplana gen. nov

Diagnosis: Anzoplaninae with small, robust body, lanceolate, broader posteriorly than anteriorly, sub cylindrical in cross section. Mouth situated just behind mid body, gonopore closer to mouth than to posterior end. Eyes in single row around anterior tip, clustered for some distance laterally in uneven rows for anterior body quarter, then sparsely in single staggered submarginal row to posterior. Creeping sole 60% of body width. Cutaneous musculature tripartite, with circular, helical muscles, with cutaneous longitudinal muscles in well-defined bundles; ventral cutaneous musculature slightly thicker than that dorsally, CMI 9.4-10.6%. Parenchymal longitudinal muscles not clearly aggregated into bundles, present in well developed subneural plate PMI 9%, with isolated fibres in weak ring zone. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, longitudinal, then mixed longitudinal and circular muscles; outer musculature with epithelium, longitudinal, circular, then mixed longitudinal and circular muscles sparse ectally, slightly stronger entally. Testes dorso-ventral, extend almost entire length of body. Efferent ducts ventral. Penis eversible, without papilla. Ovaries in anterior body third. With lateral bursae. With resorptive vesicles surrounding ovovitelline ducts. Ovovitelline ducts separately enter female genital duct; genital duct enters female antrum posterioventrally. Adenodactyls and adenomuralia present. Type species of genus: *Anzoplana trilineata* sp. nov

Etymology: *Anzoplana* is contrived from the traditional abbreviation ANZ for Australia and New Zealand and the Latin *plana* flat. Gender feminine. The planarian of Australia and New Zealand.

Distribution: Bombala, NSW; Nimmitabel, NSW; Girraween, SEQld; Dalmorton, NSW; Research, Vic (introduction); Berridale, NSW; Cootralantra Creek north of Berridale, NSW; Nr Tatangara dam, between Adaminaby and Kiandra, NSW; Mt Wilson, NSW (? introduction); Armidale, NSW.

Systematic discussion: *Anzoplana* is chiefly differentiated from other adenodactylate anzoplaninids by the presence of the ovary between anterior tip and the pharyngeal root, eversible penis, resorptive bursae either side of the pharynx, resorptive vesicles surrounding the ovovitelline duct, and both adenomuralia and adenodactyls present.

Anzoplana trilineata sp. nov

Artioposthia sp. Min Min *et al*, 1992

Material examined:

Holotype: LW 1755. Collected in Armidale, NSW by Klaus Rohde, 3 April – 27 May 1991, sectioned at 8µm, a series of 45 slides stained with MSB: anterior LSS, pre-pharyngeal TS, and posterior LSS together.

Paratype: LW 1724. Uralla, NSW sectioned at 8µm, a series of 43 slides stained with Steedman's Triple stain, pre-pharyngeal TS and posterior LSS together, immature.

Other material examined: LW678 Bombala, NSW; LW692 Nimmitabel, NSW; LW820 Girraween, SEQld; LW1318 Dalmorton, NSW; LW1533, LW 1736 Research, Vic (introduction); LW1555 Berridale, NSW; LW1556 Cootralantra Creek north of Berridale, NSW; LW1558 Nr Tatangara dam, between Adaminaby and Kiandra, NSW; LW1578 Mt Wilson, NSW (? introduction); LW1677, LW1683, LW1756 Armidale, NSW.

EXTERNAL FEATURES:

An anzoplaninid with small, robust body, lanceolate in shape, broader posteriorly than anteriorly, sub cylindrical in cross section (Fig. 8.1-1a). Mouth situated just behind mid body, gonopore closer to mouth than to posterior end. Creeping sole almost two thirds body width (61.5%). Dorsal ground colour light brown – cream, with three dark dorsal median stripes of equal width: median stripe, dark brown –

black, separated from lateral stripes by an interval (about twice width of median stripe) of ground colour with light brown mottling. Lateral stripes are lighter brown than median stripe, composed of dense mottled pigment. Longitudinal stripes pass into brown pigment of anterior end; join posteriorly. Pale ground colour extends marginally – submarginally from just behind head around entire body. Ventral surface whitish.

In common with many terricolan taxa, the median stripe is generally the most persistent of the dorsal markings. The lateral stripes may be as dark as, or lighter than the median stripe, and may be the same width or narrower than the median stripe. In some specimens fine pale mottling marginally may extend over the entire ventral surface. Dimensions of material examined are provided in Table 8.1-1.

INTERNAL ANATOMY:

Head:

Adhesive suckers with associated musculature absent. Gut extends almost to tip, overlies ganglion. With multiple eyes (Fig. 8.1-1a,b1-2), close set, in single row skirting anterior tip margin, clustered laterally in 2-3 ill-defined rows in anterior body quarter, then sparse, staggered submarginally in single row to posterior. Eyes pigment-cup 36 – 42μm diameter, with at least seven retinal clubs. Sensorial zone extends around anteroventral margin. Sensory ciliated pits simple invaginations, 14μm diameter, 9μm deep, lined by pale cyanophil ciliated anucleate epithelium

Pre-pharyngeal region:

A schematic representation of the transverse pre-pharyngeal region is provided in Fig. 8.1-1c. Dorsal, ventral epithelium equal height, 17μm thick, nucleate. Sinuous rhammites approximately 25μm long, 1.5μm diameter, derived from rhabditogen cells underlying cutaneous musculature, extend dorsolaterally to outer margins of creeping sole, densest in median, lateral, marginal zones. Epitheliosomes secreted from creeping sole. Erythrophil secretions abundant ventrally, mid-dorsally. Cyanophil secretion abundant dorsolaterally (in this species there appears to be a reversal of the "normal" distribution of cyanophil and erythrophil secretions).

Finely granular yellowish-brown pigment present below basement membrane, between fibres of cutaneous musculature and extending into ectal two-thirds of parenchymal musculature. Pigment abundant dorsolaterally, sparse ventrally. Three dorsal dark stripes characterised by coarse granular aggregations of pigment. Creeping sole flat, 1638μm wide, 61.5% of body width. Body height 1157μm. Body width: height ratio 2.2. Cutaneous musculature tripartite, with circular, helical muscles. Cutaneous longitudinal muscles in distinct bundles, not insunk. Dorsal cutaneous musculature thinner (42 – 50.4μm thick) than ventral musculature (67.2 – 72.8μm thick). CMI = 9.4% - 10.6%. (In LW1724 dorsal cutaneous musculature (33.5μm) about the same thickness as ventral musculature (39μm); CMI 6%). Parenchymal musculature well developed but not strong, parenchymal longitudinal muscles in subneural ventral plate 56μm thick, PMI = 4.8%. Dorsal, supraneural, ventral transverse muscles, dorso-ventral and peri-intestinal muscles present. (In LW1724 parenchymal longitudinal muscle plate 109μm thick, PMI 9%).

Alimentary tract:

Pharynx cylindrical, horizontal, 2124μm long, with dorsal insertion posterior to ventral insertion. Pharyngeal musculature with inner epithelium, longitudinal, then mixed circular - longitudinal muscles; outer epithelium, longitudinal, circular muscles, then mixed longitudinal - circular muscles, sparse ectally, slightly stronger entally. Pharyngeal pouch 2340μm long, 19% body length, lined by cyanophil insunk secretory epithelium, pouch wall with thin longitudinal, then circular muscles. Mouth opens close to the blind end of the pouch.

Reproductive organs:

Copulatory organs complex, with apapillate penis, with paired lateral bursae, with five musculoglandular organs (Fig. 8.1-2a,b), situated immediately behind pharyngeal pouch, within single large muscular bulb. Bulb musculature with weak inner circular, weak outer longitudinal muscles, surrounded by loosely interwoven mixed fine muscle fibres.

Testes mature, 85 - 128μm diameter, follicular, dorsoventral (surround almost entire gut, dorsally, laterally, ventrally to outer upper lateral margin of nerve cords). Testes extend anteriorly to just beyond ovaries, posteriorly almost to hind end. Sperm ductules from testes penetrate outer margin of nerve trunks, communicate with transverse sub-neural collecting ducts. Collecting ducts rise mediad, pass through lateral nerve cords, join vasa deferentia. At level of mouth efferent ducts form spermiducal vesicles lined by vacuolated cuboidal epithelium. Efferent ducts narrow, gently ascend, recurve, separately enter proximal dorsal end of seminal vesicle. Seminal vesicle lined by villiform columnar epithelium, divided into two regions: proximal duct receives coarse-grained erythrophil secretions from glands situated outside penis bulb; distal duct with shallow diverticula, receives erythrophil, fine dark cyanophil secretions. Ejaculatory duct opens into ampulla. Opening surrounded by coarse dark erythrophil granular secretions. Ampulla characterized by intramural pale cyanophil secretions that increase in cyanophilia close to epithelium through which they are secreted into cavity. Ampulla opens into anterodorsal male atrium. Penis papilla absent, penis eversible type (false papilla possibly formed by atrial folds at distal end of cavity). Male atrium largely filled by adenodactyl papillae.

Ovaries situated anteriorly, pear-shaped, 140μm diameter, dorso-ventral axis 356μm long, broader ends of ovaries almost half embedded in lateral nerve cords. Left ovary with distinct ventroposterior lobe lying below ovovitelline duct, extending 160μm caudally. Right ovary without pronounced lobe. Secondary ovary present, 106 μm long, 59μm diameter, partially embedded in nerve cord immediately below opening into ovovitelline, 390μm behind right ovary. Secondary ovary communicates with ovovitelline duct via small oviducal branch from caudal end. Ovovitelline ducts arise from dorsoposterior walls of ovaries. Proximal end of each duct expanded to form tuba, with sphincter muscle at point of contact with ovary. Tuba capacious, lined by highly vacuolate epithelium, contains sperm in process of resorption. Ovovitelline ducts pass ventrally, continue posteriorly along nerve cords to separately enter slightly expanded ventroposterior end of female. Vitellaria situated between gut diverticula, empty through dorsal wall of tuba via short narrow vitelline funnels; funnels greatly expanded, form resorptive vesicles, 40 – 85μm diameter where vitelline funnels communicate with the ovovitelline duct. Resorptive vesicles (Fig.8.1-4) lined by flattened epithelial cells with vacuolate cytoplasm. Some vesicles with sperm, others with very pale cyanophil amorphous material. Vesicles surround ovovitelline duct, extend from just behind ovaries to posteriad extent of copulatory organs at which point vesicles considerably reduced in size.

Spheroidal lateral bursae present, 640μm diameter, located either side of pharynx, communicate directly through dorsal wall of underlying ovovitelline ducts. Bursa with cortical area characterised by fine cavernous stroma of muscle fibres with cells with pale cyanophil vacuolate cytoplasm (phagocytes). Within lumen masses of sperm in intimate contact with lining epithelium; lining tall columnar epithelium with basal nuclei, greyish cytoplasm charged with erythrophil granules (lysocytes).

Glandular duct gently rises at an angle of 30° from its junction with ovovitelline ducts, enters lower rear wall of female antrum. Genital duct lined by columnar epithelium with cyanophil cytoplasm, receives coarse erythrophil ("shell gland" secretions), fine cyanophil secretions from glands in surrounding mesenchyme. Female antrum flask-shaped, with expanded proximal end, elongate narrow distal neck. Antral roof, floor of proximal portion lined by strand cells with basal nuclei with cytoplasm containing pale cyanophil secretion. Fine erythrophil strand-like secretions pass between cells into antrum, epithelium continues along ventral half of narrow distal neck of atrium almost to gonopore. Dorsal half of narrow portion of the female antrum lined by globule cells, between which pass beaded (droplet-like) erythrophil secretions. This epithelium continues in more flattened form into male antrum.

Copulatory organs with eight musculoglandular organs: with three adenodactyls (Type VI), with distinct proximal reservoirs, strongly muscularised ducts, long papillae projecting into male atrium. With five adenomuralia (Type VI), ducts lying wholly within atrial wall, with little or no papilla projecting into antrum. Secretions in adenodactyl reservoirs differ from those in adenomuralia (Table 8.1-2).

Pathology:

Ciliophoran, 12.6μm diameter, present in mesenchyme immediately underlying sensory pits within sensory margin of the anterior tip (Holotype).

Etymology:

The specific epithet *trilineata* alludes to the three dark dorsal stripes in this species, and is derived from the Latin *tri* three and Latin *linea* – line. Suffix *ata* possession of. Gender feminine.

Systematic discussion:

Anzoplana presently has only one species, *A. trilineata*. Fyfe, in an unpublished manuscript (author's collection), described a new species of *Artioposthia* collected at Brighton, Otago, New Zealand (slides OMNZ 74-29), possibly attributable to *Anzoplana*. It is the same species sent by Fyfe to Eudoxia Froehlich for comparison with Chilean taxa (Froehlich, 1978).

Anzoplana is chiefly differentiated from other adenodactylate anzoplaninids by the presence of the ovary between anterior tip and the pharyngeal root, eversible penis, resorptive bursae either side of the pharynx, resorptive vesicles surrounding the ovovitelline duct, and both adenomuralia and adenodactyls. The presence of adenomuralia and apapillate penis characterize the caenoplaninid *Newzealandia*

Lateral resorptive bursae are unusual and hitherto unrecognised in the Terricola. Those either side of the pharynx *Anzoplana* are similar in histology to the "glandular pockets" in the New Caledonian caenoplaninid *Australopacifica willeyi*. In this species paired bursae arise from the lateral walls of the female atrium immediately adjacent to the female genital canal, rather than from bursal stalks arising from the ovovitelline ducts as in *Anzoplana*. Where sperm and discharged granules are mixed in the lateral bursae of *Anzoplana*, there is breakdown of the sperm, evidenced by tinctorial changes. The presence of amorphous erythrophil and pale cyanophil material suggests extracellular digestion of the sperm and resorption of the digesta by the phagocytes. There is no evidence of intracellular digestion of sperm. The histology of these bursae, suggestive of extra-cellular digestion of excess donor sperm, is similar to that of lateral bursae in two species of the subantarctic maricolan bdellourid *Synsiphonium* described by Sluys (1988).

Table 8.1-1 *Anzoplana trilineata*: Dimensions of specimens examined.

Specimen m.m.	Length m.m	Width m.m	Mouth m.m	Mouth %	Gonopore m.m.	Gonopore %	Mouth-Gonopore	Mouth-
LW 1755	12.5	2.6	6.7	53.6	8.5	50.5	1.8	14.4
LW 1724a	31.0	3.6	19.0	61.3	23.0	74.2	4.0	12.9

Table 8.1-2. *Anzoplana trilineata.* Musculoglandular organs

Musculo glandular organ	Type	Adenodactyl or adenomuralum	Direction papilla faces	Proximal secretion: reservoir	Distal secretion: duct
Amf	VI	adenomuralum	Ventral	Erythrophil granules in globules + fine cyanophil granules	Fine erythrophil granules
Adm 1 left	VI	adenodactyl	Postero ventral		
Adm 2 right	VI	adenodactyl	Postero ventral		
Adm 3 transverse	VI	adenodactyl	Right		
Amm1	VI	adenomuralum	Right	Coarse erythrophil granules; neutrophil granules; cyanophil strands	Fine erythrophil granules
Amm2	VI	adenomuralum	Anterior		
Amm3	VI	adenomuralum	Anterior		
Amm4	VI	adenomuralum	Left		

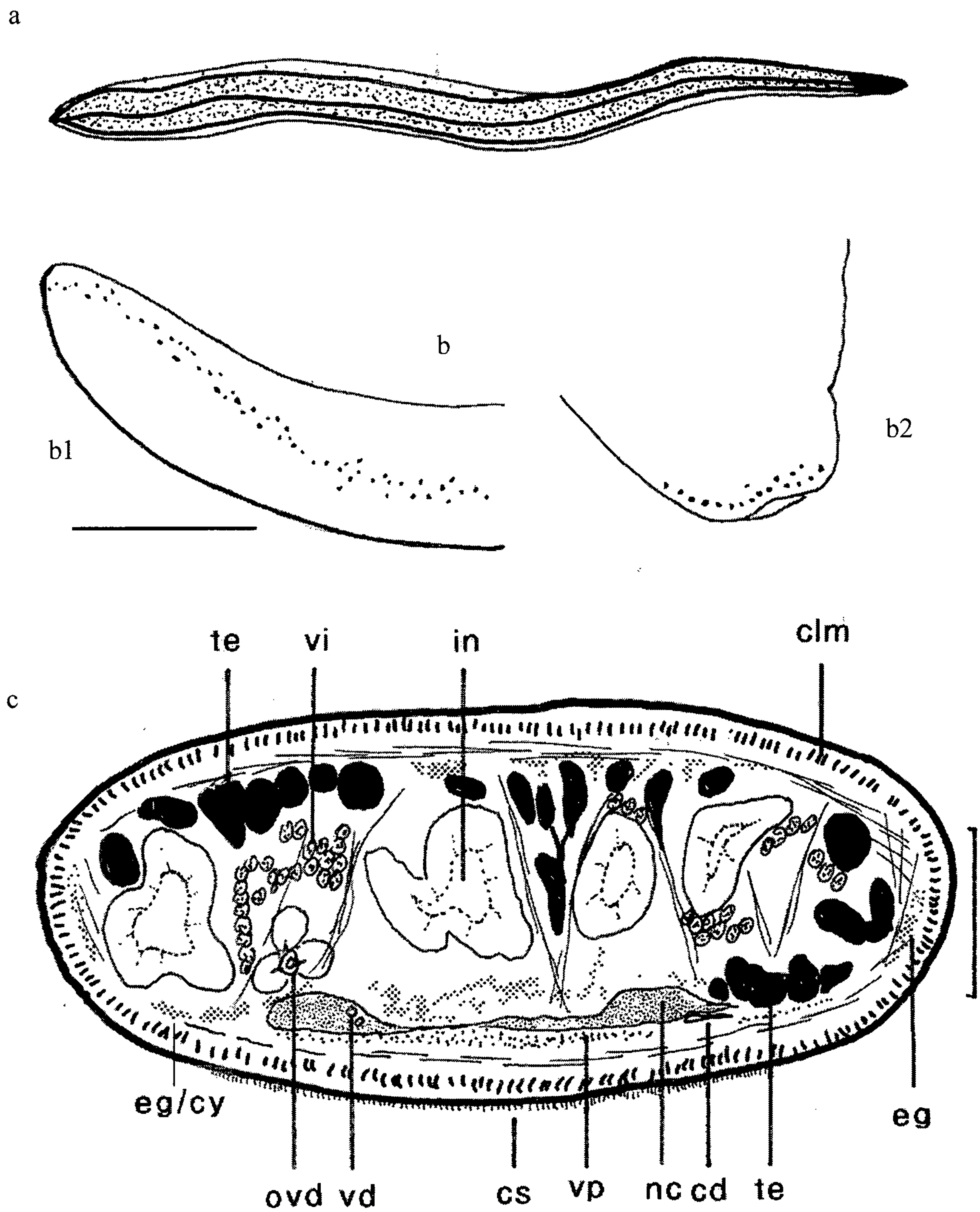


Figure 8.1-1 *Anzoplana trilineata*:

a. Whole specimen, dorsal view x5.
b. Anterior tip showing anterolateral (a) and anterior (b) distribution of eyes. Scale bar 1 mm.
c. Pre-pharyngeal region showing principal structures. Scale bar 500μm

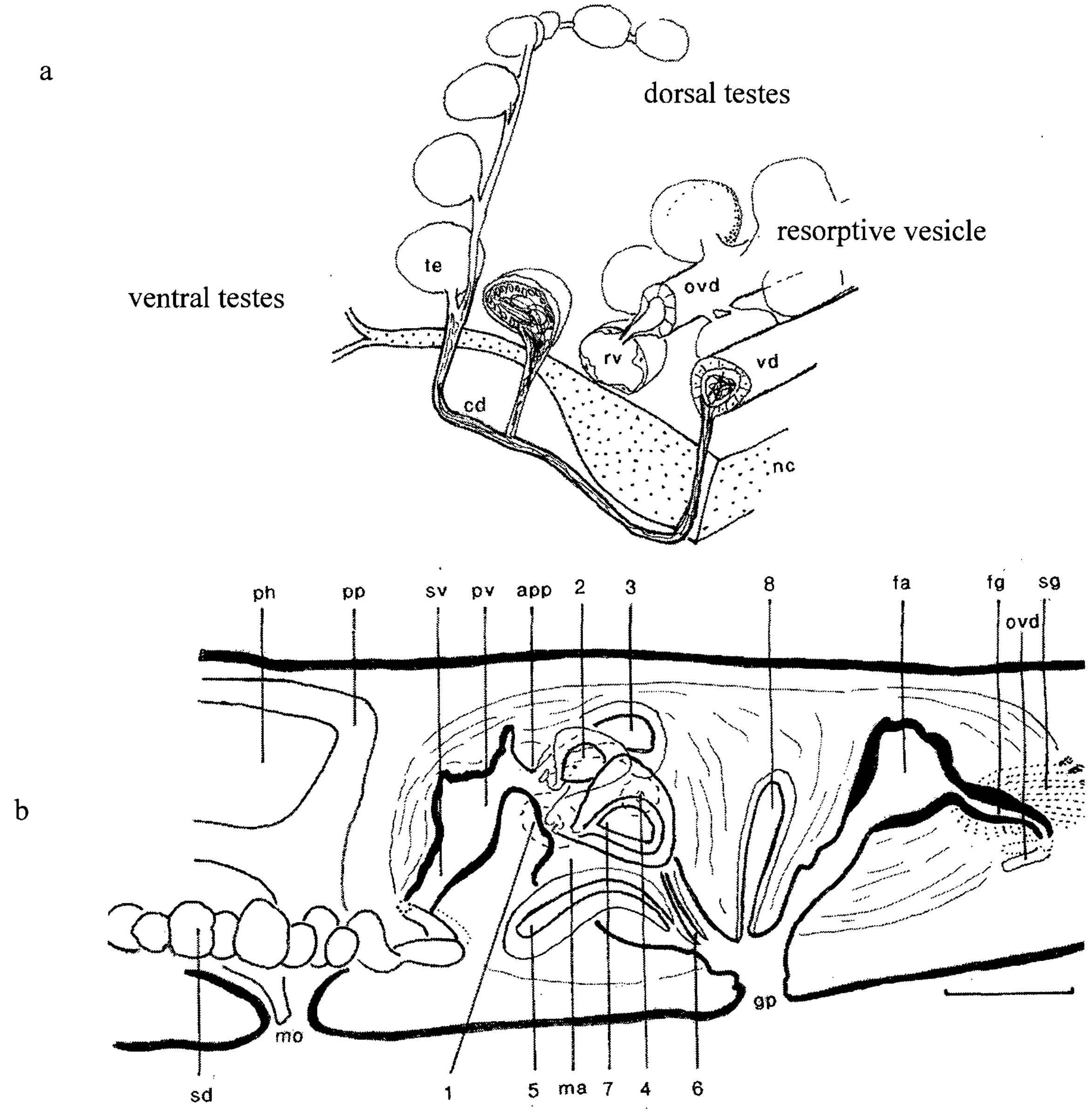


Figure 8.1-2 *Anzoplana trilineata*

a. Schematic representation of the efferent ducts passing from the dorsoventral testes to the collecting duct and vas deferens, and the ovovitelline duct with its resorptive vesicles.

b. Diagram of the copulatory organs. Numbers 1-4 are coplanar adenomuralia radially arranged (left, right, and two in an intermediate position either side of the midline facing anteriorly) in the horizontal plane, emptying into the proximal male antrum. Numbers 5-7 are adenodactyls emptying into the distal male antrum. Number 8 is an adenomuralium emptying into the common antrum. Scale bar 500μm

A8.2 Genus *Fyfea* gen. nov.

Fyfea gen.nov.

Artioposthia (part), Fyfe, 1956; Ogren & Kawakatsu 1991

Diagnosis: Anzoplaninae with small, elongate body, with mouth just behind mid body, gonopore closer to mouth than posterior end. Creeping sole more than 70% of body width. Anterior adhesive cup, sucker absent. Sensory papillae absent. Eyes ?lens-type, in single row around anterior tip, in two to three rows antero-laterally, then in staggered single row to posterior. Cutaneous musculature tripartite; circular, helical muscles, with longitudinal muscles in bundles, stronger ventrally than dorsally. CMI 22%. Parenchymal musculature with mixed longitudinal-transverse muscles in small bundles in sub-neural plate, PMI 10.8%; with strong bundles of supraneural longitudinal muscles, small bundles and single fibres of longitudinal fibres sparsely scattered in ring zone; strong supra- and infra-intestinal transverse muscles regularly spaced along body; with strong dorsoventral muscles. Pharynx cylindrical with oesophagus. Pharyngeal musculature with inner epithelium, strong longitudinal, then mixed circular-longitudinal muscles, then longitudinal muscle layer; outer pharyngeal musculature with thick layer of longitudinal muscles, then evenly spaced circular muscles, then grades into region of mixed circular and longitudinal muscles. Testes dorsoventral, sperm ducts ventral. Testes loculate, extend from midway between anterior tip and root of pharynx, to posterior end. Vasa deferentia with spermiducal vesicles; sperm ducts separately enter dorsal wall of seminal vesicle; with prostatic vesicle; penis inverted-type. Ovaries with parovarian resorptive tissue, situated between mouth and copulatory organs. Ovovitelline ducts separately enter distal end female genital canal; female genital canal enters antrum horizontally via ventro-posterior atrial wall. Vitellaria sparse. Adenodactyl present. Viscid gland absent. Type species: *Fyfea carnleyi* (Fyfe, 1956) comb.nov.

Etymology: *Fyfea* honours Marion Fyfe, 1894-1986, for her pioneering taxonomic anatomical work on the Terricola of New Zealand. Gender feminine.

Distribution: St. Col Peak, elevation 300 metres above sea level, Campbell Island, 169°10'E 52°53', and Ocean Island, Auckland Islands, Subantarctic Islands of New Zealand.

Systematic discussion: *Fyfea* presently has only one species *F. carnleyi.* Within the Anzoplaninae *Fyfea* is close to *Kontikia ashleyi* (Fyfe, 1953) (="Parafyfea" in this thesis) with which it shares the ovary situated between mouth and copulatory organs, and an inverted penis. It is distinguished from "Parafyfea" chiefly by the presence of an adenodactyl, (absent in "Parafyfea"). In Anzoplana the ovaries are situated near the anterior end, and the penis is eversible.

The inverted penis bauplan is found in Plagiostomidae, Monocelididae, some Acoela, and the maricolan taxa *Nexilis epichitonius* and *Centriovarioplana tenuis* (Sluys, 1989). It is uncommon in the Terricola, found only in *Fyfea carnleyi*, *Kontikia ashleyi* (Fyfe, 1953) (="Parafyfea"), in *Australopacifica aucklandica* sensu Fyfe 1953, (? = *Kontikia marrineri* (Dendy, 1901)), all three of which have pharyngeal - post oral ovaries, and eyes which appear to be lens-type – peripheral pigment with inner cyanophil generally featureless mass (though this may be a fixation artefact). Of particular interest are the parallels between the foregoing terricolan taxa from Auckland Islands, and the maricolan *Centriovarioplana tenuis* recorded from the subantarctic South Georgia Islands, at about the same latitude. *Centriovarioplana tenuis* has an inverted penis, ovaries located immediately anterior to the mouth on either side of the gut, and a musculoglandular organ external to the copulatory organs.

Fyfea carnleyi (Fyfe, 1953) comb.nov.

Artioposthia carneyli Fyfe, 1953; Ogren *et al* 1991, 1997
Artioposthia carnleyi Fyfe, 1953 (figures); Johns 1998

Material examined:

Type material: Lectotype: MONZ 102 St. Col Peak, 300 metres asl, Campbell Island, 169°10'E 52°53'S, collected under stones by J. H. Sorensen 28 May 1942. One series of sagittal on nine slides of the posterior half of flatworm, stain unknown.

Paralectotype: MONZ 102 St. Col Peak, 300 metres asl, Campbell Island, 169°10'E 52°53'S, collected under stones by J. H. Sorensen 28 May 1942. One whole flatworm.

Other material examined: MONZ 112 St. Col Peak, 300 metres asl, Campbell Island, 169°10'E 52°53'S, eight specimens collected under stones by J. H. Sorensen 28 May 1942. Specimens (b) 42 slides, and (f) 42 slides, both sectioned at 8?m, and stained by the Steedman's Triple and AZAN methods. MONZ 1384 W.H.D. 116. Ocean Island, Auckland Islands, one specimen collected by W.H. Dawbin 28 February 1943; MONZ 1372b labelled A49, No. 1 station, Auckland Islands, collected by W. H. Dawbin 3 February 1943 under logs. OMNZ A74-51, four slides, and A74-52 three slides, stain unknown (part of Cape Expedition material, but from which of the three localities is unknown). Dimensions of material examined are provided in Table 8.2-1.

Remarks:

In the heading of the original description the spelling of the specific epithet *carneyli* (Fyfe, 1953 p9) is an "incorrect original spelling" under Art. 32.4 (ICZN, 2000) noted by Johns (1993). It is considered here to be a printer's error. The name is correctly spelled *carnleyi* on the same page twice previously to the formal description, and also spelled correctly in the captions to the figures. Further evidence is provided in Fyfe's handwritten index cards (author's collection). Under Art 32.5.1 (ICZN, 2000) this type of spelling error must be corrected.

Fyfe (1953, p10) designated as the Type "One whole specimen and one series of sagittal sections. Nine slides in the Dominion Museum, Wellington. Cat. No. Z.W. 102." Thus the Type comprises two syntypes. The series of nine slides is here designated as the Lectotype, and the whole specimen the Paralectotype. Fyfe stated that ten specimens were collected from St Col; presently there are eight specimens in lot ZW112. MONZ 1372 examined in this study consisted of four species confused in same tube, two specimens (MONZ 1372b) are considered by here to be those collected by Dawbin from under logs in the rata forest, Musgrave Peninsula (Fyfe, 1953, p9). The incomplete slide series of this species in the Otago Museum are possibly the posterior portions of the anterior halves of specimens MONZ 112 f 1-3.

As all specimens examined by Fyfe can be accounted for, it is presumed that the two Syntypes came from the series of specimens collected at St Col peak, Campbell Island. This locality is referred to by Fyfe (1953, p9) as "Colonel Peak, Campbell Island". However no such location exists on Campbell Island. It is assumed that Fyfe considered the original locality information, given as Col Peak, to be an abbreviation for Colonel Peak. The location is St. Col peak (map and illustration in Bailey & Sorensen, 1962, p3; 20; map in Fraser, 1986 p70).

EXTERNAL FEATURES:

Fyfe (1953) described fixed specimens (Fig. 8.2-1) of this small species as having a cream dorsal ground colour with broad dark brown paired lateral stripes, separated by an interval of median ground colour wider than the lateral stripes. External to the dark stripes is an equal width of marginal ground colour. The brown stripes are composed of brown mottling, darker at the edges, which remain as thin brown stripes in bleached specimens. The median cream area may have a few brown specks that in some specimens may be concentrated to form a faint brown line. She noted that in a 11mm long immature specimen the brown stripes were not dark, were uniformly pigmented and showed no marginal differentiation. The ventral ground colour was an unspeckled cream. The eyes are small, in a single row around the anterior tip (Fig. 8.2-1b). Fyfe gives the average dimensions of the preserved specimens as 21mm long and 5mm wide. The mouth is more than half way from the anterior end, and gonopore nearer the mouth than the posterior end. Pharynx long and tubular.

All of the material from Campbell Island was bleached. Specimens from Auckland Island (MONZ 1372) exhibited pronounced dorsal margins, and the faint paired stripes described by Fyfe in bleached specimens; they also revealed faint dark submarginal stippling to the edge of the creeping sole. A dark margin to the creeping sole is present in the specimen from Ocean Island (MONZ 1384), and the penis is partly protruded.

The cross sectional body shape is markedly dorsoventrally flattened with pronounced margins, possibly a fixation artefact (MONZ 1372, 1384), to a more natural shape shallow convex dorsally and flat ventrally (MONZ 112). The average length of the specimens examined in this study, 14.8mm, (Table 1) is considerably less than that given by Fyfe, though the relative positions of the body apertures broadly accord with her description.

INTERNAL ANATOMY:

The species was briefly partially described and illustrated by Fyfe. Her description omits many currently important taxonomic characters. The sectioned Type material is incomplete, and the following description refers to the topotypic specimen MONZ 112b.

Head:

Sucker absent. Ventral parenchymal muscular plate thins out. Gut continues almost to the anterior tip. Ganglion cells prominent between anteriad extent of brain and cutaneous nerve net. Sensorial zone around lower margin of anterior tip and short distance laterally. Sensory pits simple, ciliated, tubular, 12.6µm diameter, 26µm deep. Eyes lens-type (Fig. 8.2-1c), 14µm diameter, in single row skirting anterior tip margin, slightly clustered, staggered in two or more uneven rows laterally, continuing to posterior tip in single staggered submarginal row (Fig. 8.2-2).

Pre-pharyngeal region:

Body tightly packed with muscles, testes and gut (Fig. 8.2-1d). Outer epithelium same thickness dorsally and ventrally. Rhammites 23µm long, sparse dorsally, more numerous laterally. Epitheliosomes secreted from creeping sole. Epithelium packed with granular erythrophil secretions, with abundant erythrophil secretions ventrally. Cyanophil glands sparse dorsoventrally. Creeping sole nucleate, 71% of body width. Cutaneous musculature tripartite, ventral musculature (98μm) stronger than dorsal (34μm), circular, decussate helical muscles. Longitudinal muscles in bundles, stronger ventrally (56-90μm thick) than dorsally (25-34μm thick). CMI 22.%. Parenchymal musculature strong. Sub-neural muscular plate present, 112μm thick, PMI 10.8%, with mixed musculature: longitudinal muscles in small bundles, with transverse parenchymal muscles. Ring zone present, weak, with longitudinal muscles with single fibres, small bundles. Supra-, infra-intestinal transverse muscles very strong, regularly spaced along body between gut diverticula. Dorsoventral muscles strong, between gut diverticula, testes, intersecting ventral plate.

Alimentary tract:

Pharynx cylindrical, horizontal, 11.7% of body length, with pleated internal lumen, dorsal insertion posterior to ventral insertion, with oesophagus. Pharyngeal pouch 13% of body length. Mouth in anterior third of the pouch. Inner pharynx with ciliated infranucleate epithelium in distal two thirds of pharynx, grades into nucleate secretory oesophageal epithelium occupying proximal third of pharynx and extending anteriorly to gastrodermis. Oesophageal epithelium underlain strong mixed longitudinal - circular muscles. Pharyngeal musculature inner epithelium, longitudinal, then mixed longitudinal – circular muscles; outer epithelium, thick layer longitudinal, then evenly spaced circular muscles, then grades mixed circular - longitudinal muscles.

Reproductive organs:

A schematic representation of the copulatory organs is provided in Fig. 8.2-1e. Testes extensive, loculate, 100μm - 200μm diameter, dorsoventral, occupying all space between diverticula of gut, but do not lie between gut and outer wall on sides of body. Testes begin midway between anterior tip and root of pharynx, extend to posterior tip. Efferent ducts thin-walled capillaries, difficult to trace until close to copulatory organs. Sperm ductules pass from testes to intertesticular ducts which communicate with collecting ducts lying transversely above nerve cords, commissure. Collecting ducts open into vasa deferentia. Vasa deferentia expand just behind mouth to form capacious spermiducal vesicles, lined by a non-ciliated cuboidal epithelium, with thin outer sheath of circular muscles. Spermiducal vesicles narrow, approach anteriad penis bulb, form sperm ducts, same structure as spermiducal vesicles, with thicker musculature. Sperm ducts rise, follow curvature of penis bulb, separately enter dorsal wall of seminal vesicle.

Male copulatory organs comprise seminal vesicle, with inverted penis inclined 10° to horizontal. Seminal vesicle lined by rugose nucleate columnar epithelium, receives three types of secretions: anteriad end epithelium heavily charged with coarse erythrophil plus finer cyanophil (dark blue) granules secreted in merocrine manner into vesicle, cyanophil granules dispersed, erythrophil granules clumped; posteriad end epithelium of vesicle similarly charged with same type erythrophil granules, together with amorphous cyanophil (turquoise blue) secretion which passes into lumen as strand. Vesicle epithelium with long cilia. Seminal vesicle floor occupied by inverted penis. Inverted portion with ciliated cuboidal epithelium through which pass coarse erythrophil secretion, different from erythrophil secretion of vesicle. Ejaculatory duct lined by nucleate rugose columnar epithelium through which pass amorphous erythrophil secretions which coalesce as sheets in lumen. Duct characterised by presence of long-necked cyanophil (fine dark blue granular secretion) gland cells, with swollen terminal tips projecting into lumen.

Muscular penis bulb with strong longitudinal muscles attached to ventral half of penis papilla. Muscles on dorsal half of bulb particularly strong, mixed with circular muscles, attached at roof of the common atrium and behind adenodactyl. Inverted penis with mixed musculature of strong circular muscles intersected by longitudinal muscles. Loose stroma present between ectal epithelium and musculature, extending two-thirds length of penis (compression tissue). Distal third of penis projects into atrium, surrounded by powerful circular penial extensor muscles attached to ventral half of penis, and roof of atrium forward of adenodactyl.

Adenodactyl, spheroidal shape, Type VI, situated in dorso-posterior wall of copulatory apparatus. Adenodactyl reservoir with low columnar epithelium, receives three merocrine secretions derived from adjacent mesenchymal glands: erythrophil globules, fine cyanophil (dark blue) granules, and cyanophil (turquoise) secretion from ventrad wall near duct. Duct leads from reservoir and terminates in a short papilla which projects into atrium above female genital canal; epithelium of duct and papilla are heavily charged with globular erythrophil secretions.

Atrium with folded atrial roof and relatively smooth atrial floor; lined by cocoon-making mucosa charged with cyanophil (dark blue) fine granular secretions, erythrophil globules, and dark cyanophil amorphous secretions, all derived from adjacent mesenchymal glands; cyanophil secretions appear sclerotin-forming strand cells, giving epithelium ciliated appearance. Atrium largely occupied by penis papilla. Gonopore opens below penis papilla.

Ovaries ventral, slightly embedded in nerve cords, 140μm long, 250μm wide, 100μm high, situated between mouth and copulatory organs. Resorptive parovarian tissue, not enclosed by a tunica, surrounds ovaries, extends back along oviducts short distance. Oviducts enter ovaries ventrally; lined by ciliated epithelium; with small branches behind ovary opening into adjacent resorptive tissue to receive excess donor sperm. Vitellaria reduced, distal to ovary, lying beneath gut. Ovovitelline ducts curve mediad to separately enter laterally blind end of female genital canal, do not receive secretions from adjacent shell glands.

Female genital canal mostly straight, flaring dorso-ventrally at proximal end, lined by pseudostratified columnar epithelium of cyanophil strand cells between which pass shell-gland secretions from glands in adjacent mesenchyme; with weak inner longitudinal and outer circular musculature. Female genital canal enters ventroposterior wall of atrium horizontally.

Pathology:

Gregarine sporozoites were present in the mesenchyme outside the gut wall.

Etymology:

The specific epithet designated by Fyfe (1953), given the suffix, presumably commemorates Carnley Harbour, Auckland Islands, which surrounds the Musgrave Peninsula, one of the localities where the species was found.

