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JUVENILE COLONIES OF THE GENUS *PYROSTREMMA* GARSTANG, 1929 (TUNICATA, THALIACEA)

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ABSTRACT

Four remarkable dome-shaped, apparently juvenile colonies, belonging to the genus *Pyrostremma* Garstang, 1929, are described from the Bermuda area. Comparison with juvenile colonies of *P.agassizi* (Ritter & Byxbee, 1905), and with larger colonies, fragments and loose zooids of *P.agassizi* and *P.spinosum* (Herdman, 1888), has rendered it likely, that these juvenile colonies belong to *P.spinosum*. The species of *Pyrostremma* are discussed.

INTRODUCTION

Pelagic tunicate samples, collected by the Ocean Acre Project near Bermuda and sent for identification and study to the present author, contained some remarkable small pyrosomatid colonies of a rounded form never recorded before in literature. The nature of the test projections, the absence of a colonial diaphragma and certain characters of the zooids such as the presence of "cloacal" muscles on the branchial lamellae and the oblique course of the branchial stigmata, made it clear that these colonies belong to Neumann's (1913) Pyrosomata fixata-group, at a later date raised to generic rank (*Pyrostremma*) by Garstang (1929, after Berrill, 1950).
The three known species of this genus, viz. *P.spinosum* (Herdman, 1888), *P.agassizi* (Ritter & Byxbee, 1905) and *P.vitjasi* (Ivanova-Kazas, 1960), differ clearly from the species of the only other pyrosomatid genus *Pyrosoma* Péron, 1804, in many characters (cf. Ivanova-Kazas,

1962). Incidentally, Ivanova-Kazas (1962) proposed the genus name *Propyrosoma* for the Pyrosomata fixata-group, but Garstang (1929) already assigned the name *Pyrostremma* to it, so Ivanova-Kazas' name must be considered a junior synonym. The three species are incompletely known. Undamaged adult colonies of *P.spinosum* have only recently been described and figured by Baker (1971); until then they were only known from fragments or immature colonies. Small juvenile colonies have never been recorded except for an obviously incorrect record of a 15 mm high colony by Farran (1906). The species may reach a length of 20 m. Metcalf & Hopkins (1919) supplied data on the reproduction, which are contradictory to the results obtained by Ivanova-Kazas (1962). The latter author found cyathozooids containing 30-50 stolon individuals, while the former authors only found four stolon individuals in the cyathozooid, which is the rule in the genus *Pyrosoma*. There are also contradictory statements on the presence of luminous organs in the ascidiozooids.

P.agassizi is also incompletely known, as there are no records of colonies containing zooids with gonads. It must be presumed that thus far only immature colonies have been found, although some authors did not describe the zooids of their *P.agassizi*-colonies in full. The colony size reached by this species has not been established beyond doubt, probably due to confusion with colonies of *P.spinosum*. The species was described by Ritter & Byxbee (1905) on a colony 11 cm in length. Krüger (1912) gives a maximal size of 111 cm, but as the specimen was fragmentary, lacking, moreover, the distal part, its designation as *P.agassizi* was unfounded. The zooid pictured by Krüger (1912) conforms to the zooids of *P.spinosum*, which renders it likely that the specimen of 111 cm was a moderately small colony of the latter species. The other specimens described by Krüger showed the characteristic four quadrangular processes surrounding the colonial aperture, and are thus correctly assigned to *P.agassizi*; the largest of these specimens measured 40 cm. Neumann's (1913) longest specimen was 17 cm. Metcalf & Hopkins (1919) mention maximal lengths of 12 cm. The distinction of *P.agassizi* from *P.spinosum* is based on the presence of the above mentioned four quadrangular test processes (which may sometimes be absent), while *P.spinosum* has only one very long, limp process. The shape of the zooids, the number of branchial stigmata and bars, the angle of the branchial stigmata to the horizontal axis of the zooid, the number of dorsal languets and the length of the cloacal siphon are also reported to be of distinctive importance, although Sewell (1953) has shown, that these characters vary with age and size of the zooids and are, in view of the apparent immaturity of the *P.agassizi* specimens, of doubtful value.

