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Patricia Kott ^a

^a Queensland Museum , South Brisbane, Australia

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Novel Australian Polyzoinae (Styelidae, Tunicata)

PATRICIA KOTT

Queensland Museum, South Brisbane, Australia

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Abstract

Species in the colonial subfamily Polyzoinae demonstrate a range of colonial organisations. Colony form appears to be significant at species level but not to have a phylogenetic significance at genus level, species in both speciose genera *Polyandrocarpa* and *Stolonica* having colonies either of separate zooids joined by basal stolons or they have completely embedded zooids. *Polyandrocarpa* and *Oculinaria* have characters that indicate a close affinity with solitary styelinid genera *Polycarpa* and *Cnemidocarpa*, respectively, and suggest that the subfamily is polyphyletic. *Stolonica* and other genera in the Polyzoinae, in which zooids and body organs are small and simplified, also appear to be polyphyletic assemblages of taxa but their relationships are masked by parallel evolution and convergence associated with replication and colony development. Previously overlooked in the siphonal linings of *Oculinaria australis* are overlapping spines possibly analagous with the rounded scales (see Kott 1985) in siphons of *Stolonica diptycha* (Hartmeyer, 1919). Similar armature appears to be significant at species level in Pyuridae and occasionally Styelidae and it may be further evidence of polyphyly in Polyzoinae. One of the seven species reported (*Stolonica vermiculata* sp. nov. from Lord Howe I.) is new; one (*Oculinaria australis* from a range of locations around the southern half of the Australian continent) is recorded often; and five (*Polyandrocarpa colemani* known only from the Queensland–New South Wales border, *P. colligata*, *Stolonica styeliformis* and *S. dupplicata* all from the tropical western Pacific and *Botryllocarpa elongata* from Tasmania) are seldom recorded.

Keywords: Botryllocarpa, coloniality, convergence, Oculinaria, Polyandrocarpa, polyphyletic, simplification, siphonal armature, Stolonica

Introduction

The family Polyzoinae is diverse, and probably polyphyletic, at least two genera, namely *Polyandrocarpa* and *Oculinaria*, containing species that share conspicuous characters with solitary styelinid genera *Polycarpa* and *Cnemidocarpa*, respectively (Kott 1985; Brunetti and Mastrototaro 2004). The species discussed below add evidence for this polyphyly.

The seven species discussed in this paper represent successive stages in the polyphyletic, often parallel, evolution of coloniality in the Styelidae. *Polyandrocarpa colemani* Kott, 1992 and *P. colligata* Sluiter, 1913 have similar body organs to those in the larger solitary

Correspondence: Patricia Kott, Queensland Museum, PO Box 3300, South Brisbane, Qld 4101, Australia. Email: patricia.mather@qm.qld.gov.au

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individuals of the genus *Polycarpa*, although both species are colonial and their relatively small replicated zooids are entirely embedded in colonial test. Also, there are species of *Polyandrocarpa* with similar zooids joined by basal stolons (rather than being embedded) although this difference in colony form does not appear to reflect significant phylogenetic differences at genus level. *Oculinaria australis*, which also has colonies with embedded zooids, has gonads that resemble those of the larger solitary individuals of the genus *Cnemidocarpa*, although they are present only on the right side of the body (gonads are characteristically on both sides of the body in the majority of solitary stolidobranch ascidians).

The other species discussed below, *Stolonica duplopicata* Sluiter, 1913, *S. styeliformis* Van Name, 1918, *S. vermiculata* sp. nov., and *Botryllocarpa elongata* Kott, 1990 appear to be a greater evolutionary distance from solitary ancestors than *Polyandrocarpa* and *Oculinaria*. All are from genera of the Polyzoinae with particularly small albeit separately opening zooids, small dioecious gonads (sometimes ephemeral) and reduced branchial sacs. Their true phylogeny is obscured by size reduction and convergence associated with colony development and replication. Generally in *Stolonica* spp., the zooids are conspicuously small, usually connected to one another by stolons (as *S. duplopicata* and *S. styeliformis*), with fewer than four branchial folds and numerous male, female and sometimes hermaphrodite gonads. They are significantly different from genera in the Styelinae, even though the ovaries are small sacs, more like *Polycarpa* than *Cnemidocarpa*, with only three or four eggs, and the testes each contain only a single follicle. Unlike most of the species in the genus, zooids of the new species *Stolonica vermiculata* are entirely embedded in the test, *Stolonica carnosa* Millar, 1963 from southern Australia being the only other species of the 12 known from Australian waters to have a similar habit. As in *Polyandrocarpa*, this aspect of colonial organisation does not appear to be of phylogenetic significance at genus level.