Systematic discussion:

Fyfea presently has only one species *F. carnleyi.* Within the Anzoplaninae *Fyfea* is close to "Parafyfea" with which it shares the ovary situated between mouth and copulatory organs, and an inverted penis. It is distinguished from "Parafyfea" chiefly by the presence of an adenodactyl, and reduced vitellaria. In *Anzoplana* the ovaries are situated near the anterior end, and the penis is eversible.

The inverted penis *bauplan* is found in Plagiostomidae, Monocelididae, some Acoela, and the maricolan taxa *Nexilis epichitonius* and *Centriovarioplana tenuis* (Sluys, 1989). It is uncommon in the Terricola, found only in *Fyfea* and "Parafyfea", and may also be present in the caenoplaninid *Kontikia marrineri.* Of particular interest are the parallels between the foregoing terricolan taxa from Auckland Islands, and the maricolan *Centriovarioplana tenuis* recorded from the subantarctic South Georgia Islands, at about the same latitude. *Centriovarioplana tenuis* has lensed eyes, an inverted penis, ovaries located immediately anterior to the mouth on either side of the gut, and a musculoglandular organ external to the copulatory organs. The terminations of long-necked ducts of cyanophil gland cells in the penis of *Fyfea* might be muscle fibres penetrating the ejaculatory duct epithelium, as are present in *Centriovarioplana* (Sluys 1989). Anatomical similarities between these terricolan and maricolan taxa raise the possibility of a maricolan ancestor to some subantarctic anzoplaninids (discussed Chapter 5).

The essential details of Fyfe's (1953) succinct description of *F. carnleyi* are confirmed here. Additional characters including the musculature of the body and organs, dorso-ventral testes, sperm-resorptive nature of the parovarian tissue, and the type of penis are now described. The average length of the specimens examined in this study, 14.8mm (Table 8.2-1) is considerably less than that given by Fyfe, though the relative positions of the body apertures broadly accord with her description. Also, the entry of the ovovitelline ducts into the female genital canal is depicted as dorso- and ventro-posterior (T- shaped anastomosis), with shell glands opening into these ducts. The material examined revealed that the ovovitelline ducts enter the proximal end of the female canal laterally, and that the dorsoventral flaring of the posteriad female canal could be mis-interpreted as the point of entry of the ovovitelline ducts. Fyfe (1953, Plate II, Fig. 1) shows glands entering the ovovitelline ducts, however in fact the shell glands serving the female canal partly surround but do not enter the ovovitelline ducts.

Table 8.2-1. *Fyfea carnleyi*: Dimensions of specimens examined.

Specimen m.m.	Length m.m	Width m.m	Mouth m.m	Mouth %	Gonopore m.m.	Gonopore %	Mouth- Gonopore	Mouth-
MONZ 112 a	15.0	3.5	7.5	50.0	11.5	76.7	4.0	26.7
MONZ 112 b	15.0	3.0	9.5	63.3	13.0	86.7	3.5	23.3
MONZ 112 c	15.0	3.0	8.5	56.7	11.6	77.3	3.1	20.7
MONZ 112 d	14.0	2.5	8.0	57.1	11.5	82.1	3.5	25.0
MONZ 112 e	8.0	2.0	6.5	81.3	non-sexual			
MONZ 112 fl		4.5	Anterior portions only. Possibly correspond to OMNZ A74-51 A-D or A74-52 A-C incomplete series sagittal and TS sectioned posteriors.					
MONZ 112 f 2		4.0						
MONZ 112 f3		3.0						
MONZ 1372 a	20.5	4.7	12.0	58.3	16.5	80.5	4.5	22.0
MONZ 1372 b	16.0	3.0	9.0	56.3	12.4	77.5	3.4	21.3
MONZ 1384	15.0	3.5	specimen twisted and damaged					

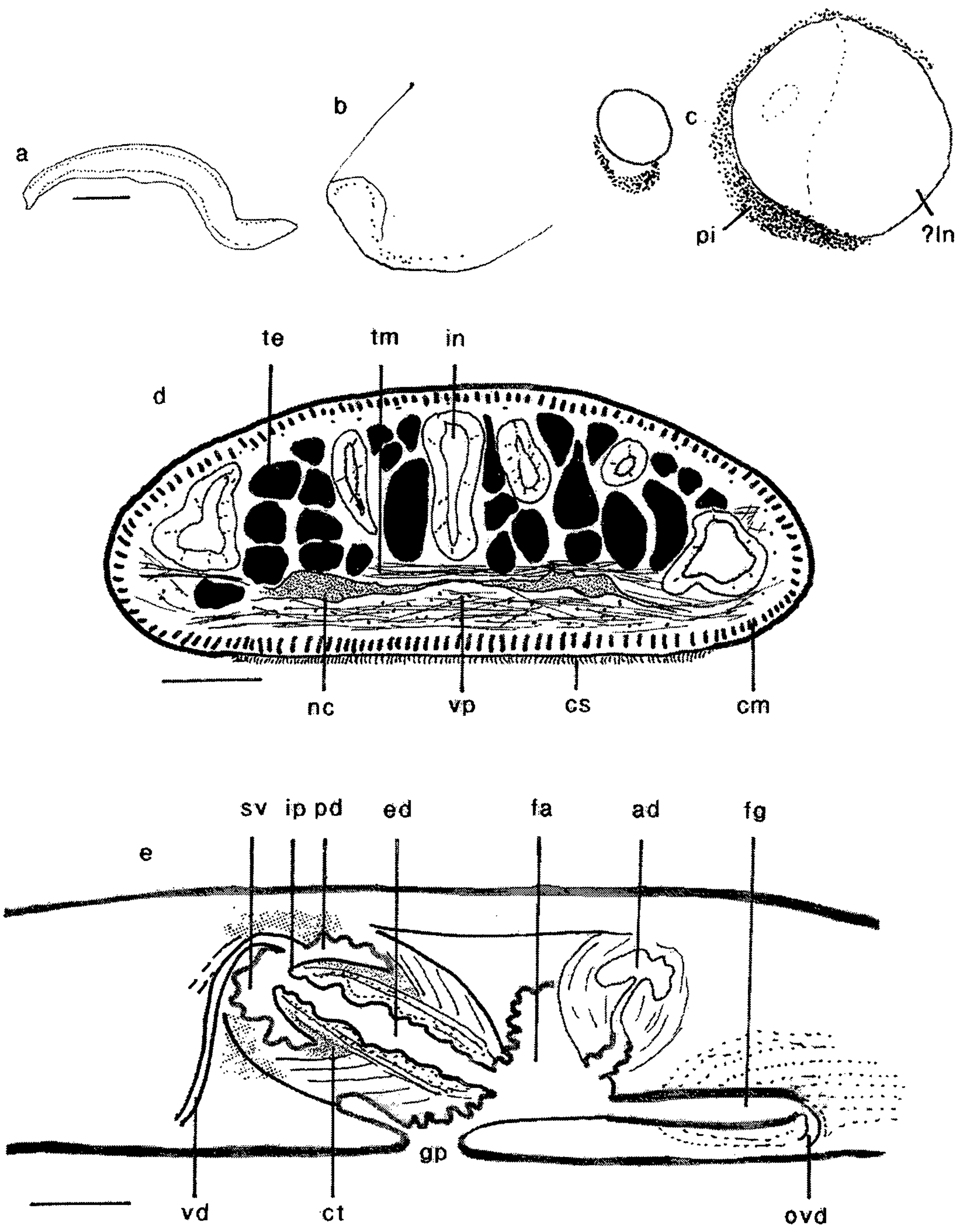


Figure 8.2-1. *Fyfea carnleyi.*

a. General form, ventral aspect, fixed specimen. Scale = 4mm
b. Anterior tip, eye pattern. Unscaled.
c. Eye, showing ? lens. X40; X100
d. Pre-pharyngeal region, transverse section. Scale bar = 500μm
e. Copulatory organs. Scale bar = 500μm

8.3 Genus *Apogaioplana* gen.nov.

Apogaioplana gen.nov.

Diagnosis: Caenoplaninae with elongate body, convex dorsally, flat ventrally. Mouth and gonopore situated in third body quarter. Creeping sole absent. Eyes absent. Anterior adhesive pad or cup absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular, helical muscles, with strong longitudinal muscles in well defined bundles, with dorsal musculature weaker than ventrally, CMI 9%. Parenchymal musculature weak; longitudinal muscles absent. Pharynx cylindrical, folded. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; outer musculature with epithelium, longitudinal, circular, then mixed circular-longitudinal muscles. Pharyngeal pouch with diverticulum. Testes ventral, lateral to nerve cords, extend to root of pharynx. Vasa deferentia enter penis bulb separately, unite, enter seminal – prostatic duct. Ejaculatory duct tubular, sinuous, strongly muscular, with intra-penial papilla. Ovovitelline ducts approach proximal end of female genital canal anteroventrally, unite, enter female genital canal via common opening. Female canal horizontal, enters ventro-posterior wall of common antrum; underlies female antrum. Musculature of copulatory organs with mixed circular-longitudinal muscles. Viscid gland present, to left of female canal, bent dorsad. Adenodactyls absent. Type species: *Apogaioplana paluma* gen et sp nov.

Etymology: The genus name is contrived from the Greek *apogaios*, from the earth, and Latin plana flat, and alludes to the presence of the species in the soil formed from well-rotted logs and litter. Gender feminine.

Distribution: Near Paluma dam, Paluma, north Queensland, in soil in decayed log, rainforest. Torresian zoogeographic sub-region.

Systematic discussion: *Apogaioplana paluma* (caenoplaninid – ventral testes) closely parallels *Geobia subterranea* (geoplaninid – dorsal testes) of Brazil in the following characters: absence of pigmentation, eyes, and creeping sole, presence of strong cutaneous musculature CMI 9% (*Geobia* CMI 8.5%), and absence of parenchymal longitudinal muscles. There are also similarities in the general conformation of the copulatory organs, and both have a penis papilla and muscular tubular ejaculatory duct. They differ in that in *A. paluma* the vasa deferentia unite within the penis bulb (unite before entering the bulb in *Geobia*), ovovitelline ducts approach the genital canal antero-ventrally (anterodorsally in *Geobia*), and viscid gland present (absent in *Geobia*).

Of the externally similar taxa within *Australoplana sensu lato*, *Apogaioplana* stands closest to *Sokoplana*. It is differentiated from this genus by the absence of eyes (present in *Sokoplana*), normal tripartite cutaneous musculature, stronger ventrally than dorsally (in *Sokoplana* dorsal and ventral cutaneous musculature are equal, plus presence of the unusual helical layer*)*, cylindrical pharynx (bell-form in *Sokoplana*), tubular ejaculatory duct (cavernous in *Sokoplana*), atrial muscular flaps (absent in *Sokoplana*) genital canal below female antrum (antrum and genital canal in-line in *Sokoplana),* mixed musculature in copulatory organs (differentiated in *Sokoplana*). Both have vasa deferentia uniting within the penis bulb, presence of a penis papilla, ovovitelline ducts entering the proximal canal through a common orifice, and viscid gland with dorsad bend, arising from inside the gonopore to the left of the genital canal. With respect to relative position and shape, the diverticulate viscid gland has some superficial similarity to the cutaneo-intestinal canal of the geoplaninid *Enterosyringia*; however they are neither homologous nor analogous structures.

Apogaioplana paluma gen et sp nov.

Material examined:

Holotype: LW 783, Near Paluma dam, Paluma, north Queensland, in soil in decayed log, rainforest, collected L. Winsor 8 March 1975; a series of pre-pharyngeal TS 16 slides, posterior LSS 78 slides, sectioned at 8µm, stained H&E, MSB.

EXTERNAL FEATURES

Body elongate, convex dorsally, flat ventrally, thick in cross section. Dorsal ground colour whitish cream with pinkish-brown anterior tip. Ventral surface white. Eyes absent. Length 79.0mm, width at mouth 7.0mm, mouth 43.0mm from anterior end (54.4% of body length), gonopore 52.2mm from anterior end (64.5% body length), distance mouth to gonopore 9.5 (12.0% of body length). Body is 5540µm wide, 2310µm high.

INTERNAL ANATOMY

Head:

The anterior end has been cleared, but not yet sectioned. Eyes, adhesive pad, absent.

Pre-pharyngeal region:

Pre-pharyngeal region (Fig. 8.3a) Dorsal and ventral epithelium equal thickness, rhammites 20µm long pack dorsal and ventral epithelium, erythrophil glands abundant, marginal to submarginal adhesive zone present. Creeping sole absent. Cutaneous musculature tripartite, with thin outer circular, decussate helical muscles, with strong longitudinal muscles in well defined bundles. Dorsal cutaneous musculature (85µm thick) weaker than ventral (135µm thick), CMI 9%. Parenchymal musculature weak, longitudinal muscles absent, with weak dorsal transverse (helical) muscles, weak dorsoventral muscles, with infraneural transverse muscles (stronger than dorsal set, not as helicoid); peri intestinal muscles weak.

Alimentary tract:

Pharynx cylindrical, folded (cuffed), lying almost horizontally within pouch. Dorsal insertion posterior to ventral insertion. Pharyngeal musculature inner epithelium, circular, then mixed longitudinal – circular muscles; outer epithelium, longitudinal, then circular muscles, then mixed longitudinal - circular muscles. Pharyngeal pouch capacious, 5% of body length, with distal diverticulum; mouth anterior of mid pouch.

Reproductive organs:

Copulatory organs (Fig. 8.3b). Testes about 200μm diameter, ventral, uniserial, lateral to nerve cord, lie beneath gut, extend dorsally between gut diverticula for about one third height of diverticula; extend horizontally to root of pharynx. Testes exhibit sequential not synchronous maturity. Sperm duct leads from mediad lower pole of each testis then passes obliquely ventrally to vas deferens lying just below level of lateral margin of nerve cords. Vasa deferentia tortuous, expanded between pharynx, copulatory organs; rise just in front of penis bulb, separately enter bulb; then each expands, forms spermiducal vesicle, narrows and unites. Common duct expands, ascends, then descends to form highly convoluted seminal vesicle - prostatic duct. Duct with tunica of circular muscles, with ciliated columnar nucleate epithelium with acidophilic margin. Seminal vesicle (proximal third of duct) receives erythrophil secretions from surrounding penial glands; prostatic duct (mid third) receives both erythrophil and cyanophil secretions; cyanophil secretions only in distad portion. Ejaculatory duct (distal third) with narrowed lumen, thickened muscular walls and epithelium that receives no secretions. Penial gland secretions absent from this region of bulb. With intra-penial papilla. Penis bulb with granular erythrophil and cyanophil secretions; erythrophil secretions derived from penial glands anterodorsal to bulb; cyanophil secretions derived from penial glands situated ventro posteriorly to bulb. Bulb with tunica of longitudinal muscle.

Male antrum conical, with two large circular, fenestrated muscular flaps: one immediately adjacent to penis papilla, other larger one protrudes into female antrum. During copulation these flaps may form a false penis. Papilla, outer muscular flap covered with low facing epithelium. Male antrum and inner muscular flaps lined by low columnar epithelium, with strongly erythrophil margin, with fine granular erythrophil, coarse globular cyanophil secretions in lumen. Atrial musculature strong, with circular then longitudinal muscles intermingled but tending towards alternating layers (as in inner pharyngeal musculature).

Ovaries not yet examined. Vitellaria extensive, situated between gut diverticula, discharge into ovovitelline ducts via short vitelline funnels. Ovovitelline ducts pass posteriorly, incurve to separately enter proximal end of horizontal female genital canal through common opening. Female genital canal below female antrum, receives shell gland secretions; shell glands surround duct, extend posteriorly. Viscid gland with distal horizontal duct 370μm long leading from common antrum, then turns inwards, upward passing to left of female genital canal; receives erythrophil, cyanophil secretions from glands surrounding duct. Female antrum with tall cocoon-making nucleate columnar epithelium with erythrophil margin; underlain by layer of circular then longitudinal mixed muscle fibres. Secretory epithelium extends around whole female antrum, grades to flattened facing epithelium lining male antrum and muscular flaps.

Pathology:

A nematode larva was present in one testis.

Etymology:

The specific epithet is from the name of the Paluma Range where the species was found. Gender neuter. The Paluma Range, and some other geographical features and township in north Queensland take their name from the Queensland colonial government survey ship HMQS Paluma which worked along the north Queensland coast in the 1880s and 1890s. *Apogaioplana paluma* – the Paluma planarian.

Systematic discussion:

Apogaioplana paluma (caenoplaninid – ventral testes) closely parallels *Geobia subterranea* (geoplaninid – dorsal testes) of Brazil in the absence of pigmentation, eyes, and creeping sole, presence of strong cutaneous musculature CMI 9% (*Geobia* CMI 8.5%), and absence of parenchymal longitudinal muscles. There are also similarities in the general conformation of the copulatory organs, and both have a penis papilla and muscular tubular ejaculatory duct. They differ in that in *A. paluma* the vasa deferentia unite within the penis bulb (unite before entering the bulb in *Geobia*), ovovitelline ducts approach the genital canal antero-ventrally (anterodorsally in *Geobia*), and viscid gland present (absent in *Geobia*).

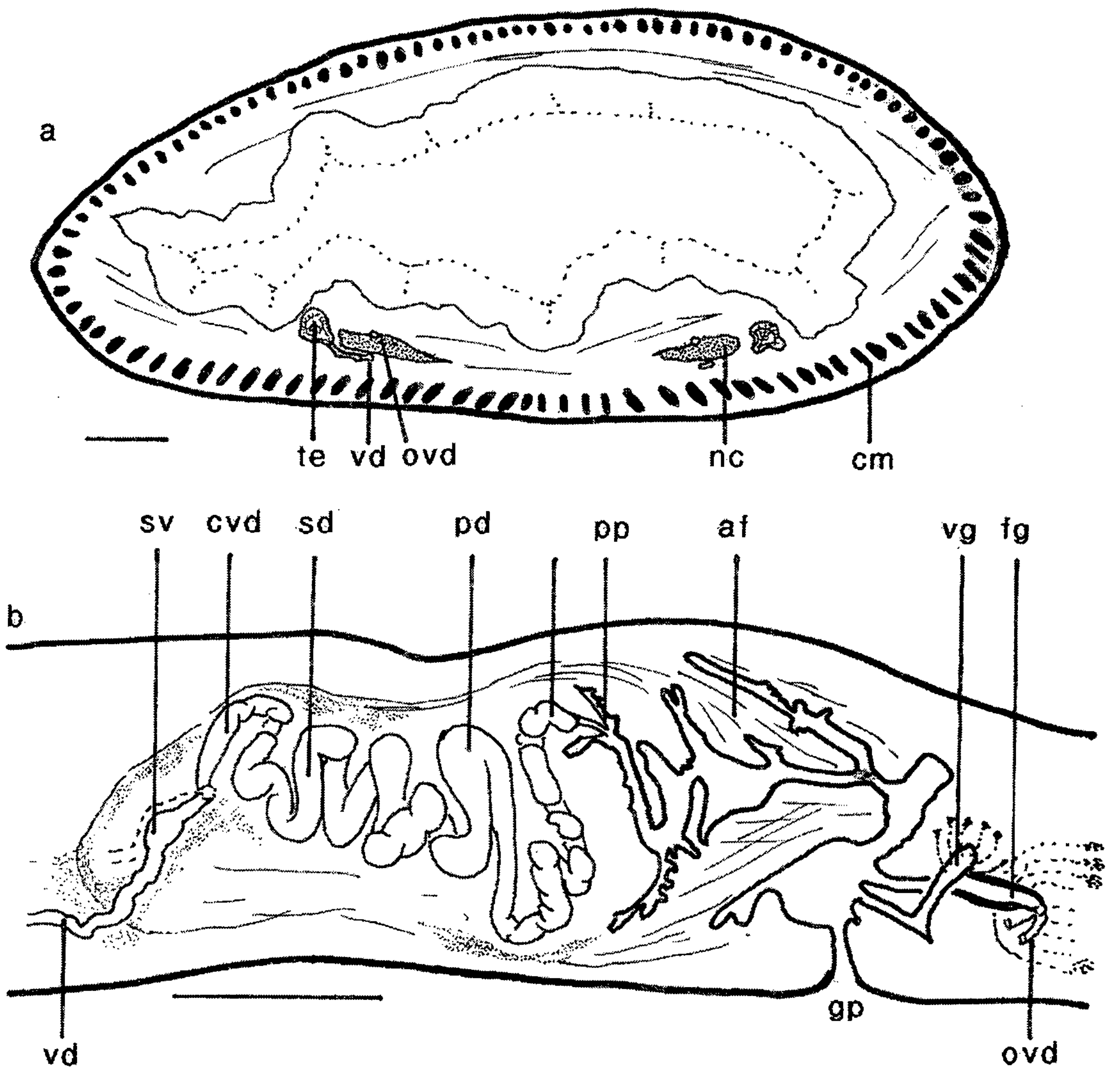


Figure 8.3 *Apogaioplana paluma*

a. Pre-pharyngeal region, transverse section. Scale bar = 1mm.
b. Copulatory organs, sagittal section. Scale bar = 1mm.

A8.4 Genus *Arthurdendyus*

Arthurdendyus Jones & Gerard, 1999 emend

Arthurdendyus Jones & Gerard, 1999
Arthurdendius Jones & Gerard, Ogren *et al* (1999)
Artioposthia (in part) Dendy, 1885a; Johns 1998
Geoplana (in part) Dendy, 1895a

Original diagnosis (Jones & Gerard, 1999): "Geoplanid land planarians with ovaries lateral to the male copulatory apparatus, adenodactyli (or accessory glands) present. Pharynx bell-shaped, not cylindrical".

Emended diagnosis (this thesis): Caenoplaninae with broad, elongate and strap-like body. With mouth situated posterior to mid body; gonopore closer to mouth than to posterior end. Ciliated creeping sole absent. Anterior adhesive pad or sucker absent. Sensory papillae absent. Eyes pigment cup-type, small, in single row around anterior end, and anterolaterally to posterior. Cutaneous musculature tripartite, strong, with circular, helical muscles, with longitudinal muscles in bundles. CMI 14%. Parenchymal musculature with strong dorsal and ventral transverse muscles, weak to absent longitudinal muscles. Pharynx plicate (collar-form). Pharyngeal musculature with inner epithelium, longitudinal, circular, thin inner layer longitudinal muscles; outer pharyngeal musculature with epithelium, circular, longitudinal, then strong circular muscles. Oesophagus present. Testes, sperm ducts ventral. Testes extend almost entire length of body. Vasa deferentia retiform distally, enter seminal vesicle horizontally, both sides, at multiple points. Penis eversible, without papilla. Male antrum capacious, elongate. Ovaries lateral to male copulatory apparatus, with lateral resorptive bursae situated behind mouth, before gonopore. Ovovitelline ducts unite, form short common duct that enters posterior female genital canal horizontally. Female genital canal horizontal, in-line with female antrum. Female antrum elongate, enters common antrum via ventroposterior atrial wall. Adenodactyls present. Type species: *Geoplana triangulata* Dendy, 1895a

Etymology: "Named in honour of Arthur Dendy for his great contributions to the study of land flatworms. Gender. Male." (Jones & Gerard, 1999). The alteration of the genus name to *Arthurdendius* by Ogren *et al* (1999) and subsequently used in their species lists (Kawakatsu *et al* 2000, 2001), is an "unjustified emendation" under Art. 33.2.3 (ICZN, 1999). The original spelling must be maintained under Art. 32.2 (ICZN, 1999).

Distribution: The genus occurs in New Zealand. Circumstantial evidence suggests that it may be adventive in the Australian and New Zealand subantarctic islands (this thesis). Two species are adventive in the United Kingdom, one of which is *A. triangulatus*, an agricultural pest and serious threat to earthworms in the U.K. and the Faeroe Islands.

Systematic discussion: Within the adenodacylate taxa of the Caenoplaninae, the combination of the presence of ovaries posterior to the pharynx at the level of the copulatory organs, the pharynx type, and absence of a creeping sole, chiefly differentiates *Arthurdendyus* from other similar taxa. *Artioposthia ventropunctata*, *A. lucasi,* and *A. mariae* have no creeping sole, but have cylindrical pharynges, and pre-pharyngeal ovaries. The subantarctic species *Fyfea carnleyi* has post-pharyngeal ovaries anterior to the copulatory organs, has a creeping sole, cylindrical pharynx, and dorsoventral testes (see the Anzoplaninae).

Arthurdendyus species have a plicate collar-form pharynx, characterized by the location of the dorsal insertion of the pharynx in the posterior third of the pharyngeal pouch. In bell-form pharynges the dorsal insertion of the pharynx is located in the mid pouch region (Graff, 1899).

Arthurdendyus vegrandis n. sp.

Material examined:

Holotype: Specimen from Lusitania Creek and Lucitania Bay, Macquarie Island, collected by R.J. Blakemore, 7 January 1998. Fixed in 70% ethanol. 50 slides of anterior tip, prepharyngeal, and posterior LSS with TS through the region of the gonopore, sectioned at 8μm, stained by MSB method.

Paratype: Specimen from Lusitania Creek and Lusitania Bay, Macquarie Island, collected by R.J. Blakemore, 7 January 1998. Fixed in 70% ethanol.

EXTERNAL MORPHOLOGY:

Both specimens (Fig. 8.4-1a) are straplike, broad, flat, tapering anteriorly and posteriorly, with slightly crenulate margins (a fixation artefact). Dorsal surface is reddish-brown, with narrow white margins extending ventrally and around both ends. Ventral surface is a uniform cream colour. Eyes very small, in single row around the anterior tip (Fig. 8.4-1b) and submarginally to posterior. Holotype measured 39 mm long and 4mm wide at mouth. Mouth is 23 mm (59%) from anterior tip, and gonopore 6.5 mm (16.6%) behind mouth. Paratype measured 32 mm long and 3mm wide at mouth. Mouth is 18.5mm (57.8%) from anterior tip; gonopore not visible.

INTERNAL ANATOMY:

Head:

Specialized adhesive structure and associated musculature absent. Anterior tip richly endowed with erythrophil secretions that may have an adhesive function. Eyes very small, pigment-cup type, 20μm diameter, in single row skirting anterior tip margin, then submarginally along sides. Retinal clubs could not be counted. Ciliated pits were not seen - the anterior tip was damaged and distorted.

Pre-pharyngeal region:

Pre-pharyngeal region (Fig. 8.4-1c). At this point width is 2580μm and height 997μm.

Epithelium thickness mostly uniform over whole body, thickest ventrally, with suggestion of adhesive margin characterised by increase in density of rhabditogen, erythrophilic glands marginally. Ciliated creeping sole absent. Rhabdoids rhammite type, 9-10μm long, most numerous submarginally, sparse dorsally, ventrally. Erythrophil epidermal secretions, finely granular, abundant dorsally, marginally, ventrally. Xanthophil secretions, finely granular, abundant especially dorsally. Cyanophil secretions present dorsally, ventrally. Cutaneous musculature tripartite, with dorsal musculature slightly thicker than ventrally. Dorsally, ventrally musculature thinnest medially, dorso-, ventrolaterally same somewhat thicker (~90μm), thick laterally (103μm) and submarginally the thickest (112μm). CMI = 14%. Parenchymal musculature well developed. Parenchymal longitudinal muscles absent. With strong dorsal and ventral parenchymal transverse muscles, weaker dorsoventral and peri-intestinal muscles.

Alimentary system:

Pharynx plicate (collar form), dorsal insertion posteriad, ventral insertion anteriad, not strongly muscularised, with oesophagus. Pharyngeal musculature inner infranucleate epithelium, longitudinal, then circular muscles; outer epithelium, circular, then thin layer longitudinal muscles. Oesophagus present, with highly folded infranucleate epithelium, with underlying circular muscle layer considerably thicker than in pharynx proper. Mouth situated approximately two thirds along the pharyngeal pouch. Lips of mouth with abundant erythrophil secretions. Pharyngeal pouch 4.8 mm long, 15% of the body length, lined by flattened nucleate epithelium containing erythrophilic granules and underlain by thin layer of longitudinal muscles external to which are numerous bundles of circular or transverse muscle fibres, strongest dorsally.

Reproductive system:

The copulatory organs (Fig. 8.4-1 d-f, Fig. 8.4-2) comprise a long penis bulb, common antrum into which discharge adenomuralia type adenodactyls, and a horizontal female genital canal.

Testes ventral, loculate, 100 - 210µm high, some 85µm in width and depth, present below and between gut diverticula, extend from anterior almost to posterior tip. Sperm duct passes from each testis to intermediate duct, then to vasa deferentia immediately below nerve cords, mediad with respect to ovovitelline ducts. Vasa deferentia lined by nucleate ciliated epithelium, pass posteriad just posterior to pharyngeal pouch, then retiform (rete vasa deferentia), then separately enter proximal seminal vesicle at multiple points laterally, then continue alongside and beyond copulatory organs to service posterior testes.

Penis bulb divided into two regions on basis of cytology and secretions: a small seminal vesicle, and elongate ejaculatory duct. Penis bulb musculature consists of inner coat of circular muscles and exterior sheath of cords of strong longitudinal retractor muscles, which together form the "basketwork musculature" (Fig 8.4-1d) described by Fyfe (1939). Penis without papilla, eversible type. Seminal vesicle 400µm long, lined by low columnar epithelium with lumenal margin heavily charged with fine bright erythrophil granules, epithelium receives secretions from cyanophil, erythrophil and xanthophil penial glands. Ejaculatory duct long, sinuate, 3.6mm long, lined by columnar epithelium characterised by presence of long-necked gland cells, with terminal tips clearly projecting into lumen. Ejaculatory duct also receives coarse erythrophil and amorphous purplish secretions, derived from glands in adjacent parenchyma, pass into the lumen.

Adenodactyls, 15, Type 1, arranged in five pairs of batteries facing each other (Fig. 8.4-5e,f). Each battery comprises three adenodactyls – upper, mid and lower. Adenodactyls with tight circular muscle around bulb, duct, external to which longitudinal muscle sheath. Reservoir lined by nucleate cuboidal epithelium charged with cyanophil and erythrophil granules derived from glands in adjacent mesenchyme, with erythrophil secretions predominating towards distal reservoir near start of duct. Duct lined by a similar secretory epithelium. Adenodactyls secrete? sclerotin compound. Atrial mucosa with tall columnar epithelium heavily charged with bright erythrophil, strongly cyanophil secretions derived from glands in adjacent parenchyma.

Ovaries located on either side of mid penis bulb, slightly embedded in dorsolateral sides of anterior quarter of lateral resorptive bursae; ellipsoidal in shape, 260µm long, 140 µm high with Keimlager in lower anteriad pole. Occlusive cells present where oviducts enter ovaries. Oviducts pass ventrad from ovaries through bursae, recurve, continue posteriorly then unite to form common ovovitelline duct.

Lateral bursae, one each side of penis bulb, sausage-like, 2mm long, 160µm diameter enclosed within very thin muscular tunica. Ovovitelline duct opens into bursa immediately before entering ovary. Bursa with deeply meandering duct lined by highly folded cuboidal epithelium. Bursal epithelium consists of two main cell types: cells with vacuolate pale greyish-blue cytoplasm (phagocytes), and granule cells charged with strongly erythrophil fine granules and coarse clumps (lysocytes). Vitellaria extensive, surround intestinal diverticula.

Female duct sinuoid, almost horizontal, with three regions: common ovovitelline duct 30µm long with ciliated low cuboidal epithelium, passes directly to proximal genital canal lined by tall non-ciliated columnar epithelium, with pale, almost colourless cytoplasm charged with fine pale purplish granules, and bright erythrophil globules derived from glands dorsal to copulatory organs. Canal narrows sharply, passes directly into distal duct some 1.2mm long, with muscular flap in roof. Epithelium of distal canal similar to antrum, receives strongly erythrophil globular secretions, but lacks conspicuous bright cyanophil secretions of antrum.

Distal canal expands and opens into common antrum, 880µm long, with gonopore in mid floor (Fig. 8.4-1f). Atrial floor lined by ciliated low cuboidal nucleate pigmented epithelium. Atrial walls with four prominent longitudinal folds on each side (Fig. 8.4-

1e). Adenodactyls (adenomuralia) in batteries, embedded in atrial walls, discharge secretions into lateral horizontal mucosal creases formed by folds in atrial walls.

Etymology:

The specific epithet *vegrandis* is Latin, meaning not very large, diminutive, alludes to the species being the smallest of the six described *Arthurdendyus* taxa.

Systematic discussion:

The morphology, general pattern of markings, and internal anatomy of *A. vegrandis* are very typical of New Zealand *Arthurdendyus* species. The general colour and markings of the species are similar to *A. testacea* and *A. australis.* Although the specimen is not fully mature it is possible to provide a reliable differential diagnosis as the number of adenodactyls in a particular species is constant and not seasonal (Fyfe, 1944, 1956). The species has 15 pairs of adenodactyls and in this character differs from *A. triangulatus* (three pairs) and *A. albidus* (one pair). The arrangement of the multiple adenodactyls in the atrial walls of the species differs from *A. australis* in which a grouping of adenodactyls is present ventral to the mouth of the ejaculatory duct, and multiple small conical (Type I) adenodactyls present "which project from the sides and two muscular flaps hanging from the roof of the antrum" (Fyfe, 1947).

The testes are immature with spermatids present in the lumen, and the rete vasa deferentia are not prominent, probably reflecting the immaturity of the specimen. The penis is eversible, without distinct papilla; what looks like a papilla in the longitudinal sections is in fact an anteroventral pocket in the wall of the common antrum. The phagocytes, lysocytes, and general histology of the lateral bursae are similar to those observed in resorptive bursa involving extracellular digestion in certain other taxa (this thesis). It is considered here that in the lateral bursae of *A. vegrandis* there is extracellular digestion of donor sperm by lysocyte granules, and phagocytosis of the digesta.

A.vegrandis could be an introduction to Macquarie Island. It has similarities with an undescribed species from the mountains north west of Christchurch, New

Zealand (P. Johns, pers. comm.). However Johns' species has not been found further south, or on Stewart Island where boats to Macquarie Island probably docked from time to time (P. Johns to P. Greenslade, pers. comm.). At present Johns' species is considered distinct from *A. vegrandis*. All the NZ subantarctic island specimens with similar shape to this species have had dorsal stripes, and no pale margin. No earthworms were found in the area where the flatworm was present, though earthworms are abundant elsewhere on the island. This observation, together with the type of pharynx present in this species, is circumstantial evidence supporting the view that *A. vegrandis* is vermivorous.

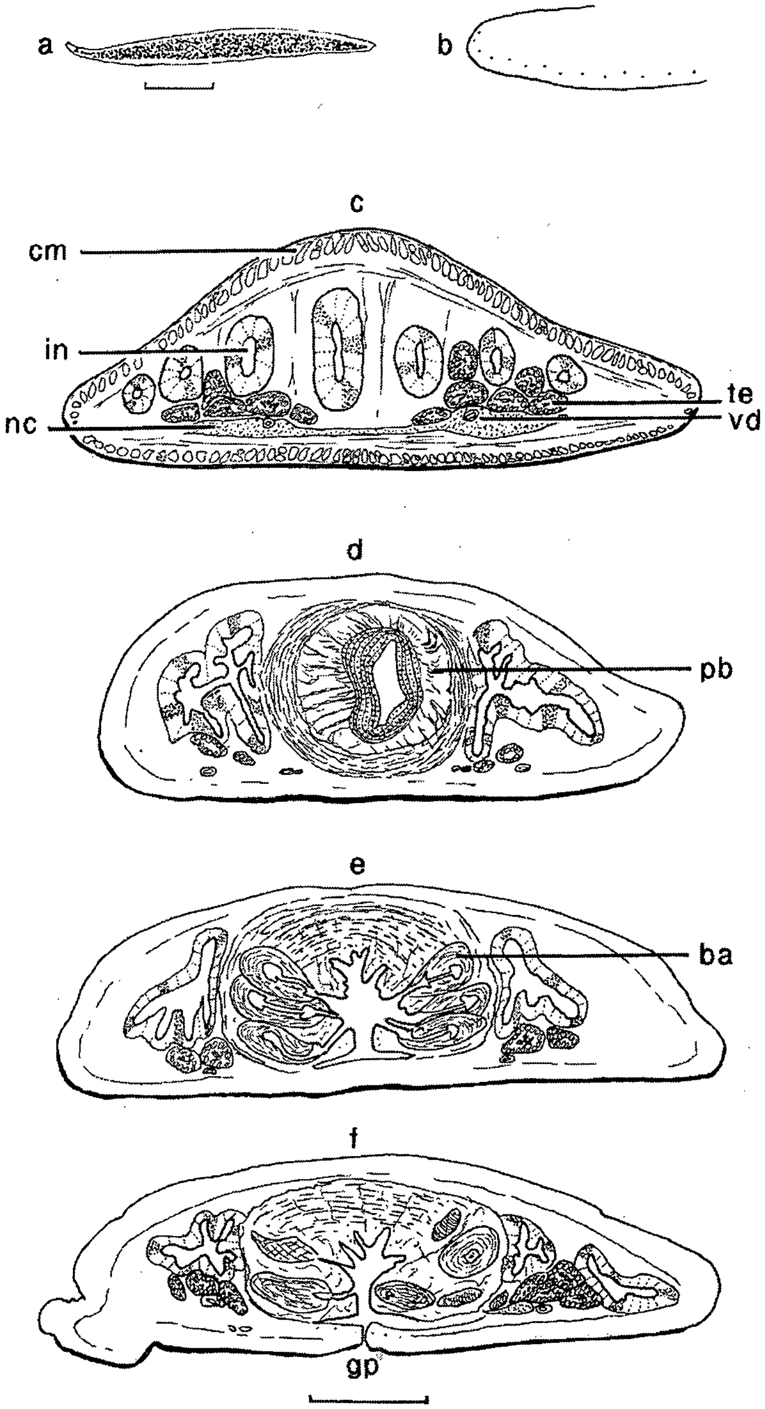


Figure 8.4-1 *Arthurdendyus vegrandis*

a. Whole specimen, dorsal surface. Scale 10mm.

b. Anterior end, eye pattern. Unscaled.

c. Pre-pharyngeal transverse section. Scale bar (for c-f) 500μm.

d-f Transverse sections through copulatory organs.

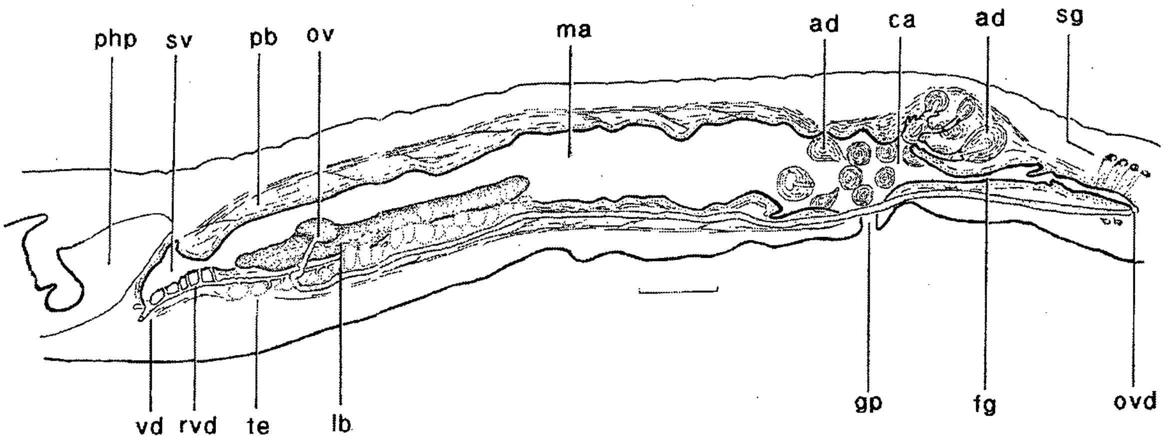


Figure 8.6-2 *Arthurdendyus vegrandis* – copulatory organs. Scale bar = 500µm.