P.vitjasi, finally, has been described recently by Ivanova-Kazas (1960) on the basis of a colony of 47 cm long and 5 cm in diameter, containing sexually mature zooids. The colony possessed no colonial processes at its aperture; the zooids possessed a number of branchial stigmata and bars higher than in *P.agassizi* and almost equal to the number in *P.spinosum*. Furthermore, the cloacal siphon possessed a long tentacle-like appendix hanging down the interior cavity of the colony. The present author, however, is of the opinion, that the main basis for the distinction of a separate species has been the important discovery by Ivanova-Kazas (1956) of a reproductive process in this species, considerably different from that in the genus *Pyrosoma*, and in *Pyrostremma spinosum* as it was described by Metcalf & Hopkins (1919). Later, Ivanova-Kazas (1962) discovered the same deviating reproductive process in *P.spinosum*, proving Metcalf & Hopkins' interpretation wrong. This different process in which 30-80 primary ascidiozooids might give rise to a new colony, instead of four as is the case in *Pyrosoma*, may be responsible for a different growth of the colonies in both genera. Ivanova-Kazas (1962) reports a difference in development of the stolon individuals in the cyathozooid of *P.spinosum* and *P.vitjasi*; the former produces a regular 8-shaped sling of about 30-50 stolon individuals, while the latter produces a much more confused sling of 50-80 stolon individuals. This different arrangement might be reflected in the structure of the juvenile colony or even in the mature colony. The study of juvenile *Pyrostremma* colonies seems thus of some interest Next to the remarkable colonies mentioned above,

small colonies of *P.agassizi* have been studied for the present paper as well. For comparison some larger colonies, fragments and loose zooids of both *P.agassizi* and *P.spinosum* are considered also.

MATERIAL

The major part of the colonies originated from the Atlantic Ocean. A few examples were taken from Indo-Pacific Dana-samples. Dr. C.F.E. Roper (United States National Museum, Washington, D.C., USNM) is thanked for the arrangement of the loan of Ocean Acre material (collected with financial support of the U.S. Navy) and South Atlantic "Walther Herwig"-material. Dr. E. Rasmussen (Zoologisk Museum, Copenhagen, ZMUC) kindly permitted the loan of the Dana-material. The Ocean Acre cruises were all held in the immediate vicinity of Bermuda.
Acre Cruise 11-13B, 11-13C, 13-3M, 13-6B, 13-7M, 13-9P, 13-10M, 13-11A, 13-11C, 13-24M, 13-29M, 13-31B, 13-32C, 14-24B. (ZMA/USNM). Walther Herwig st. 431-II (30°07'S 03°24'E), 439-II (24°19'S 00°23'E) (USNM).
Dana Expeditions st. 3561 II (04°20'S 116°46'W), 3561 X (04°20'S 116°46'W), 3640 VI (41°47'S 176°55'E), 3716 I (19°18.5'N 120°13'E), 3912 III (06°52'N 79°30'E), 3917 VI (01°45'N 71°05'E) (ZMUC).
Tridens Expedition 1972, st. 5 (42°23'N 12°38'W), st. 9 (39°26'N 23°22'W) (ZMA).

DESCRIPTION OF THE DOME-SHAPED COLONIES FROM THE BERMUDA AREA (Figs. 1A-B, 2A)

Four dome-shaped, opaque or more or less transparent, firm colonies collected during Acre Cruise 13, were brought to my attention by Dr. S. van der Spoel (ZMA). They were of the following sizes: height 18 mm, diameter 30 mm (ACRE 13-9P); height 18 mm, diameter 20 mm (ACRE 13-6B); height 20 mm, diameter 25 mm (ACRE 13-3M); height 20 mm, diameter 25 mm (ACRE 13-11A).
The upper surface of the colonies is globular and bears small triangular spines such as found in the species of *Pyrostremma*. The interior of the colony contains a shallow cavity which opens widely at the underside. The colonial walls are quite thick. The under surface is rounded, which completely rules out the possibility that the colonies might represent the top fragments of larger colonies. A remarkable feature is the asymmetry of the under surface of the colonies. At one side a distinct outcrop of the wall is present; this might be the initial stage of a colonial process, such as described for *P.spinosum* (cf. Baker, 1971).
The colonies are clearly juvenile as they contain zooids without any trace of gonads. Length of the zooids: up to 5.8 mm. The branchial stigmata run at a variable but sharp angle to the longitudinal axis of the zooid. The number of branchial stigmata varies from 21 to 35, apparently linked to the size of the zooids. The number of branchial bars varies from 15 to 29, also apparently correlated with the size of the zooid. The oral siphon is short, the cloacal siphon may be as short or more elongated (length up to 1.3 mm). Luminous organs are present at the anterior border of the branchial basket in most specimens. Some zooids show dots of presumably luminous material on the wall of the cloacal siphon. Endostyl sharply arched. Branchial muscles strongly developed, situated in two groups ventral to the ganglion and ventral to the oral aperture. Cloacal musculature situated on the branchial lamellae, sometimes linear in shape, sometimes spindle-shaped. Neither testis nor ovarium could be found. Dorsal languets present in varying number, up to 8. Most zooids have stolon buds in various sizes. The arrangement of the zooids in the colony seems regular; in the largest colony they are spirally arranged in several layers.

