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New and revised terrestrial flatworm taxa (Platyhelminthes: Tricladida: Terricola) of Australia and the Subantarctic Islands of New Zealand

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ABSTRACT: Within the context of ongoing taxonomic revisions of terrestrial flatworms from Australia and the Subantarctic Islands of New Zealand: (1) a new subfamily of the Terricola, the Anzoplaninae, is erected, and some subantarctic terricolan taxa are reassigned to the new subfamily; (2) diagnoses for the subfamily Caenoplaninae and genus *Coleocephalus* are emended; (3) the new genera *Anzoplana* and *Fyfea* are erected; and (4) the new species *Anzoplana trilineata* is described. A lectotype is designated for *Fyfea carnleyi* (Fyfe).

KEYWORDS: Platyhelminthes, Terricola, terrestrial flatworms, Geoplanidae, Anzoplaninae, Caenoplaninae, Cape Expedition, Subantarctic Islands, taxonomy, new subfamily, new genera, new species.

Introduction

During the period 1941–45 of the Second World War, Allied coast-watchers stationed on the New Zealand Subantarctic Islands operated under the wartime code name of the 'Cape Expedition'. In addition to their military duties, they undertook biological and geological fieldwork (Falla 1953; Fraser 1986), which included the collection of terrestrial flatworms (Terricola). From this material Fyfe (1953) later described four new flatworm species, *Geoplana ashleyi, Artioposthia carnleyi, Geoplana ranuii* and *Coleocephalus fusca*. The Cape Expedition Terricola material is now mostly held by the Museum of New Zealand Te Papa Tongarewa.

New Zealand has five of the 24 Subantarctic Islands and island groups lying between latitudes 50° and 60°S – the Snares, the Auckland Islands, Campbell Island, the Bounty Islands and the Antipodes Islands (Fraser 1986). Previously, only four species of terrestrial flatworms were known from these islands. Graff (1899: 386) described *Geoplana moebiusi* from four poorly preserved specimens collected by Krone from the Auckland Islands, probably during the German Transit of Venus Scientific Expedition of 1874, of which Krone was a member (Fraser 1986: 146). A sole specimen is held in the Natural History Museum, Vienna. In November 1907, the Philosophical Institute of Canterbury mounted a scientific expedition to the Auckland, Campbell, Antipodes, Bounty and Snares islands. Dendy (1909: 672) later described *Geoplana subquadrangulata* var. *enderbyensis, Geoplana antarctica* and *Geoplana aucklandica* (later correctly renamed by Dendy (1911: 100) as *G. marrineri*) from the material collected. Searches of museum collections worldwide have failed to locate Dendy's material, and the specimens are presumed lost.

The present taxonomy of terrestrial flatworms is largely based upon internal anatomical characters. The terrestrial flatworms of Australia and New Zealand are the most poorly known anatomically of the Terricola worldwide (Ogren et al. 1997), and consequently for over a century the taxonomy of the austral terrestrial flatworms has been severely constrained (Johns 1993, 1998; Winsor 1991, 1998a). Fyfe's descriptions of flatworm taxa from the Subantarctic Islands were largely confined to details of the external features and anatomy of the reproductive organs. Most of her species were placed in what are now mainly 'blanket' genera. Consequently, it has been very difficult to reassign her species correctly to present genera, as her descriptions lack some data essential in current taxonomy.

For this reason the Terricola from the Subantarctic Islands, including the Cape Expedition flatworm collection, are being re-examined and redescribed together with pertinent Australian taxa. This will also provide morphological data essential for the total-evidence approach to flatworm systematics (Littlewood et al. 1998; Winsor 1998b; Baguñà et al. 2001), in which molecular and morphological data are used together to best construct and understand the phylogeny of terrestrial flatworms and their inter-relationships within the Tricladida. However, complementary specimens for molecular studies are still required.

This paper concerns the erection of a new subfamily of the Terricola, reassignment of some of Fyfe's taxa into the new subfamily, and emended diagnoses for the Caenoplaninae and genus *Coleocephalus*, and includes descriptions of new genera and species. Of particular interest and possible phylogenetic significance are parallels in the anatomy of some subantarctic terricolans with those of some austral marine triclad flatworm taxa (Maricola).

Materials and methods

Specimens selected for histology were processed to paraffin wax, longitudinally sagittally (LSS) and transversely sectioned (TS) at 8 µm, and stained using polychrome methods described elsewhere (Winsor 1998b, 1998c). Determination of the Cutaneous and Parenchymal Muscular Indices (CMI and PMI, respectively) follow Winsor (2003), and Winsor & Stevens (2005). Nomenclature and type of adenodactyls follows Winsor (1998b). Only principal synonymies are provided, as detailed lists of references are available elsewhere (Ogren & Kawakatsu 1991). Sources of specimens together with registration numbers are indicated by the following abbreviations: Museum of New Zealand Te Papa Tongarewa, Wellington, N.Z. (MONZ–ZW or MONZ–W); Museum of Tropical Queensland, Townsville, Queensland, Australia (MTQ–G); Otago Museum, Dunedin, N.Z. (OMNZ); and the author's collection (LW).

Systematics

Family *Geoplanidae* Stimpson, 1857

CURRENT 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.

The Geoplanidae now has four subfamilies: the Geoplaninae (Ogren & Kawakatsu 1990), which occurs largely in South and Central Americas; the Caenoplaninae (Ogren & Kawakatsu 1991), mainly centred in the Australo-Pacific region; the Pelmatoplaninae (Ogren & Kawakatsu 1991) in South-east Asia and the Indo-Pacific; and a new subfamily from Australia, New Zealand and the Subantarctic Islands.

Anzoplaninae new subfamily

DIAGNOSIS: Geoplanidae with dorsoventral testes and ventral efferent ducts. 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. Eyes pigment-cup type, in a single row around the anterior end, generally continuing posteriorly, may extend dorsally.

SYSTEMATIC DISCUSSION: Within the triclad flatworms, ventral testes and efferent ducts, regarded as the primitive or plesiomorphic condition (Meixner 1928; Sluys 2001), are present in the Planariidae and Dendrocoelidae (in part) of the Paludicola and in most of the Maricola. In the Terricola, the plesiomorphic condition is present in the Rhynchodemidae, Bipaliidae and Geoplanidae (Caenoplaninae and Pelmatoplaninae). Dorsal testes and efferent ducts are present in the Dendrocoelidae (in part) of the Paludicola, and in the Terricola only in geoplaninid taxa, and are considered to be a derived (apomorphic) condition (Meixner 1928; Sluys 2001). Within the Geoplanidae, the position of the testes, together with other characters, has provided the basis for the erection of the subfamilies:

Caenoplaninae and Pelmatoplaninae with ventral testes, and the Geoplaninae with dorsal testes (Ogren & Kawakatsu 1990, 1991). The dorsoventral position of the testes in the Terricola (Winsor et al. 1998) is an apomorphy (Winsor 2003) intermediate between ventral and dorsal testes. Consistent with this is the erection of the Anzoplaninae to accommodate those geoplanid Terricola with dorsoventral testes. Members of the subfamily occur in Australia, New Zealand and the Subantarctic Islands, and include *Artioposthia alfordensis* (Dendy, 1896), *Artioposthia subquadrangulata* (Dendy, 1895), *Artioposthia ventropunctata* (Dendy, 1892), *Australopacifica aucklandica* (Dendy, 1901), *Fyfea carnleyi* (Fyfe, 1953) and *Kontikia ashleyi* (Fyfe, 1953).

Anzoplana new genus

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. Sensorial margin passes anteroventrally around the anterior tip. Sensory papillae absent. Anterior adhesive cup, sucker absent. Creeping sole 60% of body width. Cutaneous musculature tripartite, with circular and 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. Testes dorsoventral, 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 canal; genital canal enters female antrum ventroposteriorly (postflex condition). Adenodactyls and adenomuralia present. Viscid gland absent.

TYPE SPECIES: *Anzoplana trilineata* new species.

ETYMOLOGY: The name *Anzoplana* refers to the Australian and New Zealand planarian, and derives from the traditional abbreviation ANZ, for Australia and New Zealand, combined with the Latin *plana* = flat. Gender feminine.

DISTRIBUTION: Bombala, NSW; Nimmitabel, NSW; Girraween, SE Qld; Dalmorton, NSW; Research, Vic (introduction); Berridale, NSW; Cootralantra Creek north of Berridale, NSW; nr Tatangara dam, between Adaminaby and Kiandra, NSW; Mt Wilson, NSW (where it is possibly introduced); 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 located on either side of the pharynx, resorptive vesicles surrounding the ovovitelline duct, and presence of both adenomuralia and adenodactyls. The presence of dorsoventral testes in *Anzoplana* immediately differentiates it from the caenoplaninid genus *Newzealandia*, otherwise characterised by the presence of adenomuralia and an apapillate eversible penis.

Anzoplana trilineata new species (Figs 1–6)

Material examined

HOLOTYPE: MTQ-G 23586 (formerly LW 1755). Collected in Armidale, NSW, by Klaus Rohde, 3 April 1991, sectioned at 8 µm, a series of 45 slides stained with the MSB method: anterior LSS, pre-pharyngeal TS, and posterior LSS together.