A8.5 Genus *Australoplana*

Australoplana Winsor, 1991c

Caenoplana (in part) Moseley, 1877
Geoplana (in part), Fletcher & Hamilton 1888
Australoplana Winsor, 1991c; Ogren *et al* 1993b
Australopacifica (in part) Ogren & Kawakatsu, 1991

Diagnosis (emended from Winsor, 1991c): Caenoplaninae with elongate, strap-like body, broadly convex dorsally, flat ventrally. Mouth situated in posterior third of body, gonopore closer to mouth than to posterior end. Creeping sole less than a third body width. Eyes pigment cup-type, very small (pin-point), in single row around anterior tip, then sparsely submarginally to posterior end. Anterior adhesive pad or cup absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular, helical muscles; with very strong cutaneous longitudinal muscles in bundles; dorsal musculature weaker than that ventrally, CMI 8.7 – 15.6%. Parenchymal longitudinal muscles very weak or absent. Pharynx cylindrical, folded, with oesophagus. Pharyngeal musculature with inner epithelium, circular, then longitudinal muscles; outer pharyngeal musculature with epithelium, longitudinal, then circular muscles. Testes ventral, lateral to nerve cords, extend from just behind ovaries to between pharynx and copulatory organs. Vasa deferentia enter penis bulb separately, unite, enter sinuous tubular, seminal duct, prostatic duct. Ejaculatory duct tubular, sinuous, strongly muscular, with intra-antral penis papilla. Ovaries in anterior third, with tuba. Ovovitelline ducts unite at posterior end of female genital canal. Female genital canal horizontal, enters ventro-posterior wall of common antrum; underlies elongate female antrum. Musculature of copulatory organs comprises mixed circular and longitudinal muscles. Viscid gland absent. Adenodactyls absent. Type species: *Australoplana sanguinea* (Moseley, 1877).

Etymology: The genus name *Australoplana* is derived from the Latin *austral*, southern, and Latin *plana*, flat. Gender feminine. The Southern Planarian

Distribution: Found in restricted areas of the cool temperate moisture regions of the Bassian zoogeographic subregion in southeastern mainland Australia, and possibly in Tasmania.

Systematic discussion: Three provisional groups were recognized by Winsor (1991c) in the genus *Australoplana sensu lato*:

- the *Australoplana sanguinea* group comprising the species *sanguinea, rubicunda; alba, alba roseolineata,* and *minor* (now *Australoplana sanguinea, A. minor* (provisionally), and *Nelipoplana (Nelipoplana) alba,* this thesis);
- the *Australoplana typhlops* group comprising *typhlops* and previously undescribed species (now *Bassioplana typhlops*, *Sokoplana kanangra,* and *Apogaioplana paluma* this thesis); and
- the New Zealand Group containing *Australoplana sanguinea alba sensu* Jones (1981), and undescribed species (now *Nelipoplana (Peokrypta) enigma*, this thesis) placed in a separate group because of the alleged presence of parenchymal longitudinal muscles which was a significant departure from the parenchymal musculature in the other taxa.

Comparison of *Australoplana* with these new genera follows. For each genus there is as yet undescribed material.

Australoplana is mainly differentiated from *Nelipoplana* and *Apogaioplana* by the presence of a creeping sole (absent in *Nelipoplana* and *Apogaioplana*), cylindrical pharynx (bell form in *Nelipoplana*), dugesiid-type pharyngeal musculature (non-dugesiid in *Nelipoplana* and *Apogaioplana*), and female genital canal underlying the female antrum (female genital canal and antrum in-line in *Nelipoplana* and *Apogaioplana*). *Australoplana* shares with *Nelipoplana Peokrypta enigma* a muscularised, tubular prostatic and ejaculatory duct. However the penis papilla in *Australoplana* appears to be fixed (as in *Nelipoplana (Nelipoplana) alba*), not erectile (as in *Nelipoplana (Peokrypta) enigma*). *Australoplana* is distinguished from *Bassioplana* by the presence of eyes (absent in *Bassioplana*), pharynx type and musculature (dendrocoelid musculature in *Bassioplana*), fixed penis papilla (erectile in *Bassioplana*) and details of the female copulatory organs. A comparison of externally similar taxa is provided in Table 8.5-1.

Australoplana sanguinea (Moseley, 1877)

Caenoplana sanguinea (Moseley, 1877);
Geoplana rubicunda Fletcher & Hamilton, 1888
Australoplana sanguinea (Moseley, 1877); Winsor, 1991b
Australopacifica sanguinea (Moseley, 1877); Ogren & Kawakatsu, 1991
non *Geoplana sanguinea,* Dendy, 1892d
non *Geoplana alba* Dendy, 1891
non *Geoplana alba roseolineata* Dendy, 1892a
non *Rhynchodemus testaceus* Hutton, 1880
non *Geoplana sanguinea alba sensu* Jones, 1981

Material examined:

MNH 1877.11.2.10 *Caenoplana sanguinea* Moseley, 1877, Holotype: Parramatta, NSW, Coll. H.N. Moseley, April-June 1874, amongst earth at the roots of a Eucalyptus stump; single sexual specimen, sectioned 10μm, stained H&E posterior portion, LSS; AM 18454 *Geoplana rubicunda* Fletcher & Hamilton, 1888, Presumptive Holotype: Label in pencil "*Geoplana sanguinea* Moseley Springwood, Bl.Mt". Single sexual specimen, sectioned 8μm, stained H&E, Gomori trichrome, anterior HS /TS 40 slides, pre-pharyngeal region TS 3 slides, posterior LSS 43 slides. The specimen was originally part of the old collection that missed registration in 1908. Dimensions correspond to the second of eight spirit specimens of *G. rubicunda* Fletcher & Hamilton, 1888, *the* dimensions of which were provided by these authors, page 370. The label may be explained by the comment by Dendy that "it seems probable that Fletcher and Hamilton's *G. rubicunda* is identical with *G. sanguinea,* a conclusion at which I understand Mr Fletcher has himself now arrived." (Dendy, 1892, page29); W1889 *Geoplana sanguinea* Gordon, NSW, Coll. T. Steel December 1903; AM W1857 *Geoplana sanguinea* Pennant Hills, NSW, Coll T. Steel June 1917, single sexual specimen sectioned 8μm, stained Steedman's Triple, anterior LSS 54 slides, pre-pharyngeal region TS / posterior LSS 54 slides.

Permission was not granted to fully section the Holotype (MNH 1877.11.2.10), and sections from one slide in the mid region of the copulatory organs washed off. The Holotype of *G. rubicunda* (AM W18454), whilst entirely sectioned was a young mature specimen; similar problems were encountered with lifting sections in the same region. AM W 1857 was entirely sectioned, is fully mature, and is almost identical anatomically to the Holotype of *A. sanguinea.* Descriptions of the internal anatomy of the species are largely based upon AM W1857, augmented by data of specimens MHN 1877.11.2.10 and AM W18454. Dimensions of spirit specimens are provided in Table 8.5-2.

Distribution:

A. sanguinea is found in a small area of some 330 square kilometres, bounded by Springwood, Pennant Hills, Gordon, and Parramatta, west of Sydney, NSW. All records appear to be from areas of natural habitat, now mostly urbanized. The most recent record is a specimen collected in 1917; none of the records are from urban gardens or nurseries. The species is uncommon, possibly rare. It may still survive in small pockets of natural vegetation within the area of occurrence, and in National Parks to the west and north east of the early localities.

EXTERNAL FEATURES:

Original diagnosis (Moseley, 1877 p. 285): "*Caenoplana sanguinea*.. closely resembles *C. coerulea,* with the exception that it is coloured of a uniform light red, which is lighter upon the under surface of the body.. Actual length when living 7cm; breadth 4mm". The Holotype was in two parts and was possibly incomplete (Fig. 8.5-1a-c), part probably having been taken for sectioning by Moseley. Ventral surface with a conspicuous median longitudinal pale zone 0.6mm wide. Eyes small, in a single row around the anterior tip (Fig. 8.5-1d).

Original diagnosis *Geoplana rubicunda* (in Fletcher & Hamilton, 1887, p370): "*Geoplana rubicunda* ..Body tapering gradually anteriorly, more abruptly posteriorly, convex dorsally, flat ventrally (or somewhat concave in the median line), thin much depressed, contrasting markedly with *C. coerulea* in this respect. Dorsal surface of a brick red, somewhat darker in the anterior portion of the body and in the median line, otherwise fairly uniform; no indication of any stripes; undersurface of a lighter tint; in spirit the colours fade considerably. Eyes smaller and more difficult to make out than usual.... Length of a living specimen extended 60mm, breadth 2mm". Holotype with pale ventral median longitudinal zone about 1mm wide. Eyes in a single row around the anterior tip (cleared specimen).

INTERNAL FEATURES:

Head:

Adhesive suckers with associated muscular specializations absent. Anterior bracing by dorsal transverse and subneural transverse parenchymal muscles. Eyes very small (pin point), pigment cup-type, 70-85μm diameter, in single row around anterior tip, submarginally to posterior. Sensory pits small, simple, sparse, absent around anterior tip, present anterolaterally, approximately 14μm diameter, 28μm deep (AM W18454. 7.5μm diameter, 28μm deep), with proximal fine cyanophil granules.

Pre-pharyngeal region:

Dorsal (12.6μm) thinner than ventral (21.6μm) epithelium. Rhabdoids of rhammite type, 12.6μm long, present dorsolaterally, ventrally, sparsely over creeping sole. Xanthophil secretions abundant dorsolaterally, ventrally, lighter over creeping sole. Cyanophil secretions present dorsally, more numerous ventrolaterally. Ciliated creeping sole 16% body width (MNH Holotype 16%; W18454 17%). Cutaneous musculature tripartite, with circular, decussate helical, and strong longitudinal muscles in bundles. CMI 8.5 - % (MNH Holotype 13%; W18454 12.8%). Parenchymal musculature with strong dorsal, infraintestinal and infraneural diagonal muscles in bundles, with dorsoventral muscles; longitudinal muscles sparse to absent.

Alimentary tract:

Pharynx cylindrical, elongate, folded back within itself, with inner pharynx with ciliated infranucleate epithelium, then circular, longitudinal, then ectal circular muscles; outer pharynx with longitudinal, circular, then ectal longitudinal muscles;

Oesophagus present, with rugose infranucleate ciliated epithelium, then thick layer of circular muscles, thin layer of longitudinal muscles, then thin ectal layer of circular muscles. Pharyngeal pouch 5.1mm long; 8.8% body length (W18454, 4mm long, 7.6% body length) including posterior diverticulum. Mouth situated approximately mid pouch. Pouch with flattened (almost squamous) nucleate epithelium with finely granular cyanophil cytoplasm, inner longitudinal, circular, longitudinal musculature. Diverticulum present, with thicker pouch-type epithelium, receives granular cyanophil secretions from elongate gland cells surrounding diverticulum, cyanophil granules secreted in apocrine manner. Diverticulum receives numerous nephridial exit canals from abundant protonephridial elements in surrounding mesenchyme.

Reproductive organs:

Copulatory organs (Fig. 8.5-1e AM W18454). Testes ventral, laterodorsal to nerve cords, uniserial, staggered, spheroidal, some 170μm diameter, 270μm high, extend from just behind ovaries almost to pharynx. Sperm ductules exit lower testicular poles, pass ventrally below nerve cord, enter longitudinal collecting ducts linked by intermediate ducts that open into sub-neural vas deferens. Vas deferentia rise behind pharynx, form spermiducal vesicles, then separately pierce penis bulb, unite, enter seminal duct. Seminal duct receives fine granular cyanophil, erythrophil secretions; prostatic duct receives fine granular erythrophil secretions. Both seminal, prostatic ducts tortuous, with low columnar ciliated epithelium, weak circular muscles. Penial bulb with outer sheath of weak longitudinal, helical muscles, with inner weakly muscularised stroma; penial glands present in surrounding mesenchyme. Prostatic duct passes into long sinuous ejaculatory duct, with strong circular musculature, with ciliated cuboidal epithelium. Ejaculatory duct opens into male atrium through strongly muscularised intra-antral conical penis papilla, with anucleate facing epithelium. Male atrium elongate, with secretory epithelium, with erythrophil granules in globules secreted in apocrine manner. Atrial roof above penis papilla with secretory epithelium with cyanophil globules secreted in apocrine manner.

Ovaries, elongate, lie on lateral nerve cords approximately 4mm from anterior tip. Ovovitelline duct enters ovary from posterolateral side via tuba, sphincter;

continues posteriorly along dorsal side of lateral nerve cords, behind copulatory organs incurve, unite, form common ovovitelline duct, passes into proximal swollen end of female genital canal. Female genital canal horizontal, with strong circular musculature, receives shell glands, opens from lower posterior atrial wall; female atrium with large surface area, with cocoon-making epithelium (sclerotin cyanophil strand cells, erythrophil globule cells), with highly folded roof, deeply horizontally folded lateral posterior wall (tongue-like, Fig. 8.5-1e af).

Male, female atria approximately equal length. Gonopore situated centrally, with lateral atrial walls either side of gonopore with secretory epithelium receiving fine granular cyanophil secretions. Atrial musculature very strong, with inner longitudinal then intermixed circular, longitudinal muscles. Vitellaria extensive, surround intestinal diverticula, open into ovovitelline duct via short vitelline funnels. Viscid gland absent. Glandulomuscular organs (adenodactyls) absent.

Pathology: Phoretic nematode larvae present in mesenchyme (W18454). Gregarine sporozoan cysts present in W1857.

Etymology:

The specific epithet *sanguinea* from the Latin *sanguineus* – blood red, alludes to the blood-red colour of the species. Gender feminine. *Australoplana sanguinea* – the Blood-red Southern Planarian.

Systematic discussion:

A case of mistaken identity: resolution of the *sanguinea* species problem.

Since 1877, every taxonomist working on the austral Terricola has confused *Australoplana sanguinea* (Moseley, 1877) with taxa of similar external morphology. Dendy (1895b, page 729) succinctly captured the essence of the problem, which has persisted to the present, noting "I have at length ventured to revise the nomenclature of the common and widely distributed *Geoplana sanguinea*, which has been described under a different name by nearly every writer who has dealt with it. The reasons for this confusion lie in its variability in colour, the absence of definite markings, and the poorness of the original description." Dendy went on to unwittingly further confuse the picture, and in so doing underlined the limitations of species determinations based solely upon external characters. Histological studies of the Types and other specimens of relevant taxa within the context of this thesis have resolved the problem.

Of the numerous literature records of the species *sanguinea* only those of Moseley (1877), and Fletcher & Hamilton (1888) (*rubicunda*) are in fact *sanguinea sensu stricto*. Of the seventy nine specimen lots comprising some 150 specimens identified as *sanguinea* held in various collections, many of which support literature records, only four are specimens of *sanguinea sensu stricto*, described here from Springwood, Pennant Hills, Parramatta and Gordon. No attempt is made in this thesis to do other than cite the principal synonymies and non-synonymies for *sanguinea*. Literature records are summarized in the Index to Land Planarians of the World (Ogren *et al* and Kawakatsu *et al*), and shall be dealt with at length elsewhere.

Australoplana sanguinea sensu lato comprised at least five species presently assigned to three genera.

The initial source of confusion lay in Moseley's (1877) inaccurate generic diagnosis of *Caenoplana* and poor external description of his *Caenoplana sanguinea* from Parramatta NSW:

1. The generic description was incorrect in that –

    a) "eyes absent from the front of the anterior extremity" – the eyes are present around the anterior tip;
    b) "but present in two lateral elongated crowded patches placed just behind the anterior extremity .." – this is true for *C. coerulea*, but incorrect for *C. sanguinea* in which the eyes are in a single row.
    c) "without an ambulacral line", which is true for *C. coerulea* . However there was no mention in the description of the pale mid ventral zone present in *C. sanguinea*, clearly evident in the Holotype and noted by Graff (1899).
    d) "Mouth nearly central", which is true for *C. coerulea*; in C. *sanguinea*

the mouth is displaced posteriorly in the second third of the body.

The genus in fact comprised two genera (Winsor, 1991a) – *Caenoplana* (*coerulea* and *subviridis)* and *Australoplana* (*sanguinea*).

2. The external morphology of *C. sanguinea* was likened to that of *C. coerulea* "Closely resembles *C. coerulea* ..". This is a fair observation of the spirit preserved Holotypes, though the description does not state that the comment refers to preserved material. The main points of difference in the Holotypes are eye pattern, cross sectional body shape, position of body apertures, and ventral marking. There is no close similarity between living specimens of these species – *C. sanguinea* is broad, straplike and dorsoventrally flattened, whereas *C. coerulea* is thick, elongate and sub-cylindrical in cross sectional shape.

The inaccuracies concerning the distribution of eyes in the generic description, and poor description of *C. sanguinea,* misled Fletcher and Hamilton (1888) in their descriptions of new Australian Terricola. They stated, "We have never met with an example of this species" (Ibid p 363). Later in the same paper (Ibid, page 370) they described from the Blue Mountains, NSW, *Geoplana rubicunda*, now shown to be synonymous with *sanguinea* (this thesis). They also inadvertently introduced a second point of confusion into their account by including in their species, " six specimens above-mentioned were among a number of planarians obtained at one of the Sydney nurseries, and given to us by Mr Masters" (Ibid, page 370). Although most of these six specimens have been lost, the dimensions cited (Ibid, page 370) and external examination of one extant specimen suggest that they were species of *Nelipoplana.*

Dendy (1891) described *Geoplana alba* (now *Nelipoplana alba* this thesis) from the eastern highlands and elsewhere in Victoria, and Spencer (1891) provided further records. Later Dendy (1892e) considered that *sanguinea* = *rubicunda*, and that *sanguinea*, especially small "Indian Red" coloured specimens from Castlemaine (now *Nelipoplana enigma*), probably represented the darker red colour forms of *alba.* The colour of *alba* and other pale species is now known to often reflect the colour of the ingesta. He included the New Zealand species *Rhynchodemus testaceus*, now *Artioposthia testacea*, in the synonymy for *sanguinea* (Dendy 1895c) and later found difficulty distinguishing between *sanguinea* and his *Geoplana triangulata australis* (now *Artioposthia australis*) (in Dendy 1897); his Invercargill specimen of *sanguinea* is *Artioposthia australis* (in Fyfe, 1948 page 64), and likewise probably his *sanguinea* from Lake Mahinapua (AM W1993). In his monograph of the Terricola, Graff (1899) considered *alba, alba roseolineata,* and *rubicunda*, but not *testacea* to be synonymous with *sanguinea.* Steel (1901) described *sanguinea* from Tasmania, where he found it co-occurring with *G. typhlops* (originally described as an eyeless form of *alba* by Dendy who later placed it in a separate species – now *Bassioplana typhlops* this thesis).

Fyfe (1948), within the context of her taxonomic revision of New Zealand Terricola, resolved the identity of Dendy's Invercargill *sanguinea* (*Artioposthia australis*) and tried to resolve the identity of the "real *G. sanguinea*". She histologically examined and described the copulatory organs of non-Type specimens identified by Steel as *Geoplana sanguinea* from NSW, Victoria and Tasmania, from the collections of the Australian Museum. All the specimens were *Nelipoplana alba* (Dendy) (this thesis).

Jones (1981), in attempting to determine the identity of a species from the Scilly Isles examined sections of the *Caenoplana sanguinea* Holotype (sectioned earlier by LW), and a non -Type specimen from near Ballarat, Victoria identified by Dendy as *Geoplana alba.* The Scilly Isles specimen appeared to share characters of both *sanguinea* and *alba*, though had a unique character, "some longitudinal muscle bundles dorsal to the ventral nerve cords" (Jones 1981 page 842) absent in the other two taxa. Unable to resolve the identity of the species, Jones referred to it as *Geoplana sanguinea* (Moseley) var *alba (Dendy)* – now *Nelipoplana enigma* (refer to the systematic discussion on this species under *Nelipoplana*, this thesis).

What can be regarded as *Dendy's Dictum* – that " *sanguinea* is described under a different name by nearly every writer who has deals with it" (Dendy, 1895c) continued to hold true. Ball & Reynoldson (1981) synonymised within *Geoplana sanguinea* the species *rubicunda, alba,* and *sanguinea* var *alba*; the synonymy of the latter two species was not accepted by peer taxonomists. Later, Ogren & Kawakatsu (1991) placed *sanguinea* within the inclusive genus *Australopacifica* and synonymised within *Australopacifica sanguinea* the species *rubicunda,* together with numerous austral literature records of specimens referred to or identified as *sanguinea*. Under *alba* they synonymised *alba roseolineata* and *sanguinea* var *alba* sensu Jones, and curiously, assigned *alba* to *Caenoplana*, their emended generic diagnosis of which does not apply to the species. Winsor (1991c) erected *Australoplana* to accommodate the small-eyed, broad, strap-like species with posteriorly displaced body apertures. Within the genus he recognized three broad species groups, considered at the beginning of this discussion, which are accepted by peer taxonomists.

Table 8.5-1
Australoplana s.l.
Comparative data

Taxon	eyes	c'sole	cutmusc	CMI	Pharynx	PP divertic	Px inner	Px outer
Australoplana	Y	Y	tripartite	10 -18%	cyl fold	Y	cm lm cm	lm cm
Apogaioplana	N	N	tripartite	9.0%	cyl fold	Y	cm mix lm	lm cm lm
Bassioplana	N	Y	tripartite	11.8 -13%	bell	Y	cm mix cm	cm lm
Sokoplana	Y	N	tripartite +	11.0%	bell	N	lm cm lm	lm cm lm
Nelipoplana Nelipoplana	Y	N	tripartite	15.5 - 18%	bell	Y	lm cml m	lm cm lm
Nelipoplana Peokrypta	Y	N	tripartite	9.6 -11.7%	bell	Y	lm cm lm	lm cm lm

Taxon	penis pap	sv - pd	musc	gc-fa	viscidgl
Australoplana	Y	tube	mixed	under	absent
Apogaioplana	Y	tube	mixed	under	Y bent
Bassioplana	poorly diff	tube	different'd	inline+	Y
Sokoplana	Y	sv+p cav	different'd	inline	Y bent
Nelipoplana Nelipoplana	Y	sdv / pcav	mixed	inline	Y
Nelipoplana Peokrypta	poorly diff	tube	mixed	inline	absent

Key to headings:
Taxon, eyes present, creeping sole present, cutaneous musculature, Cutaneous Muscular Index, Pharynx type
Pharyngeal pouch diverticulum presence, Inner pharyngeal musculature, outer pharyngeal musculature,
Penis papilla presence, seminal vesicle-prostatic duct type, bulb musculature, genital canal-female antrum relative positions, viscid gland presence

Key to responses:
Y = yes, present; N = no, absent. Cyl = cylindrical, fold = folded, cm = circular muscle, mix = mixed circular and longitudinal muscles, lm = longitudinal muscles, poorly diff = poorly differentiated (papilla absent), tube = tubular type, sv+p cav = cavernous seminal vesicle and prostatic ducts, sdv = spermiducal vesicle, pcav = prostatic vesicle cavernous, bent = viscid gland with bend

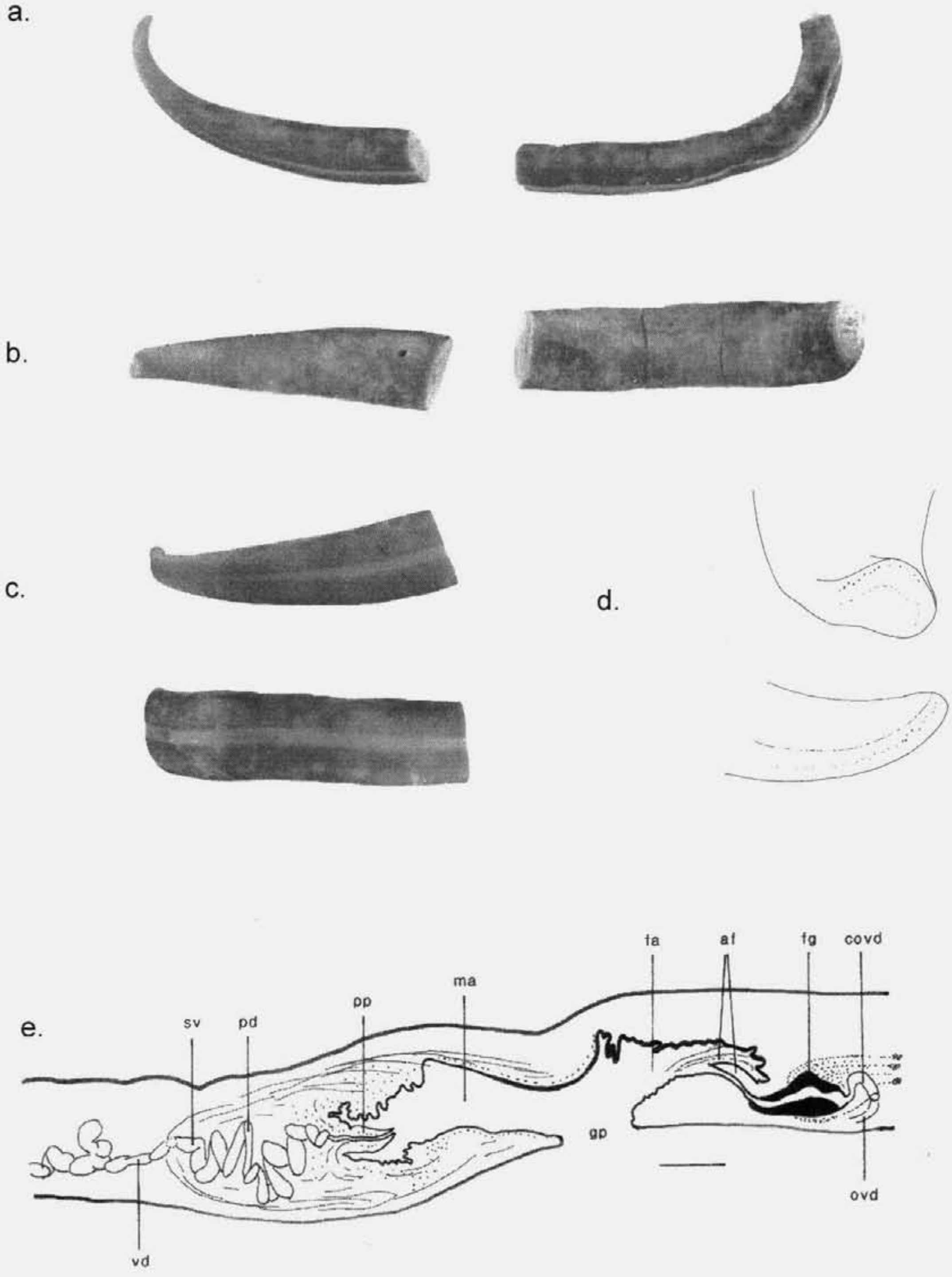


Figure 8.5-1 *Australoplana sanguinea* (Moseley, 1877)

a. Holotype, MHN 1877.11.12.10. Lateral aspect (b) dorsal aspect (c) ventral aspect. Length anterior piece 16mm, length posterior piece 17mm. (d) Holotype. Anterior end showing eye pattern. Unscaled.

e. Copulatory organs AMW18454. Mature. Scale bar = 500μm

8.6 Genus *Barringtoplana* gen.nov.

Barringtoplana gen.nov.

Diagnosis: Caenoplaninae with small, broad body, tapered slightly more anteriorly than posteriorly. With mouth just behind mid body, gonopore in last body quarter. Creeping sole almost entire width of body. Anterior adhesive pad or sucker absent. Sensory papillae absent. Eyes pigment cup-type, in single row around tip, submarginally along body. Cutaneous musculature bipartite, with layer of helicoid muscles underlain by well-developed sheath of cutaneous longitudinal muscles in bundles. Cutaneous musculature developed more strongly ventrally than dorsally. CMI 5.2-6.3%. Paranchymal musculature weak, with transverse-oblique muscles in ventral plate. Pharynx cylindrical, with distinct oesophagus. Pharyngeal musculature with inner epithelium, thin circular, then mixed circular-longitudinal muscles. Outer pharyngeal musculature with epithelium, longitudinal, then broad band of weak mixed circular-longitudinal muscles. Testes, sperm ducts ventral. Testes extend from just behind ovaries, to just beyond female copulatory organs. Vasa deferentia unite, then enter bulb, seminal duct, prostatic duct; with muscular ejaculatory duct, with partly sheathed penis papilla, with specialized secretory elements. Ovaries anterior, pre-pharyngeal. Ovovitelline ducts with tubae; unite, form common duct, enters female genital canal ventroposteriorly, female canal expanded, enters dorsoposterior female antrum. Adenodactyls present. Viscid gland absent.

Etymology: *Barringtoplana*, The Barrington Tops Planarian, a name contrived from the name of the location where it was found, and the Latin *plana,* flat. Gender feminine. Type of genus: *Barringtoplana harrisoni* (Wood, 1926)

Locality: Barrington Tops, and Sharpes Creek, Barrington Tops National Park, NSW, Australia, 156°26' E 32°02'S; Point Lookout, New England National Park, NSW; Copeland Tops State Forest, north west of Gloucester, NSW, 151°51'E 32°01'S.

Systematic discussion: The presence of adenodactyls in the copulatory organs led Wood (1926) to assign the species *harrisoni* to the genus *Artioposthia.* Her succinct description of *A. harrisoni* did not include details of the eyes and eye pattern, or a description of the histology of the internal structures such as body musculature.

Artioposthia was later found to be heterogenous and was divided into five groups, chiefly on the basis of body musculature (Winsor, 1991c). *A. harrisoni* was tentatively allocated to Group 5 characterized as "body robust, elongate; convex dorsally, slightly concave ventrally; with strong cutaneous longitudinal muscles, the ventral muscles developed slightly more developed than those dorsally; parenchymal longitudinal muscles weak or absent". Re-examination of the Type specimen of *A. harrisoni* revealed characters that excluded the species from *Artioposthia*, but required that it be accommodated in a new genus *Barringtoplana.*

Barringtoplana shares with the caenoplaninids *Caenoplana* and *Kynagoplana* (this thesis), the apomorphy of a bipartite cutaneous musculature, though stronger dorsally than ventrally. The parenchymal musculature in *Barringtoplana* is predominantly composed of helicoid muscles, reduced to a ventral plate; longitudinal parenchymal muscles are absent. *Barringtoplana* differs from *Caenoplana* and *Kynagoplana* in external morphology, the relative position of the body apertures, the extreme width of the creeping sole, single row of eyes, absence of parenchymal longitudinal muscles, presence of an oesophagus, and presence of adenodactyls and a penis papilla. *Barringtoplana* is differentiated from taxa within Artioposthia chiefly by its bipartite cutaneous musculature and unusual glandular sheathed penis papilla.

Barringtoplana harrisoni (Wood, 1926) comb.nov.

Artioposthia harrisoni Wood, 1926; Winsor 1991c; Ogren & Kawakatsu 1991

Material examined:

Holotype: AM W2351. A series of five microslides, serial sections 8µm thick, stained with (? Erlich's) haematoxylin, and eosin, mounted in Canada Balsam. The series comprises the anterior end, LVS, two slides A, B, and posterior end, TS, three slides, A, B, C, registered 21 April, 1927.

Paratype: AM W2363, a single specimen, 3mm wide, divided into an anterior portion 17 mm long, and a posterior portion 5mm long, registered 22 April 1927. The body apertures are not clear. These two portions appear to be from the same specimen.

Wood (1926) did not designate a Type in her paper, though the description of the external morphology and microanatomy is based on the sectioned specimen. Both the microslides and the specimen are labelled "Type" in Wood's handwriting. The letter from Wood to the Director of the Australian Museum (Letter No. 285/27) does not provide further information.

Missing Type material. The 17mm long specimen was sectioned at 8µm (indicated on the microslides). The anterior portion of the sectioned specimen measures 3mm. The transverse sections of the posterior equate to a length of 3.7mm. This leaves an 8.4 mm pre-pharyngeal portion of the original specimen missing, estimated to be 226 sections, the equivalent of the capacity of one microslide, corroborated by the number of sections on other slides in this series. The anteriad section of posterior slide A shows the penis bulb and the region Wood termed the seminal vesicle. The first section of posterior slide B, which should show the continuation of the prostatic vesicle, is in fact is well forward of the copulatory organs.

Other material: AM 10211, single specimen, near Point Lookout, New England National Park, bank of stream, collected by J. A. Bishop, 1 April 1961; LW 1280, single immature specimen, Copeland Tops State Forest, north west of Gloucester, N.S.W., 151°51'E 32°01'S; LW1283b, single immature specimen, Sharpes Creek, Barrington Tops National Park, 156°26' E 32°02'S, N.S.W. Dimensions of specimens of *B. harrisoni* examined are provided in Table 8.6-1.

EXTERNAL FEATURES:

Wood (1926) described this attractive small species as having a dorsal surface ground colour of creamish white, with a wide median stripe of ground colour bounded on either side by a narrower black stripe with a definite median border and an indefinite lateral border. According to Wood, laterally the body is marked off by a number of small dark brown spots. The ventral surface is white. At the anterior end the black stripes of the dorsal surface broaden, become brownish in colour and extend submarginally towards the ventral surface.

The external morphology of B. *harrisoni* (Fig. 8.6-1a, b) LW1280 is close to Wood's description, though the mouth is just behind mid-body, rather than well before mid body as indicated by Wood for the Type specimen. The median stripe extends almost to the anterior tip, and right to the posterior tip. Irregular longitudinal dark brown striae and mottling extend dorsolaterally from the dark stripes on either side of the light median stripe. The eyes are distinct, in a single row around the anterior tip and along the margins until lost in the dark pigment. The ventral surface is a uniform cream colour, with the pale sensorial zones delineated by a thin fuzzy line of brown pigment.

INTERNAL ANATOMY

Head:

Without adhesive structure or associated specialization of musculature in anterior end. Gut extends almost to extreme tip, overlain by parenchymal musculature and secretory elements, underlain by ganglion, ovaries and testes.

Sensory pits simple, tubular, 50μm deep, in non-pigmented zone around the underside of anterior tip and short distance ventro-laterally. Eyes pigment cup type, 23 - 42μm diameter, in single row around tip and anterior body (Fig. 8.6-1c), sparsely in submarginal row (number of eyes, and number of retinal clubs in each ocellus could not be ascertained).

Pre-pharyngeal region:

A schematic representation of the transverse pre-pharyngeal region is provided in Fig. 8.6-1d. Dorsal epithelium thinner (17μm) than ventral epithelium (22.6μm). Rhabdoids are rhammite type 12.6 - 14.4μm long, secreted from dorso lateral epithelium, continuing almost to margin of ciliated creeping sole, sparsely through the latter. Epitheliosomes secreted through the ventral epithelium. Erythrophil glands numerous dorsolaterally and ventrally anteriorly, cyanophil glands present ventrally. Fine granular yellow-brown pigment present in epithelium in regions corresponding to paired dark dorsal stripes. Creeping sole epithelium ciliated, nucleate, 2300μm wide, 99% of body width. Cutaneous musculature bipartite, with thin sheath of helical fibres, oriented more circularly than obliquely, strongest dorsally, together with well-developed bundles of longitudinal muscles. Longitudinal muscle bundles weak dorsally (12.6 - 19.8μm high), strongest ventrally (23.4 - 32.4μm high) where muscle fibres divided by dorso-ventral fibres into irregular compact bundles. Dorsal cutaneous musculature 22-28μm high, ventral cutaneous musculature 36-42μm high, postpharyngeal height of body midline 1103μm. CMI is 5.2 - 6.3%. Parenchymal musculature well developed, present as ventral plate of strong meshwork of transverse-oblique fibres, similarly developed dorsally but thinner. Parenchymal longitudinal muscles absent. Strong peri-intestinal muscles present.

Alimentary system:

Pharynx cylindrical, horizontal, 530μm long, with ventral pharyngeal insertion anterior to dorsal insertion. Pharyngeal pocket 736μm long, 4.3% of body length, with mouth situated almost three quarters along pouch. Diverticula absent. Pharyngeal musculature with folded inner infranucleate ciliated epithelium, thin circular, then mixed circular-longitudinal muscles. Outer pharyngeal musculature with infranucleate ciliated epithelium, longitudinal, then broad band of weak mixed circular-longitudinal muscles. Oesophagus 240μm long, present forward of pharyngeal insertion where inner circular muscle layer becomes acentric, thicker ventrally, increasing in thickness from 53μm distally to 356μm proximally; inner epithelium flattened, nucleate and non-ciliated, with sharp transition to gastrodermis. Gastrodermis is heavily loaded with phagocytosed digesta, and has an almost syncytial appearance (possibly from 4-12 hours post feeding, based on criteria provided by Jennings (1959) from observations on *Microplana terrestris*). Gut diverticula extend almost to anterior tip brain.

Reproductive organs:

Copulatory organs complex, extend over 1.3mm, compact, with eleven adenodactyls, with blunt penis papilla, within a crowded common atrium (Fig. 8.6-2a, b, c, d, e, f; Fig. 8.6-3, 1-8). Antrum differentiated dorsoventrally: dorsal-half lined by sclerotin-forming cuboidal to low columnar, nucleate, often papillate, secretory epithelium restricted mostly to sulci in atrial wall at base of adenodactyls, penis papilla, and sheaths surrounding some adenodactyls and distal penis. Ventral-half of atrium and adenodactyls with flattened nucleate facing epithelium. Gonopore located in anterior third of atrial floor.

Adenodactyls: Nomenclature of the adenodactyls (Table 8.6-2) follows the original description (Wood 1926), with those adenodactyls posterior to the gonopore considered "female" and those anterior of the gonopore "male". With respect to bilateral symmetry they include three unpaired, and eight paired adenodactyls. Three of the adenodactyls are sheathed (Fig. 8.6-1 e-h). In these adenodactyls the subterminal portion of the adenodactyl is partly enclosed along its length by a sheath derived from the atrial wall. The outer margins of these sheaths bear intraepithelial glands, comprising a low columnar papillate epithelium through which fine ducts discharge cyanophil sclerotins - in essence a secretory ridge or margin. Immediately inside the sheaths are fine longitudinal folds that are regarded as sulciform glands.

Type IV and Type V of adenodactyls present. All adenodactyls are covered by a thin flattened nucleate epithelium over most of their surface, underlain by a prominent basement membrane. Musculature underlying the outer and duct epithelia of both types of adenodactyl is similar consisting of an outer circular muscle layer underlain by longitudinal muscles. The ectal adenodactyl musculature is slightly stronger than that surrounding the central duct and reservoir.

