ON THE FUNCTIONAL MORPHOLOGY OF THE FAMILY VERTICORDIIDAE (BIVALVIA) WITH DESCRIPTIONS OF NEW SPECIES FROM THE ABYSSAL ATLANTIC

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[Plate 58]

To C.M.Y.
and with appreciation to *they who rather dive than soar* (Wordsworth) quoted
by Jeffreys in his description of '*Lyonsia*' *formosa* taken by the 'Lightning'
and 'Porcupine' Expeditions

CONTENTS

This study forms part of a larger study on the ecology and functional morphology of deep sea bivalves of the Atlantic. Eighteen living species of the family Verticordiidae are described, of which eight are new species. The descriptions include shell morphology and a detailed analysis of anatomy, particular attention being paid to the mantle, gills and alimentary canal.

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The Verticordiidae are only taken in deep water and form a small but persistant fraction of the bivalve fauna. They have a morphology that is intermediate between species of the order Anomalodesmacea and the septibranch species of the Poromyidae and Cuspidariidae, and this study shows that the latter two families have been derived from the Anomalodesmacea. The structure of the hinge is very similar to that of species of the latter order as, too, is the gill which, although reduced, is typically eulamellibranch in form. Progressive reduction in the size and the number of lamellae of the gill is evident. With reduction there is an increase in the extent of the gill membranes that are attached by tissue fusion to the mantle, the body and the septum between inhalent and exhalent apertures, i.e. an intermediate stage between the eulamellibranch and septibranch conditions.

In contrast, most of the eighteen species have a stomach identical to that of the septibranch families. However, one or two species show limited ciliated surfaces intermediate in extent between the anomalodesmacean, as exemplified by *Lyonsia*, and the septibranch condition.

In addition, the Verticordiidae show features peculiar to themselves. The mantle edge is glandular. The glands take the form of discrete multicellular radial structures. The region of inhalent and exhalent tentacles is richly supplied with papillae that secrete an adhesive fluid. The secretion has two functions; to assist the animal to maintain a position at the surface of the very soft abyssal sediment, and to capture food organisms such as copepods. The sticky tentacles are spread out over the surface of the sediment. On capture the food is 'licked' off the tentacles by an inhalent valve and falls, or is carried, to a posteriorly facing buccal funnel formed by the expanded lips. The palps are extremely reduced in size. Oesophagus and stomach are muscular and the stomach is lined with a scleroprotein and is a crushing organ. It is interesting to note that the rectal region of the hind gut is expanded, probably to assist in further digestion of food remains. This is a further example of hind gut modification in abyssal bivalves, where it is essential that food should be utilized to the full.

Other unusual features are the large size of the kidney, often extending along each side of the body as far forward as the mouth. Associated with the kidney is a lacunar system of unknown function. The Verticordiidae are hermaphrodites, producing small numbers of large eggs. Prodissoconch measurements indicate that they have at most a short pelagic life. However, individual species are widespread, many being found on both sides of the Atlantic from arctic to equatorial latitudes.

INTRODUCTION

Since 1962, the abyssal fauna of the Atlantic has been investigated by Dr H. L. Sanders of the Woods Hole Oceanographic Institute and his co-workers. The aims and methods used in these continuing investigations have been described by Sanders, Hessler & Hampson (1965) and Sanders & Hessler (1969).

The present paper forms part of a series on the taxonomy, ecology and functional morphology of deep sea bivalves (Allen 1971, 1973; Allen & Sanders 1966, 1969, 1973; Sanders & Allen 1973). Although individual stations show a wide range of variation, bivalves form approximately 10 % by number of the abyssal benthic fauna. Three groups predominate in the soft oozes, namely the Protobranchia, Thyasiridae and Septibranchia. The Septibranchia form a small but constant portion of the fauna. While total numbers are small, never more than 5 % of the total number of bivalves present, the numbers of species may be 20 % of those present at any one station. The distributional pattern of the Septibranchia is echoed by the members of the family Verticordiidae. Although there has been differing opinion as to whether the Verticordiidae are members of the Anomalodesmacea or the Septibranchia there is no doubt that they have a very large number of septibranch characters.

HISTORICAL

The Verticordiidae are among the least known of the recent bivalves and this is largely due to their rarity and restriction to deep water. Their taxonomy is both complex and confusing. They were first recorded as fossils – the earliest from the Eocene – the type genus *Verticordia* (S. Wood) being a Crag species† (Gray 1840; 1842; Sowerby 1844). Sowerby (1844) quotes

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† The type species being *V. cardiiformis* (Sowerby 1844).

Wood's manuscript description of this specimen and points out its similarity to a shell† described by Philippi (1844) and referred by him to the genus *Hippagus* of Lea (1833). However, Jeffreys (1878, 1881) and Dall (1886), who re-examined Lea's specimens, showed that *Hippagus* Lea is a mytilid, close to the genus *Crenella*. da Costa (1850) had earlier and similarly agreed that the specimens in the Philippi collection were not the same as *Hippagus* and concluded that they were to be placed in the genus *Iphigenia* of Schumacher (1817). Woodward (1851–6) disputed both opinions, believing that there was no resemblance to either *Hippagus* or *Iphigenia*, and resurrected the genus *Verticordia*. This conclusion was confirmed by Seguenza (1860) who gave detailed descriptions of *V. acuticostata* (Philippi) and *V. granulata* Seguenza, both fossil species from Sicily. In the same year Fischer (1860) also concluded that *Verticordia* and *Hippagus* were separate genera and, in addition to the three species already referred to, listed another fossil species within the genus *Verticordia* (*V. parisiensis*, Deshayes 1856–65) and two shallow water recent species, namely, *V.* (= *Trigonulina*) *ornata* (d'Obigny) and *V.* (= *Hippagus*) *novemcostatus* (Adams and Reeve)‡ from Samarang (Adams & Reeve 1848). Subsequent to this date a number of species, both fossil and recent, were included within the Verticordiidae (see, for example, Fischer 1862, Adams 1862 – for a complete list of recent species see appendix, p. 521). *V. japonica* (probably synonymous with *V. acuticostata*) Adams was the first recent species for which the anatomy was described. However, there were no specific verticordiid characters given in this description. Fischer (1862) repeated this description, appending a list of species which he included in the genus *Verticordia*.

Meneghini (1851) established a new genus *Pecchiolia* for the miocene fossil *Chama argentea* Mariti (= *C. arientina* Brocchi) to which was added the fossil *Pecchiolia arenosa* (Raynwal) (= *V. macrodonta* Seguenza) by Appelius (1870). A little later, G. O. Sars (1872) added a recent species to this genus. This latter species had first been collected off the Norwegian coast by Sars' father, who had named it *Lyonsiella abyssicola* but without description (M. Sars 1868). *Pecchiolia abyssicola* was also recorded by Jeffreys (1881) from the extensive dredgings that were taking place at this time off the west of Scotland and Norway. Sars (1872) pointed out that *P. abyssicola* was closely related to *Verticordia*, *Hippagus* and *Trigonulina*, but at the same time noted that there were differences between the shell characters of *P. abyssicola* and *V.* (= *P.*) *argentea* and *V.* (= *H.*) *acuticostata*.

This latter work came at the beginning of an era of extensive zoological and palaeontological explorations and, in particular, when sampling of deep-sea muds was producing rich rewards in new species. Coincident with this was an awareness by biologists on both sides of the Atlantic of the considerable taxonomic confusion that existed and as a result a number of papers appeared within a short time of one another, some attempting to clarify the taxonomy of the verticordiids, some adding more species and some doing both of these (Seguenza 1876; Jeffreys 1876, 1881; Verrill 1880, 1882*a*, *b*, 1884, 1885; Dall 1881, 1886, 1889*a*, *b*). That of Heilprin (1882) sets a high standard in analysing the verticordiid position, being concerned specifically with the problem identified by Sars (1872), yet in the final analysis he makes no clear and specific conclusion as to whether or not *Hippagus*, *Verticordia* and *Pecchiolia* are congeneric, although on balance he favours separate identity. In contrast, Jeffreys (1881) believes that *Verticordia* (Wood) was a synonym of *Pecchiolia* (Merghini).

For reasons of confused synonymy and common usage, Friele (1879, 1886) reintroduced the

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† *H. acuticostatus* Philippi, 1844.

‡ Later shown to be a member of the Carditidae.

generic name *Lyonsiella* for *Pecchiolia*. There was no doubt about the confusion, for Chenu (see, for example, Pecchioli 1852) thought *Pecchiolia* to be a subgenus of *Diceras* Lamarck, and Woodward (1851–6), among others, regarded it as being synonymous with *Isocardia* Lamarck. But despite this confusion, the description by Sars (1872) of *Lyonsiella* (= *P.*) *abyssicola* was the first in which both shell and anatomy of a living species of the Verticordiidae were described with any degree of accuracy, and from which uniqueness of the group was evident. In comparison with groups suggested by other authors to be related to the Verticordiidae (Trigonidae, H. & A. Adams 1858; Woodward 1868; Deshayes 1856–65; Chenu 1842; Carditidae, Phillipi 1844; Cyprinidae, Woodward 1851–6; A. Adams 1862; Chamacea, Stoliczka 1870–1†), Sars (1872) was also able to point out the similarity of the verticordiid species to the Anatinidae (= Anomalodesmacea), and to *Lyonsia* and *Mytilimeria* in particular. By 1880 most authorities (e.g. Jeffreys 1881; Tryon 1882) agreed that the verticordiids were most closely related to the Anatinidae and to *Lyonsia* in particular. In fact it will be shown that the species *Lyonsia formosa* described by Jeffreys (1881) should be included in the Verticordiidae (see p. 447 *et seq.*). But, no clear distinctions between the genera were made before those of Dall (1886) which defined the sub-genera, *Verticordia*, *Trigonulina*, *Euciroa*, *Pecchiolia*, *Halaris* and *Lyonsiella*. Subsequently Dall (1892, 1895, 1903) extended his observations on the group and added further genera – *Euciroa* and *Halicordia*.

Most of the authors mentioned up to this point described new species or extended the localities of existing species, and from the 1880s to the present time new genera and species have been described and discussions continued on specific and generic synonymies. In the course of our review of the literature of this group we have been able to compile a check list of the recent species with relevant authority, and this we present as an appendix on p. 521. Furthermore, we have been able to define more precisely the characters of the genera and these we give at the beginning of morphological section.

In 1888, Pelseneer reported on investigations that he had carried out following a suggestion by Dall (1886) that *Cuspidaria* had neither gills or palps. Pelseneer (1888*a*, *b*) found that, instead of the usual filamentous gill, there was a membrane and that palps, although small, were present. He also compared *Cuspidaria* with *Lyonsiella* and concluded that the membrane in *Cuspidaria* could be explained in terms of further modification of the lyonsiellid condition and that, the form of the gill of *Lyonsiella* was intermediate between the eulamellibranch gill of *Lyonsia* and the septum or 'membranous gills' of *Cuspidaria* and *Poromya*. He concluded that the latter two genera were sufficiently distinct from the Anatinacea (*sensu stricto*) to erect a subgroup, the Septibranchia, for the genera *Poromya*, *Silenia* and *Cuspidaria*; the first two he included in the family Poromyidae and the latter in the family Cuspidariidae. However, although he distinguished the intermediate position of *Lyonsiella* he did not include the genus within the Septibranchia, but referred to it as belonging to the group Anatinacea *s. lat.*

The dichtomy has remained until the present; on the one hand the Septibranchia being regarded by some as a major subdivision of the Bivalvia and on the other, the families that form the Septibranchia being recognized by others as extremely modified members of the Anomalodesmacea (= Anatinacea). Nevertheless, within the Anomalodesmacea the 'Septibranch' families have retained their separate identity in recent classifications at an ordinal or subordinal level as members of the Poromyoidea or Poromyacea (Dall 1886; Pelseneer 1911; Ridewood

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† It was Stoliczka (1870–1) who first proposed the family Verticordiidae, to include *Pecchiolia*, *Verticordia* and *Allopagus* (= *Hippagus* Deshayes).

1903; Thiele 1935; Newall 1965). While the Verticordiidae have been regarded as members of the Poromyacea, it is only in recent years that they have been included in the Order Septibranchia by adherents of that classification (Clarke 1962; Vokes 1967; Nakazima 1967; Knudsen 1970).

Definitions of the recent genera of the family Verticordiidae

Family: Verticordiidae Stolicza 1870

Type species: Verticordia cardiiformis (Sowerby 1844)

Shell valves with characteristic, rounded trapeziform outlines, usually with a radial sculpture of folds, ribs or finer lines and usually with a granular or minutely spined surface, the surface ornamentation arranged above or parallel to the radial lines, inner surface and valves nacrous; umbos usually prominant, forwardly directed and incurved, with or without a depressed lunule; hinge weak, with or without teeth, if teeth are present usually restricted to a single rounded cardinal on the right valve anterior to the opisthdetic ligament, a few species also with a lateral tooth on the right valve; the ligament, most if not all of it internal, includes a lithodesma; inhalent aperture very large, usually surrounded by tentacles; gill filaments much reduced in length and connected to mantle and foot by a membrane; foot usually with a functional byssus in adult, palps reduced, but lips expanded to form large conical mouth that is directed posteriorly; stomach usually clothed in a thick muscular layer; hermaphrodite; tubular glands, radially arranged, may be present at mantle edge.

Genus: Verticordia S. Wood (in Sowerby 1844)

Synonomy: Hippagus Phillipi 1844, non Lea 1833; *Iphigenia,* von Schumacher 1817; da Costa 1850; *Hippella,* Mörch 1861; *Verticordia,* Paetel 1875

Type species: Verticordia cardiiformis (Sowerby 1844)

(*The mineral conchology of Great Britain,* **7**, p. 68)

Shell may be slightly inequivalve and valve margins flexuous, with radial lines or folds, pustulate, with deeply impressed lunule; umbos raised, incurved and anteriorly directed; shell surface granular or with minute spines; right hinge margin with a large, rounded, hooked tooth† that fits under the rim of the hinge margin of the left valve, the bearing surface of the left valve being smooth and thickened; in some species there is a very fragile and small, flattened, wafer-thin tooth in each valve, dorsal to the cardinal tooth but these are so easily broken that they may well not be seen; right valve usually with a projecting lunular margin which rests on a thickened shoulder of the left valve; in some species there is an elongate posterior lateral tooth on the right valve which extends from a point posterior to the lithodesma as far as the posterior adductor muscle and is inclined slightly away from the shell margin; ligament internal and opisthodetic; lithodesma large and broad.

Various subgenera of *Verticordia* have been proposed at times (see Dall 1886; Thiele 1935). Most are not clearly defined, however a possible exception is *Trigonulina* d'Orbigny 1845, which includes those forms with an elongate lateral tooth on the right valve. Other subgenera are: *Haliris* Dall (1886), while Iredale (1930) (as was his usual wont and with no other reason than

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† Thiele (1935) does not include this character in his description of the genus and specifically states (erroneously) that the subgenus *Verticordia* is without a hinge tooth.

'it seems unwise to class varied styles of living shells with *V. cardiiformis*') erected *Vertambitus*, *Setaliris*, *Spinisipella* and *Vertesphaera*. *Haliris* on first consideration appears to be clearly defined. Dall (1886) reports a short lateral tooth close to the umbo of the left valve in adult specimens, although this was not mentioned in the first account of the type species *V. fischeriana* Dall (1881). However, this may well have been mistaken for the lithodesma still attached to the valve. Dall (1886) also reports a small cardinal tooth on the left valve – a point already discussed in the generic description of *Verticordia* (p. 405). Dall (1881, 1886) does not mention the lateral tooth that is present on the right valve (Dall 1886, Plate II, fig. 4*a*). Thiele (1935) distinguished the subgenus by none of these characters, but by the many thick folds and by the umbo not pointing forwards. The former character is found in species of other genera and in the case of the latter character the umbos point forward in the type species (Dall 1886, see figures 4*a*, *b*). Thus, on present evidence, it would seem wise not to include *Haliris* as a subgenus.

Genus: Lyonsiella M. Sars (1868), Friele 1879

Synonomy: Lyonsiella M. Sars 1868 (named but not described); *Pecchiolia* G. O. Sars 1872, non Meneghini 1851; *Lyonciella* Friele 1886; *Lyonsiela* Thiele 1912

Type species: Lyonsiella abyssicola (G. O. Sars 1872)

(University programme for 1869, Christiana 1872, p. 25, pl. 3, figures 21–43)

Shell fragile, with radial lines or folds, pustulate or with minute spines, with or only a slight indication of a lunule; valve margins may be flexuous and slightly overlapping, valves somewhat inequivalve; no hinge teeth, but part of the margin of the left valve immediately anterior to the umbo thickened; umbo anteriorly directed, may be large and incurved; lithodesma elongate and posterior margin may be notched; ligament internal, but small strip of outer layer may be seen between the valves.

The subgenus *Proagorina* Iredale (1930) differs in no way from the above description.

Genus: Euciroa Dall (1878) 1881

Synonomy: Euciroa Dall 1878 (named but not described), *Verticordia* Dall 1881

Type species: Euciroa elegantissima (Dall 1881).

(*Bull. mus. Comp. zool.* **9**, p. 106)

Shell surface granular or with minute spines, suborbicular or with the posterior margin narrowly rostrate, inflated; umbones prominent and slightly curved forward; lunule broad, lanceolate and depressed; right valve with a strong pointed, slightly curved, cardinal tooth below the umbo and usually a low, sublamellar posterior lateral tooth; left valve with an anterior and posterior cardinal tooth, the anterior one being moderately stout and more or less fused with the hinge margin, also an additional narrow low ridge along the ventral edge of the ligamental groove; ligament internal, lithodesma stout and broad.

The above definition of the genus is a modification of that of Dall, Bartsch & Rehder (1938). Previously to this there had been several definitions given by Dall (1881, 1886, 1895), and Thiele (1935) and these conflict with that above. Thus, in his account of *V.* (*E.*) *elegantissima* Dall (1881) states that 'on the left valve... the ligament is separated by a projecting septum from the fossette for the right cardinal tooth; except this septum be so considered, there are no teeth in the left valve' and this he later confirms (Dall 1886) in his definition of the genus when he states that the hinge is essentially like that of *Trigonulina*. Later still, Dall (1895) returns to the definition of the genus, pointing out that up to this paper 'it could at most form a section of the older group (*Verticordia*)'. However, he presents new evidence from the anatomy and reports that *Euciroa* differs from *Verticordia* in that the foot is laterally compressed, while in the description of *E. pacifica* he states that there is 'no trace of a byssal groove or gland'. If confirmed, this would be a major difference from *Verticordia*. Other features that he mentions, such as the presence of lateral palps and details of the gill and septum, in no way differentiate *Euciroa* from *Verticordia*. Curiously, in the final account (Dall *et al.* 1938), no mention is made of the lack of the byssus gland, either in the description of the genus or that of *E. pacifica*. However, Knudsen (1967) reports that the foot of *E. rostrata* is laterally compressed and that he did not observe a byssus gland. Surprisingly he only mentions a cardinal tooth on the right valve and further states that *E. pacifica* is without a lateral tooth. Certainly the various accounts of hinge characters are in conflict.

It would seem that on all available evidence, on shell characters alone, *Euciroa* cannot be readily distinguished from *Verticordia*. However, accepting that the byssus is lacking in the adult and the lateral compression of the foot, the genus *Euciroa* should be retained but subject to future confirmation.

Note that species in which the posterior shell margin is beak-shaped (sub-rostrate) have been included in the subgenus *Acreuciroa*, Thiele & Jaeckel (1931).

Genus: Policordia Dall *et al.* 1938

Type species: Policordia diomedia Dall *et al.* 1938

(*Bernice P. Bishop Museum, Bull.* **153**, p. 217)

Shell, suborbicular, devoid of granulations and spines, but radial ridges may be present as well as growth lines, inflated, not gaping, umbos prominent, strongly curved and anteriorly directed, the hinge is slightly sinuous anteriorly, thickened and toothless; lithodesma moderately broad.

Genus: Halicardia Dall 1895

Synonomy: Haloconchia Dall 1900

Type species: H. (= *Mytilimeria*) *flexuosa* (Verrill & Smith 1881)

(Verrill 1881, *Am. J. Sci.* **21**, p. 302)

Shell pustulate, inflated, trapeziform or trigonal shape with a triangular depressed lunule; there is a strong ridge or keel from the umbo to the posterio-ventral marginal angle, in addition there may be other less strong radial ribs; internal, strongly arched opisthodetic ligament, the right arm of lithodesma sometimes longer than the left; anterior dorsal hinge margin thickened, with an obscure, rudimentary tooth on the right valve; no outer demibranch; foot with posterior projecting heel.

Genus: Halicardissa Dall 1913

Type species: H. (= *Verticordia*) *perplicata* (Dall 1889)

(*Proc. U.S. natn. Mus.* **12**, p. 278, pl. 8, figure 1)

Shell pustulate, inflated, trapeziform or trigonal shape with a few strong ribs, one of which may be stronger than the others, there may be additional obscure ribs; lunule very small and deep; a single strong conical tooth on right valve; lithodesma short, wide and subtriangular; outer demibranch present; gills reported to be free distally; no heel.

It is possible that on further investigation *Halicardissa* may prove to be synonymous with *Halicardia*.

Genus: Laevicordia Seguenza 1876

Synonomy: Laevicordia Seguenza 1876. Non *Laevicordia* Thiele 1935

Type species: L. (= *Verticordia*) *orbiculata* Seguenza 1876

(*Rc. R. Acad. Sci. fis. nat. Napoli*, **15**, p. 104)

Shell without ribs but finely granulated, inflated with prominent umbo which is strongly incurved over region of lunule; cardinal tooth rudimentary, little more than a prominence of the incurved margin of the shell.

This genus is very similar to, and may prove not to warrant, distinct separation from *Lyonsiella*.

Soot-Ryen (1966) also tentatively included the genus *Thraciodora* Iredale within the family Verticordiidae. Iredale (1924) had proposed this name for *Thraciopsis arenosa* (Hedley 1904). Unfortunately, the anatomy is unknown. The shell characters do not particularly resemble those of other verticordiids, for the shell is elongate, compressed with the umbos subcentral. Thus, in shape and shell characters, the genus more closely resembles members of the families Thraciidae and Myochamidae. It is suggested that consideration of this genus be deferred until the anatomy has been described.

KEY TO THE RECENT GENERA OF THE FAMILY VERTICORDIIDAE

1.	Shell surface granular, pustular, or, with microscopic spinules	2
	Shell surface smooth (growth lines, radiating lines or ribs may be present)	*Policordia*
2.	Shell with one to four strong radiating ribs, the one from the umbo to the posterior ventral angle of the shell margin usually being the strongest. Other lesser ribs may be present	3
	If radiating ribs present, all approximately the same size	4
3.	Cardinal tooth on right valve very small or rudimentary; foot with posteriorly directed heel	*Halicardia*
	Cardinal tooth on right valve, strong and conical in shape; foot without heel	*Halicardissa*
4.	With radiating lines or ridges	5
	Without radiating lines or ridges	*Laevicordia*
5.	Hinge with teeth	6
	Hinge without teeth	*Lyonsiella*
6.	Without functional byssus in adult	*Euciroa*
	With functional byssus in adult	*Verticordia*

Descriptions of species collected from the abyssal Atlantic

We have arranged this section, so that for each genus there is an extensive description of one species. Other species of the same genus, although no less closely examined, are compared with this key description and in this way we hope will emphasize differing features but avoid unnecessary repetition. Type material has been housed in the Museum of Comparative Zoology (M.C.Z.), Harvard University.

Lyonsiella abyssicola (G. O. Sars, 1872)[†]

						no. of specimens
Atlantis II	23. v. 62	sta. D	39° 54.5′ N, 70° 35′ W	466.7–508.7 m		5
Atlantis II	25. viii. 64	sta. 73F	39° 46.5′ N, 70° 43.3′ W	1470–1330 m	E.S.	10
Atlantis II	18. xii. 66	sta. 131	39° 38.5′ N, 70° 36.5′ W 39° 39.0′ N, 70° 37.1′ W	2178 m	E.S.	6
Atlantis II	18. viii. 66	sta. 118	32° 19.4′ N, 64° 34.9′ W 32° 19.0′ N, 64° 34.8′ W	1135–1153 m		2
Chain	6. vii. 65	sta. 87	39° 38.7′ N, 70° 40.8′ W	1102 m	E.S.	52
Chain	5. v. 66	sta. 105B	39° 56.6′ N, 71° 03.6′ W	530 m	E.S.	19
Atlantis II	19. ii. 67	sta. 165	07° 47.0′ S, 33° 59.0′ W 07° 43.0′ S, 33° 58.0′ W	3909 m	E.S.	1
Sarsia	24. vii. 67	sta. S63	46° 17.5′ N, 4° 45.2′ W	1336 m	E.S.	2
Discovery	18. iii. 68	sta. 6709	27° 29.8′ N, 15° 20.1′ W	2351 m	E.S.	1
Discovery	19. iii. 68	sta. 6710	27° 23.6′ N, 150° 39.6′ W	2670 m	E.S.	1

Distribution:

North and west coasts of Norway, from Spitzbergen to Denmark, off the English Channel, west of Ireland, Bay of Biscay, off the coast of Spain, Faroes, west and east Greenland, north-east Iceland, many North Atlantic Stations across to the U.S. coast, Marthas Vineyard (Massachusetts), off Fernando Po and the Azores.

It occurs from 38 m (west Greenland) to 3909 m (Sta. 165, *Atlantis II*). *Lyonsiella abyssicola* was the first species of the genus to be described. It was reported by M. Sars in 1868 but without description and four years later, G. O. Sars (1872) described the shell and anatomy and, in deference to Jeffreys (1881), ascribed it to the genus *Pecchiolia* Meneghini, originally proposed for a miocene fossil. Jeffreys (1881) had also discovered the species in the samples taken by the 'Lightning' and 'Porcupine' expeditions and, in his report, Jeffreys (1881) discusses the nomenclature of the species. However, Friele (1879) later showed that this species differed from the fossil *Pecchiolia* and established the genus *Lyonsiella*. To date, no recent species have been recorded of the genus *Pecchiolia*, although some past authorities, e.g. Verrill (1884) have referred species of *Lyonsiella* to this genus (see appendix). From past records, *Lyonsiella abyssicola* appears to be the most commonly occurring species of the family and is certainly the best known. It is also by far the most common species of verticordiid obtained in the present sampling programme of the Atlantic deep-sea benthos.

The shell

The shells were measured from the umbo to the ventro-posterior corner (figures 1, 2, L–L′). The size of the present specimens ranges from 1.3 mm to 5.7 mm. An extensive description of the external features of the shell is to be found in the account of G. O. Sars (1872). The shell is very inequilateral, the oval, trapezoidal shape characteristic of the genus. The shell is inflated

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[†] For synonomy, see appendix.

and the free edges are sinuous. The latter feature is particularly noticeable anterior to the large, incurving, anterior facing umbos, and also dorsal to the position of the exhalent siphons. The right valve is somewhat larger than the left and tends to overlap the latter, particularly posteriorly. One individual was observed in which this was reversed, the left valve being the larger.

From the large number and wide size range of the animals collected, it was possible to produce a sequence of drawings showing the variation in the shape of the shell and the way in which the outline changes with increasing size. Smaller animals tend to be square, while larger animals are much more elongate and trapezoidal in shape (figure 2). Here, as in the case of other species, the outline of the shell is not constant, and there is considerable variation in the dimensions and the angles of all portions of the shell.

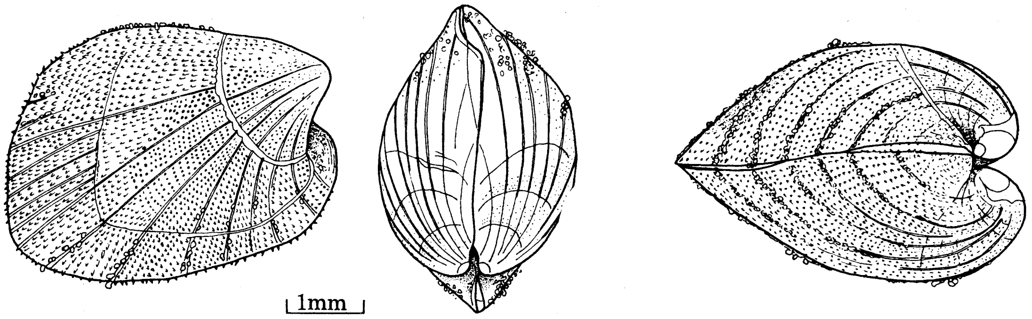

FIGURE 1. *Lyonsiella abyssicola*: lateral, dorsal and anterior views of the shell of a specimen taken at station 87 (*Chain*, 6 July 1965).

The adult shell (SH) is thin and fragile, white, but because of the punctate ornamentation, usually with sediment adhering to it. The ornamentation consists of hexagonal spines projecting from the surface of the periostracum and arranged in radiating rows from the umbone. (See plate facing p. 479.) In addition, there are radiating lines occurring at approximately every 4th to 8th row of punctae. In scanning e.m. photographs, these appear as rough, narrow indentations. To these stick sand grains and animal skeletons, particularly *Foramenifera*, and these give a characteristic encrusted pattern. The radiating lines vary according to the size of the animal, in the smallest specimens as few as four and in the largest, between fifteen and twenty. The lines run from the umbo to the edge of the shell and in larger specimens there are additional lines extending from the edge but not reaching the umbo.

Growth lines are fine but do not show any marked regularity. Many shells show one or two more definite concentric markings which probably are the result of earlier repair of damage to the shell margin (figure 1).

Internally the adductor scars can be seen but the division into 'quick' and 'catch' areas is not distinguishable. The adductor muscles are equal in size. There is also a scar along the mantle edge but no pallial sinus. The hinge is without teeth and is almost smooth. There is a very slight ledge or projection on the right valve anterior to the lithodesma, and this is overlapped by the rim of the left valve. The lithodesma lies in a groove between the two valves posterior to the umbo. It is about twice as long as it is wide and is wedge-shaped in cross section (figure 3*a*, *b*, *c*).

The opisthodetic ligament is somewhat similar in structure to the ligament of *Loripes* (Allen 1960). The posterior part of the posterior outer layer (LO) is divided, the upper half being attached to the outer rim of the valves and the inner part dorsal to the inner layer (LI). The wedge-shaped dorsal surface of the lithodesma (L) divides the ligament into two halves except for a tenuous connexion of posterior outer layer (figure 3*b*). The anterior outer layer is a small wedged shape structure at the anterior end of the lithodesma. Fused periostracum secondarily extends the ligament posteriorly and anteriorly for some distance.

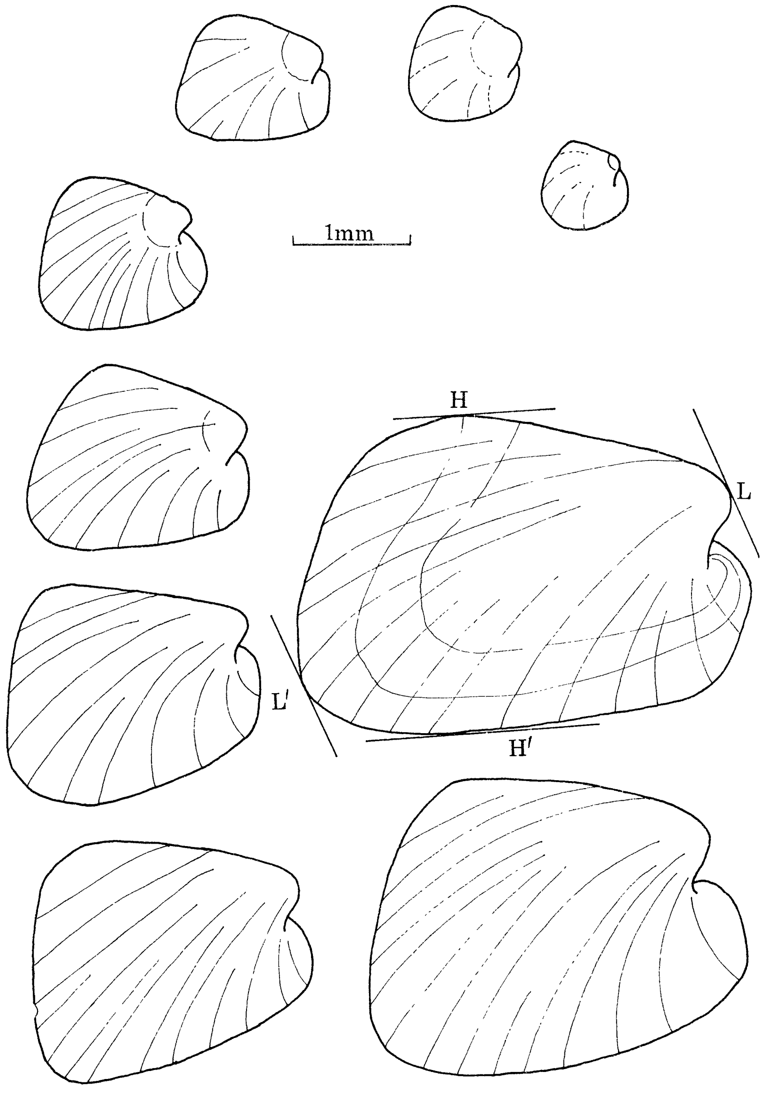

FIGURE 2. *Lyonsiella abyssicola*: outlines of the right valves of nine specimens to show variations in shell shape with increasing size. H–H′, height and L–L′, length measurements.

The mantle

The mantle edge consists typically of the three lobes with the gland cells secreting the periostracum in the groove separating the outer (OL) and middle lobes (ML). The inner muscular lobe (IL) is well developed and fairly extensive fusion limits the extent of the pedal gape so that it occupies approximately half of the ventral margin (PGP, figure 4) as well as forming well-developed inhalent and exhalent apertures. In the region of the pedal aperture and as far as the ventral limit of the inhalent aperture the sensory middle lobe consists of two non-papillate folds which merge as a single fold which continues round the periphery of the aperture.

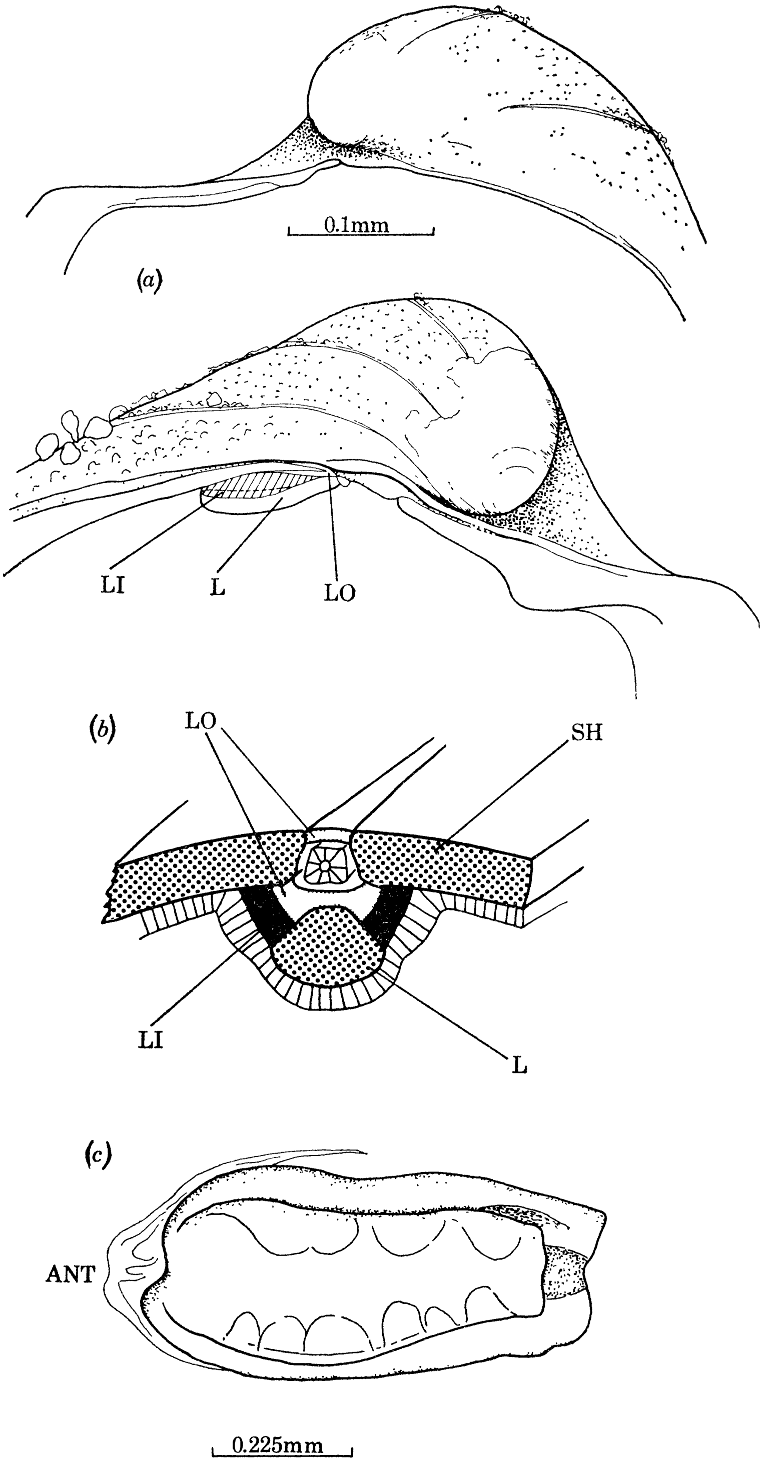

FIGURE 3. *Lyonsiella abyssicola.* (*a*) Lateral views of hinge area of left and right valves; (*b*) diagram of a transverse section through hinge, lithodesma and ligament; (*c*) dorsal view of lithodesma.

At irregular intervals between the anterior limit of the pedal gape and the dorsal side of the inhalent aperture are series of multicellular radial glands; the number varies between 9 and 14, depending on the size of the animal (figure 5*a*, *b*, MG). The glands are elongate (approximately 80 μm long) and arranged vertically to the margin of the mantle edge and lie in the space between two sets of muscles that retract the outer and middle sensory lobes respectively. In cross-section they are oval (approximately 20 μm in diameter, figure 5). The cells stain extremely densely and it is difficult to determine a duct system by means of a light microscope.

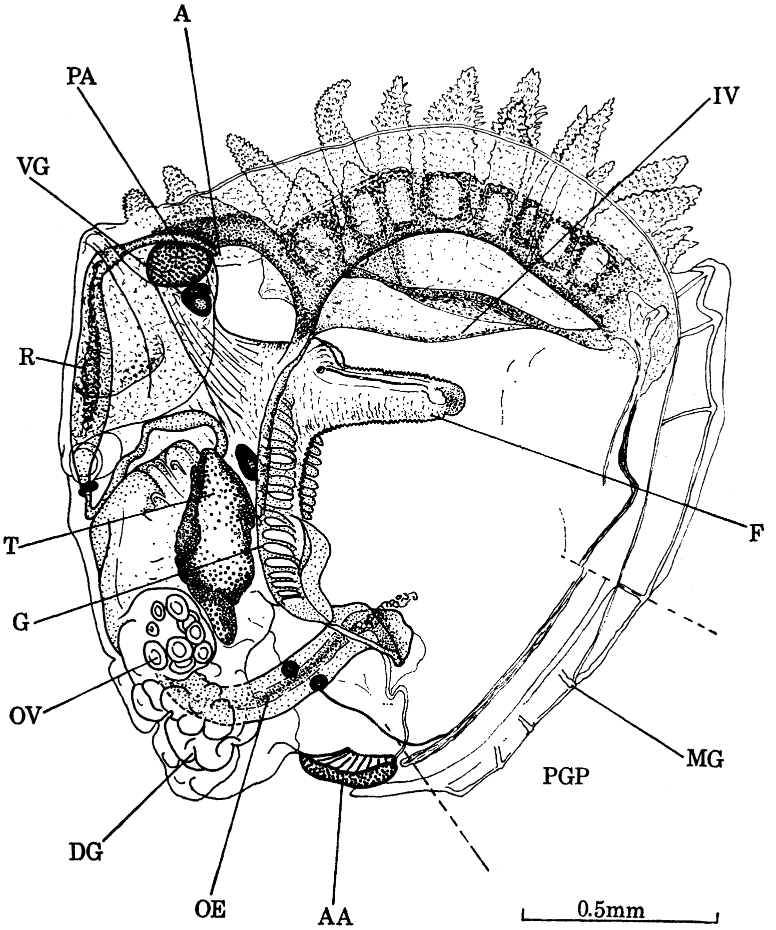

FIGURE 4. *Lyonsiella abyssicola*: lateral view of whole mount to show gross anatomy.

Sections indicate that there is a central column of gland cells (GC) surrounded by an outer unicellular wall separated from the column by a space (SP) which is particularly well defined at the proximal end. The ducts open to the inside of the inner of the two sensory folds, the position being marked by a circular pad of cells, the ducts fanning around this to open at the perimeter of the pad (figure 5*a*). Although not present in every species, these glands appear to be characteristic of the family, for we know of no other comparable structures in the mantle of other Bivalvia. It is difficult to ascribe a function to them not having observed living material, however, the mantle edge and shell of *L. abyssicola* (and also all other members of the family) have fine particles of sediment and skeletal remains of animals and algae adhering to them. It may be that these glands have an adhesive function.

The anterior adductor muscle (AA) is oval in shape and slightly smaller than the more rounded posterior muscle. The anterior adductor muscle is situated just anterior to the umbos level with the mouth, while the posterior adductor muscle (PA) is distant from the umbo. Both lie close to the shell margin. The 'quick' and 'catch' portions cannot be distinguished.

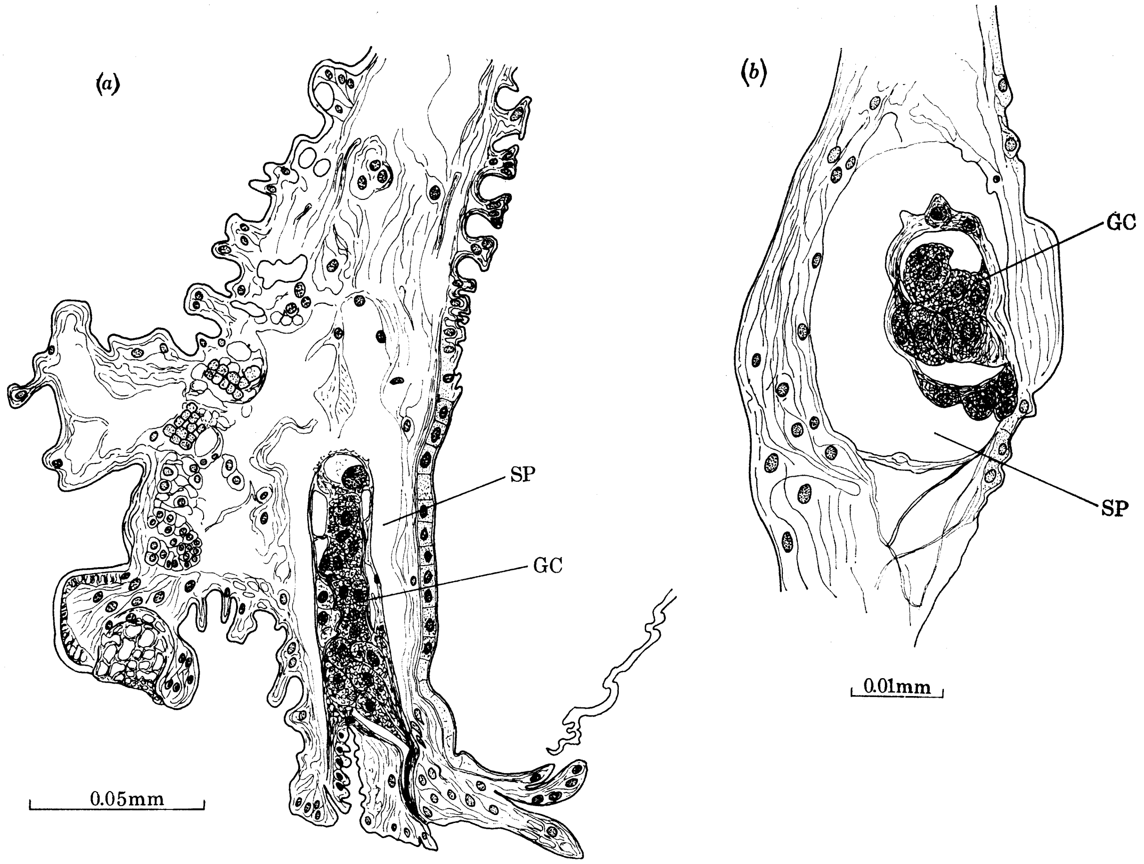

FIGURE 5. *Lyonsiella abyssicola.* (*a*) Longitudinal section through a radial mantle gland and the mantle edge; (*b*) transverse section through a radial mantle gland.

Inhalent aperture

The inhalent aperture (IA) is huge and occupies approximately $\frac{3}{4}$ of the posterior shell border. It is surrounded by a ring of approximately 14 large tentacles (IT) and there is a second, outer ring (OT) of approximately 10 smaller tentacles (figure 6). In addition there are three tentacles positioned to the dorsal side of the exhalent aperture (EA figures 4, 6). The number varies somewhat according to the size of the specimens (note Sars (1872) recorded 12 inner and 16 outer).

The tentacles are conical structures which appear to be greatly contracted in preserved specimens. However Sars (1872) illustrates a living specimen in which the tentacles are extended little more than the present preserved specimens and living specimens obtained from Bergen confirm this. The tentacles are covered with conical projections which give an arborescent appearance (figure 7*a*). The tentacles like the rest of the mantle edge, are covered with adhering fine deposits (SA). High power observations show that at the tip of each conical projection there are a few densely staining gland cells with individual ducts (D) opening to the tips. Surrounding the gland cells is a 'network' of ill-defined vacuolated cells (figure 7*b*). The gland cells presumably provide the adhesive material to which particles adhere and also form the mechanism by which food is captured (see p. 417).

The tentacles of the inner ring are so inserted at the rim of the inhalent aperture that in their contracted state they project inwards across the aperture (figure 6). Internal to the rim of the

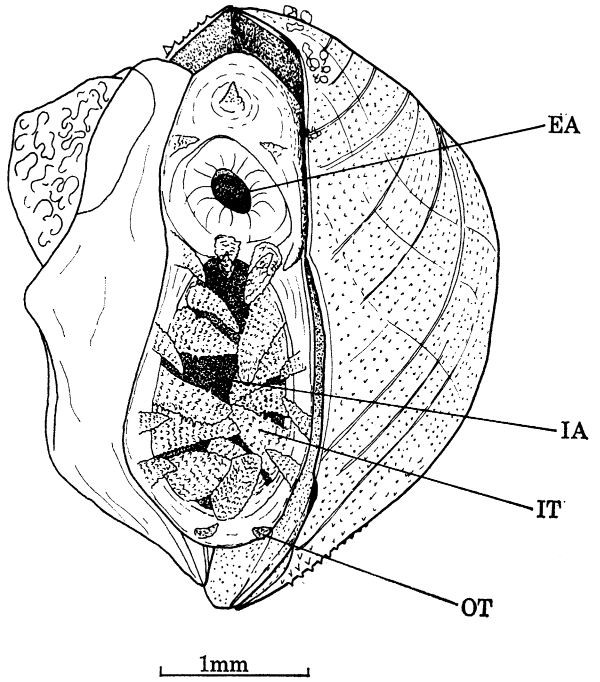

FIGURE 6. *Lyonsiella abyssicola*: posterior view of the apertures of a specimen with the left valve removed.

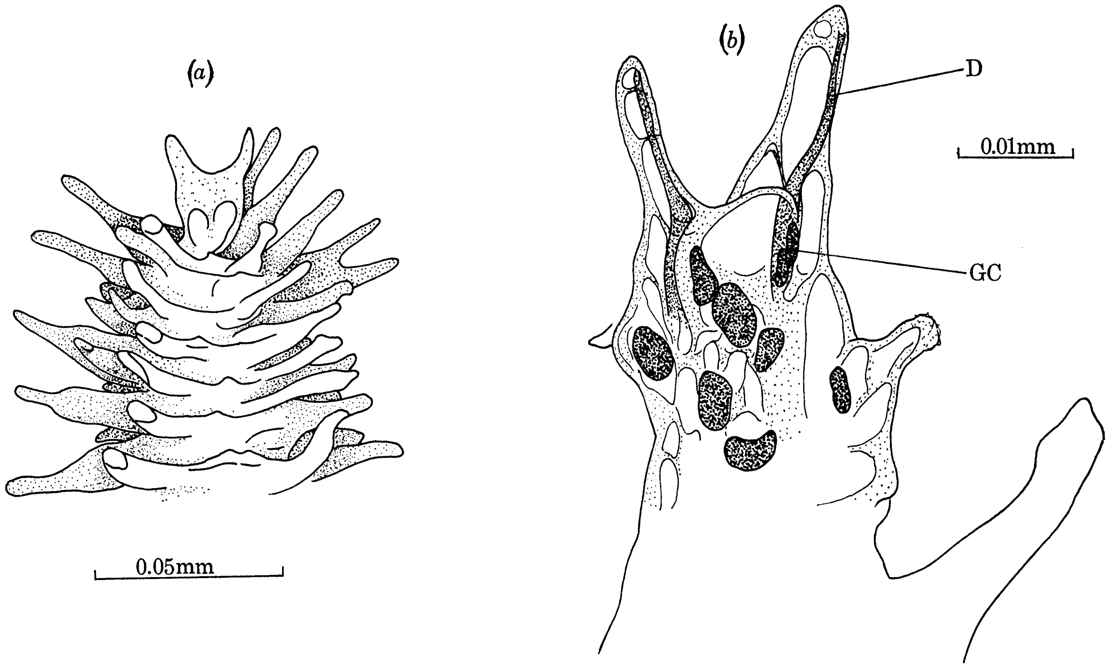

FIGURE 7. *Lyonsiella abyssicola*. (*a*) Whole mount of the tip of a tentacle to show the arrangement of the papillae; (*b*) high power drawing of a whole mount of a single papilla.

