THE RAFFLES BULLETIN OF ZOOLOGY 1995, **43**(2): 469-474

A NEW COLONIAL *STYELA* (ASCIDIACEA: STYELIDAE) FROM AN ISOLATED MARINE HABITAT, KAKABAN ISLAND, EAST KALIMANTAN, INDONESIA

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ABSTRACT. - A new species of *Styela* from a lagoon on a raised atoll is colonial, a habit not previously known for species of this genus. The lagoon is surrounded by a coral ridge 40 to 60m above sea level. There appears not to be a direct connection between the lagoon and the surrounding sea, and water exchange is limited, occurring only through submarine filtration channels. Speciation possibly resulted from isolation of a population of *Styela canopus*, the probable sister species. Coloniality is well established in the apparently monophyletic subfamily Polyzoinae in which the relationship between the genus *Polyandrocarpa* and the solitary genus *Polycarpa* (Styelinae) parallels that between the present new species and other *Styela* spp.

INTRODUCTION

The ascidian reported on below is from the former lagoon of a raised coral atoll. The lagoon, now enclosed by a coral ridge 40 to 60m above sea level, forms a lake (Halimeda Lake) with a maximum depth of 11m and 5km^2 in area. There is no direct sea water influx into the lake, which is connected to the sea only through submarine caves, tunnels and solution channels - the tidal range in the lake being only 11cm, compared with 2.5m in the sea surrounding the island. The pH of the lake water is 7.8 at the surface and 7.6 on the bottom. The salinity ranges between 23 to 26 parts per thousand. The lake contains a great abundance of *Halimeda opuntia* and *H.tuna*, and is surrounded by a narrow band of mangrove, mostly *Rhizophora* spp. All the ascidians were taken from roots of *Rhizophora mucronata* about 0.5m below the surface.

Thus, sea water influx, as far as has been determined, is submarine. Since gene flow between populations of ascidians occurs mainly through larval dispersal and recruitment and dispersal of gametes, usually in surface waters, it would appear to be a relatively rare occurrence between this lake and outside waters, and populations in the lake probably are isolated to some extent.

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Only one other species, *Ecteinascidia nexa* Sluiter, 1904, has been taken from the same location as the new species described below. It also has a wide range in the western Pacific (see Kott, 1985). However, despite its possible isolation from outside populations, the specimens taken from Halimeda Lake, mixed in a clump of weed (*Hypnea* sp.?), do not appear to depart from other known specimens of the species in any aspect of their morphology.

TAXONOMY

Styela complexa, new species
(Figs. 1, 2)

Type Locality. - Kakaban Island, East Kalimantan, Indonesia (02 08'35" N, 118 31'13"E, Halimeda Lake, roots of *Rhizophora mucronata*, 0.5m depth, coll. T. Tomascik, QM G308341 holotype, QM G308342-3 paratypes.

Description. - The species is colonial. Posteriorly zooids are embedded in a thin mat of common test. Smaller zooids 2cm long (QM G308343) project free of common basal test mat for about half their length. As zooids increase in length (to about 5 cm) they are joined together basally by a smaller proportion of their total length, i.e. common test is always about 1 cm thick, except in the longest (5 cm zooids) which are broken off basally and may have been connected only by stolons. Zooids are cylindrical, to about 1cm in diameter throughout, although preserved specimens probably are contracted. The outer surface of the tough but slightly translucent test is rough, raised into crowded elevations and wrinkles which are smaller but more pronounced anteriorly, tending to flatten posteriorly. Distinctly 4-lobed sessile apertures are at rounded anterior end of body, branchial aperture terminal or subterminal and atrial aperture about one third of distance down dorsal surface.

Small overlapping scales on test lining siphons are about 0.01 mm wide and 0.03 mm long overall, with rounded margins and long bases. Branchial tentacles simple, from 8 in smaller specimens to about 24. Dorsal tubercle with C-shaped slit, open interval turned to right. A longish-oval neural ganglion extends a short distance behind dorsal tubercle. Dorsal lamina plain-edged, extending to oesophageal opening at posterior end of long body. Branchial sac with four well-formed, parallel folds on each side. Branchial formula for right side E3 (12) 4 (11) 5 (10) 4 (7) DL. In each mesh 6 to 8 stigmata crossed by parastigmatic vessel. Relatively short oesophagus leads to more or less spindle-shaped stomach with fine parallel, longitudinal folds extending full length of its internal wall and a small anteriorly projecting caecum at the pyloric end. Stomach occupies half to three-quarters of ascending limb of gut loop. Immediate post-pyloric part of gut curves posteriorly, descending limb almost parallel to ascending limb (including stomach) of loop. Rectum extends anteriorly forming deep secondary loop before terminating in anus near atrial aperture. Anal border divided into about 12 short rounded lobes. Gut attached to body wall by a series of fine ligaments, rather than being embedded in it.