PARATYPE: MONZ–W.001553 (formerly LW 1724). Collected Uralla, NSW, L. Winsor 10.ix.1990, sectioned at 8 µm, a series of 43 slides stained with Steedman's Triple stain, pre-pharyngeal TS and posterior LSS together, immature.

NON-TYPE MATERIAL: LW678 Bombala, NSW; LW692 Nimmitabel, NSW; LW820 Girraween, SE Qld; LW1318 Dalmorton, NSW; LW1533, LW 1736 Research, Vic (introduced); LW1555 Berridale, NSW; LW1556 Cootralantra Creek north of Berridale, NSW; LW1558 nr Tatangara dam, between Adaminaby and Kiandra, NSW; LW1578 Mt Wilson, NSW (?introduced); 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. 1). 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 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

Table 1 *Anzoplana trilineata*: dimensions of specimens examined.

Specimen	Length (mm)	Width (mm)	Mouth (mm)	Mouth (%)	Gonopore (mm)	Gonopore (%)	Mouth–gonopore (mm)	Mouth–gonopore (%)
MTQ–G 23586	12.5	2.6	6.7	53.6	8.5	50.5	1.8	14.4
MONZ–W.001553	31.0	3.6	19.0	61.3	23.0	74.2	4.0	12.9

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 dorsal marking. 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 marginal mottling may extend over the entire ventral surface.

With multiple eyes (Fig. 2a,b), closely 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. Dimensions of material examined are provided in Table 1.

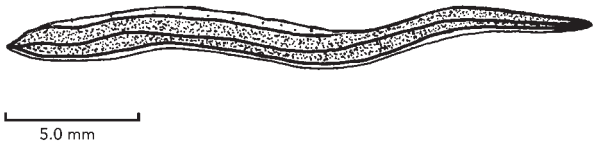


Fig. 1 *Anzoplana trilineata*: whole specimen, dorsal view.

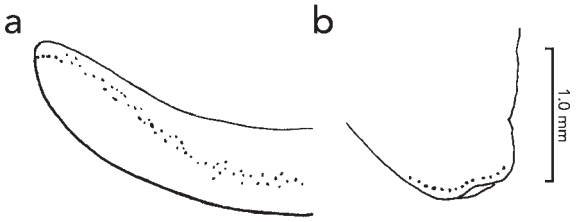


Fig. 2 *Anzoplana trilineata*: anterior tip (a) anterolateral view; (b) distribution of eyes.

Internal anatomy

HEAD: Adhesive suckers with associated musculature absent. Gut extends almost to tip, overlies ganglion. Eyes pigment-cup type, 36–42 µm 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. 3. Dorsal and ventral epithelium of equal height, 17 µm thick, nucleate. Sinuous rhammites approximately 25 µm long, 1.5 µm in 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. Granular erythrophil secretions from mesenchymal glands abundant ventrally, mid-dorsally. Granular cyanophil secretions from mesenchymal glands 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. Body 2664 µm wide. Creeping sole flat, 1638 µm wide, 61.5% of body width. Body height 1157 µm. Body width : height ratio 2.2. Cutaneous musculature tripartite, with circular and helical muscles. Cutaneous longitudinal muscles in distinct bundles, not insunk. Dorsal cutaneous musculature thinner (46 µm thick) than ventral musculature (70 µm thick). CMI = 10%. (In the paratype, dorsal cutaneous musculature [33.5 µm], about the same thickness as ventral musculature [39 µm]; CMI 6%.) Parenchymal musculature well developed but not strong, parenchymal longitudinal muscles in subneural ventral plate 56 µm thick, PMI = 4.8%. Dorsal, supra-

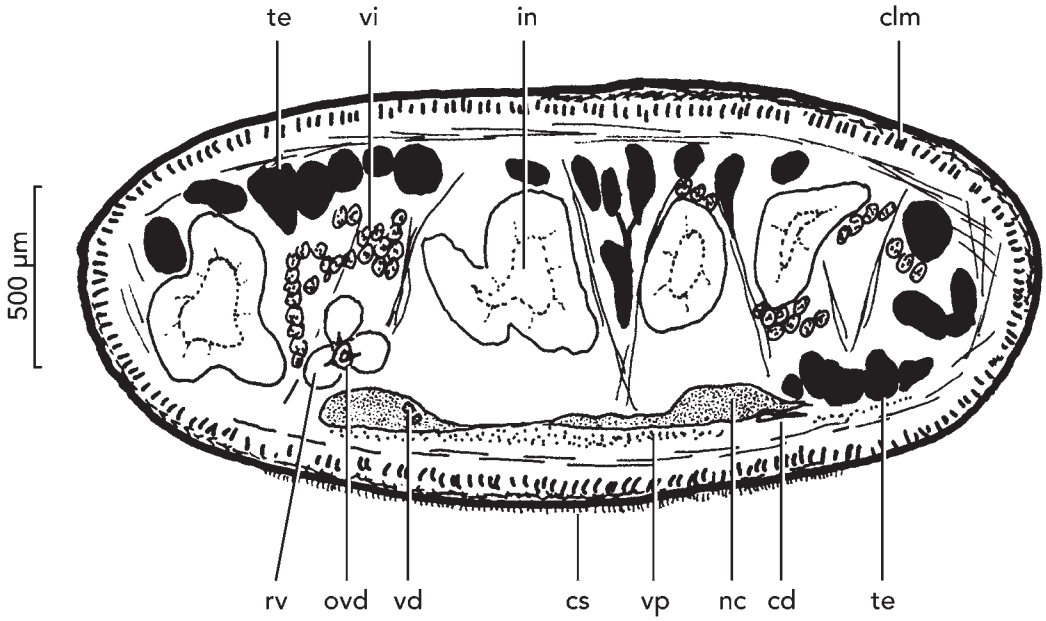


Fig. 3 *Anzoplana trilineata*: transverse section of the pre-pharyngeal region showing principal structures.

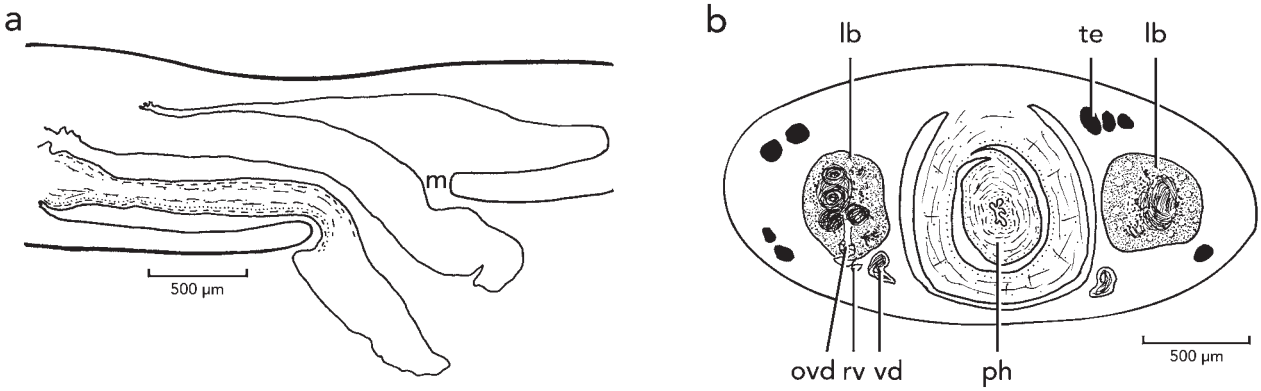


Fig. 4 *Anzoplana trilineata*: (a) pharynx, LS (MONZ–W.001553); (b) simplified transverse section of the pharyngeal region illustrating the pharynx and lateral bursae (MTQ-G 23586).

neural, ventral transverse, dorsoventral and peri-intestinal muscles all present. (In the paratype, the parenchymal longitudinal muscle plate is 109 µm thick, PMI 9%.)

ALIMENTARY TRACT: Pharynx (Fig. 4a,b) cylindrical, horizontal, 2.2 mm long, 17.6% of body length, with dorsal insertion posterior to ventral insertion. Inner pharyngeal musculature comprises subepithelial longitudinal, then mixed circular–longitudinal muscles; outer pharyngeal musculature with subepithelial longitudinal, circular muscles, then mixed circular–longitudinal muscles, sparse ectally, slightly stronger entally. Pharyngeal pouch 2.3 mm long, 19% body length. Mouth opens in the hindquarter of the pouch. Diverticulum absent. Oesophagus absent.

REPRODUCTIVE ORGANS: Copulatory organs complex, with apapillate penis, with paired lateral bursae, with five musculoglandular organs, male and female antra situated immediately behind pharyngeal pouch, within single large bulb with thin outer muscularis. Bulb with weak inner circular muscles, weak outer longitudinal muscles, surrounded by loosely interwoven mixed fine muscle fibres.

