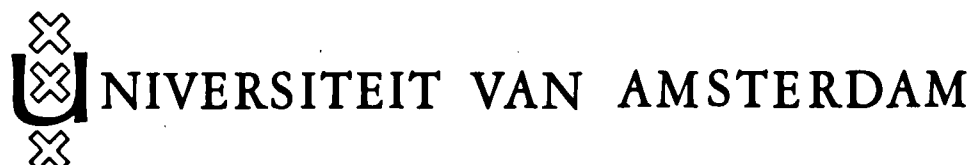


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HISTOLOGY OF THE SEMINAL VESICLES IN THE "SAGITTA SERRATODENTATA-GROUP"

(CHAETOGNATHA)

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ABSTRACT

The histology of the seminal vesicles of *Sagitta serratodentata*, *S. pseudoserratodentata*, *S. pacifica*, *S. tasmanica*, and *S. bierii* is described. To conclude from the structure of these vesicles *S. serratodentata*, *S. pseudoserratodentata*, and *S. pacifica* are closely related. For both *S. tasmanica* and *S. bierii* no relations with other species could be traced. *S. bierii* is considered the most primitive species of the group.

INTRODUCTION

General descriptions of the seminal vesicles in chaetognaths were given by Hertwig (1880) and Grassi (1883). Tokioka (1939), commenting on the structure of the seminal vesicles in different species, distinguished four types of seminal vesicles. Those found in the *Sagitta serratodentata*-group (Tokioka's *serratodentata* type) were found to be the most complex, consisting of a knob with

various structures and a trunk. According to Tokioka, the form later described as *S. pacifica* Tokioka, 1940, shows 5 to 10 chitinous teeth; *S. serratodentata* Krohn, 1853, has two pointed papillae, and *S. pseudoserratodentata* Tokioka, 1939, a finger-shaped protuberance. Thomson (1947) described *S. tasmanica* as a new subspecies with, on the seminal vesicle, a small pyriform knob.

S. selkirki Fagetti, 1958, from Chilean waters shows a seminal vesicle with numerous soft protuberances on the knob. *S. bierii* Alvarifio, 1961, has a triangular to pear-shaped seminal vesicle with one prominence on the knob.

To determine the taxonomic value of the different types of the seminal vesicles one has to know the function, morphology, anatomical homologies, and ecological importance of those differences. The following study is an attempt to arrive at such an interpretation, on the base of histologi-

cal studies.

In an earlier paper (Pierrot-Bults, 1974) the taxonomy and zoogeography of the *serratodentata*-group were discussed. Possible relationships between the constituting taxa were indicated which can be evaluated now by the present results.

MATERIAL AND METHODS

The material on which this study is based is preserved in the following museums:

- B.M. : British Museum (Natural History), London;
 U.S.N.M. : United States National Museum, Washington;
 Z.M.U.C. : Zoologisk Museum, Copenhagen;
 R.M.N.H. : Rijksmuseum van Natuurlijke Historie, Leiden;
 Z.M.A. : Zoölogisch Museum, Amsterdam.

Numerals in parentheses in the text and in the explanation to the figures refer to the numerals in table I.

All specimens were fixated and preserved in formalin 4% or alcohol 70%. The unique specimen of *pseudoserratodentata* could only be studied for the general morphology and not be sectioned. This specimen and the holotype of *S. bierii* were drawn

without staining. The *S. bierii*-like specimen from African waters (15) together with the specimens 3, 9, 12 and 17 of table I were stained with KOH-Alisarine-Cresyl after De Fluiter (Pierrot-Bults, 1974) to study the general morphology.

The other specimens of *S. serratodentata*, *S. tasmanica*, *S. bierii*, *S. selkirki* and *S. pacifica* were embedded in paraffine and cross-sectioned 5 μ thick. The *serratodentata* specimen 2 was stained with Haematoxyline-eosine. The remaining specimens were stained after Crossmon. Staining methods were adapted after Romeis (1948). When not mentioned otherwise the Crossmon stained specimens are used for the descriptions.

MORPHOLOGY OF THE SEMINAL VESICLES

The general morphology of the seminal vesicles of the *serratodentata* type was described by Tokioka (1939). They consist of a voluminous knob, on which this study is particularly focussed, and a trunk, situated laterally of the tail segment between the posterior and caudal fins, touching the former. They are placed with the knob pointing in an anterior direction. Dependent on development and filling the long axis of the vesicle may shift its position from parallel to perpendicular to the body axis.

