

Five new species of *Monocelis* Ehrenberg, 1831 (Platyhelminthes: Proseriata) from eastern Australia

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Six species of the genus *Monocelis* Ehrenberg, 1831 have been found in eastern Australia. All are new to science. Five of them are formally described here. Three species (*M. rupisrubrae* sp. nov., *M. nexilis* sp. nov., and *M. corallicola* sp. nov.) have two clearly set pigmented eyespots lateral to the statocyst. They differ in details of the copulatory organ and karyotype. No clear synapomorphies among them or with other species of the genus could be detected. *Monocelis beata* sp. nov. and *M. macrobulbus* sp. nov. present extremely elongate, longitudinally oriented copulatory organs. They are sister species, and phylogenetic relationships with *M. galapagoensis* Ax and Ax, 1977 and *M. hopkinsi* Karling, 1966 are proposed. Australian *Monocelis* have distributions limited to recognized biogeographical provinces in eastern Australia: *M. corallicola*, *M. beata* and *M. macrobulbus* in the northern Australian Zone, *M. rupisrubrae* and *M. nexilis* in the 'Overlap Zone' of the central east coast and *Monocelis* sp. A in the southern Australian Region.

KEYWORDS: *Monocelis*, Australia, systematics, biogeography.

Introduction

The genus *Monocelis* Ehrenberg, 1831 is among the largest of the genera in the family Monocelididae, and one of the most difficult taxa within the whole Proseriata, owing to the paucity of specific characters and slight differences among species (Karling, 1966). The monophyly of this genus has never been questioned, although assessment of phylogenetic relationships within it has scarcely been attempted. At present, assessment is made more difficult both by the very few morphological features felt to have phylogenetic weight and by the inadequate description of numerous species.

The genus is probably cosmopolitan: though, due to lack of investigation, reports are lacking for many areas, especially in the southern hemisphere. *Monocelis* has never been recorded hitherto in Australia.

The first reports of proseriates from the Australian marine interstitial were from the region of Darwin (Martens and Curini-Galletti, 1989; Curini-Galletti and Martens, 1991). Previously, mesopsammic fauna was known only from studies on acoels (Winsor, 1990), on kalyptorhynch rhabdocoels (Curini-Galletti and Puccinelli, 1990) and on macrostomids (Faubel *et al.*, 1994). Research on the Australian

turbellarian fauna has been largely restricted to the macroscopic (i.e. triclads and polyclads) or the symbiotic fauna (e.g. umagillids and temnocephalids). To further our understanding of interstitial turbellarian fauna in Australia, particularly along the east coast, we undertook a study of mesopsammic Proseriata. This research yielded six species of the genus *Monocelis*, all new to science. Five of them are described and discussed here. The sixth, of which material was insufficient for formal description, is nonetheless reported, in the light of the exceedingly scanty knowledge of diversity and biogeography of the Australian Proseriata.

Materials and methods

Material was collected from sandy habitats by scooping up the superficial layer of sediment. Extraction of the animals from the sediment was with $MgCl_2$ decantation (Martens, 1984). Preservation techniques routinely adopted for Proseriata were used (Martens *et al.*, 1989b) and animals were not anaesthetized when prepared for microscopical analysis. Specimens were fixed in hot (60°C) Bouin's fluid, embedded in 56°C Parablast and serial sagittal sections cut at 2–4 μm , stained with Mayer's haematoxylin and eosin and mounted in Depex.

Pore indices, used in species description, give the relative distances between mouth and the different genital pores (Karling, 1966): (a) mouth-vagina; (b) vagina-male pore; (c) male pore-female pore.

Karyological techniques used were as described by Curini-Galletti *et al.* (1989). Relative lengths (r.l. = length of chromosome \times 100/total length of haploid genome) and centromeric indices (c.i. = length of short arm \times 100/length of entire chromosome) were obtained from measurements of camera lucida drawings of 5–10 metaphase plates for each species. Idiograms are based on karyometrical data presented in the karyotype formula: haploid genome absolute length in μm , fundamental number, relative length and centromeric index of each chromosome; chromosome nomenclature between parentheses (m = metacentric; sm = submetacentric; st = subtelocentric; t = acrocentric). The fundamental number is derived according to Matthey (1949) and chromosome nomenclature follows Levan *et al.* (1964).

Histological material is stored in the collections of the Queensland Museum.

Abbreviations in Figures

b—bursa; br—brain; co—copulatory organ; e—pigmented eyespots; eg—eosinophilous glands; fd—female duct; fg—female glands; fp—female pore; gid—genito-intestinal duct; gl—gut lumen; m—mouth; ma—male antrum; mp—male pore; ms—muscle sheath; o—oviduct;	ov—ovaria; pg—prostatoid glands; ph—pharynx; pp—penis papilla; ppe—proximal penis; ps—prostatoid secretion; pt—prostatoid tissue; r—rhabdite; sd—seminal duct; st—statocyst; t—testes; vd—vaginal duct; vi—vitellaria; vm—vaginal muscle(s); vp—vaginal pore; vs—seminal vesicle.
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Genus *Monocelis* Ehrenberg, 1831

Monocelis rupisrubrae sp. nov.

(Figs 1, 6 A–G)

Material examined

HOLOTYPE: Australia, Queensland, Moreton Bay, Redcliffe, Oyster Point; extreme

high intertidal among mangroves, mixed sediment (gravel, shell fragments) with high silt content; September 1993, sagittally sectioned: G211656; PARATYPES: same data as holotype (July, August 1993): G211657–60.

Other material. Several studied alive, 22 studied karyologically. Abundant at type locality.

Etymology

The name is coined after the type locality (from Latin *rupes*: cliff, and *ruber*: red).