Type IV adenodactyls small, 2μm (Adf) to 390μm (Adm1) long, weakly muscularised, with secretory gland ducts in stroma passing between sparse circular, radial and longitudinal muscles; small reservoir in proximal duct with pale-staining cyanophil secretions; distal duct with erythrophil secretions, secreted into a subterminal expansion of duct.

Type V adenodactyls large, with sheathed adenodactyl Adf2 (left) representative of this group (Fig. 8.6-1c-g): adenodactyl 490μm long, with reservoir maximum diameter 89μm, combined reservoir and duct 320μm long; duct in two regions: the proximal part 120μm long, continuous with reservoir, receives strongly cyanophil secretions; distal duct receives pale staining cyanophil secretions. Cyanophil glands 18μm long, with nuclei 9μm diameter, located in dorsad mesenchyme immediately below rhabditogen cells pass secretions via elongate necks to Type V adenodactyls; just before entering adenodactyls secretions become strongly cyanophil. Distal duct tapers from 22μm diameter just below proximal duct, to almost 6μm diameter at the tip, with pale cyanophil secretions derived from glands in adjacent wall of copulatory apparatus discharge into distal duct over most of length; secretions delivered via fine elongate gland cell necks grouped into discrete bundles surrounding distal duct.

Testes ventral, loculate, lie below gut, along nerve cords from which they extend laterad almost to rhabditogen cells, and dorsad about half way up body. Testes begin just behind ovaries, extend posteriorly to just behind copulatory organs; measure 190μm high, 90μm long, and 180μm wide. Testicular funnel fine, passes from lower pole of each testis to intertesticular duct immediately below testes, intertesticular ducts as network, feed into intermediary ducts that traverse lower nerve cord. Intermediary ducts link collecting duct lying below with vas deferens lying above medial margin of the lateral nerve cord on either side. Intermediary and collecting ducts lined by low cuboidal nucleate non-ciliated epithelium.

Vasa deferentia, lined by nucleate epithelium with stereocilia, pass posteriorly, almost doubling diameter towards copulatory organs. Approximately 1.8 mm forward of the last section of mid penis is missing, thus entry of the vas deferens into the penis bulb could not be determined in the Type specimen.

Penis bulb surrounded on either side by gut, merges with mesenchyme immediately below dorsal cutaneous musculature. Portion of bulb protrudes into atrium. Single adenodactyl directed towards right posterior of atrium arises from mid base of bulb (Fig. 8.6-4a). Ejaculatory duct opens into atrium via flattened insunk papilla surrounded by a secretory meatus, lying within sheath formed from concentric fold of atrial wall (Fig. 8.6-4b). Sheath surrounding tip of the penis with slightly papillate nucleate epithelium similar to that of adenodactyl sheaths. Penial glands in bulb discharge secretions at meatus; secretions appear blue-grey, more related to cocoon formation rather than copulatory functions. Secretory ridge. present on angular margins of penis papilla. Penial retractor muscles very strong, arise at lateral margins of the bulb, interconnect with lower sides of atrium extending almost to atrial floor. Circular muscles sparse, present around outer dorsal bulb and scattered throughout inner bulb; light circular musculature surrounds ejaculatory duct.

Penis bulb appears highly spongiform due to large number of fine secretory gland ducts it contains. Three types of penial glands present:

(a) erythrophil glands, close to atrial margin of bulb that secrete into crease formed between atrial wall and penis bulb protruding into male atrium. Secretions coarse granules 0.7μm diameter with gland nuclei 1.7μm diameter;

(b) weakly erythrophil glands immediately adjacent to ejaculatory duct.

(c) cyanophil glands largely situated in outer dorsal bulb probably servicing adenodactyl arising from lower right aspect of penis bulb. Secretion fine grained to amorphous, possibly sclerotin pre-cursor; gland cell nuclei 1.4μm diameter.

Only the mid and distal portions of the ejaculatory duct are present, and it is difficult to clearly determine the functional regions of the ejaculatory duct. The seminal vesicle is probably the widest potion of the duct, diameter 125µm, in the upper right of the bulb. The duct then narrows to some 90µm and twists down mediad in what is probably the prostatic region. In these two regions, the duct is lined by a nucleate cuboidal epithelium that secretes fine erythrophilic granules, derived from the adjacent bulb, in an apocrine manner like (b) above. The duct further narrows to about 50µm and the lining epithelium is less secretory.

Ovaries ventral, 1.25mm from the anterior tip, 200µm long, 100µm high, and 100µm wide, half embedded in lateral nerve trunks. Right ovary slightly smaller and more loculate than left ovary. Germinal centre (keimlager) lies just behind point where oviduct enters ovary. Oviduct with expanded proximal end forming a tuba that enters dorsomediad side of ovary, with muscular sphincter and occlusion cells present at point of insertion. Oviducts pass posteriorly along top of lateral nerve trunks, almost immediately behind ovary. Vitellaria small, situated between lower poles of adjacent testes; communicate with ovovitelline duct via short vitelline funnels. Ovovitelline ducts, with nucleate non-ciliated epithelium with cyanophil margin, surrounded by retiform tissue, comprising necks of secretory cells. Ducts continue well behind copulatory organs, then rise steeply, uniting to form common ovovitelline duct with pseudostratified nucleate epithelium with pale pink homogeneous cytoplasm with cyanophil margin. Common duct passes directly to female genital canal, which takes the form of a shallow U-shape with lowest portion expanded, then narrowing in diameter where it opens through median upper rear wall of atrium; with musculature of inner circular muscles and outer weak sheath of longitudinal muscles. Genital canal lined by non-ciliated columnar epithelium proximally; epithelium grades to one with dirty-maroon coloured erythrophil cytoplasm, lumenal margin of the epithelium is cyanophil and looks almost cuticular, receives secretions from erythrophil shell glands present in surrounding stroma.

Pathology:

There is a heavy infection of Gregarine sporozoites in the gut

Etymology:

The species is named in honour of Professor Lancelot Harrison, leader of the University of Sydney expedition to Barrington Tops, January and February 1925.

Ecology:

Other species found in the area include *Caenoplana coerulea*, *Kynagoplana citrina,* and *Platydemus assimilis* (Wood 1926). The specimen from Copeland Tops (about elevation 610 metres above sea level) was found in dry open forest on a ridge, in association with *Caenoplana coerulea* and *Parakontikia atrata.* At Sharpes Creek the specimen was found at about 1,000 metres above sea level in tall closed eucalypt forest together with *Caenoplana coerulea, C. variegata, Parakontikia atrata,* an *Australoplana* sp., and the nemertean Argonemertes *hillii.*

Systematic discussion:

In general body shape, the distribution of eyes and body apertures, pharynx, general conformation of the copulatory organs, and especially the unusual penis and associated secretory elements, B. *harrisoni* is similar to in the Amazonian geoplaninid species *Geoplana (Geoplana) ruiva* (Froehlich & Froehlich 1972). The main differences between these two species are the ventral testes and presence of adenodactyls in *B. harrisoni.* The male and female atria of *G (G) ruiva* are deeply folded, and it is not difficult to envisage, in another developmental lineage, the sequestration of secretory elements to form adenodactyls as in *B. harrisoni.*

Secretion of penial gland substances through gland necks piercing the penis papilla resulting in a secretory meatus is not common in the Terricola. In *G (G) ruiva* erythrophil glands open over the surface of the penis papilla, whilst cyanophil glands open from the basal half of the papilla and cresentic fold (Froehlich, 1972, p. 36). In *B. harrisoni* the papilial glands are cyanophil, the glands of the atrial fold erythrophil, and secretory ridges are also present. Species of the South American geoplaninid genus *Gigantea* has secretory ridges over the penis papilla. These secretory ridges share some similarity to the glandular ridges present on copulatory organs in *Barringtoplana,* though the former have discrete musculoglandular organs present, rather than deriving secretions from distant glands as in *B. harrisoni.*

The species is unusual in that in the Type specimen, from the dimensions provided by Wood, the mouth is well forward of the mid body, and the body apertures lie in the mid third of the body. In the immature Copeland Tops specimen the mouth is just behind the mid-body. It is conceivable that Wood mis-identified the anterior tip when measuring her specimen, and hence the relative positions of the body apertures are reversed. If this assumption is correct, then in the Type, the mouth lies 10.0 mm and gonopore 13 mm from the anterior tip, with mouth 58.8% and gonopore 76.5% of the body length. The relative position of the mouth in this situation accords well with specimens in the author's collection: LW1280 and LW1283b.

Because of the missing Type material Wood's statement that "the vasa deferentia unite just behind the pharyngeal region to form a slightly expanded vesicula seminalis", and her figure showing that the ducts appear to unite at the point they enter the penis bulb, cannot be confirmed. Thus the character states for the entry of the vasa deferentia into the penis: vasa deferentia enter bulb separately, or vasa deferentia combine to form a common sperm duct which then enters the bulb, cannot be determined from existing Type material.

Adenodactyls: Wood identified four paired and two un-paired adenodactyls: five situated near the "male aperture" and five near the "female aperture". In this study an additional adenodactyl, Adf', Type IV, was found just anterior of Adf on the right side. Wood's Figure 4 of the reconstruction of the genital organs in the region of the genital atrium depicts a very idealised bilateral symmetry, not noted in the specimen. The sheath-like structures present on three of the adenodactyls, and also around the penis, are an unusual apomorphy. A similar sheath is noted on one adenodactyl of *Artioposthia adelaidensis* (Graff, 1899, Ad*, text figures p229, 230, and atlas plate 32, figure 8). It is clear that these structures, together with the atrial sulci and secretory ridges, all secrete cocoon-making material and that the secretory elements appear to be the same. From the shape and arrangement of these structures, it is postulated that sclerotins could be secreted as a continual sheet or tube.

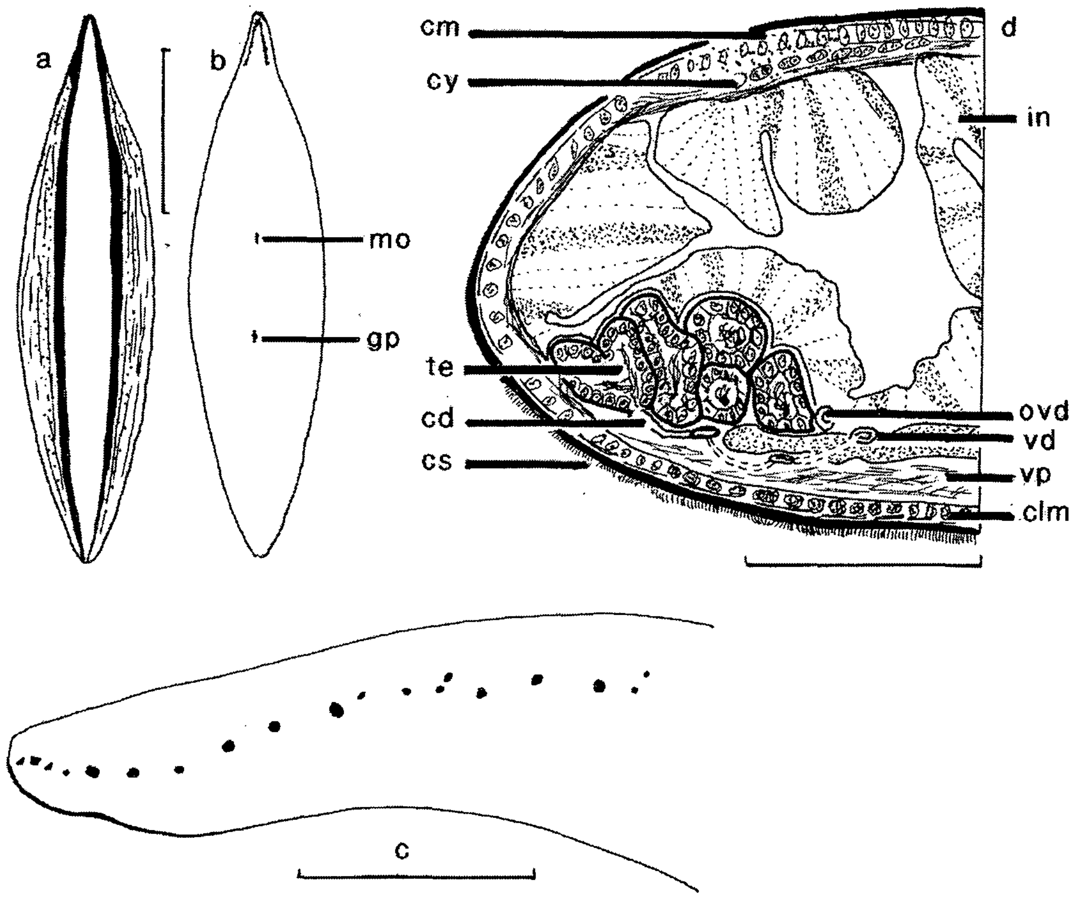


Figure 8.6-1 *Barringtoplana harrisoni* (Wood, 1926)

a. Dorsal aspect (after Wood 1926). Scale bar 5mm.
b. Ventral aspect (after Wood 1926)
c. Anterior end showing eye pattern. Scale bar 500µm.
d. Pre-pharyngeal region, transverse section. Scale bar 500µm.

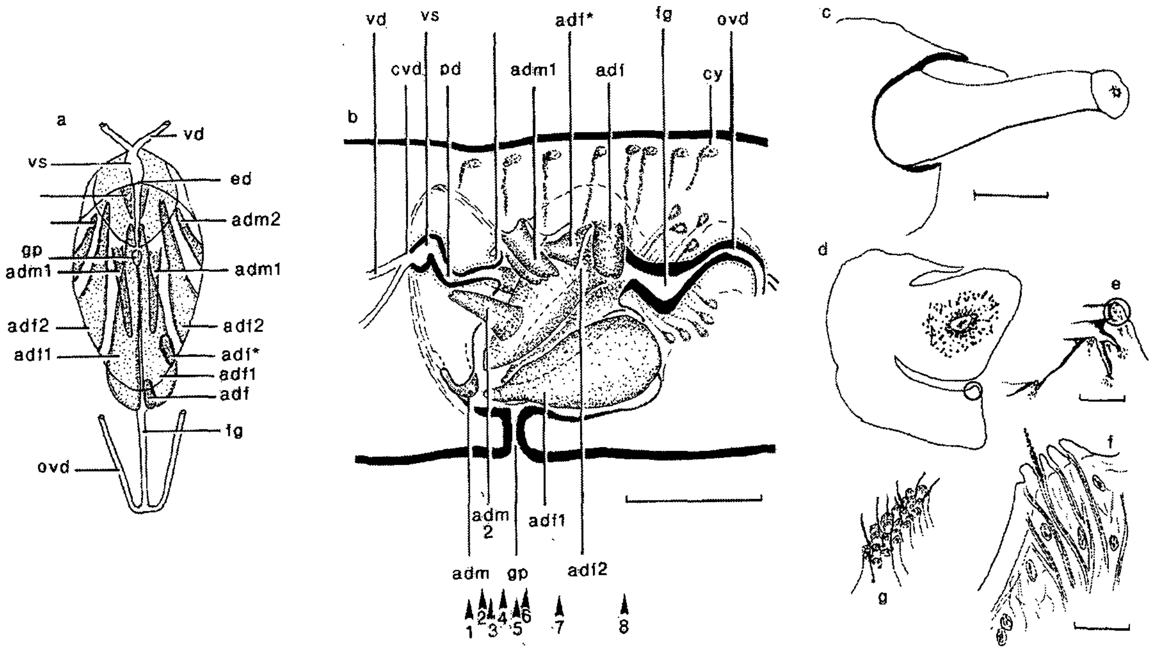


Figure 8.6-2 *Barringtoplana harrisoni* (Wood, 1926)

a. Copulatory organs, plan view (after Woods 1926), scaled to Fig. 8.6-2b. afd* indicates an adenodactyl present in the original sections but not noted by Wood 1926.
b. Copulatory organs, sagittal view. Scale bar 500µm. The numbers and arrows refer to the transverse sections depicted in Fig. 8.6-3
c. Sheathed adenodactyl. Scale bar100µm.
d. Sheathed Type V adenodactyl, transverse section showing sulci (to same scale as c.).
e. Intraepithelial glands with papilliform epithelium secreting sclerotin-like substance. Scale bar 25µm.
f. Detail of the papillae between which pass the secretions. Scale bar 20µm.
g. Impression of the appearance of the papillate epithelium. Unscaled.

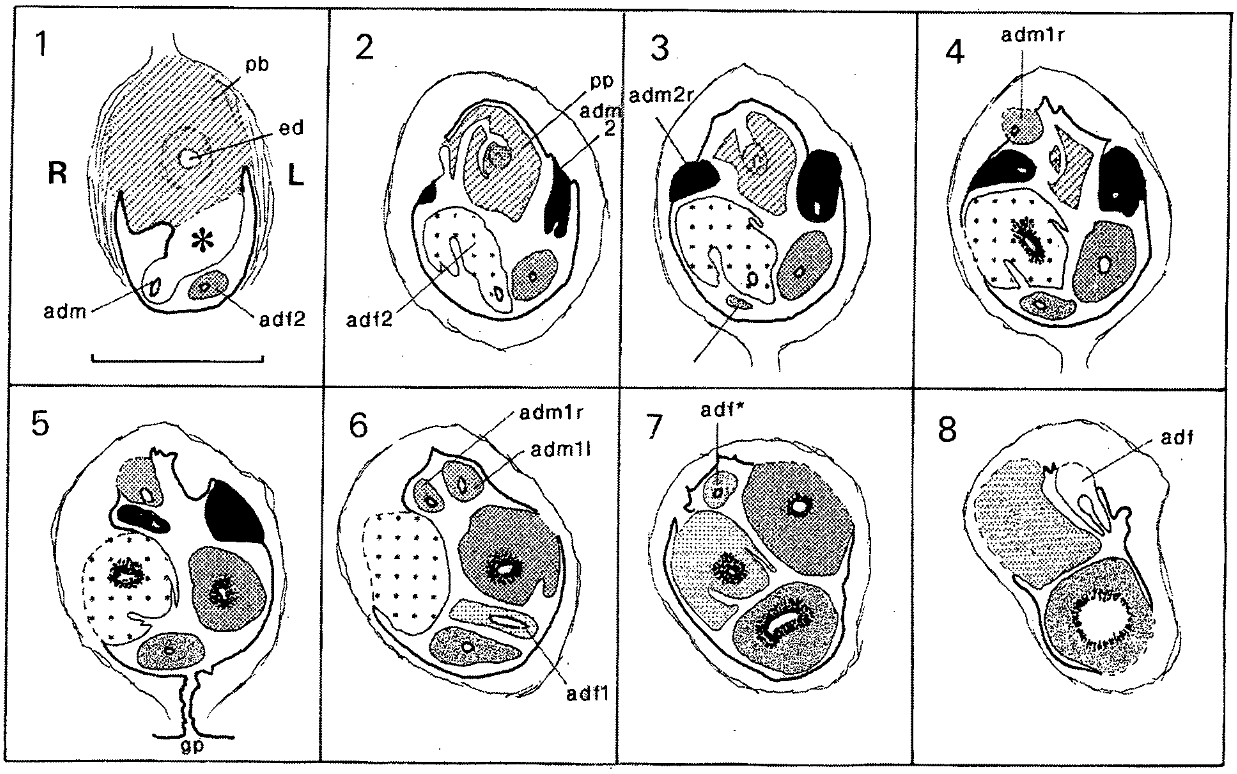


Figure 8.6-3 *Barringtoplana harrisoni* (Wood, 1926)

Transverse sections through regions of the copulatory organs illustrating relationships between the adenodactyls. Each numbered illustration corresponds to a number at the foot of Figure 8.6-2 b, indicating the area in the copulatory organs through which these transverse sections are taken.

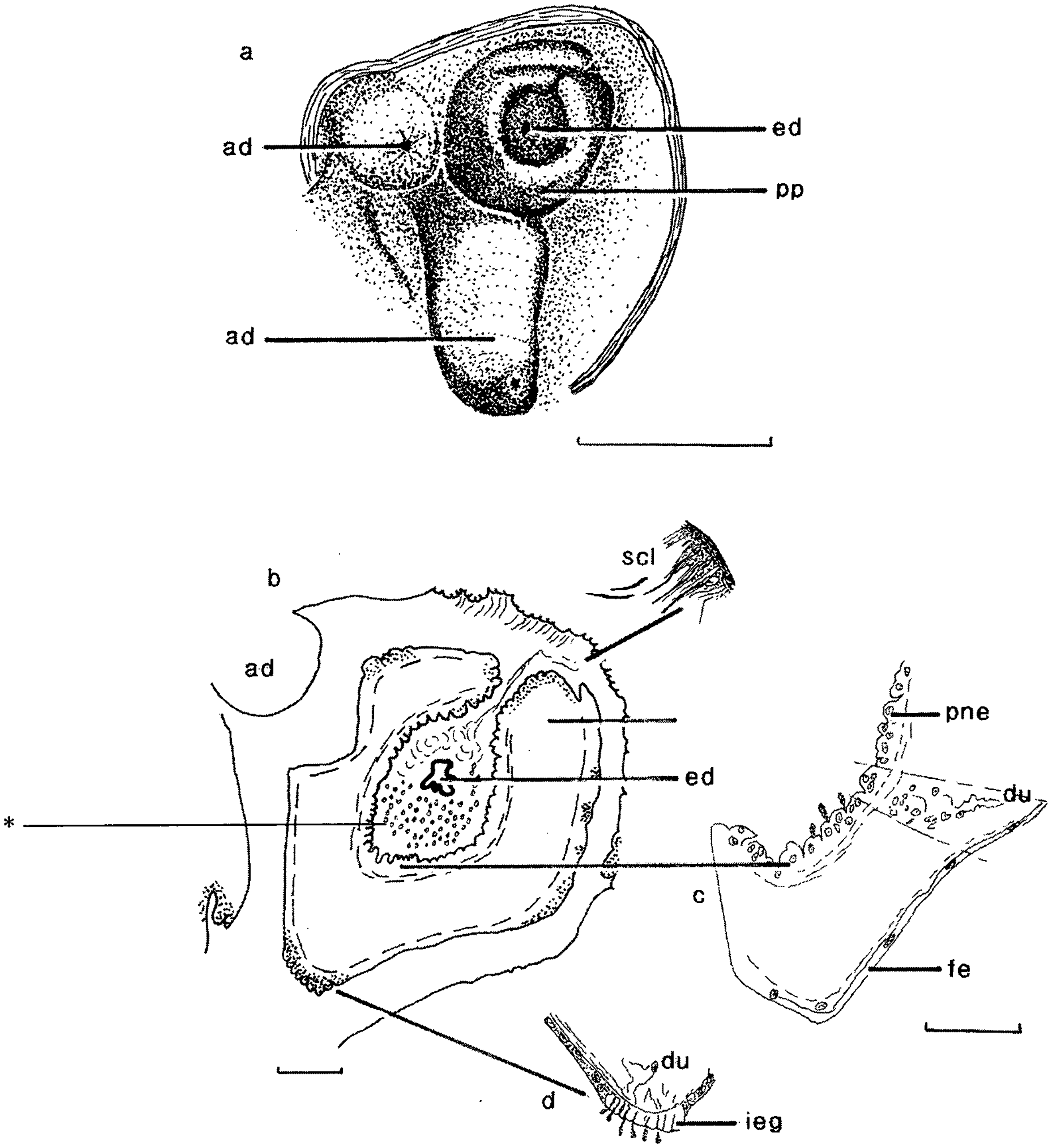


Figure 8.6-4 *Barringtoplana harrisoni* (Wood, 1926)

Details of the penis papilla and associated structures.

a. Impression of the appearance of the sheathed penis papilla and associated adenodactyls. Scale bar 200µm.
b. Transverse section through the penis papilla showing openings of penial glands (*) adjacent to the ejaculatory duct. Scale 50µm.
c. Details of inner secretory elements in penis sheath. Scale 50µm.
d. Details of the intraepithelial gland of the outer sheath. To same scale as d.

8.7 Genus *Bassioplana* gen.nov.

Bassioplana gen.nov.

Diagnosis: Caenoplaninae with elongate, strap-like body, convex dorsally, flat ventrally. Mouth in hind third of body, gonopore about midway between mouth and posterior end. Creeping sole 15% body width, present almost to anterior tip. Eyes absent. Anterior adhesive cup or pad absent. Sensory papillae absent. Cutaneous musculature tripartite, with circular muscles, with helical muscles almost longitudinally oriented ectally, almost circular entally; with strong longitudinal muscles in large bundles, dorsal musculature developed slightly more than ventrally, CMI 13%. Parenchymal musculature weak; longitudinal muscles sparse, very weak, single fibres. Pharynx bell-form. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; outer pharyngeal musculature with epithelium, circular, then longitudinal muscles. Testes ventral, dorsolateral to nerve cords, extending from behind ovaries to pharynx. Vasa deferentia enter penis bulb separately, unite, then pass into seminal vesicle anterodorsally. Ejaculatory duct tubular, weakly muscular; penis papilla present, poorly differentiated. Penis eversible type. Ovaries anterior. Ovovitelline ducts with shell glands distally (become paired genital (glandular) canals); paired genital canals enter dorsoposterior wall of female antrum separately. Female antrum almost horizontal, in ventro-posterior wall of common antrum. Antral musculature differentiated. Viscid gland present. Male antrum with adenodactyls (adenomuralia). Type species: *Bassioplana typhlops* (Dendy, 1894a).

Etymology: The genus name *Bassioplana* is derived from the name of George Bass (1771-1803), explorer and naturalist, who explored the southeastern coastline of New South Wales and Victoria, and who, with Mathew Flinders circumnavigated Tasmania. Gender feminine. The name commemorates Bass, and alludes to distribution of the species in the Bassian zoogeographic sub-region – The Bassian Planarian.

Distribution: Cool temperate zone of the Bassian zoogeographic sub-region, in northern, central, and southeastern Tasmania, and the north eastern highlands, Victoria.

Systematic discussion: Within the caenoplaninid genus *Australoplana sensu lato* in Winsor (1991c) a narrow creeping sole was found to be present in two groups: the *Australoplana typhlops* group, now *Bassioplana* gen.nov. and the *Australoplana sanguinea* group, now the restricted genus Australoplana. *Bassioplana* is differentiated from *Australoplana* chiefly by the absence of eyes (present in *Australoplana*), bell-form pharynx (cylindrical in *Australoplana*), mixed inner pharyngeal musculature (mixed musculature absent in *Australoplana*), poorly differentiated penis papilla (well differentiated in *Australoplana*), paired female genital canals separately entering the female antrum (single genital canal in *Australoplana*), presence of adenomuralia in male antrum (absent in *Australoplana*), and presence of a viscid gland (absent in *Australoplana*).

Bassioplana typhlops (Dendy, 1894a) comb. nov.

Geoplana alba Dendy, 1891; Dendy 1892f

Geoplana typhlops Dendy, 1894a; Graff 1899; Steel 1901b; Smith & Convey 1973; Winsor 1976; 1980

Australoplana typhlops (Dendy, 1894a), Winsor 1991c; Ogren *et al* 1993b

Australopacifica typhlops (Dendy, 1894a), Ogren & Kawakatsu 1991

Localities in literature:

Tasmania: Mount Wellington, Hobart, Parattah (Dendy, 1894a, b); Table Cape, Launceston (Steel, 1901); Hobart (Winsor, 1980). Victoria: Mitta Mitta Valley (Winsor, 1976).

Material examined:

Geoplana typhlops (Dendy, 1894a), AM G3189, Table Cape, Tasmania, Collected: vi. 1901.T. Steel, a series of 41 microslides: prepharyngeal region, 6 slides, TS, 8µm, MSB, Steedman's tripe; pharyngeal and copulatory region, LSS, 10µm, MSB; (anterior end has been cleared but not yet sectioned). AM G3188, Table Cape, Tasmania, June, 1901, T. Steel; AM W1844, Launceston, Tasmania, in garden, 19 February 1900, H.S. Dove; Trevallyn Hills near Launceston, Tasmania, 1899, H.S. Dove; TMAG, Blackman's Bay, Tasmania, 24 August, 1937, and Da 7, 6 September, 1937, both collected L. Rodway; QVML 1957.19.11, Cradle Valley, Tasmania, A. Connell; TMAG, Blackman's Bay, Tasmania, 27 October 1980, Mrs Clark; Department of Lands, Parks & Wildlife, P005, Huon River campsite, Scott's Peak Road, Tasmania, 9 April 1988, S. Smith.

Other material: The syntypes of *Bassioplana typhlops* have not yet been examined and are included within the specimen lots MNH 1924.8.15.456-466: Mt Wellington, Tasmania, March 1892, Mrs Dendy and L.J. Balfour; Hobart, Tasmania, collected A. Morton; Parattah, Tasmania, collected W.B. Spencer; Great Lake, Tasmania; Maria Island, Tasmania. ZMB 2408, Tasmania, A. Dendy. The two specimens forwarded by Dendy to Graff (Graff, 1899 page 365) are not present in Graff's collection and are presumed lost.

EXTERNAL FEATURES:

Body elongate, straplike, convex dorsally, flat ventrally, margins slightly crenulate when worm at rest (Fig. 8.7-1a). Dorsal ground colour white to pale brownish white, anterior tip and ventral surface white, with creeping sole paler than rest of ventral surface. Without stripes. Mouth in hind third of body, gonopore about midway between mouth and posterior end. Creeping sole 15% of body width, present almost to anterior tip, generally evident as a translucent mid ventral strip only in the preserved specimen. Eyes absent. Anterior adhesive cup or pad absent. Dimensions of the specimens examined are provided in Table 8.7-1.

INTERNAL ANATOMY:

Head:

The anterior end has been cleared, but not yet sectioned. Eyes, and adhesive pad or sucker, absent.

Pre-pharyngeal region:

Outer epithelium slightly thicker ventrally than dorsally. Rhabdoids of rhammite type. Creeping sole 600μm wide, 14.6% of body width. Epithelium with coarse, granular xanthophil secretions (orange, coarse granules), submarginal adhesive zone present. Erythrophil secretions and rhammites present ventrally. Cutaneous musculature tripartite, with circular, decussate helical and longitudinal muscles. Helical muscles very nearly longitudinal, with ental-most fibres almost circular appearing as layer of near-circular fibres within longitudinal muscle layer; with longitudinal muscles in large bundles. Dorsal cutaneous muscles (115 - 134μm thick) slightly stronger than ventral cutaneous muscles (106-112μm thick). CMI 11.8 - 13%. Parenchymal musculature weak, comprising dorsal transverse muscles, dorsoventral muscles, peri-intestinal muscles, with moderately strong infraneural transverse-helical muscles. Longitudinal muscles restricted to few widely scattered single fibres.

Alimentary tract:

Pharynx bell-form, with dorsal insertion posterior to ventral insertion. Pharyngeal musculature with single inner circular then mixed circular and longitudinal muscles, tending towards separate layers; outer pharyngeal wall with circular, then longitudinal muscle layers. Oesophagus absent. Pharyngeal pouch very long, 9.8% body length, with small posterior diverticulum; pouch roof with massive plate of circular muscles extending laterally to form pharyngeal walls. Mouth just forward of mid pouch.

Reproductive organs:

Reproductive organs (Fig. 8.7-1b). Testes ventral, uniserial, dorso-lateral to ventral nerve cords, mature, extend from behind ovaries to pharynx. Sperm ductule passes from ventral testicular pole, joins collecting duct passing below nerve cord to join sub-neural vas deferens. Just beyond anterior-most end of horizontal penis bulb vasa deferentia incurve, expand slightly, then separately penetrate the bulb rising to unite at proximal end of bulb to form tubular seminal vesicle that receives fine acidophilic secretions, rises, narrows slightly then becomes prostatic duct that receives cyanophil secretions. Duct then curves downwards posteriorly, expands, convolutes (twists) once, narrows to form short ejaculatory duct, then opens via poorly differentiated penis papilla into capacious male antrum. Penis papilla with columnar epithelium similar to male antrum, but without acidophilic secretions; papillial epithelium underlain by strong interwoven musculature. Male antrum lined by columnar epithelium charged with packets of erythrophil granular merocrine secretions, together with weakly cyanophil granular apocrine secretions. Penis bulb surrounded by strong sheath of longitudinal muscles (retractors); strongly muscularised (circular and oblique-longitudinal muscles) around ejaculatory duct and papilla. Male antrum weakly muscularised, with sparse longitudinal muscles below epithelium; with extensive xanthophil granular secretions. Musculoglandular organs (adenomuralia, Type III) with xanthophil granular secretions, open into antrum via fine papillae in proximal ends, deep mucosal folds, present near distal ventral lip male antrum. Common antrum communicates directly with male antrum; lined by tall secretory columnar cocoon-making epithelium, antral musculature differentiated, with circular then longitudinal muscle layers under epithelium. Gonopore displaced towards posterior (female) end of common antrum.

Ovaries not yet examined. Vitellaria extensive, surround outer gut between branches; short vitelline ducts enter ovovitelline duct. Ovovitelline ducts present mid upper surface of lateral nerve cords, pass posteriorly, then well behind viscid gland sharply incurve mediad. Here become paired genital canals, receiving copious xanthophil secretions from adjacent shell glands along entire length; rise steeply anterodorsally to separately enter rear wall of short flask-shaped female antrum.

Female antrum almost horizontal, lined by columnar epithelium charged with fine acidophilic granules, concentrated around neck of antrum where enters common antrum. Viscid gland present just inside posterior lip of the gonopore; comprised of short duct lined by cuboidal epithelium then posterior diverticulum which curves slightly dorsad, receives mainly coarse granular cyanophil secretions together with droplet-like erythrophil (orange-red) secretions. Cyanophil secretions derived from cells immediately surrounding, ventroposterior to viscid gland.

Systematic discussion:

Within the caenoplaninid genus *Australoplana sensu lato* in Winsor (1991) a narrow creeping sole was found to be present in two groups: the *typhlops* group, now *Bassioplana* gen.nov. and the *sanguinea* group, now the restricted genus Australoplana. *Bassioplana* is differentiated from *Australoplana* chiefly by the absence of eyes (present in *Australoplana*), bell-form pharynx (cylindrical in *Australoplana*), mixed inner pharyngeal musculature (differentiated in *Australoplana*), poorly differentiated penis papilla (well differentiated in *Australoplana*), paired female genital canals separately entering the female antrum (single genital canal in *Australoplana*), presence of musculoglandular organs (adenomuralia), and presence of a viscid gland (absent in *Australoplana*). Externally *Bassioplana* can be differentiated from similar taxa in having the mouth and gonopore displaced more posteriorly, and greater relative distance between mouth and gonopore.

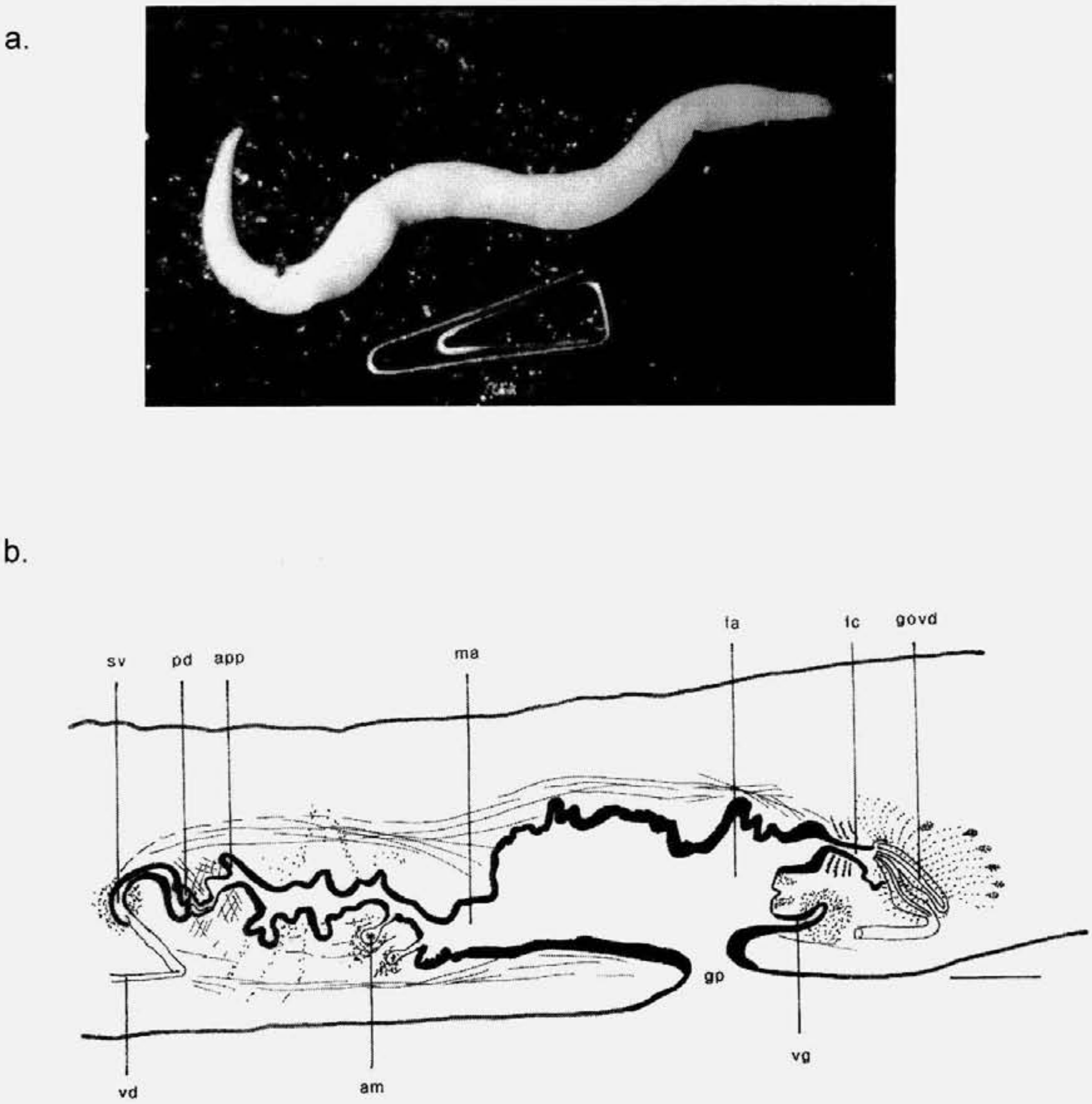


Figure 8.7-1 *Bassioplana typhlops* (Dendy, 1894b)

a. Photograph of living specimen of *Bassioplana typhlops*, Hobart, Tasmania.

b. Copulatory organs. Scale bar 500μm.

8.8 Genus *Coleocephalus*

Genus ***Coleocephalus*** Fyfe, 1953 emend
Coleocephalus Fyfe, 1953
Coleocephalus Fyfe: Ogren and Kawakatsu 1991; Johns 1998

Original diagnosis (Fyfe 1953): "Geoplanidae with hooded anterior end partly covering an oval glandular area on the ventral surface". Emended (Ogren and Kawakatsu 1991) to include: "penis papilla present; adenodactyls present".