Botryllocarpa (see *B. elongata*) and *Chorizocarpa* also have small, entirely embedded zooids that retain their separate openings to the exterior, flat branchial sacs without any folds and the greatest reductions in zooid size and simplification in the Polyzoinae, having only three internal longitudinal vessels, and a single sex gonad on each side of the body. Similar small, embedded zooids occur in the Botryllinae in which complex common cloacal systems are developed as well. These common cloacal systems are analogous with the colonies and cloacal systems in certain Holozoidae, Polyclinidae and Didemnidae in the Aplousobranchia (see Kott 1985). However, *Botryllocarpa* spp., *Chorizocarpa*, and species of Botryllinae have an unusual gastric caecum which arises from the suture line along the lateral or postero-lateral margin of the stomach, crosses the stomach at right angles to its longitudinal axis and terminates in a round bulb that often bends anteriorly into the pole of the gut loop, and may indeed indicate a phylogenetic relationship between these taxa.

The novel (for the subfamily Polyzoinae) siphonal armature found in *Oculinaria australis* Gray, 1868 resembles that often described in species of the family Pyuridae and some Styelidae. Although the presence of these spines is regarded as a reliable character at species level in both families, it does not necessarily indicate a direct relationship between them and cannot be regarded as a reliable indicator of phylogeny at that level. In the Polyzoinae siphonal armature has previously been reported in *Stolonica diptycha* (Hartmeyer, 1919), which has rounded scales rather than spines (Kott 1985). The occasional presence of siphonal armature can be regarded as evidence of a polyphyletic origin of Polyzoinae.

Although the traditional basis for the separation of Polyzoinae from the solitary Styelinae is their colonial habit, this does not appear to reflect their true phylogeny. Replication in the Styelidae (which is relatively simple budding involving the pallial or stolonial ectoderm) has

been recorded in species closely related to solitary forms (see Kott 1995). It probably has been selected for on more than one occasion in different taxa, sometimes from ectodermal vessels in the main body of the test and sometimes from vessels in the root like outgrowths at the base of solitary individuals. Subsequent progressive size reduction and simplification of the zooids as a consequence of replication and developing colonial organisation appears to reflect parallel and convergent evolution which has masked the true phylogeny of these taxa.

Nevertheless, although there is strong evidence of the sister-group relationships between *Polycarpa* and *Polyandrocarpa*, *Cnemidocarpa* and *Oculinaria* and *Botryllocarpa*, *Chorizocarpa* and Botryllinae, intra-generic relationships of *Stolonica* and other genera of the Polyzoinae remain obscure and there is insufficient available data to resolve and clearly establish their polyphyletic status.

Of the species discussed here, *Oculinaria australis* is the only one known from a number of records around the southern half of the continent. Nevertheless, a number of its significant characters were not reported in previous descriptions—possibly because its characteristic external appearance resulted in ready identification and the sandy specimens were only superficially examined. *Botryllocarpa elongata* is reported (from Tasmania) for only the second time, *Polyandrocarpa colligata*, previously known from Aru I. and the Java Sea, is recorded from Australia for only the first time and, despite the very large size of its colonies, *P. colemani* has been reported on only three previous occasions. One species, *Stolonica vermiculata* sp. nov. (from Lord Howe I.), is newly described, a large colony of the known tropical species *S. duploplicata* Sluiter, 1913 is newly recorded, and *S. styeliformis* Van Name, 1918 is recorded from the Gulf of Carpentaria for the second time.

Taxonomy

Polyandrocarpa colemani Kott, 1992

(Figures 1A, 5A)

Polyandrocarpa colemani Kott 1992, p 641.