Testes mature, 85–128 µm in diameter, follicular, dorsoventral (Figs 3, 4b, 5), surround almost entire gut

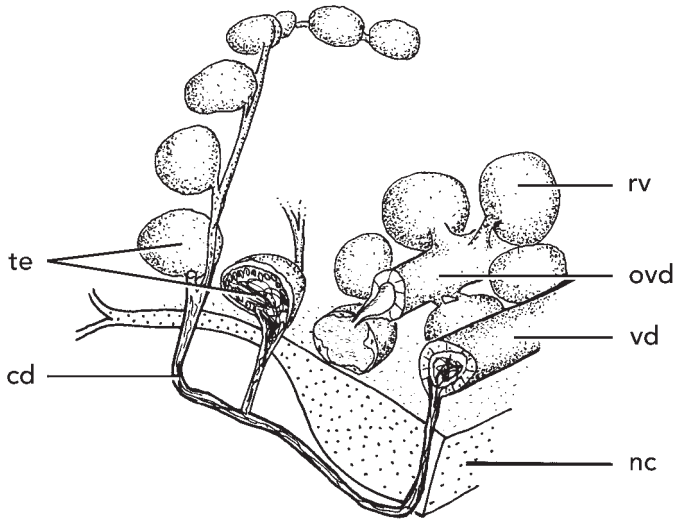


Fig. 5 *Anzoplana trilineata*: schematic representation of the efferent ducts passing from the dorsoventral testes to the collecting duct and vas deferens, and the ovovitelline duct with its resorptive vesicles. Unscaled.

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 subneural 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 and separately enter proximal dorsal end of seminal vesicle. Seminal vesicle lined by villiform columnar epithelium, divided into two regions: proximal region receives coarse-grained erythrophil secretions from glands situated outside penis bulb; distal region (prostatic vesicle) with shallow diverticula, receives both granular erythrophil and fine dark granular cyanophil secretions. Ejaculatory duct opens into ampulla. Opening surrounded by coarse granular dark erythrophil secretions. Ampulla characterised by intramural granular pale cyanophil secretions. These secretions increase in cyanophilia as they approach the epithelium, through which they are then secreted into the cavity. Ampulla opens into anterodorsal male antrum. Penis papilla absent, penis eversible type (false papilla possibly formed by antral folds at distal end of cavity). Male antrum largely filled by adenodactyl papillae.

Ovaries situated anteriorly, pear-shaped, 140 µm in diameter, dorsoventral axis 350 µm long, broader ends of ovaries almost half embedded in lateral nerve cords. Left ovary with distinct ventroposterior lobe lying below ovovitelline duct, extending 160 µm caudally. Right ovary without pronounced lobe. Secondary ovary present, 106 µm long, 59 µm in diameter, partially embedded in nerve cord immediately below opening into ovovitelline duct, 390 µm 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 genital canal. Vitellaria situated between gut diverticula, empty through dorsal wall of tuba via short narrow vitelline funnels; funnels greatly expanded, form resorptive vesicles, 40–85 µm in diameter where vitelline funnels communicate with the ovovitelline duct. Resorptive vesicles (Fig. 5) lined by flattened epithelial cells with vacuolate cytoplasm. Some vesicles with sperm, others with very pale amorphous cyanophil 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 (Fig. 4b), 640 µm in diameter, located either side of pharynx, communicate directly through dorsal wall of underlying ovovitelline

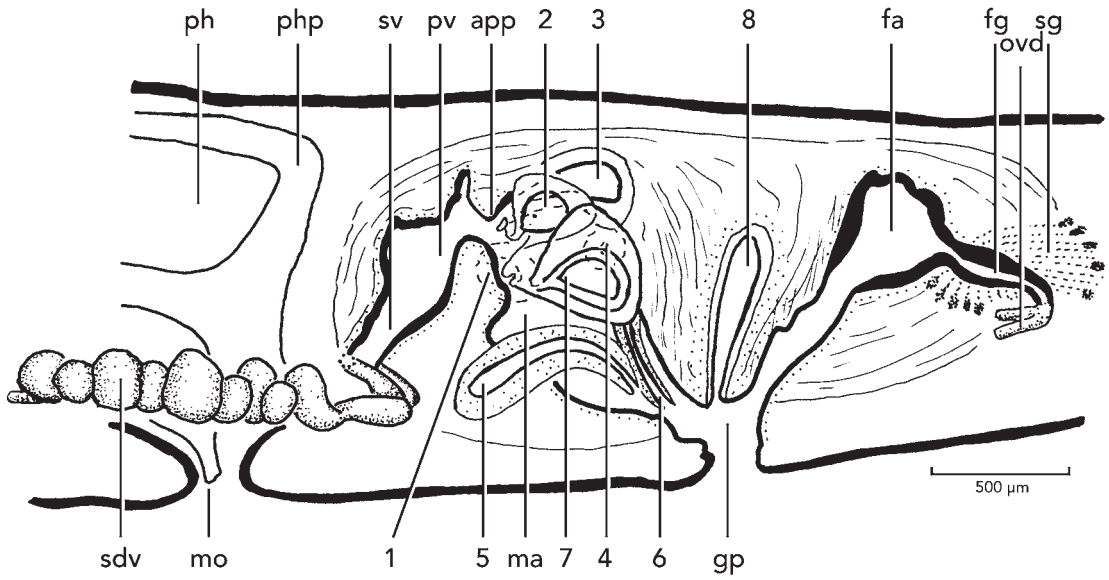


Fig. 6 *Anzoplana trilineata*: diagram of the copulatory organs (holotype). Numbers 1–4 are coplanar adenomuralia radially arranged (left, right, and two in an intermediate position either side of the midline facing anteriorly) in the horizontal plane, emptying into the proximal male antrum. Numbers 5–7 are adenodactyls emptying into the distal male antrum. Number 8 is an adenomuralium emptying into the common antrum.

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 fine erythrophil granules (lysocytes).

Female genital canal 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 granular 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 granular cyanophil secretion. Fine granular erythrophil strand-like secretions pass between cells into antrum, epithelium continues along ventral half of narrow distal neck of antrum 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 (Fig. 6) with eight musculoglandular organs: with five adenomuralia (Type VI, Fig. 6 numbers 1–4, 8), with distinct proximal reservoirs greater in diameter than the strongly muscularised ducts lying wholly within the antral wall, with little or no papilla projecting into antrum; with three adenodactyls (Type VI, Fig. 6 numbers 5–7), with distinct proximal reservoirs, strongly muscularised ducts, long papillae projecting into male antrum. Secretions in reservoir of adenodactyls differ from those in the adenomuralia (Table 2). Antra with subepithelial circular muscularis surrounded by loosely interwoven mixed fine muscle fibres.

PATHOLOGY: Ciliophoran, 12.6 µm in 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 + Latin *linea* = line + suffix *ata* = possession of. It is a feminine adjective in apposition, meaning the 'three-striped *Anzoplana*'.

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*. The species will be described elsewhere. It is the same

Table 2 *Anzoplana trilineat*: musculoglandular organs (MGOs) in the copulatory apparatus. The MGO number corresponds to the numbering in Fig. 6.

MGO no.	Adenodactyl or adenomuralum	Direction papilla faces	Proximal secretion: reservoir	Distal secretion: duct
1	adenomuralum	Right	Coarse erythrophil granules; neutrophil granules; cyanophil strands	Fine erythrophil granules
2	adenomuralum	Anterior		
3	adenomuralum	Anterior		
4	adenomuralum	Left		
5	adenodactyl	Right	Erythrophil granules in globules + fine cyanophil granules	Fine erythrophil granules
6	adenodactyl	Posteroventral		
7	adenodactyl	Posteroventral		
8	adenomuralum	Ventral		

species sent by Fyfe to Professor Eudoxia Froehlich for comparison with Chilean taxa (Froehlich 1978: 19).

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 dorsoventral testes in *Anzoplana* immediately differentiates it from the caenoplaninid genus *Newzealandia*, otherwise characterised by the presence of adenomuralia and an apapillate eversible penis.

Lateral resorptive bursae are unusual and hitherto unrecognised in the Terricola. Those on either side of the pharynx in *Anzoplana* are similar in histology to the 'glandular pockets' in the New Caledonian caenoplaninid *Australopacifica willeyi* (Busson 1903: 401). In this species, paired bursae arise from the lateral walls of the female antrum 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 extracellular 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).

Fyfea new genus

Artioposthia (in part) Fyfe, 1953: 9; Ogren & Kawakatsu 1991: 37.

DIAGNOSIS: Anzoplaninae with small, elongate body, with mouth just behind mid body, gonopore closer to mouth than posterior end. Eyes in single row around anterior tip. Sensorial margin passes anteroventrally around the anterior tip. Sensory papillae absent. Anterior adhesive cup, sucker absent. Creeping sole more than 70% of body width. Cutaneous musculature tripartite; circular and helical muscles, with longitudinal muscles in bundles, stronger ventrally than dorsally. CMI 22%. Parenchymal musculature with mixed longitudinal–transverse muscles in small bundles in subneural 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. Testes dorsoventral, sperm ducts ventral. Testes extensive, numerous, occupy parenchyma between intestinal diverticula, 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 bursae, situated between mouth and copulatory organs. Ovovitelline ducts separately enter distal end of female genital canal; female genital canal enters antrum horizontally via ventroposterior antral wall (postflex condition). With a common antrum. Vitellaria sparse. Adenodactyl present. Adenomuralia absent. Viscid gland absent.