JUVENILE COLONIES OF *P.AGASSIZI* (Figs. 1C-D, 2B)

No juvenile colonies in the size range given above are known of *P.spinosum* and *P.vitjasi*, although Farran (1906) attributed a 1½ cm long colony to the former species; the presence of four quadrangular test processes in his specimen identifies it, however, as *P.agassizi*. In fact, all *P.agassizi*-colonies recorded in literature, with the possible exception of some of Krüger's (1912) specimens, deserve to be termed "juveniles", as none of them has been reported to contain zooids with gonads.

Juvenile colonies of *P.agassizi* in the size range of the above described colonies are morphologically very different. The present material contains specimens of the following sizes: height 41 mm, diameter 9 mm (ACRE 11-13B); height 88 mm, diameter 11 mm (ACRE 11-13C); height 35 mm, diameter 8 mm (Dana st. 3912 III); height 35 mm, diameter 8 mm (Dana st. 3912 III); height 25 mm, diameter 7 mm (Dana st. 3912 III); height 20 mm, diameter 4.5 mm (Dana st. 3912 III); height 12 mm diameter 3 mm (Dana st. 3912 III); height 15 mm, diameter 4 mm (Dana st. 3912 III). Except for the ACRE-colony of 41 mm in length, all colonies showed the characteristic four quadrangular processes of the test around the colonial aperture, and the ridged aspect of the closed apex of the colony. The last feature is also found in the 41 mm ACRE-colony, so that it seems likely that it has lost its quadrangular processes in some way or another.
All these colonies are thus finger-shaped (just as the 1½ cm colony described by Farran, 1906) and resemble the older colonies of this species. The colonial wall is very thin and weak; its transparency is in sharp contrast to the somewhat milky appearance of the dome-shaped colonies. The smallest colonies (12 and 15 mm high) showed no denticulations on the outside of the test; the others did bear the characteristic triangular denticulations.
The zooids are up to 4.3 mm in length in the largest colony of 88 mm, but reach only 2.8 mm in those of 35 mm. The branchial stigmata run at a varying but sharp angle to the longitudinal axis of the zooid. Their number varies from 15 to 29. The number of branchial bars varies from 9 to 15. The oral and atrial siphon are both very short, almost non-existent. Luminous organs are situated at the anterior rim of the branchial basket. The endostyl is highly arched. Branchial muscles are hard to detect; they are situated ventrally to oral aperture and ganglion. Cloacal muscles are situated on the branchial lamellae; they are linear in shape. A few dorsal languets are present in the largest zooid. Most zooids have stolon buds in varying sizes. The arrangement of the zooids seems thoroughly irregular; no spiral pattern could be detected. A large top-zooid, showing displacement of the luminous organs as described by Neumann (1913) could not be found.

LARGER COLONIES OF *P.AGASSIZI* (Fig. 2C)

Larger colonies of *P.agassizi* do not differ from the juvenile colonies, but for size. A number of colonies and fragments have been studied, of which the largest, apparently complete, one measures 285 mm (diameter 12 mm (ACRE 14-24B)), although it lacks the characteristic quadrangular test processes and the ridged apex. Otherwise, its appearance is quite like that of colonies possessing these characters. Several other colonies had only one of the four processes, so these are probably easily lost, especially during capture.
The largest zooid encountered in colonies of *P.agassizi* is 5.3 mm in length; it has 35 branchial stigmata and 18 branchial bars. Its cloacal siphon is slightly enlarged (length 0.5 mm); no gonads are apparent. In some fragments collected by the Tridens (st. 5), the zooids show a long cloacal appendix (fig. 2C), such as has been described for *P.vitjasi*. Smaller cloacal appendices have, however, also been described for *P.agassizi*. The biggest zooid in these colony fragments measures 5.2 mm, excluding the cloacal appendix of 2 mm. The number of branchial stigmata is 30, the branchial bars number 19. No gonads are present. But for the unusually long cloacal appendix, the zooids and the colony resemble *P.agassizi*, which may point to conspecifity of *P.vitjasi* and *P.agassizi*.

PYROSTREMMA SPINOSUM (Figs. 3, 4A-B)

Material at hand of *P.spinosum* is poor: two badly preserved, one-walled fragments probably belonging to this species (measuring 100 mm long, 100 mm wide from Dana st. 3561 III and 50 mm long, 50 mm wide from WH - 439 - II); many loose zooids and a small piece of test, mostly from ACRE; three interesting one-walled strips showing the same opaqueness as the dome-shaped juvenile colonies, also from ACRE.
The two badly preserved, more or less square fragments apparently had lost the largest zooids. The longest zooid measured with the remaining zooids was 4.7 mm long. This zooid already showed the characteristic angular and elongated shape of *P.spinosum*, with a long cloacal siphon. Branchial