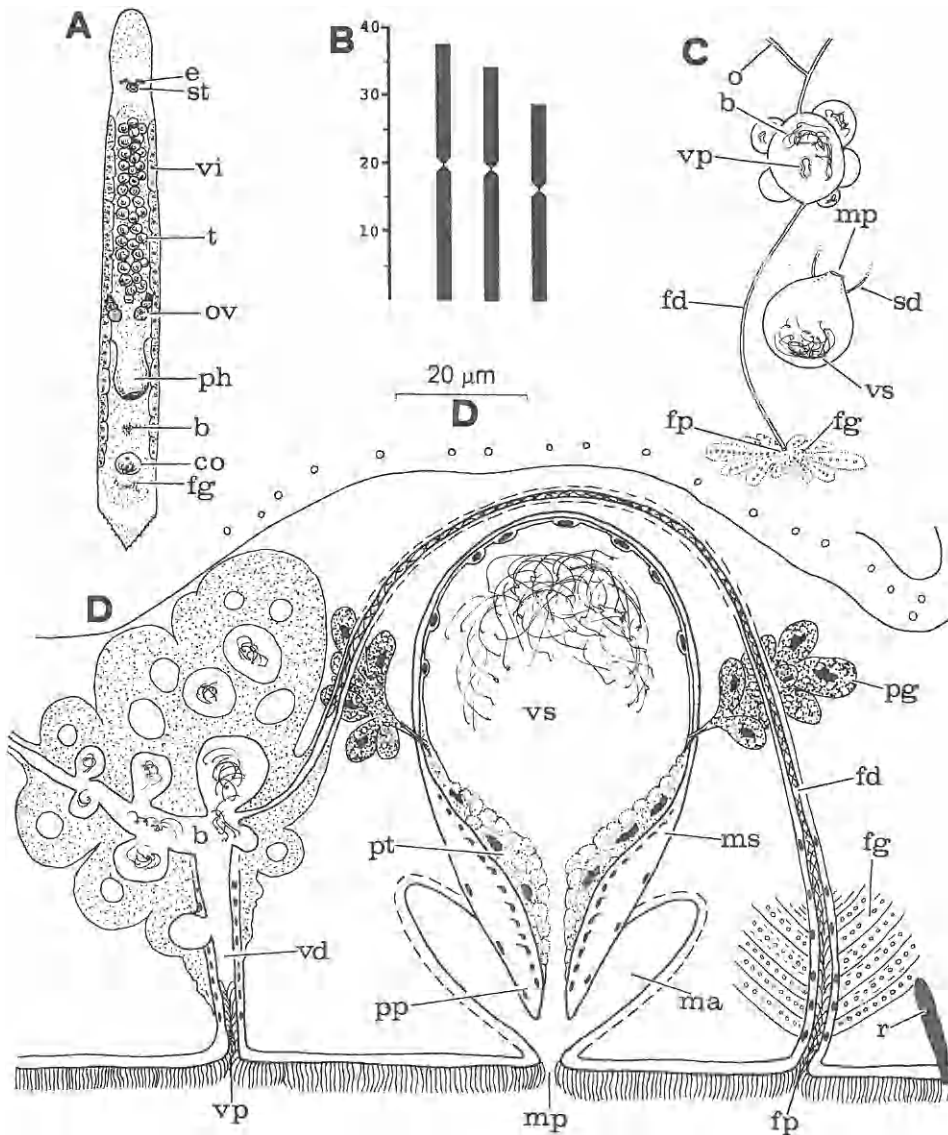


FIG. 1. *Monocelis rupisrubrae* sp. nov.: (A) general organization of a live animal; (B) idiogram; (C) general organisation of the genital organs from live animals; (D) reconstruction of the genital organs from sagittal sections.

Description

Animals slender, agile, about 1.2 mm long in sectioned material. With two clearly set pigmented eyespots lateral to the statocyst. Anterior end rounded, provided with oily drops and numerous irregular rhabdites. Posterior end rounded, with very numerous rhabdites and adhesive glands. Epithelium with insunk nuclei, ciliated all over except for the caudal tip. Cilia are short (about $2.5\text{ }\mu\text{m}$ long), slightly longer ventrally than dorsally. The pharynx is distinctly elongated and is situated in the second half of the body. Its luminal epithelium is unciliated in its proximal half; the oesophageal portion is located in its proximity third.

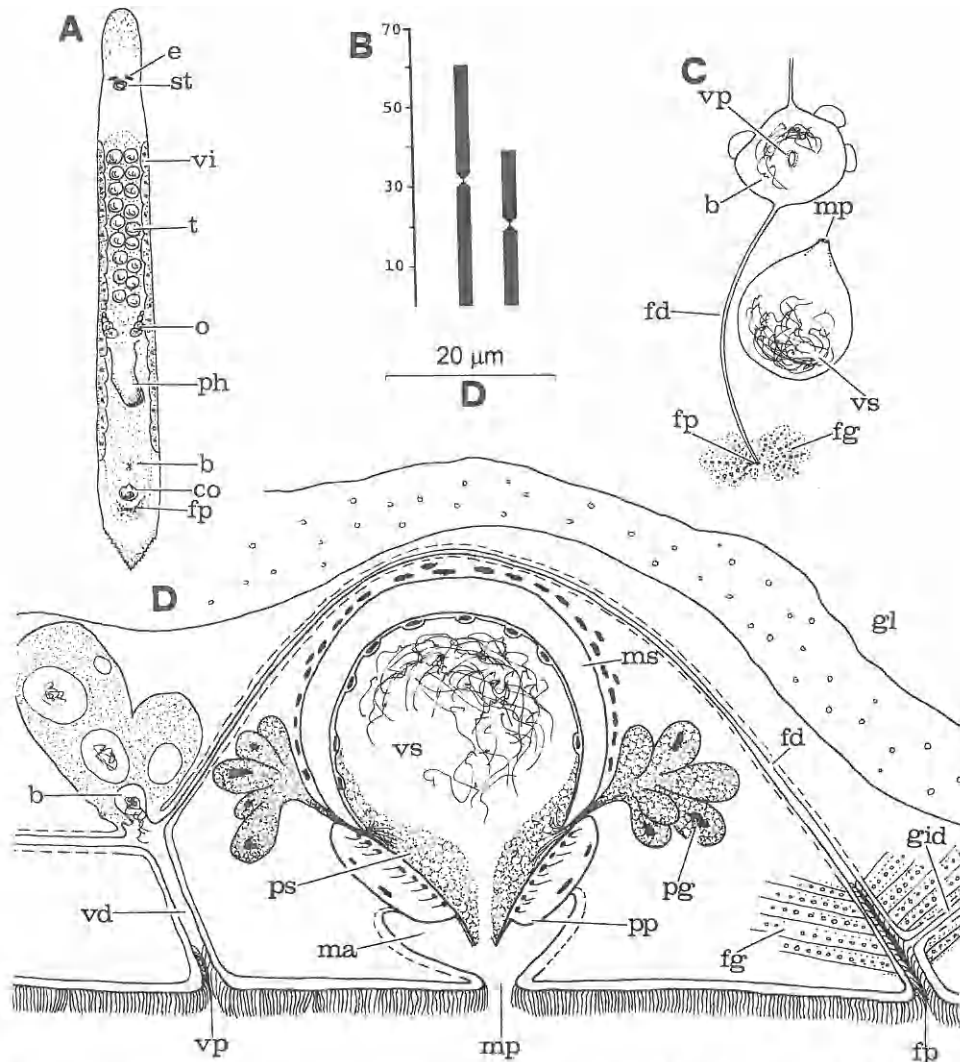


FIG. 2. *Monocelis nexilis* sp. nov.: (A) general organization of a live animal; (B) idiogram; (C) general organisation of the genital organs from live animals; (D) reconstruction of the genital organs from sagittal sections.