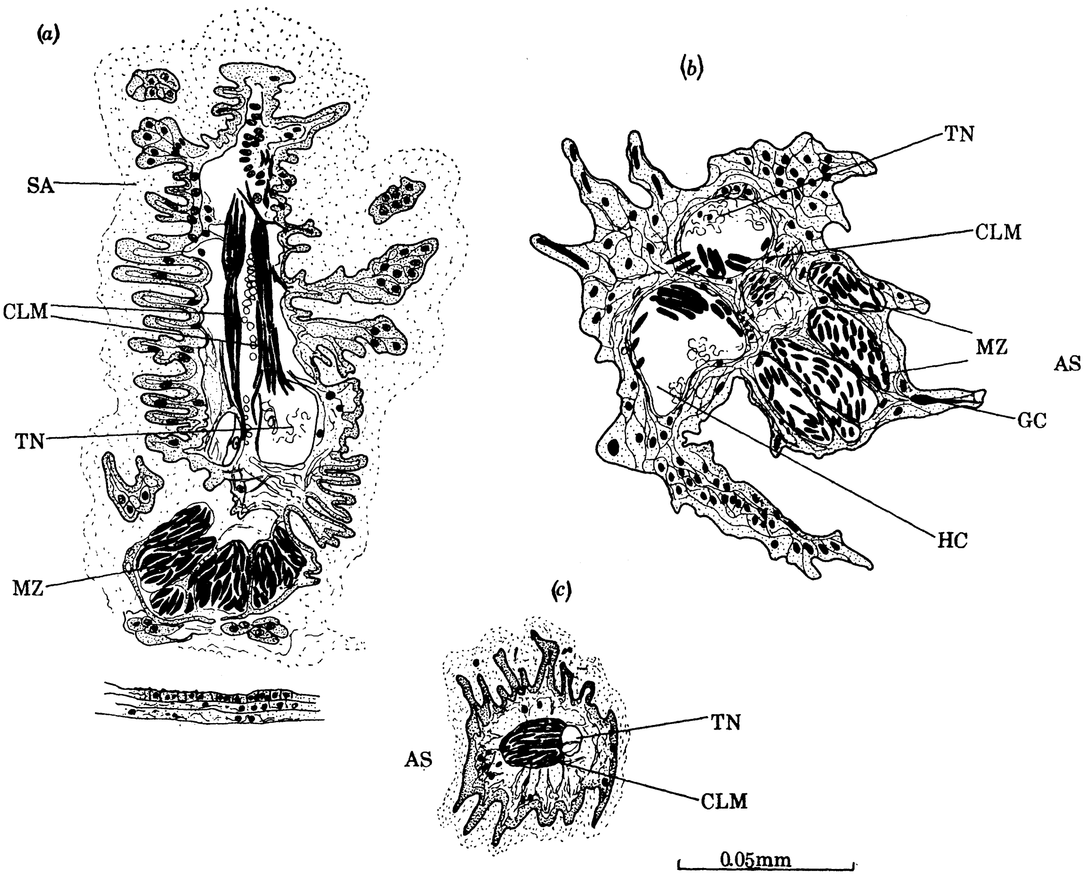

Figure 8. *Lyonsiella abyssicola*. (*a, b*) Longitudinal and transverse sections through an inner inhalent tentacle; (*c*) transverse section through an outer inhalent tentacle.

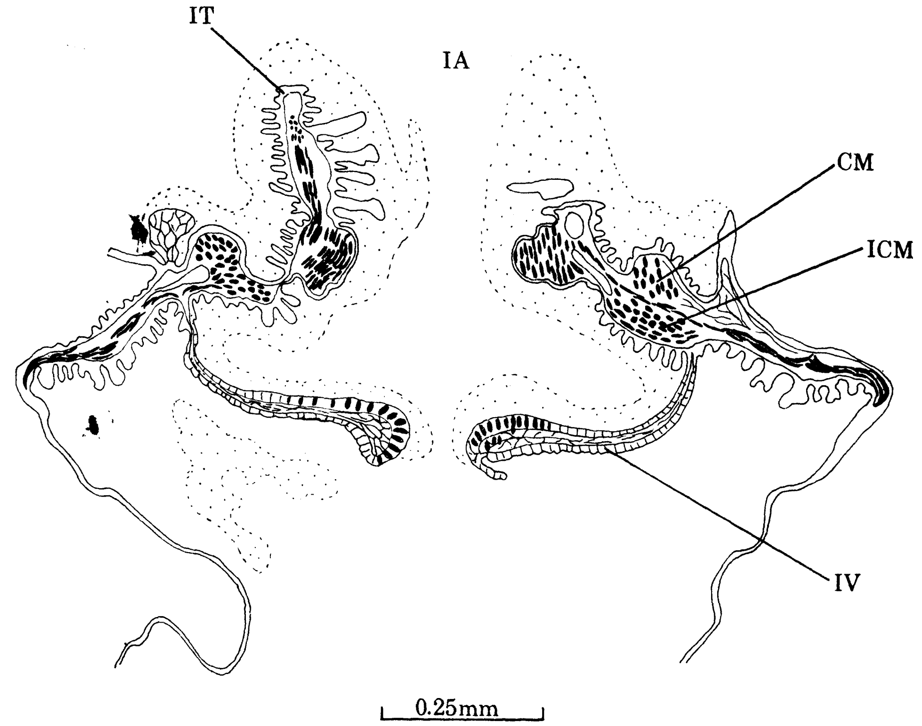

Figure 9. *Lyonsiella abyssicola*: longitudinal horizontal section through the inhalent aperture.

aperture, below the outer epithelial layer, is an encircling muscle band but this does not contribute to the musculature of the tentacles.

A group of longitudinal muscles is situated on the aperture side of the tentacle and consists of five main blocks with smaller intermediate wedge shaped bundles at the base of the tentacle (MZ, figure 8*a*). Some of the muscle fibres from the outermost bundles, and possibly the inner, extend into the base of the next adjacent large tentacle forming at least part of the outer bundles of the latter. The remaining fibres extend into a second and deeper layer of circular muscle around the aperture (CM, figure 9).

In addition, two bundles of longitudinal muscle fibres extend into each large tentacle and, from these, fibres extend into the bases of the arborescent glandular epithelial projections (CLM, figure 8*a*, *b*). These muscles are associated with the paired haemocoel cavity which runs the length of each tentacle. The longitudinal muscles are found on the inner face of each haemocoel (HC, figure 8*a*). These longitudinal fibres extend below the circular bands and insert at the mantle edge. There are longitudinal muscle fibres immediately below the epithelium of the tentacles which, in the contracted condition, extend from the apex of one fold to the next. There is also a considerable amount of connective tissue below the epithelium of the tentacles which, in the contracted condition, extend from the apex of one fold to the next and below the epithelium and around the haemocoelic spaces. This network of collagen fibres was not investigated but no obvious pattern to the network was observed.

Functionally, it appears that the tentacles are extended by hydrostatic pressure and contracted by the inner, longitudinal strands. The asymmetric outer longitudinal bundles, although taking part in the contraction, are concerned with the movement of the tentacles from an outstretched position to an infolded position over the inhalent aperture. In this way, any organism adhering to the tentacle will be brought to the aperture.

The outer ring of small tentacles differ somewhat from the inner ring in that they do not have the outer five longitudinal bundles of fibres (figure 8*c*). However, centrally there is a pair of haemocoelic spaces with associated paired longitudinal muscles which lie on the aperture side of the spaces. In this case the haemocoelic spaces are relatively smaller than those of the inner tentacles while the muscles are relatively much larger. Although they can contract and expand, they are much less capable of making powerful inwardly directed movements than are the inner tentacles. No cilia were found on the tentacles.

To the inside of the inhalent aperture is an encircling membranous collar or valve (IV) attached peripherally at the level of the outer limit of the inner circular muscles. The wall of the valve adjacent to the gill is broader than the wall next to the ventral mantle edge. Structurally the valve is relatively simple with the small space between the epithelia filled with a packing tissue, the only muscle fibres present are a few that encircle the rim of the aperture (figure 9).

Exhalent siphon

The exhalent aperture (EA) is much smaller than the inhalent (figure 6) and the shape of the aperture varies from a slit to a round opening. The edge of the surrounding tissue may be thickened. The differences in shape and tissue thickness are undoubtedly due to different degrees of contraction in the preserved animals (Soot-Ryen (1966) made similar observations on *Policordia gemma*). The circular muscle surrounding the exhalent aperture is more developed than that around the inhalent aperture. A definite, but short, exhalent siphon (ES) is formed which is 'cut away' on the ventral side. We confirm the observation of Sars (1872) that, when extended in life, the siphon is thickly covered with very fine papillae (EP, figure 10). Three tentacles are present in the exhalent region, one dorsal to the aperture, the others lateral, one to the right and the other to the left opposite the dorsal limit of the aperture (figure 6). The musculature of the siphonal tissue is more simple than that of the inhalent aperture and consists of a series of radiating strands above and below a broad and thin band of muscle encircling the aperture (RAM, figure 10). The exhalent siphon like the rest of the mantle edge and tentacles is covered with a layer of fine sediment and organic skeletal material.

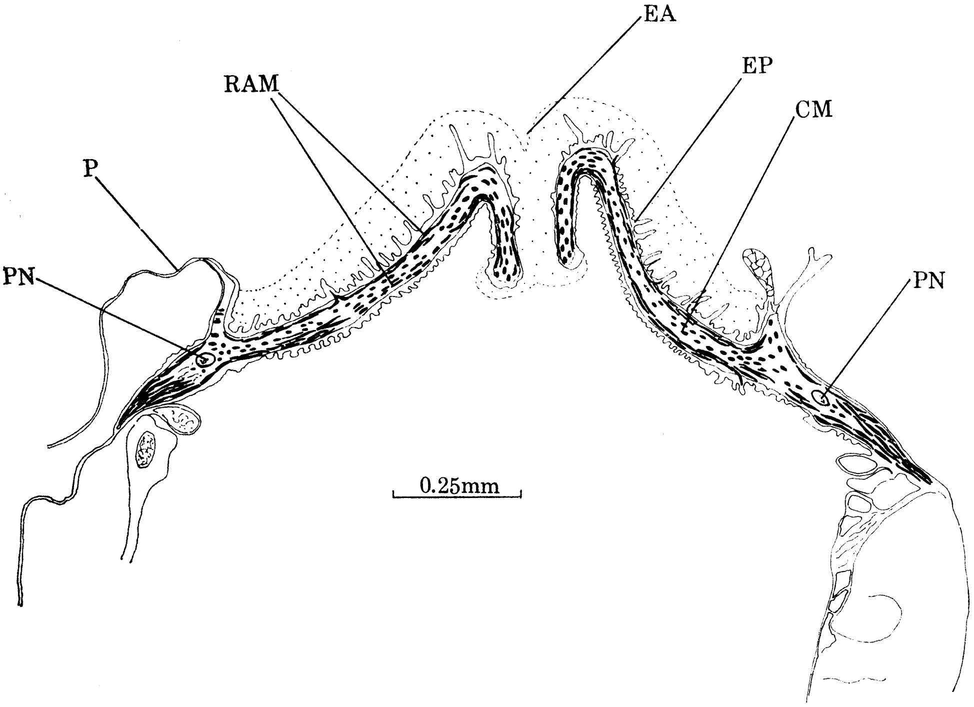

FIGURE 10. *Lyonsiella abyssicola*: longitudinal horizontal section through the exhalent aperture.

The nerves supplying the tissues surrounding the apertures are branches of the pallial nerves from the visceral ganglia (VG, figure 11). Right and left nerves skirt the ventral side of the posterior adductor muscle and run in the mantle edge close to the origin of the inner muscular layer. Below the level of the two lateral exhalent tentacles, the nerves turn inwards and give off a commissure that encircles the dorsal side of the exhalent aperture passing to the outside of the single dorsal tentacle. The pallial nerve immediately against the second branch encircles the inhalent aperture which, in its turn, gives off paired nerves to each of the inner tentacles. Within the tentacles the nerves lie close to the outer edge of the paired haemocoele (TN, figure 8). The pallial nerve continues around the periphery of the inhalent region to the outside of the outer tentacle ring (PN, figure 11).

Gills

The gills (G) extend from the anterior limit of the body, where they fit into a wedge-shaped notch between the anterior and posterior lips of the mouth, to the junction between the exhalent and inhalent apertures (SPT). Both inner and outer demibranchs are present (ID, OD, figure 12). The outer demibranch is much reduced; the ascending lamella (AL) is absent, while the descending lamella (DL) extends from the apertures to a point about two-thirds the distance to the mouth. The filaments are very short and, although eulamellibranch in form, interfilamentary junctions are present only at the ventral and dorsal edges. In an animal 4 mm long, the gill is approximately four times as long as it is deep, while in smaller specimens the gill occupies a proportionately larger area and is approximately twice as long as it is deep. Although the filaments are short there is an extended gill axis (GA) with the formation of a relatively large hypobranchial cavity (figure 13). Laterally, the demibranchs are attached by a broad membranous tissue junction to the body and mantle respectively (MB). Immediately behind the foot, the inner membranes of each side, which are formed from the extended tips of the filaments (GF) and the margin of the interfilamentary junctions, do not make a tissue fusion, but are joined together by an adhesion that appears to consist of fused, interlocking, modified frontal cilia (CF, figures 14*a*, *b*). The filaments are so short that when the gills are viewed from the ventral side they appear as two well-marked ciliated tracts on each side of the body. These tracts are (1) the ventral ciliated gutter at the free edge of the junction between ascending and descending lamellae (MGR) and (2) the exposed axis of the gill. Thus, functionally the gill consists of two pairs of conveyer belts extending from inhalent aperture to mouth (figure 12).

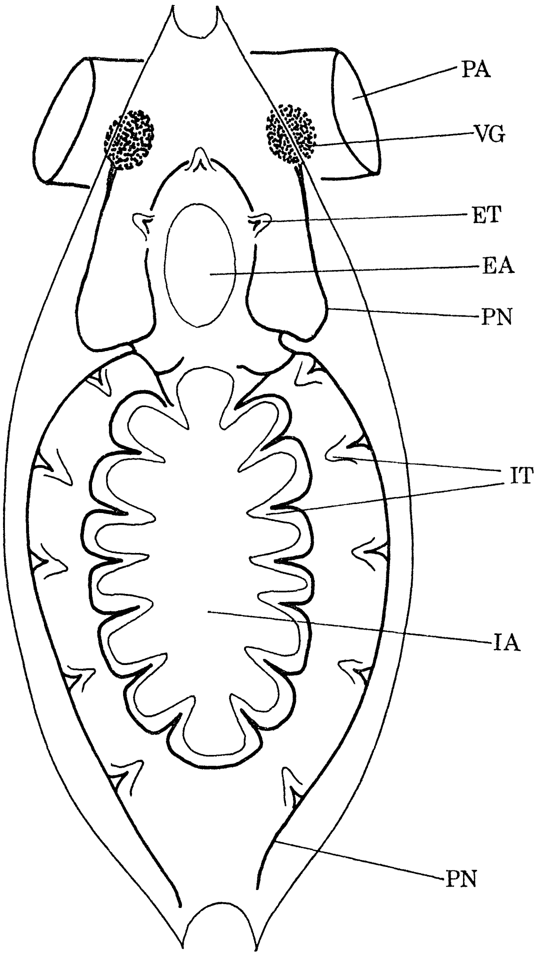

FIGURE 11. *Lyonsiella abyssicola*: diagram to show the nerve supply in the region of the aperture.

In transverse section the filaments are not greatly modified except that the lateral cilia are somewhat removed from the latero-frontal cilia, there being four or five non-ciliated cells between the two (LC, LFC, figure 14*c*). The frontal cells are very characteristic, there being on each side of the midline a row of very large cells, which are in parallel series to each other. Between these cells, in the lozenge shaped interstice, there are two smaller cells. Although all these are ciliated, because of the dominance of the large cells it appears that the frontal surface has two parallel bands of cilia (FC).

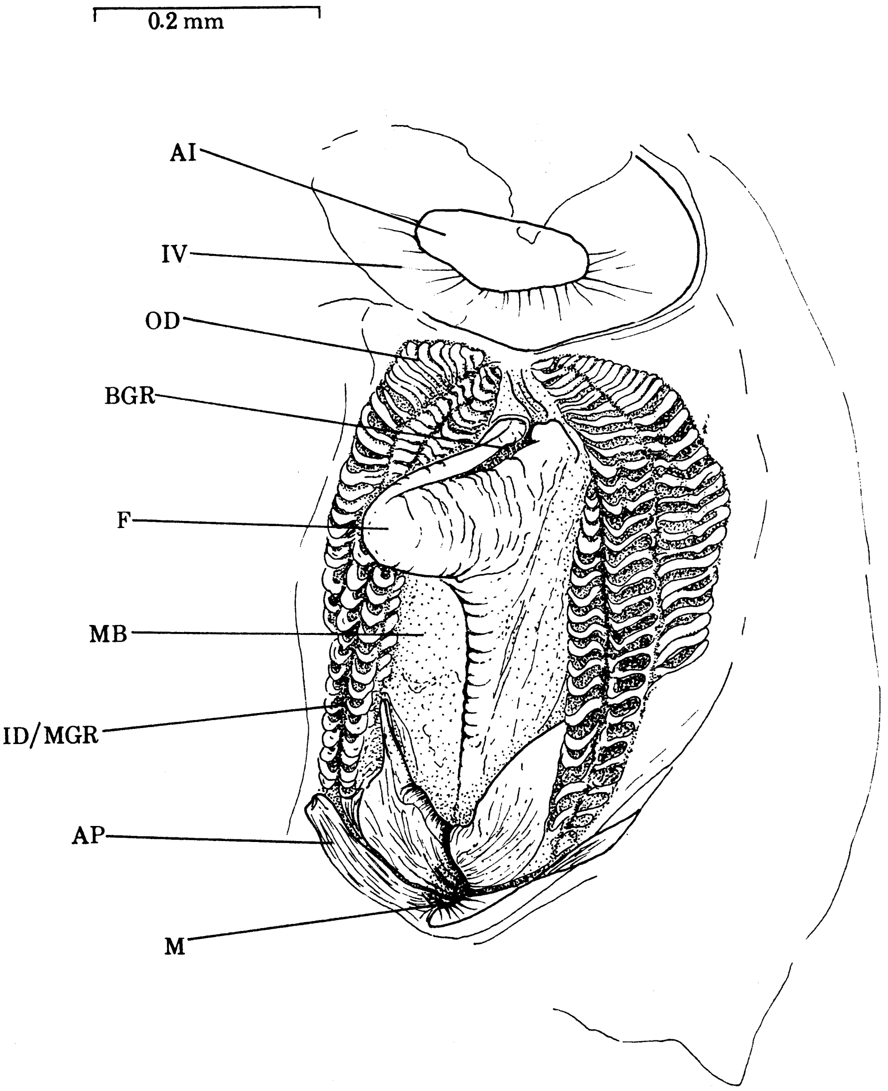

FIGURE 12. *Lyonsiella abyssicola*: ventral view of whole mount to show structures within the mantle cavity.

The longitudinal gill axis is well developed with a haemocoele and an abundance of amoebocytes (GA, figure 13). Muscles appear to be restricted to the upper part of the axis and are particularly well-developed posterior and lateral to the foot. It is by no means certain that the gill is capable of pumping movements and of acting in a similar fashion to the gills of the Protobranchia and the Cuspidariidae and Poromyidae.

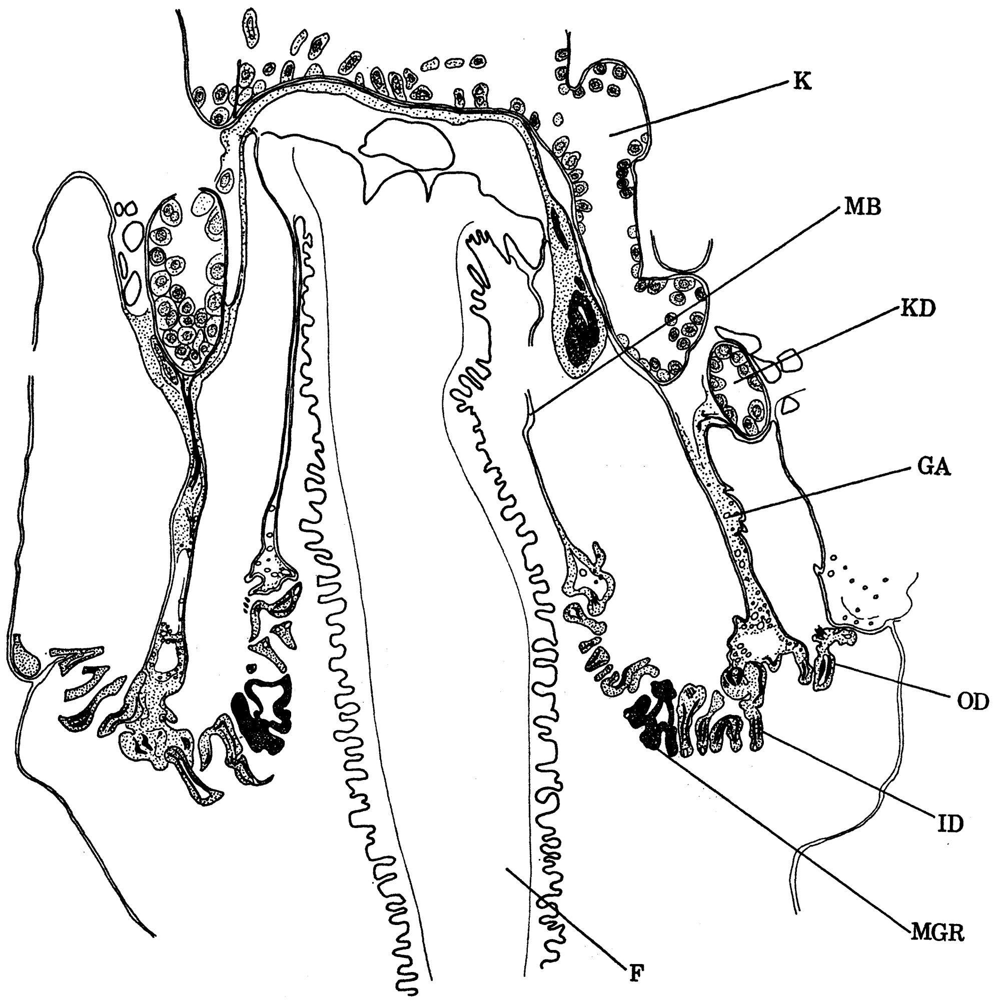

FIGURE 13. *Lyonsiella abyssicola*: transverse section through the foot, kidney and gill.

Palps

The lips and palps form an extension to the large funnel shaped mouth (M). The anterior lip (AP) forms a hood ventral to the mouth, while the posterior lips form two wing-like lateral flaps. Tissue homologous to that of the ridged part of the palps in other bivalves give rise to small extensions at the lateral limits of the lips (PL, figures 15*a*, *b* and 17). There are no obvious ridges on the inner face of the lips and palps. There is a proximal oral groove between the posterior and anterior lips and the internal longitudinal ridges of the oesophagus extend some distance into the entrance of what must be regarded as a buccal funnel (COR). The funnel is posteriorly directed in life and, because the anterior/posterior axis of the body is vertical in relation to the sediment, it forms a large cup-shaped receptacle at the bottom of the mantle cavity. Thus, material collected by the tentacles and removed by the valve will pass along the ciliated grooves of the gills, directly into the mouth. The palps are ciliated on their inner surfaces and bounded by large epithelial cells on a layer of connective tissue and muscle fibres (figure 15*a*, *b*). There is no evidence of any sorting mechanism. The ridge sorting system normally associated with the bivalve palp is not present and would indicate that there is no selection of material entering the mantle cavity.

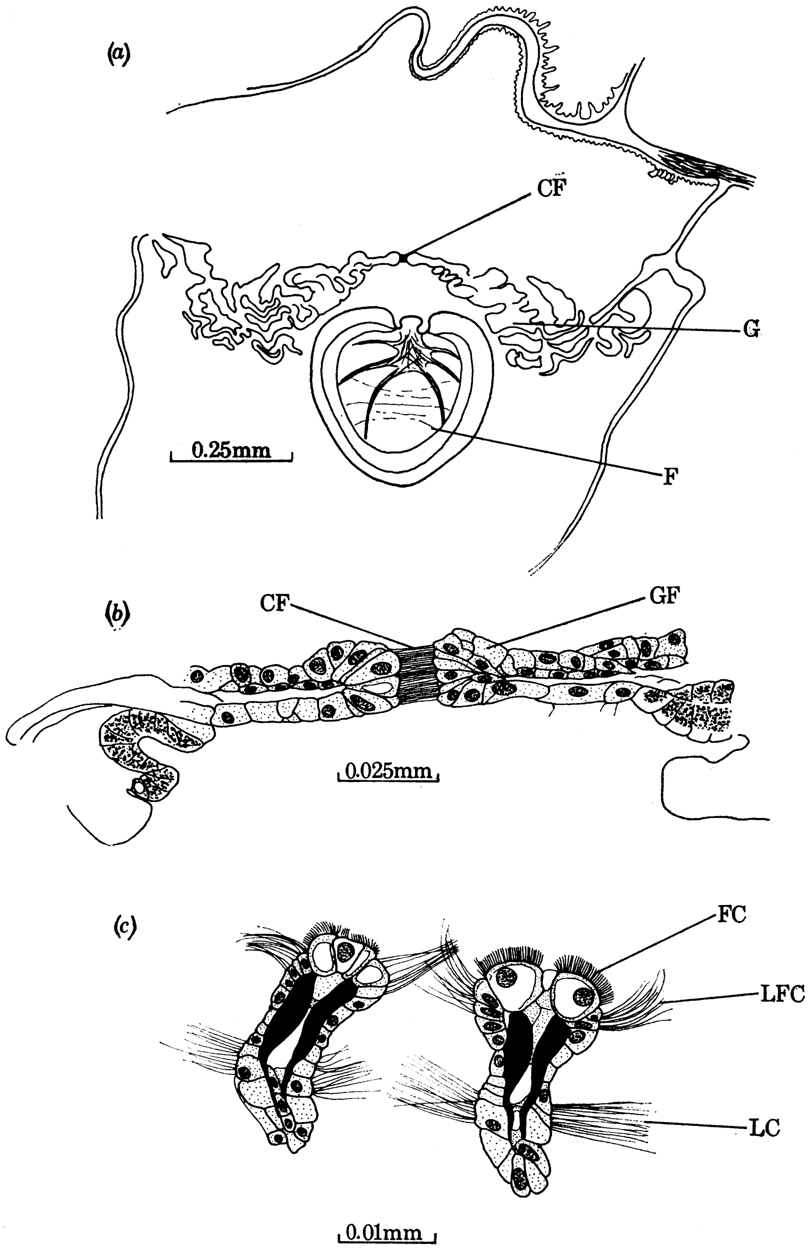

Figure 14. *Lyonsiella abyssicola.* (*a*) Transverse section through foot and junction of the ascending lamellae of the right and left inner demibranchs behind the foot; (*b*) high power of the junction shown in (*a*); (*c*) transverse section of adjacent filaments.

Gut

The gut follows a typical course and, in sequence, there is oesophagus, stomach, style sac and combined mid gut, a single loop of the hind gut passing over the posterior adductor to the anus situated immediately in front of the exhalent aperture (A, figure 4).

The oesophagus (OE) is capable of considerable dilation, a conclusion evinced by the size of the food organisms in the stomach and the highly convoluted longitudinal folds as seen in sections (figure 16). These folds, varying from 14 to 18 in number, have elongate densely ciliated epithelial cells interspersed with oval mucus secreting cells (MC), as well as occasional

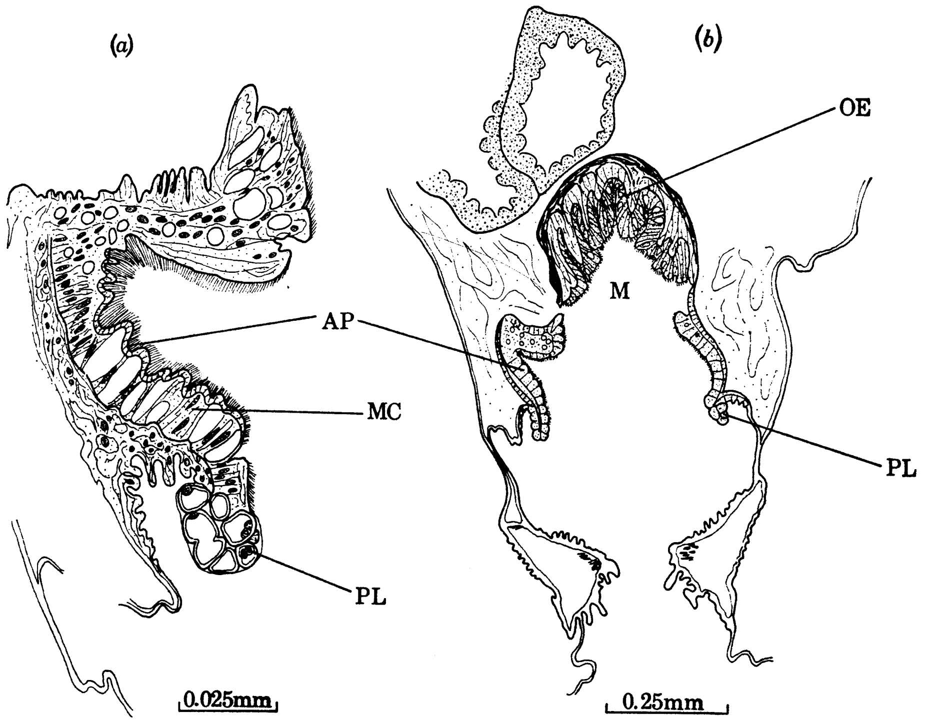

Figure 15. *Lyonsiella abyssicola*. (*a*) Transverse section through the upper (anterior) lip and palp; (*b*) transverse section of the mouth region.

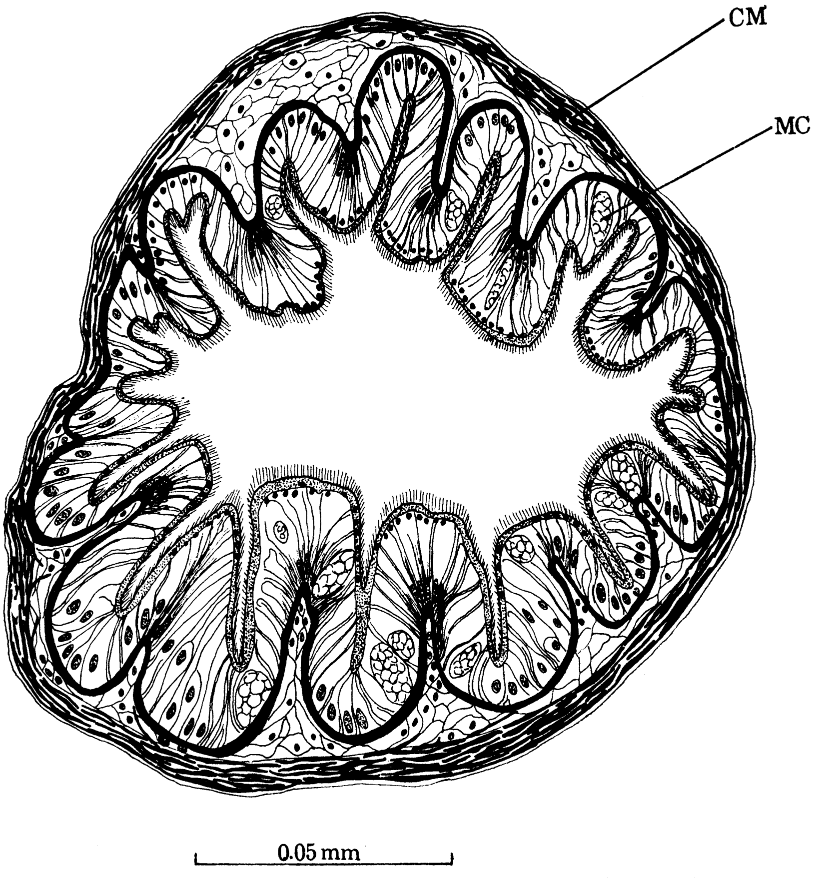

Figure 16. *Lyonsiella abyssicola*: transverse section through the oesophagus.

spindle-shaped cells with fine granular golden contents. The epithelial cells themselves have a dense layer of basal granules at the lumen surface. To the outside is a very well-developed layer of circular muscles (CM) with packing and connective tissue between it and the basement membrane of the inner epithelial cells. Some muscle fibres radiate from the circular muscle into the ridges of the folds. The presence of a muscle layer around the oesophagus and stomach is characteristic of septibranchs. Thus, Yonge (1928) describes a very similar condition in *Poromya* and *Cuspidaria*.

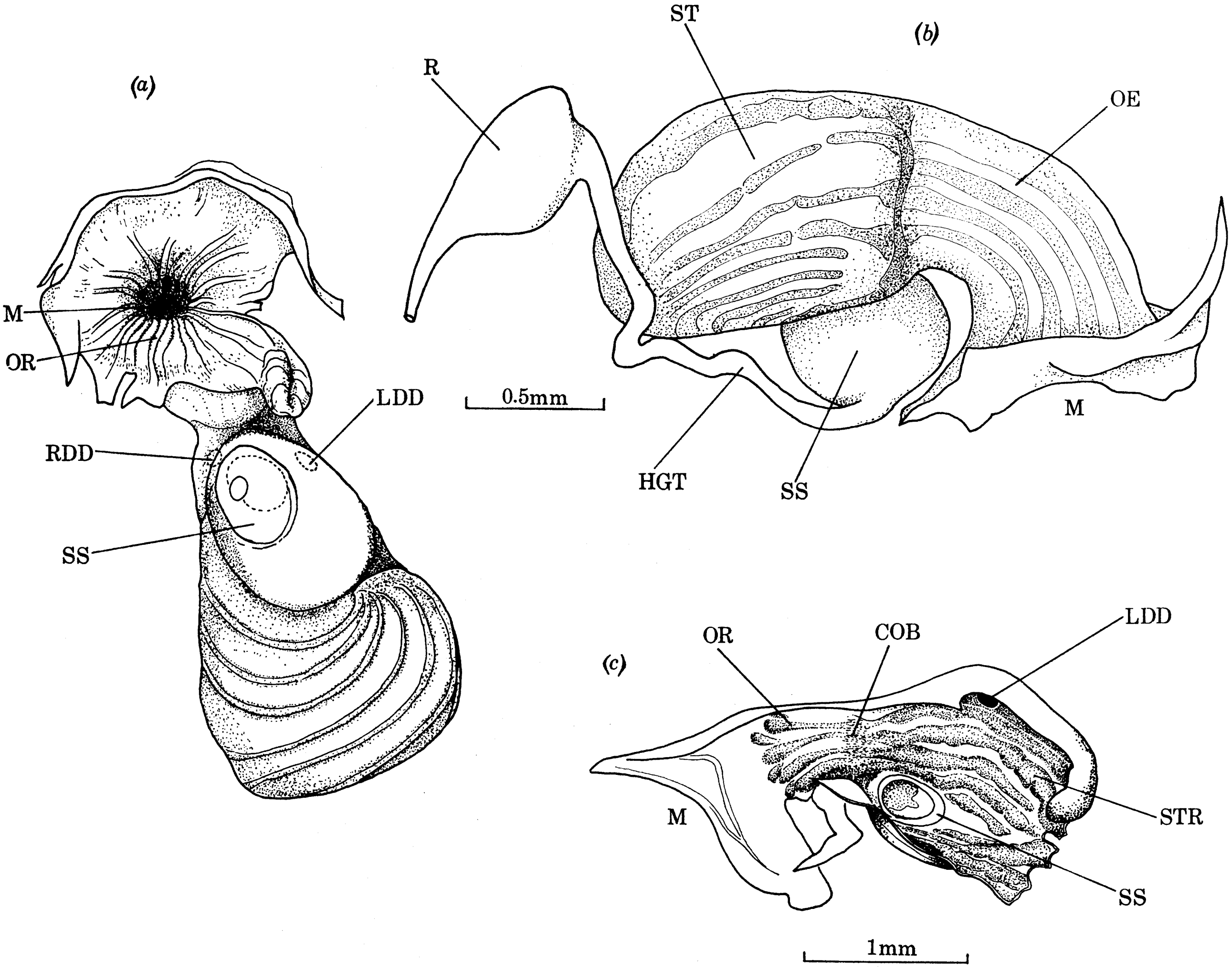

Figure 17. *Lyonsiella abyssicola.* (*a*, *b*) Ventral and lateral view of the gut; (*c*) stomach opened from the dorsal side to show internal features.

The oesophagus curves first dorsally and then posteriorly to join the anterior end of the stomach. The stomach (ST) is large and more or less globular in shape, with a posterior twist to the left that forms a shallow, broad pocket. The inner wall of the stomach is ridged (STR) and some of the lateral ridges are in line with those of the oesophagus. However, there is a break between the ridges of oesophagus and stomach in the form of a ciliated circumoesophageal band (COB). In the dorsal region of the stomach the ridges are less pronounced. There is no dorsal hood. There are approximately nine main ridges which terminate in the postero-lateral pocket (figure 17*a*, *b*, *c*). Immediately behind the oesophageal opening in a ventro-lateral position are

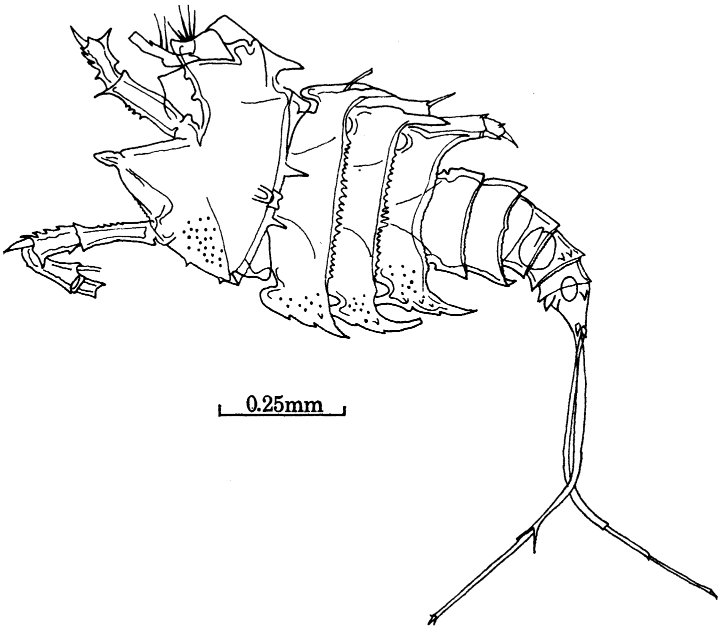

Figure 18. Whole mount of cervinid copepod removed from the stomach of a specimen of *Lyonsiella abyssicola*.

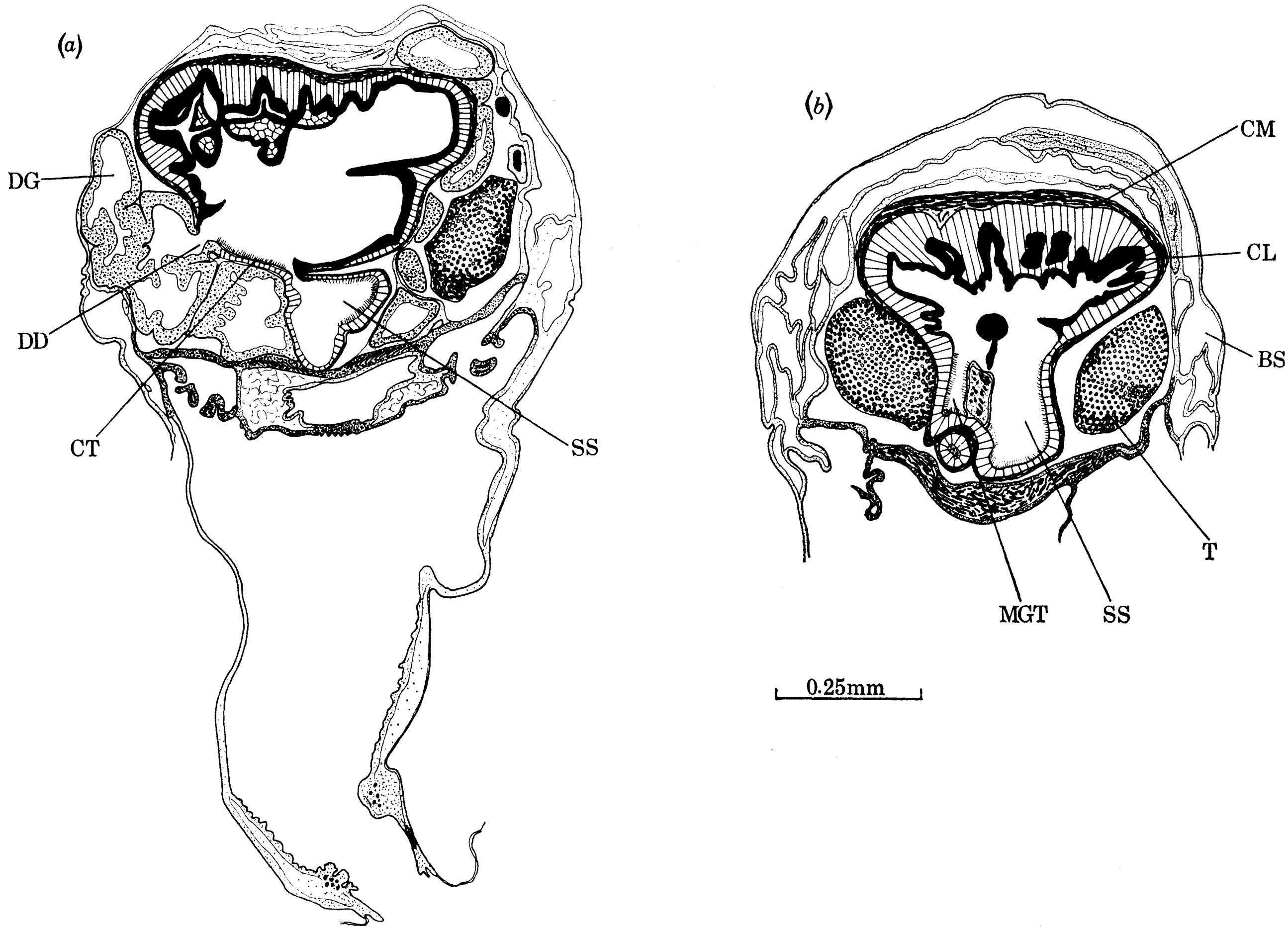

Figure 19. *Lyonsiella abyssicola*. (*a*, *b*) Transverse sections through the anterior and central regions of the stomach.

right and left openings to the digestive diverticula (LDD, RDD) and posterior to these, but still close to the ventral edge of the oesophageal aperture in the ventral floor of the stomach, is the opening to the combined style sac and mid gut.

Ciliation within the stomach is minimal. From each of the two apertures of the digestive diverticula there is a ventral ciliated tract leading to the mid gut aperture. Both the right and left apertures of the diverticula are situated close beside the circumoesophageal ciliated band (figure 17*a*, *c*). The left opening is placed slightly posterior to the right. Apart from these few small ciliated areas, the stomach is lined with scleroprotein which is thickened at its junction with the oesophagus and also at the opening of the style sac (TC, CL, figures 19*a*, *b* and 20*a*). This lining appears to be more flexible than the gastric shield of other bivalves. The heavy outer covering of muscles of the oesophagus is continued over the entire outer surface of the stomach

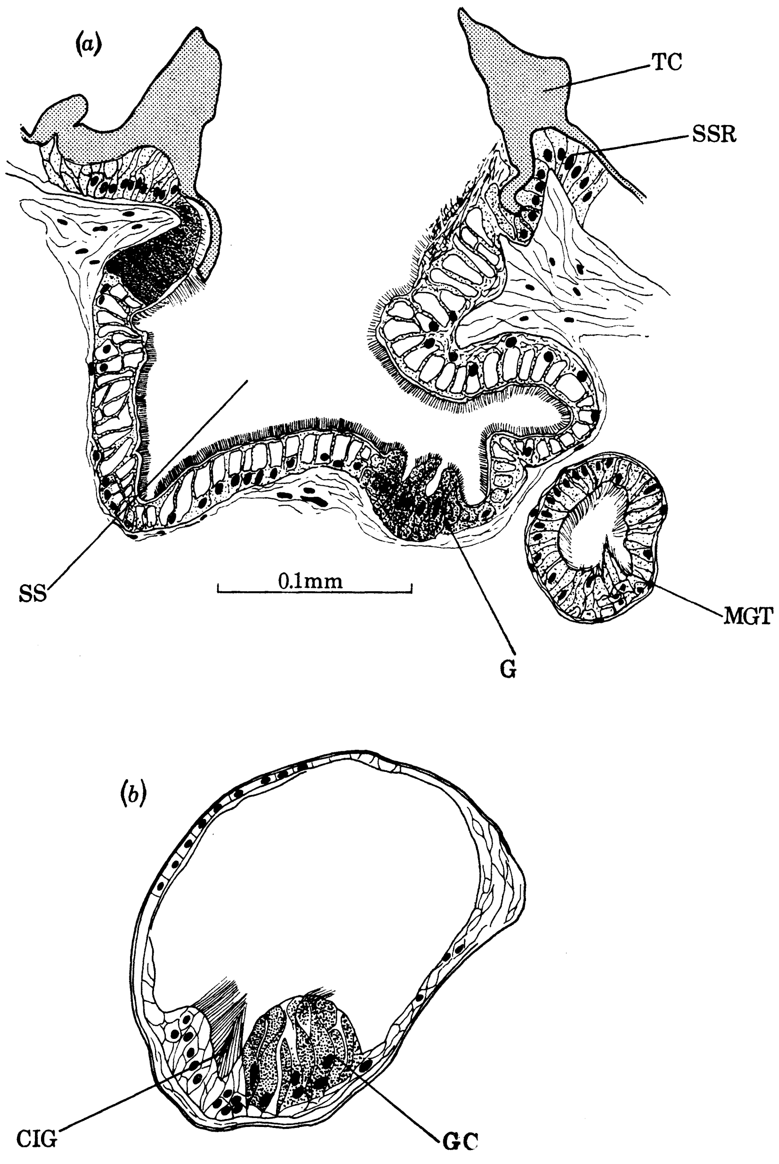

FIGURE 20. *Lyonsiella abyssicola.* (*a*) Longitudinal section through the style sac; (*b*) transverse section through the rectum.

(figure 19*a*, *b*). Thus, the stomach functions as a crushing organ with the ventral ciliation forming a conveyer belt system to the digestive diverticula and from them to the mid gut. There is no evidence of any sorting of food material within the stomach.

From whole mounts and the dissection of two specimens, food remains in the stomach (IF) consist of small Crustacea and skeletons of plant cells and Protozoa together with a large quantity of spicules and unidentifiable skeletal remains similar to that adhering to the tentacles. The largest crustacean, a harpacticoid copepod of the family Cerviniidae (probably *Pontostratiotes* sp., see Por 1969) (figure 18) was 2 mm long and 0.5 mm wide at its widest point, while the largest skeletal remains measured 1.0 mm in diameter.

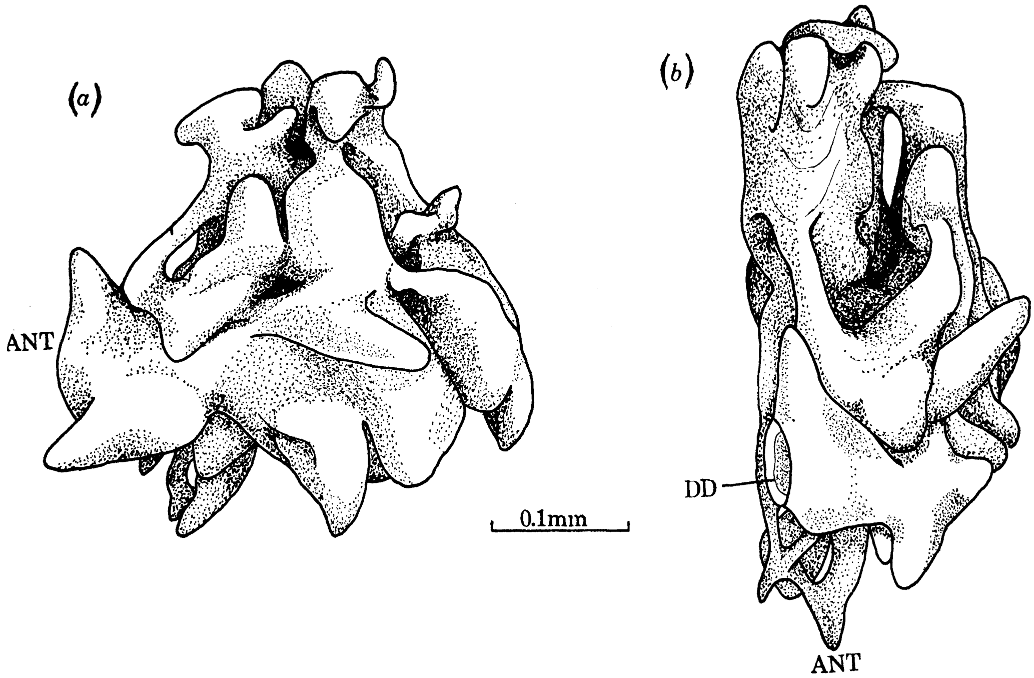

FIGURE 21. *Lyonsiella abyssicola*: whole mount of left digestive diverticulum, viewed from the side (*a*) and from below (*b*) to show branching and anastamosis of the tubular region.

The mid gut and style sac together form a short, globular structure opening on the ventral side of the stomach, close to the entrance from the oesophagus. The mid gut is to the right side of the style sac and separated from it by a pair of short typhlosoles (SS, MGT, figure 19).

The style sac, though short and broad, resembles that of other bivalves having a cuboid epithelium with a regular densely ciliated surface. Glandular cells, secreting style and enzymes (Reid 1966), are present in the typhlosole and mid-gut epithelium (GC, figure 20). There is a thin layer of muscle to the outside and this is much thinner than that surrounding stomach and oesophagus. A style (S) was observed in one of the preserved specimens. This is surprising because of the time taken to haul in and process the specimens from deep water (8–12 h), for it is well known that a crystalline style can dissolve quickly under adverse conditions. The style stained heavily in p.a.s. No tooth was identified on the gastric shield, indeed, the design of the stomach is such that a solid style would, at first sight, be functionally improbable. However, there is no evidence of any material from the stomach being forced into the style sac. The latter was empty in all other specimens examined. Thus, despite the carnivorous habit, style enzymes appear to be still available.