stigmata: 36, branchial bars: 22.
The loose zooids included a fair number of sexually mature individuals showing a developed testis and/or a developed ovary, which appears as a small globule posterior to the intestine. No developing cyathozooids are present. The cloaca of some zooids shows a fairly long cloacal appendix; many lack luminous organs. The smaller zooids (under 30 mm) are hardly distinguishable from those of *P.agassizi*, as their cloacal siphons are short and the branchial baskets are rounded rather than angular. The largest loose zooid (fig. 3) measured 14.3 mm (including a cloacal siphon of 5.2 mm). Its number of branchial stigmata is 53, its number of branchial bars 35.
The one-walled strips from ACRE 13-11C and ACRE 13-13B are thought to represent fragments of the long colonial process reported for this species by Baker (1971). This author states, that he does not know whether this colonial process bears zooids or not. The present three strips are of varying length (20 mm, 250 mm and 100 mm); their width varies from 18 to 30 mm. The long pieces are frayed at both ends, but the small one is smoothly rounded at one end and frayed at the other, and thus may represent the terminal fragment of the colonial process. The sides of all three are smoothly rounded and unfrayed, which excludes the possibility that the strips are fragments of the colony proper. All pieces bear zooids which are arranged fairly regularly: near the rim they are pointing sideways, in the centre of the strip they lie perpendicular to the longitudinal axis, the cloacal aperture at the smooth under surface of the strip, the oral aperture at the denticulated upper surface. The zooids are of varying length. Some have an extremely short cloacal siphon, others a more elongated one (fig. 4A-B). The larger zooids possess testes and/or ovaries; they lack luminous organs. The longest zooid measured 10.4 mm (including a cloacal siphon of 2.5 mm).
Presumably the dome-shaped juvenile colonies described above belong to this species. The zooids seem to conform to those of *P.spinosum* as is apparent from fig. 5, in which the number of branchial stigmata and branchial bars of specimens of both *P.agassizi* and *P.spinosum* are compared. Also one zooid of *P.vitjasi* is represented in fig. 5; it is based on the figures supplied by Ivanova-Kazas (1960). Apparently, the number of branchial bars is relatively greater in *P.spinosum* than in *P.agassizi*, although this is only true in larger zooids.

DISCUSSION

If the dome-shaped colonies described above do indeed belong to *P.spinosum*, it would mean that there must be considerable difference between *P.agassizi* and *P.spinosum* in the way the growth of a new colony is initiated. The present material and literature data seem to indicate that the arrangement of the zooids in larger colonies of both species is also different. Ivanova-Kazas (1962) described a difference in the arrangement and number of stolon buds in the cyathozooids of *P.vitjasi* and *P.spinosum*; in the latter species they are arranged in a regular 8-shaped sling, in the former the arrangement appears confused. It may be expected that the observed differences in the cyathozooid are reflected in the juvenile and also adult colonies.
The two *Pyrostremma* colonies described by Farran (1909) as *P.spinosum*, seem to be correctly assigned to that species, judging from the figures and the description he gives. Both are about 90 cm long and 19 cm wide. Whether they represent whole specimens is hard to decide; both colonies lack colonial processes. Some zooids showed ovaries. This would mean that *P.spinosum* reaches sexual maturity at a colonial length of at least 90 cm. The possibility, that Farran's specimens are mature colonies of *P.agassizi*, however, can not be excluded.
Discussing the genus *Pyrostremma*, some comment might be justified on a recently described new species *Pyrosoma sedentarium* Sebastian, 1971. From the very vague photographs and drawing supplied by Sebastian (1968, 1971) it is clear, that this species has affinities to *Pyrostremma*, as the zooids show an oblique course of their branchial stigmata and bars, and their endostyl is curved. Where the cloacal musculature is situated is not indicated. The shape of the cloacal siphon in the drawing (Sebastian, 1968) seems to be different from that in the photograph (Sebastian, 1971). What is indicated as a bud in the photograph is obviously an ovary or cyathozooid. The specimen, which was taken with

a dredge allegedly lived sedentary; it is stated to form a wide carpet on the sea floor (beyond the 100 fathom line along the coast of India). The author makes no attempt to compare his material with literature data on other pyrosomatids. It seems incongruous that the cloacal aperture lies at the under surface of the "carpet", which would mean that waste products are deposited underneath the "carpet". Although the present author has not studied the type material of this new species, there seems to be ample room for the suggestion, that *Pyrosoma sedentarium* is nothing else than a large piece of a huge colony of *P. spinosum*.