Distribution

New records: Queensland (Palm Beach reef, QM G308755, G321000). Previously recorded (see Kott 1992): New South Wales (Ararwarra, Coffs Harbour, Cook I.). The species is known from 9–12 m in a restricted geographic area on the northern New South Wales coast and just north and south of the Queensland–New South Wales border.

Description

Colonies are invariably large (to 1 m maximum dimension), tough and leathery with an even surface, the zooids completely embedded in the surface layer of test and the independently opening round incurrent and excurrent apertures project only slightly from the surface. Kott (1992) noted that colonies are found along the top of ridges where they are exposed to maximum current flows. Newly recorded colonies are vertical lamellae, to 1 m high but only about 5–10 cm thick, with zooids opening all around the surface. They are fixed firmly to rocky substrates but although the test is particularly tough it is probable that the edge of the colony is presented to the prevailing current rather than their wider surfaces. The internal test in the centre of the colony has criss-crossing test vessels from the zooids.

Figure 1. (A) *Polyandrocarpa colemani* (QM G308755): left and right pallial wall showing gut and gonads. (B, C) *Polyandrocarpa colligata* (QM G308758): (B) colony surface; (C) gut loop. (D–H) *Oculinaria australis* (SAM E3267): (D) portion of colony; (E) inner pallial body wall on right showing gonads; (F) inner pallial body wall on left showing gut and gonads; (G, H) siphonal spines. In (G), the open base of the spine in the centre of the light micrograph is showing; in all the other spines, only the hollow centres of the pointed tips are in focus. Scale bars: 1.0 mm (A); 2.0 mm (B, D–F); 0.2 mm (C); 0.05 mm (G, H).

Zooids are crowded and parallel to one another. They are narrow, to 1.5 cm long, and difficult to remove from the test. The body wall is particularly muscular with almost continuous circular bands externally around a layer of internal longitudinal muscles. The body wall lining the atrial cavity is crowded with vesicles. The branchial aperture is anterior on a short siphon and the atrial siphon is a similar length and projects from the mid-dorsal surface. In living colonies the zooids presumably lie at an angle to the surface. The dorsal tubercle has a transverse or curved slit. The endostyle in these zooids is almost the whole length of the branchial sac and the four branchial folds on each side also are straight and extend the full length of the branchial sac. Branchial folds have up to eight internal longitudinal vessels per fold and seldom more than one between. The gut forms a short, curved loop in the posterior third of the body. The oesophagus is moderately long and narrow and the long stomach, two-thirds of the length of the proximal limb of the gut loop, with 18 internal longitudinal folds, gradually increases in diameter to the distal end where it narrows abruptly to the intestine. The intestine curves into the pole of the loop and the descending limb curves postero-dorsally to form the secondary curve of the gut loop before

turning anteriorly into the vertical rectum. A flat-topped endocarp is in the gut loop between the stomach and descending limb of the intestine. Short teardrop-shaped polycarps with five to eight pairs of male follicles beneath the ovarian sac are in one or sometimes two overlapping rows of up to six per row along each side of the body with their relatively long ducts directed toward the atrial aperture.

Remarks

Although there is some variation in the form of the colonies, they always are tough with a smooth surface and crowded zooids. Even in situ photographs do not show a great difference in the orientation of the apertures of this species, which must be especially dependent on prevailing external currents to separate the incurrent and expelled ciliary streams of water.

These colonies are unusually large for separately opening stolidobranch species in which there is no internal common cloacal cavity in which the positive water pressure maintains the turgidity of the colony. In the present case the strength of the test appears to constitute the main support for the large colonies. The species is also unusual in that the majority of *Polyandrocarpa* species do not have completely embedded zooids. *Polyandrocarpa colligata* Sluiter, 1913 from the Aru I. does have completely embedded zooids although it has an encrusting colony rather than the massive one of the present species, a vertical rather than a horizontal slit on the dorsal tubercle, small endocarps on the body wall rather than a single large flat-topped one in the gut loop, a smooth-rimmed anus and a shorter stomach than the present species (see below).

The very restricted geographic range is not often encountered in the Ascidiacea, especially in view of the large conspicuous colonies which are unlikely to be overlooked by scuba divers.