The hind gut (HGT) passes dorsally behind the stomach as a narrow tube and then turns posteriorly toward the posterior adductor muscle. Between the posterior stomach wall and the adductor muscle the hind gut expands to form a pear-shaped section (R) before narrowing once again as it passes over the posterior adductor muscle to the anus. This section, which varies in its degree of inflation, usually contains the broken up remains of ingested material. At this point this is not formed into discrete faecal pellets but forms a diffuse mass. On the floor of the expanded rectal section there is a ciliated groove defined by thickened epithelial ridges (CIG,

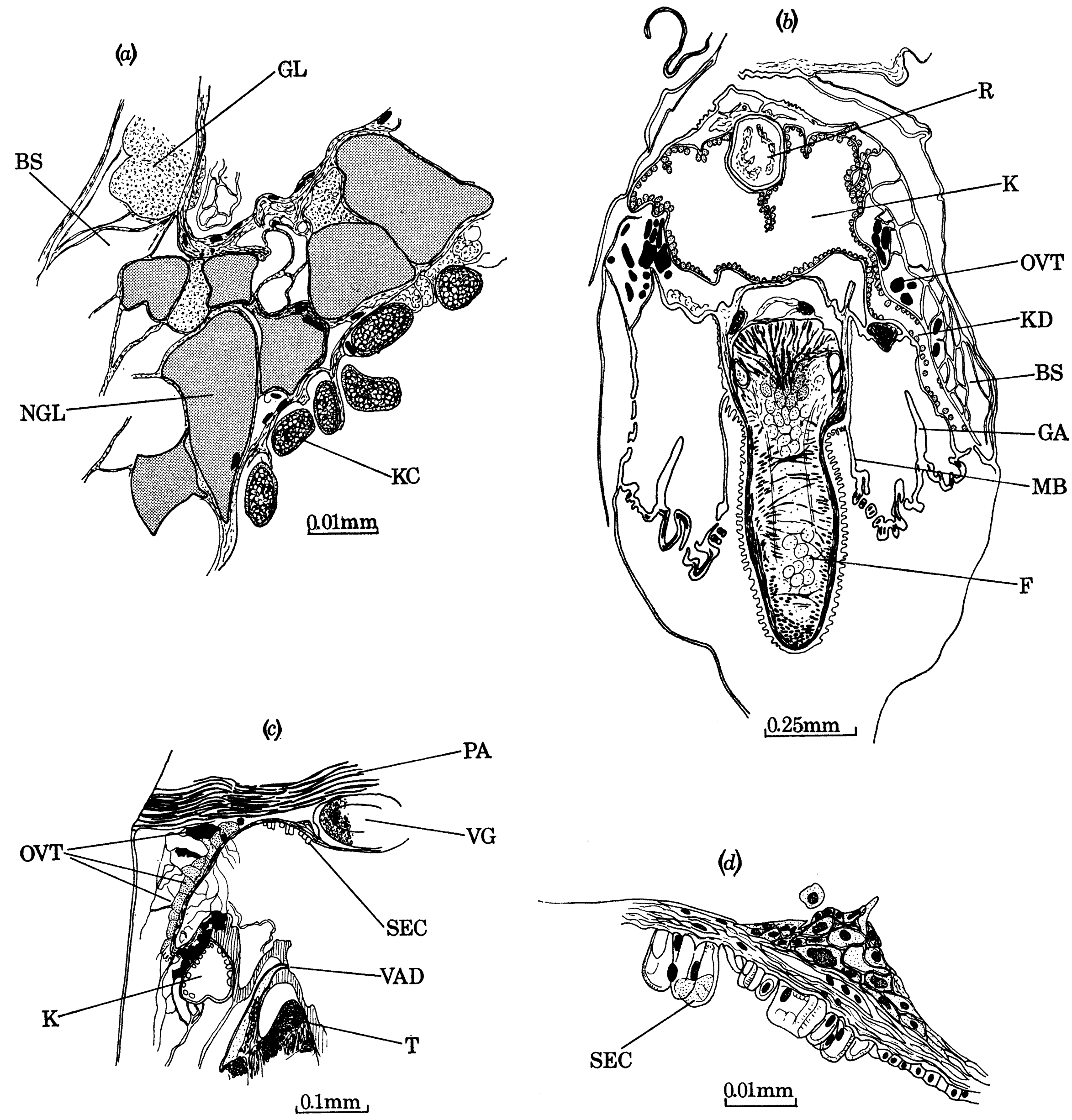

FIGURE 22. *Lyonsiella abyssicola*. (*a*) Transverse section of lacunal system adjacent to the wall of the kidney; (*b*) transverse section of a specimen through the kidney; (*c*) oblique section through the region of the posterior adductor muscle and gonadial ducts; (*d*) detail of specialized epithelial cells adjacent to the visceral ganglion.

figure 20*b*). Many abyssal bivalves extend and enlarge the hind gut, much more so than is the case here (Allen & Sanders 1966, 1973; Sanders & Allen 1973). This is undoubtedly to ensure that further digestion of refractile organic materials can occur either by retaining the material in the hind gut sufficiently long to allow bacterial decay to occur and/or to allow enzymes to act.

Digestive diverticula

The digestive diverticula (DG) form a brown mass of blind ending tubules on both sides of the body and which extend into the umbonal region. Of the two main ducts, the right is slightly more anterior than the left and somewhat larger. The main ducts are very short (approximately 8 cells long) and branch almost immediately. The tubules are bounded by a thin membrane but in the region of the main ducts there is a muscle layer present. Instead of irregular dichotomous branching of secondary ducts leading to spherical or oval tubules, the short main ducts immediately give way to a lobulated hollow interconnecting mass of tubule tissue (figure 21*a*, *b*). Histologically the tubule tissue appears to be similar to other lamellibranch bivalves such as *Cardium* (Owen 1970) with scattered groups of basiphil cells in the mass of larger digestive cells. The material was not sufficiently well fixed to determine whether the basiphil cells are flagellated. The digestive cells have typical macrovesicles and, at least from light microscope examination, appear not to differ from those of non-carnivorous bivalves.

Kidney

As in other bivalves, the paired kidney (K) abuts the anterior wall of the posterior adductor muscle. The left and right sides are joined below and in front of the inflated rectal region of the hind gut immediately posterior to the heart and stomach (figure 22*b*). The kidney is very extensive and in *Lyonsiella abyssicola*, in common with other species of the genus, there are left and right ventral extensions into the ventral and anterior part of the body as far forward as the mouth. These extensions, which have not been reported in other bivalves, are joined to the rectal part of the kidney by an elongate, tubular neck, the kidney pore to the mantle cavity opening half way along this neck. The kidney lumen is extensive and lined with a typical renal epithelium of cuboid cells with large numbers of cell inclusions (KC, figure 22*a*).

Reproductive system

L. abyssicola is hermaphrodite. The paired testes (T) are relatively small, oval, and positioned one to the right and the other to the left ventral side of the body, but dorsal to the neck of the extension to the kidney. There is a short duct and pore (VD, VAD) opening to the mantle cavity ventral to the kidney pore. The ovary, also paired to the right and left of the body, is more extensive, covering much of the lateral area of the stomach, with the short oviduct opening dorsal and posterior to the aperture of the kidney (OV, figure 23). Approximately 120 ova of varying size are present in specimens 3.5 mm total length; the largest ova measure 150 μm maximum length. Analysis shows that no specimen less than 1.5 mm total length has maturing eggs, while all specimens of 3.0 mm and above have, with the proportion of specimens with maturing eggs increasing as the length increases from 1.5 to 3.0 mm (figure 24).

Closely associated with the reproductive system, kidney, and blood spaces of the posterolateral part of the body and mantle, is a series of lacunae, the function of which can only be a matter of speculation. The tissue extends from the posterior ventral limit of the ovary across the neck of the kidney, under the posterior half of the testis to the posterior wall of the posterior

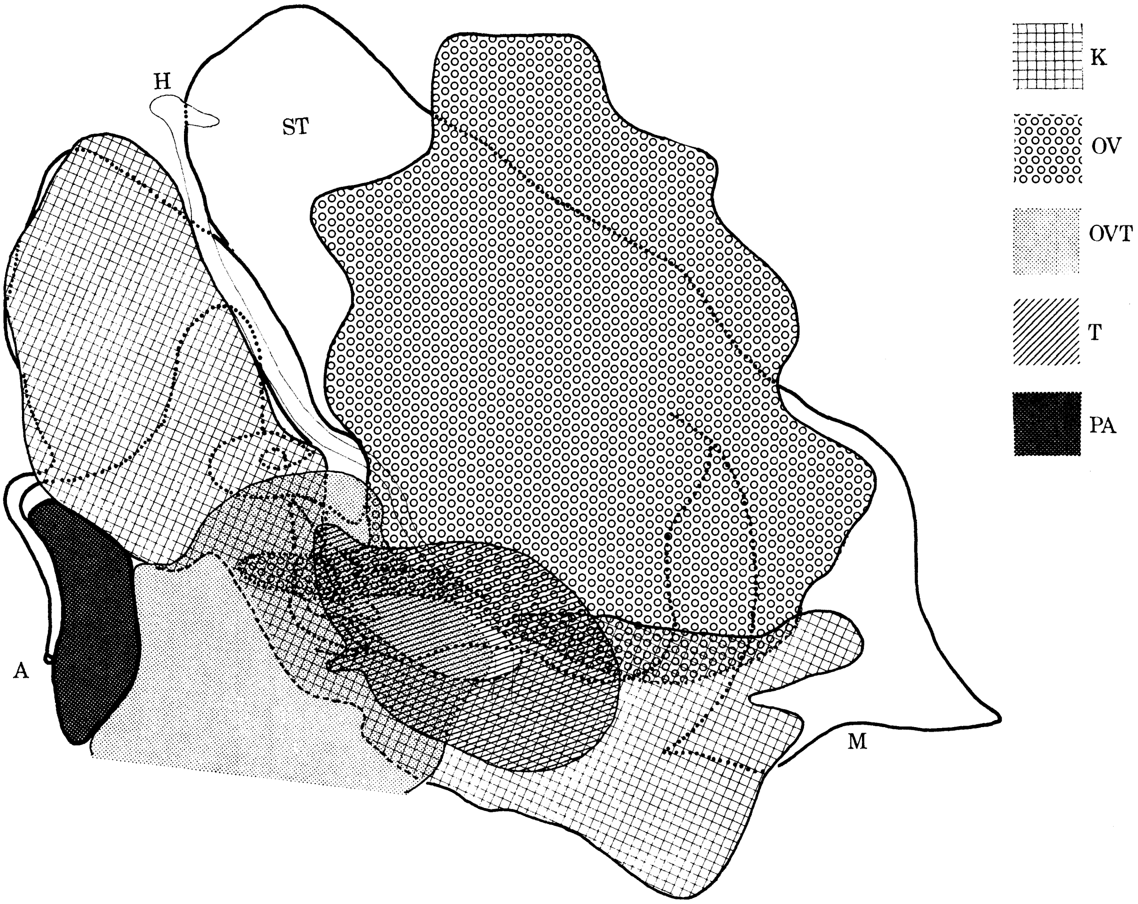

FIGURE 23. *Lyonsiella abyssicola*: lateral diagrammatic view of the gonads, kidney and lacunal system in hatched outline and superimposed on an outline of the gut. This diagram was obtained by analysis of a complete series of transverse sections and this is accurate in terms of extent and relation of the parts.

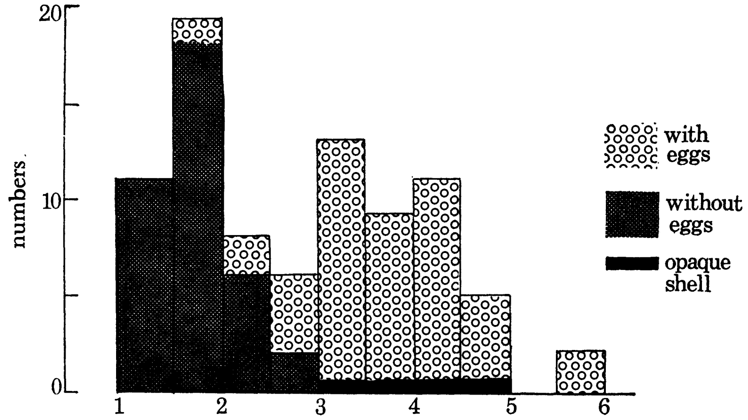

FIGURE 24. *Lyonsiella abyssicola*: to show the size range and maturity of specimens taken from all stations sampled between 1962 and 1968.

adductor muscle (OVT, figures 22*a*, *c* and 23). Most of the tissue lies between the kidney and the hypobranchial cavity. The lacunae are 10–35 μm wide and are either filled with a uniform non-granular substance (NGL) which stains darkly in trichrome stains (with orange G or with haemotoxylin) or with a fine granular network which does not stain in the trichrome stain (GL). Surrounding the lacunae are small basal cells and overlying the tissue laterally is a network of small blood sinuses (BS). No ducts were observed from the cells to the hypobranchial cavity, although the contents of the lacunae have all the appearance of a glandular secretion (figure 22*a*). Possibly if the contents are secretory they would be transported from the tissue via the blood system. Also characteristic of this region are a group of enlarged cuboid epithelial cells on the dorsal side of the hypobranchial cavity and on either side of the anus (SEC, figure 22*c*, *d*). These do not take up any stain but have a brilliant golden refractile appearance under the light microscope. Again, there is nothing to indicate function.

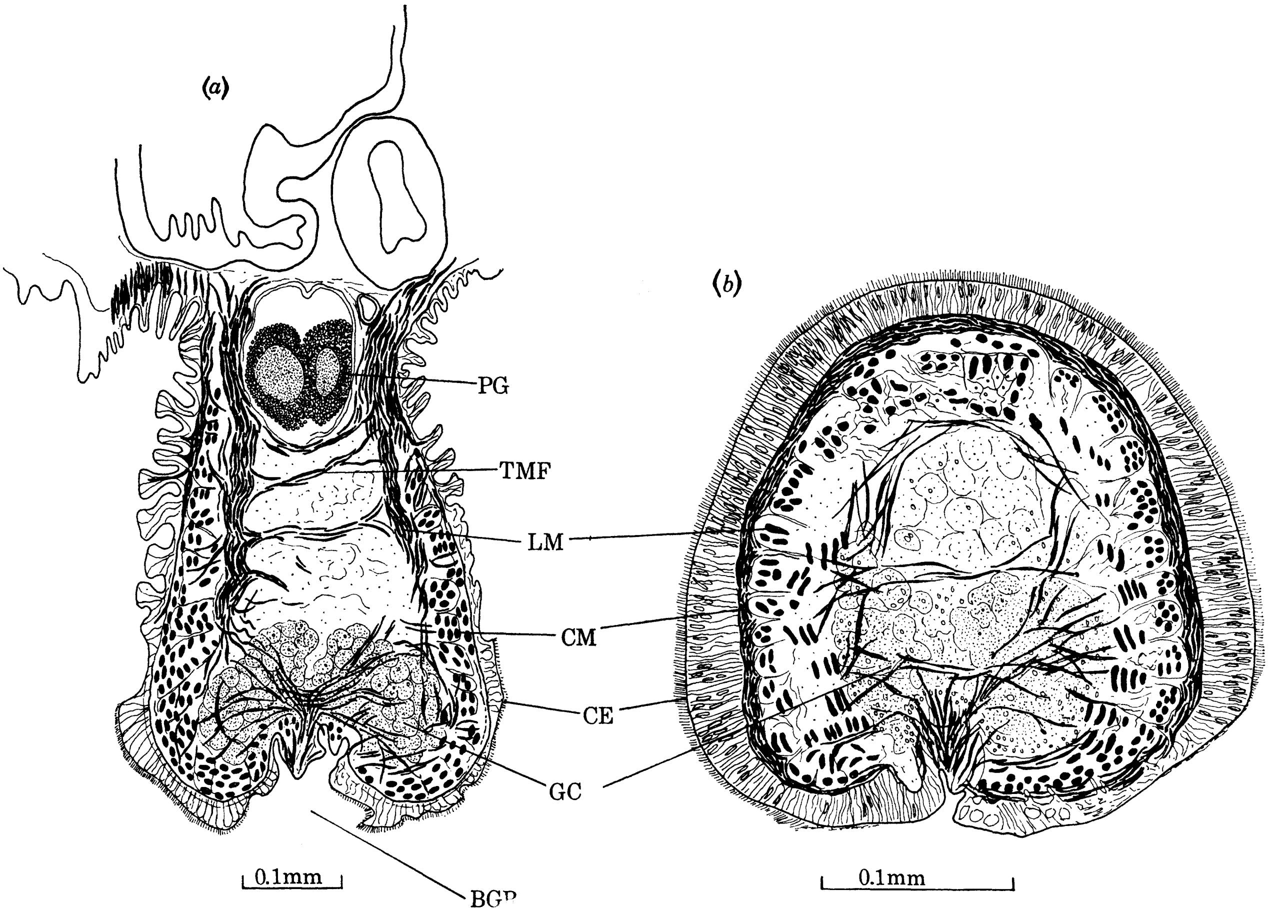

FIGURE 25. *Lyonsiella abyssicola*. (*a*, *b*) Longitudinal and transverse sections through the foot.

The foot

The small, vermiform foot (F), whose heel is not pronounced, is located posteriorly to the small pedal gape (PGD) allowing it access to the sediment. The outer surface is finely wrinkled in preserved specimens and in life it is presumably capable of considerable extension. The musculature consists of an outer circular muscle layer, an inner layer of longitudinal muscle and a central region of transverse muscle fibres running through connective tissue. There are also bundles of inner longitudinal muscle (figure 25*a*, *b*). There is a pair of major retractor muscles inserted above the posterior adductor (BRM). The tip of the foot is ciliated. There is a byssus gland (BG) and a byssal groove that runs sagittally along the posterior face of the foot. The gland is functional in the adult although very few threads (B) are present at any one time (*ca.* 6). Some of the longitudinal and transverse muscle fibres connect with the basement layer of the epithelium of the byssal groove (BGR, figure 25*a*, *b*). The gland cells of the foot are of two kinds. Both are located within the connective tissue, one, staining heavily with haemotoxylin, is peripheral to the other, and discharge via long slender ducts between the epithelial cells to the outside or into the byssal groove. The second type gives a strong positive reaction with alcian blue or p.a.s. stains and individual cells with ducts lead to the deepest part of the byssal groove. The cell contents of these latter glands are finely granular. Both glands are present along the entire length of the byssal groove and proximally the groove connects with a short duct within the heel of the foot at the head of which the p.a.s. positive gland cells are arranged in a fan of six radiating blocks. The channels between the blocks connect with the main byssal duct. This arrangement in *Lyonsiella abyssicola*, although not so complex, is little different from that of, say, *Mytilus*, except that there is no ring of glands and ducts at the tip of the foot producing an attachment disk. Instead of a disk the ends of the byssus strands are subdivided into a number of fine extensions.

The paired rounded cerebral ganglia (CG) are situated on the sides of the oesophagus equidistant between the mouth and stomach. The oval-shaped pedal ganglia (PG) are situated in the body of the animal somewhat anterior to the foot just above the line of the gill. The visceral ganglia (VG), situated just in front of the posterior adductor muscle, are large, presumably to service the large tentacular area.

Although the blood volume is probably large, the heart is small, both auricles and ventricle being little more than the diameter of the long branchial vessel which originates from a central position on the gill axis (H, figure 23). The heart is dorsal to the hind gut and situated in a wedge-shaped space between the posterior dorsal wall of the stomach and the anterior dorsal wall of the kidney. The pericardium is also small and from its posterior wall there is a short renopericardial duct.

Lyonsiella subquadrata (Jeffreys 1881)

						no. of specimens
Atlantis II	20. ii. 67	sta. 167	07° 58.0′ S–07° 50.0′ S, 34° 17.0′ W	943–1007 m	E.S.	4
Sarsia	19. vii. 67	sta. S56	43° 43′ N, 3° 47.8′ W	641 m	E.S.	2
Discovery	15. iii. 68	sta. 6696	28° 06′ N, 13° 28′ W	1780 m	E.S.	1

Distribution:

North America Basin, off Virginia; West Europe Basin, off Cape Mondego and north of Hebrides; Mid Atlantic Ridge, Azores, 298–3340 m.

The shell of *L. subquadrata* was described initially, and briefly, by Jeffreys (1881) from material taken by the Porcupine Expedition of 1869 and then further by Verrill & Bush (1898) from a single left valve taken off Virginia. Fortunately we have been able to compare our specimens with both the type material in the British Museum and other specimens in the Smithsonian Museum (no. 63239) (figure 26*a–d*). The shell is very fragile and most specimens show evidence of damage at the margin with subsequent repair. Because of this, and possibly because of a natural tendency to variation, shells of this species show marked differences in shape (figure 28), some being distorted by an indentation at the anterior ventral edge of the shell, somewhat reminiscent of the condition in *Thracia distorta* (Allen 1961). Characteristic of the species are the very large incurved umbos which are anterior in position, and also the more or less straight posterior dorsal shell margin (figures 27*a*, *b* and 28). The anterior and posterior curvature of the shell is much less constant in outline. Unevenly spaced growth lines are present, and the fine surface spinules are arranged in radiating rows in younger specimens. In larger specimens the latter may not be so obvious, many of the spinules being lost. The present specimens range in size from 1.0 to 2.6 mm in total length and 0.6–1.6 mm in height.

Internally the shell is nacreous and the adductor muscle scars barely distinguishable. The hinge plate of the left and right valves is thickened and relatively broad with small irregular

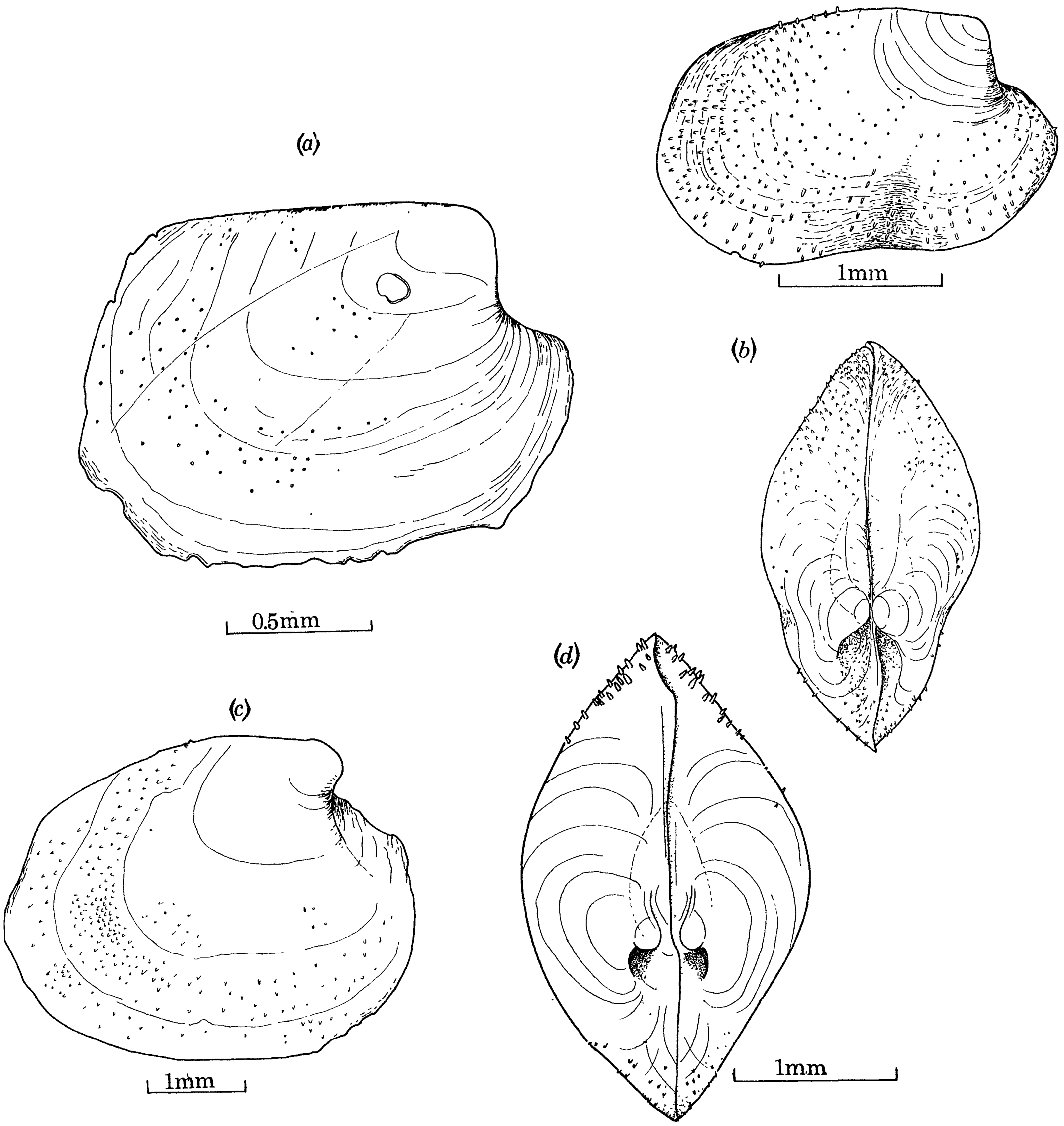

FIGURE 26. *Lyonsiella subquadrata*: lateral view of the right valve of specimen no. 63239 from the Porcupine Expedition (U.S. National Museum); (*b*) lateral and dorsal view of a shell from station 167 (*Atlantis*, 20 February 1967) to show marked variation in shell shape; (*c*) lateral view of the right valve of a specimen from the Porcupine Expedition (British Museum, Natural History); (*d*) dorsal view of typical specimen from station 167.

bulges and hollows but no teeth (figure 27). The lithodesma is twice as long as broad with a U-shaped notch at the posterior end. The opisthodetic ligament is similar to that of *L. abyssicola.*

No account has been given to date of the anatomy of this species. The following account, as with the subsequent accounts of other species of *Lyonsiella*, emphasizes differences from the description of *L. abyssicola.*

FIGURE 27. *Lyonsiella subquadrata.* (*a*) Lateral views of the hinge of two right valves, the lower tilted to show inside outline of the shell below the umbo; (*b*) lateral views of the left and right valves of a specimen from the British Museum (Natural History).

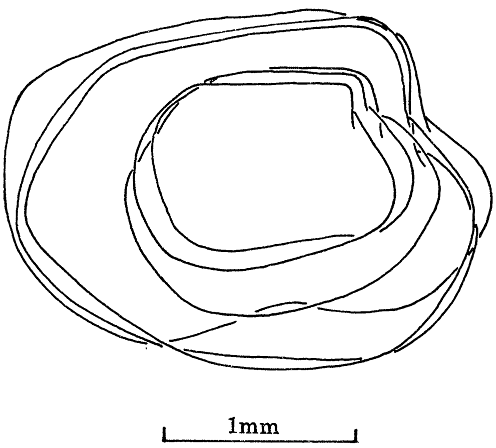

FIGURE 28. *Lyonsiella subquadrata*: lateral view of the right valves of six specimens to show variations in outline.

Radial mantle glands are not present but the extent of mantle fusion is similar to that of *L. abyssicola* with a moderately large pedal gape (figure 29). There is a well-defined exhalent siphon, which in one preserved specimen is extended to a greater extent than in any other species examined. It is suspected that this is a specimen in which fortuitous relaxation of the siphon has been maintained during fixation. There are no fringing tentacles in the exhalent region but two small conical papillate 'tentacles' are present, one on each side of the ventral margin of the base of the siphon. The inhalent aperture is not so large as that of *L. abyssicola.*

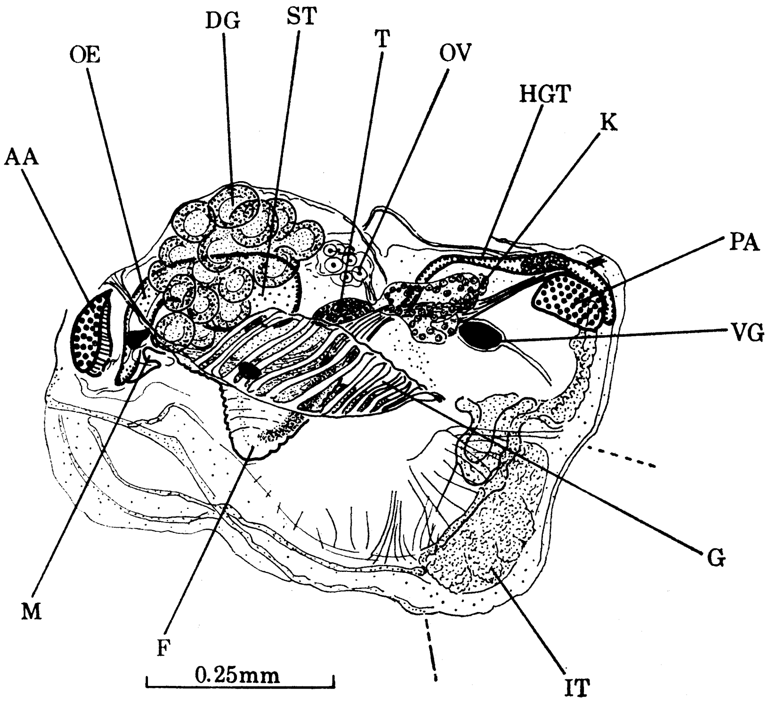

Figure 29. *Lyonsiella subquadrata*: lateral view of whole mount to show the soft part morphology.

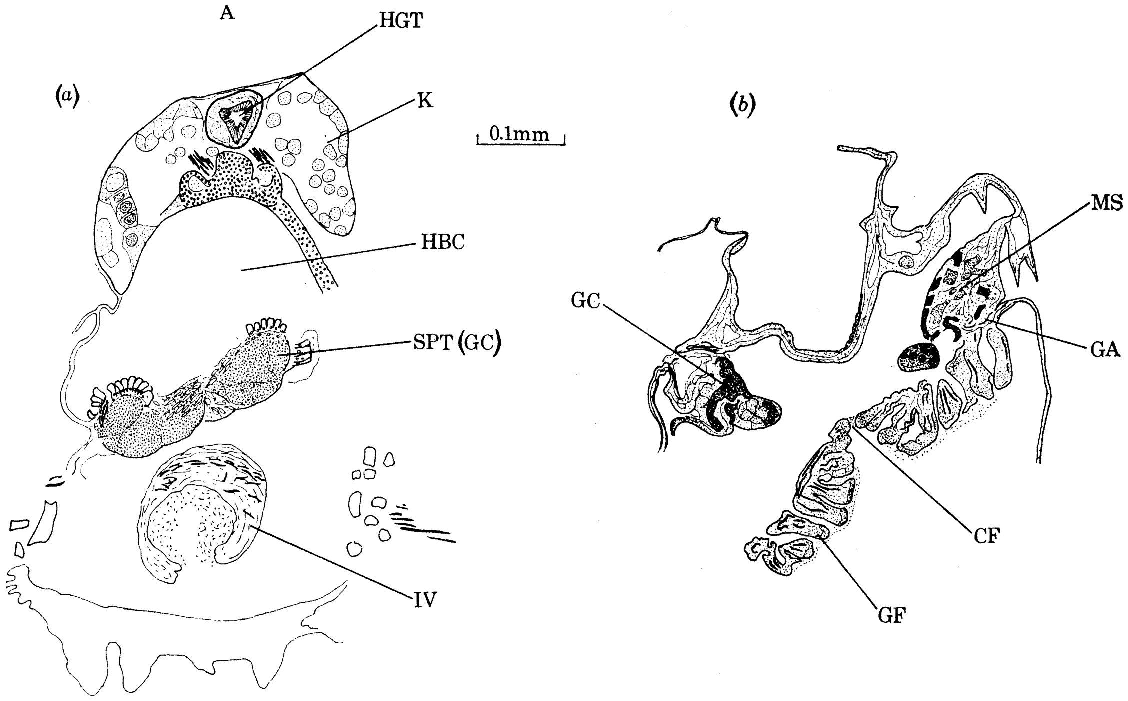

Figure 30. *Lyonsiella subquadrata*. (*a*) Transverse section through body immediately anterior to the posterior adductor muscle; (*b*) transverse section of gill posterior to the foot.

There are 8–12 broad flap-like tentacles lateral to the aperture, the second most ventral pair being larger than the remainder. Internal to these are a further 8–10 tentacles which are more conical in shape. The number is directly related to the size of the animal. Histologically, the region of the apertures is similar to that in *L. abyssicola*. The exhalent siphon does not differ in any significant way to that of *L. abyssicola*, while the tentacles are similar to the smaller tentacles of *L. abyssicola* with a double core of longitudinal-muscles in the centre of the haemocoele. The epidermis of the inner tentacles is papillate and glandular and sediment and skeletal remains adhere to it.

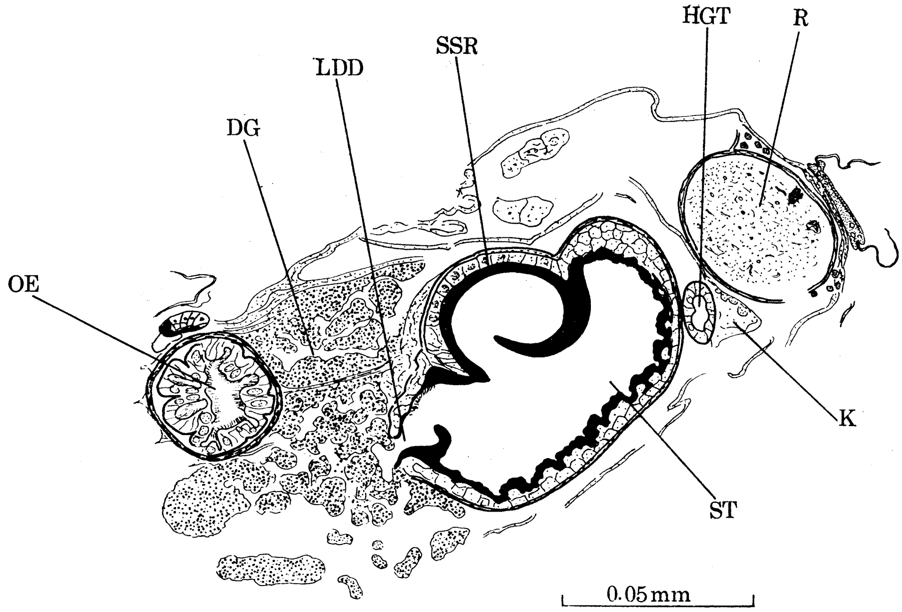

FIGURE 31. *Lyonsiella subquadrata*: longitudinal horizontal section through oesophagus, stomach and rectum.

To the inside of the inhalent aperture the inner epithelium of the mantle is well supplied with mucus glands. There are also well-developed radial pallial retractor muscles extending from the inner muscular layer into the mantle tissue in the region of the inhalent aperture and, to a much lesser extent, along the ventral mantle margin. In life the ventral mantle margin and the apertures must be able to retract within the confines of the shell. The inhalent valve is well developed and the septum between the apertures is very thick, and glandular, the epithelium being particularly thick and pad-like laterally on the hypobranchial side (figure 30*a*, *b*). The gill axes are attached to each side of the septum (figures 29, 30*a*, *b*). The gill consists of the descending lamella of the inner demibranch, the ventral ends of the anterior filaments of which are slightly upturned. Interfilamentar connexions are restricted to the free edge and the tip of the short upturned section. The filaments are moderately elongate in comparison with most verticordiids and vary in number from 11 to 13. They extend from the septum to the posterior limit of the oral hood. The axis is attached horizontally across the centre of the body and the free edge of the gill is level with the ventral limit of the body and its junction with the foot. Posterior to the body the filaments of left and right lamellae join in the midline via a fused ciliary connexion similar to that described in *L. abyssicola*.

The palps proper (as distinct from the lips) of *L. subquadrata*, while similar to those of *L. abyssicola*, are even further reduced to a few cells at the extremities of the greatly extended lips. The upper lip forms a hood ventral and posterior to the backwardly directed mouth (figure 29). The gut is also similar in basic form to that of *L. abyssicola*. The wide, ridged, muscular oesophagus opens into the anterior dorsal part of the stomach. The stomach is very large and, apart from a small ciliated area between the oesophagus, the two apertures to the digestive diverticula and the mid gut, it is completely lined with a sclero-protein layer. This is extended to form a collar around the head of the style (figure 31). The stomach is less muscular than that of *L. abyssicola* the muscles being best developed close to the oesophageal aperture and the entrance to the style sac. The short style sac lies to the left side and is lined with heavy, even, cilia. It is combined with the mid gut, the latter being to the right side. The hind gut extends from the ventral limit of the style sac dorsally where it expands into a large thin walled chamber before terminating in front of the exhalent aperture (figure 31).

Kidney and gonads are similar to those of *L. abyssicola*. Similarly, there is a well-defined functional byssus gland. The byssus threads terminate by subdivision into a tuft of fine anchor threads.

Lyonsiella perplexa sp.n. (figures 32–4)

Material: Holotype: M.C.Z. 272671

						no. of specimens
*Chain**	29. vii. 65	sta. 76	39° 38.3′ N, 67° 57.8′ W	2862 m	E.S.	3

Shell small, thin, inflated, slightly inequivalve with posterior margin flexed to the right; umbo anterior, very large and incurved; dorsal shell margin straight, posterior shell margin curves steeply so that the ventral half is almost vertical to the dorsal margin; anterior shell margin is angular, the first section from the umbo being relatively straight; the ventral margin is also angular, the central portion not quite parallel to the dorsal margin; the maximum length measurement extending between the antero- and postero-ventral corners of the shell; the shell surface is ornamented with radiating lines of fine pointed granules or spines, those at the ventral margin being somewhat larger than those closer to the umbo; a few widely spaced concentric growth lines present. Ligament opisthodetic and internal, hinge without teeth; lithodesma small, twice as long as wide, posterior edge relatively broad with a shallow central notch. Shell length of largest specimen 5.1 mm.

The shell characters of *L. perplexa* are very similar to those of *L. quadrata* Hedley. *L. perplexa* differs mainly in having an angular anterior shell margin, that in *L. quadrata* being curved, with a result that the anterior limit of the shell is more centrally placed (figure 32). The spines on the shell surface of *L. quadrata* are larger than those of *L. perplexa*, but this may be because the specimens of *L. quadrata* are three times as large as *L. perplexa*. In addition there is a great difference in geographical locality and depth of the two species, *L. quadrata* occurring in the Tasman Sea at depths of 146 and 183 m whereas *L. perplexa* was taken from the Bermuda–Woods Hole traverse (Sanders, Hessler & Hampson 1965) and off Surinam at depths of 2862–4429 m.

The anatomy, while similar to that of *L. abyssicola*, shows a number of differences (figure 33). Mantle fusion is restricted to the formation of posterior inhalent and exhalent apertures, the pedal gape is extensive occupying the entire ventral margin. No radial mantle glands are present and it should be noted that the shell of *L. perplexa* is largely clean of adhering bottom deposits. The adductor muscles are very small, the posterior muscle being oval in cross-section, the anterior very slender and crescent shaped. Both muscles lie very close to the shell margin. The inhalent aperture occupies most of the posterior mantle margin. It is surrounded by a

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* See additional records on page 531.

single ring of 10–12 conical papillate tentacles, arranged as 5 or 6 pairs, and which are structurally similar to those of *L. abyssicola*. Internal to the aperture is a very well-developed valve which has a broad dorsal face, the lateral margins tapering ventrally so that it appears to have an inverted shovel shape. The dorsal extension is presumably correlated with the marked reduction in the number of gill filaments (see below). The exhalent aperture is flanked by three conical tentacles, two lateral and one dorsal, which can be completely retracted within the shell by use of a series of short retractor muscles of even length, extending along the entire length of the posterior mantle margin.

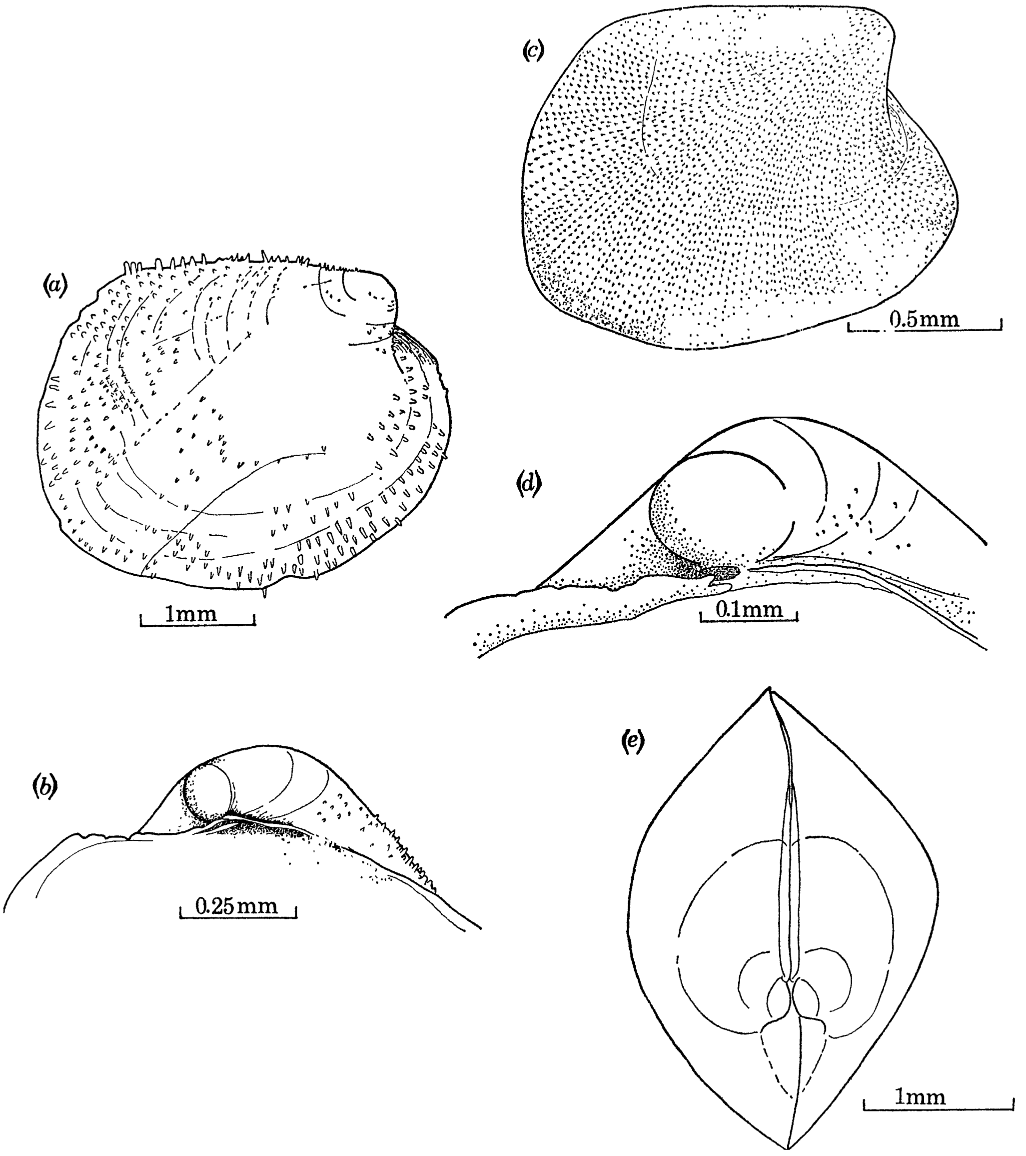

FIGURE 32. *Lyonsiella quadrata*. (*a*) Lateral view of type specimen from the British Museum (Natural History); (*b*) lateral view of the hinge of the type specimen; *Lyonsiella perplexa* (*c*) lateral view of specimen from station 76 (*Chain*, 29 July 1965); (*d*) lateral view of hinge of right valve; (*e*) dorsal view of shell.

The gills are extremely reduced, the outer demibranch is missing while the inner demibranch consists of a descending lamella of approximately 12 filaments. These are very short, the spaces between them forming a series of pores between the lower mantle and hypobranchial cavities (figures 33, 34*b*). Posteriorly the filaments stop short of the junction between inhalent and exhalent apertures, the distance being bridged by the valve. The gills are permanently attached to the mantle and body and, posteriorly, they are joined together by a membranous sheet.

The upper lip (AP) of the mouth is much extended ventrally beyond the limit of the anterior adductor muscle and lies close to the mantle edge. It is expanded to form a pair of distal wings of a channel leading to the oesophagus. The wings have a tissue attachment to the mantle ventral to the anterior adductor muscle. Whether the wings are homologous, or in part homologous, to the palps is debatable, if palps are to be regarded as extensions of the lateral corner, of the lips, then they are. However, there are no ridges on the internal face typical of the lamellibranch palp. The lower lip (PP) is not extended or enlarged, instead it is represented as a narrow band connecting the end of each gill. There are no lateral extensions of the lower lip, although the membrane that extends from the gill axis to the mantle is extended on either side of the mouth and attaches close to the ventral edge of the anterior adductor muscle (figure 34*a*). In the region of the mouth and lips there are many gland cells in the mantle epithelium.

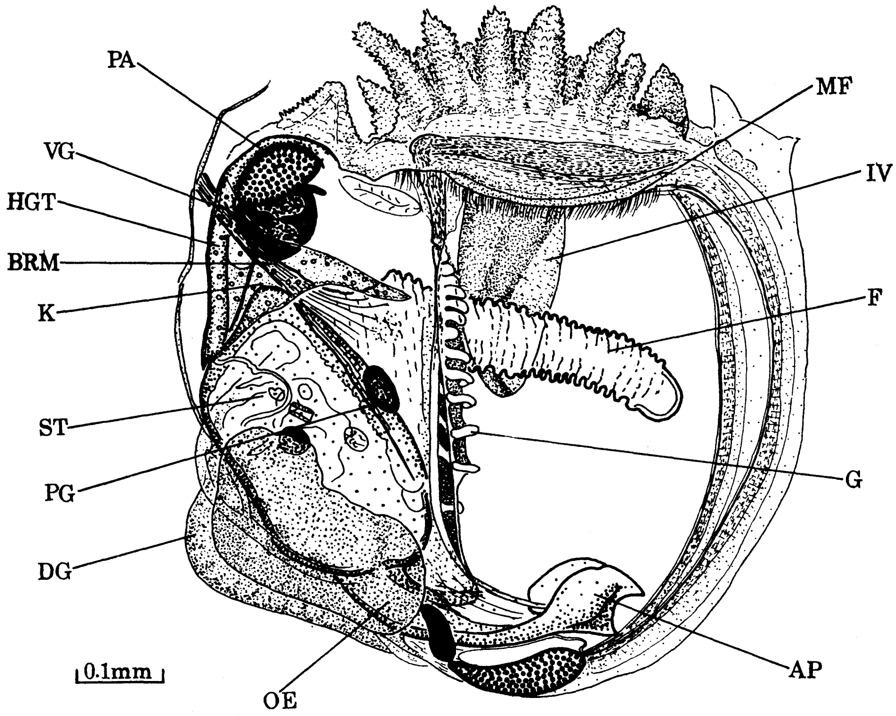

FIGURE 33. *Lyonsiella perplexa*: lateral view of a whole mount to show the soft part morphology.

The oesophagus is short and muscular. The stomach is huge, taking up much of the body above the foot. The digestive gland is anterior to and overlying the anterior part of the stomach. There are two apertures to the digestive glands close to the oesophagus and a very small and very short combined style sac and mid gut slightly to the left of the mid-line anterior on the ventral floor of the stomach. The hind gut passes behind the stomach to the dorsal side and then posteriorly over the posterior adductor muscle. The hindgut anterior to the posterior adductor muscle is not as distended as in other species of *Lyonsiella* (figure 33). The only food remains seen in the stomach were those of large diatom frustules. This species is remarkable for the large size of the visceral ganglia. Together they are larger in volume than the posterior adductor muscle, presumably their size being correlated with the increased innervation of region of the apertures and tentacles and their associated musculature. Pedal and cerebral ganglia are also prominant but not so large as the visceral. The byssus gland is small.

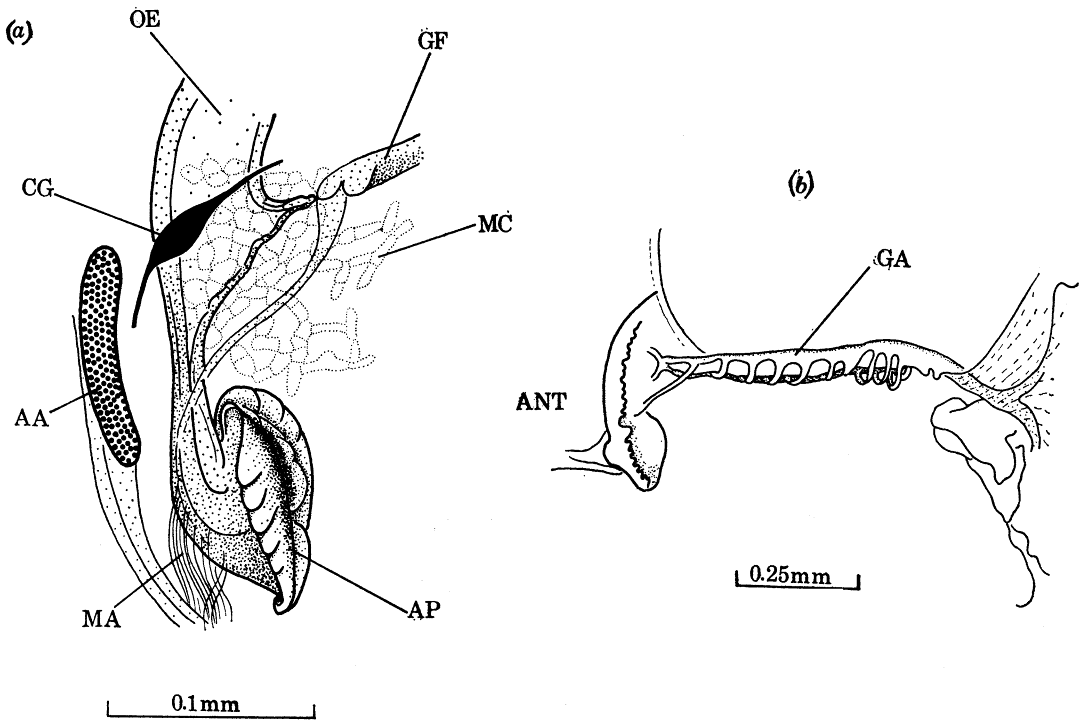

FIGURE 34. *Lyonsiella perplexa*. (*a*) Lateral view of the mouth; (*b*) lateral view of left inner demibranch.

Lyonsiella frielei sp.n. (figures 35, 36)

Material: Holotype: M.C.Z. 272672

						no. of specimens
*Discovery**	sta. 6714	20. iii. 68	27° 13′ N, 15° 41′ W	3301 m	E.S.	1

Shell small, thin, moderately inflated, slightly inequivalve, the right valve overlapping the left, anterior and posterior shell margins flexed (figure 35); shell length and height approximately equal; posterior and dorsal margins only slightly curved meeting in a sharply defined but rounded angle, ventral and anterior margins are more or less continuously curved, the anterior margin extending little beyond the level of the well-defined umbos; umbo directed forwards and inward, lunule relatively deep; approximately 11 radiating lines present on each valve, originating at the umbo and extending to the ventral margin and the lower part of the anterior and posterior margins; between the lines and parallel to them are 3–6 lines of very small surface spines, also radiating rows of spines on the posterior-dorsal angle of the valves; hinge without teeth; lithodesma small and elongate; opisthodetic ligament internal and similar to that of other species of *Lyonsiella*.

The larger specimen measures 3.6 mm total length and the species is named in memory of Dr Herman Friele for his work on North-Atlantic Arctic Mollusca and on species of the Verticordiidae in particular.

* See additional records on p. 531.

One shell was opened and the body, mounted as a whole, being lightly stained with Erlich's haemotoxylin (figure 36*a*, *b*). The morphology is very similar to that of *L. perplexa*, and in the following account the differences between the two species are stressed. There are no specialized mantle glands. The inhalent and exhalent regions are very extensive, both being surrounded by typical conical papillate tentacles (figure 36*a*, *b*). There are nine pairs of large tentacles to either side of the inhalent aperture and internal to them a similar number of somewhat smaller tentacles, together with a tertiary series of very small fine tentacles close to the bases of the larger. There is a further large primary pair lateral to the junction of the two apertures. There is a single large tentacle dorsal to the exhalent aperture with one lateral pair close beside it. Between these latter and the large primary pair at the junction, there are two smaller tentacles on each side, making seven tentacles peripheral to the exhalent siphon together with a tertiary series. Owing to the contracted state of the specimen, it is difficult to give the precise number of the latter. In form and histology, they do not differ from preceding descriptions. There is an inhalent valve but this is not so obvious as that of *L. perplexa* although this difference is probably due to differences in contraction during preservation. Judging from the similarity of gill form of the two species, it might be expected that the valve would be as extensive as that of *L. perplexa*.