Male genital organs. About 20 testes in two irregular rows are present in front of the pharynx. The copulatory organ is nearly spherical, about $40\text{ }\mu\text{m}$ long and $32\text{ }\mu\text{m}$ wide. It consists of a globular seminal vesicle, lined with a nucleated epithelium, surrounded by a thick muscular layer (with inner circular and outer longitudinal muscles). The muscular coating progressively decreases in thicknesses distally. Just distally to the point where the prostatoid glands pierce the bulb walls, the muscular coating is very thick, and forms a 'collar' around the distalmost portion of the copulatory organ. Part of this 'collar' protrudes into the male antrum, and together with a short, apparently unciliated thin-walled portion of the ejaculatory duct, forms a broadly conical penis papilla. Internally, the distal half of the copulatory organ is coated with the granular secretion of the prostatoid glands, whose nuclei lie outside the bulb. The male antrum is unciliated; it opens to the exterior via the male pore.

Female genital organs. Ovaries lie in front of the pharynx. Vitellaria stretch from the level of the first testes to in front of the copulatory organ. Posterior to the pharynx, the two oviducts fuse into the common female duct. Caudally, the duct widens into a small vacuolar bursa of the resorbiens type. It consists of a few vacuoles containing sperm. Ventral to this bursa, the vaginal duct originates: it is short, nearly straight, slightly backward oriented and unciliated, apart from its most distal portion. It opens to the outside through a vagina. The portion of the common female duct caudal to the bursa runs posteriorly close to the male organ and opens caudally through the female pore. This portion is ciliated at least in its distal part. Just before the female pore, a short communication with the gut lumen is present (genito-intestinal duct). Around the female pore, female glands are present.

Pore ratio: $a \gg c \geq b$.

Karyology

Species has two chromosomes in its haploid set. Karyotype formula of the specimens from the type locality: $9.4 \pm 1.0\text{ }\mu\text{m}$; 4; Chrom. 1: 60.78 ± 2.17 ; 46.56 ± 1.16 (m); Chrom. 2: 39.22 ± 2.17 ; 46.25 ± 2.52 (m).

The specimen from Coffs Harbour had a nearly identical karyotype: $9.4 \pm 0.6\text{ }\mu\text{m}$; 4; Chrom. 1: 59.38 ± 2.39 ; 46.73 ± 1.45 (m); Chrom. 2: 40.62 ± 2.24 ; 45.76 ± 2.34 (m).

Remarks

Among the earlier described species with two pigmented eyespots, with a vagina and with distance a longer than distance b (viz. *Monocelis durhami*, *M. oculifera*, *M. anta*, *M. tabira* and *M. rupisrubrae*) only *Monocelis oculifera*, *M. anta* and *M. tabira* have a nearly globular copulatory organ smaller than $50\text{ }\mu\text{m}$. None of them, however, presents the peculiar arrangement of the bulb musculature present in the new species, with a 'collar', thicker than the rest of the muscular coating, surrounding the distalmost portion of the copulatory organ. Among the other differences present: *M. oculifera* is similar to the new species in all pore relations; however, it has fewer testes, a copulatory organ nearly half the size, and its bursa is not of the resorbiens type. *M. anta* has almost the same number of testes and the copulatory organ is in the same size range; the two species differ for pore relation a:b, approaching 1:1 in *M. anta*, and 3:1 in *M. nexilis*. Furthermore, *M. anta* has a larger bursa, consisting of more vacuoles, and a precerebral gut diverticulum. *M. tabira* is similar in bursa structure and has a copulatory organ comparable in size with *M. nexilis*. It has

however many fewer testes (2–8), a much shorter pharynx, pore relation $b:c$ about 1:1 (it is about 1:1.5 in *M. nexilis*). *M. tabira* has been described as without rhabdites (Marcus, 1950). Specimens from Puerto Rico (Caribbean), agreeing anatomically in any other respect with the original description of *M. tabira*, had dot-like rhabdites (Curini-Galletti, 1991), different from the new species. Furthermore, the Caribbean specimens had a karyotype with $n = 3$ (Curini-Galletti, 1991), while *M. nexilis* has $n = 2$.

The chromosome number of *M. nexilis* is not found in any other *Monocelis* species karyologically described so far. Since its genome length is average for the genus (Curini-Galletti, 1991; Martens and Curini-Galletti, 1987; this paper), the reduction from the chromosome number $n = 3$, plesiomorphic for the genus (Martens and Curini-Galletti, 1987), is most likely to be the result of a chromosome fusion.

Monocelis corallicola sp. nov.

(Figs 3, 6I)

Material examined

HOLOTYPE: Australia, Queensland, Heron Is., Shark Bay; intertidal in coarse sand with shell and coral fragments (October 1993), sagittally sectioned: G211664.

Paratypes: same data as holotype: G211665–8.

Other material. Four specimens observed alive; four studied karyologically. One specimen from Green Is., intertidal in coarse sand with shell and coral fragments (September 1993), observed alive and used for karyology.

Etymology

From Latin 'inhabitant of corals'. The name refers to the localities where the species has been found, both being coral cays on the Great Barrier Reef.

Description

Animals slender in shape, agile, about 1.2 mm long in sectioned material. With two clearly set pigmented eyespots lateral to the statocyst. Anterior end rounded, provided with oily drops. Posterior end rounded, with numerous short rod-shaped rhabdites and adhesive glands. Epithelium with insunk nuclei, ciliated all over except for the caudal tip. Cilia are longer ventrally (about $4\ \mu\text{m}$) than dorsally (about $3\ \mu\text{m}$). In the brain the central tissue (neuropile) is lined with a thin membrane and surrounded by numerous nuclei: anteriorly it abuts the statocyst. The short pharynx is situated in the second half of the body. The luminal epithelium is ciliated only in its distal half; the oesophagus is about one third of the length of the pharynx.

Male genital organs. Testes (4–5) are arranged in a median row in front of the pharynx. The copulatory organ is ovoid, dorso-ventrally elongated ($33\ \mu\text{m}$ long, $24\ \mu\text{m}$ wide). It consists of an ovoid seminal vesicle, lined with a nucleated epithelium, surrounded by a thick muscular coating (with inner circular and outer longitudinal muscles). The penis papilla is about 0.33 the length of the whole copulatory organ, and is acutely conical. The bulb is surrounded by prostatoid glands whose necks pierce the bulb walls. Internally, the distal portion of the bulb is coated by the secretion of the prostatoid glands, together with a glandular tissue with few nuclei. The male antrum is not ciliated; it opens to the outside via the male pore.