TABLE I

MATERIAL USED

1	<i>S. serratodentata</i>	22° 02'N 20° 35'W	5-XII-1964	Z.M.A.	1 specimen
2		31° 59'N 63° 43'W	27- IV-1969	U.S.N.M.	1 specimen
3		25° 11'N 19° 35'W	31- I-1965	Z.M.A.	1 specimen
4	<i>S. pseudoserratodentata</i>	"Californian waters"		B.M.	1 specimen
5-6	<i>S. pacifica</i>	31° 33'S 30° 07'E	27- I-1930	Z.M.U.C.	2 specimens
7-8		00° 27'S 126° 54'E	11- IV-1930	R.M.N.H.	2 specimens
9		Great Barrier Reef Exped.	1929	B.M.	1 specimen
10	<i>S. tasmanica</i>	44° 54'N 55° 56'W	7-III-1953	Z.M.A.	1 specimen
11		51° 57'S 167° 38'E	28-III-1912	B.M.	1 specimen
12		45° 00'N 16° 06'W	5- VI-1966	Z.M.A.	1 specimen
13	<i>S. bierii</i> holotype	30° 06'N 118° 25'W	24- IV-1958	U.S.N.M.	1 specimen
14		"Californian waters"		B.M.	1 specimen
15	<i>S. cf. bierii</i>	04° 16'N 08° 18'W	10- I-1948	Z.M.U.C.	1 specimen
16-17	<i>S. selkirki</i>	Juan Fernandez	21-XII-1959	Z.M.A.	1 specimen

The wall cells are rather thin except on the anterior side where they form a glandular area.

The opening to the exterior is situated on the anterolateral side, either somewhat towards the dorsal side (*S. pacifica*) or the ventral side (*S. pseudoserratodentata*) (Tokiooka, 1939).

In figure 1 the seminal vesicles of the taxa of the "*S. serratodentata*-group" are compared, based on the original descriptions of the taxa. The seminal vesicles of *S. tasmanica* and *S. selkirkii* (figs. 2a and 2b, respectively) show the same morphology although their sizes differ. The specimen of *S. tasmanica* drawn (10), has lost the soft protuberance on the anterolateral side which is frequently found in this species. *S. bierii* (fig. 2c) shows a rather simple type of seminal vesicle with one slight protuberance on the anterior side of the knob. The lateral margin of the knob seems to have a glandular function. Figure 2d shows the seminal vesicle of a specimen from West-African waters. This specimen and also its vesicles show the same characters as *S. bierii* from the East-Pacific. *S. serratodentata*, *S. pseudoserratodentata*, and *S. pacifica* are shown in figures 2e, 2f and 2g, respectively. The knobs in these 3 taxa show on the anterolateral side the same cell types; in *S. serratodentata* they form two papillae, in *S. pseudoserratodentata* one papilla, and in *S. pacifica* a row of teeth-like structures.

HISTOLOGICAL RESULTS

S. tasmanica and *S. selkirkii* (figs. 2a, b, 3-4, 11)

The seminal vesicle consists of a clearly demarcated knob and trunk. The knob is less conspicuous than in *S. serratodentata*. Anteriorly, it consists of a layer of glandular epithelium. Laterally, this epithelium is cuboid, without a glandular function and is lined exteriorly by a structureless layer, the cuticle. Antero-exteriorly the glandular epithelium is covered by a bunch of protuberances made up of loose tissue. This is shown in figure 2b for *S. selkirkii*. The specimen of *S. tasmanica* (10) shown in figure 2a has lost these protuberances, which, however, are frequently found in this species.

Figure 3 shows part of a cross-section through

the knob of *S. tasmanica*. The protuberances appear to consist of longitudinally stretched cells with large basal nuclei and a glandular function. The nuclei stain homogeneously green.

The slightly reticulated cytoplasm stains green and shows numerous secretion granulae in the middle of the cells. Near the cell top these granulae become larger and change into secretory droplets. Contrary to the secretion filling the lumen of the knob which stains green, the external secretion of the protuberances is staining red.

A cross-section through the knob of *S. selkirkii* (fig. 4) shows the protuberances lined with the glandular cells of the knob. These consist of columnar epithelium with large basal nuclei showing red-staining chromatine. The cytoplasm is slightly vacuolized and reticulated. Numerous secretion granulae staining green can be observed, both in the inner glandular cells as well as in the lumen of the knob.

Laterad of the protuberances, the epithelium is interrupted by a double row of epidermal cells with very dark-green staining basal nuclei and light-green staining cytoplasm (fig. 11). The two rows are encircled by a continuous basal membrane. The cells are not glandular, they are arranged so as to form with their top walls a straight line where they touch. Figure 11 shows this layer in anterior view. This complex probably is the place of the initial burst of the seminal vesicle. Underneath these epithelial rows of cells, no glandular cells are present so that they discharge immediately to the lumen of the vesicle. No other tissues are found on top of these epithelial rows. The glandular cells of the protuberance are orientated with their top towards the median line of the two epithelial cell rows.

According to Ghirardelli (1968) in *S. enflata* Grassi, 1883, and *S. bipunctata* Krohn, 1853, the small cup which closes the orifice of the seminal vesicle can be detached quite easily together with the spermatophore. This cup may be fixed to the body of a specimen of the same species, thus attaching the spermatophore. The cells closing the orifice of the seminal vesicle must then be able to secrete an adhesive substance. Laterally the knob is covered with a cuticle and a layer of simple cuboidal epithelium, without glandular function.

The trunk of the vesicle consists of a layer of

cuticle with a layer of simple epithelium underneath with clear nuclei and very light-green staining cytoplasm. The lumen of this trunk is full of sperm, staining red and green.

S. bierii (figs. 2c, d, 5-6)

The seminal vesicle consists of a knob and a trunk, but the division is less clear than in the other species of the group (fig. 2c). The knob lacks the elaborate structure seen in *S. pacifica* and *S. serratodentata*.