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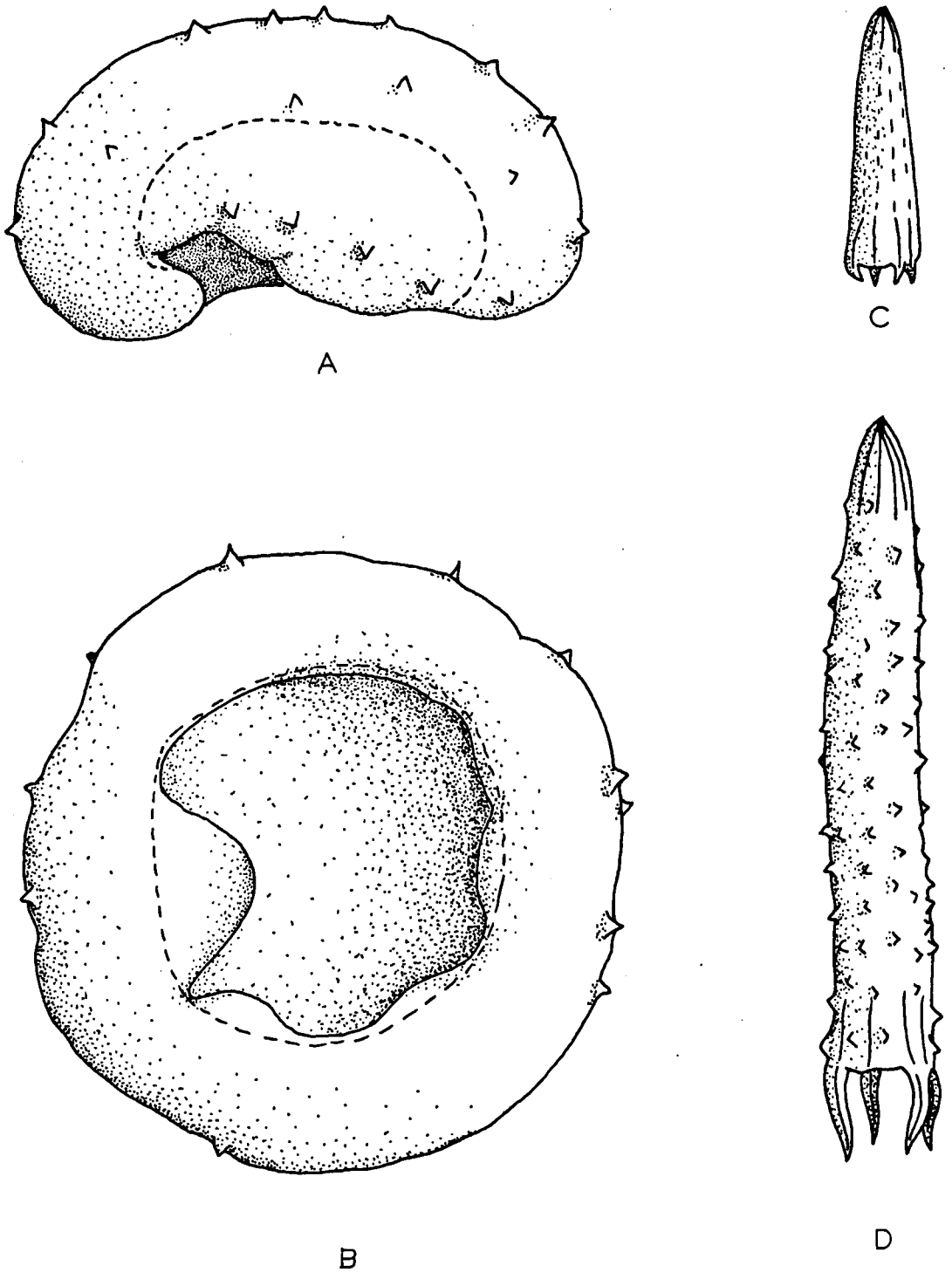

Fig. 1. Juvenile colonies of *Pyrostremma* spp. A, lateral view of a dome-shaped colony from the Bermuda area; B, ventral view of the same (diameter 30 mm); C, juvenile colony of *P.agassizi*, 15 mm high; D, juvenile colony of *P.agassizi*, 35 mm high.