Female genital organs. Ovaries lie in front of the pharynx. Vitellaria stretch from

in front of the first testes to just in front of the copulatory organ. From the ovaries, the two oviducts extend caudally over the pharynx. Posterior to the pharynx, they fuse into the common female duct. In front of the copulatory organ, the female duct is connected to a few dorsal vacuoles with sperm, which constitute a small bursa of the resorbiens type. Ventrally to the bursa, the vaginal duct originates: it is short and straight, ciliated at least distally. Its most distal portion, close to the vaginal pore, is surrounded by circular muscles. Posterior to these structures, the female duct is large, lined with an irregular, high epithelium, surrounded by few weak circular muscles, and appears unusually large even in semi-squashed living specimens (Fig. 3 C). The

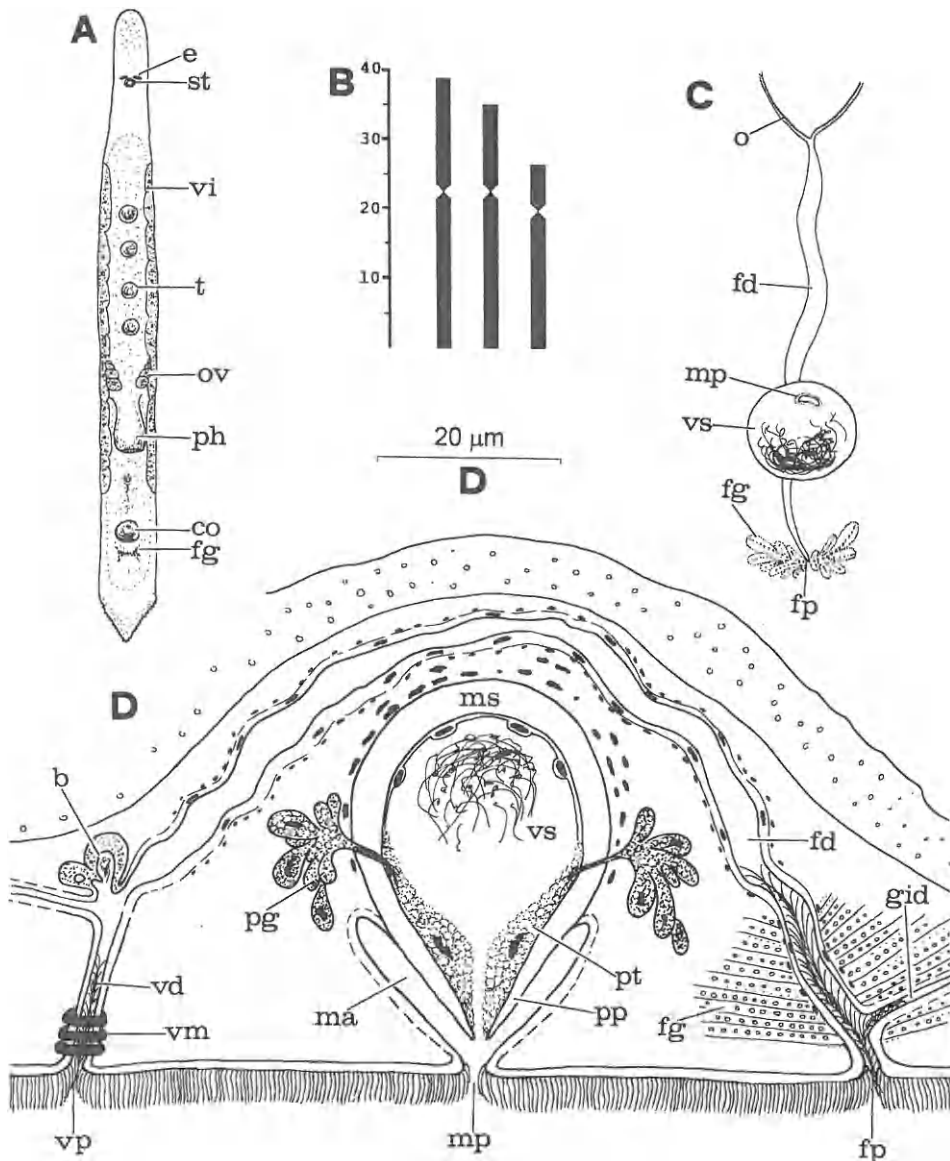


FIG. 3. *Monocelis corallicola* sp. nov.: (A) general organization of a live animal; (B) idiogram; (C) general organisation of the genital organs from live animals; (D) reconstruction of the genital organs from sagittal sections.

most distal part, posterior to the copulatory organ, is ciliated, and is connected to the gut lumen through a genito-intestinal duct. The female duct opens to the outside through the female pore, surrounded by very numerous female glands.

Pore ratio: $a \gg b \approx c$.

Karyology

Species has three chromosomes in its haploid set. Karyotype formula of specimens from the type locality: $11.3 \pm 0.6 \mu\text{m}$; 6; Chrom. 1: 38.90 ± 0.49 ; 41.86 ± 3.31 (m); Chrom. 2: 35.14 ± 0.66 ; 35.74 ± 0.97 (sm); Chrom. 3: 25.99 ± 0.21 ; 25.06 ± 2.29 (sm).

The specimen from Green Island had a nearly identical karyotype: $11.4 \pm 0.9 \mu\text{m}$; 5; Chrom. 1: 38.78 ± 0.87 ; 41.47 ± 2.65 (m); Chrom. 2: 34.20 ± 1.46 ; 34.56 ± 2.38 (sm); Chrom. 3: 27.03 ± 1.87 ; 23.39 ± 1.54 (st). Differences in nomenclature of Chrom. 3 (and hence in fundamental number) are due to its position close to the border between submetacentric and subtelocentric classes, and do not seem significant.

Remarks

The new species is uniquely characterized by features of the female genital system. The only other species with a distinctly swollen female duct, probably acting in some stages for sperm storage, is *M. pictocephala* Martens and Curini-Galletti, 1989, from Sulawesi. In this species, however, no genito-intestinal connection has been observed. Furthermore, it also lacks pigmented eyespots, has a characteristic pigment band in front of the statocyst, and the swelling of the female duct is more marked postpenially, thus forming a postpenial bursa (Martens and Curini-Galletti, 1989).

Among the *Monocelis* species with two eyespots and similar size of copulatory organ, only *M. oculifera* and *M. tabira* have fewer than 10 tests at maturity. In addition to the differences in structure of the female duct, both these species lack a genito-intestinal duct. Furthermore, *M. oculifera* has pore relation $a:b$ about 3.5:1, while it is about 2:1 in the new species. *Monocelis tabira* either lacks rhabdites (Marcus, 1950) or has tiny dot-like rhabdites (Curini-Galletti, 1991); *M. corallicola* has small rod-shaped rhabdites.

Monocelis heata sp. nov.

(Figs 4, 6 M)

Material examined

HOLOTYPE: Australia, Queensland, Heron Is., in front of the Research Station; lower intertidal in medium to coarse sand with shells fragments (October 1993); specimen studied alive and sagittally sectioned: G211669. PARATYPE: same data as holotype: G211670.

Other material. One specimen used for karyology.