Certain *Polycarpa* spp. contain crowded vesicles as in the present species (see *P. pedunculata*: Kott, 1985). However, *Polycarpa* is distinguished from the present genus by its solitary habit.

Polyandrocarpa colligata Sluiter, 1913

(Figure 1B, C)

Polyandrocarpa colligata Sluiter 1913, p 68.

Polyandrocarpa robusta Sluiter 1915, p 6; 1919, Taf. 1.

Distribution

New record: Queensland (Great Barrier Reef Seabed Biodiversity Survey, 16.705°S, 146.125°E, 33.9 m, QM G308758). Previously recorded: Aru I. and the Java Sea (Sluiter 1913, 1915).

Description

The specimen is a tough, encrusting colony with small dorso-ventrally flattened zooids completely embedded in the test. The sessile apertures of each zooid open separately to the exterior. The body wall contains crowded vesicles forming a foamy layer lining the atrial cavity while the outer muscular layer of the body wall is thin and delicate. A vertical, sometimes sinuous, slit is on the dorsal tubercle. The branchial sac has four folds on each

side with the internal longitudinal vessels arranged according to the following formula: E0(4)1(8)1(2)1(6)0DL. The gut forms an open and relatively short loop with the rectum turned anteriorly to form an angle with it. The pear-shaped stomach, with about 12 longitudinal folds and a short curved caecum, is in the middle third of the proximal limb of the gut loop. The outer curve of the gastric caecum is joined to the descending limb of the gut loop by a short ligament. A row of six to eight elongate polycarps is along each side of the mid-ventral line. Each polycarp consists of a paired row of male follicles (up to 18 in each row) beneath the ovarian tube. A few small endocarps are scattered on each side of the body wall.

Remarks

Like the present species, the subtropical *P. colemani* has embedded zooids and a foamy layer of vesicles in the body wall and closely resembles the present species. *Polyandrocarpa colemani* is distinguished from the present one by its massive colony with a network of vessels in the internal or basal test, a horizontal slit on the dorsal tubercle, a large flat-topped endocarp in the gut loop, longer stomach occupying at least three-quarters of the proximal limb of the gut loop and a thicker layer of muscles in the body wall. In the present species the gonads are in a single series along each side of the mid-ventral line, while in *P. colemani* the polycarps are in one or two rows on each side at varying distances from the mid-ventral line to a single row along each side of the atrial aperture.

Oculinaria australis Gray, 1868

(Figures 1D–H, 5B)

Oculinaria australis Gray 1868, p 564; Kott 1985, p 226 and synonymy.

Distribution

New records: Western Australia (Warnboro); South Australia (Kangaroo I., SAM E3267); Tasmania (One Tree Point, QM G308760); New South Wales (Warren Head-Ulladulla, Sydney Harbour QM G304560). Previously reported (see Kott 1985): Western Australia (Dongara, Wonerup, Cockburn Sound, Albany); South Australia (Great Australian Bight, Wright I., West I.); Tasmania (Stanley); Victoria (Rams Head, off Lakes Entrance, Port Phillip Bay); New South Wales (Port Jackson). Records of the species indicate a temperate species with a continuous range around the southern half of the continent.

Description

In situ photographs of the newly recorded specimen show it to have pink apertures showing through the sand. In preservative, it has a characteristic appearance, with the lower half of the zooids completely embedded in a solid basal mat of sandy common test and the anterior half of each zooid free and covered with thin, brittle, sand-impregnated test. The terminal free end of each zooid is more or less flattened, circular, with a small central four-lobed branchial aperture and is surrounded by a rounded marginal fold. The atrial aperture is a similar four-lobed aperture on the dorsal side of the free part of the zooid, behind the marginal fold that surrounds the flat anterior surface. Both apertures, especially the atrial one, are obscured by the sand embedded in the colony. A slight iridescence can be detected

in the test around the apertures and lining the short siphons. This iridescence is caused by minute overlapping siphonal spines, their points directed toward the opening of the siphon. They have a slightly sinuous, curved profile, the pointed tip curving out and the posterior end of the base curving in. Near the base of the siphon the spines have a flattened, frayed posterior end and the base of the spine is completely open. Further up the siphon each side of the posterior end of the spine is closed in, meeting the opposite side in the midline and leaving only a small circular opening about halfway along the base, beneath the hollow terminal pointed projecting part of the spine. The spines are about 0.136 mm from the posterior end of the base to the terminal tip of the spine.