Ventrally the knob consists of a disk-like structure on which the soft tissue forming the single papilla is situated (figs. 2d and 5). The disk consists of a layer of cells with large dark-staining nuclei on the margin of the disk and the connective tissue in the centre. The disk is situated in about the same place as the two papillae, the teeth-like row, or the soft protuberances in *S. serratodentata*, *S. pacifica* and *S. tasmanica*, respectively, but does not show any similarity in structure with either of them.

The knob consists dorsally of a layer of epithelium with very large dark-staining nuclei, covered on the outside by a thin cuticle. This epithelial layer has a glandular function, filling the lumen of the knob with secretory product. The cells at the lateral margin of the knob do not show this glandular function (fig. 5). The glandular epithelium on the dorsal side of the knob continues along the median side.

The trunk of the seminal vesicle consists of a layer of glandular epithelium on all sides (fig. 6), which provides the lumen of the trunk with secretion. Embedded in this secretion sperms can be observed, staining green. The trunk is externally covered by a cuticle. The specimen of *S. bierii* used for sectioning showed one vesicle broken down and one vesicle partly filled.

S. serratodentata (fig. 2e, 7-9)

The seminal vesicle consists of a clearly demarcated knob and trunk. *S. serratodentata* bears two papillae on the anterolateral side (fig. 2e), although some variation does exist. Sometimes only one papilla is present and in old vesicles which were probably filled and emptied several times the whole knob structure may be lost or damaged.

In cross-section these papillae consist of large cells with large apical nuclei (fig. 7). These nuclei show red staining chromatine. The cytoplasm stains dark green and is rather homogeneous, although slightly more hyaline apically. Lining the inner side, a columnar epithelium with large basal nuclei is found. These nuclei show light-red staining chromatine. The cytoplasm is reticulated and vacuolized, showing small and large green staining secretion granulae. The lateral sides of the knob of the vesicle consist of a layer of uni-stratified columnar epithelium with basal nuclei showing less chromatine than the glandular epithelium. The outside of this epithelium bears a cuticle-layer.

Figure 8 shows part of a cross-section through the knob just below the papillae. The wall of the knob consists here of a layer of epithelium with clear nuclei, containing a small contents of chromatine, without glandular function and covered by a cuticle. The lumen of the knob is filled with green staining secretion granulae, like those seen in the glandular cells in figure 7.

Figure 9 depicts part of a cross-section through the trunk of a seminal vesicle. This wall consists of a connective-tissue-like layer covered with cuticle. The lumen of the trunk is filled with a sperm mass staining partly red, partly green.

S. pacifica (figs. 2g, 10, 12-13)

The knob of the seminal vesicle of *S. pacifica* is the most conspicuous in the whole group. The anterolateral side is covered with a mass of large, very dark-green staining cells with apical nuclei (fig. 10). These nuclei show a small amount of red staining chromatine, but they are rather hyaline. The cytoplasm in these cells is homogeneously staining dark-green. This anterolateral cell mass is homologous with the cells forming the papillae in *S. serratodentata* (fig. 7) and forms the tooth-like row described by Tokioka (1939) as chitinous teeth in *S. pacifica*. The assumption that chitin is present in these "tooth cells" is incorrect. A component like secreted chitin was not found and the staining did not give any indication of the presence of chitin, neither in the "tooth cells" of *S. pacifica* nor in the papilla-cells of *S. serratodentata*.

The cross-section of which part is shown in figure 8 is partly through the knob, partly through the trunk of the vesicle. Underneath the "tooth cells" a glandular epithelium, in this part of an inactive appearance, is found. A few basal nuclei are staining homogeneously green and the cytoplasm is vacuolized and reticulate, staining very light-green, whereas no secretory products are seen. More anteriorly this glandular epithelium shows green staining granulae in the cells, the same secretory product was observed in the lumen of the knob. In figure 10 a red-and-green staining sperm mass is seen in the lumen of the trunk.

More towards the tail wall the lumen is lined by a uni-stratified epithelium with homogeneously green staining nuclei and light-green staining cytoplasm. This epithelium is covered by a cuticle. Laterad of the "tooth-cells" in the figure a few cells with dark-green staining nuclei are indicated. These probably are the posterior most cells of the place of initial burst.

Figure 12 illustrates a cross-section through the anterior part of the knob showing the place of such an initial burst. The same type of cell configuration was observed in *S. selkirkii* (fig. 11). On the lateral side of the vesicle the place of initial burst is characterized by a simple epithelium. In cross-section the cells constituting the tooth-like row are seen on both sides of this epithelium (fig. 13).

According to Tokioka (1939) the place of initial burst is situated on the dorsal side of the vesicle, but in my slides this could not be ascertained, sometimes it is seen on the dorsal side, but in other instances it is situated more ventrally. This may be due to the damaging effect of embedding and staining.

S. pseudoserratodentata (fig. 2f)

Unfortunately no specimens of *pseudoserratodentata* were available for histological sections. Consequently, figure 2f gives the intact seminal vesicle of *S. pseudoserratodentata*. The seminal vesicles of this species resemble very closely those of *S. serratodentata* (fig. 2e).