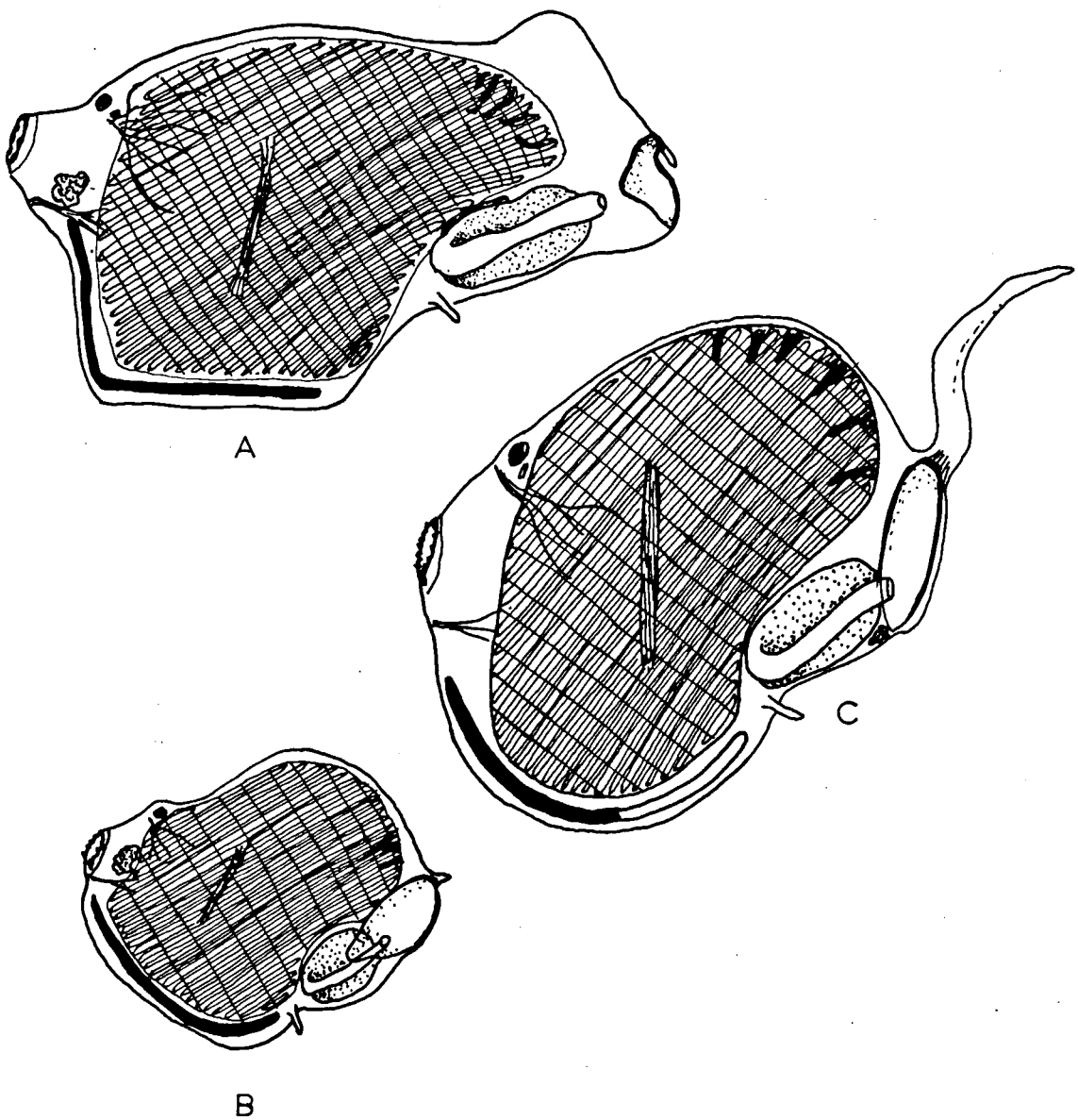

Fig. 2. Ascidiozooids from a dome-shaped juvenile colony (A, 5.2 mm), a juvenile colony of *P. agassizi* (B, 2.9 mm) and a larger colony of *P. agassizi* containing zooids with an elongated cloacal appendix (C, 4.5 mm).