The body wall is delicate, with thin muscle bands radiating a short distance down the body, which is closely attached to the test. Crowded simple branchial tentacles are at the base of the branchial siphon. The duct of the neural gland has a simple opening on the dorsal tubercle. Four deeply curved branchial folds are in the branchial sac and the branchial formula is: E8(12)7(14)6(12)3(12)1DL. There are 8–10 stigmata per mesh. The gut, attached only very loosely to the body wall by few ligaments, forms a simple open loop diagonally across the posterior end of the left side of the body. The oesophagus is narrow and opens abruptly into the broad cardiac end of a pear-shaped stomach with about 28 internal folds. Gonads are not present on the left side of the body, but on the right up to seven long narrow straight ovarian tubes converge from around the ventral border toward the atrial aperture, which is about halfway down the dorsal surface in a concavity behind the bulge where the body forms a rim associated with the anterior marginal fold of the test. The long, narrow ovarian tubes have two rows of about 20 crowded male follicles per row beneath them and occasionally extending around their sides. Vasa efferentia extend around the sides of the ovary to join the vas deferens which runs along the centre of its mesial surface, opening at the base of the short oviduct.

Remarks

The siphonal armature and the position of the atrial aperture outside the anterior marginal fold are two of the most striking characteristics of this species but both were previously overlooked. Their presence has been confirmed in re-examined specimens from Victoria (QM G9592 and G11857).

Pyura tasmanensis Kott, 1985 has siphonal spines that resemble those in the present species both in size and shape, although their base is more closed in than those in the present species and they have a flange developed. *Ctenyura tortuosa* Kott, 1985 has similar but shorter spines and the spines in some *Microcosmus* species are also similar although their points are better developed and at a greater angle to the base. Certain species of the Styelinae also have siphonal armature but it is more often scales than spines. Scales are present in *Styela* spp. and a number of *Cnemidocarpa* spp. (see Kott 1985) although *Cnemidocarpa intestinata* Kott, 1985 and *Polycarpa olitoria* (Sluiter, 1890) have spines. The only other species of Polyzoinae (besides the present one) known to have siphonal armature is *Stolonica diptycha* (Hartmeyer, 1919) although it has scales rather than spines (see Kott 1985). It appears that no higher taxon level phylogenetic significance can be attached to either the form or the presence of siphonal armature.

Gonads of the present species suggest an affinity with *Cnemidocarpa* rather than most known species of *Polyandrocarpa* with their short, numerous, polycarp-type gonads. *Polyandrocarpa abjornseni* (Hartmeyer and Michaelsen, 1928) is the only exception with two

longish-oval gonads on each side of the body, although each has only six pairs of male follicles and is readily distinguished from the present species.

***Stolonica duplopicata* Sluiter, 1913**

Stolonica duplopicata Sluiter 1913, p 67.

Amphicarpa duplopicata: Kott 1985, p 244 and synonymy.

Distribution

New record: Western Australia (NW Port Hedland, QM G308080). Previously recorded (see Kott 1985): Western Australia (Montebello Is, Port Hedland, Cape Preston, Dampier Archipelago), Torres Strait, Philippines. The newly recorded colony was trawled from 35 m in muddy sand.

Description

The newly recorded colony is large, with zooids adhering to one another along their sides although their only organic continuity appears to be through the thin basal stolons. The test is thin and paper-like and the siphon linings are black. Zooids are as previously described with two branchial folds on each side of the body, a short gut loop enclosing a single endocarp and loosely attached to the body wall by ligaments. Large clumps of small male follicles with short ducts are along each side of the mid-ventral line. Female ovaries were not detected, although the specimens otherwise conform with previous descriptions.

Remarks

The absence of female gonads from this large specimen tends to confirm previous suggestions that gonads in this group of colonial styelids are variable (see Millar 1963).