The knob consists of a glandular inner epithelium, its lumen is filled with secretory products. On the anterolateral side one finds a single papilla, composed of large cells with clear nuclei.

The cells seem to be homologous with the cells giving rise to the papillae of *S. serratodentata* and the "tooth cells" of *S. pacifica*. The trunk of the seminal vesicle consists of a thin layer of tissue surrounding the lumen of the trunk which is partly filled with sperm.

DISCUSSION

The vesicles in the *serratodentata*-group are composed of two parts, the knob and the trunk.

The morphology of the trunk is fairly similar in all the taxa of the group, the knob shows a clear diversity (fig. 2). Specific differences are found in the structural characters of the anterior part of the knob. The cytology of the knob structure in *S. serratodentata*, *S. pseudoserratodentata*, and *S. pacifica* indicates a close relationship between the three taxa. The large dark staining cells forming the two papillae, the single papilla and the "tooth-cells" are homologous.

The relationship of *S. serratodentata*, *S. pseudoserratodentata*, and *S. pacifica*, and at the other hand, *S. tasmanica* is less clear. The knob structure of *S. tasmanica*, with its soft glandular protuberances, takes a separate position.

The same is true for *S. bierii* which has one soft protuberance at the anterior side. The structure of the knob of *S. bierii* does not reveal a close relation between this species and any of the others in the *serratodentata*-group. The presence of glandular epithelium throughout the trunk seems to be a primitive feature. The same is found in very simple seminal vesicles like those found in *S. planctonis* (vide Pierrot-Bults, 1975) where the glandular layer is found on all sides of the vesicle.

In how far the shape and structure of the seminal vesicle is relevant to the transmission of sperms is uncertain. The literature references on sperm-transmission from the seminal vesicles to the seminal receptaculum in the ovaries do not point to a direct contact of sexual organs. It is very dubious whether the differences in vesicle structure constitute a mechanical barrier to the precopula (Jägersten, 1940; David, 1958; Dallot, 1967; Ghirardelli, 1968). Essential differences in the opening and closing mechanism of the vesicle (the place of initial burst), which are directly linked with the possibility of refilling of this

organ, could not be traced. In all taxa of the group refilling seems possible because the mechanism for opening and closing is present.

No obvious explanation is available for the differences found in the structure of the seminal vesicles within the "*serratodentata*-group". Comparing the histological structure with the other taxonomic characters (Pierrot-Bults, 1974), a discrepancy is obvious for some of the taxa. The great difference between *S. tasmanica* and *S. serratodentata* is not reflected in their resemblance in other characters. Ibanez (1969) found a close relationship between *S. pacifica*, *S. pseudoserratodentata*, *S. serratodentata* and *S. tasmanica*. *S. bierii* was somewhat less close but still in the same group as far as his analyses were concerned. The study of Grant (1967) established a close relationship between *S. serratodentata* and *S. tasmanica*, indicating the possibility of interbreeding in contact zones.

The relationship of *S. pacifica*, *S. pseudoserratodentata* and *S. serratodentata* as seen by their distribution pattern (Pierrot-Bults, 1974) is strongly supported by the histological structure of their seminal vesicles, the latter having an elaborate knob and a simple trunk wall.

The distribution of *S. tasmanica* points to a close relationship with *S. serratodentata*, but the structure of the seminal vesicle does not support such a relationship, since the vesicle of *S. tasmanica* shows a different knob structure and a somewhat thicker trunk wall.

The position of *S. bierii* is less clear. The distribution of this taxon in south- and central-eastern Pacific waters and in south-eastern Atlantic waters, together with the more primitive characters of the seminal vesicle structures, particularly the trunk wall covered with glandular epithelium, indicate a relic-distribution.