TYPE SPECIES: *Fyfea carnleyi* (Fyfe, 1953) new combination.

ETYMOLOGY: The name *Fyfea* honours Marion Fyfe (1894–1986), for her pioneering taxonomic anatomical work on the Terricola of New Zealand. Gender feminine.

DISTRIBUTION: St Col Peak, 300 metres asl, Campbell Island, 169°10' E 52°53' S, and Ocean Island, Auckland Islands, Subantarctic Islands of New Zealand.

SYSTEMATIC DISCUSSION: *Fyfea* presently has only one species, *F. carnleyi*. Within the Caenoplaninae, *Fyfea* shares with *Kontikia ashleyi* (Fyfe, 1953) some morphological characters – the ovary situated between mouth and copulatory organs, and an inverted penis. It is distinguished from *K. ashleyi* chiefly by the presence of an adenodactyl (absent in *K. ashleyi*). In *Anzoplana*, the ovaries are situated near the anterior end, and the penis is eversible. The antrum is not differentiated histologically or structurally into male and female parts, and is regarded here as a common antrum.

The inverted penis *bauplan* is found in Plagiostomidae, Monocelididae, some Acoela and the maricolan taxa *Nexilis epichitonius* and *Centriovarioplana tenuis* (Sluys, 1989). This type of penis is uncommon in the Terricola, and found only in *Fyfea carnleyi*, *Kontikia ashleyi* (Fyfe, 1953) and *Australopacifica aucklandica* sensu Fyfe, 1953 (? = *Kontikia marrineri* (Dendy, 1901)), all three of which also have pharyngeal to post-oral ovaries. Eyes in these taxa appeared to comprise peripheral pigment with an inner cyanophil featureless mass, considered to be a fixation artefact (R. Sluys, pers. comm. 2002); the eyes are the pigment-cup type. Of particular interest are the parallels between the foregoing terricolan taxa from Auckland Islands, and the maricolan *C. tenuis* recorded from the subantarctic South Georgia Islands, at about the same latitude. *C. 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. Whether this is simply an example of character convergence, or indicates some relationship between these marine and terrestrial flatworm taxa, is presently unknown.

Fyfea carnleyi (Fyfe, 1953) new combination (Figs 7–12)

Artioposthia carneyli Fyfe, 1953: 9, Fig. 2, Pl. 2: Fig. 1, Pl. 3: Fig. 2; Ogren & Kawakatsu 1991: 37; Ogren et al., 1997: 78, 90. Incorrect original spelling.

Artioposthia carnleyi Fyfe, 1953; Johns, 1998: 466. Justified emendation.

Material examined

Lectotype: MONZ–ZW 102 St Col Peak, 300 metres asl, Campbell Island, collected under stones by J.H. Sorensen 28 May 1942. One series of sagittal sections on nine slides of the posterior half of flatworm, stain unknown. **Paralectotype**: MONZ–ZW 102 St Col Peak, 300 metres asl, Campbell Island, collected under stones by J.H. Sorensen 28 May 1942. One whole flatworm.

NON-TYPE MATERIAL: MONZ–ZW 112 St Col Peak, 300 metres asl, Campbell Island, eight specimens collected under stones by J.H. Sorensen 28 May 1942. Specimens (b) 42 slides sectioned at 8 µm, and stained by the Steedman's Triple and AZAN methods. MONZ–ZW 1371 labelled A49, No. 1 station, Auckland Islands, three specimens collected by W.H. Dawbin 3 February 1943 under logs, immature, 21 slides, AZAN. MONZ–ZW 1381, Port Ross, Auckland Island, single specimen collected by J.H. Sorenson 27 May 1947 under old timber. MONZ–ZW 1382 Sandy Bay, Enderby Island in Port Ross, Auckland Island, single specimen collected by R.K. Dell 18 March 1954 under logs, rata forest, 34 slides, AZAN. MONZ–ZW 1384 W.H.D. 116. Ocean Island, Auckland Islands, one specimen collected by W.H. Dawbin 28 February 1943. MONZ–ZW 1390B Campbell Island, single specimen collected by C.M. Clark 10 August 1962, 50 slides, AZAN. 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 3.

REMARKS: In the heading of the original description, the spelling of the specific epithet *carneyli* (Fyfe 1953: 9) is an 'incorrect original spelling' under Article 32.4 (ICZN 1999) noted by Johns (1998). It is considered here to be a printer's error. The name is correctly spelled *carnleyi* twice on the same page, before 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 Article 32.5.1 (ICZN 1999) this type of spelling error must be corrected.

Table 3 *Fyfea carnleyi*: dimensions of specimens examined.

Specimen	Length (mm)	Width (mm)	Mouth (mm)	Mouth (%)	Gonopore (mm)	Gonopore (%)	Mouth–gonopore (mm)	Mouth–gonopore (%)
MONZ–ZW 112 a	15.0	3.5	7.5	50.0	11.5	76.7	4.0	26.7
MONZ–ZW 112 b	15.0	3.0	9.5	63.3	13.0	86.7	3.5	23.3
MONZ–ZW 112 c	15.0	3.0	8.5	56.7	11.6	77.3	3.1	20.7
MONZ–ZW 112 d	14.0	2.5	8.0	57.1	11.5	82.1	3.5	25.0
MONZ–ZW 112 e	8.0	2.0	6.5	81.3	non-sexual			
MONZ–ZW 112 f		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–ZW 112 g		4.0						
MONZ–ZW 112 h		3.0						
MONZ–ZW 1371 a	13.0	2.2	7.0	53.9	9.7	74.6	2.7	20.8
MONZ–ZW 1371 b	11.5	1.7	6.0	52.2	8.5	73.9	2.5	21.7
MONZ–ZW 1371 c	10.7	1.6	6.0	56.1	8.0	74.8	2.0	18.7
MONZ–ZW 1381	< 10	Specimen curled and immature						
MONZ–ZW 1382	8.2	3.0	3.5	42.7	5.1	62.2	1.6	19.5
MONZ–ZW 1384	15.0	3.5	Specimen twisted and damaged					
MONZ–ZW 1390 B	20.0	3.5	11.0	55.0	15.0	75.0	4.0	20.0

Fyfe (1953: 10) 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 designated here 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 MONZ–ZW 112. Specimen MONZ–ZW 1371, examined in this study, consisted of four species confused in the same tube; two specimens (MONZ–ZW 1371) are considered here to be those collected by Dawbin from under logs in the rata forest, Musgrave Peninsula (Fyfe 1953: 9). The incomplete slide series of this species in the Otago Museum (OMNZ A74-51) possibly comprises the posterior portions of the anterior halves of specimens MONZ–ZW 112 f, g, h.

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: 9) as 'Colonel Peak, Campbell Island'. However, no such location exists on Campbell Island. It is presumed 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: 3; 20; map in Fraser 1986: 70).

External features

Fyfe (1953) described fixed specimens (Fig. 7) 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 (Fig. 8). Lateral 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, which in some specimens may be concentrated to form a faint brown line.

She noted that in an 11-mm-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. Eyes are 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. 9).

Fyfe (1953) gives the average dimensions of the preserved specimens as 21 mm long and 5 mm wide. The mouth is more than halfway from the anterior end, and gonopore nearer the mouth than the posterior end. Pharynx is long and tubular.

All of the material from Campbell Island was bleached. Specimens from Auckland Island (MONZ–ZW 1371) 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–ZW 1384), and the penis is partly protruded. Specimen MONZ–ZW 1382 is robust, dark brown dorsally, paler ventrally with an unpigmented tip and 'canoe' shaped with strongly curved dorsum and concave ventral surface.

The cross-sectional body shape is markedly dorsoventrally flattened with pronounced margins, possibly a fixation artefact (MONZ–ZW 1372, 1384), to a more natural shape that is shallow convex dorsally and flat ventrally (MONZ–ZW 112). The average length of the specimens examined in this study, 14.8 mm (Table 3), is considerably less than that given by Fyfe, though the relative positions of the body apertures broadly accord with her description.

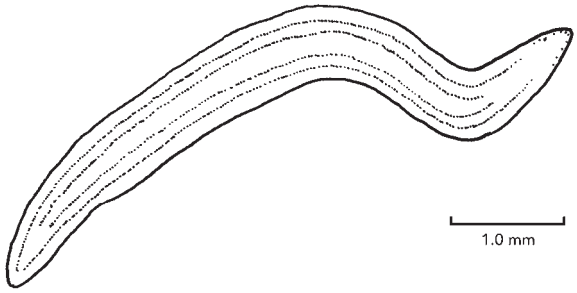


Fig. 7 *Fyfea carnleyi*: general form, dorsal aspect, fixed specimen.