Gonads characteristic of *Styela*, with from 6 to 10 large lobed and branched testis follicles in the body wall around, but separated from, the proximal half of each sinuous ovarian tube. One or two gonads on right, converge to atrial aperture. Two gonads on left, one extending down into secondary gut loop, and one crossing body wall anterior to pole of primary gut loop. Vasa efferentia extend from each testis follicle to join vas deferens running along centre of each ovarian tube, opening at base of oviduct opening. As zooids increase in length, testis follicles become more branched, lobes and branches longer and narrower, and follicles

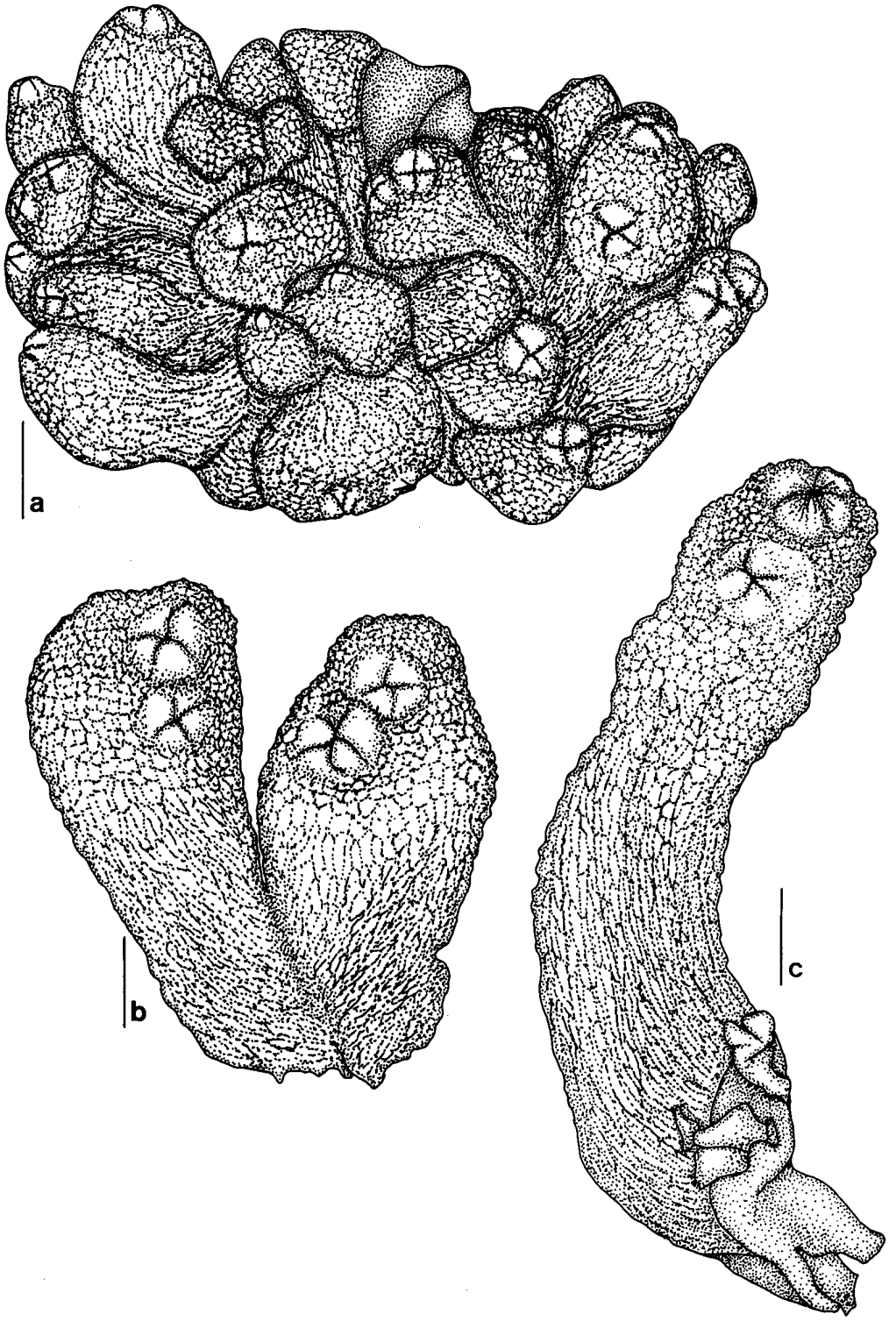

Fig. 1, *Styela complexa*, new species, external appearance (scales, 5mm), (a) portion of colony with short zooids - QM G308343; (b) portion of colony with long zooids - QM G308341; (c) single long zooids believed to have been part of a colony, possibly joined by stolons - QM G308342.