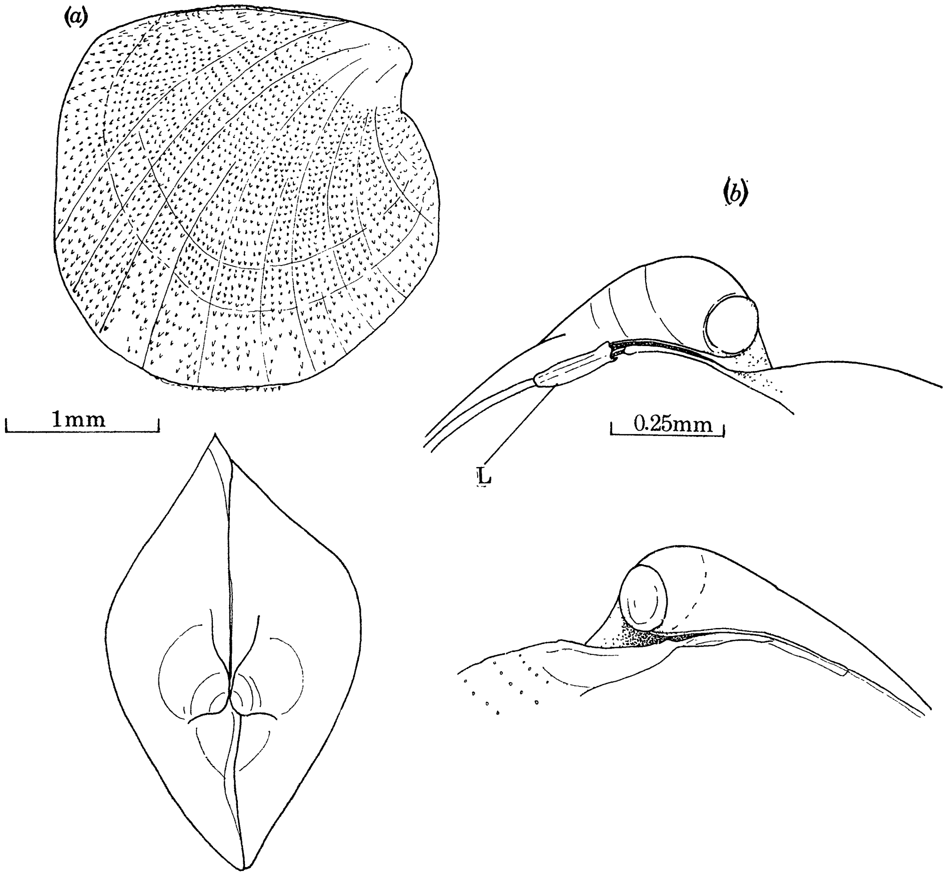

FIGURE 35. *Lyonsiella frielei*. (*a*) Lateral and dorsal view of shell; (*b*) lateral views of left and right hinges.

Lacunal tissue is particularly well developed. The adductor muscles are dissimilar in size and shape, the posterior being oval and particularly small, while the anterior is three times as large and an asymmetrical crescent shape. The visceral ganglion, like that of *L. perplexa*, is very large, but differs in shape, being elongate. It bridges the gap between the pedal retractors and the posterior adductor muscle (figure 36*b*). The gills are reduced, and comprise the descending lamella of the inner demibranch with single inter filamentar pores, there being 17–18 filaments in all. The mouth and lips lie anterior to the anterior adductor muscle, and both upper and lower lips are well developed and form the typical verticordiid funnel-shaped mouth. The stomach is relatively smaller than that of *L. perplexa*, with digestive gland covering most of the anterior, dorsal and lateral surfaces. The configuration of the gut differs little from that of other species of *Lyonsiella*, there being a typical enlarged rectal region. The kidney is extremely large and extends on either side of the body as far forward as the oesophagus. There is a well-developed, functional byssus gland (figure 36*b*).

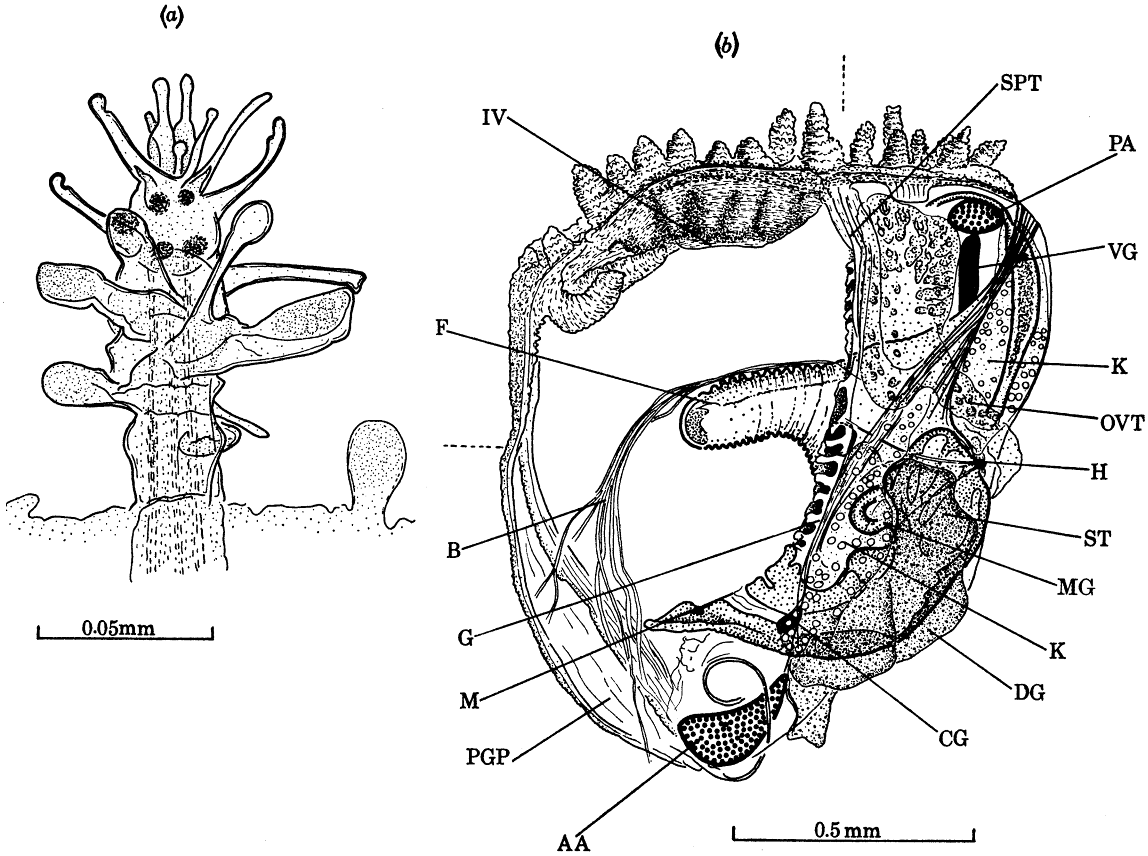

FIGURE 36. *Lyonsiella frielei.* (*a*) Whole mount of an inhalent tentacle; (*b*) lateral view of a whole mount to show the soft part morphology.

Lyonsiella smidti (Smith 1885) Friele 1886†

Material from:

						no. of specimens
Chain	3. vi. 65	sta. 83	34° 46.5′ N, 66° 30′ W	5000 m	E.S.	1
Chain	5. vii. 65	sta. 85	37° 59.2′ N, 69° 26.2′ W	3834 m	E.S.	2
Chain	14. xii. 65	sta. 93	34° 39′ N, 66° 26′ W	5007 m	E.S.	1

Distribution:

Mid Atlantic, Globigerina ooze, 1018–5007 m

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† For synonomy see appendix 1.

In 1879 Friele described a new species which he called *Lyonsiella jeffreysi* (type material, Bergen Museum, see figure 92), while in 1885 Smith, overlooking this description, applied this name to a Challenger specimen (figure 37). Friele (1886) pointed out that the Challenger specimens and his type material were not the same and proposed the name *L. smidti* for the Challenger specimen. Dautzenberg (1927) confused the issue further when he referred to the Challenger specimens as *L. smithi* and Soot-Ryen (1966) has since transferred the species to the genus *Laevicordia*. Because there is clear radial shell ornamentation (figure 37*a*, *b*) this transfer cannot stand, the species conforming in all particulars to the genus *Lyonsiella*.

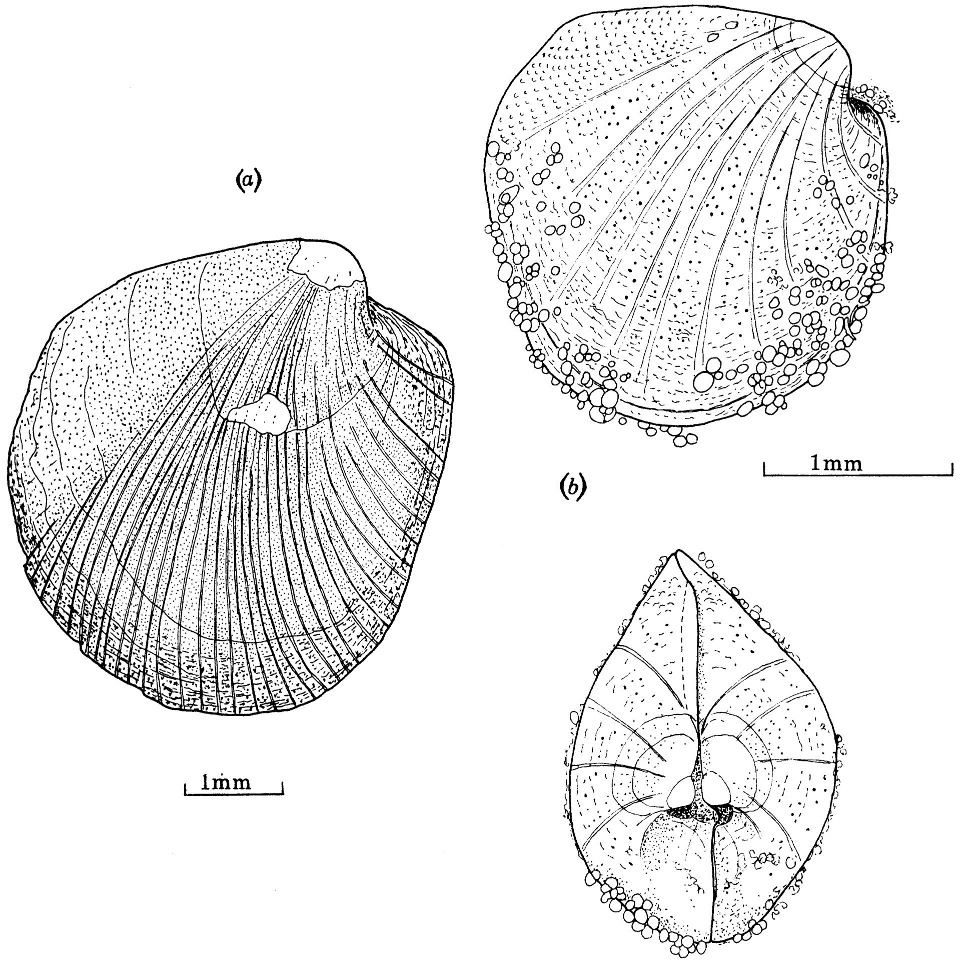

FIGURE 37. *Lyonsiella smidti*. (*a*) Lateral view of right valve of type specimen from the British Museum (Natural History) and labelled *L. jeffreysi*; (*b*) lateral and dorsal view of shell of a specimen taken from station 85 (*Chain*, 5 July 1965).

The present material was compared with the somewhat damaged type material in the British Museum, and in spite of a disparity in size they clearly belong to the same species (figure 37*a*, *b*). The maximum length of the present specimens is 3.2 mm and on one is a larval shell which is 250 μm long and 180 μm high. The shell is brown in colour with sand grains and foraminifera tests adhering to it. The shell surface is ornamented with 12 or more radiating lines and fine spinules, those spinules at the posterior end of the shell being stouter and more scale-like than the rest. The left valve slightly overlaps the right posteriorly. The hinge is without teeth, the lithodesma is relatively short and narrow and the internal ligament being similar to those described previously (figure 38).

The mantle edge is fused to form inhalent, exhalent and pedal apertures. The fusion only involves the inner muscular fold and is not extensive, that between pedal and inhalent apertures being little more than about 40 μm in length. The region of the apertures is greatly developed, more than in any other species of *Lyonsiella* seen to date, and this is at the expense of the pedal aperture, the latter being restricted to the anterior ventral margin of the mantle (figure 39*b*). Within the mantle there are a series of radial mantle glands in the region of the pedal aperture, approximately eight to each edge. These are similar to those in *L. abyssicola* and consist of a narrow cylindrical column of heavily staining densely granular gland cells (figures 39*b*, 40*a*, *b*). The ducts are not obvious in vertical section, but from whole mounts there appear to be at least three present distally. The gland lies between inner and outer mantle epithelia and opens just inside the outer limit of the middle, sensory fold (figure 40*a*). The terminal part within the sensory lobe is surrounded by crescent shaped connective cells which are possibly contractile.

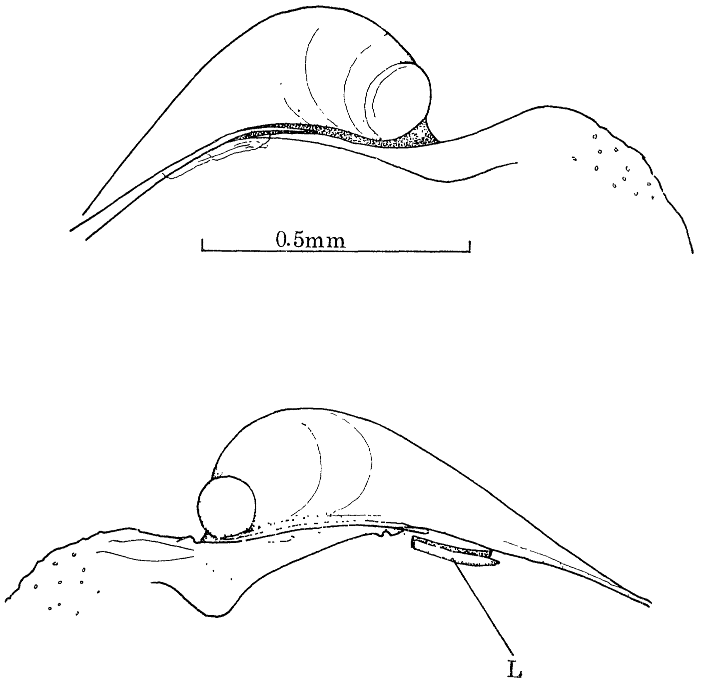

FIGURE 38. *Lyonsiella smidti*: lateral views of the left and right hinges.

Both exhalent and inhalent apertures are extremely large, the inhalent being three or four times the size of the exhalent. There are 14 large tentacles surrounding the inhalent aperture, these being conical with many adhesive papillae on their surface. The exhalent aperture is surrounded by 16 small tentacles and a somewhat larger single tentacle to the dorsal side of the aperture (figure 39*a*). The musculature of the large tentacles is not so complex as that in *L. abyssicola*. There is a pair of central longitudinal muscles with transverse musculature between them. These longitudinal muscles extend in part into the mantle behind the aperture as a series of retractor muscles. The remainder join a small number of muscles encircling the aperture. Well-developed asymmetrical longitudinal muscle bundles of the type described in *L. abyssicola* are not present (figure 39*c*). However, there are scattered peripheral longitudinal muscle fibres below the epithelium of the tentacle, as well as the fibres encircling the aperture. Internal to the inhalent aperture is the usual funnel shaped valve which has a single finger-like process at its ventral limit. The exhalent aperture is exceptionally large as is the supra-branchial cavity (figure 39*b*). It is almost certain that in life the periphery of the aperture can be extended as a short siphon. Evidence for this is twofold; one, that the peripheral tissue is relatively broad, even in the contracted state; and two, that there is a series of retractor muscles in the thickened mantle adjacent to the aperture (figure 39*b*). The mantle epithelium in the region of the apertures is supplied with many mucus gland cells. The adductor muscles are very small and rounded in shape and attached close to the shell margin. The visceral ganglion immediately anterior to the posterior adductor muscle is large, as is the pedal ganglion (figure 39*b*).

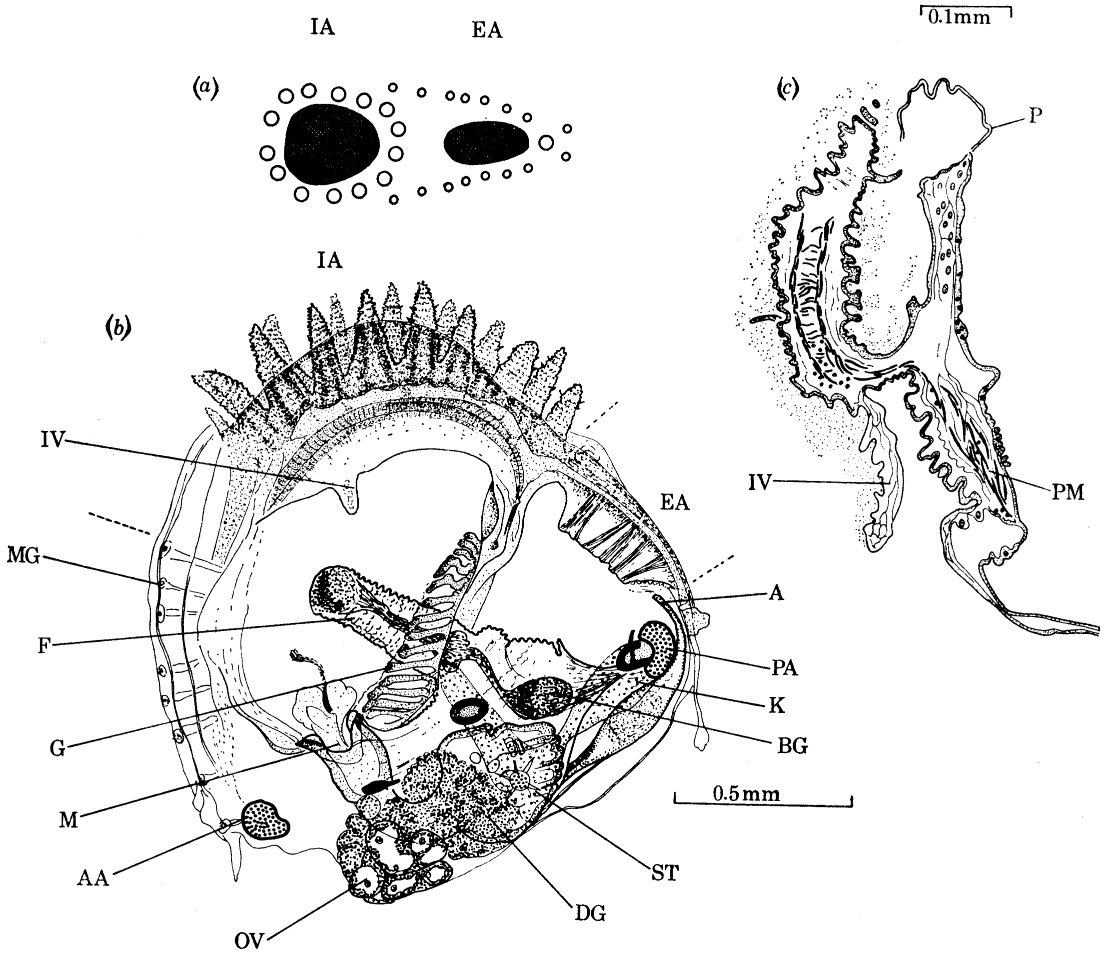

FIGURE 39. *Lyonsiella smidti*. (*a*) To show the arrangement of the tentacles surrounding the inhalent and exhalent apertures; (*b*) lateral view of a whole mount to show the soft part morphology; (*c*) longitudinal section through an inhalent tentacle and the adjacent mantle edge.

The gills comprise both outer and inner demibranchs. The filaments are short and carried lateral to the axis so that ascending and descending lamella are not easy to define. The ascending lamella of the inner demibranch was not observed, while that of the outer demibranch, if present, is restricted to the very fringe of the gill edge. Both demibranchs unite either with the body or mantle by tissue fusion. Posterior to the foot it may be that in life there is similar ciliary fusion to that described in *L. abyssicola*, although in whole mount preparations the gills are not fused in the mid line posterior to the foot even though there is tissue extension of the inner gill edge. Both demibranchs extend from the inhalent valve to the mouth, the inner originating a little further posterior than the outer demibranch. Posteriorly the gill is carried on a ridge of mantle epithelium which is glandular on its lower face (MS, figure 41*a*, *b*). This ridge then merges with the posterior dorsal edge of the inhalent valve.

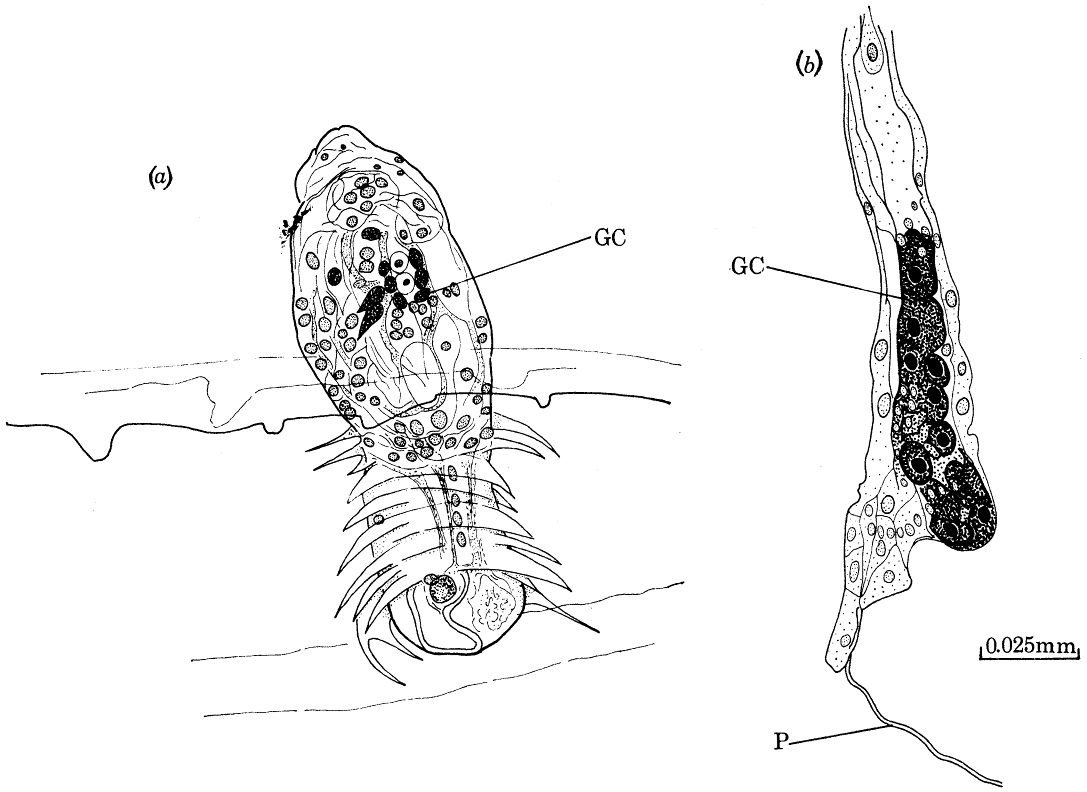

FIGURE 40. *Lyonsiella smidti*: radial mantle gland. (*a*) Whole mount in lateral view; (*b*) longitudinal section.

The lips and palps appear to be less prominent than in other species of *Lyonsiella*. However, the whole mount specimen shown in figures 39, 42*a* is in the act of swallowing an unidentified larva and the lips may well be more contracted than at other times. As a corollary to this observation it should be noted that the lumen of the oesophagus of this specimen is much wider than other species, presumably being dilated to accept the prey (FO, figure 42*a*). Gland cells are present in the mantle epithelium surrounding the mouth and are similar to but possibly not homologous with the golden refractile cells that occur close to the anus in *L. abyssicola* (cf. figures 22*d*, 42*b*). The gut follows a similar course to that described previously, with an extremely large stomach lined with scleroprotein, a very reduced style sac and mid gut, and a dilated rectal region in the hind gut. The digestive gland lies across the anterior half of the stomach.

The ovary lies far forward, anterior and dorsal to the oesophagus and anterior to much of the digestive gland. In contrast, the testis is far removed from it and lies dorsal to the byssus gland. The kidney is large and extends to where the anterior margin of the foot joins the body.

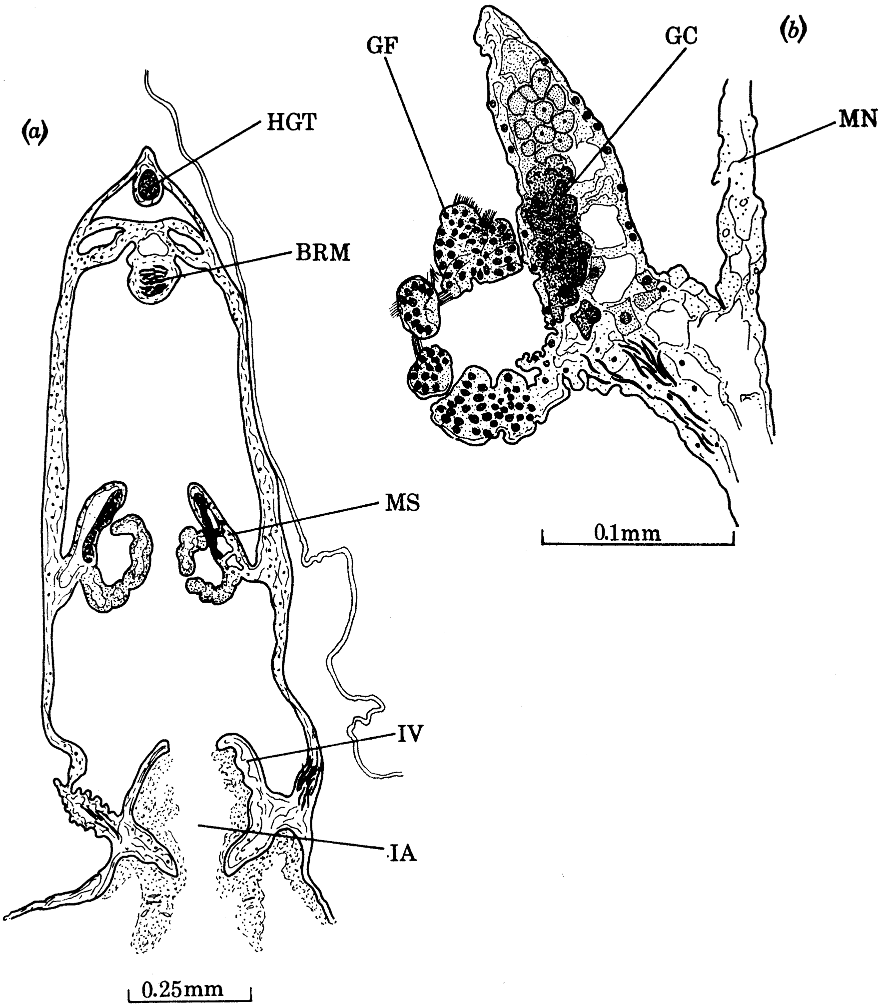

FIGURE 41. *Lyonsiella smidti.* (*a*) Transverse section posterior to the foot to show gill attachment to mantle shelf; (*b*) enlarged drawing of mantle shelf.

Lyonsiella formosa (Jeffreys 1881)

Material from:

						no. of specimens
Atlantis II	5. ii. 67	sta. 142	1.0° 30.0′ N, 17° 51.5′ W	1624–1796 m	E.S.	8
Atlantis II	13. ii. 67	sta. 155	00° 03.0′ S, 27° 48.0′ W	3730–3783 m	E.S.	1
Atlantis II	14. ii. 67	sta. 156	00° 46.0′ S, 29° 28.0′ W 00° 46.5′ S, 29° 24.0′ W	3459 m	E.S.	4
Discovery	15. iii. 68	sta. 6696	28° 06′ N, 13° 28′ W	1780 m	E.S.	2
Discovery	18. iii. 68	sta. 6709	27° 29.8′ N, 15° 20.1′ W	2351 m	E.S.	1

Distribution:

Off Canaries, Azores, Bay of Biscay, Gulf of Mexico, 366–3783 m.

This species was originally described by Jeffreys (1881) as *Lyonsia formosa* and, in general, the elongate shape of the adult shell resembles that genus. Jeffreys (1881) did not describe any of the soft parts but described the shell accurately and he was clearly impressed with it, writing that it is '*a most lovely shell, and one of the prizes of the deep sea dredger*'. We hope that any deficiencies in Jeffrey's description are compensated by our figures of specimens from the present material which we compare with Jeffreys' specimens from the Smithsonian collection (no. 61238) (figure 43*a*–*f*).

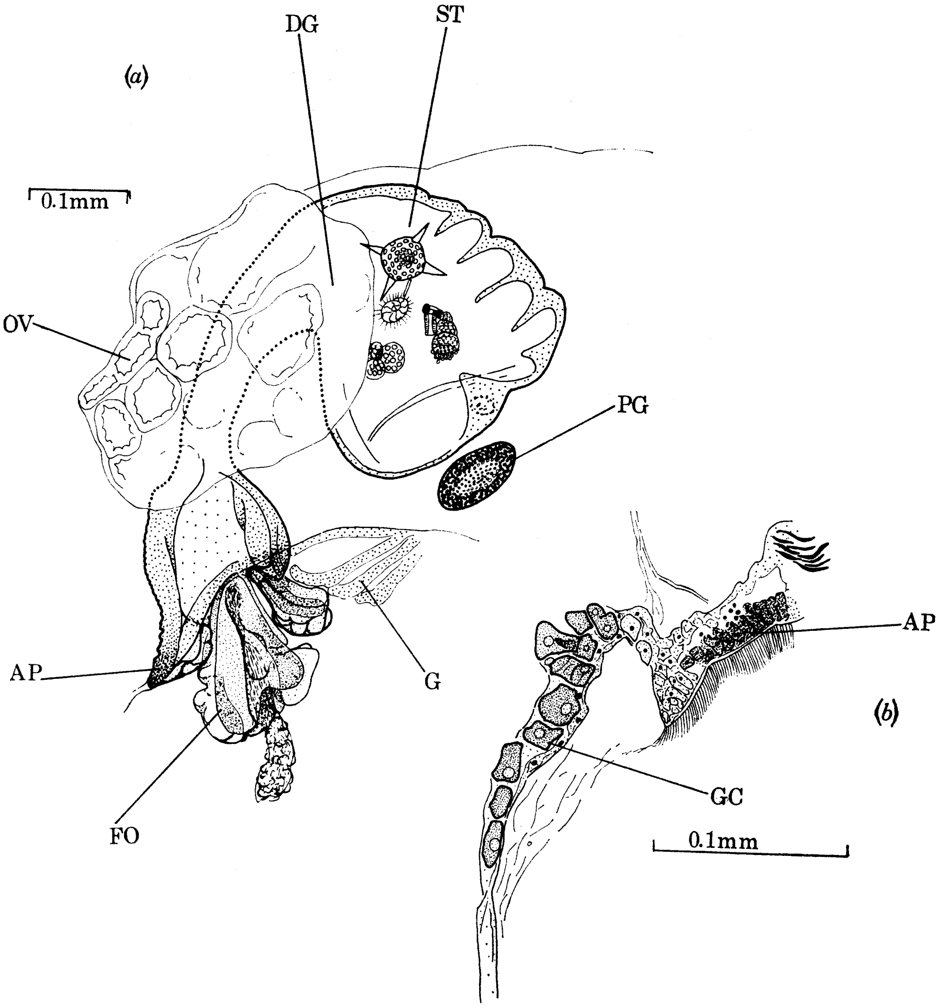

FIGURE 42. *Lyonsiella smidti.* (*a*) Lateral view of mouth and stomach (note a larva is in the process of being swallowed and there are remains of Radiolaria and Foraminifera in the stomach); (*b*) transverse section of anterior lip and adjacent mantle.

The largest adult shells (8.0 mm total length) are elongate, with the umbo anterior in position. The ventral edge is extended posteriorly with, in the largest shell, two postero-ventrally directed angles, where the crests of the two most anterior crests of radiate ridges meet the margin. Other ridges radiating posteriorly from the umbo meet the irregular posterior margin. This margin in particular shows evidence of considerable and continuous damage during the lifetime of the animal. Many large specimens have a postero-dorsal gape when the valves are closed. Both the shape of the shell and the number of ridges present varies during the lifetime of the shell. The shape of the smallest specimens in our collection is typically trapezoidal with one or two posterior radiating ridges (figure 44). As the shell grows, it becomes more elongate and the number of ridges increases to at least twelve. The most anterior ridge and sometimes the second

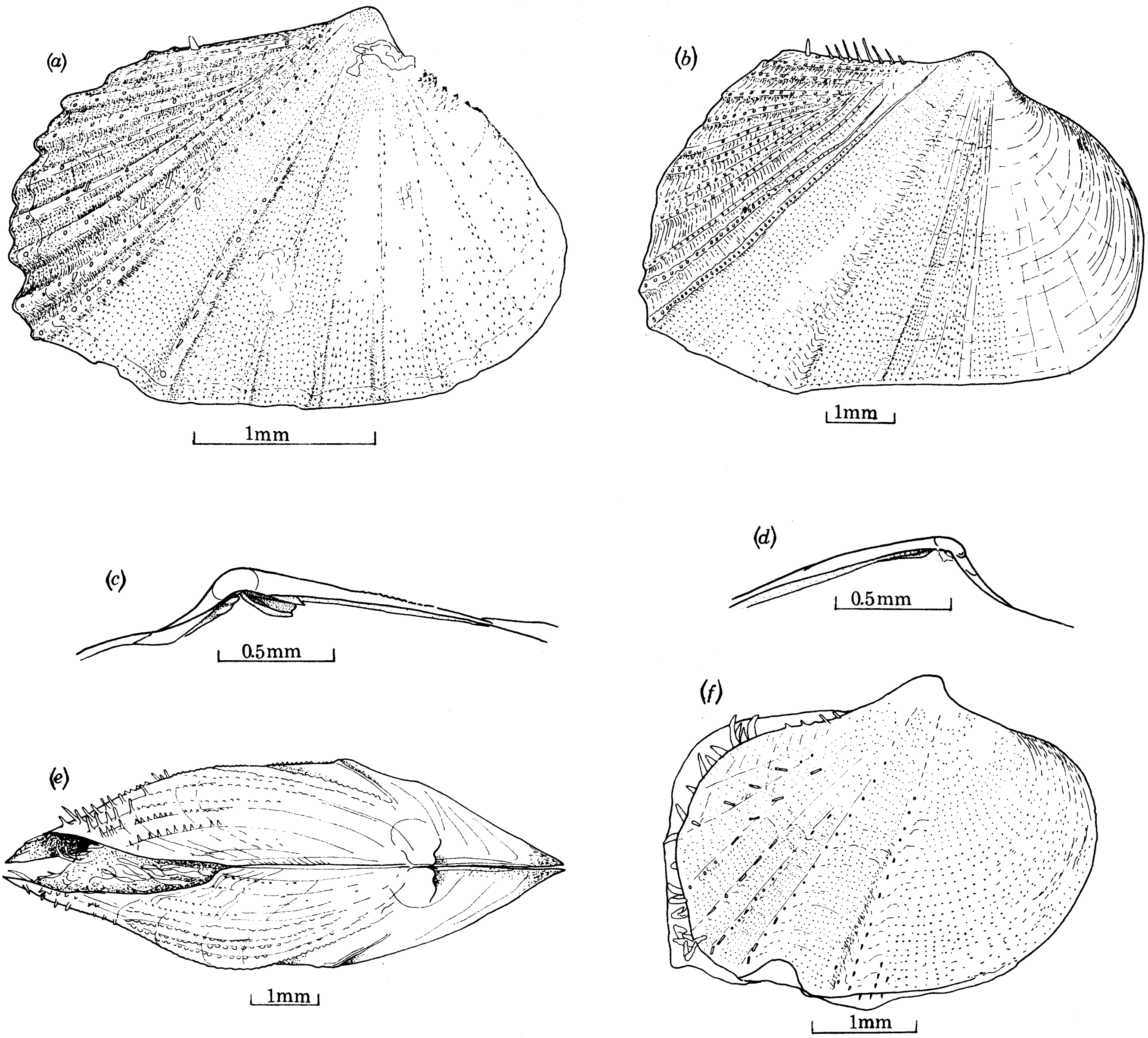

Figure 43. *Lyonsiella formosa*. (*a*) Lateral view of the right valve of specimen no. 61238 (U.S. National Museum); (*b*, *e*, *f*) lateral and dorsal views of specimens taken from station 142 (*Atlantis*, 5 February 1967); (*c*, *d*) lateral views of right and left hinges.

most anterior, being more widely separate from the others. Each ridge bears a single row of spines, set in large sockets, the spines are frequently lost, their position being indicated by the surviving pits or sockets. Elsewhere on the shell surface are smaller spines or pits in radiating rows but these are not set on raised ridges. Irregular growth lines are present. The hinge is smooth, without teeth, although there is a small thickening of the hinge margin immediately anterior to the umbo (figure 43*c*, *d*). There is a very small, boat-shaped lithodesma which has a sharply truncate anterior margin. The lithodesma lies immediately posterior to the umbo with the ligament attached to its mid-central dorsal face. The mantle edge is fused to form inhalent and exhalent apertures, but because fusion between the pedal gape and the inhalent aperture is minimal (figure 45), the pedal gape is extensive. The free mantle edge is not thickened, the inner muscular lobe forms a shelf, the middle and outer lobes being clearly defined (figure 46*b*). There are no specialized radial mantle glands, although there are large cells each with a prominent nucleus and clear cytoplasm below the middle sensory fold, however, these do not appear to have a glandular function. The sensory lobe is papillate (figure 46*a*). The inhalent and exhalent apertures are flanked by three ill-defined rows of unevenly spaced tentacles, the outer rows are the largest, the inner the smallest. They vary in number with the size of the specimen, the maximum number recorded for the present specimens was 45 (figure 47*a*, *b*). The 6–8 tentacles situated at the ventral limit of the inhalent aperture are much larger than the remainder and more spatulate in shape. Most are unbranched, narrow, finger-like structures, profusely covered in elongate papillae (figure 47*d*). The mantle edge is much thicker in the region of the apertures and the tentacles stand on a thickened perimeter that surrounds both apertures.

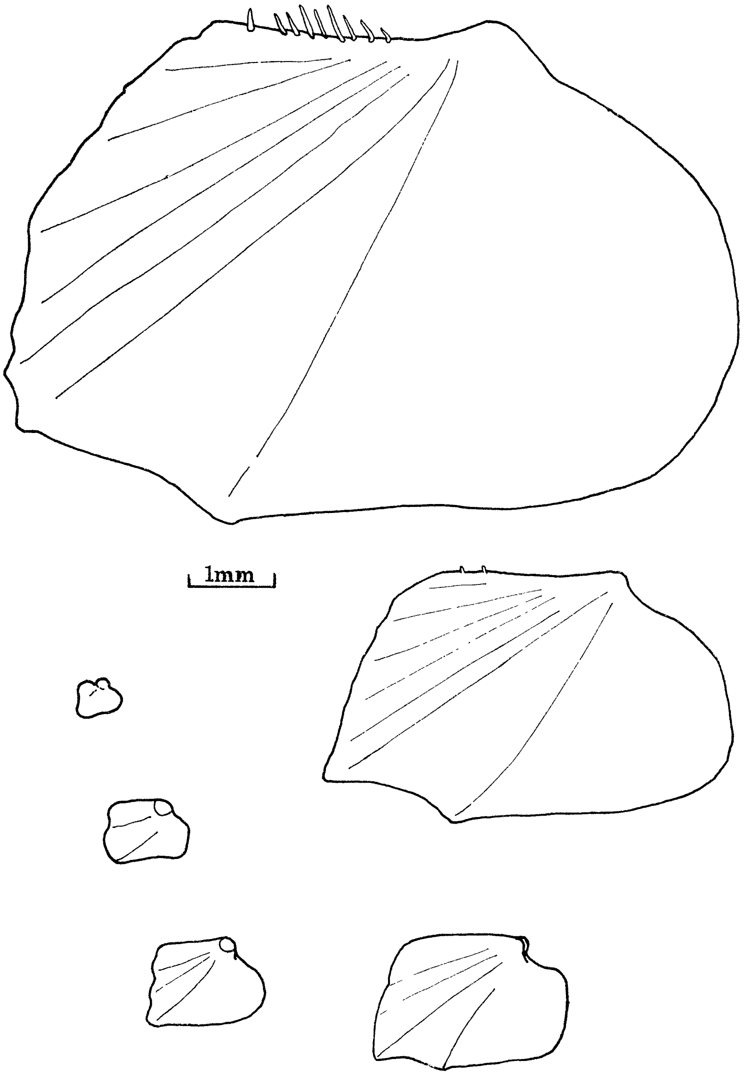

FIGURE 44. *Lyonsiella formosa*: outlines of the right valves of various specimens to show changes in form with increasing size.

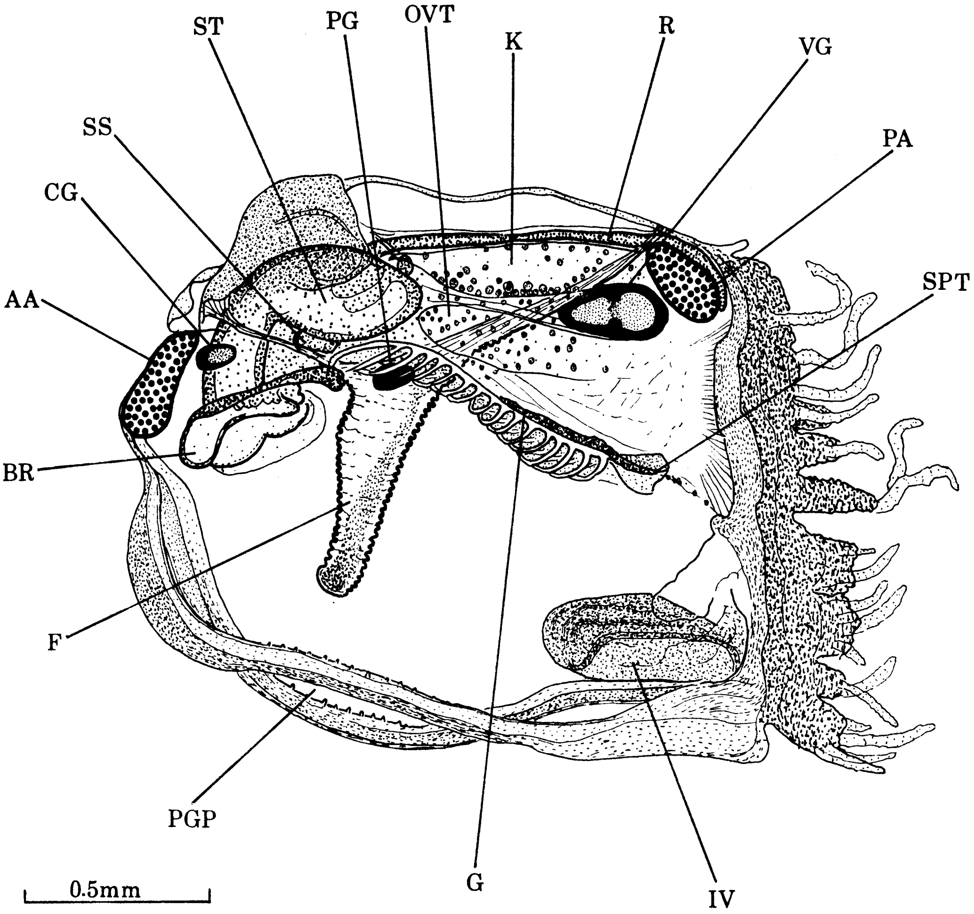

FIGURE 45. *Lyonsiella formosa*: lateral view of whole mount to show details of the soft part morphology.

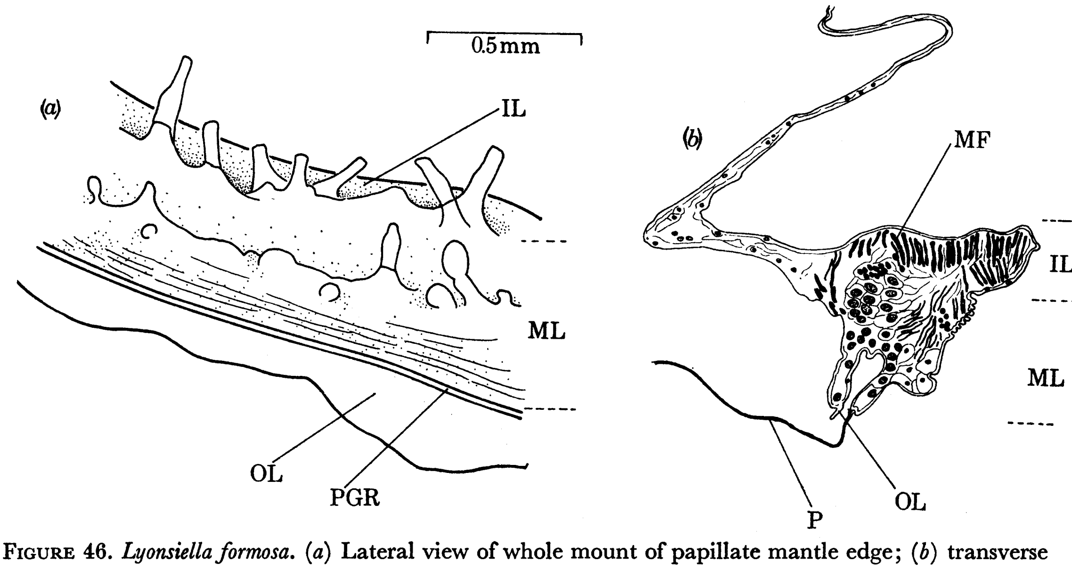

FIGURE 46. *Lyonsiella formosa*. (*a*) Lateral view of whole mount of papillate mantle edge; (*b*) transverse section of the mantle edge.

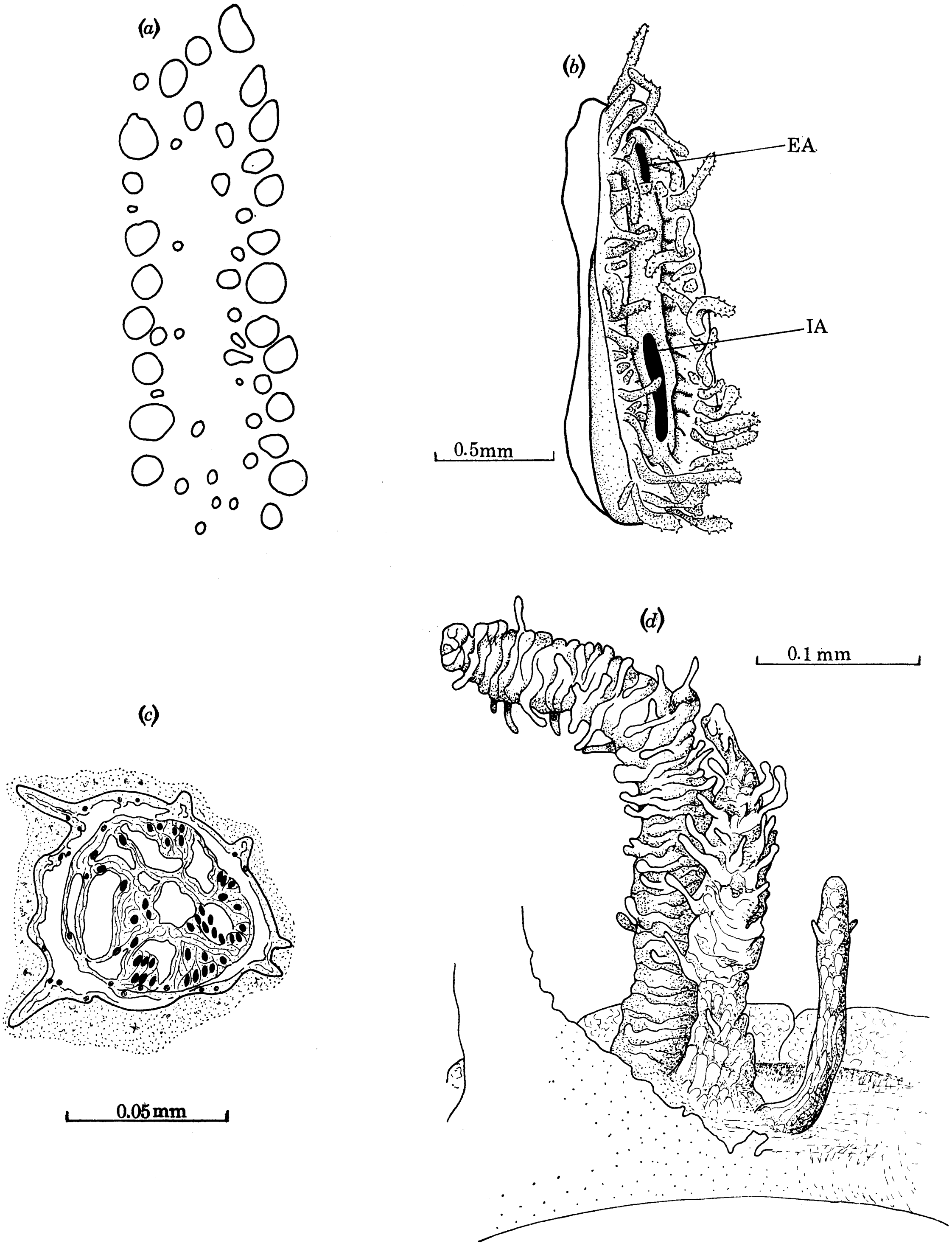

FIGURE 47. *Lyonsiella formosa*. (*a*) Plan of the siting of the inhalent and exhalent tentacles in posterior view; (*b*) posterior view of the apertures and associated tentacles; (*c*) transverse section of an inhalent tentacle; (*d*) whole mount of three adjacent inhalent tentacles.

In cross-section, each tentacle has a central core of tissue which is arranged in the form of a spoked wheel, longitudinal muscles running through the tissue. The hub and spokes form the walls of 6–8 longitudinal haemocoelic spaces (figure 47*c*). Between the central core of tissue and the epidermis of the tentacle is an outer annular haemocoele with a few tissue cross connections. The longitudinal muscles extend into a circular band of muscle at the perimeter of each aperture. No asymetrically placed muscles are present in the base of the tentacle.

To the inside of the bases of the inner tentacles the encircling band of muscle forms a thin sheet below the outer epithelium of a diaphragm surrounding the aperture. To the inside of the inner epithelium of the diaphragm is a second sheet of encircling muscle fibres and between the two sheets are bundles of regularly arranged radial muscles which extend peripherally to form short retractors within the mantle anterior to the apertures. Connecting fibres extend across the septum between the apertures, these form a cross between the encircling muscles of the exhalent and inhalent apertures.

The musculature associated with the inhalent aperture is better developed than that of the exhalent. Posterior to the inhalent aperture and extending into the mantle cavity is a large valve. This is a tongue of tissue attached peripherally to the inside of the lateral and ventral walls of the inhalent aperture (figures 45, 48*a*, *b*). The tongue is elongate and trough shaped, the concave face held below the gill. Together, these form a broad channel down which material entering the inhalent aperture will pass towards the mouth. The internal structure of the valve is similar to the diaphragm surrounding the aperture.