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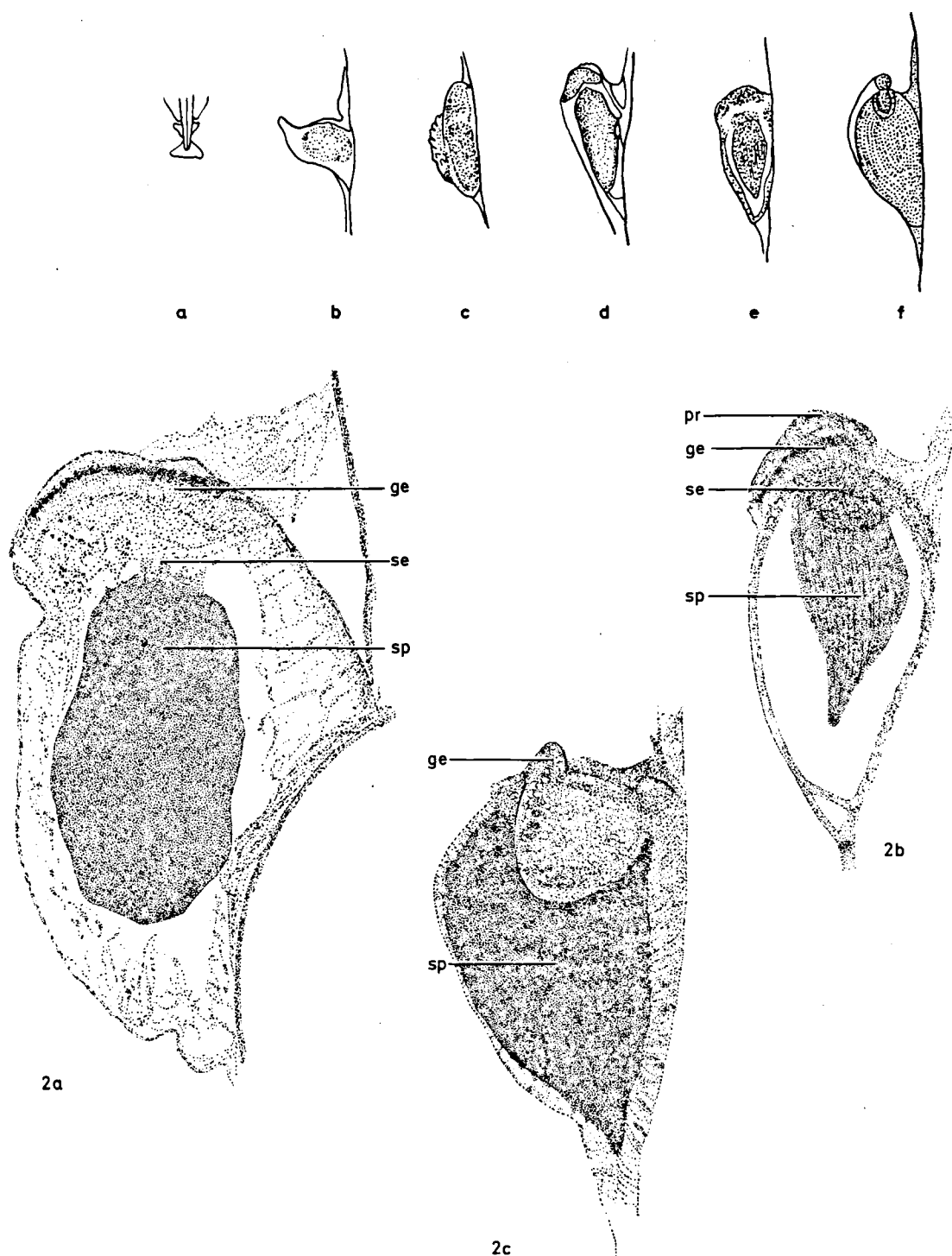


Fig. 1. Seminal vesicles based on the original illustrations of
 a, *S. serratodentata* Krohn, 1853; b, *S. pseudoserratodentata* Tokioka, 1939; c, *S. pacifica*
 Tokioka, 1940; d, *S. tasmanica* Thomson, 1947; e, *S. selkirki* Fagetti, 1958; f, *S. bierii*
 Alvarado, 1961.

Fig. 2. Seminal vesicles of a, *S. tasmanica* (12); b, *S. selkirki* (17), and c, *S. bierii* (13).

Numerals in parentheses refer to the numerals in table I.

ge: germinal epithelium; se: secretion product; sp: sperm; pr: protuberances.