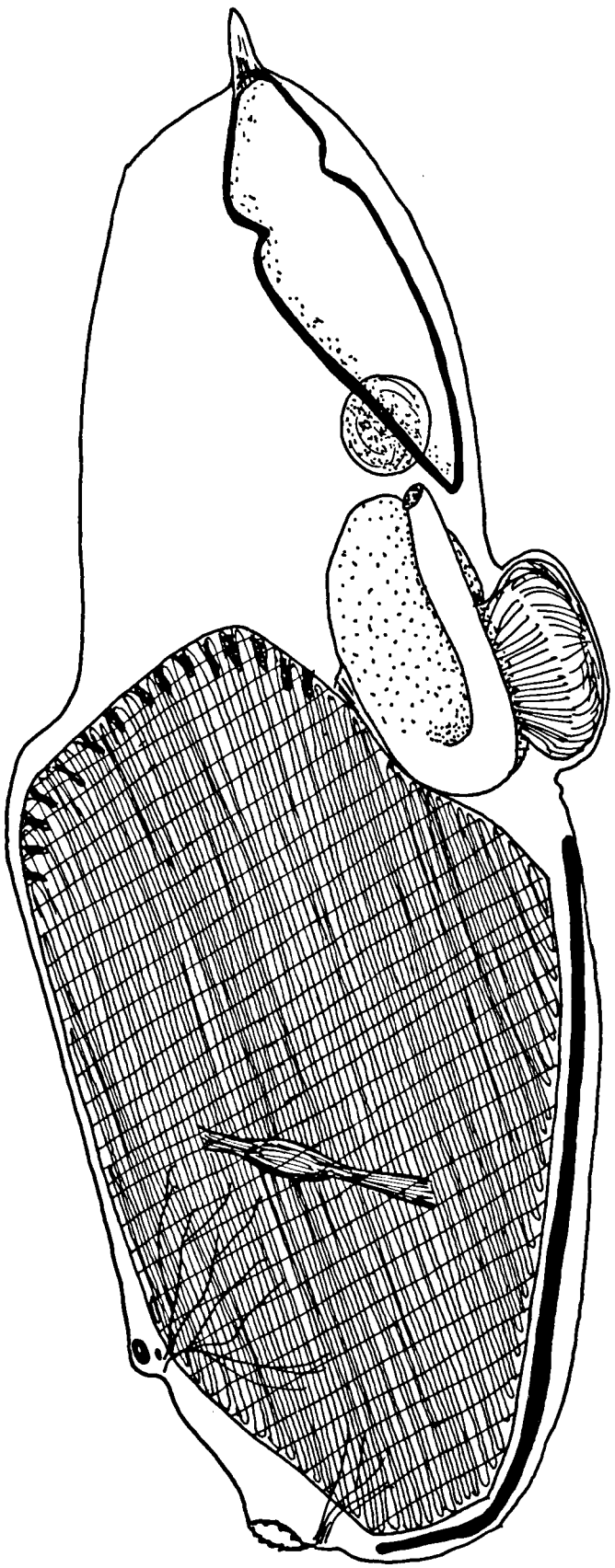

Fig. 3. A mature zooid of *P. spinosum* (13.0 mm).