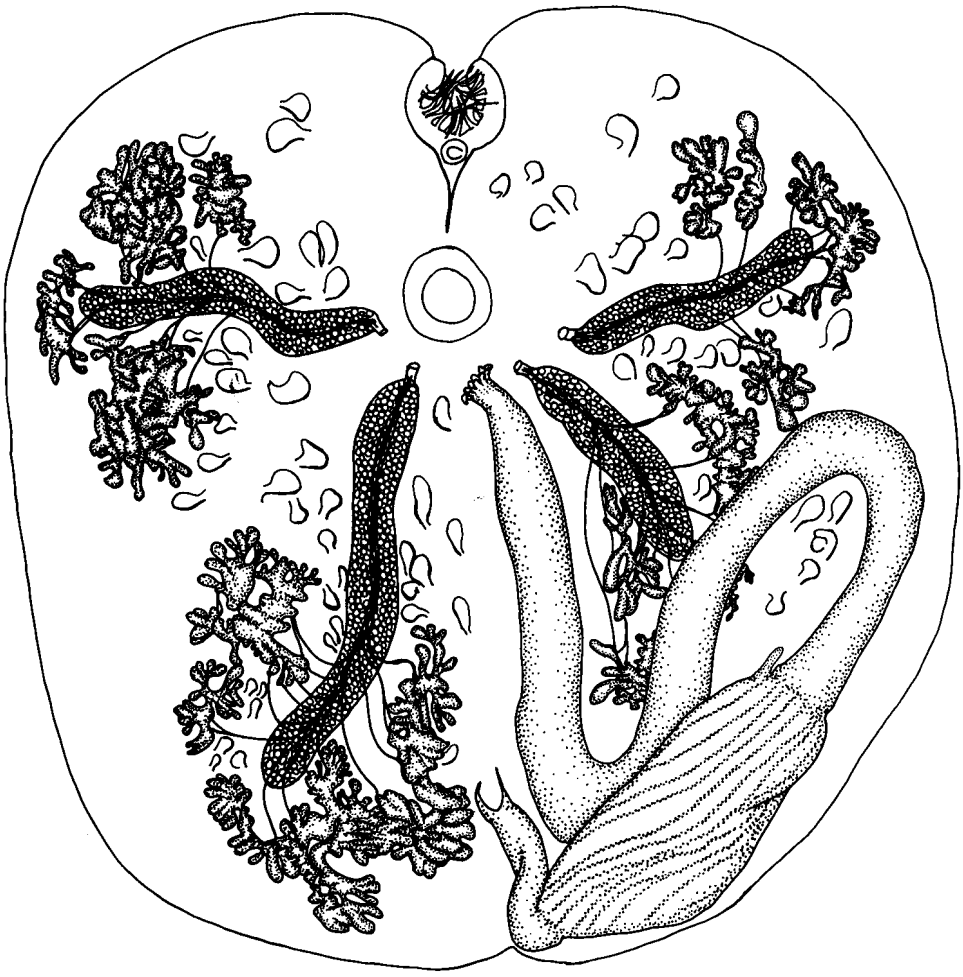

Fig. 2, *Styela complexa*, new species, body opened around ventral mid-line showing gut, gonads and endocarps embedded in the parietal body wall - QM G308341 (scale, 1.0mm).

spread over a greater area. Small endocarps are scattered on body wall, but not on either gut or gonads. A few are on body wall between the ascending and descending limbs of primary gut loop.

Remarks. - The new species is unusual in its colonial habit. Although it shares this habit with the subfamily Polyzoinae, it appears closely related to the genus *Styela* (subfamily Styelinae), while most polyzoinids appear to be related to the genus *Polycarpa*. Indeed, the present specimens have the same relationship to *Styela* as *Polyandrocarpa* has to *Polycarpa*, *Polyandrocarpa* differing only in its size and colonial habit from *Polycarpa*. Other genera of the Polyzoinae are, very likely, derived from *Polyandrocarpa*, the process of replication (interrupting individual zooid growth) gradually resulting in selection for smaller, more simplified zooids. Polyzoinae appear to be monophyletic, having small polycarp gonads, rather than long ones resembling those of either *Styela* or *Cnemidocarpa*. The present new species does not appear to have a range of taxa deriving from it, and does not justify the

erection of a new subfamily. It is the only colonial species known with a direct affinity with *Styela*. It appears to have evolved in isolation in this unusual location, probaby from *Styela canopus* (Savigny, 1816), which has a cosmopolitan range (see Kott, 1985).