Etymology

From Latin *beatus*: living in paradise. It refers both to the place where the animal occurs (the idyllic Heron Is.) and to Dr Beate Sopott-Ehlers, for her contribution to the knowledge of the Proseriata.

Description

Animals very slender, about 1.2 mm long (from sections). Without pigment or pigmented eyespots. Anterior end rounded, provided with oily droplets. In sections, the cephalic region in front of the statocyst appears provided with vacuolated polygonal cells (precerebral gut). In the brain the central tissue (neuropile) is lined with a thin membrane and surrounded by numerous nuclei; anteriorly it abuts the statocyst. Posterior end variable in shape in living organism, with elongate rhabdites (about 7–8 μ m) and adhesive glands. Epithelium ciliated all over the body

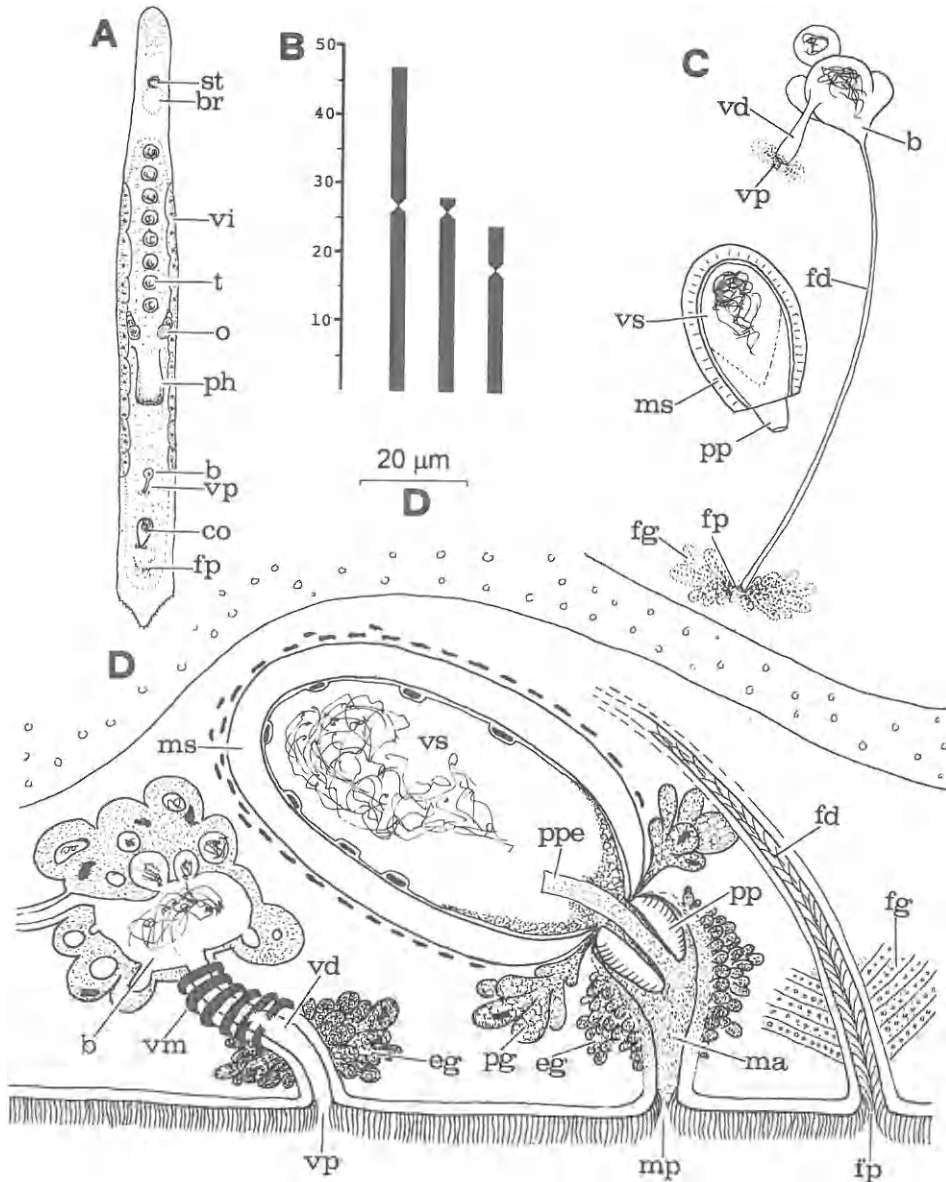


FIG. 4. *Monocelis beata* sp. nov.: (A) general organization of a live animal; (B) idiogram; (C) general organisation of the genital organs from live animals; (D) reconstruction of the genital organs from sagittal sections.

except for the caudal tip. Cilia are longer ventrally (about $4\text{ }\mu\text{m}$) than dorsally (about $2.5\text{ }\mu\text{m}$). Few, large (up to $15\text{ }\mu\text{m}$) glands are present caudally. The pharynx is elongate and situated in the second half of the body. Its cilia (absent at its most distal tip and in its inner half) are about $1.5\text{ }\mu\text{m}$ in length. The inner proximal part (oesophagous) is lined with a high epithelium. Numerous pharyngeal glands are present.

Male genital organs. About 8 testes in one medium row are present in front of the pharynx. The copulatory organ is markedly ovoid ($74\text{ }\mu\text{m}$ long, $37\text{ }\mu\text{m}$ wide). It is obliquely elongated along an antero-posterior axis, and backwardly oriented. It consists of an ovoid seminal vesicle, lined with a nucleated epithelium, surrounded by a very thick muscular coating (about $5\text{ }\mu\text{m}$ thick), easily seen even in living animals. It has inner circular and outer longitudinal muscles. The penis papilla has a muscular portion, about 0.16 the length of the whole copulatory organ, conical, surrounded by a thick muscular layer, and protruding into the male antrum. The main part of the unciliated ejaculatory duct has very thin walls, is inverted into the bulb, and forms a proximal penis. The distal portion of the bulb is surrounded by prostatoid glands, whose nuclei lie outside the copulatory organ, and whose cell bodies pierce the wall of the bulb at the base of the penis. Their secretion thinly coats the distal inner part of the bulb. The male antrum is comparatively long; its walls are entirely surrounded by extremely numerous, tiny eosinophilous glands. Their secretion filled up the male antrum to a degree that it was impossible to ascertain whether it is ciliated or not in the specimens available. The male antrum opens to the exterior via the male pore.

Female genital organs. Ovaries lie just in front of the pharynx. Vitellaria stretch from the level of the first testes to the level of the bursa. Posterior to the pharynx, the two oviducts fuse into the common female duct. Caudally, the duct widens to form a bursa of the resorbiens type. It consists of a large number of vacuoles, many of which contain sperm, around a central cavity, filled with sperm. This bursa is connected to the outside through a rather long vaginal duct, whose unciliated epithelium, in its proximal part, is surrounded by numerous circular muscle cells. Distally, muscle cells are absent, and the duct is surrounded by numerous eosinophilous glands, with very dense granular content. The portion of the common female duct caudal to the bursa runs posteriorly over the male organ and opens caudally through the female pore. At least the most distal portion of the duct is ciliated. Around the female pore, female glands are present.