***Stolonica styeliformis* Van Name, 1918**

(Figure 2)

Stolonica styeliformis Van Name 1918, p 107; Tokioka 1967, p 165; Millar 1975, p 278.

?*Amphicarpa duplopicata*: Kott 1972, p 50.

Distribution

New record: Northern Territory (Gulf of Carpentaria, 16°37.30'S, 140°10.871'E, trawled sample no. 372, coll. CSIRO, QM G308759). Previously recorded: Northern Territory (Gulf of Carpentaria, Kott 1972); Philippines (Van Name 1918; Tokioka 1967; Millar 1975).

Description

Zooids are small, sandy, rounded, spherical to oval or triangular in outline, to 1.0 cm maximum dimension. Each is connected to a network of basal stolons by a short stalk, the test is thin, translucent and flaccid, and sand is embedded in the surface, entirely covering the zooids and their stalks. Some brown pigment is in the test at the anterior end of the

Figure 2. *Stolonica styeliformis* (QM G308759). (A) External view of zooids; (B) internal pallial body wall on right. Scale bars: 2 mm (A); 1.0 mm (B).

body. Apertures are close together on the upper surface. The body wall adheres closely to the internal layer of test and is separated from it only with difficulty. Two branchial folds are on each side of the body and sometimes an incipient third fold, consisting of crowded vessels that spread out posteriorly, is in the ventral part of the branchial sac. A branchial formula is E1(4)2(10)4(6)3DL1(8)3(5)1(4)E. Four stigmata are in a mesh in the centre of one side of the branchial sac. An S-shaped vertical slit is on the dorsal tubercle. The gut is thick and forms a relatively short loop across the posterior end of the body with the rectum turning anteriorly almost at right angles to it. The relatively short stomach with about 16 gastric folds occupies the middle third of the proximal limb of the gut loop. The anus is bilabiate. The distal end of the stomach is connected with the distal limb of the gut loop by a short ligament. Rows of endocarps are on the body wall on each side. Neither gastric caecum nor gonads were detected in the newly recorded specimens, which appear to have been frozen.

Remarks

The majority of the specimens doubtfully assigned to *Amphicarpa duplopicata*: Kott, 1972 from the Gulf of Carpentaria appeared to have been dried out and only the external test is present. The internal organs were determined from only one specimen from a different location. Only two branchial folds were reported and it is probable that a third incipient fold, as in the present specimens, could have been overlooked.

The type specimens from the Philippines, like those reported by Millar (1975) and Tokioka (1967), are similar to the Northern Territory specimens, being sandy, upright zooids attached to basal stolons by short vertical stalks and with the body wall closely adherent to the test. The dorsal tubercle has a vertical slit. The branchial sac has similar numbers of internal longitudinal vessels and stigmata per mesh and Millar (1975) did find a specimen with incipient second and most ventral (fourth) folds. The gut is thick forming a short loop with the rectum turned anteriorly. The anal border is smooth as in the present specimens. A small gastric caecum was detected only in the specimens Millar (1975) examined. Gonads, consisting of small ovarian sacs in a row along each side of the

mid-ventral line and groups of single pear-shaped male follicles scattered on the body wall, are present in the Philippine specimens.

Both Van Name (1918) and Tokioka (1967) report especially large, robust colonies with four brown longitudinal bands in the test radiating from the branchial siphons. These are not reported by the other authors and although brown pigment is in the test around the anterior end of the body, bands of pigment were not detected in the present zooids.

Stolonica vermiculata sp. nov.
(Figures 3, 5C)

Distribution

Type locality. New South Wales (Lord Howe I., 13 m, coll. N. Coleman, 17 July 2002, syntypes QM G308501).

Figure 3. *Stolonica vermiculata* sp. nov. (QM G308756, holotype). (A) Colony surface; (B) ventral view of zooid showing rectum curving around branchial sac; (C) dorsal view of internal body wall of the zooid, branchial sac and the upper half of the zooid removed; (D) testis follicles; (E) larva. Scale bars: 0.2 mm (A); 0.4 mm (B, C); 0.1 mm (D, E).