Apart from its colonial habit, the individual zooids of the present species are distinguished from *S.canopus* by their long, cylindrical bodies, sessile apertures, more numerous stigmata per mesh (six to eight rather than the two or three in *S. canopus*), very small endocarps on the body wall, small and very few endocarps in the gut loop, and the size and shape of the flattened, lobed testis follicles (which appear to become more branched than any others known in the Styelidae).

Another unusual aspect of this species is its capacity to tolerate the relatively low salinity of the lake. Only two species of ascidians are known to accommodate consistently low salinity (see Kott, 1985). One is *Molgula manhattensis* (de Kay), the other is *Styela plicata* (Lesueur). The latter species is, with *S.canopus*, similar to the present one, which may have inherited some capacity to accommodate brackish water from a common ancestor. (Specimens of *Ecteinascidia nexa* recorded from the Halimeda Lake with the present species suggest that this species also may tolerate low salinity)

The reproductive strategies of the present species are not known, no larvae have been detected, although the ovarian tubes of the specimens are largely expended. The occurrence of viviparous larvae, internally fertilised and brooding in the atrial cavity as in all previously known colonial species (see glossaries in Kott 1985, 1990, 1992: viviparity and incubation of embryos), could confirm a longer evolutionary history for this isolated species than would be the case if viviparity had not yet replaced an oviparous habit. Further, only part of three different adult colonies were collected, and the method of budding is not known. The form of the colony suggests that it occurs in test vessels at the posterior end of the zooids.

The only other case of budding in a species of Styelinae observed by the author was brought to her attention by Myriam Preker of the Heron Island Research Station. The bud was from a basal root-like projection or holdfast from the stalk of *Cnemidocarpa stolonifera* held in a small aquarium tank. This demonstrates the capacity of members of the class Ascidiacea to produce replicates - a capacity that has been selected for principally in the Aplousobranchia, but also in some taxa of Phlebobranchia and Stolidobranchia. In the latter sub-order coloniality occurs universally in Polyzoinae and Botryllinae, both in the family Styelidae. The present new species is the first known colonial species in the other sub-family (Styelinae) of the Styelidae.

NOTES ON COLONIALITY

Aggregates of individuals are known in certain species in the Styelinae. These include *Polycarpa tumida* Heller and *Dendrodoa grossularia* (Beneden). *Polycarpa tumida* Heller (see Monniot, 1972) from Bermuda and the tropical Atlantic is found in aggregates or as solitary individuals. The aggregates are irregular, individuals ahere to one another by varying amounts of the surface test and can readily by separated. There does not appear to be any basis for the view that the aggregates form by replication.

Of more interest in relation to the evolution of the colonial habit is a cnemidocarp-like styelid *Dendrodoa grossularia* (Beneden) which has regular aggregates (like those of the

present species) and viviparous larvae (usually a characteristic of colonial forms). Berrill (1950) insists that vegetative replication is not involved, and the aggregations, rather than being true colonies of cloned zooids of one genotype, are thought to be the result of a short free-swimming larval life and the absence of a light sensitive ocellus, larvae accordingly settling around the parents. The relatively large larvae of *D. grossularia*, with well developed ampullae, do resemble viviparous larvae of the Polyzoinae rather than those of the Styelinae, which are small, have few larval or adult organs, and (with the exception of a few species of *Polycarpa*: see Kott 1985) develop from externally fertilised eggs. It is hard to understand how *Dendrodoa grossularia* larvae are not dispersed when they are said to be free-swimming for many hours, even though the aggregations form only in protected sites. However, if Berrill is correct and many genotypes are present in the aggregations, and if the larvae of the present species in due course are found to be viviparous, the relationship between *Dendrodoa grossularia* and *Cnemidocarpa* is analagous, rather than homologous, with the relationship between the present species and the genus *Styela*. Further, it suggests that the evolution of viviparity is associated with the colonial habit, rather than with the process of replication.

ACKNOWLEDGMENTS

I am grateful to Dr Tomas Tomascik, EMDI (Environmental Management Development in Indonesia) who submitted the material to me for identification, and to whom I am indebted for the habitat notes (above). I am grateful, also, to Miss Sue List, who did the line drawings.

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Received 03 Jun 1995
Accepted 09 Oct 1995