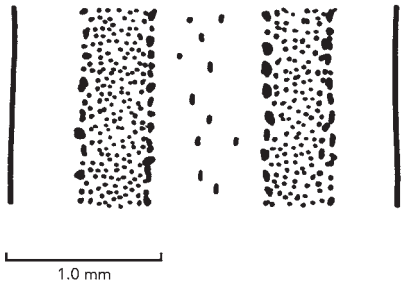


Fig. 8 *Fyfea carnleyi*: dorsal stripe pattern (after Fyfe 1953: 9, text figure 2).

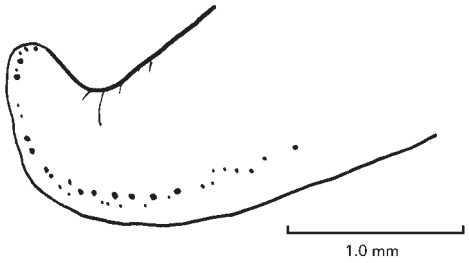


Fig. 9 *Fyfea carnleyi*: anterior tip, eye pattern.

Internal anatomy

The species was briefly and only partially described and illustrated by Fyfe. The sectioned Type material is incomplete, and the following description refers to the topotypic specimen MONZ–ZW 112 b.

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, 12.6 µm in diameter, 26 µm deep. Eyes pigment-cup type, 14 µm in diameter.

PRE-PHARYNGEAL REGION: Body tightly packed with muscles, testes and gut (Fig. 10a). Outer epithelium same thickness dorsally and ventrally. Rhammites 23 µm 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. Body 2528 µm wide. Creeping sole nucleate, 1798 µm wide, 71% of body width. Body height 1033 µm. Body width : height ratio 2.4. Cutaneous musculature tripartite, with circular and decussate helical muscles, with longitudinal muscles in dorsal bundles 30 µm thick, ventral bundles 73 µm thick. Dorsal cutaneous musculature 34 µm thick, thinner than ventral (98 µm thick). CMI

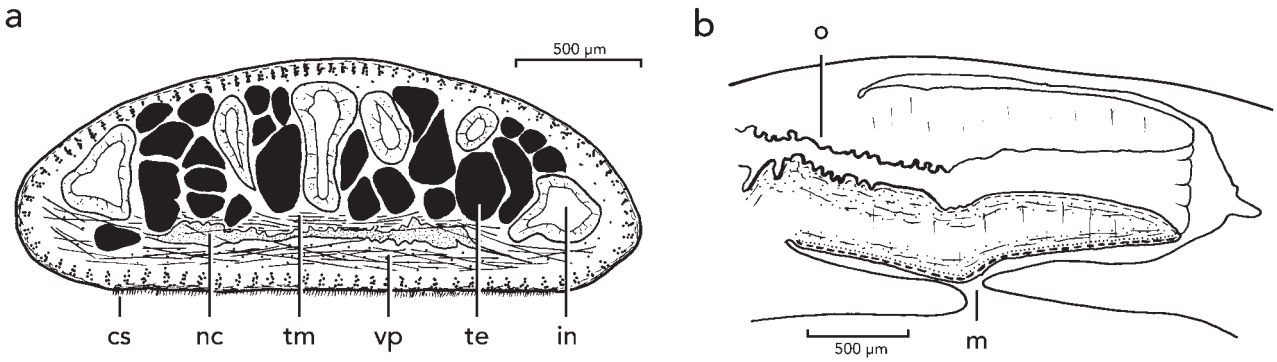


Fig. 10 *Fyfea carnleyi*: (a) pre-pharyngeal region, transverse section; (b) pharynx, LS (MONZ–ZW 112 b).

22.%. Parenchymal musculature strong. Subneural muscular plate present, 112 µm 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 (Fig. 10b) cylindrical, horizontal, 1.8 mm long, 11.7% of body length, with pleated internal lumen, dorsal insertion posterior to ventral insertion, with oesophagus. Inner pharyngeal musculature with subepithelial longitudinal, then mixed circular–longitudinal muscles; outer pharyngeal musculature with a thick subepithelial layer of longitudinal, then evenly spaced circular, muscles that grade into mixed circular–longitudinal muscles. Inner pharynx, with ciliated infranucleate epithelium in distal two-thirds of pharynx, grades into nucleate secretory oesophageal epithelium occupying proximal third of pharynx and extends anteriorly to gastrodermis. Oesophageal epithelium underlain by strong mixed circular–longitudinal muscles. Pharyngeal pouch 2 mm long, 13% of body length. Mouth in anterior third of the pouch. Small diverticulum present.

REPRODUCTIVE ORGANS: Copulatory organs (Fig. 11) contained within a poorly defined sheath of mixed longitudinal and circular muscles that merge into the body parenchymal musculature dorsally. With a common antrum.

Testes extensive, 100–200 µm in diameter, dorsoventral (Fig. 10a), occupying all the 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 with 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, and inverted penis inclined 10° to horizontal. Seminal vesicle lined by wrinkled (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 that 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 coalesces 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.

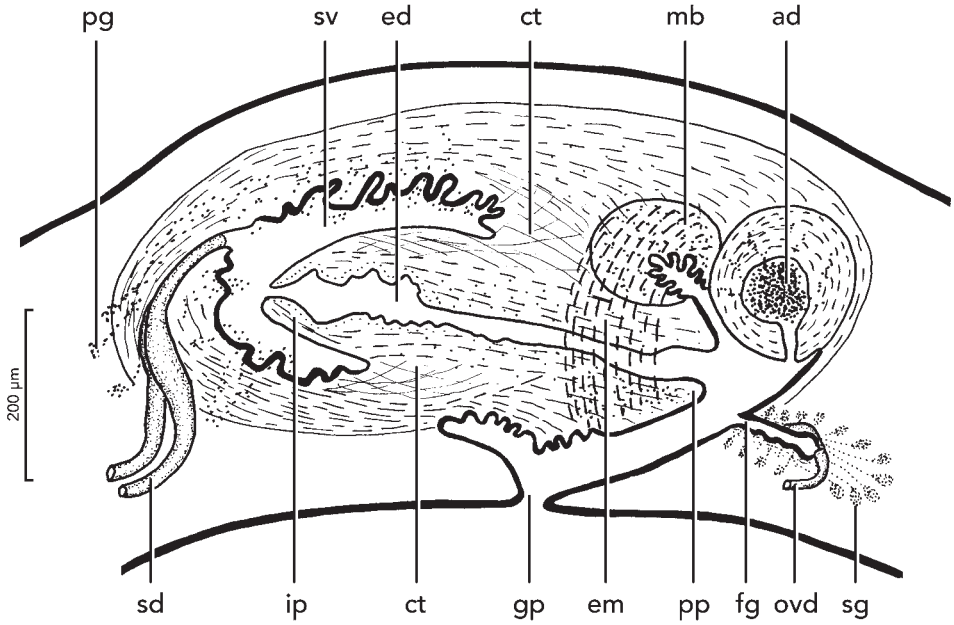


Fig. 11 *Fyfea carnleyi*: copulatory organs.

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 a muscular bolster in the roof of the common antrum and behind the 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, considered here to facilitate penial extension). Distal third of penis projects into antrum, surrounded by powerful circular penial extensor muscles attached to ventral half of penis, and to the muscular bolster in the roof of antrum forward of adenodactyl.

Adenodactyl spheroidal shape, Type VI, situated in dorsoposterior 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 amorphous cyanophil (turquoise) secretion from ventrad wall near duct. Duct leads from reservoir and terminates in a short papilla that projects into antrum above female glandular canal; epithelium of duct and papilla are heavily charged with globular erythrophil secretions.

Common antrum largely occupied by penis papilla. Antral roof formed by strong bolster of circular muscles and by adenodactyl; posterior wall weakly muscularised (slight extension of bulb musculature), with relatively smooth floor. Antrum 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 as sclerotin-forming strand cells, giving epithelium ciliated appearance. Gonopore opens below penis papilla.

Ovaries ventral, slightly embedded in nerve cords, 140 µm long, 250 µm wide, 100 µm high, situated between mouth and copulatory organs. Parovarian bursa not enclosed by a tunica, surrounds ovaries, extends back along oviducts short distance. Oviducts enter ovaries ventrally; lined by ciliated epithelium; with small branches (Fig. 12) behind ovary opening into adjacent parovarian bursa to receive excess donor sperm. Vitellaria reduced, distal to ovary, lying beneath gut. Ovovitelline ducts curve mediad to enter separately laterally blind end of female genital canal (postflex condition), do not receive secretions from adjacent shell glands.

Female genital canal mostly straight, flaring dorsoventrally 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

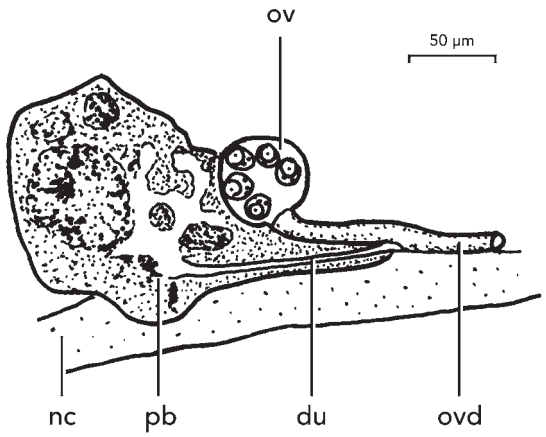


Fig. 12 *Fyfea carnleyi*: left ovary and associated parovarian bursa.

circular musculature. Female genital canal enters ventro-posterior wall of antrum horizontally.