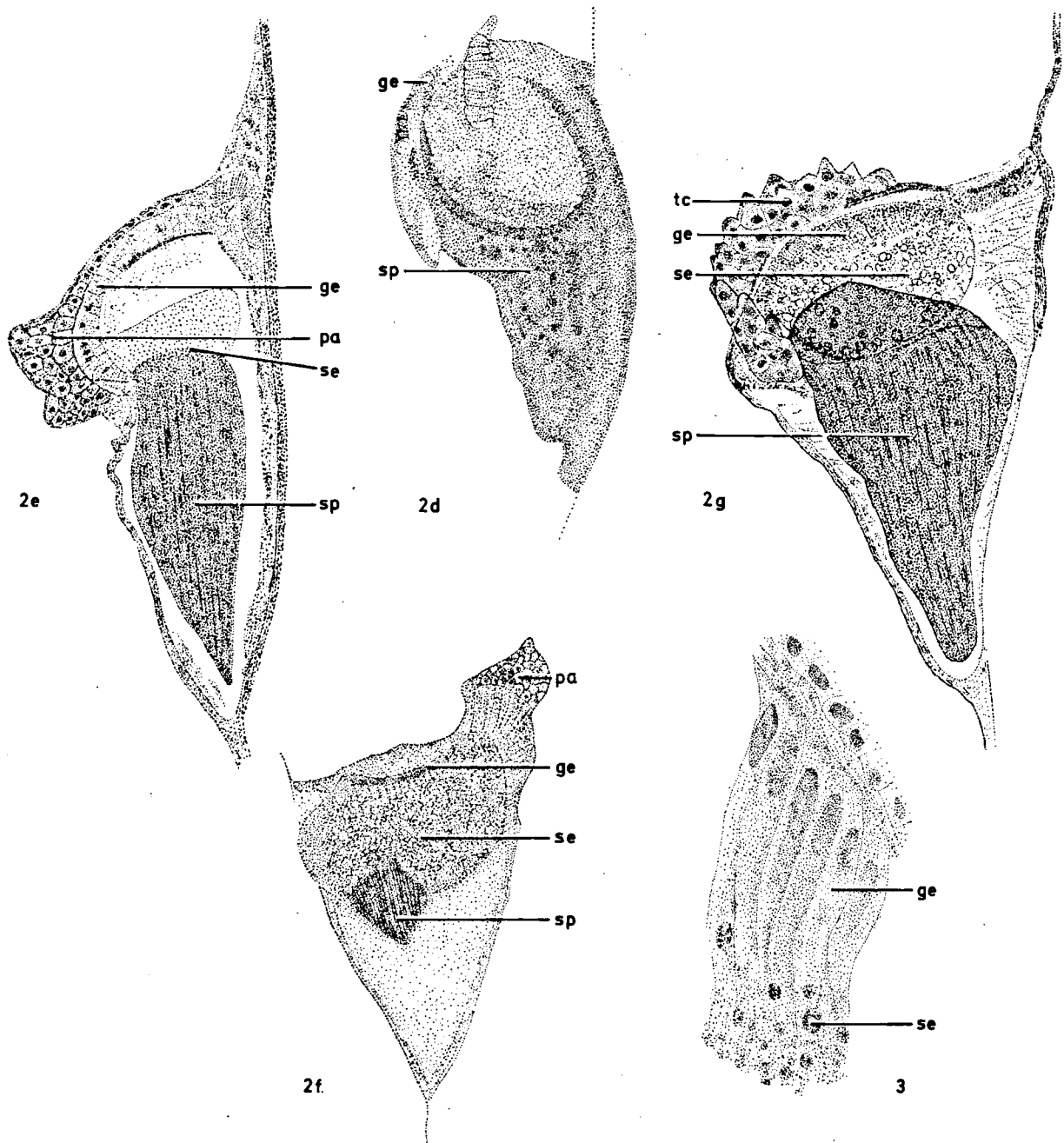


Fig. 2. (contd.) Seminal vesicles of d, *S. cf. bierii* (15); e, *S. serratodentata* (3); f, *S. pseudo-serratodentata* (4), and g, *S. pacifica* (9).

Fig. 3. Cross-section through the knob of the seminal vesicle of *S. tasmanica* (10) showing the soft glandular protuberances.

Numerals in parentheses refer to the numerals in table I.

ge: germinal epithelium; se: secretion product; sp: sperm; pa: papilla; tc: tooth cells.