Pore ratio: $a > b > c$.

Karyology

Species has three chromosomes in its haploid set. Karyotype formula: $9.2 \pm 0.5\text{ }\mu\text{m}$; 4; Chrom. 1: 47.25 ± 1.37 ; 43.05 ± 1.27 (m); Chrom. 2: 28.35 ± 0.06 ; 4.3 ± 0.70 (t); Chrom. 3: 24.41 ± 1.45 ; 23.82 ± 3.22 (st).

Remarks

In addition to the new species described above, the only *Monocelis* species with a copulatory organ distinctly elongated, approaching or even surpassing a ratio length-width 2:1, are *M. galapagoensis* Ax and Ax, 1977 from Galapagos, and *M. hopkinsi* Karling, 1966, from California. In both these species, however, the copulatory organ is oriented dorso-ventrally, and thus perpendicular to the ventral surface (see Ax and Ax, 1977, fig. E, p. 8; Karling, 1966, fig. 42, p. 511). *Monocelis beata*, on the contrary,

has a nearly horizontal, backwardly oriented copulatory organ, with a markedly more muscular coating, and with a well developed, muscular portion of the penis, protruding into the male antrum. None of the above species has a precerebral gut. Furthermore, in *M. galapagoensis* granular secretions are lacking within the copulatory bulb (which is only 50 μm in length), and there is no vagina. *Monocelis hopkinsi*, in addition to the above quoted differences, has about 30 testes, a larger copulatory organ, which is up to 90 μm in diameter, not ovoid in shape, having a rather sharply pointed proximal part. Furthermore, in *M. hopkinsi* pore relation a : b is about 1 : 1.5, while it is 1.5 : 1 in *M. beata*.

Similarly to the new species, *M. anta* has a precerebral gut diverticulum. It has, however, about 30 testes, a pyriform copulatory organ, vertically oriented, with a comparatively small, globular vesicula seminalis. Furthermore, this species has two clearly set pigmented eyespots, lateral to the statocyst, which are absent in *M. beata*.

Monocelis macrobulbus sp. nov.

(Figs 5, 6 L)

Material examined

HOLOTYPE. Australia, Queensland, South Mission Beach, medium to high intertidal, medium to coarse sand (September 1993), sagittally sectioned: G211671.

Other material. Same data as holotype, two specimens studied alive, two specimens used for karyology.

Etymology

From Greek *macro*s (large) and Latin *bulbus* (bulb); the name, used on apposition, refers to the remarkably large relative size of the copulatory bulb of the species.

Description

Animals slender in shape, about 1.5 mm (from sections). Without pigment or pigmented eyespots. Anterior end rounded, provided with oily droplets. Posterior end elongate with adhesive glands. Epithelium ciliated except for the caudal tip. It is provided all over the body with elongate rhabdites, about 5.5 μm long. Cilia short, longer ventrally (about 2.3 μm) than dorsally (about 2 μm). Few large glands are present caudally. The pharynx is elongate and situated in the second half of the body. The luminal part is ciliated for 0.5 of its length, and has a large, conspicuous oesophageal portion, with high nucleated epithelium.

Male genital organs. About 30 testes are arranged in two median rows in front of the pharynx. The copulatory organ is large (about 90 μm in total length, up to 27 μm wide), ovoid, elongated along an antero-posterior axis, backwardly oriented, with its most distal tip nearly perpendicular to the longitudinal axis. It consists of an ovoid seminal vesicle, lined with a nucleated epithelium, surrounded by muscular layers of inner circular and outer longitudinal muscles. Distally, the vesicle bends towards the ventral surface. This portion is almost filled by the granular secretion of the prostatoid glands whose cell bodies lie outside the copulatory organ. The prostatoid secretion fills the area so massively that only a small lumen connects the seminal vesicle to the most distal part of the bulb, which is surrounded by a thin muscular layer. Parts of the ejaculatory duct, with very thin walls, is inverted into this area

(proximal penis). It is short and apparently ciliated. It is connected by threads to the inner walls of the bulb (contracted during inversion?). The male antrum is small, surrounded by numerous tiny eosinophilous glands, whose secretion fills the antrum itself, thus obscuring observation. However, the antrum seems to be ciliated. It opens to the outside via the male pore.

Female genital organs. Ovaries lie in front of the pharynx. Vitellaria stretch from the first testes to the level of the copulatory organ. A small bursa of the resorbiens type, lined by a vacuolar tissue, is present ventrally to the seminal vesicle, and hidden by the latter in living specimens. It extends ventrally into a tube-like structure. Though a vaginal pore has not been clearly seen in the specimen sectioned, we interpret this structure as a vaginal duct, and we assume that a vagina is likely to be present in the species. In the proximal portion of the vaginal duct, numerous tiny