Diagnosis emended (this thesis): Caenoplaninae with small, robust body, broadest in posterior body third, tapering gradually to anterior tip; more abruptly to posterior end; flat to slightly concave dorsally, with sharply rounded margins, convex ventrally; with sucker antero-ventrally. Sensory papillae absent. Eyes pigment cup-type, in single row around anterior tip, continuing in submarginal row to posterior end. Mouth and gonopore situated in hind third of body. Creeping sole 70% or more of body width. Cutaneous musculature tripartite, very strong, with circular, helical muscles, with longitudinal muscles in bundles, developed equally dorsally and ventrally, CMI 22-24%. Parenchymal musculature with strong dorsal and ventral transverse muscles; longitudinal parenchymal muscles weak or absent. Pharynx plicate, collar-form. Pharyngeal musculature with inner epithelium, then mixed circular-longitudinal muscles; outer musculature with epithelium, longitudinal, then circular muscles. Testes ventral, extend from anterior body to posterior tip. Vasa deferentia ventral to nerve cords. Penis eversible, without papilla. Ovaries just forward of root of pharynx, with parovarian resorptive tissue. Ovovitelline ducts join, form common duct that enters female genital canal ventroposteriorly. Female genital canal horizontal, enters female antrum through ventroposterior wall, below adenodactyls. Adenodactyls present. Viscid gland absent. Type species: *Coleocephalus fusca* Fyfe, 1953

Etymology: Fyfe (1953) did not indicate the etymology of the taxon names. *Coleocephalus* is derived from the Greek *koleus* – sheath, and kephale – head, and alludes to the hooded anterior end. Gender masculine.

Distribution: Auckland Islands: Horseshoe Lake, Ranui Cove, and Port Ross on Auckland Island, and from Enderby Island (Fyfe, 1953).

Remarks: Although Fyfe (1953) was unable to find testes in her material, Ogren and Kawakatsu (1991) provisionally included the genus in the Caenoplaninae, confirmed here. The testes are ventral. Examination of the Type and other material has shown that the hooded anterior end, alluded to in the generic epithet, is an unreliable character. It is a fixation artefact. Ogren and Kawakatsu (1991) interpreted an adenodactyl papilla in Fyfe's figure as a penis papilla. The penis is apapillate. At present there is only one described species of *Coleocephalus*, though possibly more than three undescribed species are represented in collections (Johns, 1998).

The differential diagnosis between the three caenoplaninid taxa with anterior adhesive suckers and pads, *Coleocephalus fuscus, Pimea monticola,* and *Thosteelia mesibovii,* is provided elsewhere in this thesis (this appendix, 8.14 systematic discussion).

Coleocephalus fuscus Fyfe, 1953

Coleocephalus fusca Fyfe, 1953; Johns 1993; Johns 1998
Coleocephalus fuscus Fyfe, Ogren and Kawakatsu 1991

Material examined:

Holotype MONZ ZW104. Enderby Island, Auckland Island group, collected 12 February 1945 by W.H. Dawbin It comprises 20 microslides in two series - the anterior end (sagittal sections17 slides), and posterior end (sagittal sections - an incomplete series of 3 slides considered to have probably been a series of five microslides, now with the first and last slides, which may well have contained testes, missing). The sections are stained with a bichrome, mounted in Canada Balsam and are badly faded. The heights of the complementary ends of the sections of the anterior and posterior portions differ, and there is a strong possibility that two different specimens are represented in the Holotype.

Type Locality: Not stated in the original paper. Given as Enderby Island, Auckland Islands in the MONZ Register. All material came from the Auckland Islands.

Other material: MONZ ZW 1370, single sexual specimen, sectioned at 8μm, stained with MSB and AZAN, and the slides labelled as ZW 110A. The specimen was originally confused together with another species in a tube with label "*Geoplana aucklandica* collected at Stony Peak, Auckland Islands, M.G. Easton 26.4.1945. Cape Expedition" ZW110. According to Fyfe (1953) only a single specimen of *G. aucklandica* was collected from this location. The exact location in the Auckland Islands for this specimen of *C. fuscus* is uncertain.

Distribution: All specimens (? 10) were obtained from the Auckland Islands: one each from Horseshoe Lake, Ranui Cove, and Port Ross on Auckland Island, and several from Enderby Island (Fyfe, 1953).

EXTERNAL MORPHOLOGY:

Body small, robust, broadest in posterior body third, tapering gradually to anterior tip; more abruptly to posterior end; flat to slightly concave dorsally, with sharply rounded margins, convex ventrally (Fig. 8.8-1a.b). Mouth, gonopore in posterior third. Sucker present; shallow, ellipsoid-shaped depression anteroventrally. Dimensions of Holotype and MONZ ZW 1370 provided in Table 8.8-1).

Markings: "The dorsal surface is uniformly light brown with broad marginal bands of dark brown fading to paler brown at the edges. The ventral surface is cream with faint broad marginal bands of fawn. The sides of the worm turn up to form a definite edge making the dorsal surface flat and the ventral surface convex, which is the opposite of the usual arrangement." (Fyfe, 1953).

MONZ ZW1370 light brown dorsal ground colour ("museum brown"), with paired broad lateral dark blotchy brown stripes separated by median interval of ground colour 0.3mm wide extending along two-thirds posterior body. External to dark lateral stripes are 0.3mm wide intervals of ground colour lying along sharply rounded margins. Darker brown colour extends to distinct outer ventral zone. In life the specimen could be described as a dark brown flatworm with thin light coloured median and marginal stripes.

Eyes in single row around anterior tip, more widely spaced in staggered submarginal row to posterior tip (Fig. 8.8-1c). Sensorial zone passes around anterior tip below eyes, tapering off forward of hind end of sucker.

INTERNAL ANATOMY:

Head:

Sucker cotyloplanid type. Cutaneous longitudinal muscles, not insunk, undivided, act as retractor muscle. Parenchymal dorsoventral muscles strong, anchored in dorsal and ventral cutaneous musculature. Parenchymal dorsal transverse muscles strong, interlaced with dorso-ventral muscles to form corset (*Muskelgeflecht*). Parenchymal ventral transverse muscles strong, more than twice thickness (112μm) anteriorly than in pre-pharyngeal region (50μm). Sucker epithelium anucleate, nonciliated. Sucker with three secretions (Table 8.8-2), erythrophil and xanthophil elements concentrated sub-intestinally, ventral rhabditogen cells subneural. Dorsal rhabditogen cells just below cutaneous musculature. Haftpapillen absent. Gut extends almost to tip. Eyes pigment cup type, 20 - 28μm diameter, with 3-4 or more retinal clubs. Sensory pits simple, ciliated, 30μm deep.

Pre-pharyngeal region:

Pre-pharyngeal region Fig. 8.8-d. Epithelium almost same thickness dorsally and ventrally, receives eight types of secretions (Table 8.8-2). Adhesive margins dorsolateral, slightly raised, rhabdoid-free, with coarse xanthophil, cyanophil secretory elements. Ciliated creeping sole 70% of body width. Cutaneous musculature tripartite, developed equally dorsally and ventrally; dorsally well developed, thickest submarginally, thinner towards margins, thinnest mid-ventrally. CMI 24% (median) Parenchymal musculature comprises broad strong dorsal, supraneural, ventral transverse muscles, and strong dorsoventral muscles. Transverse muscles intermesh mid dorsally with thick dorsoventral muscle fibres to provide dorsal corseting. Numerous strong dorsoventral muscles provide additional bracing. Longitudinal parenchymal muscles absent. Nephridial canals present ventrally either side of midline below gut.

Alimentary:

Pharynx (Fig. 8.8-2a,b) plicate, collar-form type, ventral insertion anterior to dorsal insertion; inner and outer musculature of both comprise subepithelial longitudinal then circular muscles. Pharyngeal pouch 2.5mm long, 15% body length; mouth in hindquarter of pouch. Diverticulum absent. Oesophagus absent.

Reproductive system:

Copulatory organs (Fig. 8.8-2c) in posterior quarter of body immediately behind pharyngeal pouch, without overall muscular investment; penis bulb, adenodactyls discrete. Penis bulb situated on right hand side of copulatory complex. Gonopore opens into common antrum.

Adenodactyls, Type VI, all with elongate papillae, ten: anterior (male) side, three; left mid lateral wall, two; posterior (female) side, five. Adenodactyl reservoir larger than duct, with fine erythrophil apocrine and granular xanthophil secretions; proximal duct receives globules of erythrophilic secretions, distal duct receives cyanophil secretions. Adenodactyl papillae and common antrum with nucleate cocoon-forming cyanophil secretory columnar epithelium.

Testes (ZW1370) triserial, ventral, above middle and lateral margins of nerve cords, in parts extend dorsad to mid body between gut diverticula; extend from anterior body third to posterior end behind copulatory organs; testes larger posteriorly (80 -120μm) than anteriorly (40-70μm); sperm ductules arise from ventral testicular poles, collecting ducts and vasa deferentia ventral to nerve cords. Vasa deferentia with capacious spermiducal vesicles; sperm ducts pierce penis bulb separately and join, common sperm duct enters anterior wall of seminal vesicle. Penis bulb musculature weak; longitudinal muscles in open mesh ectally, with retractor function for penis.

Common sperm duct, seminal vesicle with ciliated low columnar epithelium, with fine xanthophilic droplet secretions. Prostatic vesicle thin walled, capacious, with erythrophil secretion derived from glands in bulb musculature. Ejaculatory duct curves mediad; opens through antral roof. Ejaculatory duct slot-like, shape horizontal sinuoid, with nucleate lightly cyanophilic columnar epithelium, with erythrophil apocrine secretion; with ental circular muscles, ectal longitudinal muscles, within loose sheath of mixed circular and longitudinal muscles; region of distal ejaculatory duct with strong circular contractor muscles; ejaculatory duct, penis bulb and antral musculature intermeshed. Penis papilla absent. Penis eversible type.

Ovaries pear-shaped, slightly loculate, 125µm long, 285µm high, enclosed within thin fascia, pre-oral, embedded in mid lateral nerve cords, some two thirds distance between anterior tip and mouth. Parovarian resorptive tissue present, loculate, surrounds ovaries dorsally and posteriorly. Proximal ovovitelline duct communicates with resorptive tissue and upper pole of ovary, separately open into female genital canal distal to proximal (blind) end. Female canal almost horizontal, enters ventroposterior antral wall; proximal end of duct receives shell gland secretions. Vitellaria extensive, between and above gut diverticula, anterior to posterior, discharge via short vitelline funnels into ovovitelline ducts.

Functional anatomy:

Extension and retraction of the sucker would be accomplished by a combination of cutaneous longitudinal muscles and the dorsoventral parenchymal muscles. The strong parenchymal dorsal transverse muscles interlaced with the dorso-ventral muscles would provide essential corseting of the anterior end during retraction and bending of the anterior end bearing the sucker. Contraction of these parenchymal muscles, particularly the thick ventral transverse muscles would amplify the speed and displacement of the anterior end.

The ventral convexity of fixed specimens is a fixation artefact. Overall body musculature is stronger ventrad than dorsad. On fixation, contraction of the strong bundles of supraintestinal and ventral transverse muscles, coupled with contracted cutaneous musculature results in displacement of body volume dorsad to the more weakly muscularised body. This produces a ventral convexity, hooded anterodorsal tip, and probably the pronounced margins.

In MONZ ZW1370 the most striking histological feature is the presence of transverse cutaneous wrinkles, particularly evident in longitudinal sections with the appearance of cell nests in the epithelium, also noted in the Type. They are a fixation artefact possibly due to severe agonal contraction. The phenomenon has been observed in individuals of other taxa. The width of the ciliated creeping sole was difficult to determine as the epithelium was poorly preserved in the outer ventral zone. The sole is at least 70% of the body width.

A penis papilla and intra-penial papilla are absent. However a pseudophallus might be formed from the adjacent adenodactyl papillae. The distal region of the ejaculatory duct where it enters the antrum, is strongly muscularised by circular contractor muscles that would evert the penis. As a consequence, the adenodactyl papillae that protrude into the antrum probably behave as a bolster to the eversible penis, in a similar manner to that depicted (Fyfe, 1956, p 506) in *Newzealandia moseleyi*.

Adenodactyls: The antral epithelium in *C. fuscus* lacks the apocrine secretions normally associated with the sclerotin globules, though the cyanophilic sclerotin strand secretions are present. The adenodactyls appear to produce a sclerotin protein - initially in erythrophilic globules formed in the adenodactyl reservoir through apocrine secretion. These are coated by coarse xanthophilic proteinaceous granules in the reservoir and proximal duct. As the mass passes down the adenodactyl duct it is further coated by fine erythrophilic secretions from the duct. As it enters the papilial duct it is coated by the sclerotin strands and passes into the antrum. The acidophilic globules are intact in this layered sclerotin. At a later stage they disappear leaving small empty vesicles in the mass. This is possibly the condensation stage. The erythrophilic globules do not become chromophobic. From the arrangement of the papillae in the antrum, simultaneous secretion from the adenodactyls would create a more or less spherical sheet of sclerotin which could wrap around the egg mass (eggs plus vitelline granules plus shell gland secretion) as it is expelled via the female canal.

Etymology:

Fyfe (1953) did not indicate the etymology of the specific epithet, *fuscus*, from the Latin dusky, dark or swarthy. It presumably alludes to the overall dark brown dorsal pigmentation of the species. Ogren and Kawakatsu (1991) considered the genus name to be masculine (Art 30 (a) (iii) ICNZ 2000), and corrected the spelling of the specific epithet from *fusca* to *fuscus*.

Pathology:

Gregarines in various developmental stages are present in the gastrodermis and gut lumen. Numerous phoretic nematode larvae are present in the outer body wall, parenchyma, and one is present in an adenodactyl papilla. There is no evidence of host response at any of the infection.

Biology:

Fyfe (1953) noted that the only mature specimen was collected in April, and that all immature specimens were collected in February (Fyfe, 1953). The latter show well developed female organs and ducts, slightly developed adenodactyls, and no testes. The species appears to be protogynous. The Holotype is not fully mature as it lacks testes (though they may have been present in the missing slides). The spermiducal vesicles and seminal vesicle contain sperm. The spermiducal vesicles do not exhibit the diverticula noted in MONZ ZW1370. Fyfe states that the number of adenodactyls could not be estimated accurately because of their lack of complete development. However this was found not to be the case; both the Holotype and MONZ ZW1370 each have ten adenodactyls. The latter specimen was fully male-mature, with ripe testes, and sperm throughout the male reproductive tract. Sperm were also present in the ovovitelline ducts and in the resorptive tissue. Vitelline cells in the extensive vitellaria looked immature (large nucleus to cytoplasm ratio), with cyanophil cytoplasm and absence of characteristic cytoplasmic granules. The habitat of *C. fuscus* is not known.

Systematic discussion:

Type specimen: Fyfe (1953) stated that the Type comprised "One whole worm and a series of sagittal sections (21 slides) in the Dominion Museum, Wellington. Cat. No. Z.W. 104." She did not specify the specific locations from which the syntypes were collected. Only microslides were received by the museum and were designated as the Holotype (R.K. Dell, personal communication).

Hood: The hood observed by Fyfe (1953) in the Type and other material, and included by her in the generic diagnosis of *Coleocephalus* was not present on the Stony Peak specimen examined by the author. A ventriflexed, "hooded" end has been observed in fixed specimens of other taxa in which it is clearly an artefact. Hooding of the anterior tip has not been seen by me in living specimens of cotylate Terricola. Dendy (1897, p259), in his description of Australopacifica *cucullata*, recorded that the "Body in life much flattened when at rest with no noticeable peculiarity in shape. In spirit, however, the shape is very characteristic .... The anterior tip strongly curved ventrad, beak-like, with smooth incurved margin forming a kind of hood, deeply excavated beneath and bearing eyes along the edge ..." The specific epithet of this species means hooded. He also observed (Dendy, 1896, p 211) a similar appearance in the anterior end of spirit-preserved specimens of *Australoplana latissima* (Dendy), a species he considered closely related to *A. cucullata*. The hooded anterior in *Coleocephalus* is considered here to be a fixation artefact, and for this reason this variable and unspecific character has been deleted from the generic diagnosis of *Coleocephalus*.

Planoconvex transverse body shape: As previously indicated, the planoconvex appearance of the transverse body with pronounced ridges in *C. fusca* is considered to be a fixation artefact reflecting strong transverse parenchymal musculature. Similarly with *Pasipha ercilla* (Froehlich) (1978, p29, Fig.37), which also has very strong dorsal and ventral transverse parenchymal muscles, and strong dorsoventral muscles in bundles. *Pelmatoplana treubi* Graff (1899, plate 5, Fig. 14), *Bipalium semperi* Graff (1899, plate 9, Fig. 3), and *Rhynchodemus michaelseni* Graff (1899, plate 17, Fig. 32) all exhibit this feature; their internal anatomy is unknown.

Pharynx: Fyfe stated that "the pharynx differs from the usual tubular type in being very much branched, each branch having its own opening into the peripharyngeal cavity. The pharynx is plicate (collar form), the folds of which in sagittal section can give the appearance of multiple branches described by Fyfe (Fig. 8.8-5).

A comparison between the three austral caenoplaninid taxa with anterior adhesive suckers and pads, *Coleocephalus fuscus, Pimea monticola,* and *Thosteelia mesibovii,* is provided in the systematic discussion for *Thosteelia mesibovii,* Appendix 8.14.

Table 8.8-1. *Coleocephalus fuscus*: dimensions of Type and other material.

Character	**Type ZW104**	**ZW 1370**
length (mm)	25	16.5
width (max, mm)	7.0	6.0
height (µm)	1350	1359
mouth from anterior tip (mm)	20	12.1 (73.3%)
gonopore from anterior tip (mm)	?	13.8 (83.8%)
mouth-gonopore (mm)	?	1.7 (10.3%)
adhesive sucker length x width (mm)		
Body, width µm (pre-pharyngeal)	?	3800
creeping sole, width (µm)	?	2670
creeping sole, width as % body width	?	70
dorsal epithelium, height (µm)	14-16	28
ventral epithelium, height (µm)	17-20	23
dorsal cutaneous musculature, thickness (µm)	145	177
ventral cutaneous musculature, thickness (µm)	145	177
Cutaneous Muscular Index (CMI %)	22	24
dorsal transverse parenchymal muscles, thickness (µm)	108	70
ventral transverse parenchymal muscles, thickness (µm)	108	64
Parenchymal Muscular Index -transverse muscles (PMIt %)	16	9.9

Table 8.8-2 *Coleocephalus fuscus* ZW 1370: secretions from outer epithelium

Secretion	Epithelium from which secreted	Histochemical entity
rhabdoids	dorsal to outer ventral; outer sucker	
epitheliosomes	ventral	
erythrophil, fine granular	dorso-ventral; sucker	PAS +ve. Glycoprotein
cyanophil A (blue-green)	ventral	Alcian Blue +ve, Acid mucin
xanthophil A (coarse brown-orange)	marginal adhesive zone; sucker	basic protein
cyanophil B dark blue	marginal	
erythrophil, coarse granular	Submarginal to outer ventral; intermixed	
xanthophil B		basic protein

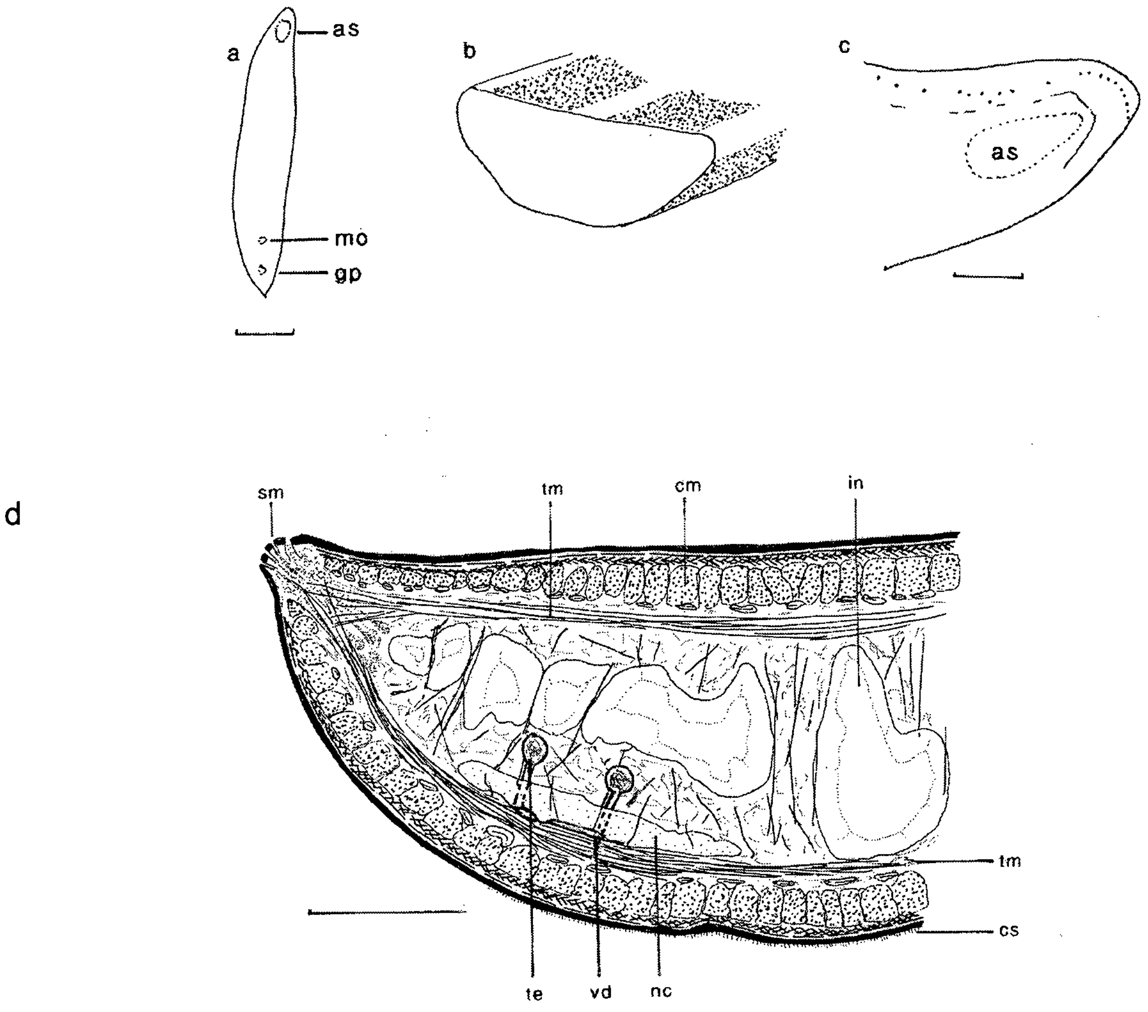


Figure 8.8-1 *Coleocephalus fuscus* (Fyfe, 1956) ZW1370.

a. Whole specimen, ventral surface showing anterior sucker. Scale bar = 3mm

b. Dorsal stripe pattern. Unscaled.

c. Anterior end showing eye pattern and anterior ventral sucker. Scale bar 1 mm.

d. Pre-pharyngeal region. Transverse section. Scale bar 500μm.

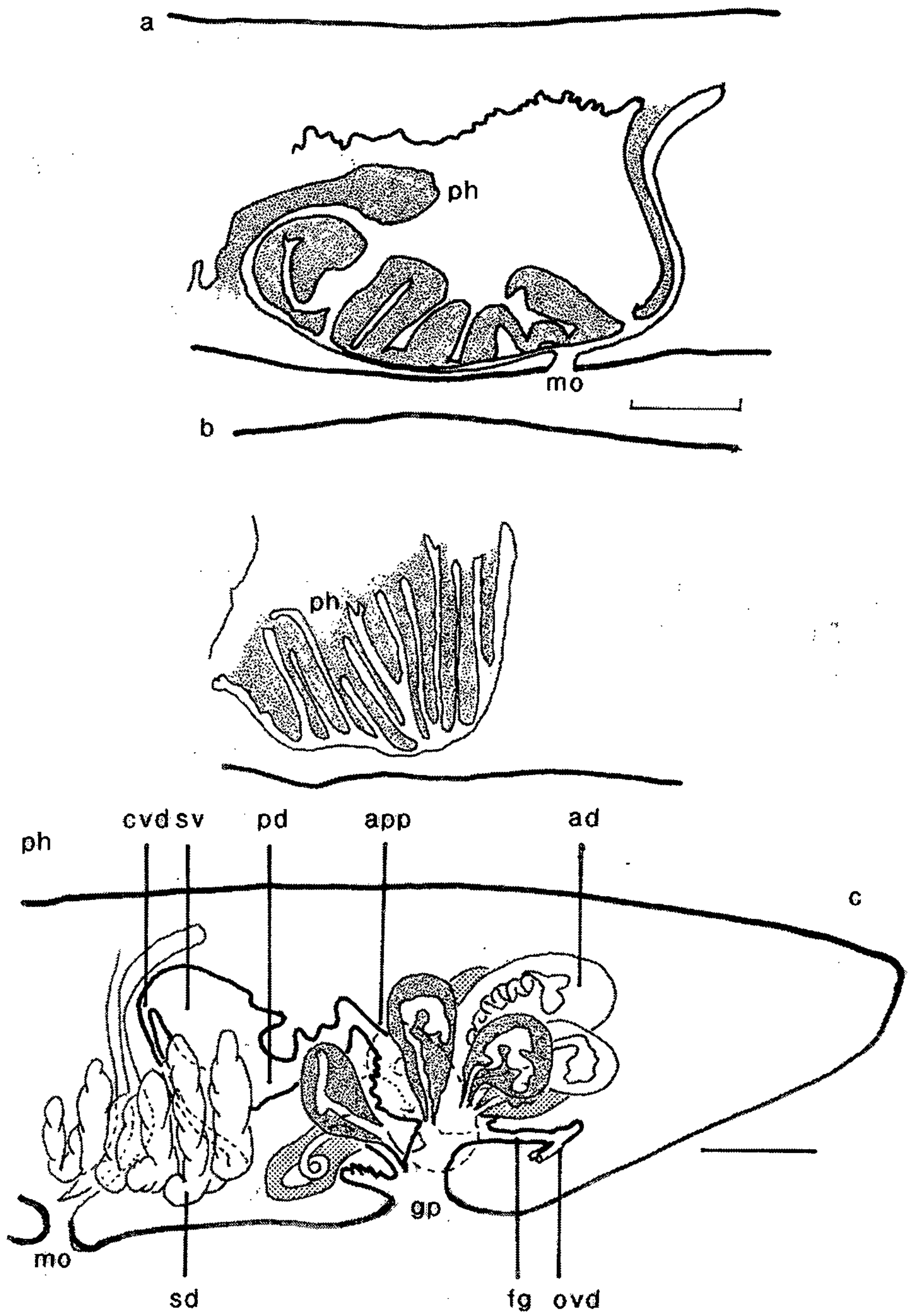


Figure 8.8-1 *Coleocephalus fuscus* (Fyfe, 1956) ZW1370.

a. Plicate (collar-form) pharynx, median sagittal section. Scale bar 500μm (same for b, following).

b. Plicate pharynx, lateral section, giving the appearance of multiple mouths reported by Fyfe (1956).

c. Copulatory organs. There are 10 adenodactyls. Scale bar 500μm.

8.9 Genus *Danidoplana* gen. nov

Danidoplana gen. nov

Diagnosis: Caenoplaninae with small elongate body, subcylindrical in cross section, mouth in first half close to mid body, gonopore closer to mouth than to posterior end. Creeping sole more than 60% body width. Anterior adhesive sucker, pad or cup absent. Sensory papillae absent. Eyeless. Cutaneous musculature tripartite, weak, with circular, helical muscles, longitudinal muscles in bundles, with ventral musculature stronger than that dorsally. CMI 4%. Parenchymal musculature weak, with subneural longitudinal muscles present as sparse single fibres, not organized in ring-zone or distinct plate. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; with outer epithelium, longitudinal, then circular muscles. Testes and sperm ducts ventral. Testes extend from ovaries to just anterior of copulatory organs. Vasa deferentia separately enter penis bulb, penis papilla present. Ovaries closer to anterior tip than to pharynx, female genital canal enters antrum horizontally. Adenodactyls. Viscid gland absent.
Type of genus: *Danidoplana palatris*

Etymology: *Danidoplana* is contrived from the Greek *danos* dry, parched, burnt, ide = forest, and the Latin *plana* flat. feminine. The name alludes to the open dry sclerophyll woodland where members of the genus occur. The dry forest planarian.

Distribution: In the Eyrean and warm temperate moisture zone of the Bassian zoogeographic sub-regions, west, central, and northeastern Victoria.

Systematic discussion: In general habitus *Danidoplana* is similar to *Lenkunya*, *Tasmanoplana,* and *Parakontikia.* It is distinguished from these genera in being eyeless, lacking a ring zone or subneural plate of strong parenchymal longitudinal muscles, and differing in pharyngeal musculature. It shares with *Lenkunya* and *Tasmanoplana* a broad creeping sole and penis papilla, and relative positions of the body apertures.

Danidoplana palatris sp. nov.

Material examined:

Holotype LW548, Woolshed Road, 2.4km west of Eldorado, Victoria 146°30'E 36°14'S, 13.8mm long, 2.0mm wide, mouth 5.5mm from the anterior end, height 979μm. Sectioned at 7μm, stained with Steedman's Triple stain; anterior TS and posterior (pre-pharynx) LSS, 17 slides.

Other material examined:

LW318 6.5km south of Ararat, Victoria, LL; LW351 Amherst, 16km south of Maryborough, Victoria, 143^{0}10'E 37^{0}09'S; LW357 4.8km north of Dunolly, Victoria, 143°41'E 36°49'S; LW363 4.8km north of Natte-Yallock, Victoria, 143°29'E 36°56'S; LW469 (sectioned) 5.1km south of Nagambie, Victoria, 145°09'E 36°50'S; LW550 Chiltern, Victoria, 146°36'E 36°10'S: LW (autolysed) Moore's Flat, 12.9km west of Maryborough, Victoria 143°35'E 37°04'S; MV unregistered, Black Springs, 9.7km west of Beechworth, Victoria, 146°39'E 36°22'S.

EXTERNAL FEATURES:

The dimensions of the Holotype and other preserved specimens are provided in Table 8.9-1. Species small, elongate with sharply tapering extremities, subcylindrical in transverse section, eyeless (Fig. 8.9-1a-c), posterior with pronounced tip. Mouth generally forward of midbody, with gonopore just behind mouth. Dorsal ground colour fawn - pale brown, with five dark brown dorsal - submarginal stripes all approximately same width, as follows: fine median dark brown stripe, 0.1mm wide, separated from lateral stripes by narrower strip of ground colour. External to lateral stripes coarse brown mottling extends to marginal zone, followed by interval of ground colour, then dark submarginal stripe. Ventral surface pale yellowish brown with pale brown mottling, densest in mid third of sole, and in arc delineating sensorial zone skirting anterior end. Outer ventral pale stripes paired, delineated by dense aggregation of pigment along inner and outer stripe margins giving suggestion of four very fine, stippled outer ventral dark stripes.

Variations: The median stripe, clearly evident in living specimens, is eventually lost in most spirit-preserved specimens. In other material there is a pale interval of ground colour immediately external to the lateral stripes, giving the suggestion of paired narrow inner and broad outer dorsal stripes. In some specimens the whole or lateral margins of the pale ventral stripes may be slightly raised.

INTERNAL ANATOMY:

Head:

Anterior suckers and associated specialized musculature absent. Sensory papillae absent. Eyes absent. Sensorial zone extends around the anteroventral margin. Sensory pits simple invaginations, 18µm deep, 7.2□m diameter.

Pre-Pharyngeal region:

Rhabdoids, rhammite type, twisted, 18-19µm long. Erythrophil secretions present, with two types of cyanophil secretions (dense dark blue staining, and a foamy secretion derived from coarse paler granules). Cyanophil secretions appear to be relatively more abundant dorsally than is normally the case. Creeping sole broad 60-70% of body width (Holotype creeping sole 1292µm wide, body width 1833µm, creeping sole 70 % body width; in LW469 body 1424µm wide, creeping sole 854µm wide, 60% of body width). Cutaneous musculature weak, tripartite, with circular, helical muscles, longitudinal muscles in distinct bundles. Ventral cutaneous musculature stronger than that dorsally, with dorsal cutaneous musculature 14.4µm thick, ventral cutaneous musculature 25.4µm thick, CMI 4 %. Parenchymal musculature weak. Longitudinal muscles present, subneural, sparse single fibres not bundled or in plate. Weak helicoid muscles present as wide mesh throughout parenchyma, possibly in part pathological lesion due to gregarines.

Alimentary tract:

Pharynx short, cylindrical, inclined 30^0 below horizontal within pharyngeal pouch. Dorsal insertion of pharynx posterior to ventral insertion; pharynx occupies approximately three quarters of pouch. Pharyngeal musculature with inner infranucleate epithelium, circular, then mixed circular-longitudinal muscles; with outer infranucleate epithelium, longitudinal, then circular muscles. Oesophagus absent However inner pharyngeal dorsal wall epithelium grades into gastrodermis over distance of 140µm with weak underlying musculature, whereas transition zone on opposing ventral wall epithelium is abrupt. Pharyngeal pouch 890µm long, 6.5% length of specimen. Small diverticulum present, 178µm long.

Reproductive organs:

Reproductive organs (Fig. 8.9-1d). Testes ventral, 114µm in diameter, situated on dorsolateral crest of nerve cords, extend in laterally staggered row from just behind ovaries posteriorly to level with male copulatory organs; immature with only spermatogonia and mid stage spermatids present. Male efferent system difficult to trace in entirety. Sperm ductule passes from outer lower testicular pole to intertesticular duct. What appear to be vasa deferentia lie on mid third of dorsal commissure. Collecting and intermediary ducts could not be confidently traced.

Copulatory organs immature, though sufficiently developed to indicate general topography. Male apparatus with spheroidal muscular penis bulb with distinct penis papilla opening into conical male antrum. Antrum lined by a flattened nucleate facing epithelium, narrows markedly before communicating with female antrum. Vasa deferentia appear to separately enter penis bulb; unclear whether they then join, or separately enter seminal vesicle. Strong longitudinal retractor muscles surround bulb; insert into dorsal roof of male antrum, ventrally around proximal antral margin.

Female antrum distinguished by secretory epithelium underlain by layer of circular muscle fibres. Female genital canal almost horizontal, distinguished by thicker mixed circular, longitudinal musculature. Gonopore partially developed within floor of common antrum; epithelium of common antrum appears weakly ciliated. Area of presumptive gonopore approximately 2.3mm behind mouth.

Ovaries anterior, situated on outer crest of lateral nerve cords, 0.5mm from anterior tip, slightly flattened, 85µm high, 106µm wide, immature. Ovovitelline ducts with slightly expanded proximal (ovary) end, which in mature individuals may be a tuba, separated from t ovary by muscular sphincter. Ovovitelline ducts lie on crest of lateral nerve cords. Ovovitelline ducts narrow, pass posteriorly towards, but not yet connected to female genital canal. Vitellaria not observed, possibly because of immaturity of specimen or pathology due to gregarines.

Pathology:

The two specimens examined histologically are both heavily infected by an aseptatinid gregarine. Sporonts measure some 9µm long and 2.8µm wide. Various intracellular stages, together with sparse black-brown spore-like spheres, are scattered in the gastrodermis. The gregarines have heavily infiltrated the surrounding parenchyma, especially throughout the dorsolateral tissues. Muscle fibres, neurones, and the subneural parenchyma and cutaneous tissues are least affected. The specimens exhibit severe gregarine-induced peri-intestinal histolytic vacuolation. Intracellular stages of gregarines were observed in most testes, though infections were light (2-3 infected cells per testis). There is a possibility that the gregarines infection of the testes could cause sterility.

Etymology:

The specific epithet palatris is derived from the Greek *palai* meaning gold nuggets, combined with the suffix *–tris*, a place for. Gender feminine. The name alludes to the occurrence of the species throughout the central and northern Victorian alluvial goldfields.

Systematic discussion:

Variation in stripe pattern: The pattern of fine pale brown stippling on the ventral surface, and the paired dark submarginal stripes are the most constant features of the markings in specimens of this species. Three variations of the dark dorsal stripes are known:

(a) One dorsal stripe consisting of a single thin dark median stripe separated by an interval of ground colour from heavy coarse dark brown mottling extending to the body margins (LW469);

(b) three dorsal stripes consisting of a single thin dark median stripe separated by an interval of ground colour from paired narrow dark brown lateral stripes, external to which is coarse dark brown mottling extending to the body margins ie. dark inner margins of the mottling forming paired lateral stripes (LW548; LW550; MV);

(c) two dark dorsal stripes separated by an interval of ground colour from heavy coarse dark brown mottling extending to the body margins. Dark median stripe absent. This variation has been seen in living specimens. The median stripe may be lost after prolonged period in alcohol preservative giving rise to this variant. (LW 318; LW351; LW357)

The absence of eyes in this species is immediately distinguishes it from *Lenkunya*, *Tasmanoplana,* and *Parakontikia.*

Table 8.9-1 *Danidoplana palatris*: Dimensions of specimens examined.

LW No	548	318	351a	351b	351c	357	363	469	550	MV
Length	13.8	Coiled	16.8	11.7	11.5	11.7	14.6	12.0	10.7	11.0+
Width	2.0		2.3	2.2	2.1	2.1	2.3	2.1	2.1	2.5
Mouth	5.5		8.1	6.1	3.6	6.2	6.4	5.1	5.1	8.0xp
Mouth%	40%		48%	52%	31%*	53%	44%	45%	48%	-
Gonopore	(2.3)									2.0

- regenerating anterior end.