PATHOLOGY: Gregarine sporozoites present in mesenchyme outside gut wall. In specimen MONZ–ZW 1371, gregarines are present in the testes, raising the possibility that these parasites might cause eventual sterility in infected specimens.

ETYMOLOGY: The specific epithet *carnleyi* designated by Fyfe (1953) presumably refers to 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 Caenoplaninae, *Fyfea* shares the characters of the ovary situated between mouth and copulatory organs, and an inverted penis, with *Kontikia ashleyi*. It is distinguished from *K. ashleyi* chiefly by the presence of an adenodactyl and by reduced vitellaria (in the author's opinion, *K. ashleyi* does not belong in *Kontikia* and will be reassigned to a new genus in a subsequent taxonomic revision). 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 *Kontikia ashleyi*, and may also be present in the caenoplaninid *K. marrineri*. Of particular interest are the parallels between the foregoing terricolan taxa from Auckland Islands, and the maricolan *C. tenuis* recorded from the subantarctic South Georgia Islands, at about the same latitude. *C. tenuis* has an inverted penis, ovaries located immediately anterior to the mouth on either side of the gut, a musculoglandular organ external to the copulatory organs, and lensed eyes, which sets it well apart from *Fyfea*. 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, or may simply reflect anatomical convergence.

The essential details of Fyfe's (1953) succinct description of *Fyfea carnleyi* are confirmed here. Additional characters, including the musculature of the body and organs, dorsoventral testes, sperm-resorptive nature of the parovarian tissue (parovarian bursae) and the type of penis, are now described. The average length of the specimens examined in this study, 14.8 mm (Table 3), 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 glandular canal is depicted as dorso- and ventro-posterior (T-shaped anastomosis) (Fyfe 1953, Pl. II, Fig 1). 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 misinterpreted as the point of entry of the ovovitelline ducts. Also, Fyfe (1953, Pl. 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.

The external features of MONZ–ZW 1382 strongly accord with the description of *Australopacifica moebiusi* (Graff, 1899) from Auckland Island, the Type of which has yet to be examined histologically. This species may prove to be conspecific with *F. carnleyi*.

Subfamily Caenoplaninae Ogren & Kawakatsu, 1990

ORIGINAL 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 paper): Geoplanidae with ventral testes and ventral efferent ducts. 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. With or without eyes. Eyes when present pigment-cup type, in a single row around the anterior end, generally continuing posteriorly, may extend dorsally.

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 and with gonopore in the third quarter. In addition, taxa with bipartite cutaneous musculature, or in which a ciliated creeping sole or eyes were absent, were not known at the time and so no provision was made for them in the diagnosis. Consequently, the subfamily diagnosis is emended. In the light of recent systematic studies of the hitherto poorly known austral Terricola (Winsor 2003), the sections of the Caenoplaninae designated by Ogren & Kawakatsu (1990) should be reassessed and redefined.

Genus *Coleocephalus* Fyfe, 1953

Coleocephalus Fyfe, 1953: 12; Ogren & Kawakatsu 1991: 33; Johns 1998: 465; Winsor 1998b: 414.

ORIGINAL DIAGNOSIS (in Fyfe 1953: 12): 'Geoplanidae with hooded anterior end partly covering an oval glandular area on the ventral surface.' Emended by Ogren & Kawakatsu (1991) to include: 'penis papilla present; adenodactyls present'.

DIAGNOSIS EMENDED (this paper): Caenoplaninae with small, robust body. Mouth and gonopore situated in hind third of body. Eyes pigment-cup type, in single row around anterior tip. Sensorial margin passes anteroventrally around the anterior tip. Sensory papillae absent. With adhesive sucker anteroventrally. Creeping sole 70% or more of body width. Cutaneous musculature tripartite, very strong, with circular and helical muscles, with longitudinal muscles in bundles, CMI 22–24%. Parenchymal musculature with strong dorsal and ventral transverse muscles; longitudinal parenchymal muscles weak or absent. 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 bursae. Ovovitelline ducts separately enter female genital canal ventroposteriorly (postflex condition). Female genital canal horizontal, enters female antrum through ventroposterior antral wall, below adenodactyls. Adenodactyls present. Adenomuralia absent. Viscid gland absent.

TYPE SPECIES: *Coleocephalus fuscus* Fyfe, 1953.

ETYMOLOGY: Fyfe (1953) did not indicate the etymology of this taxon. *Coleocephalus* is derived from the Greek *koleus* = sheath, and *kephale* = head, and alludes to the hooded anterior end of the animal. 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 & Kawakatsu (1991) provisionally included the genus in the Caenoplaninae. Examination of the Type and other material has shown that the testes are ventral, confirming the genus as a caenoplaninid. The hooded anterior end, alluded to in the generic name and included in the original generic diagnosis, is a fixation artefact, and consequently has been deleted from the diagnosis. Ogren & 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).

There are presently two cotylate caenoplaninid genera: *Coleocephalus* Fyfe, 1953, and *Pimea* Winsor, 1991 from New Caledonia. *Coleocephalus fuscus* is distinguished from *Pimea* mainly by possessing a cotyloplanid-type sucker, not the adhesive pad sucker bearing *haftpapillen* present in

Pimea, and retractor derived from cutaneous longitudinal muscles, not insunk as in *Pimea*. Eyes and sensory pits skirt the anterior tip, with strong cutaneous musculature, CMI 22–24%, strong parenchymal musculature, plicate pharynx, ovaries near pharynx root, with parovarian bursae, apapillate eversible penis, and adenodactyls. In *Pimea* the eyes are absent around and over the anterior tip, but present in a row anterolaterally. The sensory zone is restricted to anteroventrolateral patches, and is absent from the tip. It has strong cutaneous musculature, CMI 11.5%, but weak parenchymal muscles; cylindrical pharynx, ovaries are near the anterior tip, with seminal receptacle, resorptive tissue and adenodactyls absent; with intra-penial papilla, protrusible penis, and copulatory bursa.

Coleocephalus fuscus Fyfe, 1953
(Figs 13–19)

Coleocephalus fusca Fyfe, 1953: 12, Pl. 4: Figs 1–5; Johns 1993: 28; Johns 1998: 466.

Coleocephalus fuscus Fyfe, 1953; Ogren & Kawakatsu 1991: 68; Winsor 1998b: 425. Justified emendation.

Material examined

Holotype: MONZ–ZW 104. Enderby Island, Auckland Island group, collected 12 February 1945 by W.H. Dawbin. It comprises 20 microslides in two series – the anterior end (sagittal sections 17 slides), and posterior end (sagittal sections; an incomplete series of three slides considered to have probably originally been a series of five microslides, now with the first and last slides missing, which may well have contained testes). The sections are stained with a badly faded bichrome, and are mounted in Canada balsam. 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 Island Group.

NON-TYPE MATERIAL: MONZ–ZW 1370, single sexual specimen, sectioned at 8 µm, stained with MSB and AZAN, and the slides labelled as MONZ–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' MONZ–ZW 110. According to Fyfe (1953), only a single specimen of *G. aucklandica*

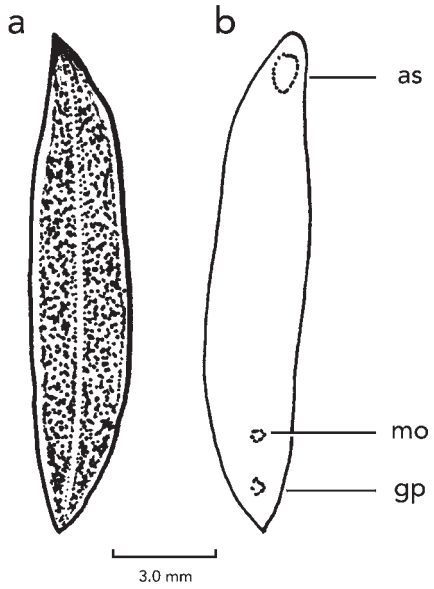


Fig. 13 *Coleocephalus fuscus*: (a) dorsal aspect; (b) ventral aspect of the whole specimen.

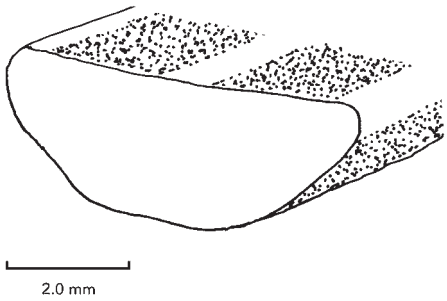


Fig. 14 *Coleocephalus fuscus*: dorsal stripe pattern.