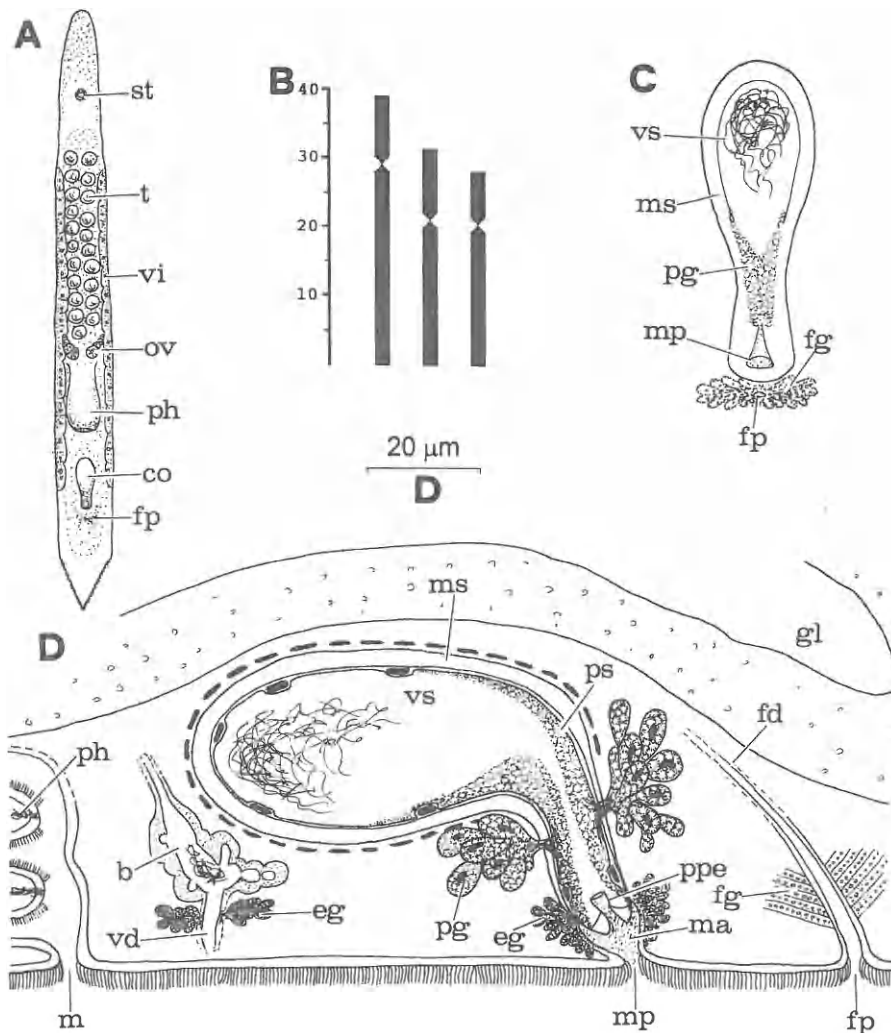


FIG. 5. *Monocelis macrobulbus* sp. nov.: (A) general organization of a live animal; (B) idiogram; (C) general organisation of the genital organs from live animals; (D) reconstruction of the genital organs from sagittal sections.

eosinophilous glands are present. The female duct opens caudally to the male copulatory organ, with the female pore, surrounded by female glands.

Pore ratio: $b > c > a$.

Karyology

Species has three chromosomes in its haploid set. Karyotype formula: $9.2 \pm 0.6 \mu\text{m}$; 6; Chrom. 1: 40.07 ± 1.80 ; 26.03 ± 4.60 (sm); Chrom. 2: 31.73 ± 2.15 ; 31.89 ± 4.45 (sm); Chrom. 3: 28.19 ± 1.48 ; 26.78 ± 5.30 (sm).

Remarks

The new species shares several similarities with *M. beata*. Both species, in fact, lack pigmented eyespots, have an elongated, backwardly oriented copulatory organ, inverted proximal penis, and numerous tiny eosinophilous glands around the male pore. Both have the vaginal duct surrounded by eosinophilous glands. However, *M. macrobulbus* is immediately recognizable by the much thinner muscular layer surrounding the copulatory organ and absence of a muscular portion of the penis protruding into the male antrum. Furthermore, *M. macrobulbus* is a larger species, with larger copulatory organ and more testes. Its karyotype is also different.

Monocelis macrobulbus is similarly distinct from all other *Monocelis* species with a narrowly elongate copulatory bulb. *Monocelis galapagoensis*, in fact, has a vertical copulatory organ, nearly half the size of that of the new species, without granular secretion within the bulb. It is without a vagina or vaginal duct. *Monocelis hopkinsi* has a copulatory organ similar in length, but less elongated, not ovoid in shape, and dorso-ventrally oriented. Furthermore, in this species distance c is longer, about double distance a . It is the opposite in the new species. Eosinophilous glands ventral to the bursa have been found in none of the above species.

Monocelis sp. A

(Fig. 6 N)

Material examined

Australia, Tasmania, Eagle Hawk Neck, beach on the protected side, intertidal in medium sand (October 1993). One specimen, immature in the female line, observed alive and used for karyology.

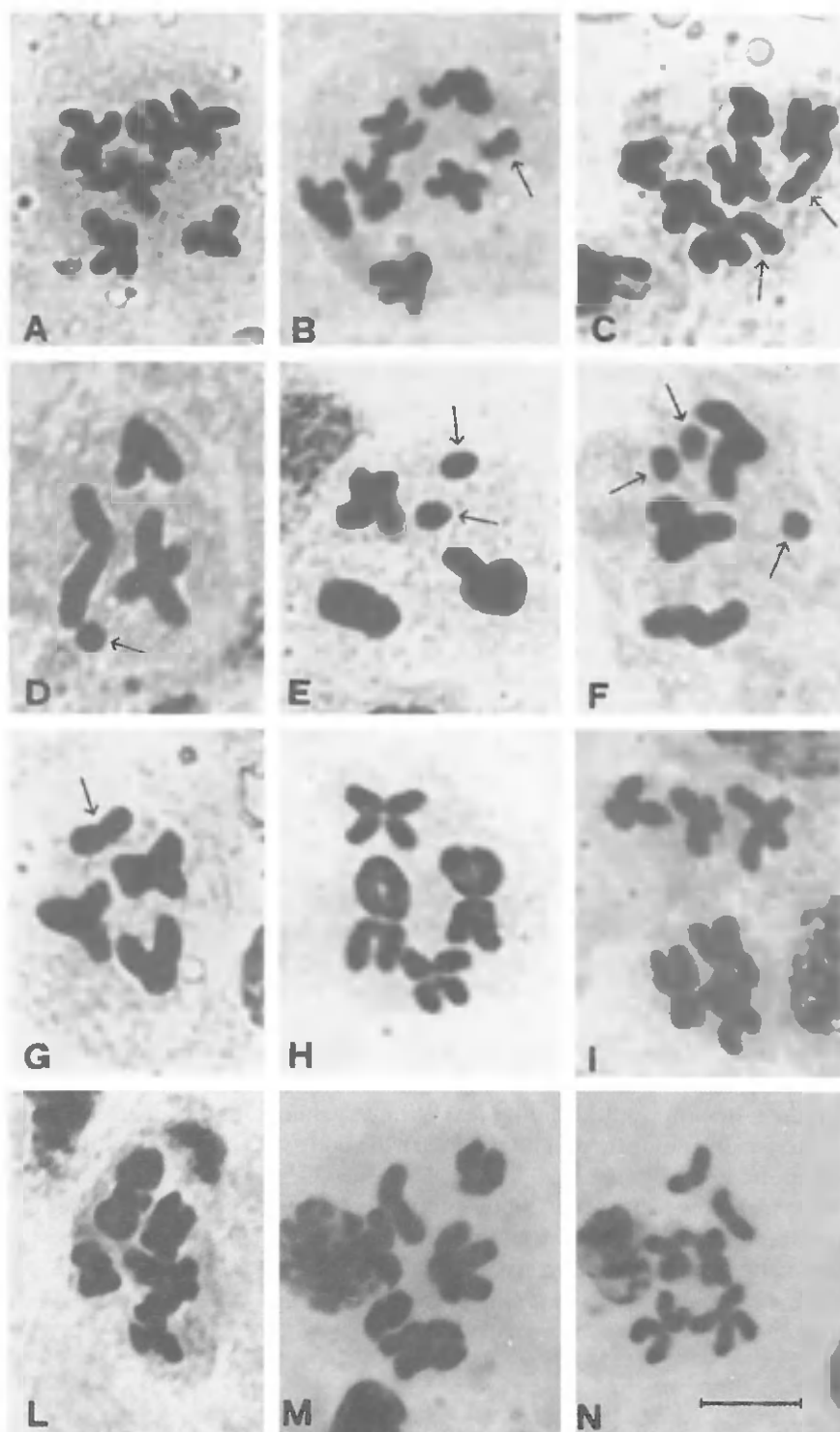
Description

Large (up to 4 mm in semi-squashed conditions), very stocky animal. With two pigmented eyespots lateral to the statocyst, and some faint, irregular black lines behind the statocyst, over the brain area. With very numerous oily droplets in front of the statocyst, and elongate rhabdites all over the body. Pharynx comparatively large, in the second half of the body.