Description

The sheet-like colonies containing small (about 4 mm diameter) dorso-ventrally flattened, circular zooids are on the test of a specimen of *Herdmania* sp. The zooids are flat on their undersurfaces and the thin test is hard to separate from the *Herdmania* that they are attached to. A continuous layer of test may be between the zooids attached firmly to the substrate but this was not clearly demonstrated. The inconspicuous, sessile apertures are on the upper surface, the atrial aperture more or less in the centre and the branchial aperture between the atrial aperture and the anterior end of the zooid. The delicate body wall, closely adherent to the thin test, has fine muscles radiating a short distance from the apertures. The meridian of the body, around which it is folded, is about halfway down the left and right sides, although the branchial sac is folded along its ventral and dorsal midlines. Six larger branchial tentacles alternate with six smaller ones inside the branchial aperture. The ciliated pit is a small, circular, anteriorly directed opening. The branchial sac is flat with up to 15 internal longitudinal vessels per side, seven transverse vessels and two long stigmata per mesh crossed by a parastigmatic vessel. The gut forms a double loop in the posterior half of the body on the left side, projecting out into the fold around the meridian. The short stomach, in the centre of the ascending limb of the loop, has 10 rounded folds and a long gastric caecum that curves around in the pole of the gut loop. The descending limb of the primary loop forms a deep secondary loop with the rectum, which curves around the dorsal edge of the folded branchial sac on to the upper surface of the zooid as it extends anteriorly to the atrial aperture. Only unisexual gonads are on the left side of the body and hermaphrodite gonads are on the right side. In these zooids a cluster of male follicles always is on the left side of the body anterior to the gut loop. In some zooids these are immature, small tear-shaped follicles each with a short duct directed toward the atrial aperture, but in other zooids with more mature male follicles they are large, lobed, overlapping pyriform masses, each with a relatively long duct that projects into the atrial cavity from near the centre of the mesial surface of the follicle and trails toward the atrial aperture. A row of five to six hermaphrodite gonads to the right of the endostyle (in the fold around the meridian) have their short, wide ducts irregularly orientated. Occasional female gonads are also present in this row along the right side of the endostyle. In the syntypes, larvae are crowded in the atrial cavity. They have triradially arranged adhesive organs, an otolith halfway along the trunk covered over by a circle of about 20 ectodermal ampullae. The larval trunk is 0.3 mm and the tail is 0.6 mm.

Remarks

The hermaphrodite gonads of the present species (with a small sac-like ovary and one or a pair of testis follicles) resemble those of many genera of the Polyzoinae, although the separate (dioecious) male and female gonads that also are present indicate an affinity with species assigned to *Stolonica* (see Kott 1990), which also have hermaphrodite and sometimes female gonads on the right side of the body and numbers of single follicle male gonads on the left. Some *Stolonica* spp. have separate male gonads on the right as well as on the left and sometimes separate female gonads as well as hermaphrodite gonads on both left and right. Kott (1990) found much of the variation in the number and disposition of the male, female and hermaphrodite gonads resulted from the ephemeral nature of the gonads and differences relating to age and sexual maturity of the zooids. This is confirmed in the present species, in which the female gonads were only occasionally detected on the left side of the body. Subsequent investigations could indicate further variation than that presently

observed in the syntypes, although, at this stage, the species appears to be characterised by the presence of separate male gonads only on the left, hermaphrodite gonads only on the right and occasionally separate female gonads only on the left.

Although previously recorded *Stolonica* spp. have from two to four branchial folds, there are no folds in the branchial sac of the present species. Nevertheless, the number of internal longitudinal branchial vessels resembles that in other species (irrespective of the presence or the number of branchial folds). This is taken as yet another indication of variability in higher-level taxa of evolving colonial zooids. Other genera of the Polyzoinae with flat branchial sacs are *Polyzoa* (which has only hermaphrodite gonads in a row on each side of the endostyle), *Metandrocarpa* (which has only separate sex gonads on each side of the body) and *Theodorella* (an indigenous New Zealand genus which has its gonads in rows either each side of or beneath the endostyle, male gonads only on the left and hermaphrodite and sometimes some separate male gonads on the right). None of these genera have the clumps of male gonads present in *Stolonica*. In this context, the disposition of the gonads is considered to be a character of greater phylogenetic significance than whether or not the branchial sac is folded.