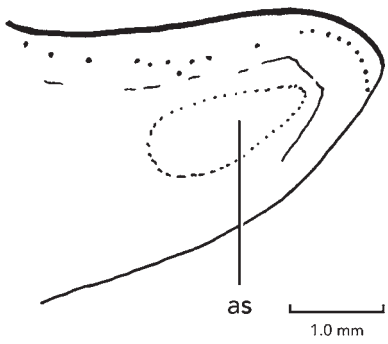


Fig. 15 *Coleocephalus fuscus*: anterior end showing eye pattern and anterior ventral sucker (MONZ–ZW 1370).

Table 4 *Coleocephalus fuscus*: dimensions of holotype and other material.

Specimen	Length (mm)	Width (mm)	Mouth (mm)	Mouth (%)	Gonopore (mm)	Gonopore (%)	Mouth–gonopore (mm)	Mouth–gonopore (%)
MONZ–ZW 104 **Holotype**	25.0	7.0	20.0	80.0	?	?	?	?
MONZ–ZW 1370	16.5	6.0	12.1	73.3	13.8	83.8	1.7	10.3

was collected from this location. The exact location in the Auckland Islands for this specimen of *C. fuscus* is therefore uncertain.

DISTRIBUTION: All specimens, possibly ten in number, 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 features

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. 13). Mouth, gonopore in posterior third. Adhesive sucker present; shallow, ellipsoid-shaped depression anteroventrally. Dimensions of the holotype and specimen MONZ–ZW 1370 are provided in Table 4.

Markings (Fig. 14): '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).

Specimen MONZ–ZW 1370 has light brown dorsal ground colour ('museum brown'), with paired broad lateral dark blotchy brown stripes separated by median interval of ground colour 0.3 mm wide extending along two-thirds of posterior body. External to dark lateral stripes are 0.3-mm-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. 15). 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 dorsoventral muscles to form corset (*muskelgeflecht*). Parenchymal ventral transverse muscles strong, more than twice thickness (112 µm) anteriorly than in pre-pharyngeal region (50 µm). Sucker epithelium anucleate, non-ciliated. Sucker with three secretions: rhabdoids, fine erythrophil and coarse xanthophil granules. Erythrophil and xanthophil elements concentrated subintestinally, ventral rhabditogen cells subneural, dorsal rhabditogen cells just below cutaneous musculature. *Haftpapillen* absent. Gut extends almost to tip. Eyes pigment-cup type, 20–28 µm in diameter, with 3–4 or more retinal clubs. Sensory pits simple, ciliated, 30 µm deep.

PRE-PHARYNGEAL REGION: Data derived from MONZ–ZW 1370; Fig. 16. Epithelium almost same thickness dorsally and ventrally, receives eight types of secretions from mesenchymal glands: rhabdoids, epitheliosomes, fine erythrophil granules (glycoprotein), coarse erythrophil granules, amorphous cyanophil secretion (an acid mucopolysaccharide), granular cyanophil secretions, coarse brown-orange xanthophil granules (basic protein), and fine xanthophil granules. Adhesive margins dorsolateral, slightly raised, rhabdoid-free, with both coarse xanthophil and cyanophil secretory elements. Body 3800 µm wide. Ciliated creeping sole 2670 µm, 70% of body width. Body height 1359 µm. Body width : height ratio 2.8. Cutaneous

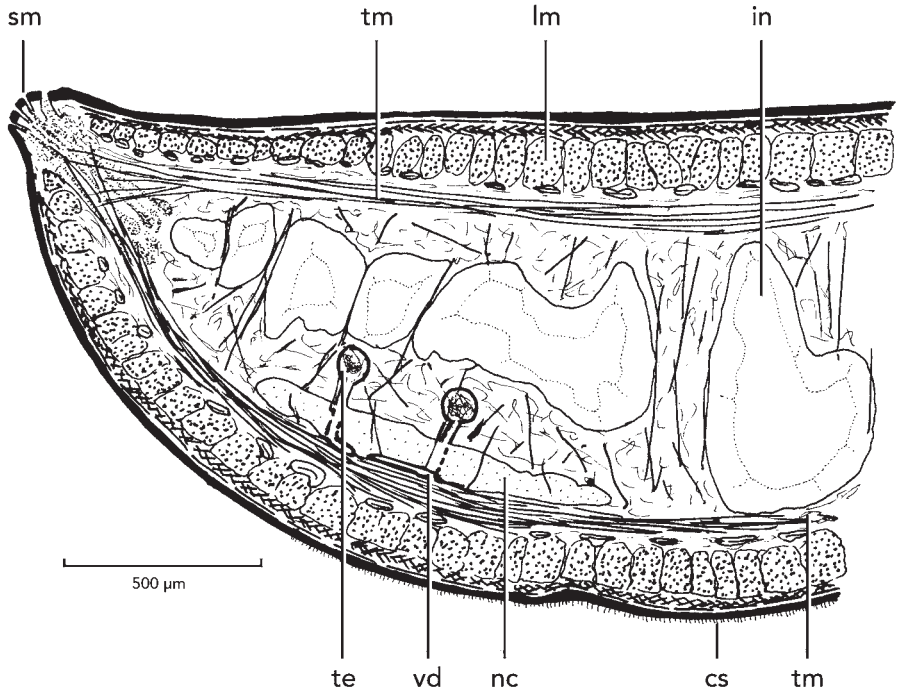


Fig. 16 *Coleocephalus fuscus*: pre-pharyngeal region. Transverse section (MONZ–ZW 1370).

musculature tripartite, with circular and helical muscles. Cutaneous longitudinal muscles in bundles, not insunk. Overall, the cutaneous musculature is developed equally dorsally (177 µm thick) and ventrally (177 µm thick); CMI 24%. 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 SYSTEM: Pharynx (Fig. 17) plicate, collar-form type, ventral insertion anterior to dorsal insertion; inner and outer musculature of both comprise subepithelial longitudinal then circular muscles. Pharyngeal pouch 2.5 mm long, 15% body length; mouth in hind quarter of pouch. Diverticulum absent. Oesophagus absent.

REPRODUCTIVE SYSTEM: Copulatory organs (Figs 18, 19) 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: Data derived from MONZ–ZW 1370. 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 (80–120 µm) than anteriorly (40–70 µm); 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, 125 µm long, 285 µm high, enclosed within thin fascia, pre-oral, embedded in mid-lateral nerve cords, some two-thirds distance between anterior tip and mouth. Parovarian bursae present, loculate, surrounding ovaries dorsally and posteriorly. Proximal ovovitelline duct communicates with bursal tissue and upper pole of ovary. Ovovitelline ducts separately enter female genital canal ventroposteriorly (postflex condition). Female genital 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.

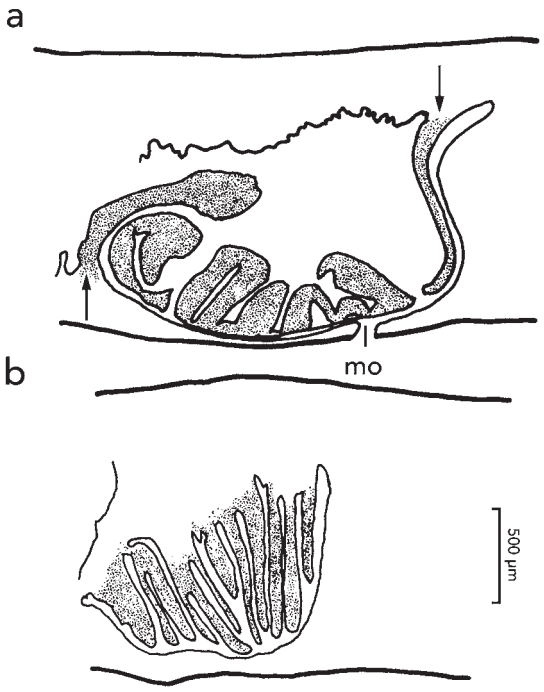


Fig. 17 *Coleocephalus fuscus*: (a) plicate (collar-form) pharynx, median sagittal section. Arrows indicate anterior (ventral) and posterior (dorsal) insertions of the pharynx (MONZ–ZW 1370); (b) plicate pharynx, lateral section giving the appearance of multiple mouths reported and illustrated by Fyfe (1956: 13, Pl. IV, Fig. 5) (MONZ–ZW 1370).

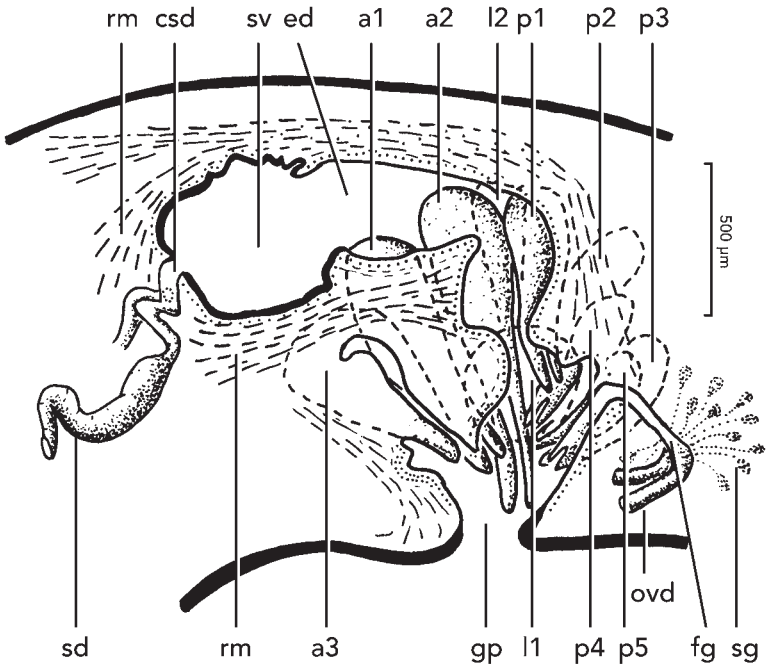


Fig. 18 *Coleocephalus fuscus*: copulatory organs. There are ten adenodactyls: anterior a1–3, lateral l1–2, and posterior p1–5 (Holotype, MONZ–ZW 104).