In most specimens the gill comprises the inner demibranchs only, the lamellae lying in the horizontal plane. The gill axis is attached close to the junction of mantle with the body, the edge of the ascending lamella of the inner demibranch being attached to the side of the body by a narrow membranous tissue junction. Immediately posterior to the foot the ascending lamellae are held together by an interlocking ciliary junction, but further posterior they too are joined by a narrow tissue membrane. The most posterior filament of each side fusing with the inward extension of the septum between inhalent and exhalent apertures. In the largest specimens a small outer demibranch is present at the posterior end of the axis and this consists of a narrow descending lamella attached to the mantle (figure 48*a*). Interfilamentar junctions are limited to the edge of the lamellae and the food groove at the junction of ascending and descending lamellae.

Few muscle fibres are present in the gill filaments or gill axis. Apart from their respiratory function, the gills must act primarily and together with the inhalent valve, as a conveyor belt for material passing from the inhalent aperture to the mouth.

The mouth, lips and palps are not formed into an open, posteriorly directed funnel, but are much modified. The modification involves (as it does in the formation of the funnel) the great extension of the anterior (upper) lip. In *L. formosa* the anterior lip recurves first posteriorly and then dorsally below and behind the mouth where it fuses with the central part of the rim of the posterior (lower) lip. The structure so formed is constricted in the horizontal plane in the mid-line and below the mouth and forms a globular flask-shaped buccal cavity below the mouth (BC, figure 49*a*, *b*, *c*). Extending laterally from the right and left sides of the neck of the sac there are a pair of fluted funnel shaped tubes (FL) which correspond to the outer sections of the upper and lower lips, the edges of which have been fused proximally. The gills, terminate at the open distal ends of these tubes (figure 49*a*). Anterior to its opening below the mouth proper, the roof of the buccal cavity is thickened in the mid-line and forms a plug to the opening (TO, figure

49*b*, *c*). The opening can also be constricted by a sphincter muscle encircling the neck. The thickened region is reminiscent of a tongue and possibly may function as such, however, the ventral side of the structure appears to be supplied with large numbers of gland cells (figure 49*b*). The walls of the flask are not muscular and there is nothing to suggest that it is capable of active contraction, however it is possible that it could be distended and that it could have a digestive function.

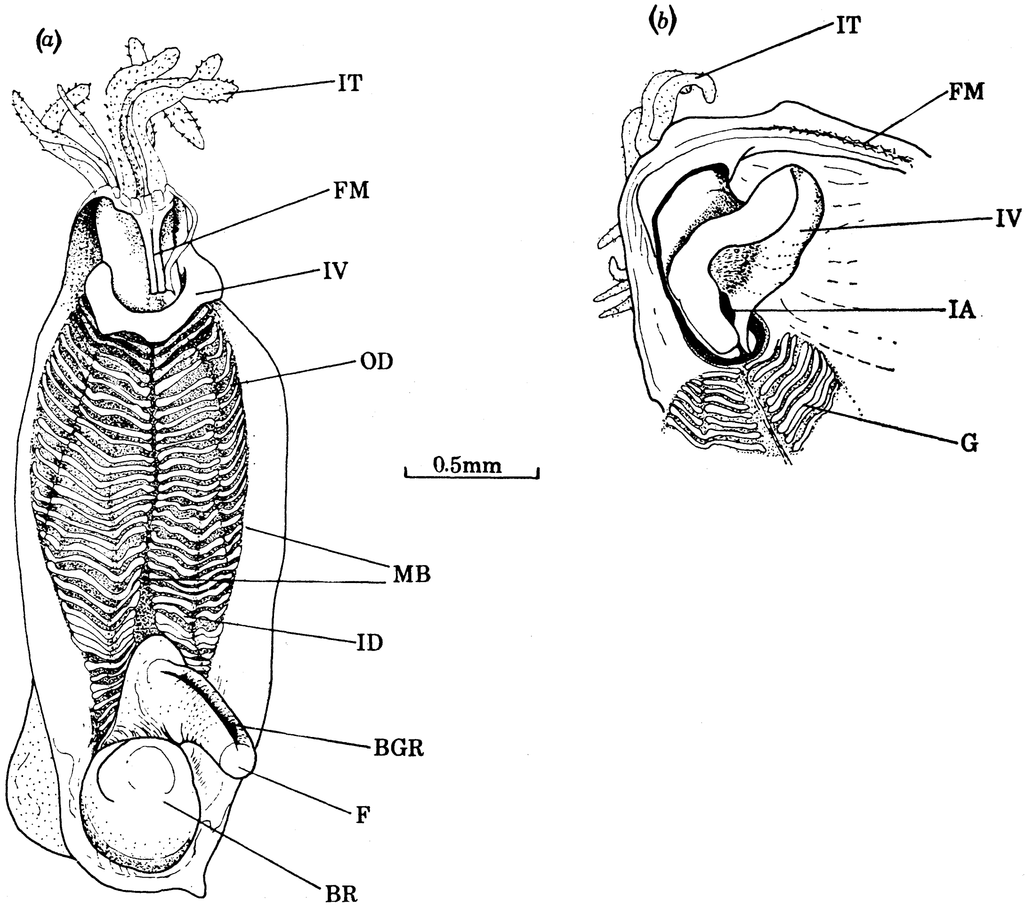

FIGURE 48. *Lyonsiella formosa.* (*a*) Ventral view of mantle cavity and associated organs, the ventral mantle margin having been removed; (*b*) detail of the inhalent valve as seen ventro-laterally.

The gut is similar to that described for *L. abyssicola.* There is a short, wide, muscular oesophagus that joins the stomach anteriorly. The large, globular ridged stomach has a fine layer of muscle externally and has an internal lining of scleroprotein. The latter has three or four folds on each side. Ventrally, close to the oesophagus, there is a very short, combined style sac and mid gut which in its turn connects with the hind gut that passes dorsally and posteriorly to the right of the stomach. That portion of the hind gut anterior to the posterior adductor muscle is not enlarged as it is in many verticordiids examined in this study. The digestive diverticula lie lateral and dorsal to the anterior half of the stomach. Short, left and right digestive ducts join the stomach between the opening of the oesophagus and that of the combined hind gut and style sac.

The visceral ganglion is extremely large, larger than the posterior adductor muscle, anterior to which it lies. The other ganglia are much smaller, although still clearly visible in the whole mount preparations. The pedal ganglion lies mid central above a small thin foot. There is a functional byssus gland and groove. The histology of the foot is similar to that described for *L. abyssicola.* The kidney is relatively large, extending from the posterior adductor muscle to the posterior lateral wall of the stomach. *L. formosa* is hermaphrodite and a system of lacunae is present, posterior to the ovary and lateral and ventral to the kidney similar to that described for *L. abyssicola.*

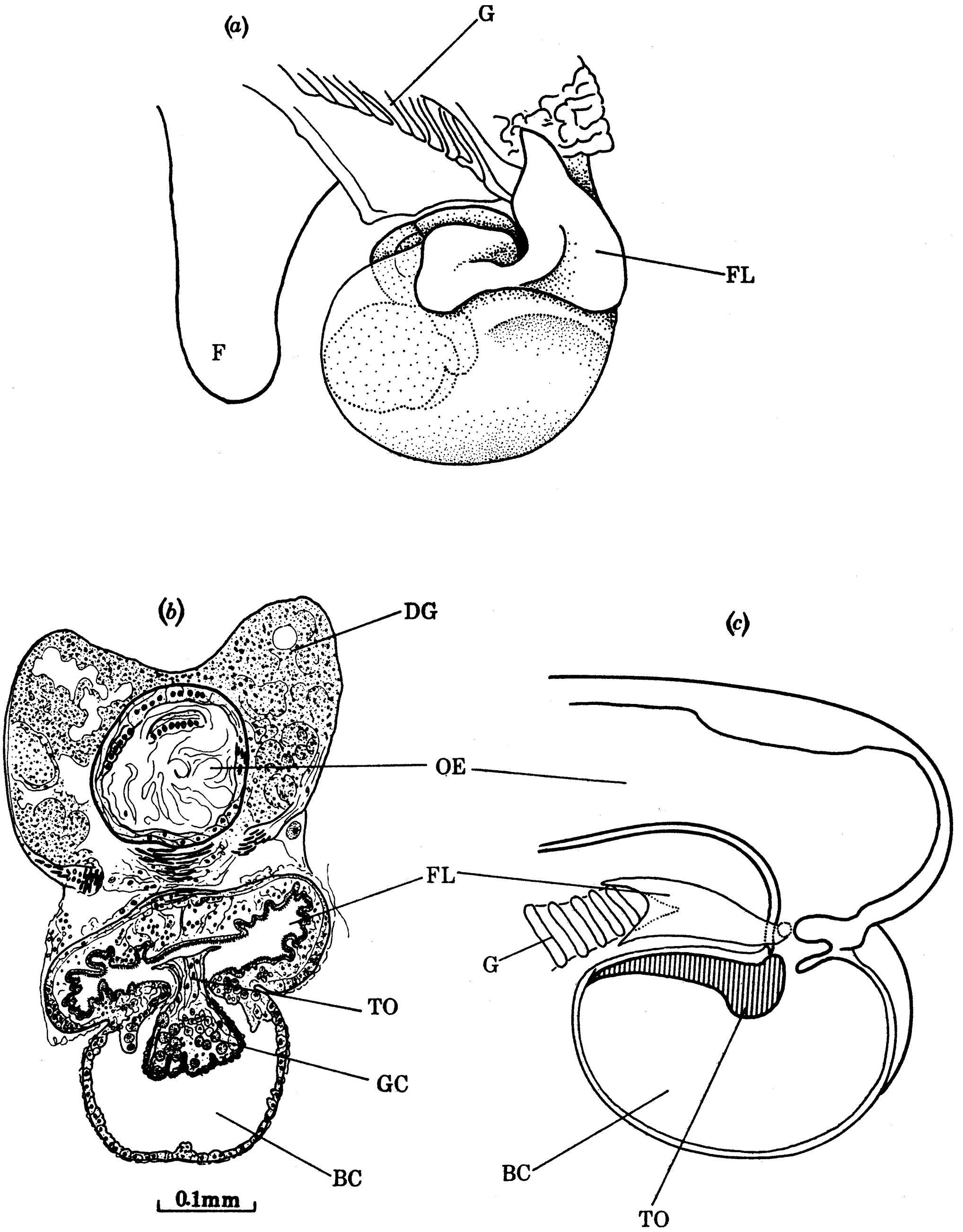

Figure 49. *Lyonsiella formosa.* Detail of the mouth region: (*a*) lateral view of right side of a whole mount; (*b*) transverse section; (*c*) semidiagrammatic lateral view of longitudinal sagittal section.

Lyonsiella fragilis, sp.n. (figure 50)

Material: Holotype: M.C.Z. 272673

						no. of specimens
*Atlantis II**	25. viii. 64	sta. 73	39° 46.5′ N, 70° 43.3′ W	1470–1330 m	E.S.	6
Chain	6. vii. 65	sta. 87	39° 48.7′ N, 70° 40.8′ W	1102 m	E.S.	1

Shell very fragile (all the specimens are partly broken), posteriorly elongate, angular, moderately inflated, slightly inequivalve; the largest specimen measures 8.9 mm, total length; posterior dorsal margin long, straight, and meets the posterior margin in a well-defined obtuse angle; anterior dorsal margin short, deeply curved below the umbos and meets the anterior margin in a well-defined but rounded angle; anterior margin nearly straight, slopes posteriorly in small specimens and is more or less parallel with posterior margin; ventral margin of all specimens is badly damaged, but from growth lines it would not appear to be strongly curved except at the posterior ventral margin; the umbos are incurved; raised radiating lines (8–18 depending on size of specimen) extend from close to the umbo to the posterior and ventral margins of each valve, the most dorsal line is adjacent to the dorsal margin, the most anterior line lies vertically below the umbo; the raised lines project at the margin of the shell to form a scalloped edge; between the lines and parallel to them are radiating rows of fine spinules, the number of rows varies (approximately 7–13) according to the varying width of the space between the lines; the rows of spinules also occur anterior to the most anterior line; irregular concentric growth lines are also present; hinge without teeth, lithodesma small and elongate, with an associated internal opisthodeic ligament dorsal to it.

While *L. fragilis* resembles *L. formosa* in overall shell dimensions and in general appearance, there are major differences in morphology (figure 50*a–d*). The pedal gape occupies the entire ventral margin and fusion between it and the inhalent aperture is minimal. Radial mantle glands are present along the mantle edge. Each duct opens at the margin of the sensory lobe opposite the point where a radial line terminates at the shell edge. They consist of a group of gland cells deep in the sensory lobe with a single central duct leading from them (figure 50*c*). The inhalent aperture is large, without papillate tentacles but the opening is flanked on either side by a large flap. The surface of the flap is finely papillate. The papillae are small, dome shaped (approximately 20 μm in diameter) and closely packed and consist of one or two cells that have a similar appearance to those at the tips of the papillae in species with tentacles. The exhalent aperture also lacks tentacles. The ventral and ventro-lateral margins of the exhalent aperture are produced to form a compressed exhalent siphonal channel. On each side there is an elongate narrow retractor muscle extending half the length of the mantle. At the base of the inhalent flaps, the muscle fibres fan out in two groups, one serving the flaps and the other the exhalent siphon. Both siphon and flaps can be withdrawn completely within the shell valves and where they lie in a shallow embayment. There is a short inhalent valve which is broad at the ventral margin of the aperture. The gills, for a verticordiid, are large and deep and cover the entire body. Both demibranchs are present. The outer demibranch consists of the descending lamella alone. This is reflected dorsally and is restricted to the posterior two-thirds of the gill axis. The posterior filaments are moderately elongate but decrease in length anterior to the posterior margin of the foot. The inner demibranch consists of both descending and ascending

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* See additional records on p. 531.

lamellae, the filaments of the latter being short and making a ciliary connexion with body and with the opposite ascending lamella posterior to the foot. The anterior filaments of outer descending lamella are very long but posterior to the foot they get progressively shorter. The filaments of the outer demibranch are present along the entire length of the gill axis. The most posterior filament of each side forms a tissue junction with the septum between the apertures. Interfilamental connexions are restricted to the margins of the lamellae.

The lips and palp form a posteriorly directed conical funnel around the mouth, similar to that of *L. abyssicola* and from this a short, broad posteriorly directed oesophagus opens into a large globular stomach. The oesophagus has a peripheral layer of circular muscle but this layer is relatively thin as compared with *L. abyssicola*. Similarly the stomach has only a tenuous layer of muscle fibres around it. Internally the stomach is not completely lined with scleroprotein,

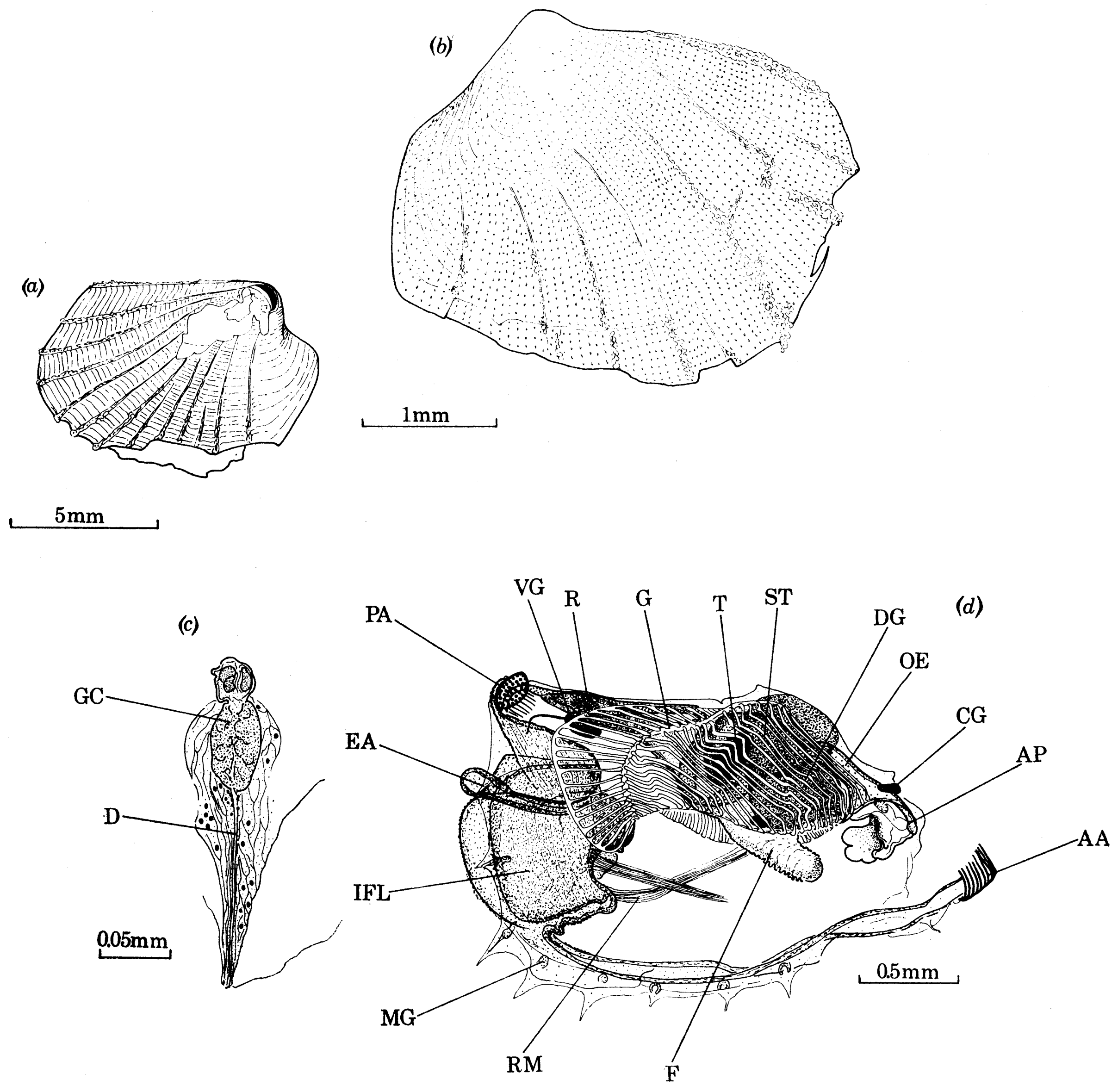

Figure 50. *Lyonsiella fragilis*. (*a*, *b*) Right and left lateral views of the shells of two specimens taken from station 73 (*Atlantis*, 25 August 1964); (*c*) lateral view of whole mount of radial mantle gland; (*d*) lateral view of the right side of whole mount to show soft part morphology.

instead this lining is restricted to the posterior dorsal, ventral and left walls to the gastric shield. There is a large tooth on the dorsal wall above the style sac. The right wall is ciliated from the opening of the oesophagus to the opening to the digestive ducts and mid gut. Sections indicate that there are a few ill-defined grooves on the right wall. There is a very small dorsal pocket in the thickness of the stomach epithelium into which the single flange of the gastric shield fits. This lies close to the tooth of the gastric shield and may be homologous to the dorsal hood of eulamellibranchs. It is extremely small and not obvious in whole mounts. The short mid gut and style sac are joined and open from the stomach ventrally close to the oesophagus as in other verticordiids. The two ducts to the digestive diverticula open ventrally and to the left and right, close to and in front of the style sac and mid gut, beside the opening of the oesophagus.

In other features, foot and byssus gland, nervous system and hermaphrodite condition, *L. fragilis* is remarkably like other species so far described, but the kidney is not large and does not extend into the anterior part of the body.

Lyonsiella compressa n.sp. (figure 51)

Material: Holotype: M.C.Z. 272674

						no. of specimens
Sarsia	12. vii. 67	sta. S29	47° 40′ N, 5° 0′ W	119 m	E.S.	1

The single specimen measures 3.2 mm total length. Shell elongate, compressed, fragile; right valve overlaps left to a slight extent; posterior dorsal margin straight; anterior margin forms a deep concavity anterior to umbos; umbos anteriorly directed; anterior and posterior dorsal margins form a sharp angle with anterior and posterior margins respectively; posterior margin slightly curved and almost vertical to dorsal margin; ventral margin barely curved for much of its length but posteriorly it curves to meet the posterior margin; ventral margin not parallel to posterior dorsal margin, but slopes away so that highest shell measurement is posterior. Shell ornamented with 15 radiating raised lines that run more or less straight from margin to umbos; apart from one terminating at the posterior ventral shell margin, these do not extend to the umbo; additional lines added by interpolation as the shell grows.

Between the lines and parallel to them are rows of small spinules, the number of rows varies from 6 to 14 depending on the distance between the radiating lines; spinules in the triangular area outlined by the posterior and dorsal shell margins and the radiating line from umbo to posterior ventral shell margin, are larger than those anterior to them; irregular concentric growth lines; no hinge teeth, lithodesma small and elongate.

Morphology is similar to that of *L. fragilis*. The major difference lies in the form of the mantle in the region of the apertures. Finger-like tentacles are present around both apertures. These vary in size, those at the dorsal and ventral limits of the apertures being the largest. Thus, there are three large tentacles at the dorsal rim of the exhalent aperture and two smaller pairs lateral to the aperture, one pair central in position, the other pair opposite the ventral margin of the aperture. There is a short inhalent siphon with four tentacles on each side and a pair of large tentacles just ventral to it. Of the tentacles around the inhalent aperture, the four most dorsal are somewhat larger than the others.

Such details of musculature as can be seen from the whole mount show that each tentacle has a central core of longitudinal muscles. The tips are cup shaped; this may not be an artefact owing to the contracted condition of the specimen but may indicate an adhesive function to the tentacles. They are not papillate. The surrounding musculature of the apertures is similar to that described in other species. The apertural region can be completely retracted within the shell, there being a broad band of short retractor muscles within the mantle anterior to the apertures. Typical verticordiid radial mantle glands are present at the posterior and posterior ventral margins of the mantle, there being approximately 18 on each margin, i.e. more than the number of ridges on the shell, and differently distributed to the ridges (figure 51*a–d*). The adductor muscles are moderately large.

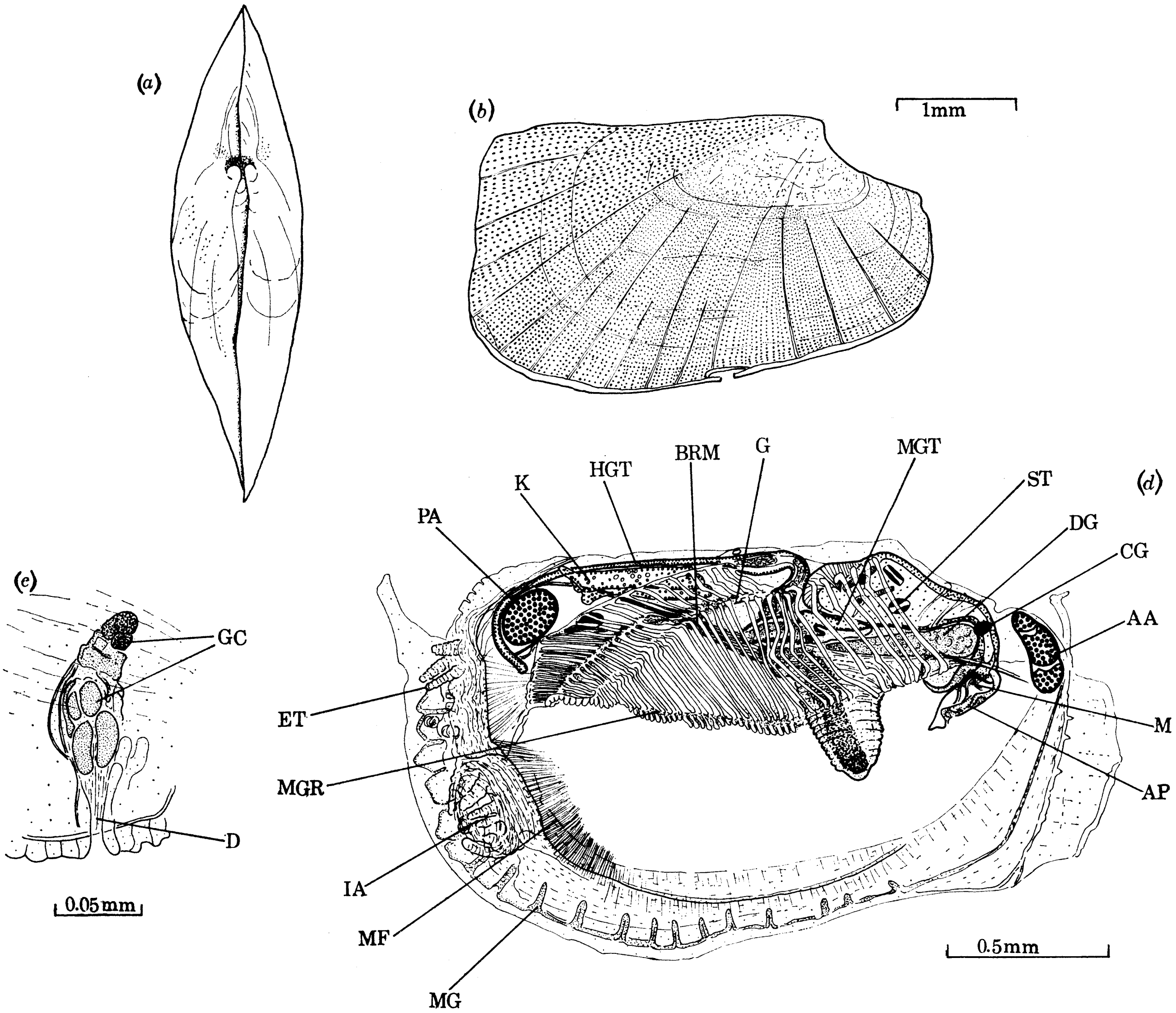

FIGURE 51. *Lyonsiella compressa.* (*a*, *b*) Dorsal and lateral view of shell; (*c*) whole mount of radial mantle gland in lateral view; (*d*) lateral view of right side of whole mount to show soft part morphology.

The gills are well developed and similar to those of *L. fragilis.* The lips and palps, however, differ and are of highly significant form. The lips are broad and extended by leaf-like palps, which form lateral extensions to the buccal funnel. Unlike all other verticordiids here described, sorting ridges are present on these palps. These comprise five ridges on the anterior (upper) palps and two (with possibly a third camouflaged by a fold in the palp) on the posterior (lower) palp. Diatom remains are present in the stomach and what little can be seen of the stomach indicates similarity to that of *L. fragilis*. The form of the gut is also similar to the latter species and there is some inflation of the hind gut in the anterior part of dorsal section close to the stomach. Digestive glands are ventral to the stomach. The kidneys are not noticeably enlarged nor are the ganglia. There is a well-developed byssus gland.

It should be noted that this specimen was collected from shallow water close to the shelf slope break at the northern edge of the Biscay Basin.

Verticordia triangularis Locard 1898

Material from:

						no. of specimens
*Chain**	30. vi. 65	sta. 77	38° 0.7′ N, 69° 16′ W	3806 m	E.S.	4
Chain	30. vi. 65	sta. 78	38° 00.8′ N, 69° 18.7′ W	3828 m	E.S.	5
Chain	5. vii. 65	sta. 85	37° 59.2′ N, 69° 26.2′ W	3834 m	E.S.	26
Atlantis II	18. xii. 66	sta. 131	39° 38.5′ N–39° 39.0′ N, 70° 36.5′ W–70° 37.1′ W	2178 m	E.S.	3
Atlantis II	5. ii. 67	sta. 143	10° 35.0′ S, 17° 44.0′ W	2095 m	E.S.	1
Atlantis II	22. v. 68	sta. 200	9° 43.5′ S–9° 29′ S, 10° 57′ E–11° 34′ E	2644–2675 m	E.S.	4

Distribution:

North of the Azores, Woods Hole–Burmuda traverse, off Angola, Mid Atlantic Ridge, off Surinam; 2178–3862 m

Until the present material was obtained, *V. triangularis* Locard (1898) was known only from a single large specimen collected by the Talisman in 1883. After comparison with a photograph of the type specimen, Dr Mêtevier of the Musée Naturelle, Paris, kindly compared our specimens with this valve and he confirmed our identification (figure 52).

The shell is roughly triangular in shape and laterally compressed in comparison with other verticordiids. In common with the *Lyonsiella* species already described there is considerable variation of the shell outline. This is in part due to changes in shape with increasing size and in part due to the repair of shell damage. The ventral and posterior regions of most specimens bear signs of repaired damage resulting in an irregular margin (figures 52, 53). The length (L–L′, figure 53) and height (H–H′, figure 53) of the shell were measured. The smallest shell measured 1.4 mm long by 1.2 mm high and the largest 13.3 mm high by 11.8 mm long. The latter is still much smaller than the 'Talisman' specimen with a length of 36 mm and height 35 mm. The larval shell can be seen clearly on some shells and has a length of 0.22 mm. The growth series (figure 53) shows that small animals are more angular than larger ones, the latter becoming rounded except in regard to the straight postero-dorsal hinge margin. The right valve is slightly larger than the left and overlaps it posteriorly (figure 52).

The shell is white but, like *L. abyssicola*, in life it appears brown and encrusted due to adhering sand grains and animal skeletons. The shell is covered with regularly spaced, fine radiating lines, 95 in a shell 6.5 mm high and 6.0 mm long (figure 52). Each line extends from close to the umbo to the edge of the shell. They are frequently obscured by sediment and are more noticeable in worn shells. Between the lines there are two or three rows of irregularly spaced short spinules which are shown to be hexagonal in scanning e.m. photographs (plate 58, facing p. 479). Each spine is housed in a rounded depression, hence the pitted appearance of worn shells. Growth

* See additional records on p. 531.

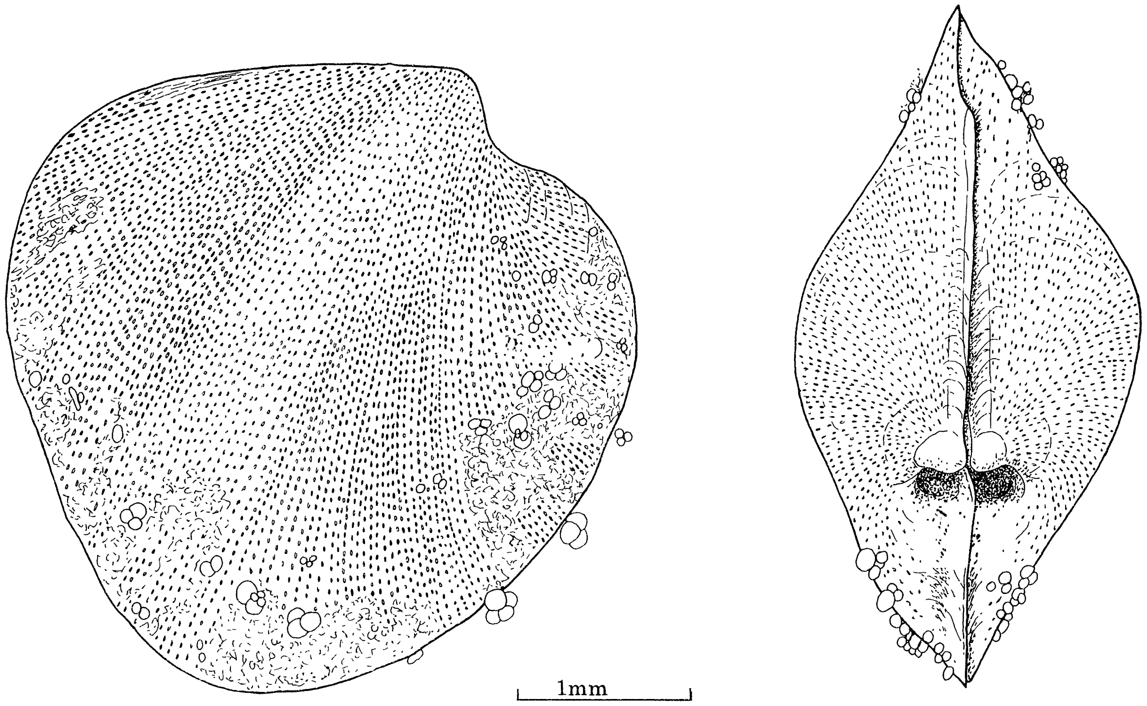

FIGURE 52. *Verticordia triangularis.* Lateral and dorsal view of shell of specimen from station 85 (*Chain,* 5 July 1965).

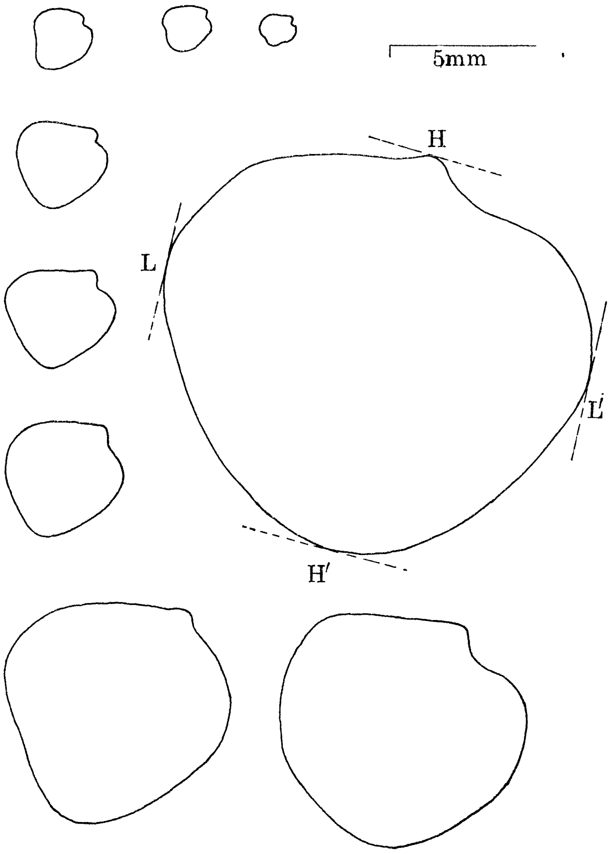

FIGURE 53. *Verticordia triangularis.* Outlines of shell margins to show variations in shape with increasing size. Points of measurement for height (H–H′) and length (L–L′) are shown for the largest specimen.

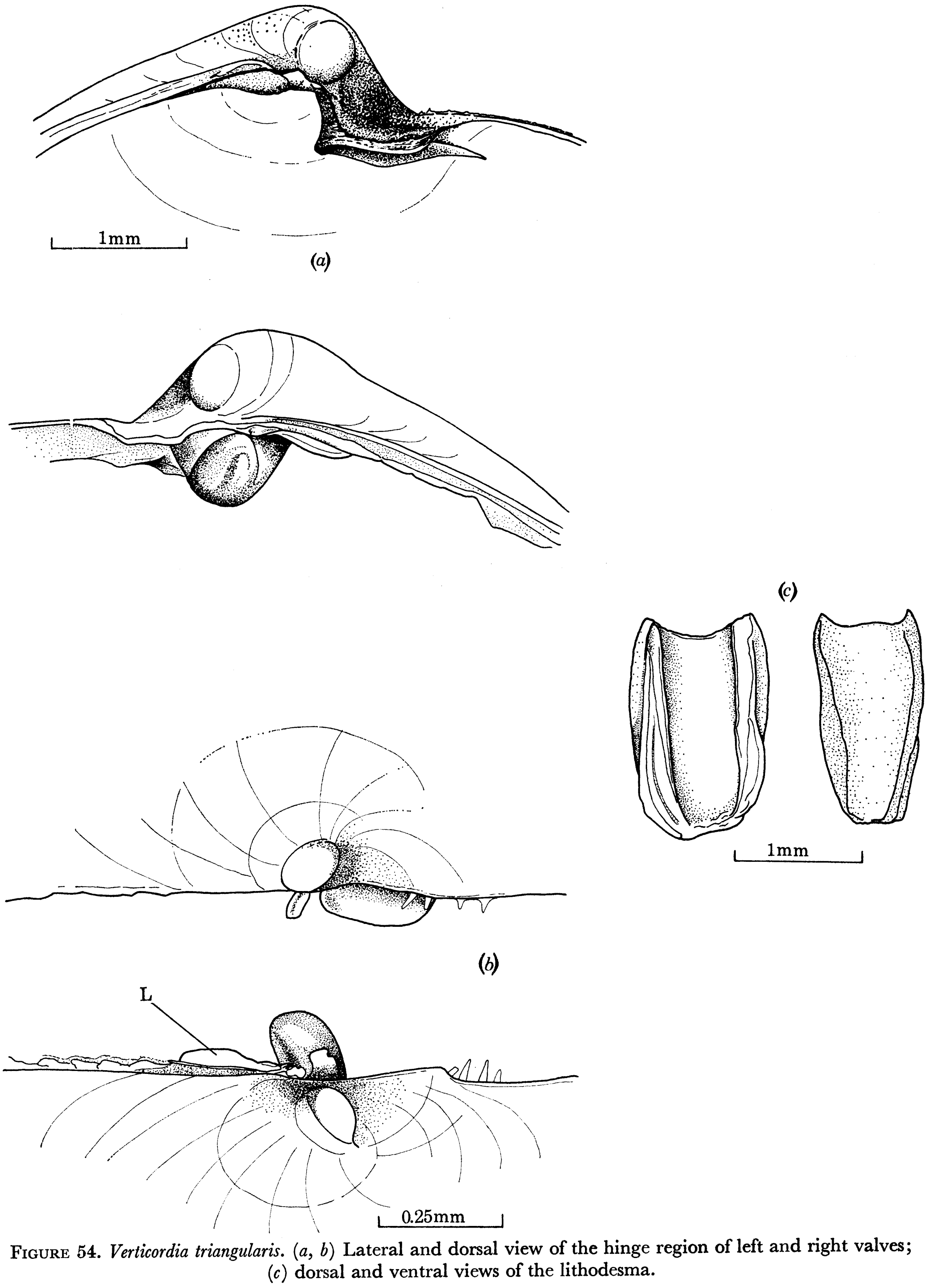

Figure 54. *Verticordia triangularis*. (*a, b*) Lateral and dorsal view of the hinge region of left and right valves; (*c*) dorsal and ventral views of the lithodesma.

lines are very fine and hard to distinguish but in some of the larger specimens there are two or three very pronounced concentric bands. Internally the shell is nacreous, the two adductor scars are faint and the pallial line almost indistinguishable.

The right valve bears a single cardinal tooth, characteristic of the genus *Verticordia*, which takes the form of a rounded boss (figure 54*a*, *b*). The tooth fits into the corresponding gap in the hinge plate of the left valve. Anterior to the socket is a small fragile projection at the edge of the shell and at the base of this are two smaller and even more fragile, scroll-like, laminae which key into two notches in the right. Although not recorded in previous descriptions, presumably because of the ease with which they are broken, these interlocking laminae are probably not to be regarded as homologous to anterior lateral teeth (figure 54*a*, *b*).

Posterior to the umbo is a small, moderately elongate, fragile lithodesma. The opisthodetic ligament (including the lithodesma) is structurally similar to that in *L. abyssicola*.

The mantle edge consists typically of three lobes but is not as well developed as that of *L. abyssicola* (figure 55*a*). It is broad with a shallow outer lobe divided from the sensory lobe by the periostracal groove. At regular intervals along its length, from the dorsal limit of the exhalent aperture ventrally to a position opposite the ventral edge of the anterior adductor muscle, there are a number of radial mantle glands within the sensory lobe. These vary in number between 25 and 35, depending on the size of the animal. Each gland is roughly cylindrical, about 140 μm long and 15 μm wide. Although longer and thinner in cross-section they are essentially similar in structure to those of *L. abyssicola* (figure 55*b*, *c*). The sensory lobe also bears small papillae scattered in a relatively broad band in the region of the pedal gape. The muscular lobe is also broad. As in other bivalves, the pallial muscles form two groups, one supplying the muscular lobe itself, the other forming the retractor muscles to the other lobes. There is an extremely well-developed pallial nerve immediately below the point of insertion of the muscles with the shell. A ciliated tract is present above the muscular layer in the region of the pedal gape and extends from a position ventral to the mouth to where the mantle margins fuse posteriorly and continues beyond this point as far as an internal dome shaped projection ventral to the inhalent aperture. Immediately posterior to this projection the tracts of each side join to form a single broad tract approximately 120 μm wide, which extends to the base of the inhalent siphon (figure 57*a*). There are gland cells in the inner mantle epithelium above and along the entire length of the ciliated tract.

The inhalent aperture is approximately half as large again as the exhalent aperture (figure 57*b*). There is no exhalent siphon. The apertures are outlined by a membranous diaphragm containing a thin layer of circular muscle fibres. The development of circular muscle surrounding the exhalent aperture is no greater than that surrounding the inhalent aperture and in neither case is it as well developed as in *L. abyssicola*. There is a thick band of septal muscles formed by the fusion of the muscular lobe separating the two apertures. There are five small tentacles around the exhalent aperture, one in a mid-dorsal position and two on each side (figure 57*b*). Like those around the inhalent aperture, they arise at the junction of the inner and middle lobes. The inhalent aperture is surrounded by a single row of 14 tentacles, the two level with the dorsal edge of the aperture being rather larger than the rest. The tentacles are short, stumpy, rounded cones covered with fine epithelial projections bearing densely staining gland cells as in *L. abyssicola*.

The musculature of the tentacles differs somewhat from that of *L. abyssicola* (figure 57*c*). A wide band of muscle encircles the perimeter of the aperture beneath the tentacles but does not supply muscles to them. Pallial retractor muscles extend into the base of each tentacle from the mantle. At the tips of the tentacles the longitudinal muscles seem to be arranged in four or five ill-defined bundles, but towards the base the organization is more diffuse. The longitudinal muscles seem to be associated with ill-defined divisions of the haemocoele, and in *V. triangularis* the haemocoele appears to be sub-divided into five or six major cavities instead of two as in *L. abyssicola*.

Situated to the aperture side of the base of each tentacle there are 10–12 small muscle blocks

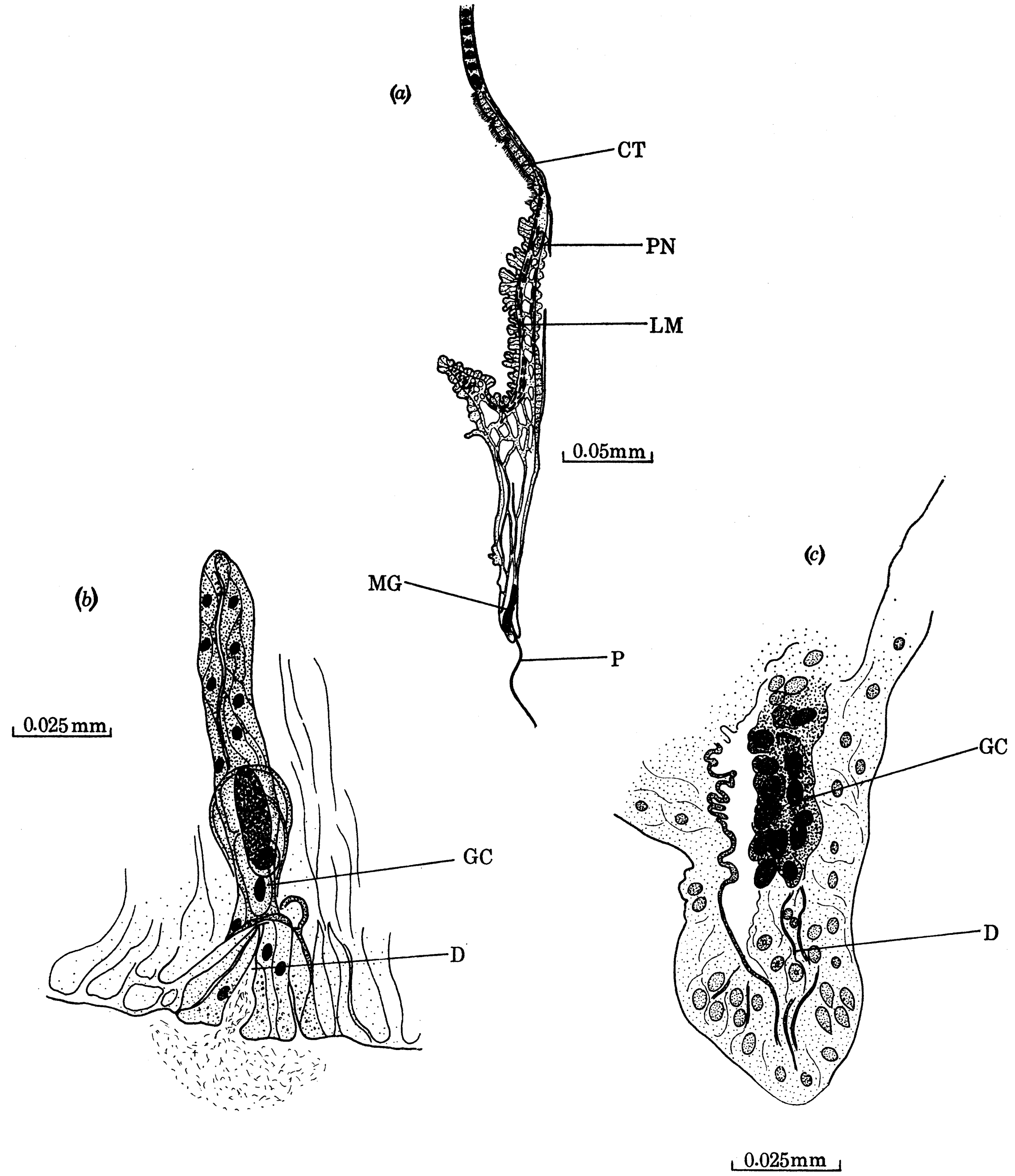

Figure 55. *Verticordia triangularis*. (*a*) Transverse section of the mantle edge in region of pedal gape; (*b*) whole mount of radial mantle gland; (*c*) longitudinal section through a radial mantle gland.

(SMB) which are also associated with compartments of the haemocoele. Unlike comparable muscles in *L. abyssicola* these seem to extend into the mantle valve to the inside of the inhalent aperture. The valve is a simple sheet of tissue containing a thin layer of encircling and radiating muscle fibres between the epithelia. The arrangement is symmetrical and the margin is not appreciably thickened. The organization of a network of collagen fibres is much more apparent in the tentacles of *V. triangularis* than it is in *L. abyssicola*. Fibres radiate from the centre of the tentacle, dividing and separating the muscle blocks at the periphery of the tentacle (figure 57*c*).

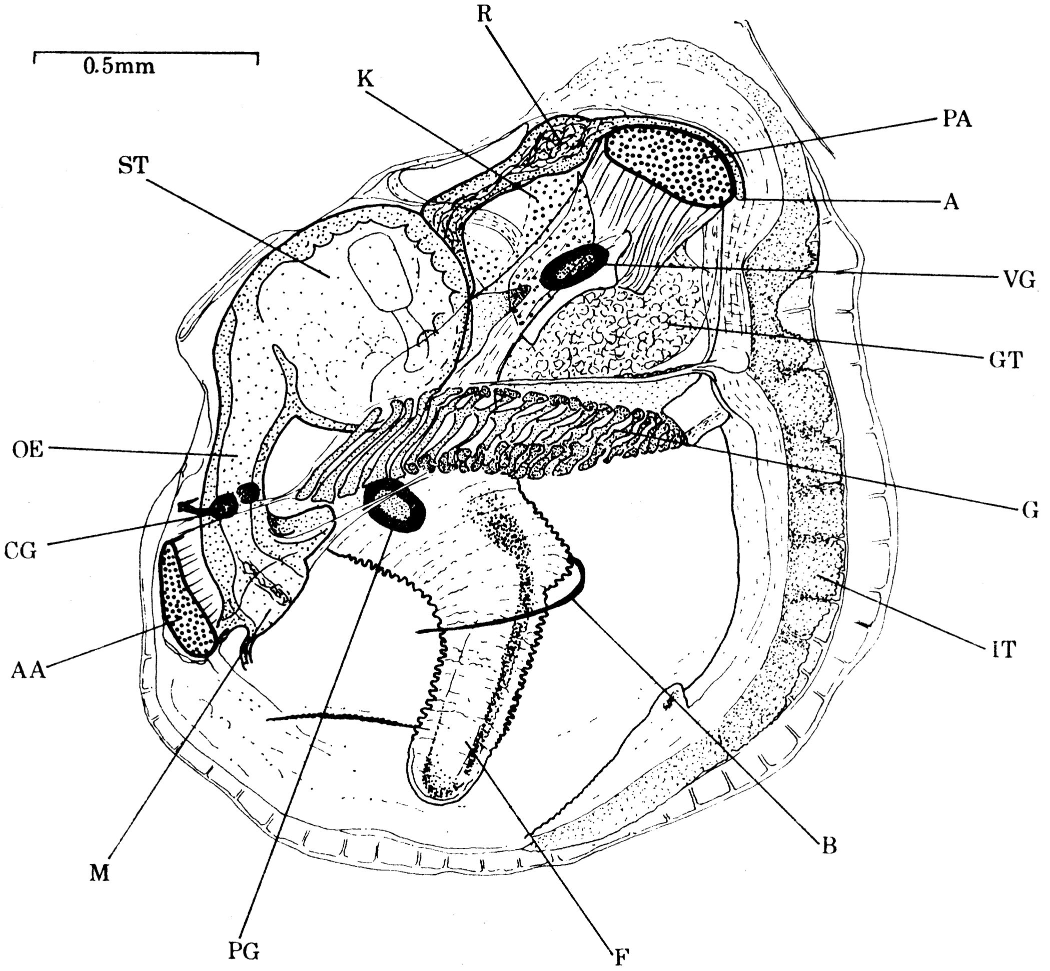

FIGURE 56. *Verticordia triangularis.* Lateral view of the left side of a whole mount to show the soft part anatomy.