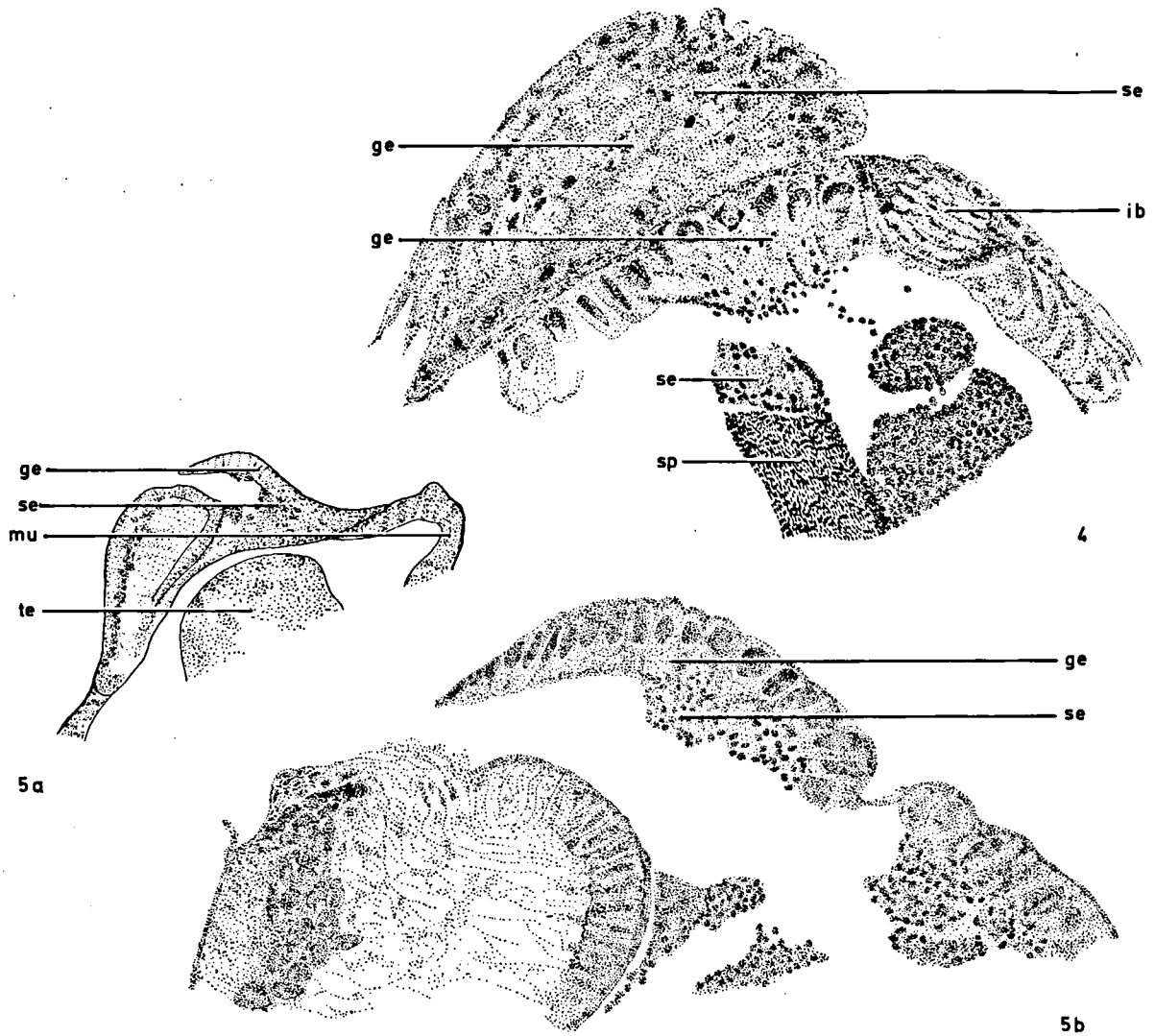


Fig. 4. Cross-section through the knob of the seminal vesicle of *S. selkirkii* (16).

Fig. 5. Cross-section through the knob of the seminal vesicle of *S. bierii* (14); a, overall picture; b, enlargement of part of the knob.

Numerals in parentheses refer to the numerals in table I.

ge: glandular epithelium; se: secretion product; sp: sperm; pr: protuberances; ib: place of initial burst; mu: muscles; te: testes.

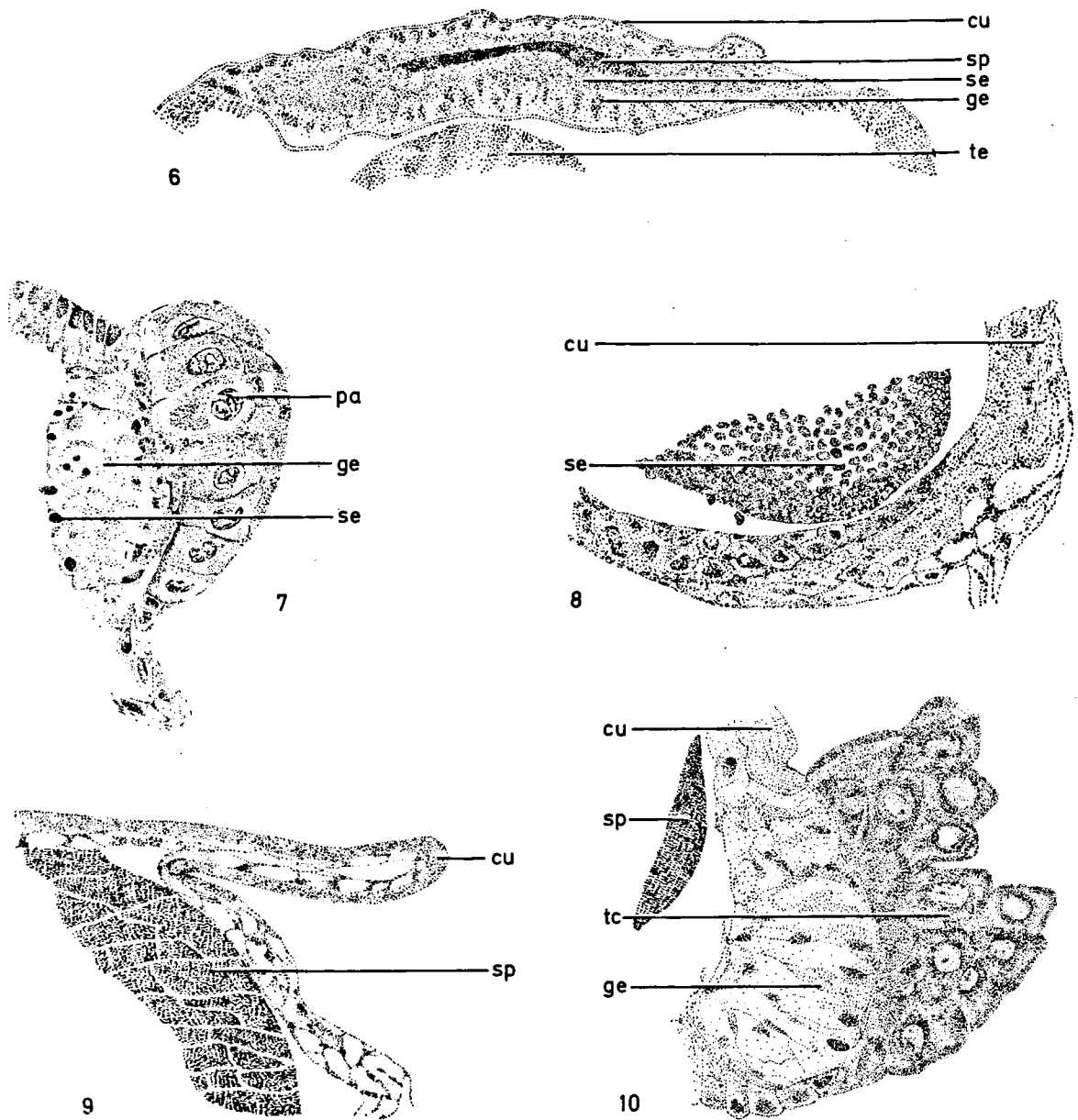


Fig. 6. Cross-section through the trunk of the seminal vesicle of *S. bierii* (14).