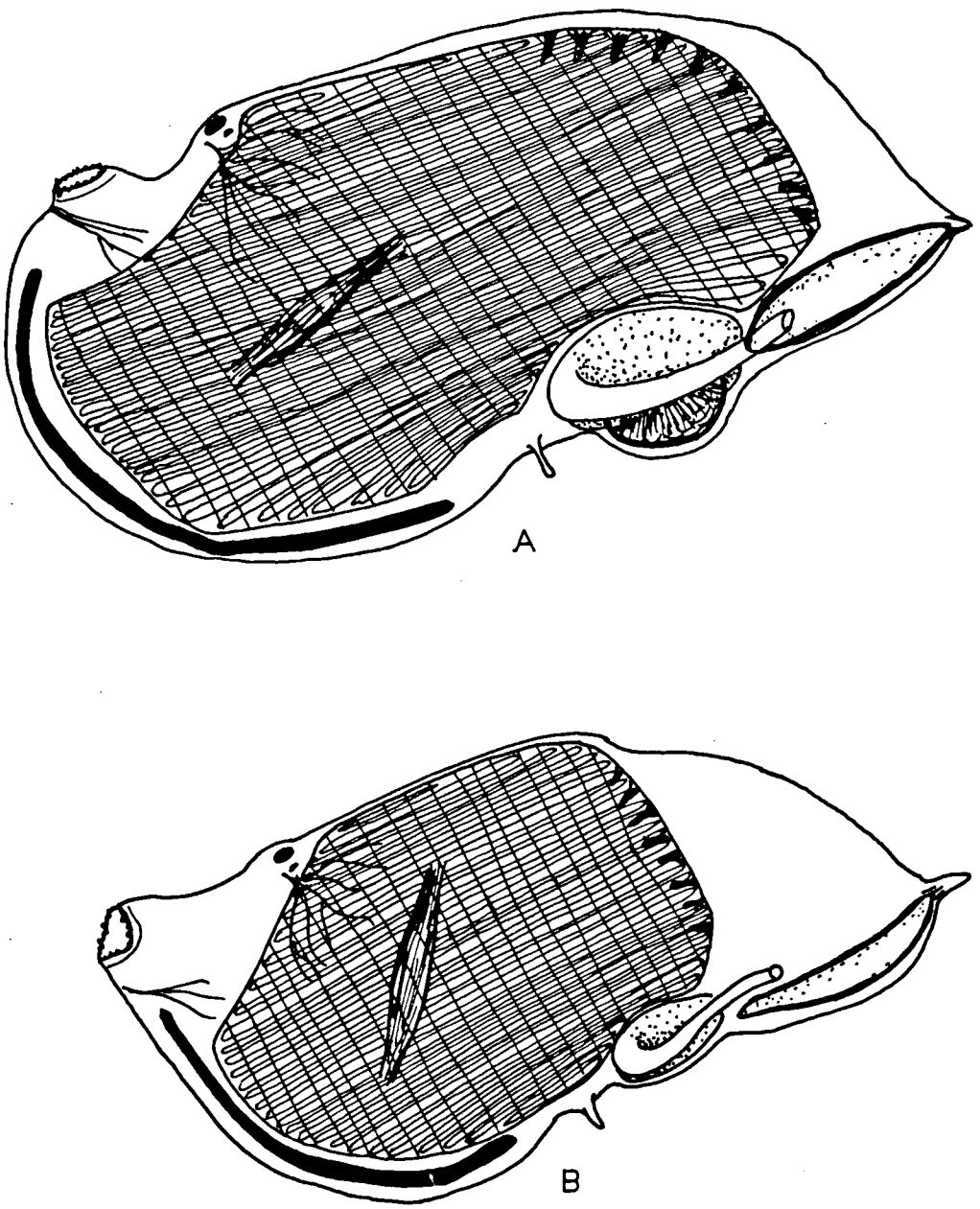

Fig. 4. Zooids from one-walled strips supposed to be fragments of the "tail" of a *P. spinosum* colony (A: 6.3 mm long, B: 7.4 mm long).

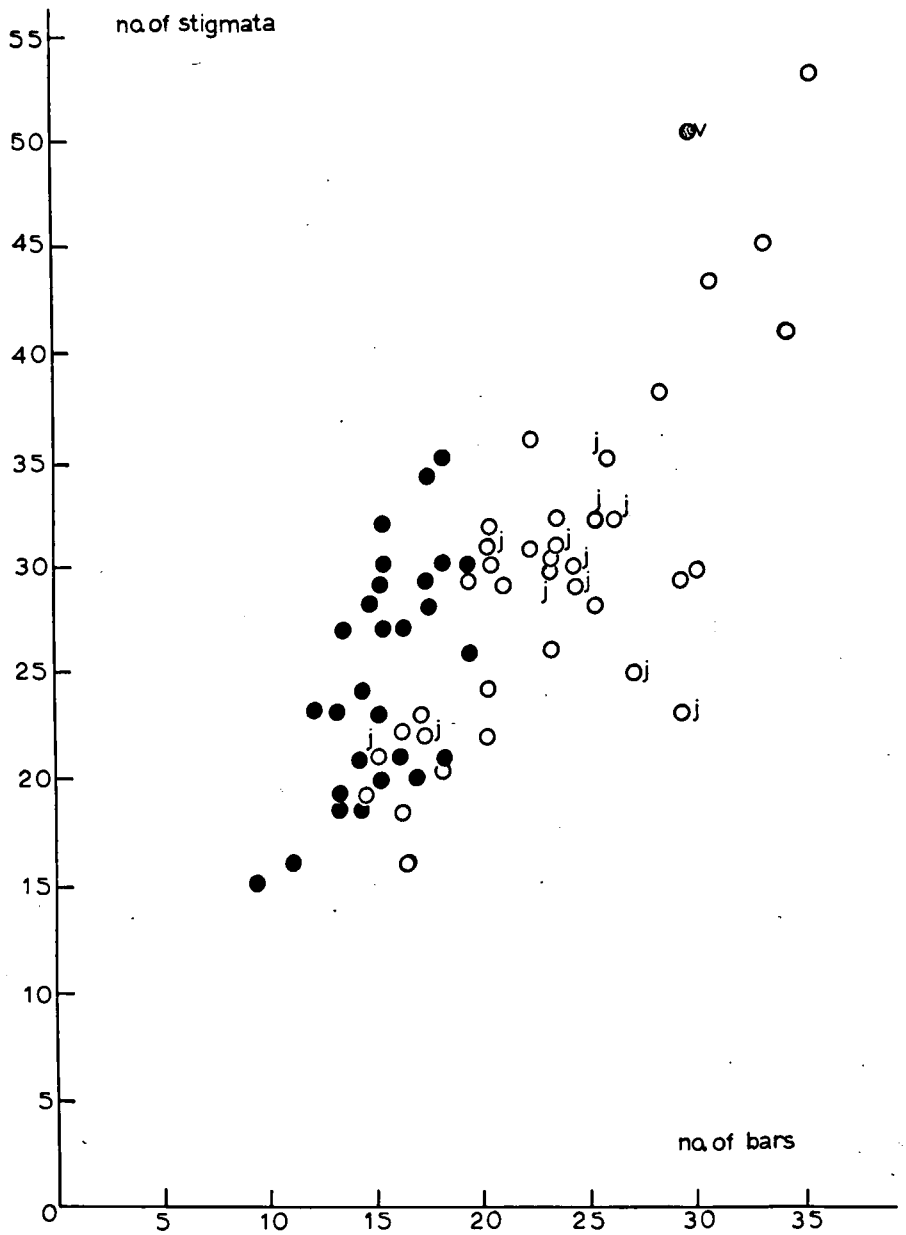

Fig. 5. Relation between the number of branchial stigmata (vertical axis) and branchial bars (horizontal axis) in zooids of *P. agassizi* (black dots) and *P. spinosum* (open circles). Zooids from dome-shaped colonies are indicated by a "j". Data given by Ivanova-Kazas (1956) for *P. vitjasi* are indicated by a "v".