The haemocoele is divided into five or six major cavities and two of these, in the mid-line, each contain a large tentacular nerve. The nerve supply to the exhalent and inhalent apertures resembles that of *L. abyssicola.*

The tentacles of the exhalent aperture are smaller than those surrounding the inhalent aperture. They, too, have a network of collagen fibres and a central region of longitudinal muscle but they lack the basal and peripheral blocks on the side nearest the aperture. In their place, there are occasional longitudinal muscle fibres within the periphery of the tentacle. The haemocoele is divided in the same way as in the inhalent tentacles and there are two nerves

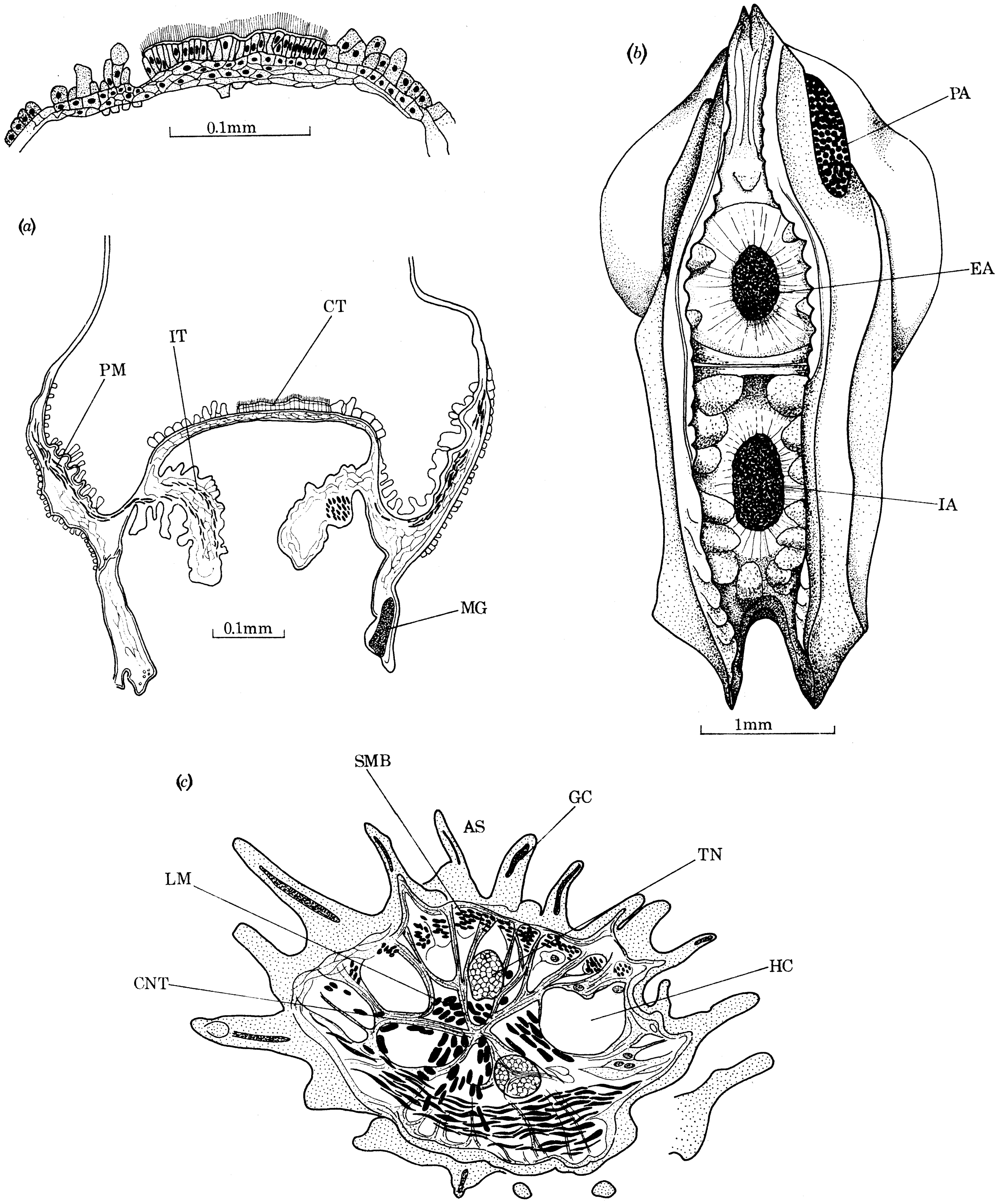

FIGURE 57. *V. triangularis*. (*a*) Transverse section through the fused mantle edges ventral to the inhalent aperture with an enlargement of the central ciliated tract; (*b*) posterior view of the apertures and associated tentacles; (*c*) oblique section through an inhalent tentacle.

present. The membrane encircling the exhalent aperture is similar to that of the inhalent aperture and contains radial and circular muscle fibres. At the ventral edge of the exhalent aperture, to the inside of the membrane, there is a region of dense staining granular cells which is flanked on both sides by large vacuolated cells which in turn line two grooves (see below and figure 59*a*, *b*).

The gills of *V. triangularis* are similar to those in *L. abyssicola*. Both inner and outer demibranchs are present and these extend from the mouth to the ventral side of the exhalent aperture. The filaments of the outer demibranch are longer than those of the inner, the most anterior filament being one third as long again as those immediately posterior to it (figure 58*a*, *b*). The outer demibranch is attached along its whole length to a thickened shelf of mantle tissue (MS), the dorsal surface of which is glandular (figure 59*a*, *b*). The glands are continuous with those of the inner mantle epithelium of the hypobranchial cavity. Posterior to the foot, the left and right mantle shelves fuse across forming a sheet of tissue which connects with the inwardly extended floor of the ventral side of the exhalent aperture. Between the inner edge of the mantle shelf and the filaments of the outer demibranch and, also, at the inner edge of inner demibranchs posterior to the foot, immediately behind the ciliary junctions there is, on the dorsal side, a thickened section of epithelium (figure 59*a*, *b*, *c*). This is composed of extremely regular elongate cells, each with a basal nucleus and granular cell inclusions distally. The cells apparently secrete a clear capping and resemble the epithelial cells of the stomach which secrete the gastric shield (SC, figure 59*b*). Their function is unknown.

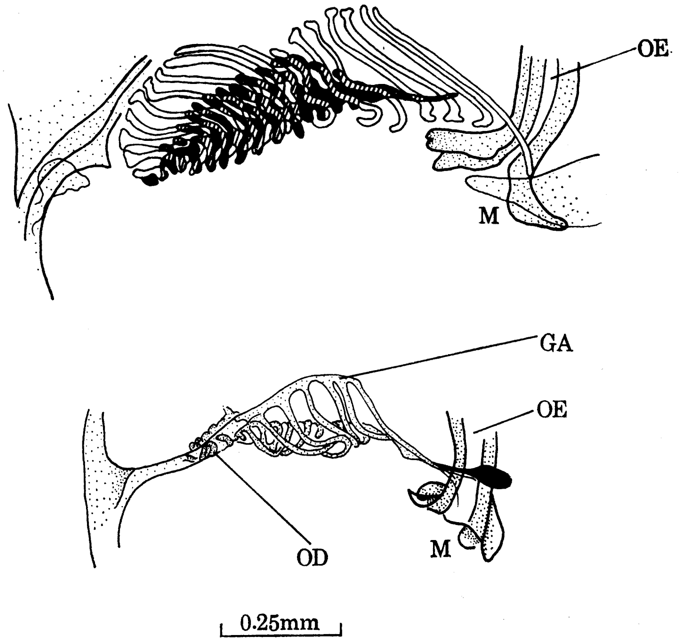

FIGURE 58. *Verticordia triangularis*. Lateral view of the right gills of two specimens. In the upper figure the outer filaments of the demibranch are shown hatched and blocked and in the lower figure (of a smaller specimen) the outer demibranch is restricted to three or four rudiments on the outer face of the posterior end of the gill axis.

The outer demibranch is reduced and without an ascending lamella. The descending lamella is reflected upwards and is incurved. The filaments of the lamellae of the inner demibranch are even shorter than those of the outer demibranch and the whole gill is flattened in the horizontal plane (figure 58*a*, *b*). Interfilamentar connexions are restricted to the gill edges and the margin between ascending and descending lamellae of the inner demibranch. There is ciliary connexion between the inner demibranchs immediately behind the foot but further posterior there is a tissue connexion with the septum between the apertures. Within the axis on the ventral side below the axial blood vessels there is a well-defined bundle of longitudinal muscle fibres (figure 60).

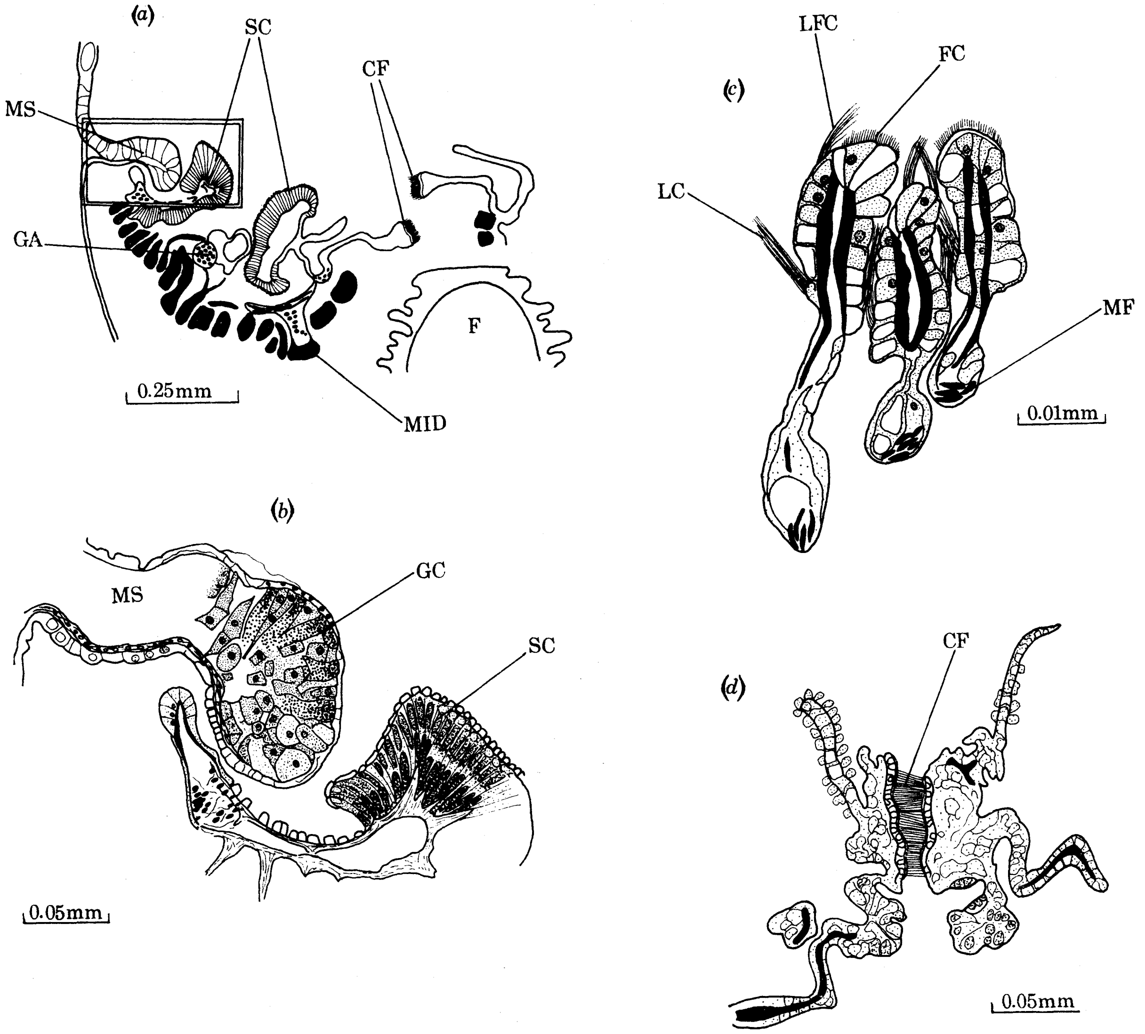

FIGURE 59. *Verticordia triangularis*. (*a*) Transverse section of the gill posterior to the foot; (*b*) enlargement of area outlined by the rectangle in (*a*) at junction of gill with mantle; (*c*) transverse section of three gill filaments; (*d*) section through the region of ciliary junction of the demibranchs posterior to the foot.

The development of muscle in the gill of *V. triangularis* is greater than that in *L. abyssicola*. The mantle shelf which is associated with the gill along its entire length has a very thin layer of muscle beneath the epithelium. The filaments of the gill are supplied with muscle fibres, abfrontally adjacent to the hypobranchial cavity (figure 59*c*). While these muscles are not restricted to certain filaments, they are generally better developed in the larger anterior filaments. Muscle fibres are also present at the margin of the inner demibranch at the edge of the ascending lamella of the inner demibranchs posterior to the foot. There is a well-defined ciliated tract running the length of the inner demibranch, at the junction between ascending and descending lamellae, and there is a similar groove running along the gill axis.

The anterior palps and lips are extended ventrally and posteriorly to form a ventral hood over the funnel-shaped, posteriorly directed mouth. The posterior palps, and lips, are also extended and form a broad roof to the hood (figures 56, 61 and 62). Laterally there is a V-shaped notch between the anterior and posterior palps at which point the gill terminates. The inner surface of the lips is covered with a ciliated epithelium which is finely ridged on the anterior lips and folded into 8–12 more definite small furrows on the posterior lips. These are continuous with some of the oesophageal ridges which number 9–28, the number depending on the size of the animal. The lips and palps are attached to the mantle by a membrane which extends laterally from the edge of the palps. This contributes a lateral extension to the funnel formed by mouth, lips and palps. Histologically the lips and palps are similar to those of *L. abyssicola*.

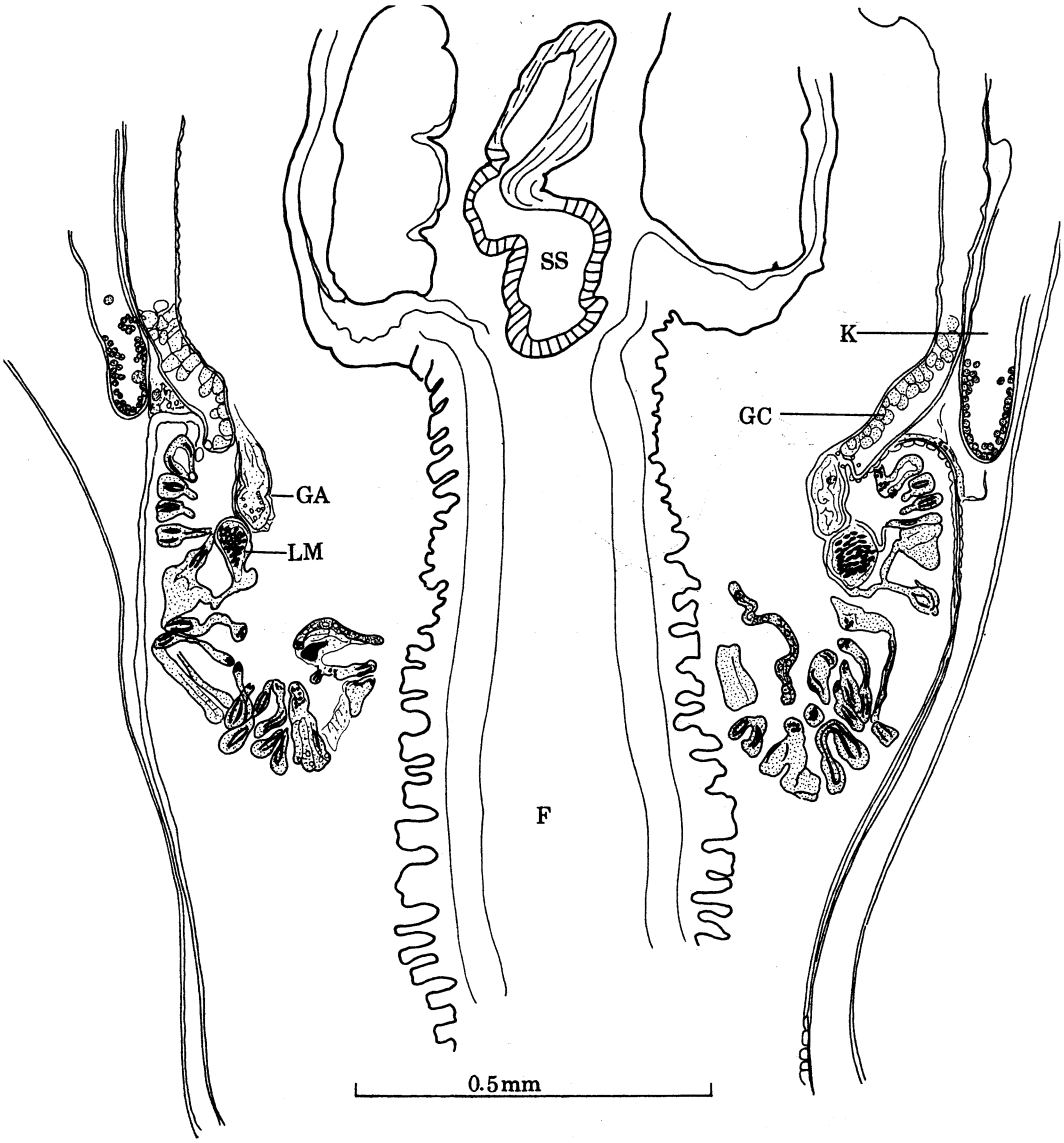

FIGURE 60. *Verticordia triangularis*. Transverse section through the gills lateral to the foot.

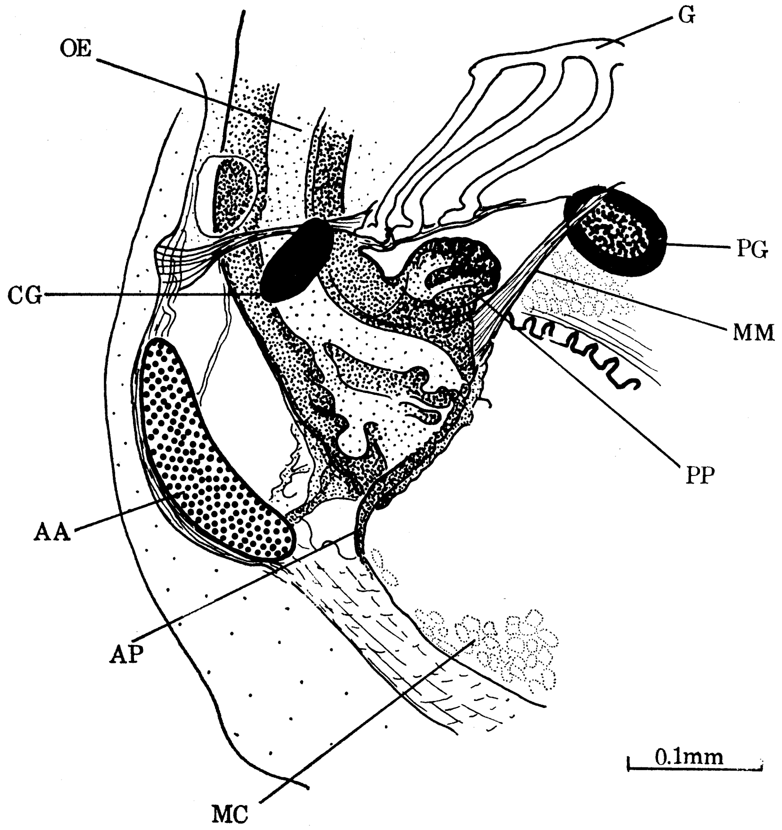

FIGURE 61. *Verticordia triangularis.* Lateral view of mouth region.

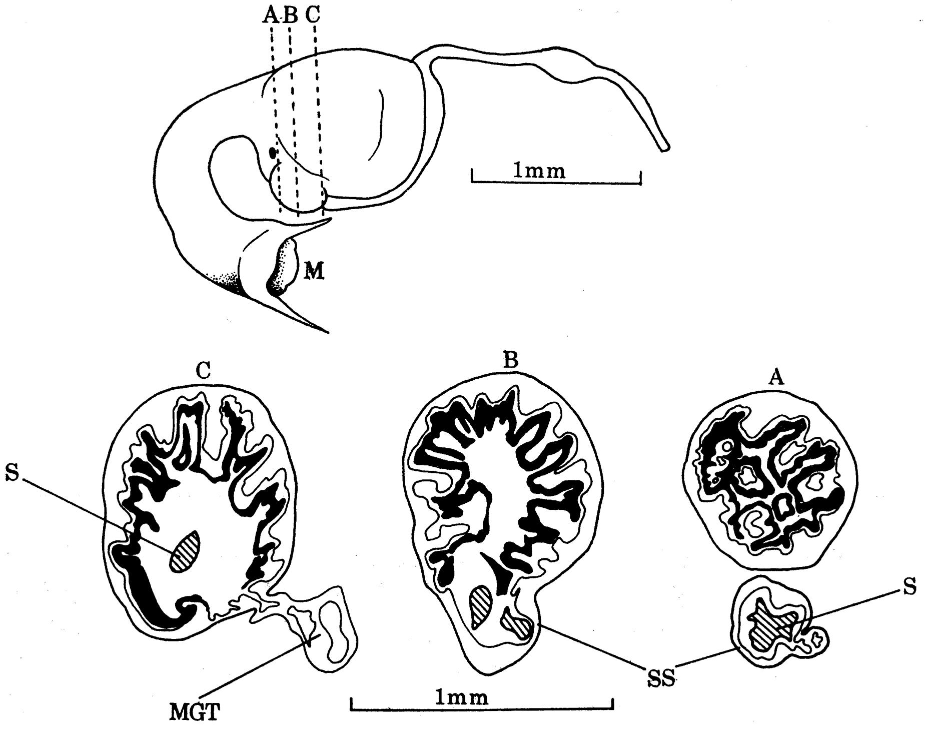

FIGURE 62. *Verticordia triangularis.* Lateral view of the left side of the gut showing the position of three vertical sections through the stomach and style sac, the sections (*a*), (*b*) and (*c*) are shown outlined below.

The course of the gut of *V. triangularis* is similar to that in species of *Lyonsiella* (figure 62); likewise the histology of the gut is similar, the stomach being completely lined with a scleroprotein cuticle except for an antero-ventral region which extends from the junction of the oesophagus to the opening of the style sac and mid gut (figure 62). Into this region first the right and then the left digestive duct opens with ciliated tracts leading from these to the style-sac opening. By removing the lining of the stomach the internal convolutions could be seen more clearly (figure 63). Dorsally, there are three main longitudinal ridges which divide anteriorly into lateral ridges. On each side there are four or five main ridges and several smaller ones. At the posterior end of the stomach there are about 20 blunt internal projections. The ridges are

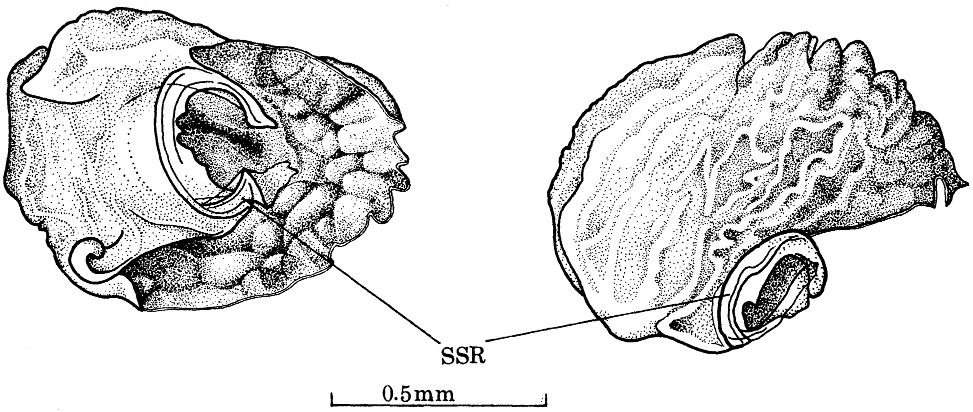

Figure 63. *Verticordia triangularis.* Ventral and lateral views of the cuticular lining of the stomach.

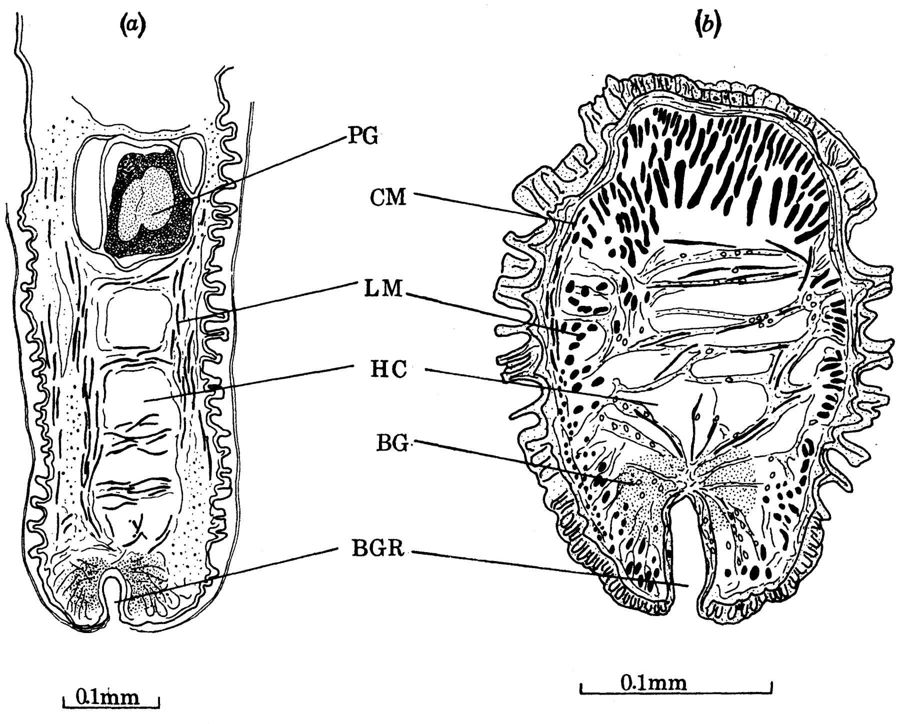

Figure 64. *Verticordia triangularis.* (*a*) Vertical section through central region of foot; (*b*) transverse section through tip of foot.

much more broken up and subdivided in *V. triangularis* than they are in *L. abyssicola*. The cuticle forms a thickened band around the oesophageal aperture and around the combined style-sac and mid gut aperture. The mid gut and style sac connect with the stomach ventrally close to the oesophageal aperture. The mid gut is divided from the style sac by typhlosoles and exits on the right side near the hind end of the style sac. The style sac has a typical cuboid ciliated epithelium and a glandular region on the inner side of the typhlosoles which secretes a style. At its base the style is irregular in cross-section and rather square, but distally the style is cylindrical and extends forwards to lie close to the aperture of the oesophagus. In preserved specimens, the style is 700 μm long and 70–110 μm in diameter.

Other organs and structures such as digestive gland, kidney, gonads and foot, are similar to those described for *L. abyssicola* (figure 56, 64*a*, *b*).

Verticordia quadrata Smith 1885

Material from:

						no. of specimens
*Chain**	5. vii. 65	sta. 85	37° 59.2′ N, 69° 26.2′ W	3834 m	E.S.	1
Atlantis II	19. viii. 66	sta. 119	32° 15.8′ N, 64° 31.6′ W 32° 16.1′ N, 64° 32.6′ W	2095–2223 m	E.S.	2
Atlantis II	18. xii. 66	sta. 131	39° 38.5′ N, 70° 36.5′ W 39° 39.0′ N, 70° 37.1′ W	2178 m	E.S.	1
Atlantis II	7. ii. 67	sta. 149	10° 30.0′ N, 18° 18.0′ W	3861 m	E.S.	2
Atlantis II	14. ii. 67	sta. 156	00° 46.0′ S, 29° 28.0′ W 00° 46.5′ S, 29° 24.0′ W	3459 m	E.S.	1
Atlantis II	5. ii. 67	sta. 144	10° 36.0′ N, 17° 49.0′ W	2051–2357 m	E.S.	1
Atlantis II	13. ii. 67	sta. 155	00° 03.0′ S, 27° 48.0′ W	3730–3783 m	E.S.	1

Distribution:

Off Palma, Canaries, Woods Hole–Bermuda traverse, Mid Atlantic Ridge, off Surinam 630–4980 m

The first description (Smith 1885) of *V. quadrata* was of a single left valve, the only other description being that of Kobelt (1888) which is merely a repeat of the original. We have redrawn the type specimen from the British Museum (figure 65*b*). In addition, examination of the verticordiid material in the U.S. National Museum showed that specimen no. 95450 (figure 65*a*) from off the north coast of Brazil at 1863 m is also of this species and not *V. woodi* as labelled. *V. woodi* is somewhat similar to *V. quadrata* but more rounded and less elongate (we also include in figure 65*d* the type specimen of *V. woodi* from the British Museum for comparison). In *V. quadrata*, the right valve overlaps the left, the dorsal shell edge being curved both anterior and posterior to the umbo (figure 65*c*). The umbos are particularly large being incurved and anteriorly directed. The shape of the present specimens is remarkably constant for a verticordiid, however, the number of radiating ridges is less constant and varies from 8 to 11 being dependent on the size of the animal. The calcareous spinules are not arranged in rows parallel to the ridges. Evidence from one preserved specimen suggests that the spines are laid down in advance of and separate from the outer layer of the shell, for in this specimen, the newly formed periostracum, as yet not covering the shell, bears a series of calcareous spinules, these presumably being formed close to the junction of the outer and middle lobes of the mantle edge (figure 68*a*).

As Smith (1885) surmised, the hinge of the right valve bears a relatively stout, hooked, single

* See additional records on p. 531.

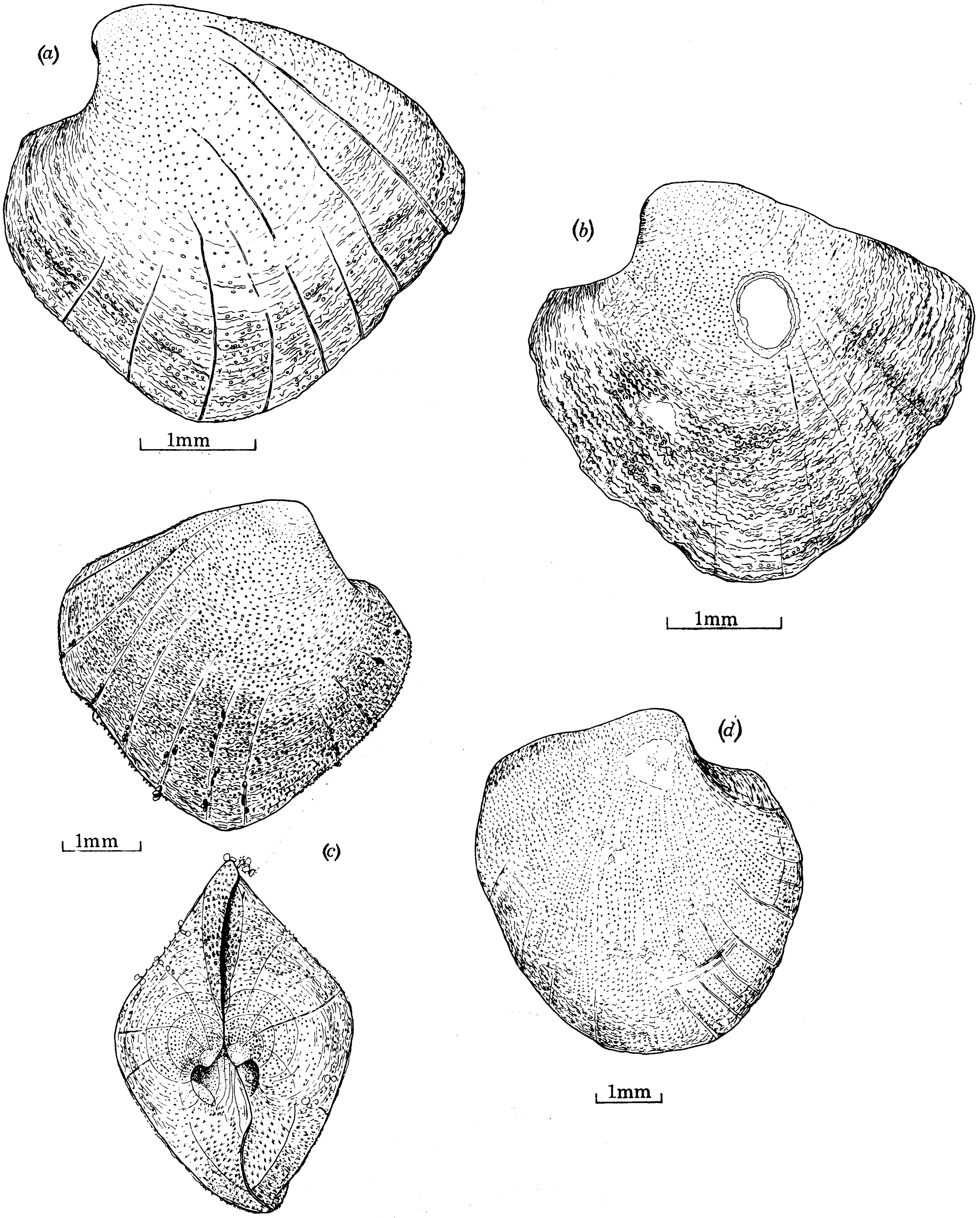

FIGURE 65. *Verticordia quadrata*. (*a*) Lateral view of the left valve of specimen no. 95450 from the Smithsonian Museum and labelled *V. woodi*; (*b*) lateral view of the left valve of the type specimen from the British Museum (Natural History); (*c*) lateral and dorsal views of shell from station 119 (*Atlantis*, 19 August 1966); *V. woodi*; (*d*) lateral view of right valve of the type specimen of *V. woodi* from the British Museum (Natural History).

curved tooth, which latches under the hinge of the left valve behind a thickened hinge plate (figure 66*a*, *b*).

The morphology is similar to that of *V. triangularis*. Radial mantle glands are present, three on each side of the pedal aperture – one anterior, one close to the inhalent aperture and one central in position. In comparison with mantle glands in other verticordiid species, the glands in *V. quadrata* are not elongate but laterally flattened and in broad outline, flask shaped. In section they appear as a mass of dark staining cells with no obvious duct system and do not

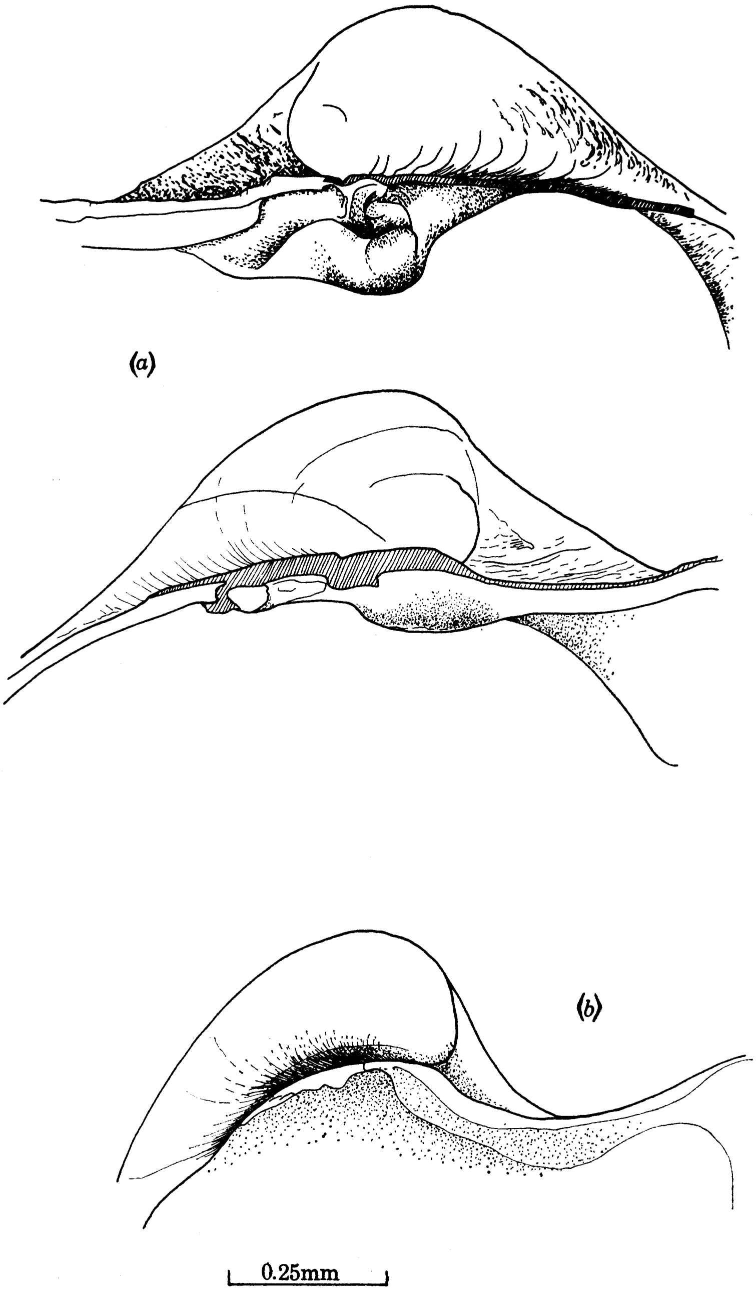

Figure 66. *Verticordia woodi*. (*a*) Lateral view of the hinge of left and right valves of the type specimen from the British Museum (Natural History); *Verticordia quadrata*; (*b*) lateral view of the hinge of the right valve of the type specimen from the British Museum (Natural History).

extend dorsal to the inner muscular mantle lobe (figure 67*a*, *b*). Small papillae are present along the middle sensory mantle lobe in the region of the pedal aperture. The pedal aperture is relatively small and anterior in position. This is owing to the great development of the inhalent aperture, which is flanked by two rows of tentacles. The outer row consists of six large tentacles on each side of the aperture and the inner row of five tentacles on each side of the aperture. In addition, there is a single unpaired tentacle ventral to the aperture and central to the ventral papillae of the inner and outer rows (figure 68*a*). There are also three tentacles, one dorsal and one on each side, flanking the exhalent aperture. The tentacles are covered with glandular papillae. The musculature of the tentacles is very similar to that of *L. abyssicola* (figure 68*b*) with asymmetrically placed basal longitudinal muscles on the inner face which are divided into three main blocks, and longitudinal muscles on either side of the inner wall dividing the haemocoele into a pair of longitudinal cavities. The epithelium is richly supplied with glandular papillae. The tentacles must function in the manner suggested for those of *L. abyssicola* (p. 417). There is a well-developed valve to the inside of the inhalent aperture and a well developed band of retractor muscles extending some distance inwards in the mantle (figure 68*c*). The adductor muscles are very small, the posterior being somewhat smaller than the anterior and in cross-section of a similar diameter to the visceral ganglion lying immediately anterior to it. The other ganglia, although moderately large, are not as well developed as the visceral (figure 68*c*).

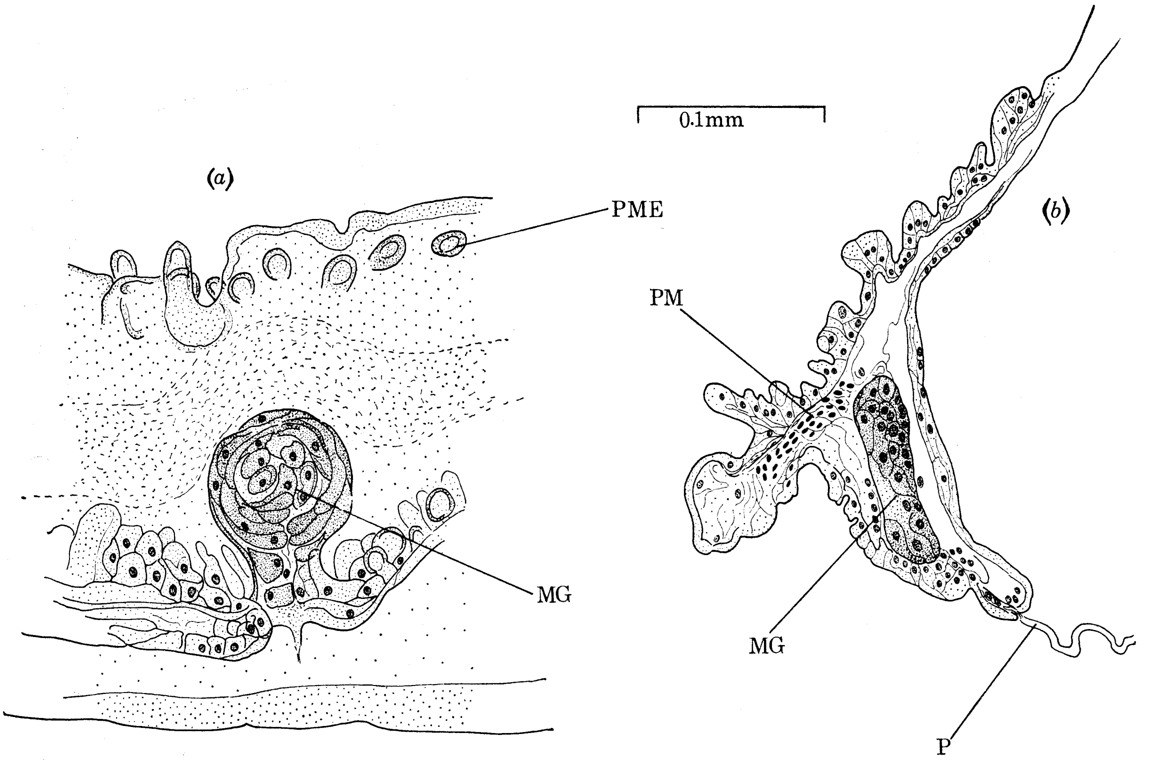

Figure 67. *Verticordia quadrata.* (*a*) Whole mount of mantle edge to show radial mantle gland; (*b*) transverse section of the mantle edge through a radial mantle gland.

The gill is much reduced and consists of an inner demibranch with about 10–12 small filaments (figure 68*c*). The posterior four filaments resemble small papillae, the more anterior filaments being united at the margin of the lamella to form a single series of pores. There is a

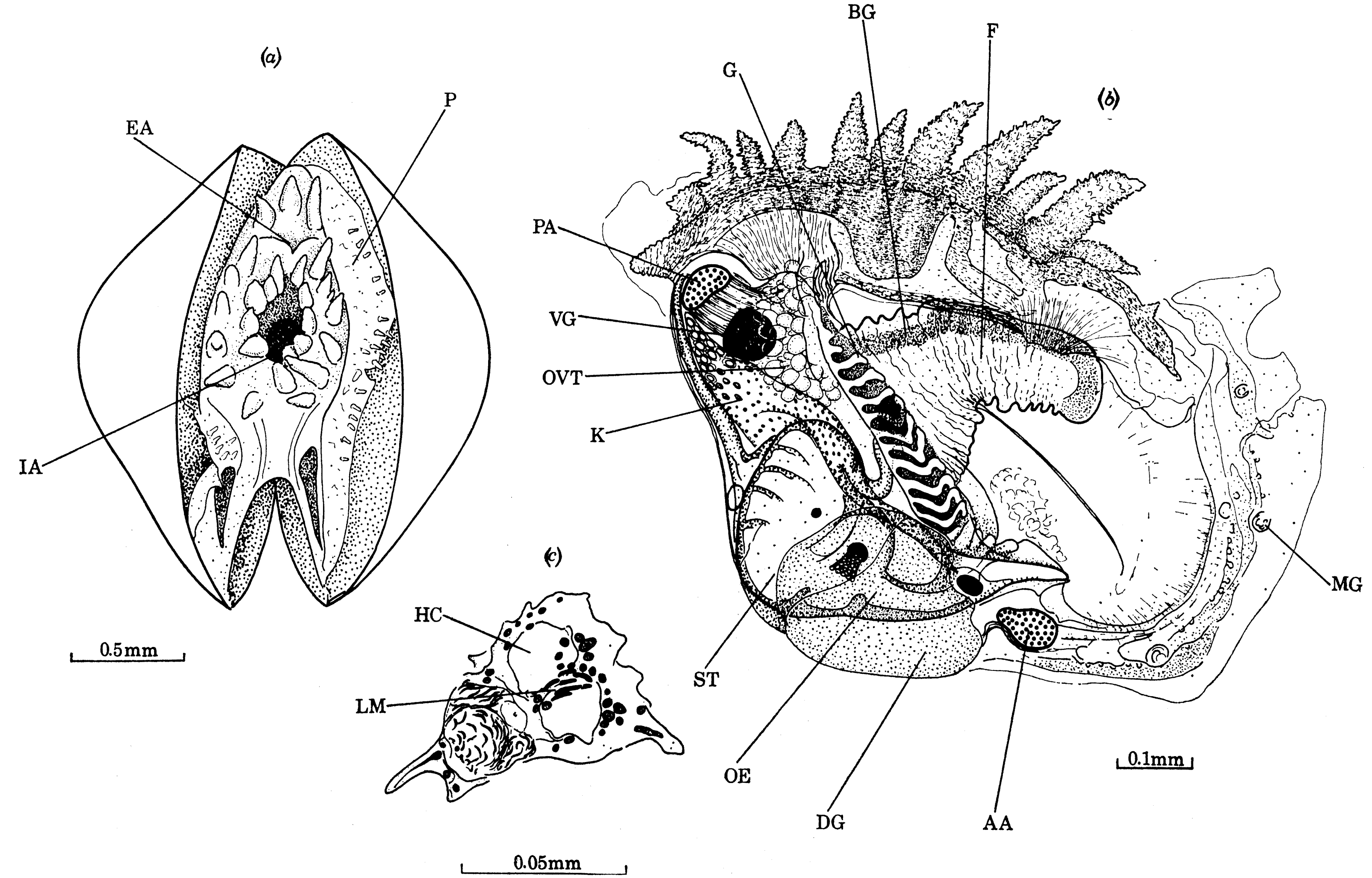

FIGURE 68. *Verticordia quadrata*. (*a*) Posterior view of the apertures and associated tentacles; (*b*) lateral view of whole mount to show soft part morphology; (*c*) transverse section of an inhalent tentacle.

shallow indentation laterally in each filament that corresponds to the food groove of the free edge. The most anterior filament lies short of the lips in preserved specimens, however the gill axis extends forward of this filament as far as the oral groove, thus ensuring ciliary continuity between gill and mouth region. Neither the anterior nor the posterior lips are greatly extended in preserved specimens and palps, *sensu stricto*, are present as a rim about six cells deep to the lateral edge of the lips. Thus, there is no voluminous hood such as has been described for the preceding species.

The gut is very similar to that described for *V. triangularis* and for species of *Lyonsiella*. The wide, muscular, ridged oesophagus opens into a huge stomach lined with scleroprotein that occupies much of the dorsal body space (figure 69). There is a short combined style sac and mid gut section opening from the floor of the stomach and connecting with a simple hind gut section which is not noticeably dilated in the kidney region. This may be due to the lack of material within the lumena of those specimens examined. The digestive gland is anterior in position and overlies the oesophagus and anterior half of the stomach. The digestive ducts are virtually non-existent, the two apertures from the stomach opening into a connecting system of tubules. The tubule cells are of two kinds, vacuolated cells and non-flagellated interstitial cells similar to those of other bivalves.

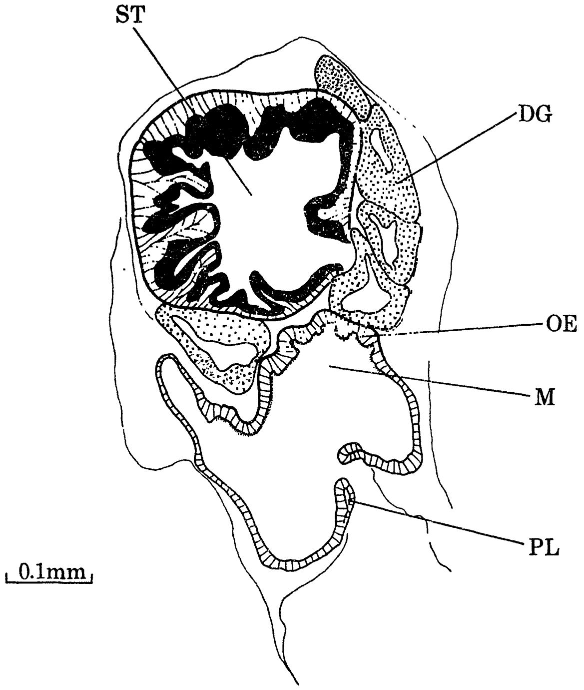

Figure 69. *Verticordia quadrata*. Transverse section through the anterior part of the stomach and mouth region.

The kidney is elongate with a pair of narrow attenuate sections, one each side of the body, extending as far forward as the oral end of the oesophagus. The specimens examined are immature – no gonadial tissue could be determined with certainty. However, a lacunal system similar to that described in *L. abyssicola* is present. Also present are large refractile cuboid epithelial cells on the dorsal side of the hypobranchial cavity (see p. 431). In this species they are concentrated particularly in the region of the visceral ganglion and overlie it laterally. It may be that their function is controlled by the ganglion (figure 70).

There is a byssal gland, the structure of both gland and foot being similar to that described in *L. abyssicola*.

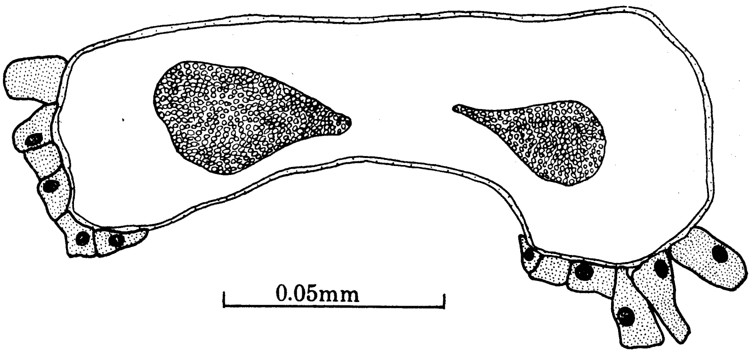

FIGURE 70. *Verticordia quadrata*. Transverse section through the visceral ganglion to show the position of the associated refractile epithelial cells.

Policordia densicostata Locard 1898

Material:

						no. of specimens
Atlantis II	25. viii. 64	sta. 73	39° 46.5′ N, 70° 43.3′ W	1470–1330 m	E.S.	1
Chain	6. vii. 65	sta. 87	39° 48.7′ N, 70° 40.8′ W	1102 m	E.S.	7 + 1 valve
Atlantis II	16. v. 68	sta. 189	23° 00′ S, 12° 45′ E	1007–1014 m	E.S.	1
Atlantis II	17. v. 68	sta. 191	23° 05′ S, 12° 31.5′ E	1546–1559 m	E.S.	2

Distribution:

Southeastern Atlantic, off Senegal, off Angola, Woods Hole –Bermuda traverse, 1007 m–2325 m

Our specimens were compared not only with the original description (Locard 1898) but with excellent recent photographs provided by the Museé d'Histoire Naturelle, Paris. The type specimen (18 mm total length) is much larger than any of our specimens (3.5 mm maximum total length), but shell shape and ornamentation are identical. In practice we found it difficult to distinguish between *P. densicostata*, *P. gemma* and *P. atlantica* (p. 494), using shell characters alone,† although in fact, *P. densicostata* is shortest in relation to height and only moderately extended in the posterior dorsal region (figures 71*a*, *b*, 79*a*, 84*a*).

The number of radiating lines on the shell is similar in the three species (30–37) but whereas the lines are slightly raised ridges in *P. densicostata* and *P. gemma* they are shallow furrows in *P. atlantica* (plate 1) which, surprisingly, proved to be a difficult feature of distinction. In addition to the radial ornamentation there are fine concentric striae which are more marked in larger specimens (figure 71*a*). The valves of *P. densicostata* are inflated and the relatively small umbos point anteriorly. Trapezoidal in lateral outline, the posterior dorsal margin of the shell is characteristically straight or almost so; the anterior dorsal margin is very short, forming a short curve to the anterior margin; anterior, posterior and ventral margins together form a deep parabolic curve. The right valve is a little larger than the left and overlaps it slightly posteriorly.