With very numerous testes (above 100), and a very large spherical copulatory organ. Of the female genital system, only the vitellaria could be clearly observed. They stretch from the level of the first testes to just in front of the copulatory organ. A faint hyaline area, presumably corresponding to an early stage of development of ovaries, was present in front of the pharynx.

Karyology

Species has three chromosomes in its haploid set. Karyotype formula:



$9.5 \pm 1.0 \mu\text{m}$; 5; Chrom. 1: 42.55 ± 0.84 ; 45.97 ± 2.46 (m); Chrom. 2: 34.56 ± 1.19 ; 45.68 ± 2.06 (m); Chrom. 3: 22.87 ± 1.44 ; 12.23 ± 1.99 (t).

Remarks

Despite extensive sampling in the area where the only specimen was found, the habitat of this large species remained elusive. Though obviously different for karyotype and pigmentation from any known species, the material is insufficient for a species description.

Discussion

The genus *Monocelis* appears to be particularly rich in eastern Australia, where about one fourth of the presently known species of the genus are present. One of the most obvious features of the Australian *Monocelis* fauna is the prevalence of species with two clearly set pigmented eyespots, lateral to the statocyst. In contrast, within the genus as a whole, species with distinct pigmented eyespots constitute a small minority. Most of them come from tropical areas or from the southern hemisphere. Ax and Ax (1977) proposed a close phylogenetic relationship for the subset of species with two pigmented eyespots and with a vagina. All of the Australian species with pigmented eyespots will thus be a part of this monophylum. Curini-Galletti (1991) suggested that the large genome size of *M. tabira*, contrasting with the very small genome size of the European *Monocelis* species (Martens and Curini-Galletti, 1987; Martens *et al.*, 1989a) could be an apomorphic feature for that species. All the species with two pigmented eyespots karyologically known (Curini-Galletti, 1991; this paper; unpublished data) have indeed large karyotypes (and hence large genome size, see Martens *et al.*, 1989a). However, it is doubtful whether these characters are real synapomorphies among the above species. Similar very large karyotypes are in fact found in the genus *Pseudomonocelis* Meixner, 1943 (Martens *et al.*, 1989a), and in other genera with a copulatory organ of the simplex type (*Minona*, *Peraclistus*) (Curini-Galletti, 1991; unpublished data). Two distinct pigmented eyespots are found as well in *Pseudomonocelis* and *Minona* species (Karling, 1978; Schockaert and Martens, 1987; Sopott-Ehlers, 1993). Both pigmented eyespots and large karyotype are, at the present level of knowledge, more parsimoniously interpreted as plesiomorphic features for the genus *Monocelis*. Presence or absence of a vagina appears to be a variable feature even in recognized sister species (see, for example, the sister pair *M. galapagoensis*–*M. hopkinsi*) (Ax and Ax, 1977), and its phylogenetic weight is dubious. At present, therefore, no phylogenetic relationship can be proposed for the Australian species with pigmented eyespots.

Monocelis beata and *M. macrobulbus* share several features: both species have an extremely elongate, backwardly oriented copulatory hulf, nearly horizontal, rich in prostatic secretion and with numerous eosinophilous glands around the male pore and the vaginal duct. This structure of the copulatory bulb is unique in the genus *Monocelis*, and is not found in *Pseudomonocelis* (Schockaert and Martens, 1987). Only two of the numerous species of the genus *Minona* (*M. dolichovesicula* Tajika,

FIG. 6. A–G. *Monocelis rupisrubrae*. (A–C) spermatogonial mitoses; (D–G) primary spermatocytes. Arrows indicate supernumerary chromosome(s) (B, C), univalent(s) (D–F) and bivalent (G) formed by supernumerary chromosomes; (H–N) spermatogonial mitoses of *Monocelis nexilis* (H); *Monocelis corallicola* (I); *Monocelis macrobulbus* (L); *Monocelis beata* (M); *Monocelis* sp. A (N). Scale bar: $5 \mu\text{m}$.

1982 and *M. trigonopora* Ax, 1956) have a somewhat comparable shape of the copulatory bulb, though the eosinophilous glands are lacking. While a thorough phylogenetic analysis of all those genera is missing, it seems parsimonious to consider the structure of the copulatory bulb and the presence of eosinophilous glands as a synapomorphy for *M. beata* and *M. macrobulbus*; and the similarities shared between the two Australian species and the *Minona* species as homoplasious features.

The karyotype of both *M. macrobulbus* and *M. beata* is peculiar due to the relative lengths of chromosomes. Chrom. 1, in fact, is distinctly longer than Chroms 2 and 3, which have comparable length. In the basic set of the genus *Monocelis* (Martens and Curini-Galletti, 1987), the chromosomes have a slight difference in length (see, for example, the karyotype of *M. rupisrubrae*, this paper). The karyotype found in the two species above is probably due to a translocation involving Chroms 1 and 2 of the basic set; it is a synapomorphy for the two species.

Two further species of the genus *Monocelis* (*M. galapagoensis* and *M. hopkinsi*) have a distinctly elongate, vertical copulatory bulb. According to Ax and Ax (1977) they are sister species. A very elongate copulatory bulb could be considered as a synapomorphy for the two species pairs *M. galapagoensis-hopkinsi* and *M. macrobulbus-beata*, with a further evolution (the longitudinal orientation) present in the Australian species, probably linked to the proportionally larger size of their copulatory organs. The four species have a transPacific distribution (NE Australia, Galapagos, California) (Sluys (1994) for possible interpretations of similar distributions in Platyhelminthes).

The distribution of the Australian *Monocelis* species appears restricted to one or the other of the generally recognized biogeographical areas of eastern Australia: (i) Northern Australian Zone (*M. beata*; *M. corallicola*; *M. macrobulbus*); (ii) 'overlap zone' (southern Queensland—northern New South Wales) (*M. nexilis*; *M. rupisrubrae*); (iii) Southern Australian Region (*Monocelis* sp. A). Within the Northern Australian Zone, species have either a mainland distribution (*M. macrobulbus*) or occur on the Great Barrier Reef (*M. beata*, *M. corallicola*; the latter at least with a wide latitudinal range).

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