As well as the absence of branchial folds, the present species is distinguished from most other *Stolonica* spp. by its embedded zooids, a habit it shares with *Stolonica carnosus* Millar, 1963 from southern Australia. The latter species has a shorter stomach with a longer curved caecum, it lacks the patches of crowded male follicles and it has separate flask-shaped male follicles and sac-like ovaries on each side of the endostyle.

***Botryllocarpa elongata* Kott, 1990**

(Figures 4, 5D)

Botryllocarpa elongata Kott 1990, p 283.

Distribution

New record: Tasmania (Tasman Peninsula, Waterfall Bay, on rock wall 12–14 m, SAM E3232). Previously recorded (see Kott 1990): Victoria (Phillip I.).

Figure 4. *Botryllocarpa elongata* (SAM E3232). (A) Zooid; (B) gut loop. Scale bars: 0.1 mm.

Figure 5. In situ images. (A) *Polyandrocarpa colemani* (QM G308755) (photograph: Merrick Ekins); (B) *Oculinaria australis* (SAM E3267) (photograph: K. Gowlett Holmes); (C) *Stolonica vermiculata* (QM G308756) (photograph: Neville Coleman); (D) *Botryllocarpa elongata* (SAM E3232) (photograph: K. Gowlett Holmes).

Description

The newly recorded colony consists of elongate, transparent heads containing one to three transversely orientated zooids, each head attached to a basal stolon by a short, narrow thread-like stalk. Zooids are spherical, about 1 mm diameter, delicate and transparent. The apertures are minute and appear to be smooth-rimmed. They open directly to the exterior on short siphons, the branchial aperture from near the undersurface of the head and the atrial aperture uppermost. Circular muscles can be seen around the apertures but were not detected on the rest of the body. The branchial sac has three internal longitudinal vessels per side, seven rows of about 18 stigmata per row and three to four stigmata per mesh. The gut forms an almost horizontal loop across the posterior end of the left side of the body. The barrel-shaped stomach has eight longitudinal folds and a caecum that arises as a narrow tube, crosses the outside of the distal end of the stomach and expands into a rounded knob in the gut loop. A large egg is attached to the atrial wall on the left side of the body, anterior to the gut loop. A testis was not detected in these zooids.

Remarks

The newly recorded specimens have been assigned to this little known genus on the basis of its separately opening apertures, its flat branchial sac with only three internal longitudinal vessels, and only one single sex (female) gonad on the left side of the body. The absence of male gonads may be either because individuals are dioecious or, more likely, the gonads are ephemeral as they so often appear to be in this subfamily. In the type specimen (Kott 1990), a single, lobed male follicle is on each side of each zooid and female gonads were not detected.

The only other known *Botryllocarpa* sp. is the type species, *B. viridis* (Pizon, 1908) from Indonesia and the Pacific coast of Costa Rica (see Kott 1990), which is reported to have fewer testis lobes and more stomach folds than the present species and a separate male and a female gonad on each side of the body.

The related genus *Chorizocarpa* Michaelsen, 1904 (see Kott 1985) is known from three species, *C. sydneyensis* Herdman, 1891 from New South Wales to the tropical western Pacific, *C. guttata* Michaelsen, 1904 from New South Wales, and *C. michaelsoni* (Sluiter, 1909) from the Torres Strait. Like *Botryllocarpa* and Botryllinae, the genus also has three internal longitudinal branchial vessels and similar colonies. However, unlike the present genus, all three of the known species of *Chorizocarpa* are reported to have only one unisexual gonad on each side, the female on the right and the male on the left (anterior to the gut loop).

Kott (1990) appears to have overlooked the unusual origin of the stomach caecum from a suture line along the outer or postero-ventral edge of the stomach, which makes a right-angled bend across the distal end of the stomach (across its longitudinal axis) and terminates in a spherical bulb in the pole of the gut loop. The caecum is similar to that found in some species of the Botryllinae and in *Chorizocarpa michaelsoni* Sluiter, 1909 (see Kott 1990). Although the present genus has similar gonads to some species of Botryllinae, it is distinguished by the absence of common cloacal systems.

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