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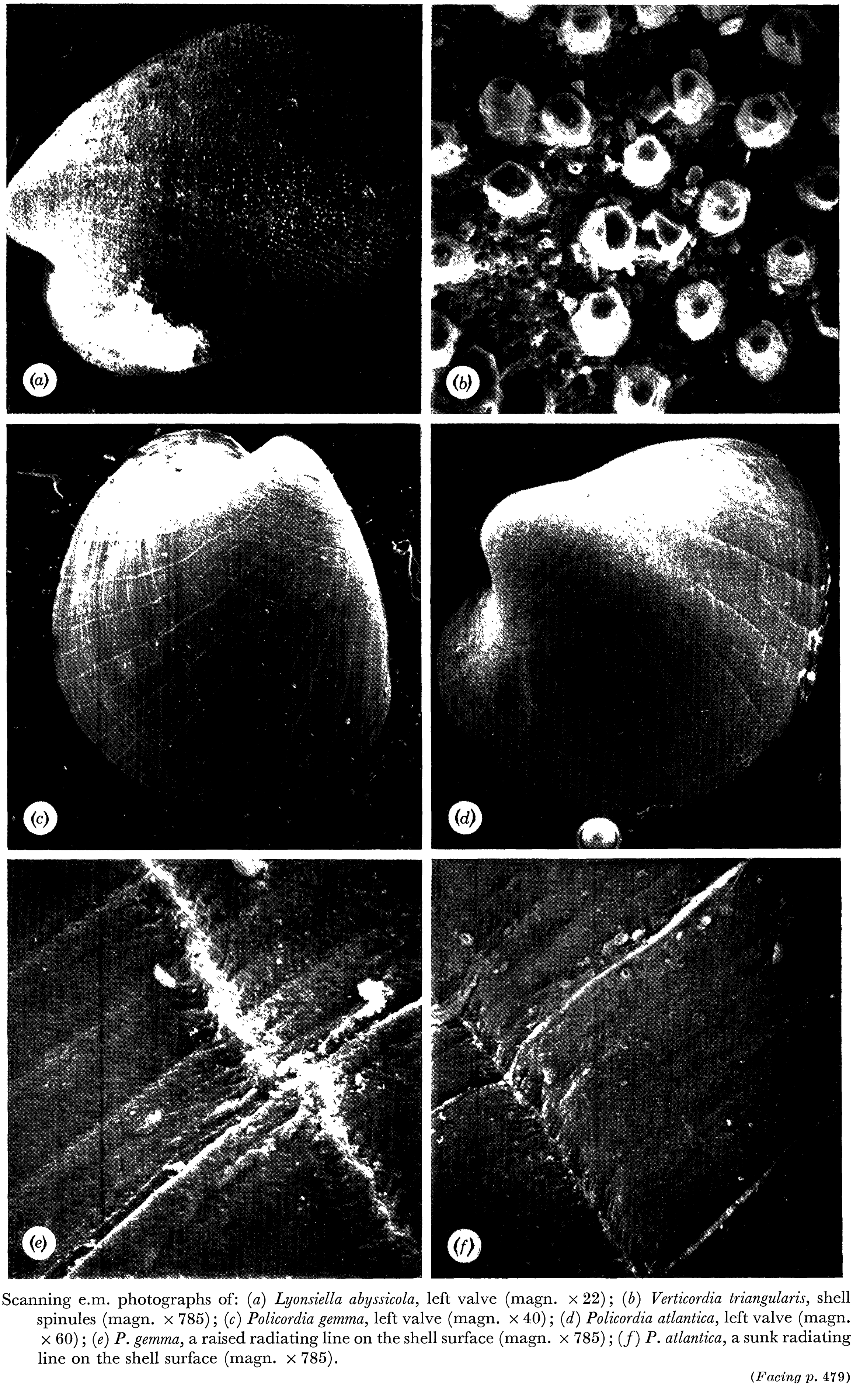
† It will be seen that there are much greater differences in morphology (p. 480 *et seq.*).



Scanning e.m. photographs of: (*a*) *Lyonsiella abyssicola*, left valve (magn. × 22); (*b*) *Verticordia triangularis*, shell spinules (magn. × 785); (*c*) *Policordia gemma*, left valve (magn. × 40); (*d*) *Policordia atlantica*, left valve (magn. × 60); (*e*) *P. gemma*, a raised radiating line on the shell surface (magn. × 785); (*f*) *P. atlantica*, a sunk radiating line on the shell surface (magn. × 785).

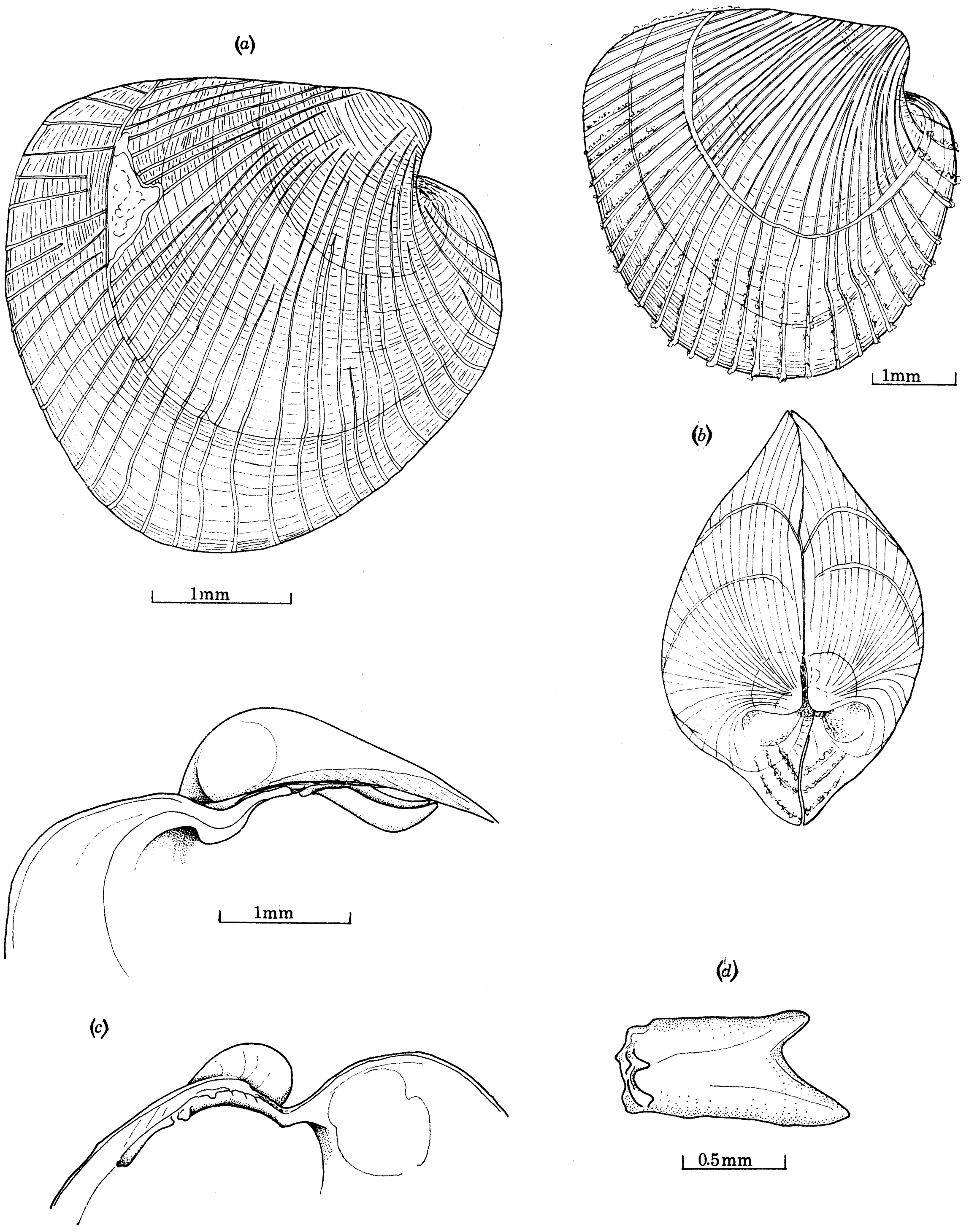


FIGURE 71. *Policordia densicostata*. (*a*, *b*) Lateral and dorsal views of the shells of specimens from station 87 (*Chain*; 6 July 1965); (*c*) detail of hinge region in lateral view; (*d*) dorsal view of lithodesma.

The free margins are sinuous, particularly anterior to the umbos (figure 71*b*). Internally the shell is very smooth, nacrous, with the anterior adductor muscle scar clearly seen, the posterior less so. The hinge region is devoid of teeth, although the shell margins below the umbo are thickened. The lithodesma lies posterior to the umbos, being a recurved plate which is irregularly truncate anteriorly and posteriorly bifid, the left posterior projection being longer than the right (figure 71*c*, *d*). The ligament is similar to that described earlier (p. 411).

The mantle margins are extensively fused anterior to the inhalent aperture resulting in a small anterior pedal gape which occupies about one quarter of the ventral edge (figure 72*a*). There are typically three mantle folds, however only in section are the middle sensory and inner muscular portions clearly distinct. Mantle glands occur along the length of the mantle edge. These are evenly spaced and close together, numbering about 30 in each mantle margin (figure 72*b*). Each gland consists of a flask-shaped portion with a central lumen, the neck opening on to the edge of the sensory lobe of the mantle. To the inside of the flask-shaped portion there is a long cylindrical portion which appears to be separate from the former (figure 73). Whole mounts show a duct leading from the cylindrical portion into the flask shaped portion. The cylindrical portion is recurved in the plane at right angles to the shell. The whole gland is approximately 175 μm long, the flask part being 35 μm at its widest point while the cylindrical part is 12 μm in diameter. As in other species, the glands stain heavily in haematoxylin.

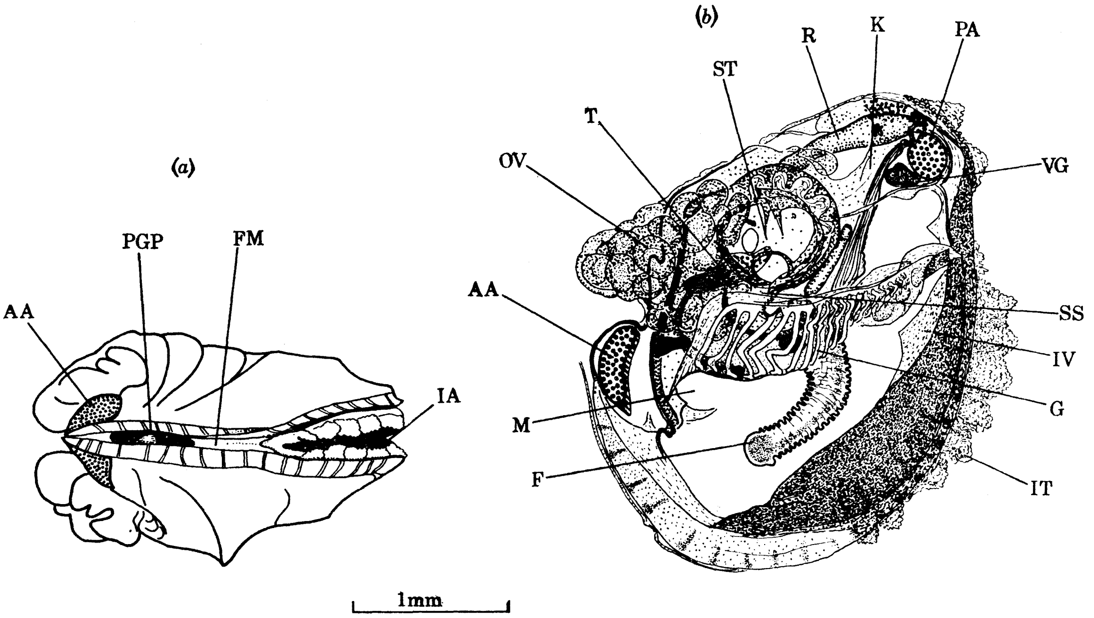


Figure 72. *Policordia densicostata*. (*a*) Antero-ventral view showing the extent of the pedal aperture; (*b*) lateral view of whole mount to show the soft part morphology.

While the inhalent aperture itself is not large, the valve and tentacular area surrounding it occupy about two-thirds of the posterior margin of the animal (figure 74*a*, *b*). The exhalent aperture is small and is bordered by lips, the right one being larger than the left which it overlaps. There are three tentacles above the exhalent aperture and two at its ventral limit. These tentacles are unbranched, conical and blunt ended with a dense covering of papillae (figures 74*a*, *b*, 75*a*).

The inhalent aperture is surrounded by about 22 tentacles, the bases of which are fused on each side. Each branches into 3–7 lobes and is densely covered with papillae (figures 74*b*, 75*a*, *c*). The musculature of the tentacle is similar to that of *P. atlantica* (p. 491 and figure 75*b*) as is the nerve supply of the siphonal region. However, *P. densicostata* differs from *P. atlantica* in that there is a concentration of glandular cells at the tip of each tentacle (figure 75*b*, *d*). Individual cells measure approximately 5 μm wide and 15 μm long and fine ducts lead from them to the outside. Little or no muscle extends into the valve of the inhalent aperture and this is not thickened at its free edge (figure 75*b*).

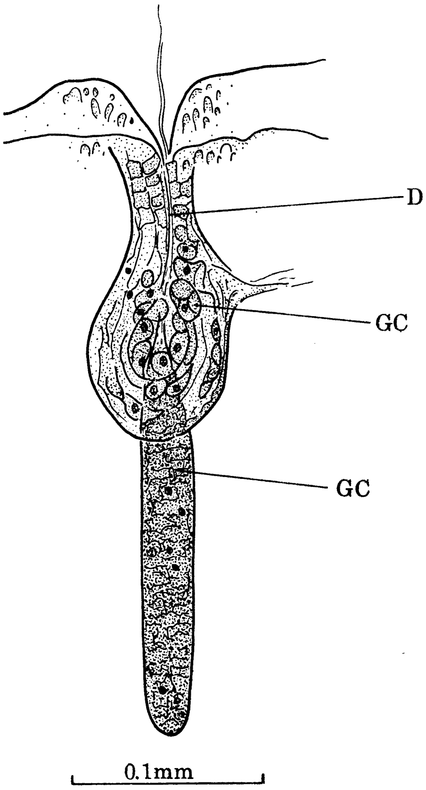


FIGURE 73. *Policordia densicostata*. Lateral view of a whole mount of radial mantle gland.

The gill is relatively well developed with both demibranchs present throughout the entire length (figure 76*c*, *d*). Although few muscle fibres are present, the gill axis is broad and thickened. The blood vessels of both axis and filaments contain large numbers of amoebocytes. Although well developed in comparison with other verticordiid species, the filaments are short and extend more or less horizontally from the gill axis. The ascending lamella of the outer demibranch fuses with the mantle and is not as long as the descending lamella. There is a ciliated marginal groove present at the junction of ascending and descending lamellae of the inner demibranch (figure 76*c*). Interfilamentar junctions are restricted to the distal ends of the filaments and the line of the marginal groove. A tissue membrane connects the inner ascending lamellae with the body. This is a more tenuous connexion than that of the outer demibranch. Immediately posterior to the foot the right and left demibranchs are united by ciliary junctions of the ascending inner lamellae, but further posterior they are connected by a membrane. There is a broad food groove along the line of the axis.

The gill of *P. densicostata* is similar to that of *P. atlantica* (p. 492) with both demibranchs present, although it is not so muscular. In cross-section the filaments are similar to those of *L. abyssicola*, with paired large frontal cells, but unlike the latter species there are more than two intermediate cells central to the large frontal cells (figure 76*a*). The lateral cilia are extremely long – reflecting the widely spaced filaments – and far removed from the frontals.

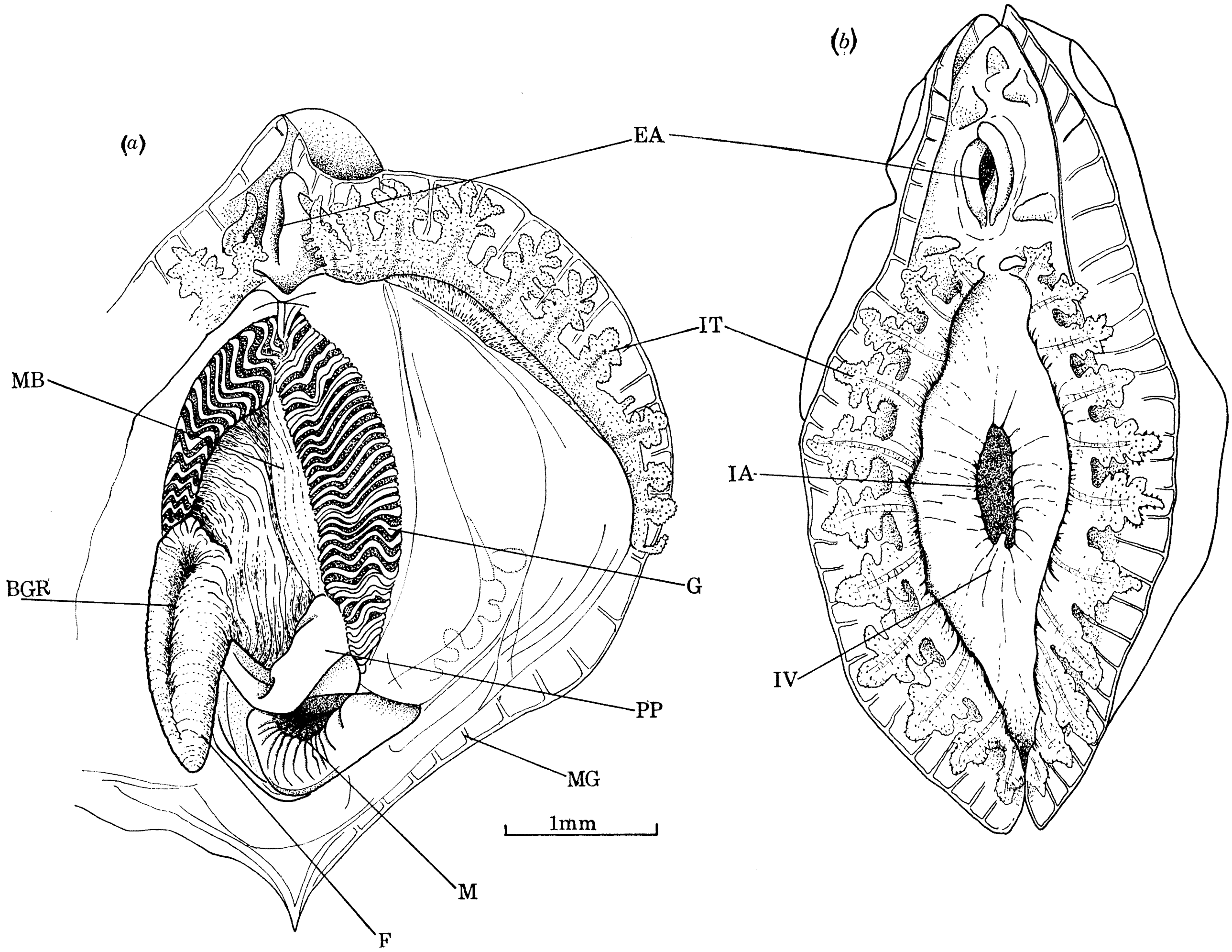


FIGURE 74. *Policordia densicostata*. (*a*) Ventral view of the mantle organs, the area of mantle fusion between inhalent and pedal apertures has been cut; (*b*) posterior view of apertures and surrounding tentacles.

The mouth region is also similar to that of *P. atlantica* and of other verticordiids possessing a ventral hood to the mouth forming a funnel with the anterior limit of the gills terminating laterally at the grooves marking the junction of dorsal and ventral lips (figure 76*b*).

The folds of the oesophagus which terminate on the buccal funnel are well marked and ten in number. The histology and general form of the oesophagus is in no way different from that previously described. The stomach, also, is similar to that described for species of *Lyonsiella* and *Verticordia* (figures 77, 78*a–d*), but differs from that of *P. atlantica* in that the dorsal ciliated tract (CT), that persists posterior to the oesophageal aperture in that species, is not so extensive in *P. densicostata*. The cuticular lining, in contrast, is more extensive than that in *P. atlantica* but remains extremely thin except for the region surrounding the style sac where it forms a thickened collar (figures 77, 78*d*). The stomach lining is extensively folded with three well-defined dorsal ridges similar to those observed in *V. triangularis*. The posterior extension of the stomach is well

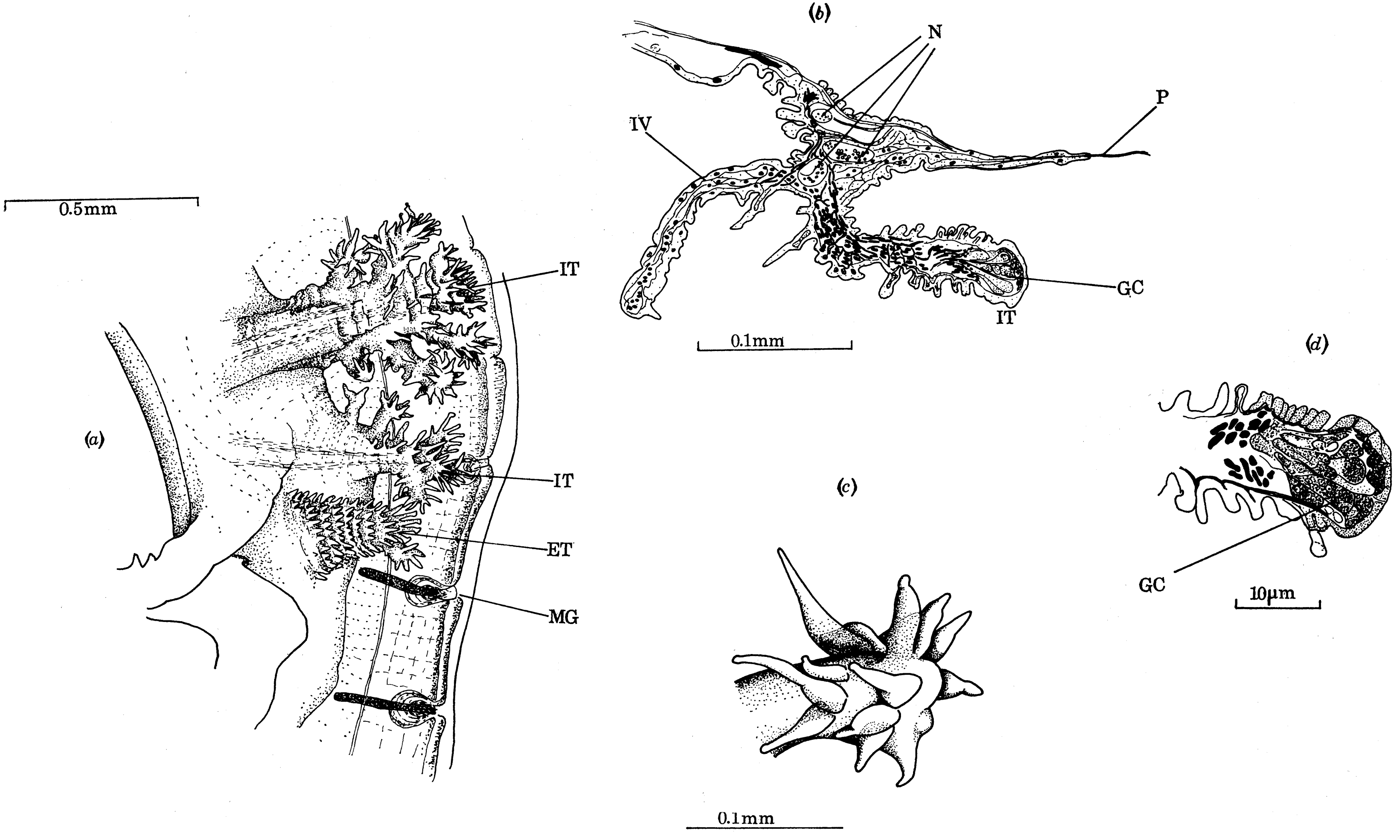


FIGURE 75. *Policordia densicostata.* (*a*) Lateral view of a whole mount of two inhalent and one exhalent tentacle; (*b*) transverse section through an inhalent tentacle and adjacent mantle edge; (*c*) whole mount to show arrangement of papillae at the tip of an inhalent tentacle; (*d*) longitudinal section through the tip of an inhalent tentacle to show the arrangement of the gland cells.

marked, the aperture of the style sac and mid gut being anterior and close to the oesophageal and left and right ducts to the digestive gland. The style sac is relatively large, although typically short (figure 77). The remainder of the gut has the usual form and histology, with a voluminous rectal portion posterior to the posterior adductor muscle (figure 78 *a–c*). The digestive gland largely lies anterior to the stomach and dorsal to the oesophagus where the latter joins the stomach.

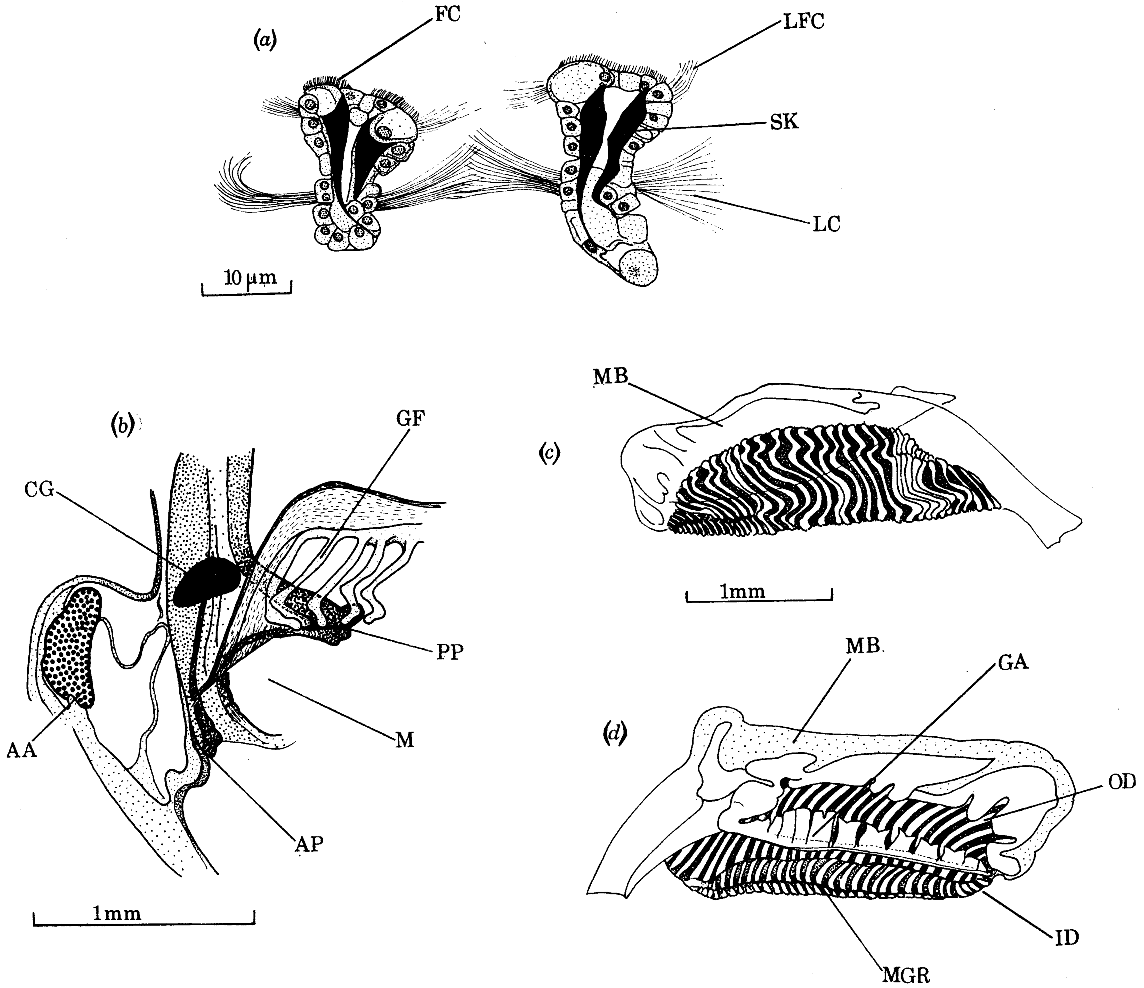


FIGURE 76. *Policordia densicostata*. (*a*) Transverse section of two adjacent gill filaments; (*b*) lateral view of mouth region; (*c, d*) outer lateral and inner lateral views respectively of a right demibranch.

The kidney overlies the posterior dorsal and lateral sides of the stomach but does not extend forward on either side of the body close to the oesophagus, as it does in some species. In other respects (e.g. form of byssus gland, position of ovary and testis) *P. densicostata* is similar to species already described.

Policordia atlantica n.sp. (figures 79–83)

Material: Holotype: M.C.Z. 272675

						no. of specimens
Atlantis II	18. xii. 66	sta. 131	39° 38.5′ N, 70° 36.5′ W 39° 39.0′ N, 70° 37.1′ W	2178 m	E.S.	2
Atlantis II	5. ii. 67	sta. 142	10° 30.0′ N, 17° 51.5′ W	1624–1796 m	E.S.	5+1 valve
Atlantis II	6. ii. 67	sta. 145	10° 36.0′ N, 17° 49.0′ W	2185 m	E.S.	3
Atlantis II	16. v. 68	sta. 185	22° 56′ S, 13° 02′ E	458–463 m	E.S.	2+1 valve
Atlantis II	23. v. 68	sta. 203	8° 48′ S, 12° 52′ E	527–542 m	E.S.	13

Specimens range in size from 1.3 mm total length to 3.7 mm total length. Shell, inequilateral, inflated, fragile and grey-white in colour; right valve overlapping left posteriorly; anterior dorsal shell margin strongly curved immediately in front of the umbos; posterior dorsal shell margin relatively straight and elongate and lies above the level of the umbos; posterior margin slopes forwards and is also nearly straight; more than 90 % of shell lies posterior to the umbo, the shell having a characteristically expanded appearance (figure 79*a*, *c*).

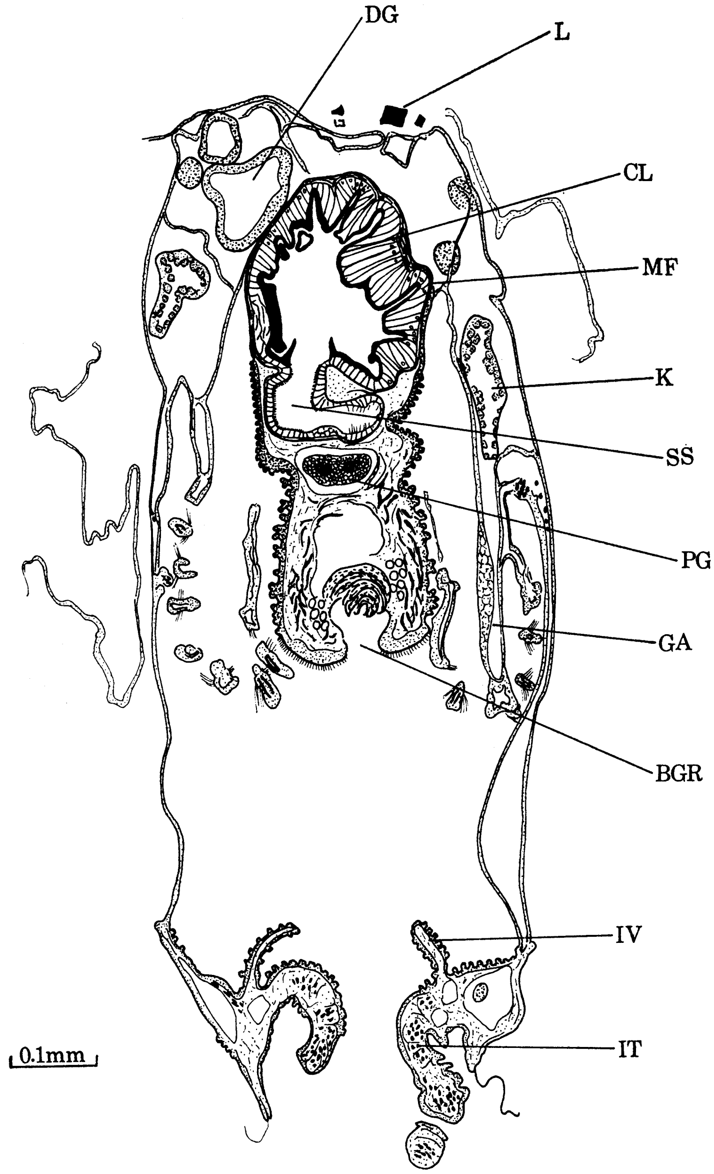


FIGURE 77. *Policordia densicostata*. Longitudinal, horizontal section through stomach and style sac.

Shell nacreous; muscle scars difficult to distinguish; hinge line smooth and without teeth; lithodesma small, forked posteriorly, the two extensions equal in length (figure 79*b*). Shell surface with no granular or spinular ornamentation, but with 15–30 radiating lines; the number varying with size; a few radiating lines extend from umbo to shell edge, others being interpolated with increasing size of shell.

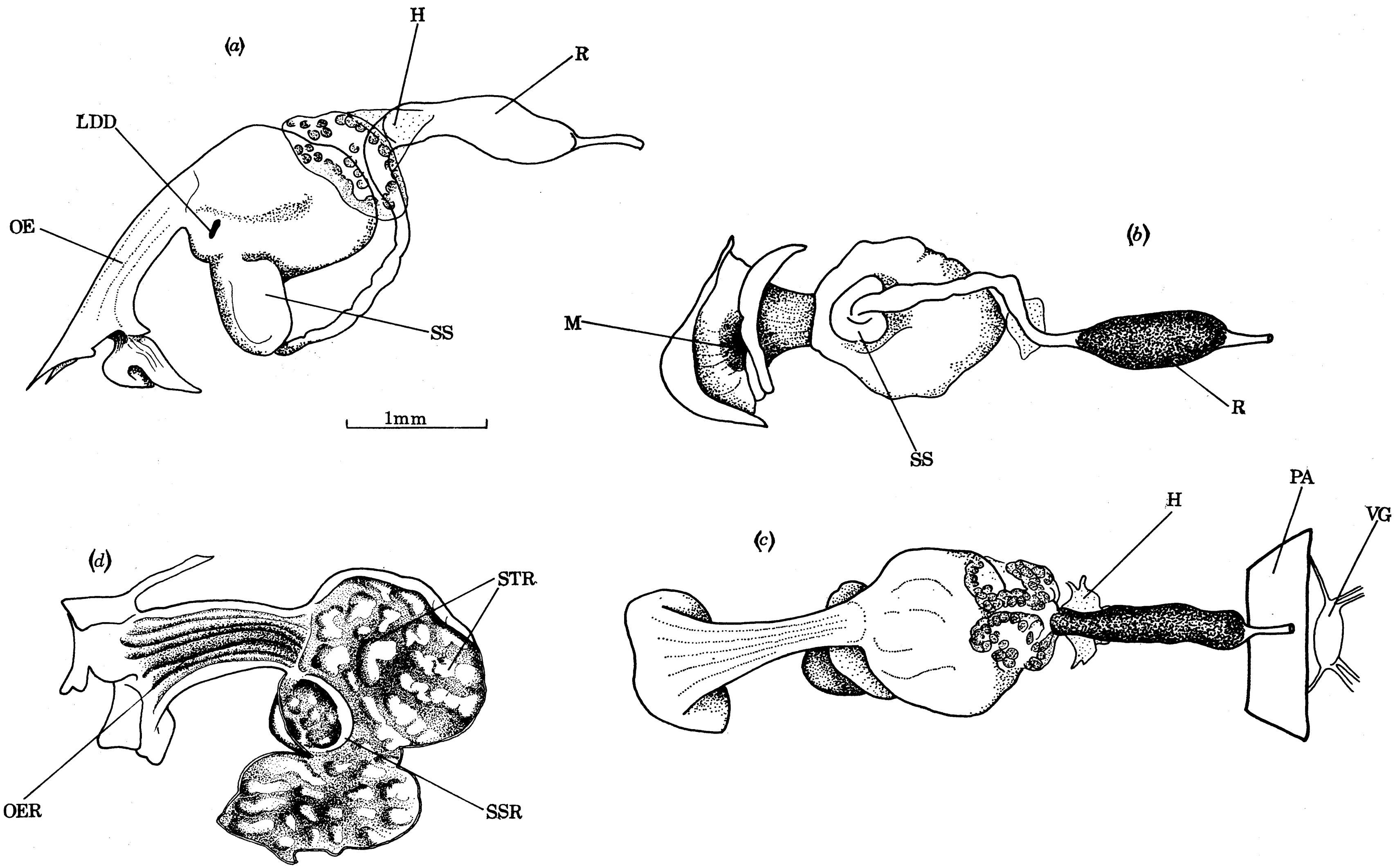


FIGURE 78. *Policordia densicostata*. (*a*, *b*, *c*) Lateral, ventral and dorsal views respectively of a dissection of an entire gut; (*d*) mouth, oesophagus and stomach of the same specimen opened along the left side to show the pattern of the internal ridges.

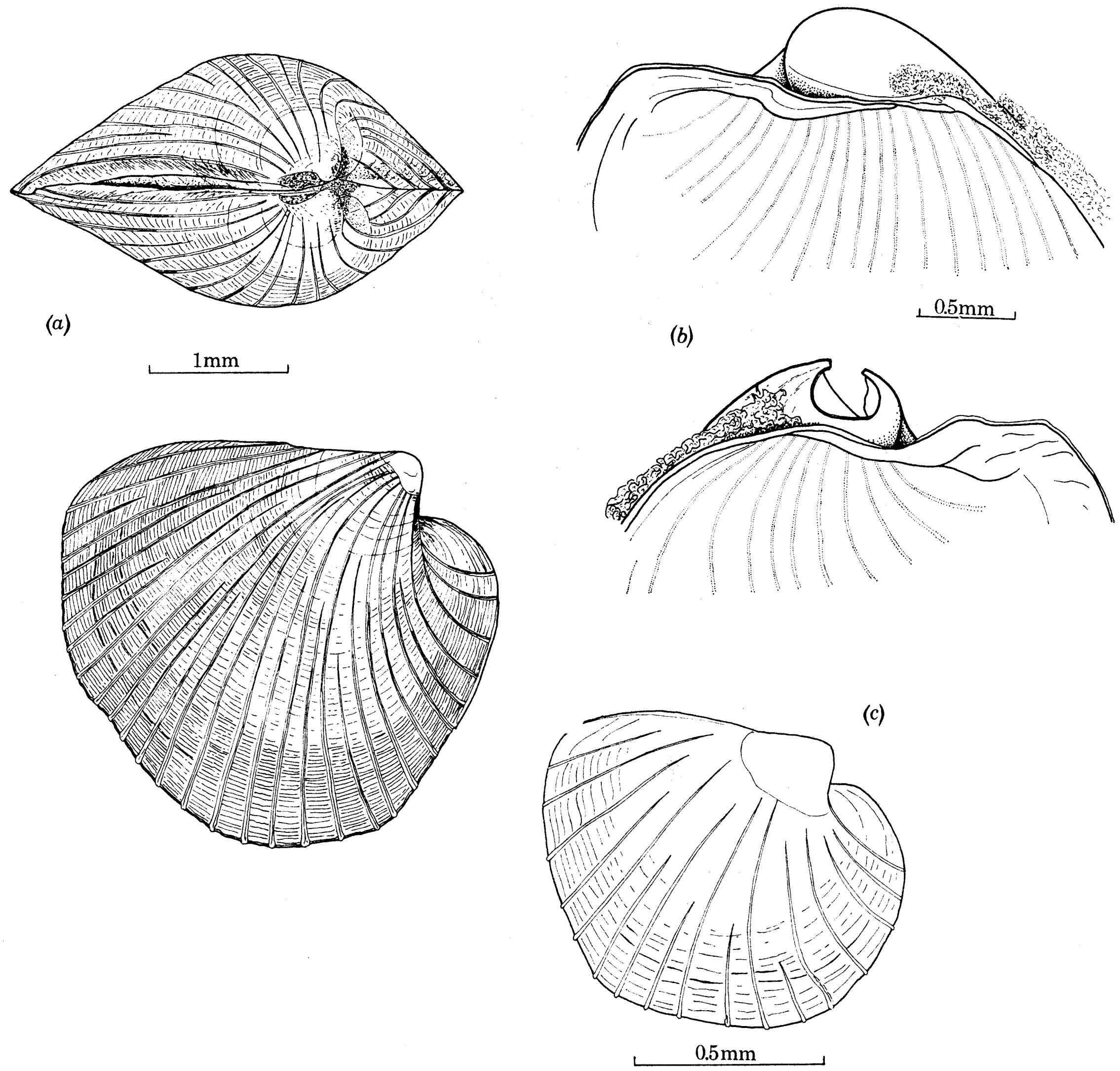


FIGURE 79. *Policordia atlantica*. (*a*) Right lateral and dorsal views of the shell; (*b*) lateral views of the hinge of the left and right valves; (*c*) lateral view of right valve of smallest specimen in collections. All drawings are of specimens taken at station 203 (*Atlantis*, 28 May 1968).

Scanning e.m. pictures show the radiating lines to be depressed grooves in the shell surface (see plate facing p. 479). In some specimens there is a raised line of soft sediment material adhering to the margin of the radiating lines. Concentric, closely spaced growth lines occur between the radiating lines.

The middle and inner folds of the mantle edge are not clearly separate although the outer fold is well defined, the periostracum being secreted within a groove between this and the sensory fold. Very few muscles are present in the mantle edge. Internal to the folds is a relatively broad band of gland cells adjacent to an inner, broad, ciliated region which extends along the region of the pedal gape inwards as far as the junction of the gill membrane in the region of the mouth (figure 80*a*). The pedal gape is restricted and anterior in position. There are 15–20 mantle glands in each mantle margin. These are not restricted to the region of the pedal gape but are fairly evenly spaced from the exhalent aperture to the level of the anterior adductor muscle. The inner part of the gland consists of an area of densely staining cells with a central

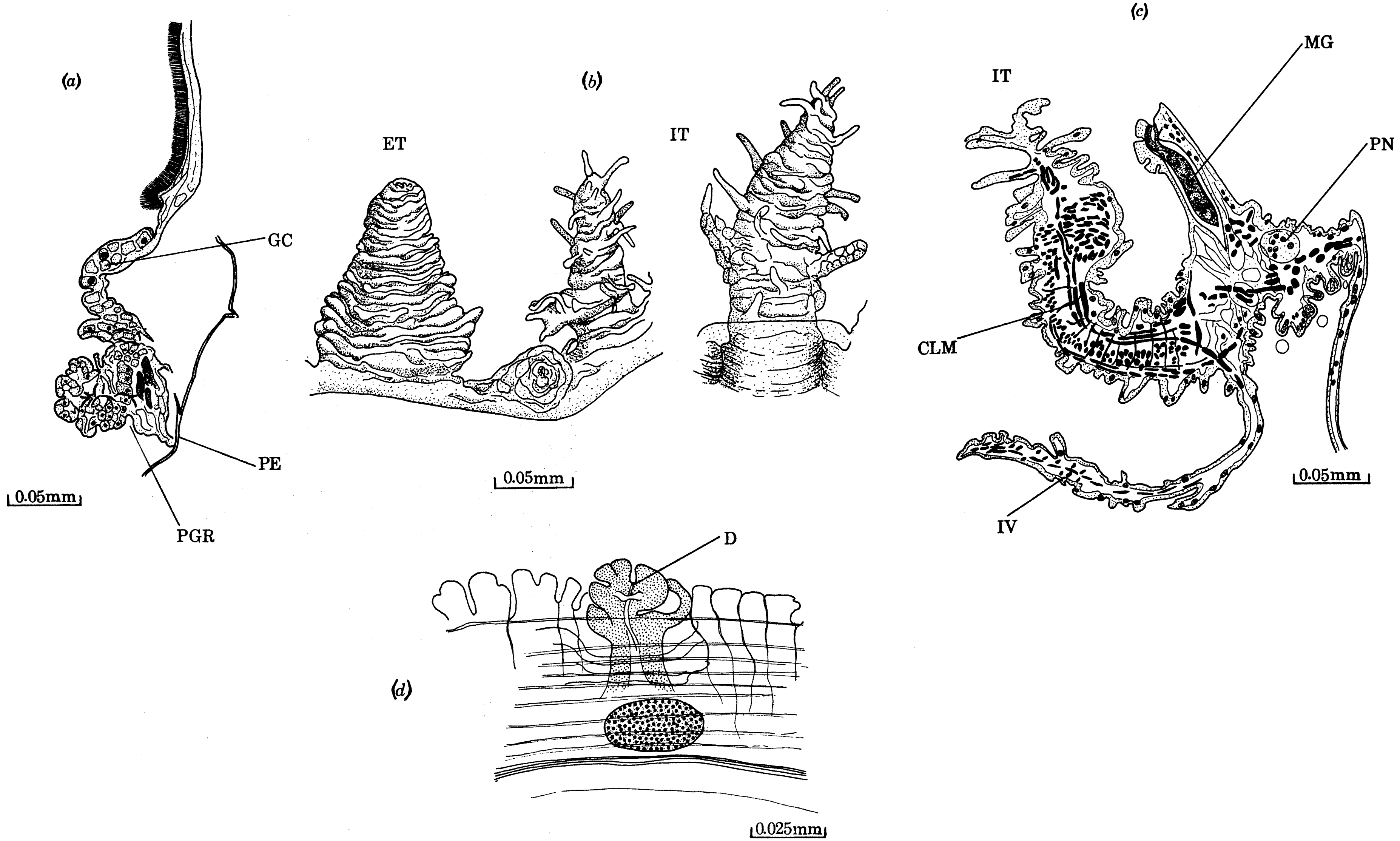


FIGURE 80. *Policordia atlantica*. (*a*) Transverse section through the mantle edge at the level of the pedal gape; (*b*) whole mounts of an exhalent and two inhalent tentacles; (*c*) transverse section of the mantle edge in the region of the inhalent aperture; (*d*) whole mount of a radial mantle gland.

duct leading from it. The duct appears to have divided opening. Internal to the glandular part is a squat oval structure, 37 μm × 15 μm in lateral dimension, that stains heavily and appears to be removed from the rest of the gland (figure 80*c*, *d*). No connecting duct or tissue is apparent between the two regions.

Dorsal and internal to the inhalent aperture there is a small ciliated projection in the region of the fused inner mantle folds. This connects with a ciliated tract on either side of the aperture and extends anteriorly along each side of the mantle to the ciliation on the inside of the pedal gape, being similar to that described for *Verticordia triangularis*.

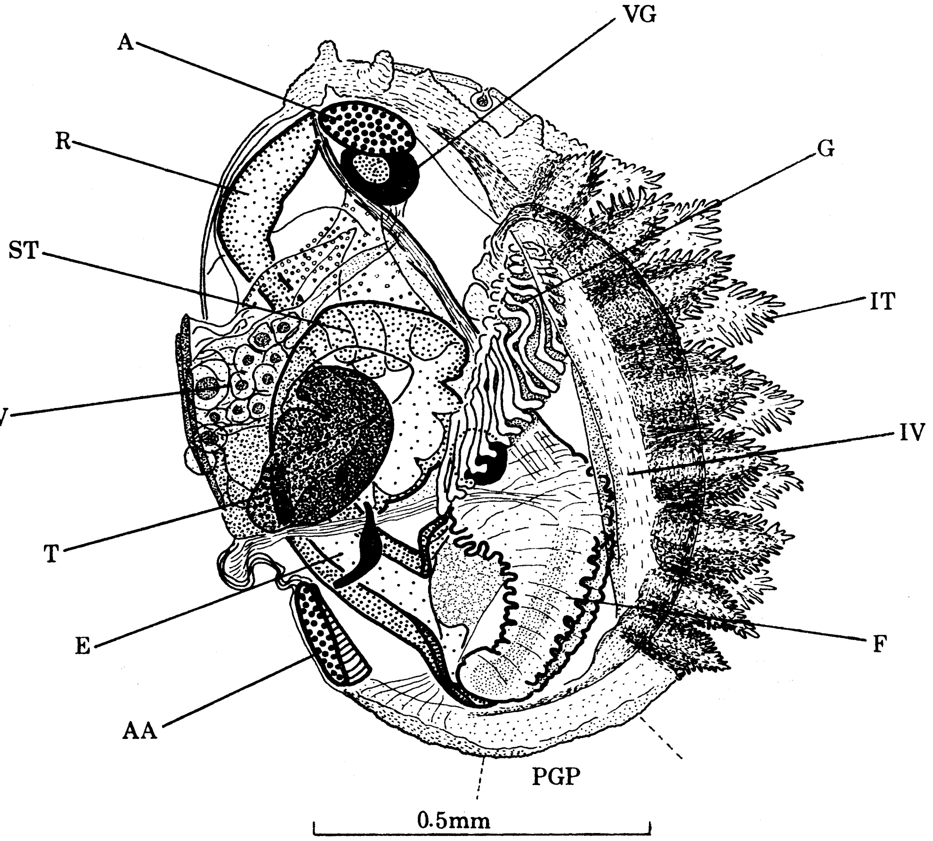


Figure 81. *Policordia atlantica*. Lateral view of whole mount to show details of soft part morphology.

The inhalent and exhalent apertures occupy the posterior and ventral margins of the animal (figure 81). The exhalent aperture is bordered by two thick lateral flaps of tissue, the flap on the right overlapping that on the left (figure 82*b*). There are five tentacles, one mid-dorsal and one on each side of the dorsal margin and a lateral tentacle on either side of the ventral margin of the exhalent aperture. Around the inhalent aperture a single row of 28 pointed papillate tentacles rings the aperture completely except for a small mid dorsal space.