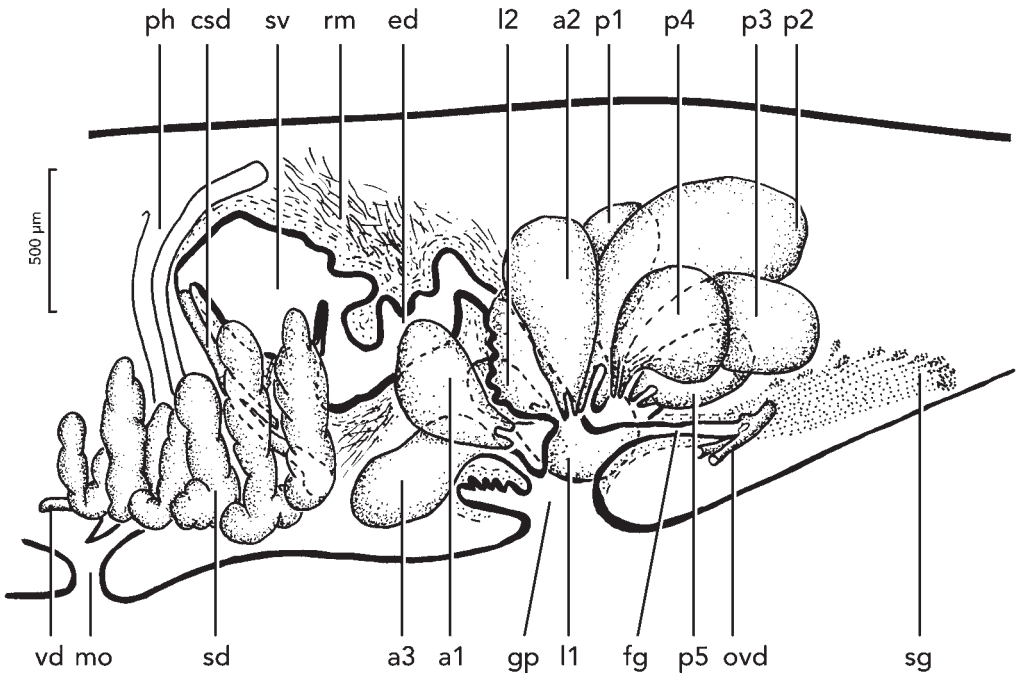


Fig. 19 *Coleocephalus fuscus*: copulatory organs. There are ten adenodactyls: anterior a1–3, lateral l1–2, and posterior p1–5 (MONZ–ZW 1370).

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 dorsoventral 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. When both the cutaneous and parenchymal musculatures are taken into account, the overall body musculature is stronger ventrally than dorsally. 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 specimen MONZ–ZW 1370, 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, which would evert the penis. Therefore, 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: 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 genital canal.

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 and parenchyma, and one is present in an adenodactyl papilla. There is no evidence of host response at any of the sites of infection.

ETYMOLOGY: Fyfe (1953) did not indicate the etymology of the specific epithet *fusca*, which is Latin = dusky, dark or swarthy. It presumably alludes to the overall dark brown dorsal pigmentation of the species. Ogren & Kawakatsu (1991) considered the genus name to be masculine (Article 30 (a) (iii) ICNZ 1999), and corrected the spelling of the specific epithet from *fusca* to *fuscus*.

BIOLOGY: Fyfe (1953) noted that the only mature specimen was collected in April, and that all the immature specimens were collected in February. The latter specimens 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 (although they may have been present in the missing slides), though the spermiducal vesicles and seminal vesicle contain sperm. The spermiducal vesicles do not exhibit the diverticula noted in MONZ–ZW 1370. 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 specimen MONZ–ZW 1370 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

Fyfe (1953) stated that the Type specimen 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 state 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, pers. comm. 1974).

HOOD: The 'hood' was observed by Fyfe (1953) in the Type and other material, and included by her in the generic diagnosis of *Coleocephalus*. A hooded anterior 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: 259), 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: 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. A similar transverse body shape is present in *Pasipha ercilla* (Froehlich, 1978) (Froehlich 1978: 29, Fig. 37), which also has very strong dorsal and ventral transverse parenchymal muscles, and strong dorsoventral muscles in bundles. *Pelmatoplana treubi* Graff, 1899 (Graff 1899: Pl. 5, Fig. 14), *Bipalium semperi* Graff, 1899 (Graff 1899: Pl. 9, Fig. 3) and *Rhynchodemus michaelseni* Graff, 1899 (Graff 1899: Pl. 17, Fig. 32) all exhibit this feature; their internal anatomy is unknown.

PHARYNX: Fyfe incorrectly 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 of *C. fuscus* is plicate (collar form, Fig. 17a), the folds of which in sagittal section can give the appearance of multiple branches described by Fyfe (Fig. 17b).

ADENODACTYLS: Fyfe stated that there were 'several adenodactyls … the number could not be estimated accurately because of their lack of complete development, but there are more than five. The reservoir is not enlarged, having the same diameter as the duct.' There are ten adenodactyls in both the holotype and specimen MONZ–ZW 1370. There is good agreement between the structure of the copulatory organs of both specimens, though the organs of the holotype are slightly more contracted than those of MONZ–ZW 1370. The adenodactyls in both specimens are mature, and the diameters of the reservoirs of the adenodactyls are greater than those of the ducts.

SPERM RESORPTIVE BURSAE: Although not noted in the original description (Fyfe 1953), parovarian bursae are present in *Coleocephalus fuscus*. The bursae in *Arthurdendyus triangulatus*, *Kontikia marrineri*, *K. ashleyi* and *Fyfea carnleyi*, previously regarded as 'parovarian tissue' (Fyfe 1937, 1953), have a sperm resorptive function. All these bursae have a similar internal structure (Winsor 2003; Winsor & Stevens 2005), comprising thin, irregular arborising folds that may fuse to appear honeycomb-like. Lysocytes and phagocytes are present, and sperm are digested intraluminally.

Concluding remarks

Two subfamilies of geoplanid terrestrial flatworms, comprising five genera and nine species, are represented in the New Zealand Subantarctic Islands. Within the Anzoplaninae they include *Fyfea carnleyi* (Fyfe), and within the Caenoplaninae they include *Artioposthia subquadrangulata* (Dendy), *A. subquadrangulata enderbyensis* (Dendy), *Australopacifica antarctica* (Dendy), *A. moebiusi* (Graff), *Coleocephalus fuscus* Fyfe, *Kontikia ashleyi, K. marrineri* (Dendy) and *K. ranuii* (Fyfe). Of these species, *Artioposthia subquadrangulata*, *A. subquadrangulata enderbyensis*, *Australopacifica antarctica*, *A. moebiusi*, *K. ashleyi*, *K. marrineri* and *K. ranuii* require evaluation, redescription, removal from blanket genera and reassignment into new and revised genera. There also remain additional new subantarctic terricolan taxa yet to be described. For these reasons, it is premature to attempt an analysis and consideration of the biogeography of the terrestrial flatworm faunas of the Australian and New Zealand Subantarctic Islands in this paper.

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Abbreviations used in figures

a	anterior adenodactyl
ad	adenodactyl
app	apapillate penis
as	adhesive sucker
cd	collecting duct
clm	cutaneous longitudinal muscle
cs	ciliated creeping sole
csd	common sperm duct
ct	compression tissue
du	bursal duct
ed	ejaculatory duct
em	extensor muscles
fa	female antrum
fg	female genital canal
gp	gonopore
in	intestine
ip	inverted papilla
l	lateral adenodactyl
lb	lateral bursa
lm	longitudinal muscle
m	mouth
ma	male antrum
mb	muscular bolster
nc	nerve cord
o	oesophagus
ov	ovary
ovd	ovovitelline duct
p	posterior adenodactyl
pb	parovarian bursa
pg	penial glands
ph	pharynx
php	pharyngeal pouch
pp	penis papilla
pv	prostatic vesicle
rm	retractor muscle
rv	resorptive vesicles
sd	sperm duct
sdv	spermiducal vesicle
sg	shell glands
sm	secretory margin
sv	seminal vesicle
te	testis
tm	transverse parenchymal muscle
vd	vas deferens
vi	vitellaria
vp	ventral plate