Fig. 7. Cross-section through the knob of the seminal vesicle of *S. serratodentata* (1) showing the papillae.

Fig. 8. Cross-section through the knob of the seminal vesicle of *S. serratodentata* (1) just behind the knob.

Fig. 9. Cross-section through the trunk of the seminal vesicle of *S. serratodentata* (1).

Fig. 10. Cross-section through the knob of the seminal vesicle of *S. pacifica* (7).

Numerals in parentheses refer to the numerals in table I.

ge: glandular epithelium; se: secretion product; sp: sperm; pa: papilla; cu: cuticle; tc: tooth cells; te: testes.

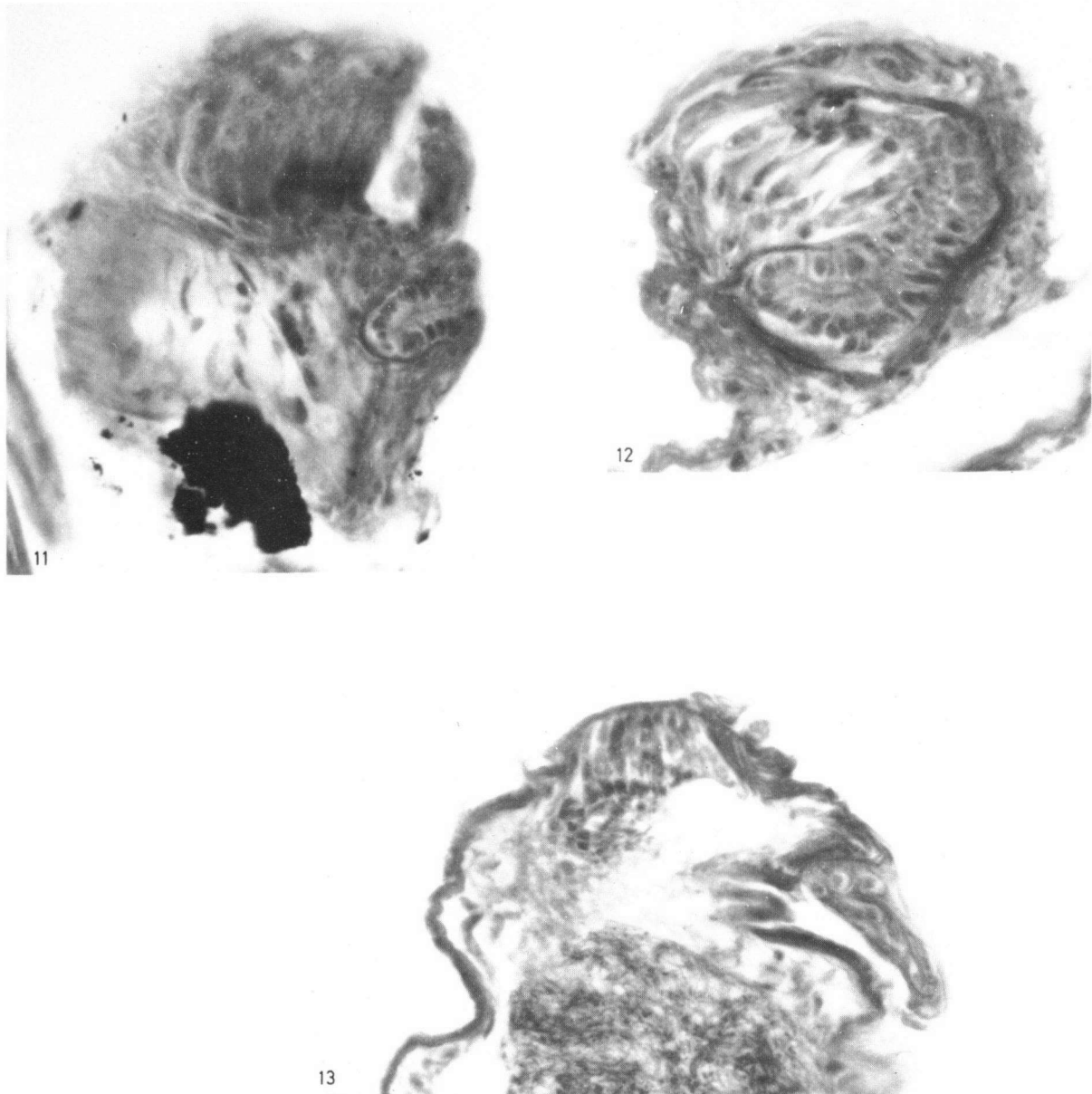


Fig. 11. Photomicrograph of a cross-section through the knob of the seminal vesicle of *S. selkirkii* (16) showing the place of initial burst.

Fig. 12. Photomicrograph of a cross-section through the knob of the seminal vesicle of *S. pacifica* (8) showing the place of initial burst.

Fig. 13. Photomicrograph of a cross-section partly through the knob, partly through the trunk of the seminal vesicle of *S. pacifica* (6) showing the place of initial burst lined on both sides by tooth cells.

Numerals in parentheses refer to the numerals in table I.

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