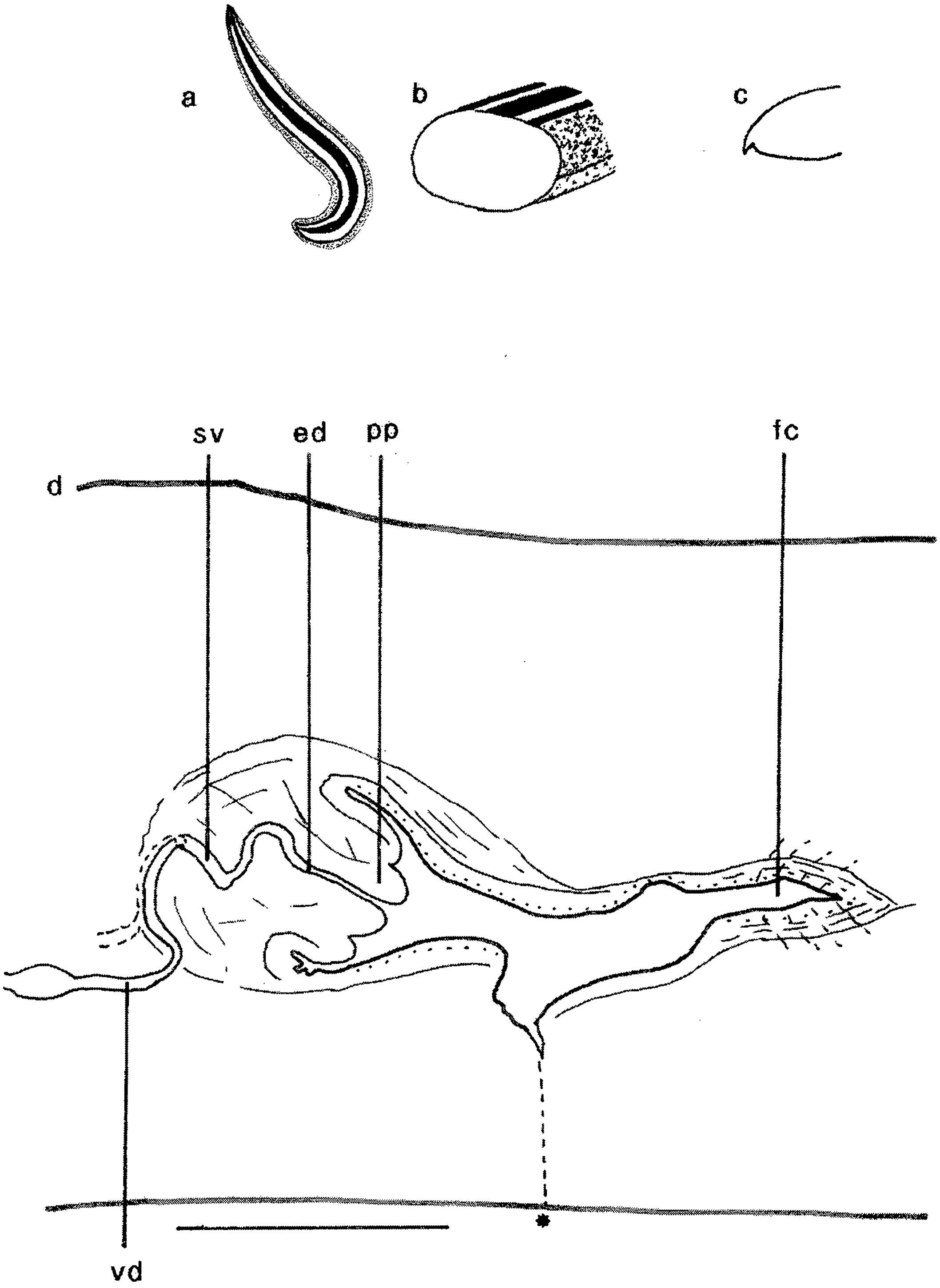


Figure 8.9-1 *Danidoplana palatris*

a. General form, X1.5
b. Dorsolateral stripe pattern, unscaled.
c. Posterior, showing pronounced tip. Unscaled
d. Copulatory organs (immature). * indicates position of putative gonopore. Scale bar = 500μm.

8.10 Genus *Kynagoplana* gen.nov

Kynagoplana gen.nov

Diagnosis: Caenoplaninae with elongate body, sub cylindrical in cross section, mouth just behind mid body, gonopore closer to mouth than to posterior end. Creeping sole more than 70% body width. Anterior adhesive pad or sucker absent. Sensory papillae absent. Eyes pigment cup-type, in single row around anterior tip, clustered anterolaterally, then in single staggered submarginal row posteriorly. Cutaneous musculature bipartite, weak, with helical, longitudinal muscles; longitudinal muscles in bundles. CMI 2.5 – 3.3. Parenchymal muscles strong, with predominantly mixed longitudinal and helical fibres in ring zone, PMI 38%. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then mixed circular-longitudinal muscles; outer musculature with epithelium, longitudinal, then mixed circular-longitudinal muscles. Testes, sperm ducts ventral. Testes biserial, extend from just behind ovaries to level of mouth. Vasa deferentia unite dorsally to form common sperm duct; joins extra-bulbar seminal vesicle; penis eversible type, papilla or intra-antral papilla absent. Ovaries pre-oral, with multiple secondary ovaries. Ovovitelline ducts unite behind copulatory organs, form common duct that enters female genital canal almost horizontally, female genital canal in-line with female antrum. Female antrum elongate, complex, comprising secretory ridges separated by highly folded glandular mucosa. Adenodactyls absent. Type of genus: *Kynagoplana citrina* (Wood), 1926

Etymology: *Kynagoplana*, the Hunter Planarian, is a name contrived from the Greek *kynagos* hunter and Latin plana flat. Gender feminine. The name is an allusion to the presence of this genus in the Hunter Region of northern New South Wales, and also reflects the nature of these predators.

Distribution: Barrington Tops, 156°26' E 32°02'S, New South Wales. *Fagus* scrub.

Systematic discussion: *Kynagoplana* shares with *Caenoplana* the apomorphy of a bipartite cutaneous musculature, and parenchymal musculature predominantly composed of mixed longitudinal and helical muscles in a ring zone. It is distinguished from *Caenoplana* by the extra-bulbar seminal vesicle, complex secretory structures in the female copulatory organs, and presence of multiple secondary ovaries.

Kynagoplana citrina (Wood), 1926

Geoplana citrina Wood, 1926
Geoplana barringtonensis Wood, 1926
Caenoplana citrina - Winsor 1991c; Ogren, Kawakatsu and Froehlich 1997
Caenoplana barringtonensis - Winsor 1991c; Ogren, Kawakatsu and Froehlich 1997
Australopacifica citrina - Ogren and Kawakatsu 1991
Australopacifica barringtonensis - Ogren and Kawakatsu 1991

Locality:

Barrington Tops, 156°26' E 32°02'S, New South Wales, Australia, collected by the University of Sydney party led by Professor L. Harrison, January and February, 1925. Found beneath a rotting log, *Fagus* scrub, and on damp moss.

Material examined:

HOLOTYPE AM W2353, sectioned at 8µm, a series of 214 microslides: anterior, 98 slides, LSS, H&E; pre-pharyngeal region, 18 slides, TS, H&E, PG, PTAH, MSB; mid region and genitalia, 60 slides, LSS, H&E, PG, MSB, PTAH; posterior portion, 38 slides, LSS, H&E. Length 70mm, width 5.5mm, mouth 38mm (54%), and gonopore 44mm (63%), 6mm behind the mouth (8.6%). The anterior tip was damaged.

Other material:

W2365, W2367, *Geoplana citrina* Williams River, collected T.G. Campbell, October 1926. Identified Lucy Wood. W2352, *Geoplana barringtonensis*, Type, Barrington Tops, sectioned at 8µm, a series of 212 microslides: anterior, LSS, H&E; pre-pharyngeal region, TS and posterior LSS, H&E, PG, MSB, PTAH; W2364 Barrington Tops, collected T.G. Campbell, October 1926. Identified Lucy Wood.

EXTERNAL FEATURES:

Dorsum very convex, with lemon yellow ground colour pale (lightly) to deeply (darkly) mottled with sienna in reticulate striate pattern, extending to submarginal zone. In mature individuals, dorsal and ventral surfaces clearly marked off from one another; less distinct in lightly mottled specimens. (Wood, 1926, Text Fig. 2). The dark straie were still visible in the Type specimen, though not on the photograph (Fig 8.10a). A thin median stripe of white to lemon yellow ground colour is sharply bordered on either side by a thin sienna stripe, the outer margins of which merge with the lateral mottling. Ventral surface flat, and has a uniform lemon yellow colour.

INTERNAL ANATOMY:

Head:

There is no adhesive structure or associated specialization of musculature in the anterior end. Simple invaginated ciliated pits, 50µm deep are present within a fine pale line running around the anterior tip immediately below the dorsal pigmentation.

According to Woods' (1926) description of *K. citrina* the "eyes are arranged in three parallel rows on either side of the body, extending from the anterior end to about the middle of the body (Text Fig. 2) ". In her description of *barringtonensis* "the eyes are very numerous and are present as minute black specks placed ventro-laterally at the extreme anterior end, and extending around the horse-shoe shaped tip and along the whole length of the body to the posterior end. They are more numerous at the anterior end." Cleared specimens of the Type specimens of both *citrina* and *barringtonensis* show the eyes pass around the anterior tip, are clustered anterolaterally, then pass in a staggered submarginal row to the posterior (Fig. 8.10b).

Pre-pharyngeal region:

Dorsal epithelium 48µm thicker than ventral epithelium 28µm. Rhabditogen cells and erythrophil glands open through dorso-lateral epithelium, crowded in marginal – submarginal zone; cyanophil glands open dorsally, predominate ventrally over creeping sole. Fine pale brown pigment present in mesenchyme. Cutaneous musculature bipartite, weak, with sheath of decussating helical fibres, and longitudinal muscles in well developed bundles. In W2353, height 2300µm, dorsal cutaneous musculature (40µm) is slightly stronger than that ventrally (35µm), CMI 3.3%. In W2352, height 2600µm, dorsal musculature (25µm) is weaker than that ventrally (40µm), CMI 2.5%. Parenchymal musculature with ring zone of mixed longitudinal and helical muscles, longitudinal muscle fibres mostly single or double, sometimes in bundles of three; ring zone is developed equally dorsally and ventrally, PMI 38% (W2352). Strong supraintestinal but weak supraneural transverse muscles. Dorso-ventral fibres pass between gut diverticula.

The epithelium of the creeping sole (W2352) poorly preserved, width of the sole is estimated at 76% of the body, based on the assumptions that there is a creeping sole (absence of rhabdoids over creeping sole; presence of cyanophil glands), and when present generally begins at the ventrad extent of the rhabditogen cells (4500µm wide).

Alimentary tract:

Pharynx cylindrical (Fig. 8.10c), about 4.3% of body length, inclined ventrad about 20° to horizontal; dorsal insertion posterior to ventral insertion. Inner pharyngeal musculature with circular muscles underlain by mixed longitudinal, circular muscles; outer pharyngeal musculature with longitudinal muscles underlain by mixed circular, longitudinal muscles; outer pharynx, posteriad third of the pharynx with infranucleate ciliated epithelium which grades to columnar, nucleate gastrodermis. Mouth situated in anterior third anterior of pharyngeal pouch; pouch with weak longitudinal musculature, with diverticulum.

Reproductive organs:

A sagittal reconstruction of the copulatory organs is provided in Fig. 8.10d. Testes ventral, mature, biserial, lying below gut diverticula at lateral margins of nerve cords; testes extend from just in front of ovaries, to level of mouth; efferent ducts pass from lower testicular poles, continue posteriorly beneath lateral nerve cords; vas deferens subneural, with nucleate, non-ciliated epithelium, rise at level of anterior end of male copulatory organs, expand to form spermiducal vesicles, then narrow, pass mediad, rise, recurve anteriorly; unite to form saccate common sperm duct. Male reproductive tract with three main parts: long seminal vesicle external to penis bulb musculature, itself lying in loose stroma; strongly muscular penis bulb enclosing ejaculatory duct (eversible-type penis without papilla); male antrum.

Seminal vesicle extra-bulbar, with ciliated cuboidal epithelium, with long, strongly muscularised sheath of circular muscles; receives cyanophil secretions from glands in the surrounding mesenchyme. Seminal vesicle tightly recurves posteriorly, passes anteriad, then curves ventrad (C-shape), then follows fairly horizontal course posteriorly before rising in S-shape to enter ejaculatory duct at proximal end of penis bulb; intra-penial papilla absent. Penis eversible type.

Ejaculatory duct capacious, situated in dorsal half of bulb, with tall columnar epithelium with brush border. Duct receives globular erythrophil secretions, weakly cyanophil granules, both secreted by gland cells in surrounding mesenchyme. Both secretions distinct in proximal duct; erythrophil globules show progressive granularity and dissociation with passage distally down duct, culminating in somewhat cyanophil substance in distal duct. Bulb very muscular, with layer of circular muscles surrounding ejaculatory duct, external to which is strong musculature of mixed circular, longitudinal and radial muscles (wickerwork), with outer sheath of longitudinal muscles. Floor of ejaculatory duct smoother than roof; duct gradually widens then narrows at termination of bulb at male antrum. Male antrum with flattened non-ciliated cuboidal epithelium up to gonopore. Anterior floor of antrum with transverse mucosal flaps covering muscular lip traversing width of antrum at point where ejaculatory duct enters antrum. Musculature of antral lip separate from penis. Sperm duct and seminal vesicle combined length approximately that of ejaculatory duct and male antrum combined length.

Ovaries multiple, mature, embedded in top of nerve cords, pre-oral, beginning 8mm from anterior tip (in W2353 there is a pair of principal ovaries, and six pairs of secondary ovaries, separated by 600-700μm, diminishing in size from a diameter of 480μm (left ovary) and 380μm (right ovary) to some 80μm. A similar arrangement is present in W2352, though the ovaries are slightly smaller and immature). Oviductules short, enter antero-dorsal end of each ovary, communicate with ovovitelline duct ventrally; vitelline funnels open into the upper side of the ovovitelline duct. Ovovitelline ducts with ciliated nucleate cuboidal epithelium, continue posteriorly along top of lateral nerve cords; form common ovovitelline duct that enters female genital canal posteriorly.

Female genital canal horizontal to slightly inclined dorsally, with rugose tall ciliated columnar epithelium, with cytoplasm dark basally, vesiculate, foamy, near lumen, with large central nuclei. Diverticulum present, posteriorly from genital canal, immediately above common ovovitelline duct; 500μm deep, bifurcate midway along length, with columnar epithelial cells with dark cyanophil (purple) cytoplasm, with fine granular cyanophil (blue) secretions from glands in adjacent mesenchyme.

Genital canal in-line with fusiform female antrum. Female antrum with capacious mid portion with highly folded (almost villiform) mucosa, with secretory ridges, with narrowed lumen either side. Erythrophil shell glands open into lumen at secretory ridges Antral roof, floor, with epithelial secretions providing sclerotin strand - globule components for cocoon formation: antral roof epithelium secretes sclerotin strand component; antral floor up to gonopore with sclerotin globule-making epithelium. Female antrum enclosed within substantial muscular tunic, stronger ventrally than dorsally, with circular muscles underlying mucosa, external to which is mixed musculature of circular, longitudinal and radial fibres. Vitellaria small, mostly subintestinal. Glandulomuscular organs absent.

Pathology:

Phoretic nematode larvae were present entally to the ventral cutaneous nerve net in W2352 and W2353. Gregarine sporozoites, 20µm long, 5µm diameter, were noted in the peri-intestinal mesenchyme in W2352 and W2353.

Etymology:

Wood (1926), alluding to the lemon yellow body colour, gave the species the specific epithet *citrina* derived from the Latin masculine *citrinus.*

Systematic discussion:

Wood (1926) assigned to *Geoplana sensu lato* the species *citrina* and *barringtonensis*, both collected from Barrington Tops. No differential diagnosis between these species was provided; rather, each was compared to other taxa. The species have similar external topography and presumably were considered separate taxa on the basis of size, perceived eye pattern, the depth of ground colour, and extent of mottling (from examination of the Type of *citrina,* the dark markings are more accurately regarded as striae rather than spots or blotches).

Both species were later transferred *Caenoplana* (*sub-viridis* group)*, chiefly* on the basis of external topology and body musculature (Winsor 1991c). In the absence of published anatomical data the species was placed in the inclusive genus *Australopacifica* (Ogren and Kawakatsu 1991).

Full histological examination of the Type specimens revealed that the *barringtonensis* specimen was immature, and that the species was synonymous with *citrina* that had line precedence in the descriptions in Wood's (1926) paper. A new genus *Kynagoplana* was erected to receive *citrina,* as characters present in the species precluded accommodation of *citrina* in *Caenoplana.*

Kynagoplana shares with *Caenoplana* the apomorphy of a bipartite cutaneous musculature, and parenchymal musculature predominantly composed of mixed longitudinal and helical muscles in a ring zone. It is distinguished from *Caenoplana* by the extra-bulbar seminal vesicle, complex secretory structures in the female copulatory organs, and presence of multiple secondary ovaries.

Kynagoplana citrina is similar to the six-striped species *Caenoplana sub-viridis* and *C. variegata.* The anatomy of the copulatory organs for both these species is unknown; the Type specimen of the former species is immature, and the Type of *viridis* is lost. Externally, *K. citrina* differs from these species in having mottling and striations fairly uniform laterally, not aggregated into additional dark lateral stripes as in members of the *C. sub-viridis* group.

The male copulatory organs include an antral lip. This structure may act as a bolster or anchor point for the floor of the ejaculatory duct during the eversion of the penis, which in some taxa appears to proceed initially through eversion of the roof of the antrum and ejaculatory duct. There are broad similarities in the topology of the apapillate male copulatory organ of *K. citrina* with those of species in the South American genus *Pasipha*, though the female copulatory structures in the latter are small and unremarkable. An *elongate* female antrum as in *K. citrina* is present in species of *Caenoplana* and *Artioposthia,* but neither of these genera has species exhibiting the glandular complexity and structures present in *K. citrina*. Multiple ovaries, exhibited by *K. citrina*, are very uncommon in the Terricola; a secondary ovary may rarely be present in addition to the normal paired ovaries, as in *Anzoplana* (this thesis). As it is uncertain whether this apomorphy is a generic or specific state, for the present it is included in the generic diagnosis of *Kynagoplana*. The female genital canal in *K. citrina* is unusual in not receiving shell gland secretions; the latter are secreted from the prominent ridges in the antrum. The foamy cytoplasm in the epithelium of the genital duct suggests a resorptive function. The diverticulum immediately above the genital canal is unusual: whether the secretions are involved in cocoon formation, lumenal digestion of excess seminal fluid, or whether the diverticulum is a vestigial genito-intestinal duct is uncertain.

Table 8.10-1. *Kynagoplana citrina* – dimensions of material examined.

Specimen m.m.	Length m.m	Width m.m	Mouth m.m	Mouth %	Gonopore m.m.	Gonopore %	Mouth-Gonopore m.m	Mouth-Gonopore %
W2353 Type *Citrina*	70.0	5.5	38.0	54.0	44.0	63.0	6.0	8.6
Wood, 1926 *citrina*	90.0	Not given	51.0	56.7	62.0	68.9	12.0	13.3
W2365 *citrina*	One specimen, ? mature. Not measured							
W2367 *citrina*	One specimen, immature. Not measured.							
W2352 Type *barringtonensis*	52.0	6.5	25.0	48	33.0	63.5	8.0	15.4
Wood, 1926 *barringtonensis*	51.0	Not given	26.0	50.9	38.0	74.5	12.0	23.5
W2364 *barringtonensis*	Two specimens, one ?sexual. Not measured.							

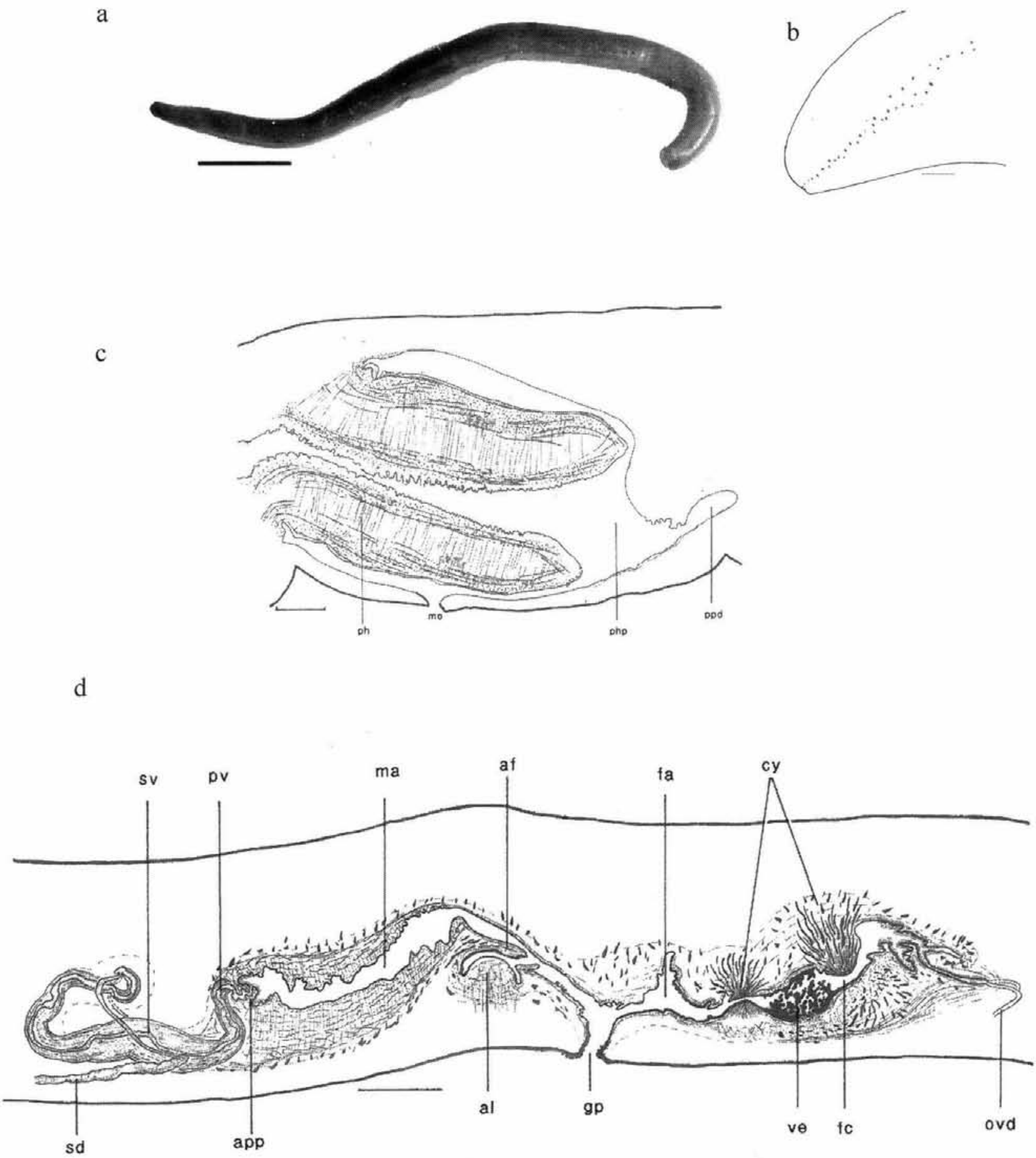


Figure 8.10 *Kynagoplana citrina*

a. Holotype specimen AM W2353. Anterior tip damaged. Scale 1 cm.
b. Anterior tip, eye pattern (W2352). Scale bar 500µm
c. Cylindrical pharynx, sagittal section, pharyngeal pouch and diverticulum. Scale bar = 500µm
d. Copulatory organs, sagittal section. Scale bar = 1mm

8.11 Genus *Lenkunya*

Lenkunya Winsor, 1991c
Geoplana (in part) Fletcher & Hamilton, 1888
Caenoplana (in part), Ogren & Kawakatsu 1991
Lenkunya Winsor, 1991c; Ogren *et al* 1993

Diagnosis: Caenoplaninae with robust body, broadly convex dorsally, flat ventrally. Mouth just anterior to mid body, or central; gonopore closer to mouth than to posterior end. Creeping sole 70-80% of body width. Eyes pigment-cup type, in single row around anterior tip, crowded in characteristic lens-shape anterolaterally, extending to anterolateral region of dorsal surface; continue in staggered submarginal row to region of pharynx, very sparse thereafter. Cutaneous musculature tripartite, weak, with longitudinal muscles in small bundles. CMI 3.6 – 5.5%. Parenchymal musculature strong, with subneural ventral plate of longitudinal muscles, with ringzone of longitudinal muscles present as single fibres, with diagonal muscles, PMI 12 – 18%. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, longitudinal, then mixed longitudinal and circular muscles; outer epithelium, longitudinal, circular, then longitudinal muscles. Testes and sperm ducts ventral. Testes extend anterior to ovary, almost entire length of body. Ovary in anterior body third. Copulatory organs complex, with highly differentiated seminal vesicle – ejaculatory duct, with well developed penis papilla. An intra-penial papilla present in some species. Male and common atria highly glandular. Adenomuralia present. Ovovitelline ducts unite to form common ovovitelline duct that enters female genital canal ventrally. Female genital canal enters antrum horizontally. Type species: *Geoplana munda* Fletcher & Hamilton, 1888.

Etymology: *Lenkunya* is an aboriginal word meaning beautiful. The origin of the dialect and language group for the word is unknown. The name alludes to the attractively marked species in this genus. Gender feminine.

Distribution: Throughout the Warm and Cool temperate moisture regions of the Bassian zoogeographic sub-region in Tasmania, Bass Strait islands, south-eastern South Australia, Victoria, Australian Capital Territory, and central eastern New South Wales, and South Western zoogeographic sub-region, Western Australia.

Systematic discussion: In addition to *L. munda*, included in this genus (Winsor 1991c) are *L. adae* (Dendy 1891), *L. frosti* (Spencer 1891), *L. adae extralineata* (Dendy 1892a), *L. adae fusca* (Dendy 1894a), *L. ornata* (Fletcher & Hamilton 1888), *L. virgata* (Fletcher & Hamilton 1888), *L. arenicola* (Steel 1901a). To these are added *L. pava* (Steel 1897) and *L. scaphoidea* (Steel 1901a) previously *Geoplana elegans* (renamed, Steel 1897). The Type specimens of *L. munda, L. ornata* and *L. virgata* are presumed lost. Preliminary investigations on non-Type material of the *L. adae* – *L. frosti* complex indicate that at least three or more species are present. Resolution of the complex must await analysis of the type and supplementary material. *Lenkunya* is differentiated from *Caenoplana* by the distinctive lens-shaped antero-lateral crowding of the eyes. It is distinguished from *Fletchamia* principally by its small robust body (elongate in *Fletchamia*), strong parenchymal musculature (weak in *Fletchamia*), pharyngeal musculature with mixed musculature only in inner pharyngeal wall (mixed musculature present in inner and outer walls in *Fletchamia*), and general morphology of the copulatory organs. *Lenkunya* is probably closely related to *Fletchamia*, and both have a similar distribution pattern. The innermost longitudinal muscle layer of the pharyngeal wall is absent in *Lenkunya adae*.

Lenkunya munda (Fletcher & Hamilton, 1888)

Geoplana munda Fletcher & Hamilton, 1888: Dendy 1891; 1892e; 1894a,b; Spencer, 1891; Graff, 1899; 1912; Steel 1900; Winsor, 1973; 1973; 1976; 1977; E.M. Froehlich 1978; Johns 1993

? *Coenoplana munda* (Fletcher & Hamilton): C.G.Froehlich, 1959

Lenkunya munda (Fletcher & Hamilton); Winsor, 1991c; Ogren & Kawakatsu 1997

Caenoplana munda (Fletcher & Hamilton): Ogren & Kawakatsu 1991

Material examined:

LW 30 Gisborne, Victoria. Fixed SUSA, LSS 30 slides10μm H&E; LW 179 Acheron, Victoria. Fixed SUSA (a) gravid, LSS / TS37 slides, 10μm H&E, (b) mature LSS/TS 50 slides H&E, MSB; LW 379 North Koroit, Victoria. 14.10.73. Tyler's fixative, TS 4 slides, 8μm MSB.

Type Locality: Hartley Vale, New South Wales. From under a log and almost submerged in the water on a swampy flat. Hartley Vale was once the site of a large oil-shale industry set up in 1872 that continued until the turn of the century (Branagan & Packham, 1967). A swampy flat is still present at Hartley Vale though now occupied by an abandoned shaft, boiler and buildings; no flatworms were found at this locality (L. Winsor, 6 August 1978).

Distribution:

Hartley Val, New South Wales northernmost extent? South to islands in Bass Strait, northern Tasmania.

EXTERNAL MORPHOLOGY:

Body small (Fig. 8.11-1a), broadest in middle, tapering evenly to anterior and posterior ends, nearly oval in cross section, flattened ventrally. Mouth just forward of mid body, gonopore close to mouth.

Markings: The original description (Fletcher & Hamilton 1888 p 369, and Plate 5, Fig. 8) is as follows: "Undersurface greyish in centre, yellowish towards the margins. Above these is a narrow median dorsal line of pale olive brown, bounded on either side by a very fine dark line, external to which is a broader band of a slightly darker brown, and this is bordered externally by a very dark brown line, which gradually merges into a rather broad band of very dark brown, which fades gradually towards its outer margin."

A more accurate description and illustration of the markings is that of Spencer (1891 p90, Plate 12, Fig. 10) "The body colour is yellow (the tint being that known as Naples yellow), varying in intensity in different specimens, and being always lighter on the ventral than the dorsal surface. On the dorsal surface are, typically, four darker bands of colour. Two of these lie one on either side of the median line, enclosing between them a narrow strip of body colour; their internal edges are sharply marked, their external ones are less defined. External to the dark lines is a band of body colour, some three times the width of the median stripe, and covered with speckles of brown, which seem to spread out from the dark bands above mentioned, and to gradually diminish in number towards the external borders. External to these light bands lies, on either side, a dark brown band, somewhat wider than the former. Each may be divided into three portions - an upper, median, and lower. The upper has its internal edge sharply marked, and is always very dark; it passes more or less abruptly into the median part, which has a characteristic speckled appearance, and is bounded externally by the third and lower portion, made up of a somewhat narrow series of dark brown speckles. This lowest part varies somewhat in definition. The four dark bands are always present, but in addition to these, there may be present on either side, just where the dorsal merges into the ventral surface, a linear row of brown speckles, tending to form a dark line along each side. The brown of the bands varies from vandyke to umber."

Eyes (Fig. 8.11-1b) densely arranged in a single row around the anterior tip and anterolaterally, spreading to anterolateral region of dorsal surface, continue to posterior tip in staggered submarginal row.

INTERNAL ANATOMY:

Head:

Anterior adhesive pad or sucker absent. Parenchymal muscles of ring zone converge, cross, and with dorsoventral muscles form open meshwork that provides corseting to anterior end. Eyes pigment cup-type (Fig. 8.11-1b), embedded in cutaneous nerve net, with 5 or more retinal clubs (difficult to ascertain), in two distinct morphological types: small eyes with greater depth than width (pigment cup up to 25μm diameter, 30μm deep), in dense dark single row skirting anterior tip and submarginally; large eyes greater width than depth (pigment cup up to 36μm diameter, 14μm deep), in crowded, pale brown, anterolateral lenticulate cluster Eyes then continue in single staggered submarginal row to posterior end. Sensorial zone skirts anterior tip and present anterolaterally. Sensory pits simple, ciliated, 11.3 – 12.6μm diameter, 18.0 – 19.7μm deep.

Pre-pharyngeal region:

Epithelium same thickness (19.7 – 22.6μm) dorsally and ventrally. Adhesive margin present. Ciliated creeping sole 80% of body width. Cutaneous musculature tripartite, weak, developed equally dorsally and ventrally, CMI 3.6%. Parenchymal musculature strong, with longitudinal muscles as single and paired fibres in subneural plate and in loose ringzone, PMI plate 13.3%, PMI ringzone 13.3-15.5%. Dorsal, subintestinal and subneural diagonal muscles, and dorsoventral muscles weak.

Alimentary tract:

Pharynx cylindrical (Fig. 8.11-1c), inclined 35° ventrad, bent, longer than pouch, with dorsal insertion posterior to ventral insertion. Pharyngeal musculature inner epithelium longitudinal (single fibre thick), circular muscles in loose bundles, then mixed longitudinal and circular muscles; outer epithelium, longitudinal (two fibres thick), circular, then longitudinal muscles. Oesophagus absent. Pharyngeal pouch 1.35mm long, 9.6% of body length. Diverticulum absent. Mouth in distal third of pouch.

Reproductive system:

Copulatory organs lie in approximately mid-body immediately behind the pharyngeal pouch (Fig. 8.11-1c). With a strongly muscularized penis bulb, with another strongly muscular bulb containing male and female antra, and female genital canal; light longitudinal musculature invests organs ventrally, extensive secretory cells present dorsally. Testes ventral, anterior to ovaries, staggered in groups of 3-4 above each other to mid body or more, beneath and between diverticula of gut, extending almost entire length of body. Testes 100µm diameter, 213-284µm dorsoventrally. Sperm ductule leads from lower testicular pole to collecting duct beneath lateral nerve cord. Intermediate duct links collecting duct with subneural vas deferens that lies in line with ovovitelline duct. Vas deferentia rise either side of pharynx to pass posteriorly above nerve cords; form spermiducal vesicles when parallel with anterior quarter of copulatory organs. Sperm ducts then recurve and rise to separately enter anterodorsal end of penis bulb, join to form common sperm duct and enter proximal end of seminal vesicle.

Seminal vesicle capacious, U-shaped, sacculate, lined by secretory epithelium; distal end opens into strongly muscular ejaculatory duct. Proximal ejaculatory duct highly convoluted, prostatic region horizontally sinusoidal, receives erythrophil secretions. Distal (penial) ejaculatory duct receives erythrophil and cyanophil penial secretions; penis papilla with secretory ducts which discharge pale erythrophil globular secretions. Penis strongly muscular, with inner longitudinal and outer circular musculature; with elongate fixed-type papilla, covered by flattened anucleate epithelium. Male antrum elongate, sheath-like, with two dorsal and two ventral large adenomuralia, with reservoirs receiving fine granular erythrophil secretion from adjacent glands in mesenchyme, secretory ducts from dorsal reservoirs multiple, thin-walled, tortuous, with multiple openings into antrum; secretory ducts from ventral reservoirs thin-walled, lumen narrow proximal to reservoirs, wider distally, opening through floor mid antrum. Male antrum opens distally into narrow copulatory canal, which in turn opens into common antrum.

Ovaries in anterior body quarter. Ovovitelline ducts enter lateral walls of ovaries; posteriorly unite to form common ovovitelline duct that enters female genital canal ventrally. Female canal almost horizontal, receives strongly erythrophil secretions from extensive shell glands measuring 18-20µm diameter. Female canal enters antrum horizontally. Cyanophil and erythrophil mesenchymal glands, both 30-36µm diameter situated just below dorsal cutaneous musculature, dense secretory canaliculi surround and open into antrum. Antrum highly glandular, lined by tall ciliated columnar secretory epithelium with basal nuclei, with intraepithelial canaliculi, receives coarse granular cyanophil secretions. Fine erythrophil secretions accumulate in the distal ends of the epithelia. Cyanophil secretion in coarse granules entering epithelium, discharged along cilia as fine cyanophil granules. Secretion in antrum laminate, alternating fine cyanophil granules (pale purplish blue) and clear vesicles. Vitellaria extensive, surround gut.

Pathology:

Both specimens of LW179 from Acheron have a light gregarine infection. Various intracellular stages are evident in cutaneous and mesenchymal tissues including testes. LW379 exhibits severe gregarine-induced peri-intestinal histolytic vacuolation.

Etymology:

The specific epithet is derived form the Latin adjective mundus meaning clean, neat, nice, and alludes to the appearance of "this pretty little planarian" (Fletcher & Hamilton 1888, p369).

Biology:

Mature specimens showing the gonopore have only been recorded in March, April and May. Copulation has been observed in April and May, cocoons in April and May, and juveniles in May (Winsor 1977). Cocoons form in the female antrum, and are discharged through the greatly thinned dorsal antral wall. The resulting scar is manifested as displacement ("fault line") of the dorsal longitudinal stripes thus possibly indicating number of cocoons hatched. Habitat typically riparian areas such as river flats, often in waterlogged conditions. At night this gregarious species can be found massing on available prey on damp creek banks. It lives in interstices in the creek banks, which are probably refugia, much of the original woodlands throughout its range in western Victoria having been felled during the gold rush.

Remarks:

The Type specimen is lost. Graff's description of the anatomy of specimens from Croydon, Victoria received from Dendy differs that that here. Graf makes no mention of the adenomuralia present in the antral walls. Dendy (1892e p37) reported a light coloured variety of *L. munda* from Heidelberg and Creswick, also found in western Victoria and on Bass Strait islands. This variety has not yet been examined anatomically. Spencer (1891) observed that the original description of *L. munda* by Fletcher & Hamilton 1888, does not tally with the drawing (Fig. 8) given by them. It is clear from the notes accompanying their paper that these authors experienced problems, particularly with shading, with the illustrations produced by the lithographer. Their description, whilst lacking fine detail, generally accords with that of Spencer (1891).

Etymology:

The specific epithet from the Latin enigma riddle, mystery, alludes to the confusion surrounding the identity of the species and it's country of origin.

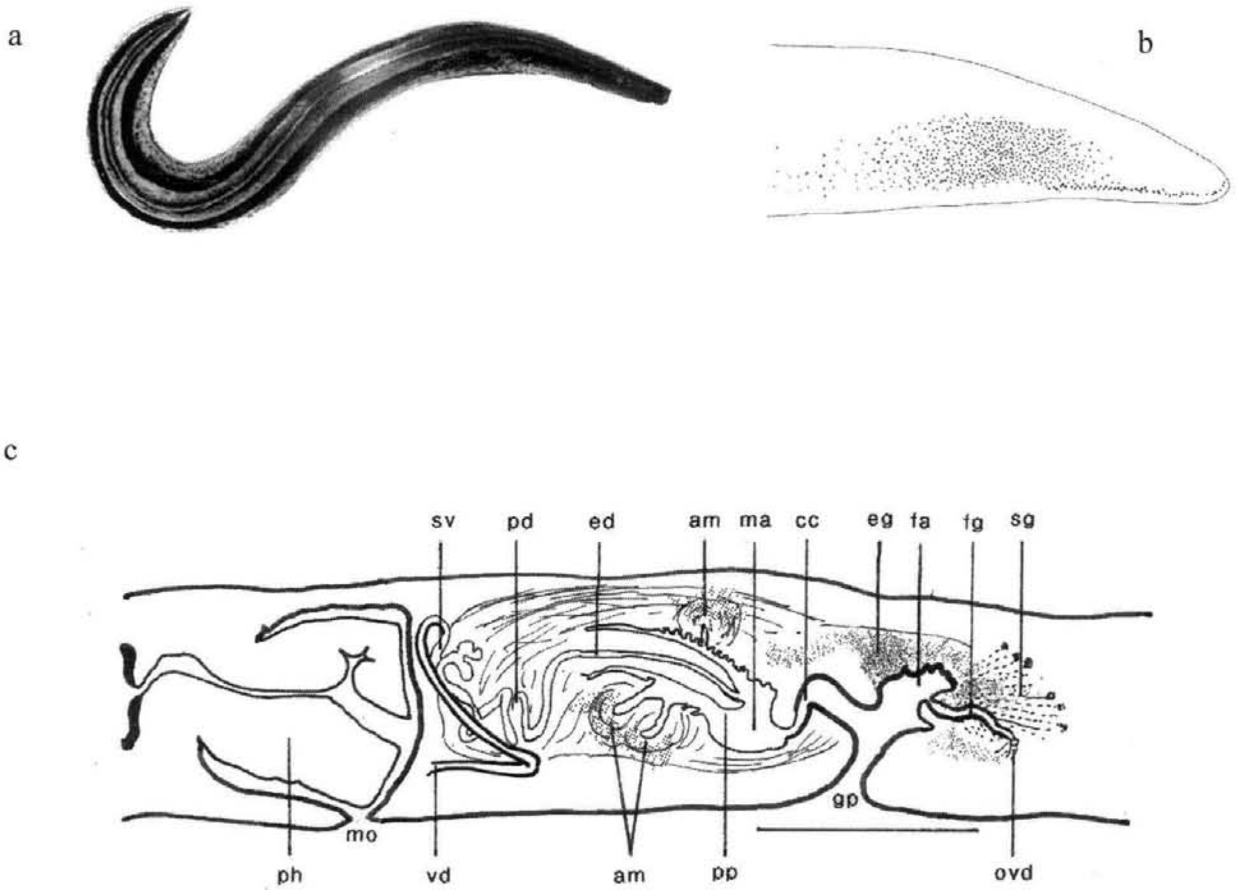


Figure 8.11 *Lenkunya munda* (Fletcher & Hamilton, 1888)

a. Whole specimen, dorsal aspect. Specimen 35mm long.

b. Anterior end, eye pattern. Unscaled.

c. Pharynx and copulatory organs. Scale bar = 500μm.

8.12 Genus *Nelipoplana* gen.nov.

Nelipoplana gen.nov.

Australoplana (part), Winsor, 1991c

Diagnosis: Caenoplaninae with elongate, strap-like body, broadly convex dorsally, flat ventrally. Mouth situated in posterior third of body, gonopore closer to mouth than to posterior end. Creeping sole absent. Eyes pigment cup-type, very small, in single row around anterior tip, then sparsely laterally to posterior end. Anterior adhesive pad or cup absent. Cutaneous musculature tripartite, with circular, helical muscles; strong longitudinal muscles in bundles. CMI 9.4 – 18%. Parenchymal longitudinal muscles very weak or absent. Pharynx bell-form. Pharyngeal musculature inner, epithelium, longitudinal, circular, then longitudinal muscles; outer, epithelium, longitudinal, circular, then longitudinal muscles. Testes ventral, dorsal to dorso-lateral to nerve cords, extend from just behind ovaries to root of pharynx. Vasa deferentia enter penis bulb separately then unite before passing into seminal vesicle. Seminal vesicle, prostatic region ejaculatory duct tubular, sinuous, strongly muscular, or spermiducal vesicles with cavernous prostatic region. Penis papilla present. Ovaries in anterior third. Ovovitelline ducts unite, form common duct that enters ventroposterior end of female genital canal. Female genital canal with expanded proximal end, almost horizontal, enters terminal end of tubular female antrum. Musculature of copulatory organs mixed, with wickerwork circular and longitudinal muscles. Viscid gland absent. Adenodactyls absent. Type species: *Nelipoplana alba* (Dendy, 1891)

Etymology: The genus name *Nelipoplana* is derived from the Greek *nelipos* barefooted, and the Latin *plana* flat, and alludes to the absence of a ciliated creeping sole in this genus. Gender feminine. The Bare-footed Planarian.

Distribution: Found in the cold, cool and warm moisture regions of the Bassian zoogeographic subregion of mainland of southeastern Australia, and Tasmania, and possibly with small pockets in cool upland sclerophyll forests in the Torresian zoogeographic subregion of southern and northern Queensland. Adventive in New Zealand and the United Kingdom.

Systematic discussion: *Nelipoplana* is differentiated from *Australoplana* chiefly by the absence of a creeping sole (narrow sole present in species of Australoplana), presence of a bell-form pharynx (cylindrical in *Australoplana*), pharyngeal musculature (*Australoplana* inner cm.lm.cm, outer lm.cm.lm) and in-line female antrum – genital canal (genital canal below female antrum in *Australoplana*). In both *Nelipoplana* and the more robust *Sokoplana* a ciliated creeping sole is absent. However *Nelipoplana* is differentiated from *Sokoplana* in having normal tripartite cutaneous musculature (additional layer of helical muscles present in *Sokoplana*), by the presence of mixed (wickerwork) musculature of the copulatory organs (well differentiated, not wickerwork in *Sokoplana*). However species of the subgenus *Nelipoplana (Nelipoplana)* share with *Sokoplana* a cavernous prostatic duct, and presence of a viscid gland, though in *Sokoplana* the bulb contains seminal vesicle and prostatic region, whilst in *Nelipoplana* the extra-bulbar spermiducal vesicles receive cyanophil secretions and appear to have the role of seminal vesicles; the prostatic region is intra-bulbar. The two genera may share a common lineage.

There are two distinct groups within *Nelipoplana*, mainly distinguished by major differences in the structure of the male copulatory organs (tubular, sinuous, strongly muscular seminal vesicle, prostatic region and ejaculatory duct, with poorly differentiated penis papilla *versus* spermiducal vesicles with cyanophil secretions (acting as seminal vesicles), with cavernous prostatic region and ejaculatory duct, with well differentiated penis papilla) and presence or absence of a viscid gland in gonad-mature specimens. These groups appear to be closely related and have in common their general external morphology and internal anatomy, with the exceptions previously noted. They may prove to be allopatric species. For this reason they are presently accommodated within the same genus. However given the quite disparate structures of the male copulatory organs, and pending the examination of other species in the genus, they are regarded here as the subgenera *Nelipoplana (Nelipoplana)* and *Nelipoplana (Peokrypta),* rather than species groups, best reflecting a possible dichotomy in a common lineage.

Nelipoplana gen et sub.gen.nov.

Diagnosis: As previously defined, with spermiducal vesicles (acting as seminal vesicles), prostatic region cavernous, small ejaculatory duct; penis papilla fixed type, encloses most of ejaculatory duct. Viscid gland present. Type species: *Nelipoplana (Nelipoplana) alba* (Dendy, 1891) gen. et sub. gen. nov.

Nelipoplana (Nelipoplana) alba (Dendy, 1891) comb. nov.

Geoplana alba Dendy, 1891; Spencer 1891; Dendy 1891
Geoplana sanguinea (Moseley, 1877), Dendy 1891; *sensu* Fyfe 1948
Australoplana alba (Dendy, 1891), Winsor, 1991c; Ogren *et al* 1993b
Caenoplana alba (Dendy, 1891), Ogren & Kawakatsu 1991
Geoplana alba var *roseolineata* Dendy, 1892a; Smith & Convey 1970;
Australoplana alba var *roseolineata* (Dendy, 1892a); Winsor 1991c
Caenoplana alba var *roseolineata* (Dendy, 1892a); Ogren & Kawakatsu 1991

Literature records and figure of sectioned material:

AM W1820, Table Cape, Tasmania, non-sexual; W2151 Blackheath, NSW, immature; W2152, Gosford, NSW, sexual; W2196 Yarraville, Victoria, found burrowing in soil, Coll. FWS Sept 1907 (Fyfe, 1948). Fyfe sectioned part of these specimen lots, and returned the unsectioned anterior portions to the Museum of Victoria, where they remain, rather than to the Australian Museum. The location of the microslides is unknown. MNH, Ballarat (Jones 1981).

Material examined:

Geoplana alba var *roseolineata* Dendy, 1892a Syntypes, Loch, Victoria, Coll. W.B. Spencer, 1891: AM W2256 a, (designated the Lectotype, Fig. 8-12-1a) sexual specimen, sectioned at 8μm, anterior HS 28 slides H&E, pre-pharyngeal region TS 4 slides, posterior LSS 22 slides, stained with Gomori trichrome, and MV G1458, (designated the Paralectotype) immature specimen, sectioned 8µm, pre-pharyngeal region TS – posterior LSS, 15 slides, stained with Gomori trichrome.

Other material:

MV Unregistered, originally from the Melbourne University Zoology Department, six slides umbered 1 – 6, sections stained by a carmine method, non-sexual, labels in ink, W.B. Spencer's hand "*G. alba* (middle) (Long. hor) Series 1"; G629 Warburton, Victoria, Coll. J.A. Kershaw, 13 Jan 1905, five sexual specimens; specimen G629a sectioned at 8µm, stained with Gomori Trichrome, pre-pharyngeal region TS 7 slides, posterior LSS 48 slides. AM W1945 Mt Blackwood, Victoria, Coll T. Steel, two sexual specimens; specimen W1945a sectioned at 8µm, stained with Gomori Trichrome, pre-pharyngeal region TS 9 slides, posterior LSS 66 slides. LW130 Mt Erica, Victoria, 2 specimens, sexual specimen sectioned at 8µm, stained H&E, pre-pharyngeal region TS 20 slides, posterior LSS 106 slides. AM. W1992 Mt Victoria, Auckland, New Zealand. Coll. T. Steel. (no date on label; suspect collected before 1894) considered to be the specimen listed as " .. near Auckland (coll. T. Steel, Esq.)" under *Geoplana sanguinea* in Dendy, A. 1894 (issued 1895). *Note on New Zealand Land Planarians Part I. Trans. Proc. N.Z. Inst. 27*: p179. Single sexual specimen, sectioned at 8µm, stained Gomori trichrome and PTAH, anterior tip TS / HS, 18 slides, pre-pharyngeal region TS - posterior LS, 30 slides. Over 200 specimens in 108 specimen lots have been examined externally.

Distribution:

Southeastern Australia including Tasmania. Adventive in New Zealand.

EXTERNAL FEATURES:

Body elongate, broad, much flattened, often with crenulate margins that disappear when the animal moves. Colour may vary from deep red to pink, peach to light orange-brown, pale creamish yellow, flesh coloured to white, and is often dependent upon the colour of ingesta. Anterior tip reddish brown – peach coloured. Ventral surface generally the same or slightly lighter than dorsal colour, evenly coloured without evidence of distinct creeping sole. May have paired red to pink coloured lateral dorsal stripes, generally with diffuse margins, dividing the back into three equal parts. Lectotype: Length 28.0mm, width 4.0mm, mouth 17.5mm from anterior tip, gonopore 2.4mm behind mouth. Specimen (Fig. 8.12-1) is a uniform blotchy brown colour. Specimen broad, flat and elongate, tapered in the anterior third, tapered more abruptly posteriorly. Dorsal surface convex, ventral surface slightly concave. Height 1642µm. Creeping sole absent.

INTERNAL ANATOMY:

Head:

Anterior sucker and muscular specialization absent; eyes small, pigment cup type, 11- 14µm diameter, situated in single row contouring anterior tip, continuing posteriorly in single submarginal row. Sensorial zone extends around anteroventral margin, sensory ciliated pits small, inconspicuous, 19µm deep, 7.5µm diameter.

Pre-pharyngeal region:

Dorsal epithelium slightly thicker (18.5µm) than ventral (14.0µm thick). Ciliated creeping sole absent. Rhabdoids rhammite type slightly sinusoidal, 14µm long, pack dorsal epithelium, continue to ventral zone. Microrhabdites sparsely secreted over ventral surface. Erythrophil secretions abundant over entire body surface. Cyanophil secretions sparse ventrally. Marginal adhesive zone absent. Cutaneous musculature tripartite, with circular, decussate helical, longitudinal muscle layers; longitudinal muscles in bundles, strong, tightly packed with fibres. Dorsal (118.4 µm thick) thinner than ventral cutaneous musculature (135.4µm). CMI = 15.5%. Parenchymal musculature with strong dorsal, ventral transverse muscles; supraintestinal, infraneural transverse muscles weaker. Dorsoventral muscles numerous, strong. Periintestinal muscles strong. Parenchymal longitudinal muscles absent.

Alimentary tract:

Pharynx bell-form, with dorsal insertion posterior to mouth, ventral insertion anterior to mouth. Pharyngeal musculature inner, epithelium, longitudinal, circular, then longitudinal muscles; outer, epithelium, longitudinal, circular, then longitudinal muscles. Pharyngeal pouch 2.7mm long, 9.6% of body length, with mouth situated mid pouch, diverticulum present, abuts front of the penis bulb.

Reproductive organs:

Copulatory organs Fig. 8.12-1b. Testes ventral, spherical to ovoid, 240μm diameter, situated under gut diverticula in staggered uniserial arrangement, lying dorsolaterally to nerve cord, beginning just behind ovaries, extending to pharyngeal root. Staggered pairs of testes connected by intertesticular duct: a sperm ductule from the lower pole of more mediad testis passes ventrolaterally to short intertesticular duct which leads directly to adjacent more laterad testis of pair. Sperm ductule passes from lower testicular pole ventrally, enters intermediary duct that passes into collecting duct at lateral margin of nerve cord. Intermediary duct connects collecting duct to vas deferens. Vasa deferentia lie immediately below lateral nerve cords in line with ovovitelline duct; pass posteriorly until level with penis bulb, rise, narrow then expand spermiducal vesicles each side of bulb. Spermiducal vesicles receive basiphilic secretions from adjacent glands; open into sperm ducts, recurve medially, penetrate penis bulb to separately enter the prostatic vesicle. Prostatic vesicle cavernous, with alveolate (honeycombed) secretory lining membrane, with coarse agglomerations of fine erythrophil granules within membrane-bound globules secreted in apocrine manner into lumen; prostatic vesicle opens into ejaculatory duct within strongly muscular penis papilla. Penis bulb musculature with outer sheath obliquely-longitudinal muscles, with innermost circular muscles, then wickerwork musculature of mixed circular, longitudinal and radial muscles; circular muscles predominate along ventral side of the prostatic region, penis papilla, muscular flap.

Ovaries anterior, elongate, some 190μm diameter, lie immediately above mid nerve cords. Ovovitelline ducts with tuba at proximal (ovary) end, with resorptive tissue; ovovitelline ducts then narrow, pass posteriorly, unite, form common ovovitelline duct, rises dorso-posteriorly at 45°, strongly curves forward passing into female genital canal ventroposteriorly. Common ovovitelline duct saccate, with tall columnar epithelium, with mid nuclei, with cyanophil margin, secretes cyanophil droplets, erythrophil granules, membrane bound globules. Female genital canal with tall columnar epithelium with central nuclei, with shell gland secretions; enters funnel-shaped female antrum, with cocoon-forming epithelium, secretes erythrophil sclerotin globules, cyanophil sclerotin strands; secretions derived from glands mainly in adjacent dorsal mesenchyme. Viscid gland present inside posterior gonopore lip; 340μm deep (including duct), 90μm diameter, with nucleate cuboidal epithelium, secretes fine erythrophil (dark red) granules, coarse xanthophil granules, both derived from secretory cells posterior to copulatory organs. Vitellaria abundant, situated between gut diverticula; communicate via short vitelline funnels with ovovitelline duct. Glandulomuscular organs (adenodactyls) absent

Table 8.12-1. *Nelipoplana (Nelipoplana) alba* (Dendy, 1891). Dimensions of type material.

DIMENSIONS	AM W2256a Lectotype (sectioned)	MV G1458 Paralectotype (sectioned)
LENGTH mm	28.0	13.0
WIDTH mm (over mouth)	4.0	1.5
HEIGHT (from sections) µm	1640	1075
MOUTH mm from anterior tip	17.5	9.0
MOUTH distance from anterior tip as % length	62.5	69.2
GONOPORE mm from anterior tip	20.0	10.0
GONOPORE distance from anterior tip as % length	71.4	76.9
GONOPORE mm from mouth	2.5	1.0
GONOPORE distance from mouth as % length	8.9	7.7
Cutaneous Muscular Index (CMI)	15.5%	16.5%

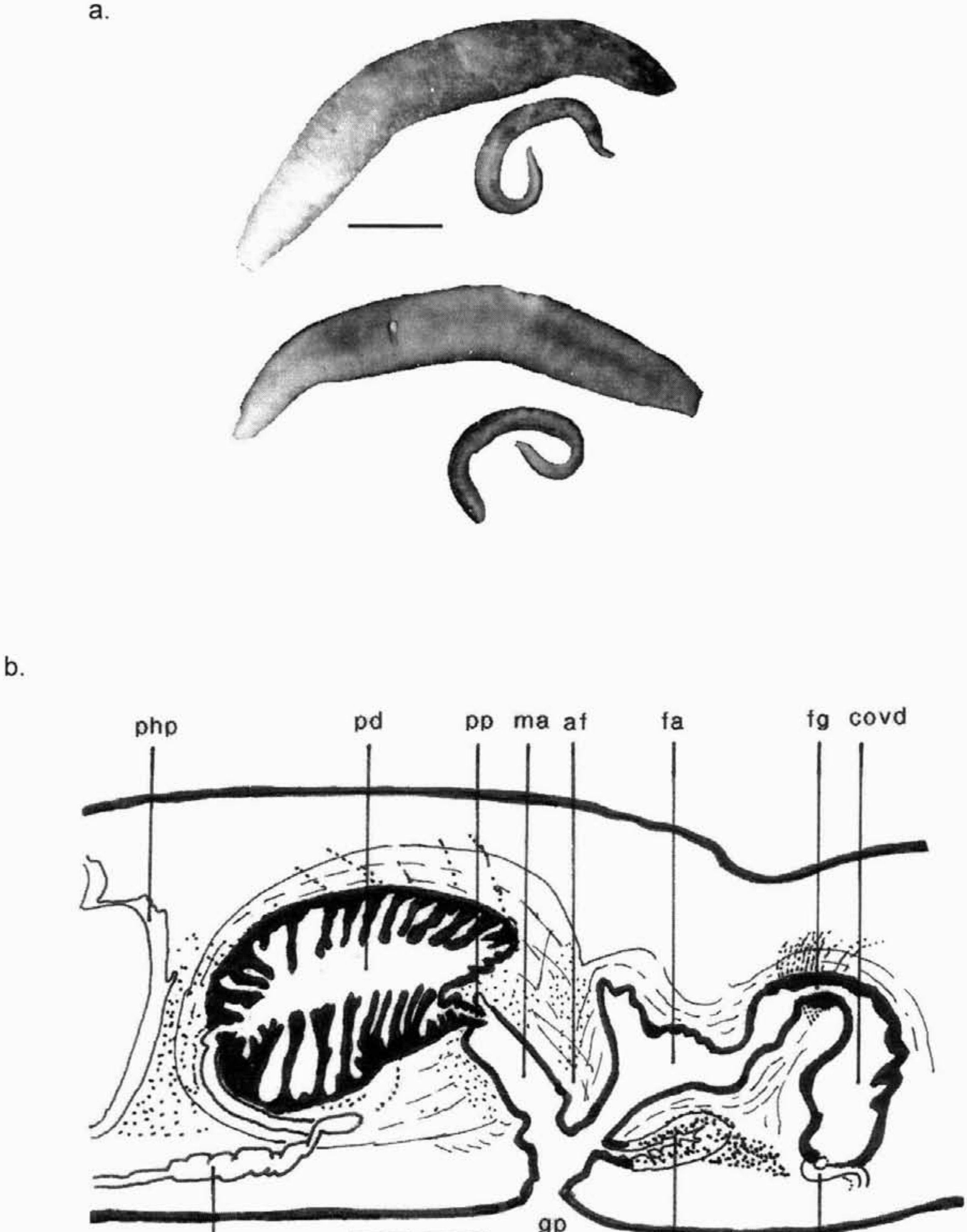


Figure 8.12-1 *Nelipoplana (Nelipoplana) alba* Lectotype AM W2256.

a. Dorsal and ventral surfaces of specimen (Lectotype is the larger of the two), Scale 5 millimetres.

b. Copulatory organs. Scale bar = 500μm

Peokrypta sub. gen. nov.

Diagnosis: As previously defined, with seminal vesicle, prostatic region, ejaculatory duct tubular, sinuous, strongly muscular; penis papilla very small, enclosing little of the ejaculatory duct. Viscid gland absent. Type species: *Nelipoplana (Peokrypta) enigma* gen. et sub. gen. et sp. nov.

Etymology: *Peokrypta*, hidden penis, contrived from the Greek *peos* penis and *kryptos* hidden, alludes to the small, poorly differentiated penis papilla in species in this genus. Gender feminine.

Distribution: Southeastern Australia including Tasmania. Adventive in New Zealand and the U.K.

Nelipoplana (Peokrypta) enigma gen. et sub gen et sp. nov.

Geoplana sanguinea (Moseley, 1877), Dendy 1892e
Geoplana sanguinea (Moseley, 1877) var *alba* (Dendy, 1890) *sensu* Jones 1981;
Geoplana sanguinea (Moseley, 1877), Ball & Reynoldson 1981
Australoplana sanguinea var *alba sensu* Jones 1981; Winsor, 1991c; Mather & Christensen, 1996; Jones & Boag 1996; Jones *et al* 1998
Caenoplana alba (Dendy, 1890); Ogren *et al* 1991
Australoplana alba (Dendy, 1890); Ogren *et al* 1993b
Australoplana sanguinea alba (Dendy, 1891*); Ogren *et al* 1998

(* *sic*)

Literature records of sectioned and figured material:

Australoplana sanguinea alba (Dendy, *sensu* Jones (1981) described from specimens obtained from the gardens at Tresco Abbey, Scilly Isles. Additional records in Belfast, Northern Ireland, and Poole, Dorset, England (Jones, 1981).

Material examined:

MV Unregistered, formerly No. 555, Melbourne University Zoology Department, with label in Dendy's hand "*Geoplana sanguinea* Moseley Castlemaine", three sexual specimens [originally seven specimens collected by T.S. Hall from under fallen bark and stones (Dendy, 1892)], sectioned 8μm and stained by Mallory-Heidenhain, pre-pharyngeal region, TS, 4 slides; posterior region, LSS, 10 slides. LW 890 11km SW of Lefroy, north eastern Tasmania, collected by LW 17 October 1975, a pair of specimens fixed *in cop*, from under log, ecotone between cleared pastoral land and low open forest on boggy, fine loamy soil; found together with native molluscs and *Artioposthia* spp. Sectioned, 8μm, stained by Mallory-Heidenhain, posterior region LSS, 26 slides. LW 1761 Adelaide, collected by T. Terrace, CSIRO, 5 July 1995, single sexual specimen, from urban garden, sectioned 10μm, stained H&E, MSB, pre-pharyngeal region TS / posterior LSS 26 slides.

Distribution:

Southeastern Australia including Tasmania. Adventive in New Zealand and the U.K.

EXTERNAL FEATURES:

"Rich Indian red above, paler below. The eyes, as in *G. alba*, very small and difficult to make out. ... The Castlemaine specimens of *G. sanguinea* are all markedly smaller than the average size of *G. alba*, but Moseley's examples seem to have been of about the same size as the latter" (Dendy, 1892). Dimensions of the three spirit-preserved specimens are provided in Table 8.12.2.

INTERNAL FEATURES:

Head:

Anterior sucker and muscular specialization absent; eyes small, pigment cup type, situated in single row contouring anterior tip, continuing posteriorly in single submarginal row. Sensorial zone extends around anteroventral margin, sensory ciliated pits small, inconspicuous.

Pre-pharyngeal region:

Dorsal epithelium thicker than ventral epithelium. Ciliated creeping sole absent. Rhabdoids present as fine sinuous rhammites 9.5-11.4µm long, numerous dorsally - dorsoventrally, continuing over but less numerous on ventral surface. Erythrophil cutaneous secretions fine granular, present over entire surface, concentrated marginally, submarginally. Xanthophil cutaneous secretions coarse granular, with distribution paralleling erythrophil secretions. Cyanophil cutaneous secretions absent. Marginal adhesive zone absent. Cutaneous musculature tripartite, with circular, helical, longitudinal muscles. Longitudinal muscles in bundles. Dorsal cutaneous musculature slightly stronger than that ventrally. CMI 9.8%. Parenchymal musculature weak, with supraintestinal transverse and infraneural transverse muscles prominent. Longitudinal muscles absent.

Alimentary tract:

Pharynx bell-form, with dorsal insertion posterior to mouth, ventral insertion anterior to mouth. Pharyngeal musculature inner, epithelium, longitudinal, circular, then longitudinal muscles; outer, epithelium, longitudinal, circular, then longitudinal muscles, with very strong ring of muscles around proximal pharynx. Pharyngeal pouch 600µm long, 3.5% body length, with elongate diverticulum, closely abuts copulatory organs.

Reproductive organs:

Copulatory organs Fig 8.12-1a,b. Testes ventral, uniserial, dorsolateral to nerve cords, mature, extend from anterior to near to pharyngeal root. Sperm ductule passes from ventral testicular pole to join collecting duct that passes below nerve cord to join sub-neural vas deferens. Vas deferens rise near pharynx, with spermiducal vesicles adjacent to pharynx, ascend to separately enter penis bulb, unite to form common duct; duct ascends, enters seminal vesicle. Seminal vesicle and prostatic region tubular, with circular muscles, coiled, lie within a loose connective tissue stroma. Seminal vesicle receives cyanophil secretions, prostatic region receives erythrophil secretions. Penis elongate, protruded within antrum, papilla not clearly differentiated from antral wall. Bulb and male antrum with strong mixed circular and longitudinal muscles, tending towards alternating (wickerwork) layers, with weakly muscularized outer open stroma. Male antrum with tall "ciliated" columnar cocoon-forming epithelium, receives predominantly xanthophil secretions from glands in surrounding mesenchyme. Common and female antra with tall columnar deeply cyanophil cytoplasm, receive fine granular cyanophil granules; common antrum with weak mixed circular and longitudinal muscles, female antrum with strong sheath of circular fibres predominating.

Ovaries not yet examined. Vitellaria extensive, surround gut between branches. Ovovitelline ducts pass posteriorly along top of lateral nerve cords, ascend to separately enter ventroposterior end of female genital canal. Female genital canal flask shaped, bulbous proximally, enters mid antral wall via narrow neck. Female antrum with cocoon-making epithelium, receives cyanophil secretions from glands in surrounding mesenchyme. Viscid gland and musculoglandular organs (adenodactyls) absent.

Internal anatomy of other material (LW 890 and LW 1761):

Both specimens share with MUZD 555 the presence of eyes, relative positions of the body apertures, the same general histology of the body wall in particular abundant erythrophil and xanthophil secretions over entire surface, absence of a ciliated creeping sole, cutaneous musculature, with LW 890 CMI 9.4%, LW1761 CMI 9.7%, absence of parenchymal longitudinal muscles; pharynx type and musculature; pharyngeal pouch with diverticulum close to copulatory organs present in LW 890, but absent in LW 1761 (possibly as specimen had recently fed, with pharynx filling pouch, and gut fully distended with ingesta). Both specimens have the same topography and histology of the copulatory organs with penis retracted in both specimens, with intra antral papilla evident in LW890, fixed *in cop*, (Fig. 8.12-1 b), and exhibiting a deeply folded male antrum typical of a fully mature specimen; the penis papilla was poorly differentiated in LW1761, and male antrum not deeply folded, the specimen probably being not fully mature.

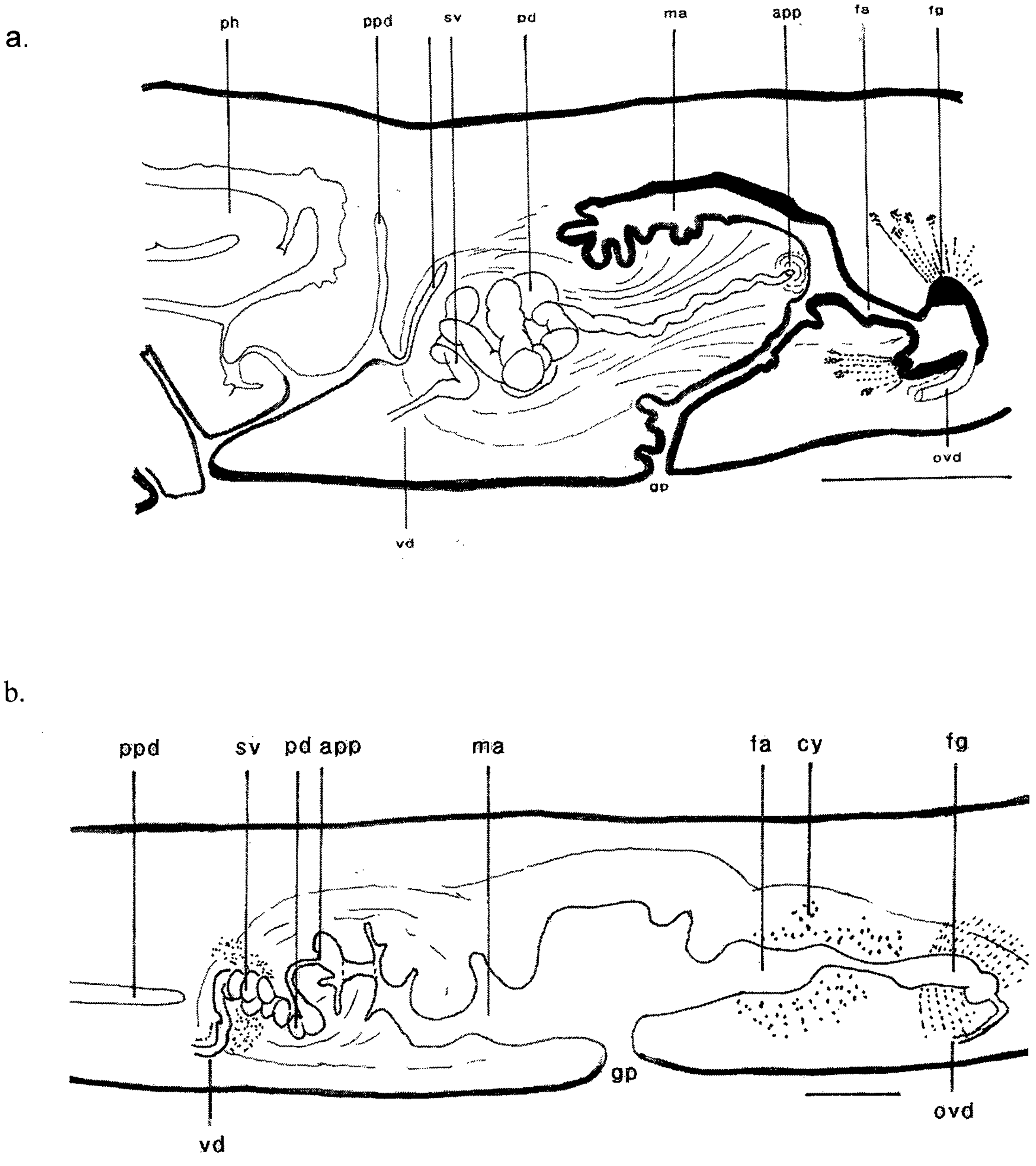


Figure 8.12-2 *Nelipoplana (Peokrypta) enigma* Copulatory organs.

a. Holotype MV MUZD 555. Castlemaine, Victoria. Scale bar 500µm. Note that the pseudophallus is partly everted. The tip lies across the antrum.

b. LW890 Lefroy, Tasmania. Penis not everted. Refer to text for discussion.

Systematic discussion:

1. *Nelipoplana (Nelipoplana) alba* (Dendy, 1891).

The Type specimens of *Nelipoplana alba* are lost. It is possible that some of the original specimens were sectioned, suggested by the carmine stained serial sections, labelled *G. alba*, Series 1, originally from the Melbourne University Zoology Department where Dendy worked in 1891, now in the collections of the Museum of Victoria. However a Lectotype and Paralectotype have been selected from the Syntypes of *Geoplana alba roseolineata* Dendy, 1892a. The latter subspecies is considered here to be synonymous with *Nelipoplana alba* (Dendy, 1891). There are no major anatomical differences between non-striped specimens (*alba*) and specimens exhibiting paired red stripes (*alba roseolineata*). The sectioned material, representing various examples of colouration from red through to white, and red striped, exhibits remarkable uniformity in the copulatory organs. Specimens from upland localities (eg. Mt Erica) in Gippsland, Victoria, tended to be larger when mature than those from the lowlands (eg. Loch). Minor anatomical differences appear to be related to maturity. They include the development of spermiducal vesicles and extent of looping in the vas deferens before entering the penis bulb, evident in fully mature specimens, and the presence of a viscid gland in gonad-mature specimens; the viscid gland was absent in specimens with patent gonopore, but immature testes. Variation in the distance between the posterior extent of the pharyngeal pouch and anterior end of the copulatory organs in specimens was also noted. Generally the two structures are separated by some 500µm of parenchymal tissue. However in the Lectotype and Paralectotype of *Geoplana alba roseolineata*, both from Loch, Victoria, the structures abutted. Similar variation in distances between these structures was noted between specimens of *Nelipoplana (Peokrypta) enigma.*

2. *Nelipoplana (Peokrypta) enigma*

The three sectioned specimens of this species examined here exhibit varying degrees of penial tumescence, but otherwise differ little with regard to general typography and anatomy; they are all considered to be the same species, *Nelipoplana (Peokrypta) enigma.* This species is considered here to be identical with

Australoplana sanguinea alba, sensu Jones (1981), described from specimens obtained from the gardens at Tresco Abbey, Scilly Isles, U.K., now found throughout other areas of the U.K., and until now, of unknown origin. The name *Australoplana sanguinea alba sensu* Jones, 1981, is not valid – the species is neither *Australoplana sanguinea* (Moseley, 1877) nor *Nelipoplana (Nelipoplana) alba* (Dendy, 1890).

There was one major point of difference between Jones' description of his species and the actual histology of specimens of *Nelipoplana (Peokrypta) enigma* described here: the presence of parenchymal longitudinal muscles in supraneural bundles, described and figured by Jones (1980 page 839, and Fig. 2). These "muscles" could be bundles of fine, thin walled longitudinal secretory ducts from subintestinal gland cells, mostly supplying the pharynx, or may be nephridial tubules common in these areas, or may be cross sections of oblique and dorsoventral muscles. Neither of the later two elements persists in longitudinal sagittal sections. In all the specimens of *Nelipoplana (Peokrypta) enigma* examined here the secretory ducts contain globular, deeply erythrophil secretions, which resemble muscle fibres in cross-section; some protonephridial end canals also resemble muscles in cross section, and could account for Jones' mis-interpretation of these structures in his Scilly Isles material. Blocks of parenchymal longitudinal muscle are absent in *N. (P). enigma.*

The fore mentioned gland and duct system, and nephridial elements are present to a varying extent in all terricolans. In *Australoplana sanguinea* and *Nelipoplana (Nelipoplana) alba* the bundles of ducts are present between nerve cords and gut and between the outer gut and testes, with generally fine erythrophil, xanthophil, and cyanophil granules present in the lumen; the ducts do not look like muscles bundles, possibly explaining why Jones stated (1980 page 842) that " these (ie. longitudinal muscle bundles) are not present in the other two specimens (of *sanguinea* and *alba*)". Tissue fixation, histological sectioning, and staining can affect the appearance of these structures, further confusing interpretation.

8.13 Genus *Sokoplana* gen.nov.

Sokoplana gen.nov.

Diagnosis: Caenoplaninae with elongate body, convex dorsally, flat ventrally. Mouth and gonopore situated in third body quarter. Creeping sole absent. Eyes pigment cup-type, very small, in single row around anterior tip, then sparsely laterally to posterior end. Anterior adhesive pad or cup absent. Cutaneous musculature tripartite, with circular, decussating helical - helico-circular, and longitudinal layers; dorsal and ventral cutaneous musculature equal; with strong longitudinal muscles in well defined bundles. CMI 11%. Parenchymal musculature weak; longitudinal muscles absent. Pharynx bell-form. Pharyngeal musculature with inner epithelium, thin longitudinal, thick circular, then thin longitudinal muscle layers; outer epithelium, longitudinal, strong circular, then loose longitudinal muscle layers. Pharyngeal pouch diverticulum absent. Testes ventral, lateral to nerve cords, extend from just behind ovaries to root of pharynx. Vasa deferentia enter penis bulb separately then unite before passing into anterior – antero-dorsal wall of seminal vesicle. Bulb lumen cavernous, with seminal vesicle, prostatic region, ejaculatory duct. Penis papilla fixed-type; papilla without glandular ducts. Ovaries anterior, with tuba. Ovovitelline ducts unite at posterior end of female genital canal. Female genital canal horizontal, enters terminal end of elongate female antrum. Musculature of copulatory organs differentiated, with outer longitudinal and inner helical muscle layers. Viscid gland present. Adenodactyls absent. Type species: *Sokoplana kanangra* gen. et sp. nov.

Etymology: The genus name *Sokoplana*, derived from the Greek *sokos* strong, and the Latin *plana* flat, alludes to the physical attributes of species of the genus, in particular the strong cutaneous musculature with the unusual additional helical muscles. Gender feminine. The Strong Planarian.

Distribution: The genus occurs in the Cool temperate moisture region of the Bassian zoogeographic sub-region of New South Wales.

Systematic discussion: A comparison of taxa, including *Sokoplana*, of similar external appearance in the old *Australoplana sensu lato* group is provided in Appendix 8. *Sokoplana* is unique amongst these taxa in having an unusual helical muscle sheath within the cutaneous musculature, also reflected in the musculature of the pharynx and copulatory organs. *Sokoplana* stands closest to *Apogaioplana*, and a differential diagnosis for these two taxa has been provided previously within the discussion for the latter genus. There is presently only one species, *Sokoplana kanangra*.

Sokoplana kanangra gen. et sp. nov.

Material examined:

AM W 10215 Green Gully, Boyd Plateau, Kanangra-Boyd National Park, N.S.W., three specimens, collected by M & G. Grey, 27 June 1971, Found in rotting logs. Specimens preserved in 70% ethanol. Holotype W10215 #1: combined pre-pharyngeal region TS and LSS posterior, 48 slides, stained AZAN. Paratypes W10215 #2 and W10215 #3.

EXTERNAL MORPHOLOGY:

"Colouring - light brownish orange with single darker orange stripe down middle" (specimen label). Robust, elongate, dorsoventrally flattened worms, dorsal side convex, ventral side slightly concave. Colour pale brownish with faint thin (0.1-0.2mm wide) median dorsal stripe; slight orange tint at extreme posterior margins. Slightly paler and uniform ventrally; no evidence of creeping sole. Dimensions of material examined are provide in Table 8.13-1.

INTERNAL ANATOMY:

Head:

Adhesive sucker and pad absent. Sensory papillae absent. Eyes small, in a single row skirting anterior tip margin, present in single staggered submarginal row to posterior end. Sensorial zone extends around anteroventral margin.

Pre-pharyngeal region:

Dorsal epithelium (14-17µm thick) overall slightly thinner than ventral epithelium (14-20µm thick). Creeping sole absent. Rhammites are of rhabdoid type, present dorsally and ventrally. Erythrophil and xanthophil epidermal secretions abundant dorsally and ventrally. Cyanophil secretions present dorsally. Marginal adhesive zone absent. Cutaneous musculature tripartite; with circular muscles (7µm thick); helical muscle layer with thick fibres, very open decussate (27µm thick), with apparent additional separate circulo-helical layer (14µm thick) part of helical layer, with fibres which anastomose with longitudinal muscle fibres (total thickness helical layer 40µm); longitudinal muscles in bundles (70µm). Ventral organization same. Dorsal and ventral cutaneous musculature equal thickness. CMI = 11%. Parenchymal musculature with weak dorsal transverse muscles more helical than transverse, strong dorsoventral muscles, weak peri-intestinal muscles. Strong infraneural transverse muscles more helical than transverse, with ventral plate of weak longitudinal muscles present as fibres not in bundles, sparse. PMI plate 1.2 - 1.4%.

Alimentary tract:

Pharynx very large bell-form type, with dorsal insertion posterior to mouth, ventral insertion anterior to mouth. Pharyngeal musculature with inner epithelium, thin longitudinal, thick circular, then thin longitudinal muscle layers; outer epithelium, longitudinal, strong circular, then loose longitudinal muscle layers. Pharyngeal pouch 6% body length, closely approximated to pharynx, without diverticulum. Mouth situated two-thirds along pouch floor. Dorsal wall of pouch with thick layer of helical muscles, tapering out anteriorly beyond pharyngeal insertion; posteriorly continuous with dorsal insertion pharynx wall.

Reproductive organs:

The copulatory organs are very large (Fig. 8.13-1). Testes 280 µm high, 200□m wide, ventral, uniserial, laterodorsal to nerve cord, underlying gut, with upwards extension between gut diverticula, extend posteriorly to root of pharynx; sperm ducts from lower testicular poles connect with intertesticular ducts lying parallel with lateral margins of nerve cords. Intertesticular ducts with tortuous paths, join transverse intermediary ducts at intervals of 570 -720μm; intermediary ducts pass under nerve cords, bifurcate, form collecting ducts which parallel then rise to anastomose with vasa deferentia. This arrangement of ducts gives appearance of vasa bifurcating then rejoining in dorsoventral plane at intervals of 270 -360μm. Anteriorly vasa deferentia embedded beneath medial margins of nerve cords above efferent ducts. Posteriorly, behind pharynx, vasa deferentia tortuous, increase in diameter, form spermiducal vesicles. Level with anterior penis bulb vasa straighten, incurve, then ascend, strongly recurve anteriorly, then separately enter bulb, unite within mid-anterior end of bulb. Common duct receives xanthophil granules from adjacent gland cells, rises then passes posteriorly, enters prostatic vesicle dorsally through roof of penial bulb.

Penis bulb highly muscular, differentiated, with very strong inner sheath helical muscles, with large fibres similar to cutaneous helical muscle fibres; with outer sheath longitudinal muscle. Penial glands situated anterior to copulatory organs; with complex penial secretory structures, secretions. Lumen divided into three regions on basis of secretions: seminal vesicle (proximal end bulb) characterised by cyanophil globular secretions; prostatic region characterised by strongly erythrophil globular secretions, then narrow ejaculatory duct characterised by xanthophil secretions. Seminal vesicle, prostatic regions with highly modified anucleate epithelium resembling reticular network of ducts: ductules of penial glands open into ampullae from which multiple terminal ducts open into lumen. Terminal duct membranes supported by septae. Fine granular erythrophil penial secretions pass through bulb musculature, enter ampullae, then coalesce within ducts to form globules that pass to distal end of terminal ductules, then secreted in apocrine manner. Ejaculatory duct epithelium grades into nucleate columnar epithelium with strongly cyanophil cytoplasm, with terminal basic protein xanthophil secretions; terminates in elongate fixed-type penis papilla. Papilla with low facing epithelium present around male antrum in proximity of papilla, underlain by longitudinal muscles external to which is very strong sheath of circular muscles with outermost layer of longitudinal muscles.

Male antrum with mixed circular and longitudinal muscles.

Gonopore large; antra with tall rugose columnar cocoon-making epithelium, with cyanophil sclerotin globules. Common antrum with interwoven muscles; female antral musculature with inner interwoven helical muscles, with strong outer circular muscles, particularly below antrum, with longitudinal-helical muscular fascia. Viscid gland present just inside posterior lip of gonopore, with narrow duct passing dorso posteriorly at approximately 30 degrees for 500μm below female antrum, expands, then rises passing left of female antrum; receives globular erythrophil, granular cyanophil secretions from glands surrounding duct. Dorsal wall of viscid gland with epithelium similar to prostatic duct - reticulate duct arrangement; ventral wall with tall columnar epithelium, with basiphilic cytoplasm. Viscid gland musculature with thin ental longitudinal, thick ectal circular muscle layers.

Ovaries not yet examined. Ovovitelline ducts are embedded in mid dorsal side of nerve cords; pass posteriorly, incurve horizontally, separately enter proximal end of genital canal via common opening. Genital canal elongate, with columnar epithelium that receives basic protein xanthophil secretions from large concentration of shell glands posterior to canal; enters female antrum horizontally. Vitellaria extensive, completely surround gut, communicate with ovovitelline ducts via short vitelline funnels. Glandulomuscular organs (adenodactyls) absent.

Pathology:

A few nematode larvae were present in the ventral musculature.

Etymology:

The specific epithet refers to the Kanangra-Boyd National Park, New South Wales, from which the species was collected. *Sokoplana kanangra* – the strong planarian of Kanangra.

Systematic discussion:

Sokoplana is unique amongst taxa of similar appearance (*Australoplana, Bassioplana, Nelipoplana)* in having an unusual helical muscle sheath within the cutaneous musculature, also reflected in the musculature of the pharynx and copulatory organs. *Sokoplana* stands closest to *Apogaioplana*, and a differential diagnosis for these two taxa has been provided within the discussion for the latter genus.

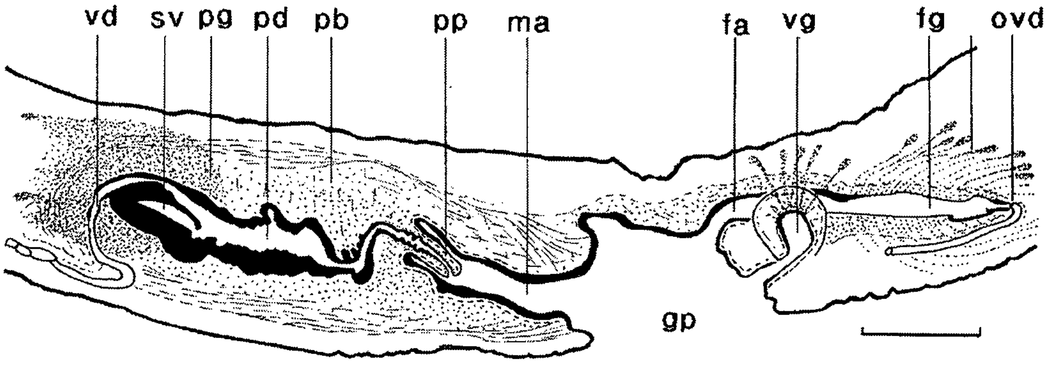


Figure 8.13-1 *Sokoplana kanangra.* Copulatory organs. Scale bar = 1mm.

Table 8.13-1 *Sokoplana kanangra*: dimensions of fixed Type specimens.

DIMENSIONS	W10215 #1 Holotype (sectioned)	W10215 #2 Paratype	W10215 #3 Paratype
LENGTH mm	109	117	99
WIDTH mm (over mouth)	5 (4440μm)	5	4
HEIGHT (from sections) μm	2050		
MOUTH mm from anterior tip	65	72	63.5
MOUTH distance from anterior tip as % length	59.6	61.5	64.0
GONOPORE mm from anterior tip	76.5	82	72
GONOPORE distance from anterior tip as % length	70.2	70.1	72.7
GONOPORE mm from mouth	10.5	10	8.5
GONOPORE distance from mouth as % length	9.6	8.6	8.6

8.14 Genus *Thosteelia* gen.nov.

Thosteelia gen.nov.

Diagnosis: Caenoplaninae with small, robust, elongate body. Creeping sole two thirds of body width. Anterior end slightly expanded, with single antero-ventral adhesive pad, incompletely bipartite. Eyes pigment cup–type, in single row around anterior tip, with slight crowding laterally, and in a single row submarginally to posterior extremity. Sensory pits simple, on either side of but not continuous around anterior tip. Cutaneous musculature tripartite, weak, unevenly developed, dorsal musculature stronger than ventral musculature. CMI 2.7 %. Ventral cutaneous longitudinal muscles insunk entally to cutaneous nerve net. Mediad dorsal cutaneous longitudinal muscles almost dorsoventral. Parenchymal musculature strong comprising strong transverse and dorsoventral muscles, and subneural plate and ringzone of longitudinal muscles. Insunk cutaneous longitudinal muscles and ventral plate acts as retractor for adhesive pad. Pharynx cylindrical. Pharyngeal musculature with inner epithelium, circular, then longitudinal muscles; outer epithelium, longitudinal, then circular muscles. With oesophagus. Penis papilla fixed-type. Female genital canal horizontal. Testes and ovaries pre-pharyngeal, half way between anterior tip and mouth. Vitellaria surround gut diverticula. Type and only species: *Thosteelia mesibovii*

Etymology: *Thosteelia* honours Thomas Steel (1858-1925) for his research on the austral Terricola and the legacy of his specimens, library and literature. Gender feminine. The specific epithet *mesibovii* is for Dr Bob Mesibov in appreciation of a long friendship, welcome help and enthusiasm in collecting Tasmanian flatworms, and a common interest in the austral cryptofauna.

Distribution: Table Cape, N.W. Tasmania, 145°44'E 40°57'S. Coastal, cool temperate Bassian. Known only from this site.

Systematic discussion: The differential diagnosis between the three caenoplaninid taxa with anterior suckers and pads: *Coleocephalus fuscus, Pimea monticola,* and *Thosteelia mesibovii,* is provided in the systemic account.

Etymology: *Thosteelia* honours Thomas Steel (1858-1925) for his research on the austral Terricola and the legacy of his specimens, library and literature. Gender masculine. The specific epithet *mesibovii* is for Dr Bob Mesibov in appreciation of a long friendship, welcome help and enthusiasm in collecting Tasmanian flatworms, and a common interest in the austral cryptofauna.

Thosteelia mesibovii gen. et sp. nov.

Material examined:

Holotype LW1035a. Length 14.7mm, width 2.6mm, mouth 7.2mm from anterior tip (49%), gonopore 9.4mm from anterior tip, mouth-gonopore distance 2.2mm. Live, creeping, length about 30mm, width about 3mm. Fixed in Tyler's fixative. Paratype LW1035b. Length 8.8mm, width 2. 1 mm, mouth 5.0mm from anterior tip (57%), gonopore absent; height 800μm; height 800μm; width creeping sole estimated 1500 - 1068μm. A series of 9 microslides, sections 7μm, stained by AZAN method. Fixed in Tyler's fixative.

Locality:

At the lighthouse, Table Cape, N.W. Tasmania. 29 October 1975 (Locality BM5), 145°44'E 40°57'S. Two specimens found under a rotting log together with *Fletchamia sugdeni*, *Australoplana sanguinea*, an *Artioposthia* species, and the nemertean *Argonemertes australiensis*. Vegetation near the lighthouse is continuous with that on the surrounding cliffs (Plate 8.15-1a). Despite intensive searching further specimens of the species have not been subsequently found. The species is considered to be native, and not cryptogenic.

EXTERNAL FEATURES:

At first sight the species is reminiscent of a small robust bipaliid (Plate 8.14-1a; Fig. 8.14-1a). Anterior end bluntly rounded with slight constriction 0.8mm posterior to tip to form slight "neck" evident in both living and fixed specimens. Body sub cylindrical in cross section, immediately broadens posterior to neck. Eyes variable in size, skirt anterior tip margin, crowd slightly laterally, and continue posteriorly in single submarginal row (Fig. 8.14-1b). Dorsal ground colour light greyish-brown. Three dark chocolate brown longitudinal stripes, all with diffuse margins, divide dorsum into approximately four equal parts. Anteriorly stripes merge into dark brown head colour, posteriorly unite before tip. Ventral surface lighter brown colour than dorsal ground colour. Anterior adhesive pad white. Creeping sole, white, begins just behind adhesive pad. Sensorial zone white, some 0.5mm long present either side at neck (Fig. 8.14-1c). Mouth situated approximately in mid body. Gonopore closer to mouth than posterior end.

INTERNAL ANATOMY (LW 1035b):

Head:

Adhesive pad anteroventral, single, incompletely bipartite (Fig. 8.14-1d-g), measuring 640μm wide, 380μm antero-posteriorly, with median longitudinal sulcus 100μm long and 50μm deep beginning 112μm from anterior margin, terminating 140μm from hind margin. Rhabdoid-free sensorial zone delineates lateral extent of pad. Adhesive secretions for adhesive pad provided by numerous rhabditogen and erythrophil gland cells (Fig. 8.14-1f-g) mainly concentrated below cerebral ganglion; some secretory elements pass dorsoventrally through ganglion. Adhesive papillae (*haftpapillen*) absent. Rhabdoids sparse in dorsal epithelium, rhabditogen cells below cutaneous musculature. Retractor musculature for pad provided by insunk ventral cutaneous longitudinal muscles together with sub-neural plate of strong parenchymal longitudinal muscles (Fig. 8.14-2a,b). Sub-neural plate divided into irregular blocks by transverse and dorsoventral muscles. Strong supra-neural transverse muscles interwoven with strong dorso-ventral muscles form protractor musculature; provide corseting in median area of interwoven muscle between gut and nerve cord (Fig. 8.14-2a). Supra-intestinal longitudinal and transverse parenchymal muscles also interwoven with dorso-ventral muscles to form corset, pronounced dorsally and combined with cutaneous longitudinal musculature which is almost dorsoventral where anterior ramus of gut is close to surface. Sensorial zones absent from anterior tip, present from outer quarter of anterior end ventrolaterally either side of "neck". Sensory pits, simple, ciliated, 40 μm deep. Glandular margin present just above sensorial zone, with xanthophil secretion. Eyes skirt anterior tip margin, pigment cup type, 20 - 36μm diameter, each with at least four retinal rods.

Prepharyngeal region:

Prepharyngeal region (Fig. 8.14-2b). Rhabdoids rhammite type, 20μm long, present dorsally to outer ventral zone. epitheliosomes sparse ventrally. Erythrophil and xanthophil secretions parallel rhammites and epitheliosomes in distribution. Cyanophil secretions present in outer ventral zone, creeping sole. Pigment, fine, granular, melanotic, present in dorsal epithelium and underlying musculature, corresponding to three dorsal stripes. Cutaneous musculature tripartite, very weak, stronger dorsally than ventrally. Longitudinal muscle bundles small, with six or less fibres per bundle, insunk entally to cutaneous nerve net. CMI 2.7 %. Parenchymal musculature strong, with supraneural transverse muscles; dorso-ventral muscles; supraintestinal transverse muscles intermingled with parenchymal longitudinal muscles in ringzone. Parenchymal longitudinal muscles in subneural ventral plate, PMI 9%, with ringzone PMI 1%. Muscle fibres in plate in small bundles, loosely aggregated, more closely packed in ringzone. Longitudinal muscles strong and divided by transverse muscle fibres into substantial muscle blocks in region between inner ventral and outer ventral zones; small bundles and individual fibres extend to cutaneous nerve net; adjacent insunk cutaneous longitudinal musculature weakest in this region. Creeping sole 50 – 71% about two-thirds of the body width. Main nephridial ducts small, 3,6μm diameter, single, supraintestinal, either side and above anterior ramus of gut.

Alimentary tract:

Pharynx cylindrical, inclined ventrad about 30° to horizontal; dorsal insertion posterior to ventral insertion (Fig. 8.14-2c). Pharyngeal musculature with inner epithelium, circular, then longitudinal muscles; outer epithelium, longitudinal, then circular muscles. Outer pharynx and posteriad third of the pharynx lumen lined by infranucleate ciliated epithelium, which grades into oesophagus. Oesophagus short, anteriad third of pharynx lumen, differentiated from pharynx by strong circular muscles underlying nucleate non-ciliated epithelium. Mouth situated in the mid ventral floor of the pharyngeal pouch. Pouch musculature comprised of weak circular muscles, with flattened nucleate lining epithelium; small diverticulum present at posteriad extent of pouch, just anteriad of male copulatory organs. Pharynx 5%, and pharyngeal pouch 10.2% of body length.

Reproductive organs:

Copulatory organs with substantial penis bulb, with penis papilla; male antrum capacious, female antrum small, female genital canal horizontal (Fig.8-14-2c). Muscular protuberance in roof of female antrum possibly an adenodactyl. Gonopore imperforate, situated close to female antrum. Testes ventral, crowded below and just between gut diverticula; extending from immediately behind ovaries to pharynx; immature. Efferent ducts indistinct. Ovaries pre-pharyngeal, half way between anterior tip and mouth, embedded in dorsal aspect of nerve cords. Ovovitelline ducts arise from dorsal surface of ovaries. Vitellaria surround gut diverticula between ovaries and pharynx.

Observations:

Thosteelia mesibovii crawls with its anterior end raised (Plate 8.14-1c) in the manner of an elapid snake. This is in contrast to the more vibratory tactile movement of other caenoplaninids that do not hold their head in this manner. The retractor muscles are antagonists to the dorsal cutaneous and parenchymal longitudinal muscles responsible for dorsiflexion of the anterior end during locomotion.

Table Cape, where *Thosteelia* was found, is a "hot-spot" of flatworm biodiversity. The locality (Plate 8.14-1a) is on the edge of steep cliffs vegetated by coastal heath complex, tea-tree and a few eucalypts. Adjacent countryside has largely been cleared for crops. A small creek flows southeast from the lighthouse to low-lying swampy ground. Remnant vegetation bordering the creek comprises tea-tree, tree ferns and fern under story. Where the road crosses the last branch of the creek before the lighthouse, under a rotting log were found *Australoplana alba* and *Artioposthia mortoni*. Literature records from Table Cape (Steel 1901b) include *Tasmanoplana lyra, T. tasmaniana* (= *T. balfouri (Graff)*), *Australoplana sanguinea, Fletchamia sugdeni, Artioposthia diemenensis, A. dovei* (= *lucasi* ex Tasmania), and *A. mortoni.*

Systematic discussion:

1. *Thosteelia mesibovii*

The foregoing anatomical description was based upon the immature Paratype. The Holotype will be sectioned and described for formal publication. The width of the creeping sole in the Paratype was difficult to determine due to poor preservation of the ciliated epithelium. The lower figure measurements are based on the assumption that the creeping sole generally begins at the ventrad extent of the rhammites (1068µm wide), the higher figure based on stereomicroscopic measurements (1500µm wide). Whilst the copulatory organs are immature, their general topography is established. The developing imperforate gonopore is 1240µm behind the mouth (14% of body length) and 6240µm from the anterior tip (71% of body length). The presence or otherwise of an adenodactyl in the female antrum will be confirmed on sectioning the mature Holotype.

At first sight *Thosteelia mesibovii* with its three dark brown dorsal stripes on pale ground colour looks like a small *Tasmanoplana lyra* (Steel 1901b). Externally it is distinguished from the latter species by a rounded anterior tip, presence of an anteroventral adhesive pad, eyes in a single row around the anterior tip with slight crowding laterally and in a staggered submarginal row along the body, and sensorial zones either side of the head. *Tasmanoplana lyra* has a tapered anterior tip, eyes in a single row around the tip, clustered laterally, then continuing posteriorly in a staggered single row, sensorial zone passing around the anterior tip, and no adhesive pad. The relative positions of body apertures are similar in both species. Internally *Thosteelia* differs from *Tasmanoplana* in having relatively weaker cutaneous and parenchymal musculatures, and has a capacious gut. With regard to musculature, *Tasmanoplana* stands closer to undescribed taxa from the subantarctic islands of New Zealand. Both species have a similar form of cylindrical pharynx, similar relative positions and extent of the gonads, and similar general topography of the immature copulatory organs.

2. *Cotylate geoplanids* - overview:

An anterior adhesive sucker or adhesive pad is present in six geoplanid genera:

a. Neotropical geoplaninid genera *Choeradoplana* and *Issoca*
b. Oriental pelmatoplaninids *Beauchampius nilgiriensis* (India) and *B. bogoriensis* (Java)
c. Austral caenoplaninids *Coleocephalus fuscus* (subantarctic Auckland Islands), *Pimea monticola* (New Caledonia), and *Thosteelia mesibovii* (Tasmania, Australia).

3. Austral cotylate caenoplaninids:

Within the Caenoplaninae *Coleocephalus fuscus* is distinguished from the other taxa mainly by a cotyloplanid-type sucker, and retractor derived from cutaneous longitudinal muscles, not insunk. Eyes and sensory pits skirt the anterior tip, with strong cutaneous musculature CMI 22-24%, plicate pharynx, ovaries near pharynx root, with parovarian resorptive tissue, apapillate eversible penis, and adenodactyls.

Both *Thosteelia mesibovii* and *Pimea monticola* have adhesive pad-type suckers, incompletely bipartite in the former, undivided and with *haftpapillen* in latter species. Both species exhibit insunk ventral cutaneous longitudinal muscles that contribute to the sucker retractor muscle. Eyes skirt the anterior tip and are slightly clustered anterolaterally in *Thosteelia*. In *Pimea* eyes are absent around and over the anterior tip, but present in a row anterolaterally. The sensory zone in both species is restricted to anteroventrolateral patches, and absent from tip. *Pimea* has strong cutaneous musculature CMI 11.5%, and weak parenchymal muscles, whilst in *Thosteelia* cutaneous musculature is weak, CMI 2.7 %, with strong parenchymal musculature, plate PMI 9%, and ringzone 1%. Both taxa have a cylindrical pharynx, and a small diverticulum in the pharyngeal pouch. In *Pimea* ovaries are near anterior tip, with seminal receptacle, and resorptive tissue absent; with intra-penial papilla, protrusible penis, and copulatory bursa. In *Thosteelia* ovaries are pre-pharyngeal, half way between anterior tip and mouth. Resorptive tissue is absent. Penis protrusible, with papilla. Adenodactyls are absent in both *Thosteelia* and *Pimea.*

4. Cotylate geoplanids - comparison of some key characters:

a. Eyes of the pigment cup type, though the distribution and number of eyes differ. In *Coleocephalus*, *Thosteelia* and *Issoca* the eyes skirt the anterior tip margin and continue along the sides of the body. In *Choeradoplana* and *Beauchampius nilgiriensis* the eyes skirt the anterior margins, but are absent from the apex. In *Pimea* the eyes are absent from the head and restricted to the sides of the neck and body.

b. Sensorial zones contour the anteroventral margin of the anterior tip in *Coleocephalus* and *Issoca*, skirts the anterior but is absent from the apex in *Choeradoplana*, and is restricted to anteroventrolateral patches in *Pimea* and *Thosteelia.*

c. Adhesive pads and suckers: *Pimea, Thosteelia* and *Issoca* have simple, single, pad-type suckers, and in *Thosteelia* and *Issoca* it is incompletely bipartite. *Choeradoplana* has two glandular pads separated by a median groove. In *Coleocephalus* and the cotylate *Beauchampius* species, the sucker is an undivided depression (cotyloplanid-type) rather than an adhesive pad.

d. Adhesive pad and sucker retractor muscles: In *Thosteelia, Pimea,* and *Choeradoplana* the ventral cutaneous longitudinal musculature is insunk entally to the cutaneous nerve net. Here it forms part of the retractor muscle for the adhesive pad and the antagonistic muscles for dorsal protractor muscles responsible for dorsiflexion of the anterior tip. Insunk cutaneous longitudinal musculature is also shared with the acotylate Chilean taxa *Gusana* and *Liana*, and an undescribed caenoplaninid that moves with curled anterior tip, from the wet tropics of north Queensland, Australia. In *Coleocephalus* and *Issoca* the ventral cutaneous longitudinal musculature is not insunk or divided, and anteriorly forms the retractor muscle.

e. In *Thosteelia mesibovii* and *Beauchampius nilgiriensis* the retractor muscles for the sucker are largely derived from parenchymal longitudinal muscles in a subneural ventral plate, a character also shared by species of the rhynchodemid genus *Cotyloplana.* Corseting (*Muskelgeflecht)* is present in head region of both *Choeradoplana* and *Thosteelia.*

f. In live specimens of Choeradoplana the anterior tip is curled to expose the sucker (Froehlich, 1956) and raised in *Thosteelia* (Winsor, unpublished observations), whilst *Issoca* keeps its sucker close to the substratum (Froehlich 1956) as does *Cotyloplana* (Winsor, unpublished observations).

g. Adhesive secretions for the pad in *Thosteelia* are chiefly rhammites and erythrophil secretions, similarly in the sucker in *Coleocephalus* in addition to abundant xanthophil secretions. In *Choeradoplana, Issoca* and *Beauchampius nilgiriensis* the secretions are chiefly erythrophil. Only *Pimea* has adhesive papillae (*haftpapillen*) in the sucker, with four types of associated secretions.

h. Copulatory organs: Between the genera there appears to be no common topology of the copulatory organs. *Choeradoplana* contains taxa with eversible, apapillate penes, and taxa with protrusible papillate penes. Similarly species in *Issoca* show considerable variation in their copulatory organs.

i. Present anatomical data for these geoplanid cotylate taxa suggests that they do not share a common lineage. Rather, some of the characters they exhibit, such as the adhesive pads and suckers, show varying degrees of convergence.

Plate 8.14-1 *Thosteelia mesibovii*

a. Table Cape, Wynyard, Tasmania (Sandscene International postcard T42, photography by Owen Hughes). Type locality near the lighthouse.
b. Specimen at rest, dorsal aspect.
c. Specimen crawling, with anterior end lifted

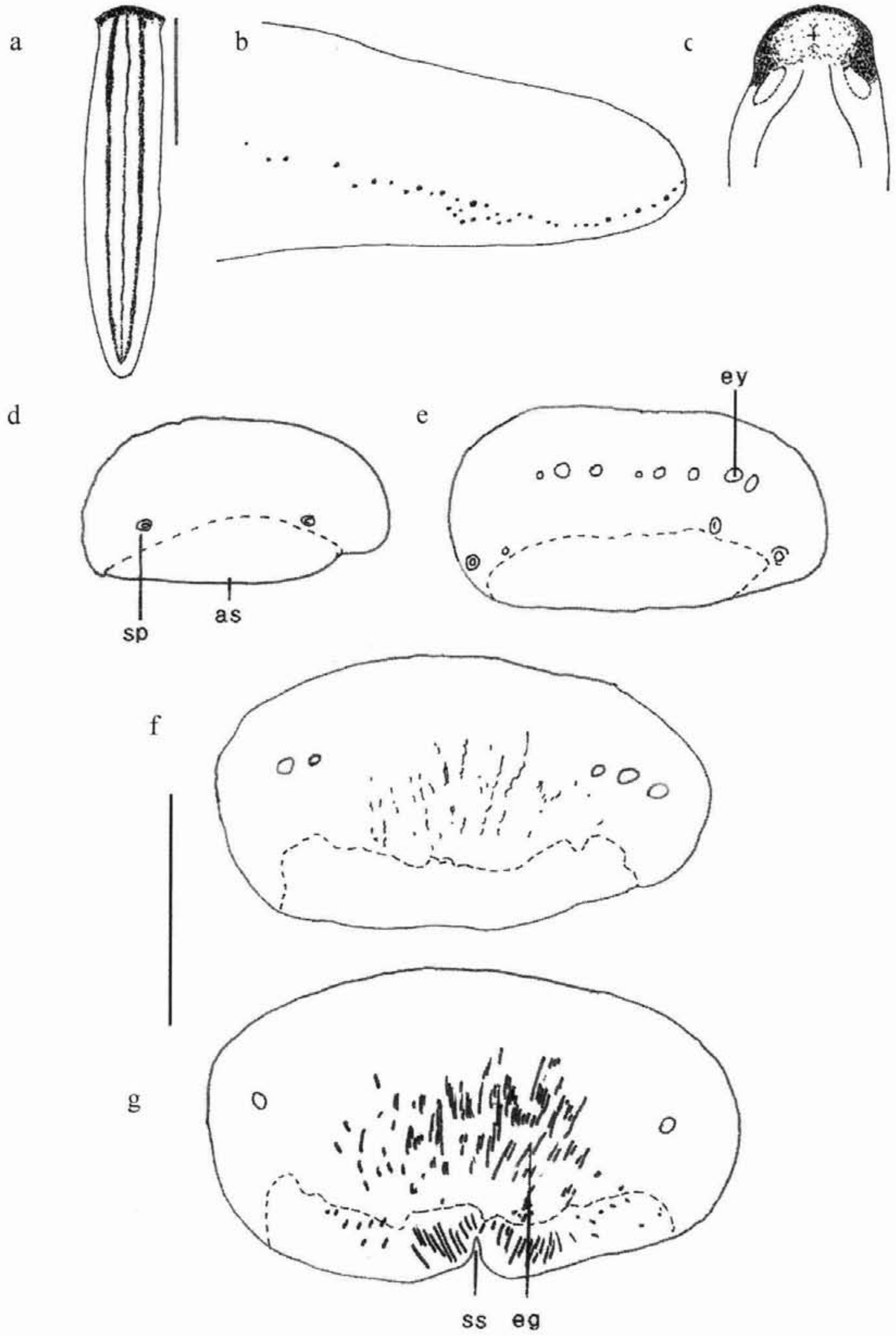


Figure 8.14 –1 *Thosteelia mesibovii*

a. Whole fixed specimen. Scale bar = 5mm.
b. Anterior end showing eye pattern x16
c. Anteroventral surface showing sucker and sensorial zones x8
d – g Transverse sections, anterior end showing sucker. Scale 500µm.

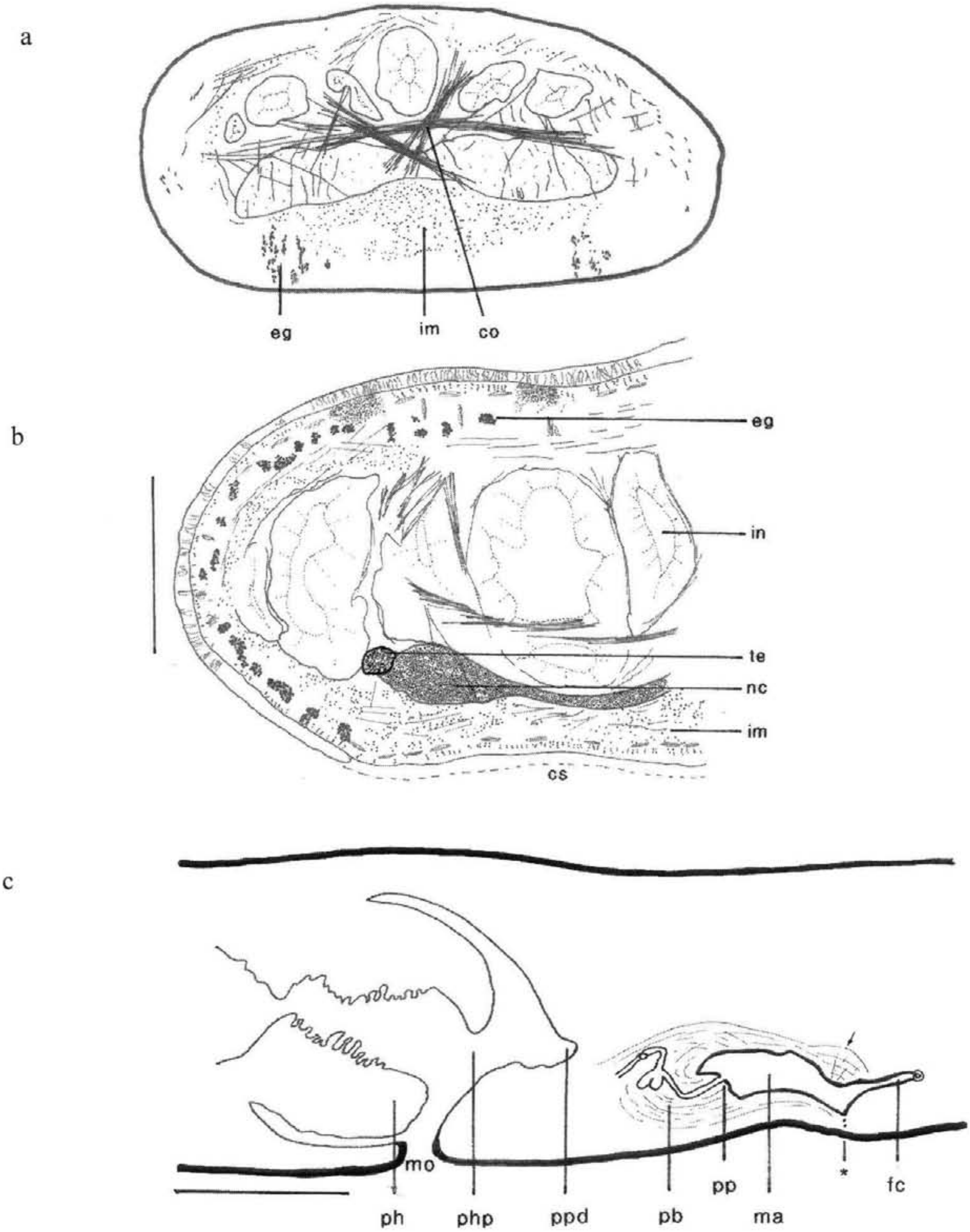


Figure 8.14-2 *Thosteelia mesibovii*

a. Anterior end behind sucker showing the corseting and insunk retractor musculature.
b. Pre-pharyngeal region. Scale bar for Fig. 8.14-8 & 9 is 500μm.
c. Pharynx and associated structures, and copulatory organs. * = putative gonopore, arrow indicates suspected musculoglandular organ. Scale 500μm.

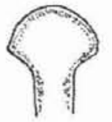
Appendix 9 Field Keys to Terricola of the Australian Region

Appendix 9.1 FIELD KEY (1) TO THE TERRICOLA FAMILIES & GENERA IN AUSTRALIA

TERRICOLA

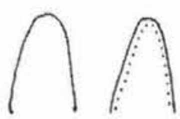
Head expanded, semilunate

Family Bipaliidae
Single introduced species *Bipalium kewense*
Found only in human modified habitat



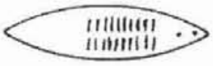
Head not expanded

Eyeless or with multiple eyes
Family Geoplanidae (refer to Key 2)

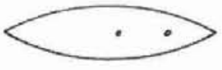


With paired dorsolateral eyes
Family Rhynchodemidae

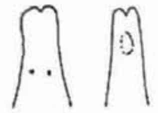
With multiple mouths, two gonopores
Digonopyla - Cape York, Queensland (one species)



With single mouth, single gonopore



With anterior adhesive sucker
Cotyloplana - north Queensland (two species)
& Lord Howe Island (two species)



No anterior adhesive sucker

Body flat and broad
Platydemus – Queensland, New South Wales,
Victoria, Lord Howe Island. Some species are introduced.

Body rounded to flat, thin, elongate

Body flat, thin, very long. Gregarious.
Dolichoplana – Queensland

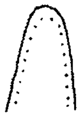
Body rounded to flat, thin, short and small. Solitary.
Rhynchodemus – Queensland, New South Wales, Victoria,
South Australia, northern Tasmania

Appendix 9.2. FIELD KEY (2) TO THE TERRICOLA GENERA IN AUSTRALIA

Family Geoplanidae

Eyeless
(Refer to Key 3)

With multiple eyes
(note that there are undescribed genera which will also key out using the following characters, and can only reliably determined by histological examination).



Eyes in single row around anterior tip and anterolaterally
(Refer to Key 4)

Eyes in a single row around tip, crowded anterolaterally

Eye crowding irregular anterolaterally

Body small, 20-35mm long, subcylindrical, with mouth just behind mid body, gonopore closer to mouth than to posterior end, creeping sole two thirds or more of body width. Ground colour pale brown with dark stripes. Gregarious. Genera and species only reliably determined by histological examination. Genera and species only reliably determined by histological examination.
Distribution: Cool to cold temperate Bassian. *Anzoplana*

Body large, 40-150mm long, convex dorsally, flat ventrally. Mouth just behind mid body, gonopore closer to mouth than to the posterior end. Creeping sole about two-thirds of body width. Genera and species only reliably determined by histological examination. Ground colour yellow to blue-green, often with pale or dark stripes. Gregarious.
Distribution: Cool to cold temperate Bassian. *Caenoplana* and *Kynagoplana*. *Caenoplana* present in Torresian subregion.

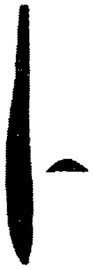
Eyes in distinctive lens-shaped cluster anterolaterally
(Refer to Key 5)

Appendix 9.3. FIELD KEY (3) TO THE TERRICOLA GENERA IN AUSTRALIA

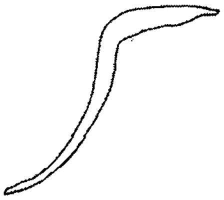
Eyeless

Body small, 20 –30 mm long, sub cylindrical, with sharply tapering extremities, with mouth just forward of mid body, gonopore short distance behind mouth. With creeping sole about two thirds of body width. Ground colour pale brown with darker brown mottling and stripes. Solitary. Distribution: Warm temperate Bassian – Eyrean
Danidoplana

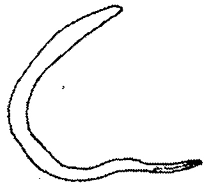
Body large, 50-100 mm long, elongate, convex dorsally to strap-like
Colour white to pale brown



Body strap-like, dorsoventrally flattened, generally white
Mouth and gonopore in hind third of body. With narrow creeping sole.
Solitary. Distribution: Cool to cold temperate Bassian.
Bassioplana

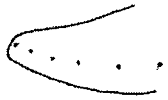


Body convex dorsally, strongly muscular, white to pale brownish colour
Mouth and gonopore in third body quarter. Without a creeping sole.
Distribution: Torresian.
Apogaioplana



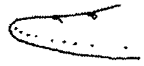
Appendix 9.4. FIELD KEY (4) TO THE TERRICOLA GENERA IN AUSTRALIA

Eyes in single row around anterior tip and anterolaterally



Eyes very small (pin-point). Body elongate, strap-like, with mouth and gonopore in posterior third of body. Colour white to blood red; may have pale brown to red stripes. Genera and species only reliably determined by histological examination.

- With narrow creeping sole – *Australoplana*
- Without creeping sole – *Nelipoplana, Sokoplana*



Solitary. Distribution: Warm to cold temperate Bassian

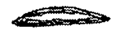
Eyes larger than pin-point size

Eyes small, generally "haloed". Body small, 20-30mm long, flattened dorsally, often with distinct inward sloping lateral margins, with mouth just behind mid body, gonopore halfway between mouth and posterior end; creeping sole about half width of body. Colour generally mottled brown. Solitary. Distribution: Cool to cold temperate Bassian.
Reomkago

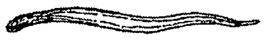
Eyes small to large, not haloed

Eyes small.

- Body up to 25mm long, strongly tapered anteriorly and posteriorly, convex dorsally, flat ventrally, mouth just behind mid body, gonopore closer to posterior end than to mouth. Creeping sole almost entire body width. Ground colour yellowish with dark brown stripes. Solitary. Distribution: Cool to cold temperate Bassian.
  Barringtoplana



- Body 30-40mm long, broad, convex dorsally, flat ventrally, with mouth just behind mid body, gonopore halfway between mouth and posterior end. Colour generally cream with brown-black stripes. Gregarious. Distribution: Cool to cold temperate Bassian.
  Tasmanoplana

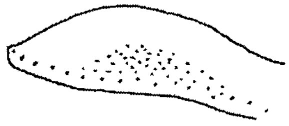


Eyes large. Body 20-30mm long, sub cylindrical, with mouth just behind mid body, gonopore closer to mouth than to posterior end, creeping sole half to two thirds or more of body width. Ground colour pale brown to black, often with dark stripes. Genera and species only reliably determined by histological examination.

- In Australia restricted to disturbed and urban habitat. Solitary. *Kontikia*
- Warm to cool temperate Bassian. Gregarious. *Parakontikia*

Appendix 9.5. FIELD KEY (5) TO THE TERRICOLA GENERA IN AUSTRALIA

Eyes in distinctive lens-shaped cluster anterolaterally



Body small, 20–30 mm long, convex dorsally, flat ventrally, with sharply tapering extremities, with mouth mid body, gonopore closer to mouth than to the posterior end. Creeping sole about two thirds to three quarters of body width.
Gregarious. Distribution: Warm to cool temperate Bassian.
Lenkunya

Body large, 50-100 mm long, elongate, convex dorsally, flat ventrally. Mouth about mid body, gonopore closer to mouth than to the posterior end. Creeping sole up to three quarters of body width. Ground colour generally pale lemon to chrome yellow, generally with brown to black stripes. Generally gregarious. Some species move about in the open on overcast days.
Distribution Eyrean to warm temperate Bassian; some species in mild areas of the cool temperate Bassian; south-western sub-region.
Fletchamia