The inhalent tentacles in preserved specimens are contracted with a much convoluted epithelium which bears fine projecting papillae (figures 80*b*, 83). There are also two moderately large lateral branches inserted close to the base of each tentacle (figure 80*b*). The exhalent tentacles are blunt-ended with a convoluted epithelium but without papillae or branches. The inhalent aperture appears as a long narrow slit bounded by a membraneous diaphragm which extends outwards to the base of the tentacles (figure 82*a*, *b*). Internally there is a thin radial

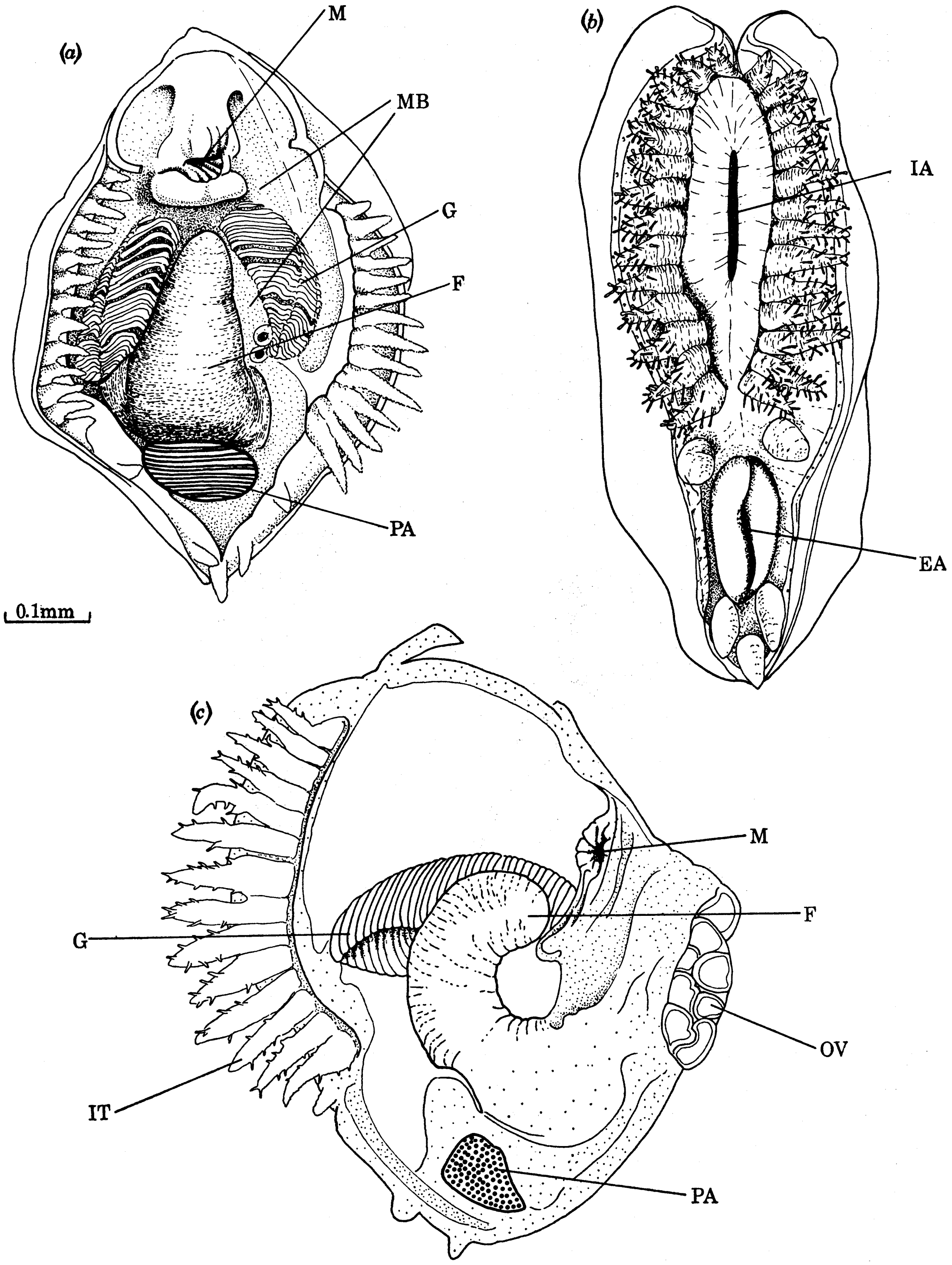


Figure 82. *Policordia atlantica.* (*a*) Postero-ventral view of the soft part morphology, note that the posterior adductor muscle (PA) is seen through the dorsal wall of the hypobranchial cavity and that the gills are free posteriorly. This is because the gill membrane posterior to the foot, and the fused mantle between the apertures, has been cut. Also cut is the fused mantle between inhalent aperture and pedal gape; (*b*) posterior view of apertures and associated tentacles; (*c*) lateral view with mantle and gill removed from the left side.

muscle layer and the rim of the aperture is thickened by a small number of circular muscles (figure 80*c*).

The musculature of the tentacles differs from that described in *L. abyssicola* and in other species. There is a central core of longitudinal muscles which are not paired. This is surrounded by a haemocoele which is crossed by scattered transverse fibres and there is a further thin, scattered layer of longitudinal muscle fibres adjacent to the basement membrane of the outer epithelium. While the peripheral longitudinal muscles are somewhat denser on the inner wall of the tentacle, there is no marked development of asymmetrical muscle blocks as seen in *L. abyssicola* and *V. triangularis*. Most of the peripheral muscle fibres extend into the inner muscular fold, with a few connecting with the radial muscles of the valve. The inner longitudinal muscles

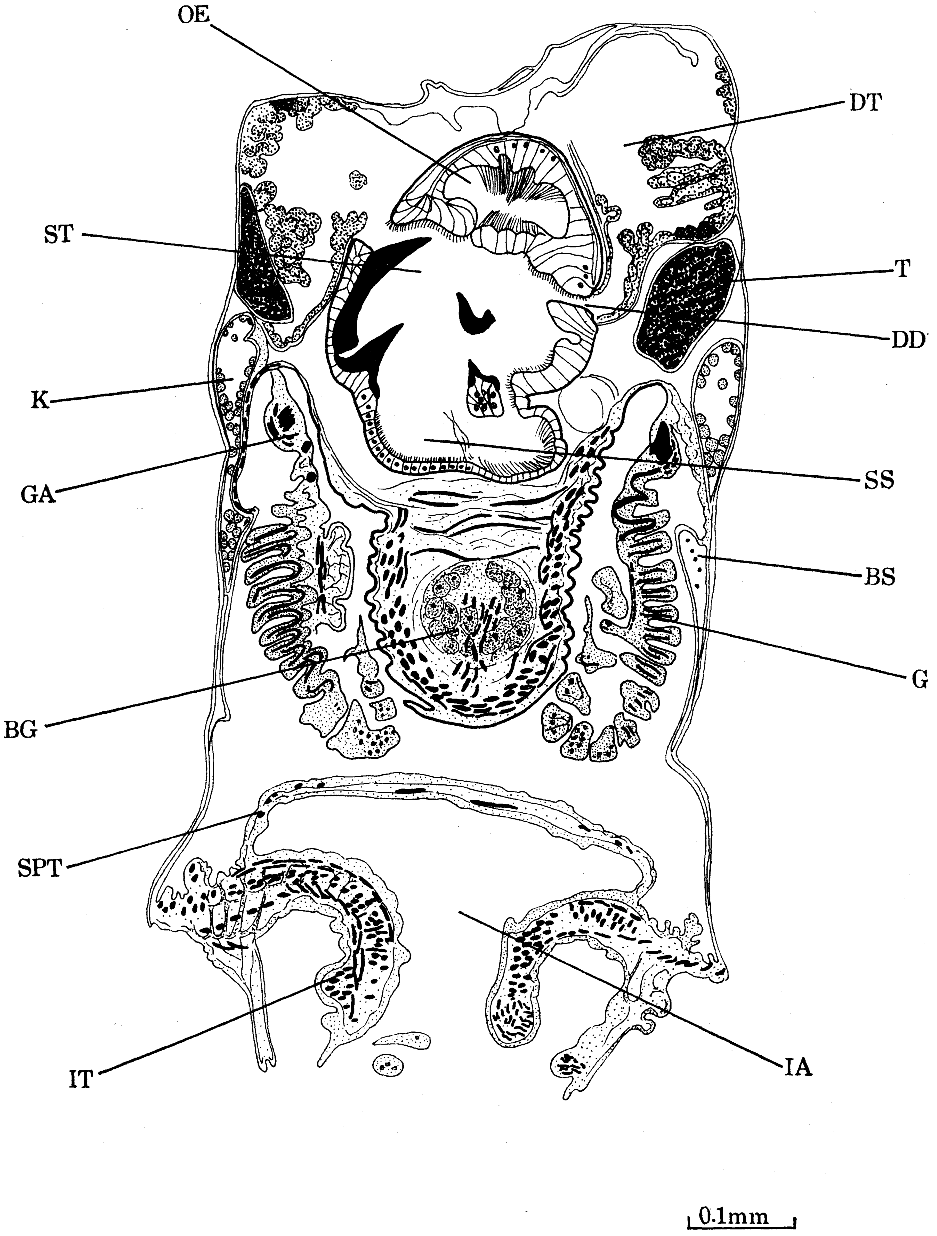


FIGURE 83. *Policordia atlantica*. Horizontal longitudinal section through the centre of the visceral mass.

merge with a thick band of muscle that encircles the aperture beneath the base of the tentacles. The paired lateral branches at the base of the tentacle are well supplied with muscles originating from the inner longitudinal series. It is probable that in life the tentacles of *P. atlantica* are displayed and behave differently to those of other species.

The gills consist of both inner and outer demibranchs. Anteriorly the gill margins are attached to the body by a tissue membrane. Immediately posterior to the foot the left and right inner demibranchs are connected to each other by ciliary junctions. Further posterior they are joined together by a membrane which is continuous with the junction between inhalent and exhalent apertures (severed in figure 82*a*). Although the 30–40 filaments lie in a horizontal plane, there are well developed food grooves at the gill axis and at the ventral limit of the gill between the descending and short ascending lamella of the inner demibranch (figure 82*a*). The gill axis is not exceptionally deep but it contains muscles which extend longitudinally along the axis close to the point of connexion of filaments with the axis (figure 83). Posterior to the foot the axes are attached to thickened extensions of the mantle wall, the structure of which is similar to that described for *V. triangularis*. Muscle fibres are also present in the interlamellar junctions above the food groove.

The lips surrounding the mouth form a funnel similar to that of previously described species (e.g. *L. abyssicola*). The funnel is contracted in preserved specimens and not so clearly trumpet shaped as it is in some species (figure 82*a*, *c*). Laterally there is a deep oral groove connecting mouth with the food groove of the gill. Other grooves (8–10) – continuations of the folds of the oesophagus – are present.

The course and histology of the gut is similar to species of *Policordia* previously described. The ridged oesophagus is bounded by a muscle layer and the inner epithelium includes conspicuous mucus cells. It joins the anterior end of the stomach dorsally and a pair of digestive ducts open one to each side just ventral to the oesophageal aperture (figure 83). A ciliated tract runs from each digestive duct aperture to the mid gut, the opening to which is also anterior in the floor of the stomach. There is also a dorsal ciliated tract that extends from the oesophageal aperture to the posterior sac-like extension of the stomach. Laterally the stomach bears a cuticular lining which bears on the right side, two thickened tooth-like projections above the opening of the style sac. No remains of a style were found in the preserved specimens. Posteriorly the stomach is highly convoluted and completely lined with cuticle. The mid gut and style sac are combined and very short. The mid gut is on the right of the style sac and subsequently continues as the hind gut along the ventral side of the stomach to its posterior limit before passing dorsally and posteriorly where it forms a swollen rectal region, anterior to the posterior adductor muscle.

The digestive diverticula consist of short right and left ciliated digestive ducts, each of which lead into large lobulate digestive tubules lateral and anterior to the stomach. Each tubule has a large lumen and four or five lobes. The outer wall of each lobe is lined with large, columnar, vacuolated cells which in sectioned specimens are in the process of producing large numbers of spherules. Also on the peripheral wall of each lobe are clusters (10–20 cells) of deeply staining non-flagellated interstitial cells. The remainder of the tubule epithelium is well defined, one cell thick, and comprises vacuolated cells not producing spherules, and isolated individual non-flagellated interstitial cells. Sections indicate a distinct difference in activity between the cells of the outer wall as compared with the cells of the inner wall adjacent to the stomach (figure 83).

Other morphological features of note include the extremely large visceral and pedal ganglia. In lateral view the visceral ganglia approach the size of the posterior adductor muscle (figure 81).

The pedal ganglion lies above the muscular part of the foot close to the style sac. The foot is large in comparison with other verticordiids, particularly *P. densicostata* and *P. gemma*, and it is directed anteriorly reflecting the anterior aspect of the pedal aperture (figure 81, 82*c*). There is a well-developed byssus gland, similar to that described earlier (p. 432). Paired ovaries lie dorsal to the stomach, the testes lie lateral to the stomach and ventral to the digestive gland (figure 83). The kidney is extensive and penetrates anteriorly on each side of the body reaching close to the oesophagus. The lacunal system and the gland cells associated with the epithelia lining the hypobranchial cavity are similar to those described for *L. abyssicola*.

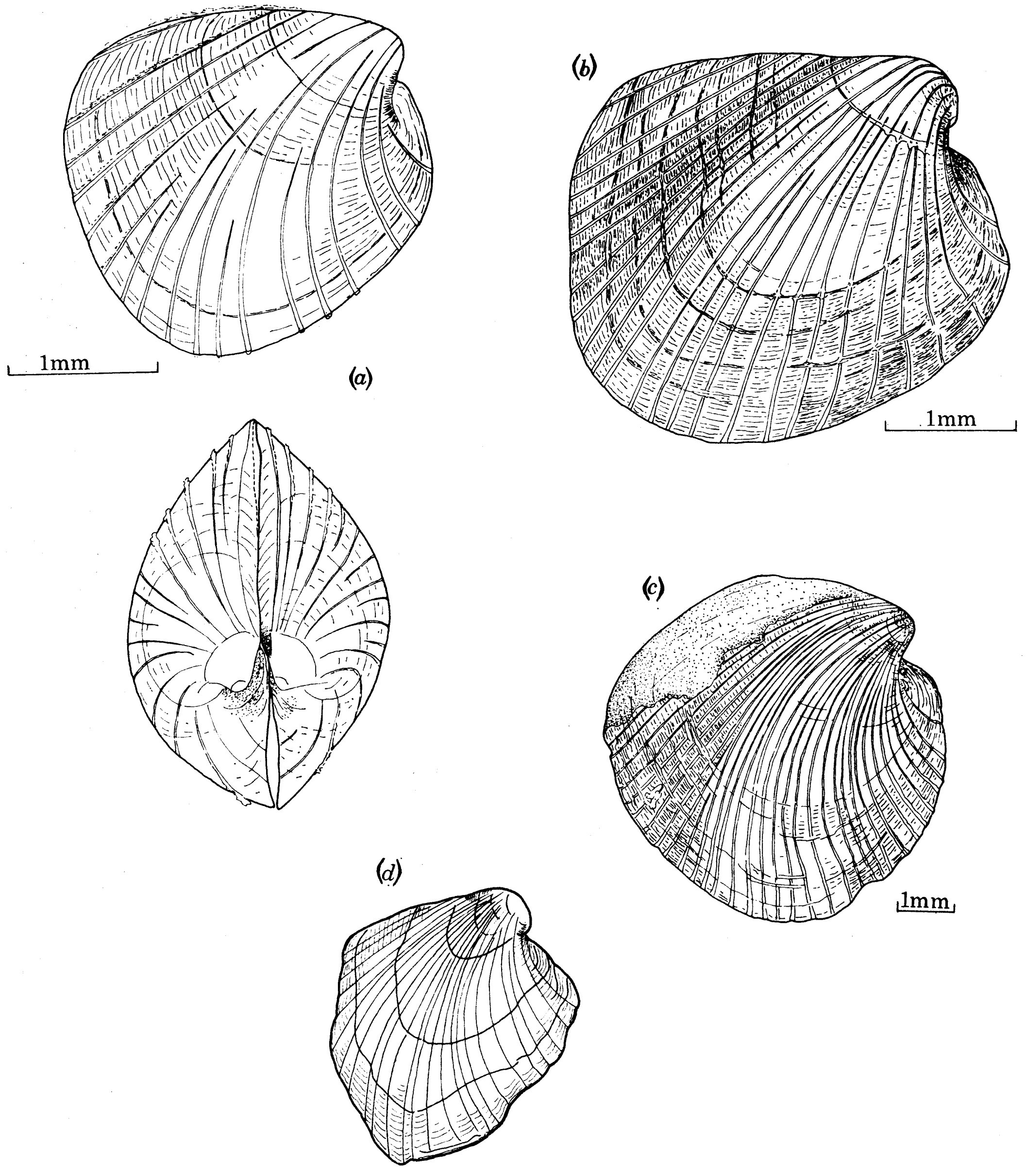


FIGURE 84. *Policordia gemma*. (*a*) Lateral and dorsal view of a specimen taken at station 85 (*Chain*, 5 July 1965); (*b*) lateral view of right valve of specimen no. 63234 of the U.S. National Museum, taken at station 1093 off Martha's Vineyard and labelled '*L. gemma*'; (*c*) similar view of specimen no. 63237 of the U.S. National Museum taken at station 10 of the 'Porcupine' Expedition and labelled '*L. insculpta*'; (*d*) similar view of a specimen from the British Museum also taken from the 'Porcupine' Expedition labelled *V. insculpta.*

Policordia gemma (Verrill 1880)

Material from:

						no. of specimens
Chain	5. vii. 65	sta. 85	37° 59.2′ N, 69° 26.2′ W	3834 m	E.S.	76+ 2 valves
Chain	30. vii. 65	sta. 78	38° 0.8′ N, 69° 18.7′ W	3828 m	E.S.	1
Atlantis II	24. viii. 66	sta. 126	39° 37.0′ N, 66° 47.0′ W 39° 35.5′ N, 66° 44.0′ W	3806 m	E.S.	2
Atlantis II	14. ii. 67	sta. 156	00° 46.0′ S, 29° 28.0′ W 00° 46.5′ S, 29° 24.0′ W	3459 m	E.S.	1
Atlantis II	17. v. 68	sta. 191	23° 0.5′ S, 12° 31.5′ E	1546–1559 m	E.S.	2
Atlantis II	24. iii. 71	sta. 256	37° 40.9′ S, 52° 19.3′ W	3906–3917 m	E.S.	2
Atlantis II	26. iii. 71	sta. 259	37° 13.3′ S, 52° 45.0′ W	3305–3317 m	E.S.	3

Distribution:

N. America Basin, W. Europe and Canaries Basin, Azores, 138–3917 m

Policordia gemma is characterized by a thin fragile shell, which varies greatly in shape. This appears to be due to natural variation in growth as well as to the repair of breaks at the shell perimeter (figure 84*a–d*). Extreme forms have been regarded as separate species, *L. gemma* (*sensu stricto*) being subrostrate with the anterior margin almost straight, while *L. insculpta* has a shorter posterior dorsal margin and a more evenly curved anterior margin. However, intermediates are well known. The *L. gemma/insculpta*, complex has been known for a considerable time (Smith 1889) and has been recently discussed by Soot-Ryen (1966)†. Both conclude that this is a single species showing extreme variation, a conclusion that has not been challenged by observations on our material with its advantage of greater numbers and well-preserved anatomy.

From our original observations we concluded that three closely related species could be recognized, namely, *P. gemma*, *P. atlantica* and *P. densicostata*. Subsequently it proved possible to distinguish *P. atlantica* by shell characters (pp. 478, 487). Distinction between *P. atlantica* and *P. gemma* is not easy and we believe that some past records of *P. gemma* may be of *P. atlantica*. Thus, we believe that specimens photographed by Soot-Ryen (1966) and named *P. gemma* (No. 9, Plate 1) and *P. insculpta* (No. 10, Plate 1), the former from Michael Sars North Atlantic deep sea expedition (station 70) and the latter from the Porcupine Expedition (station 1) and a lectotype of *P. insculpta* Jeffreys (1881), are examples of *P. gemma*. But the specimen named *P. gemma* (typical *gemma* form) (Soot-Ryen 1966, No. 8, Plate 1) will probably prove to be a specimen of *P. atlantica* (compare the photograph with figures 79*a*, *c*, 84*a–d*).

Good descriptions of the shell characters have been given by Verrill (1880, 1884), Jeffreys (1881) and Soot-Ryen (1966), and apart from confirming that the hinge is without teeth and that the lithodesma is relatively broad and short with its posterior margin excavated (figure 85*d*), further description can be limited to figure 84*a–d* which shows the range of variation shown by this species and compares one of the present specimens with previous records.

The anatomy has not been well described previously, although Soot-Ryen (1966) was able to indicate details of the gross anatomy by soaking dried specimens of the two extremes of form. While the general morphology of *P. gemma* is similar to that of *P. densicostata*, *P. atlantica* and other verticordiids, there are various differences of degree (figure 86*a*, *b*). Thus the pedal aperture of *P. gemma* is more extensive than either of the latter two genera and the mantle tissue in the region of the apertures is not thickened to the same extent although the arrangement of

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† See Soot-Ryen (1966) and appendix 1 for taxonomic history.

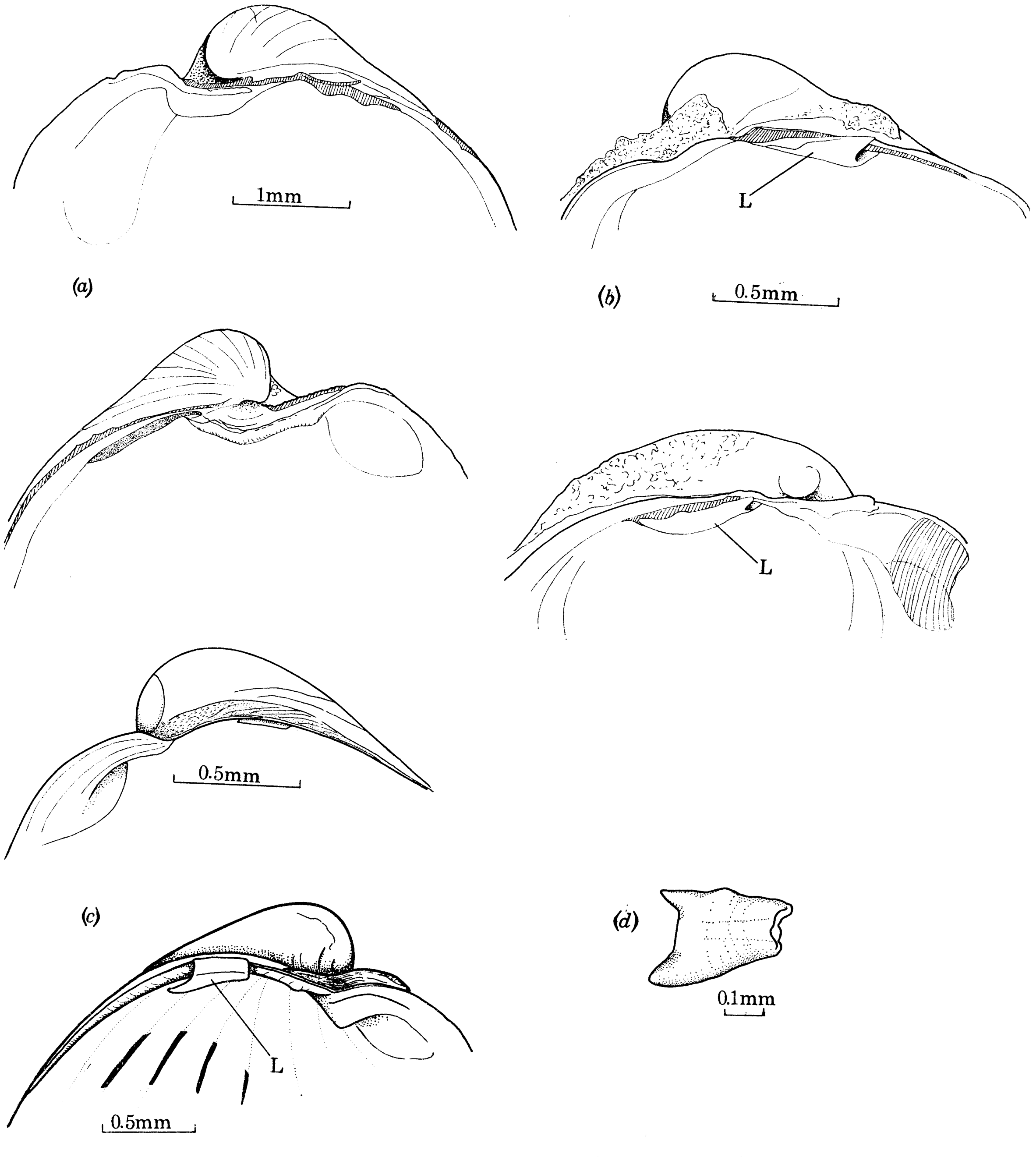

Figure 85. *Policordia gemma*. Lateral view of the hinges of the right and left valves of U.S. National Museum specimens: (*a*) no. 63237 labelled '*L. insculpta*'; (*b*) no. 63234 labelled '*L. gemma*'; (*c*) hinges of left and right valves of different shells taken at station 85 (*Chain*, 5 July 1965); (*d*) ventral view of lithodesma.

tentacles is the same. There are five tentacles adjacent to the exhalent aperture and as many as twenty around the inhalent aperture. The tentacles are more delicate than those of *P. atlantica*, those around the inhalent aperture are typically and finely papillate but unbranched (figure 87*a*). The musculature of the tentacles differs from that described for *P. atlantica* in that there is an asymetrical muscle block below the epidermis at the base of the tentacle on the side next to the aperture. In this it resembles many other verticordiids, although the muscle is poorly

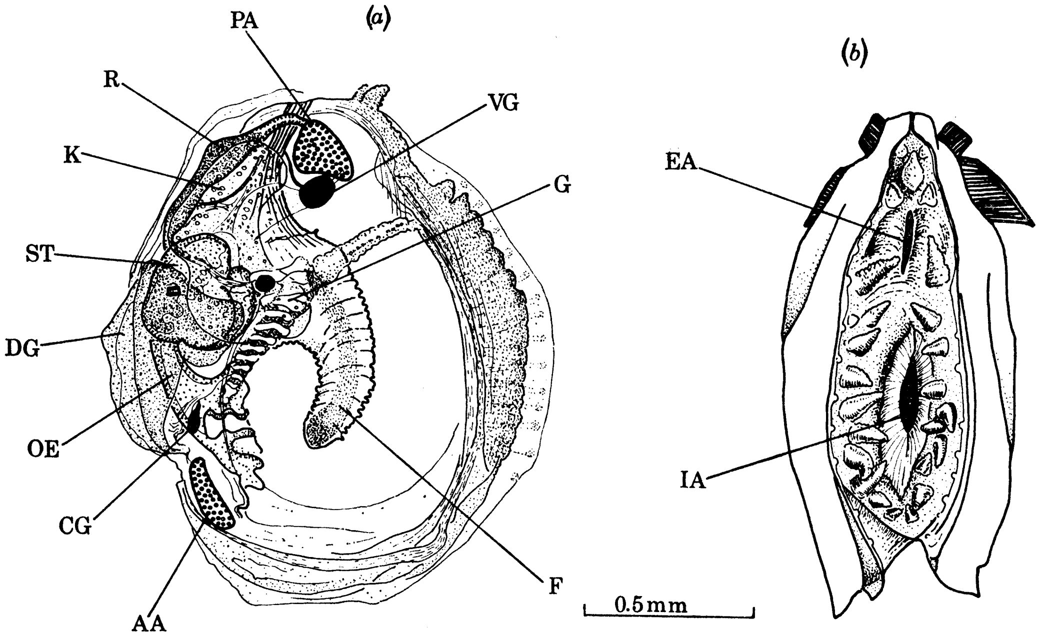

Figure 86. *Policordia gemma*. (*a*) Lateral view of whole mount to show details of the soft part morphology; (*b*) posterior view of apertures of the same specimen.

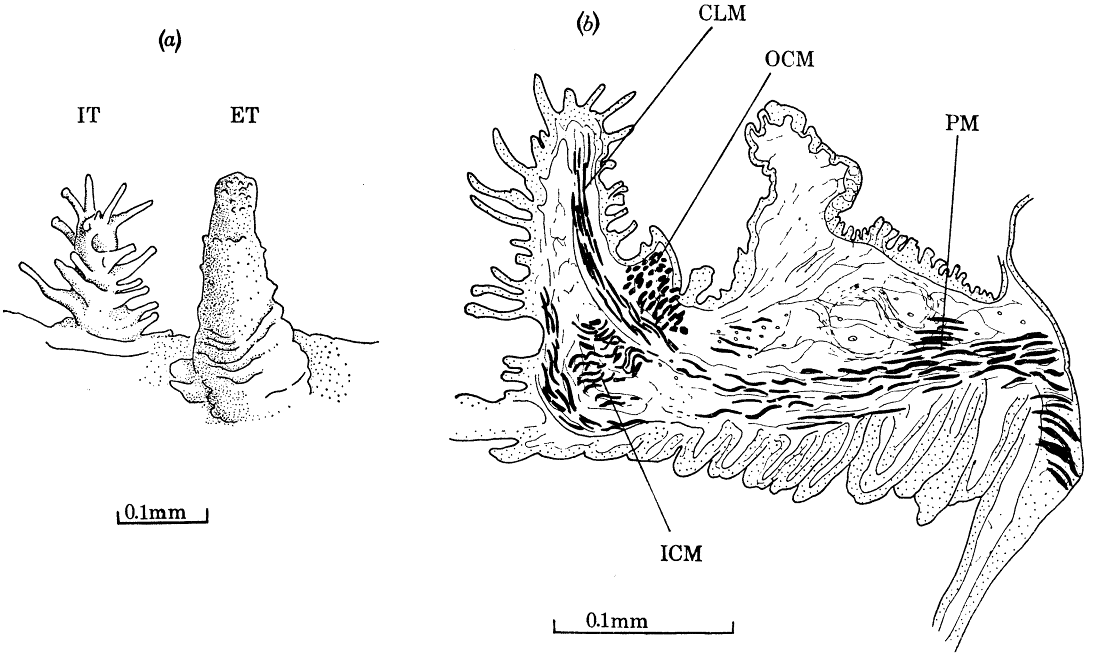

Figure 87. *Policordia gemma*. (*a*) Lateral view of whole mount of the ventral-most exhalent tentacle and dorsalmost inhalent tentacle of right side; (*b*) longitudinal section through an inhalent tentacle and mantle edge.

developed compared with that of *L. abyssicola*. As in other species the longitudinal muscles of the tentacle are derived from the pallial musculature (figure 87*b*). At the base of the tentacles there are two circular bands of muscles encircling the aperture; one band, the larger, to the outside and the other band to the inside of the main longitudinal muscle of the tentacle. The mantle valve is not as extensive as it is in other species of *Policordia*. The adductor muscles are

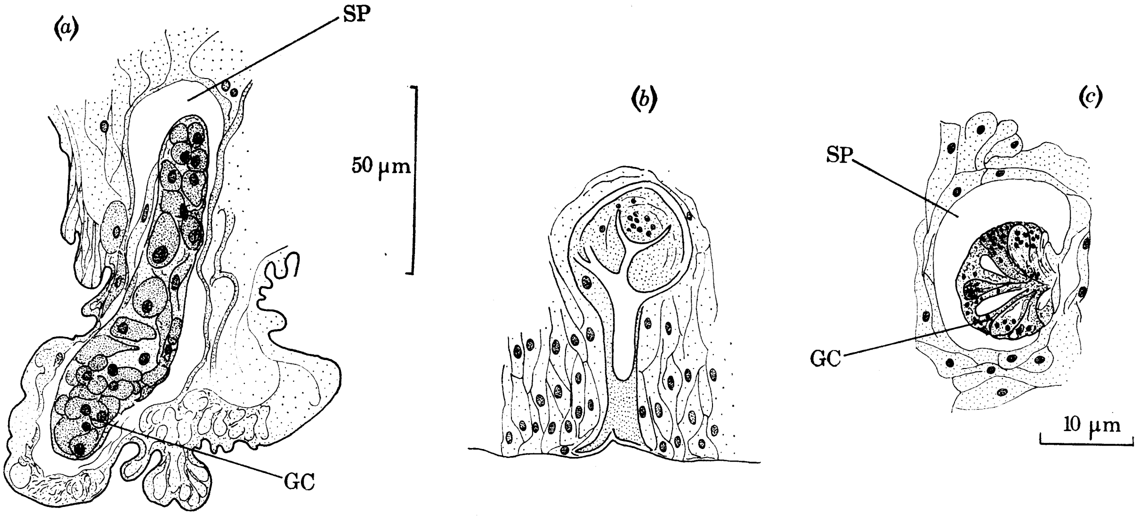

FIGURE 88. *Policordia gemma*. Radial mantle glands. (*a*) Longitudinal section; (*b*) whole mount of terminal duct region; (*c*) transverse section.

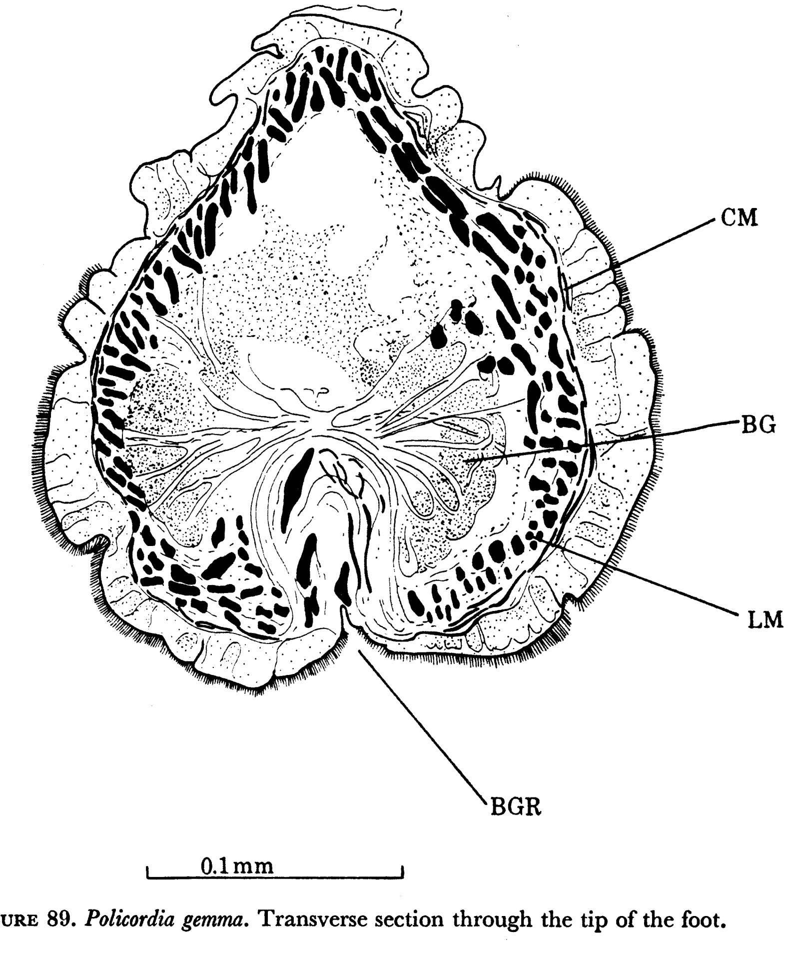

FIGURE 89. *Policordia gemma*. Transverse section through the tip of the foot.

relatively larger than those of *P. atlantica* and *P. densicostata*. The visceral ganglion although large is smaller in diameter than the diameter of the posterior adductor muscle.

Approximately twenty radial mantle glands are present in the left and right margins of the mantle. The glands are arranged approximately equidistant to each other from a point immediately ventral to the anterior adductor as far as the ventral limit of the posterior adductor. They consist of an elongate cylindrical rod of densely staining gland cells with a flask shaped terminal part that opens at the outer face of the sensory lobe. In cross-section the column of glandular cells is almost surrounded by an annular cavity within the parenchymatous cells of the mantle tissue. The cells themselves appear to have a central flask shaped cavity that opens to a duct running the length of the gland on the side that is attached to the parenchyma (figure 88*a–c*).

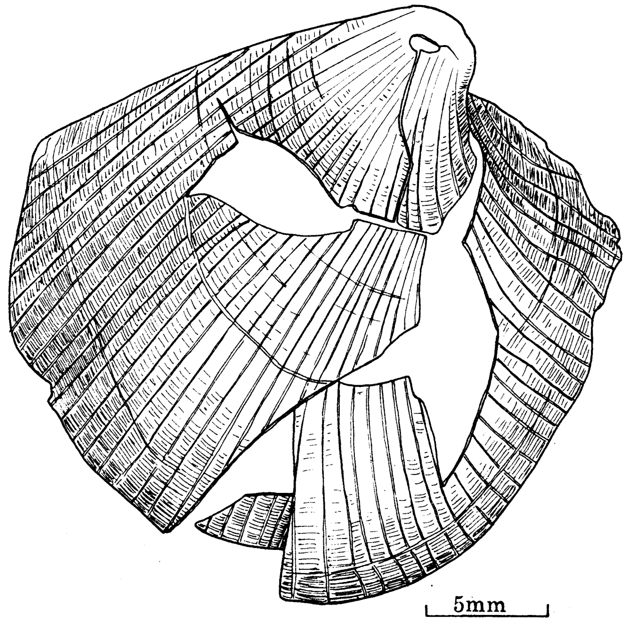

FIGURE 90. *Policordia papyracea*. Lateral view of right valve of the type specimen from the British Museum (Natural History).

Only the inner demibranchs are present, the gill axis being attached to the body close to its junction with the mantle. The filaments are very short and lie almost horizontally across the mantle cavity, there is a well-marked marginal groove between the ascending and descending lamellae.

The tips of the first two or three anterior ascending filaments are attached to the body by a membrane but, posterior to this, the ascending filaments are free of the body (or, possibly, in life attached by ciliary junctions). The gill filaments do not extend far beyond the posterior limit of the foot (figure 86*a*), however the axis joins with the septum between inhalent and exhalent apertures where together they form a tissue partition between lower mantle cavity and posterior part of the hypobronchial cavity.

The buccal cavity is a short but wide posteriorly directed funnel; the lips and palps are not greatly extended in the preserved specimens. The gut is similar to that of other species of *Policordia*. The kidney is very extensive, each side being broadly bilobed. The anterior lobe extends beyond the level of the anterior margin of the foot. The foot is anteriorly directed with a slight indication of a heel and a well developed byssus gland and groove (figure 89).

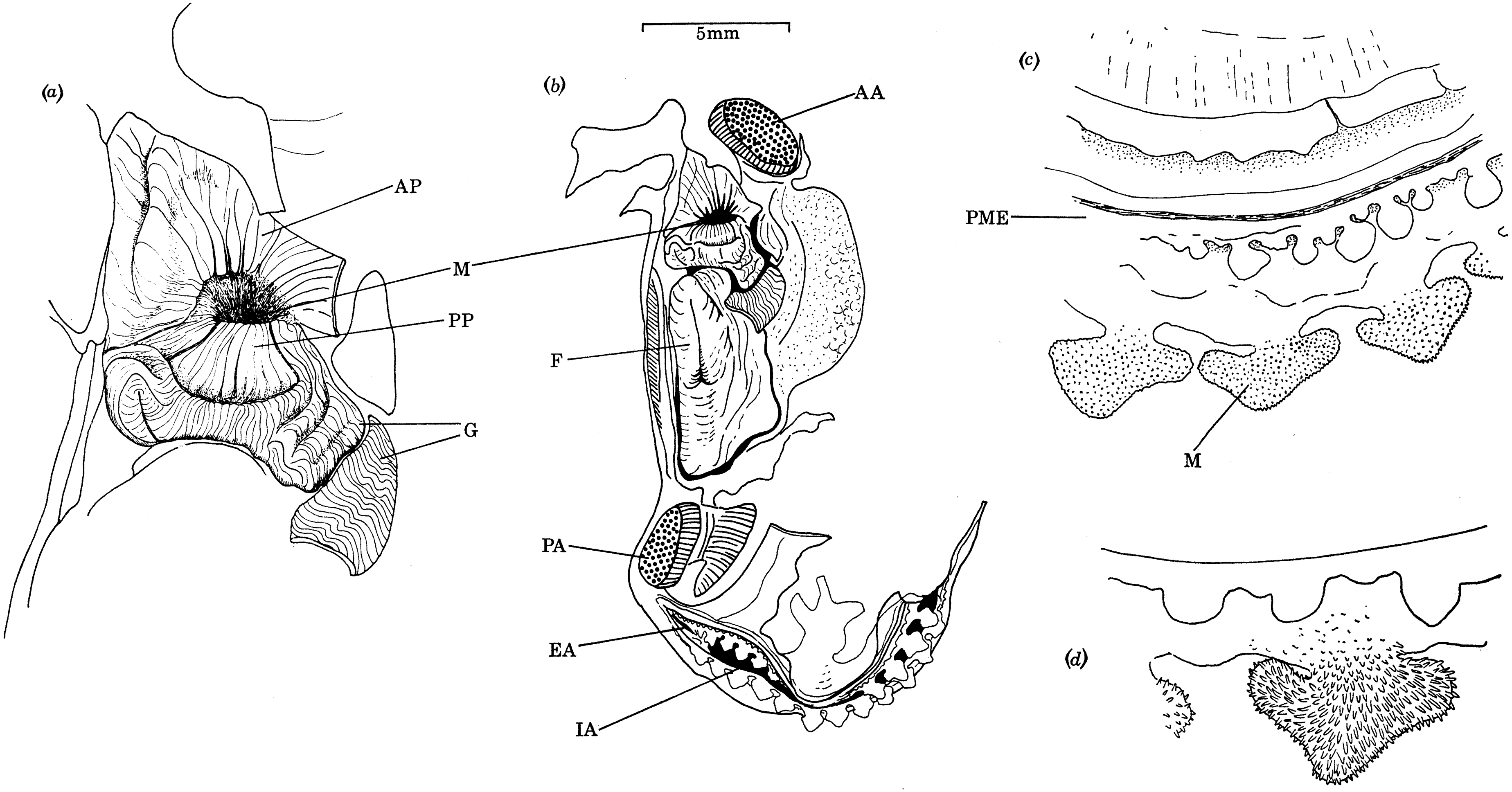

FIGURE 91. *Policordia papyracea*. (*a*) Ventral view of mouth region; (*b*) ventro-lateral view of the remaining soft parts of the type specimen; (*c*, *d*) detail of the mantle and tentacles of the inhalent region.

Policordia papyracea (Smith 1885)

Distribution:

South Australia

This species has not been recorded in our samples from the Atlantic, nevertheless, for completeness we include new information on anatomy from the type material held in the British Museum. The shell of the type is large, thin and much broken, fragments show that the shell was much repaired during life. Although we have included a more accurate figure of the type (figure 90) nothing needs to be added to the description given by Smith (1885).

The tissues are incomplete, the gills having been removed, presumably by Ridewood (1903) for his studies on the bivalve gill.

The anatomy is much the same as that of other species of *Policordia* (figure 91*a*, *b*). There is a small exhalent aperture and a very large inhalent aperture, without siphons. The inhalent aperture is flanked by tentacles and to the outside of these and extending along the entire free edge of the mantle are fringing papillae of the middle sensory lobe. These papillae vary in size and approximately alternate, one small with one large (figure 91*c*, *d*). Between the inhalent and exhalent apertures are three small, pointed, unbranched tentacles. The 24 tentacles that flank the inhalent aperture are broadly trilobed, their bases being joined by a ridge, the broad surface of the tentacle being parallel to the mantle edge. The inhalent tentacles are covered with fine, unbranched, pointed papillae (figure 91*c*, *d*).

The pedal gape is large and the region of fusion between it and the inhalent aperture is short (torn apart in the type specimen). The gill is well described by Ridewood (1903), who notes that, 'there projects, from the mantle just above the outer demibranch, a curious flap with a free lower edge'. This flap or ridge is the same structure that has been described in other species, e.g. *L. smidti* (figure 41). It should be noted that in this species as well as in *Euciroa eburnea* and *V. acuticostata* there are interfilamentar junctions between the axis and gill margin (Ridewood 1903).

The mouth is typically large and funnel-like with the lips and palps more pronounced than have been seen in any other species so far examined. Ridges are present on the lower lips but these are probably not homologous with those of other eulamellibranch palps, but appear to be a continuation of the folds of the oesophagus, those on the palp region lying at right angles, parallel to the proximal groove, i.e. at 90° to ridges of the palps of eulamellibranchs (figure 91*a*).

Little can be seen of the internal anatomy, the foot being directed anteriorly and having a well-defined byssal groove (figure 91*b*).

Policordia jeffreysi (Friele 1879)

Material from:

						no. of specimens
*Chain**	29. vi. 68	sta. 76	39° 38.3′ N, 67° 57.8′ W	2862 m	E.S.	1

Distribution:

Norwegian Sea, West of Spitzbergen, Woods Hole–Bermuda Traverse, 1198–4429 m

* See additional records on p. 531.

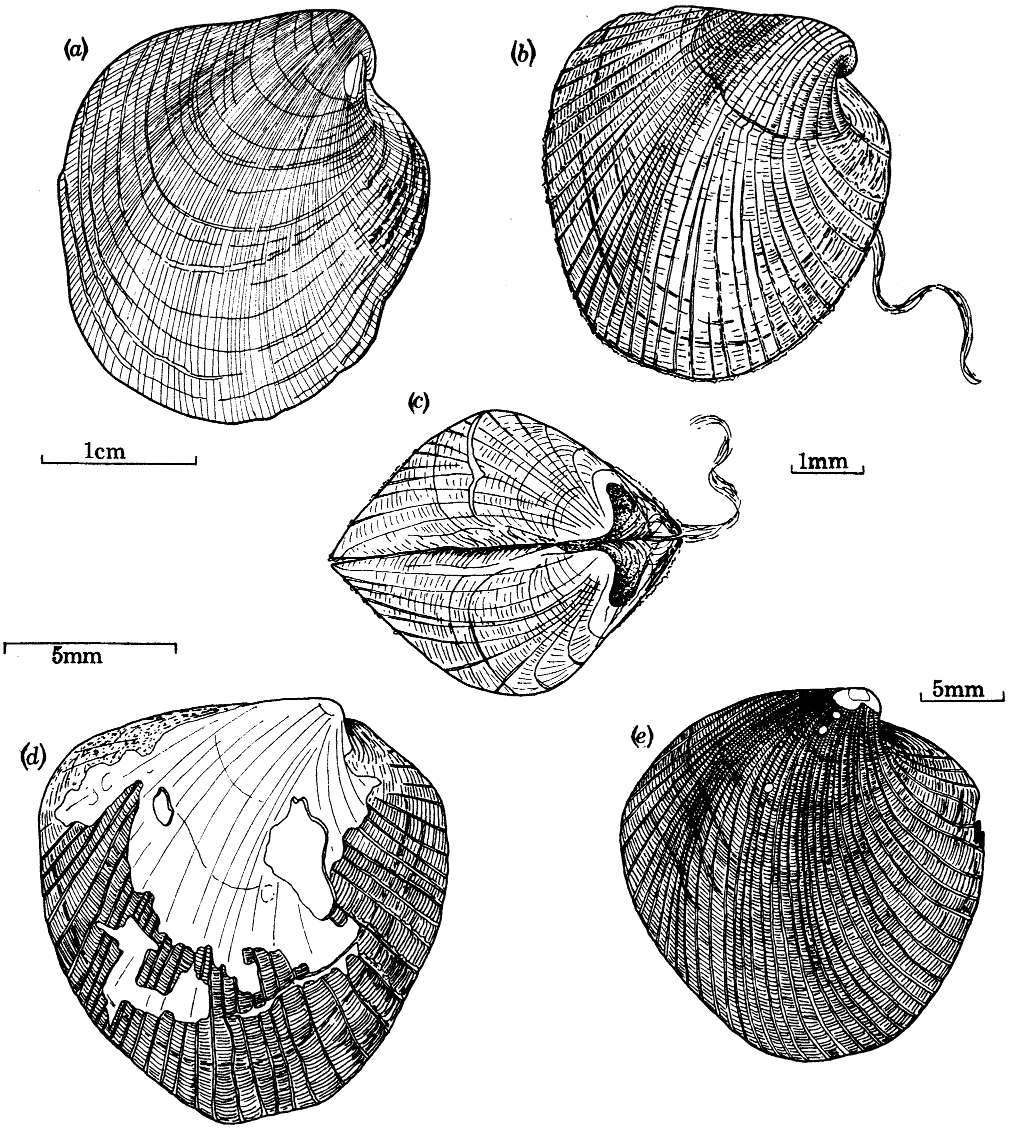

FIGURE 92. *Policordia jeffreysi.* (*a*) Lateral view of right valve of type specimen no. 21265 from Bergen Museum; (*b*) lateral view of right valve of a specimen taken at station 76 (*Chain*, 29 June 1968); (*c*) dorsal view of shell of specimen drawn in (*b*). *Policordia radiata*; (*d*) lateral view of right valve of specimen no. 97137 from the U.S. National Museum. *Policordia alaskana*; (*e*) lateral view of right valve of specimen no. 679071 from the U.S. National Museum.

The present specimens are identical to the type material from the Bergen Museum (no. 21265) (figure 92*a*, *b*). The Bergen specimen is distorted at a point on the anterior ventral margin where the byssus is probably extended. *P. jeffreysi* is characteristically inflated with large incurved umbos and a deep lunule, this is in contrast to *P. alaskana* and *P. radiata*, which have similar trapezoidal shapes but which have a much less pronounced umbo and are not so inflated (figure 92*d*, *e*). No hinge teeth are present in *P. jeffreysi*, the lithodesma is moderately elongate and broad and posterior to the umbo (figure 93). The posterior edge is slightly excavated (length 4.8 mm).

Only one specimen is available but it was possible to remove the body for examination. Unfortunately this proved to be considerably damaged and distorted and only limited details of the gross morphology could be determined (figure 94*a*, *b*). This is similar to that of other species of *Policordia*. The inhalent aperture, together with its surrounding tentacles dominates the mantle. Some 28 squat papillate tentacles are present, fringing the aperture laterally and 3 simple conical tentacles lie dorsal to the exhalent aperture (figure 94). The sensory lobe of the mantle is papillate along its entire length. Other features of note included the well-defined membrane between gill, mantle and the junction between inhalent and exhalent apertures, and the very large number of byssal threads which presumably were sufficiently strongly attached both to the substrate and the byssal axis within the byssal groove as to tear the foot apart when the animal was removed from its substrate on collection. This species has by far the best developed byssus of all here examined.

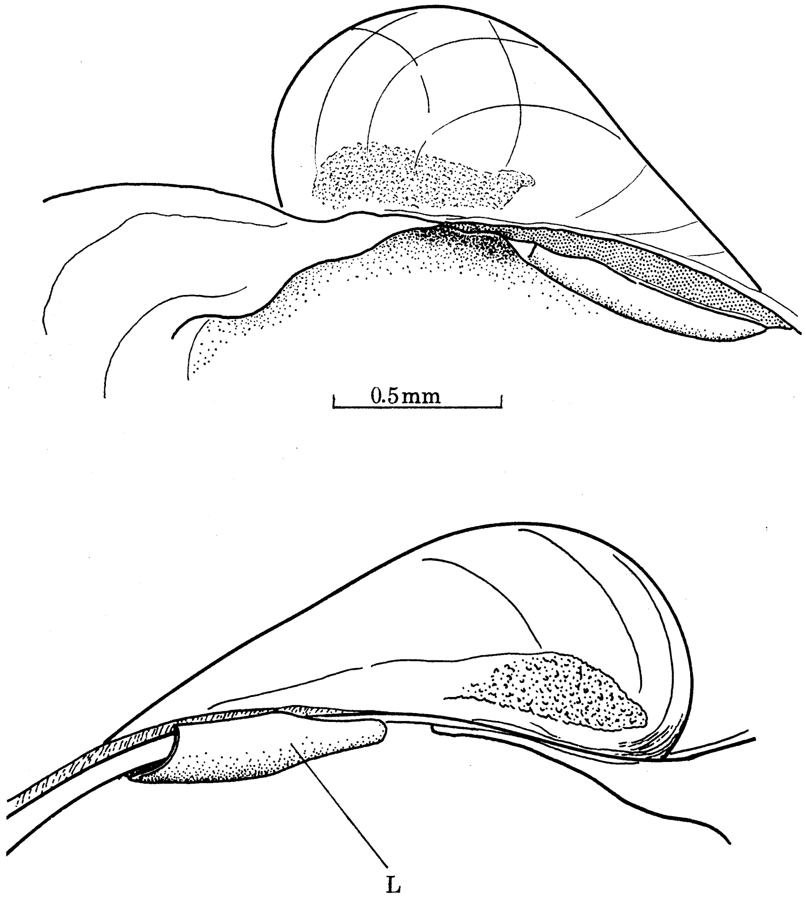

FIGURE 93. *Policordia jeffreysi*. Lateral view of hinge region of both valves of specimen taken at station 76 (*Chain*, 29 June 1968).

Policordia insolita n.sp. (figures 95, 96)

Material: Holotype: M.C.Z. 272676

						no. of specimens
Chain	4. v. 66	sta. 103	39° 43.6′ N, 70° 37.4′ W	2022 m	E.S.	2
Atlantis II	18. xii. 66	sta. 131	39° 38.5′ N, 70° 36.5′ W 39° 39.0′ N, 70° 37.1′ W	2178 m	E.S.	8
Atlantis II	17. v. 68	sta. 191	23° 05′ S, 12° 31.5′ E	1546–1559 m	E.S.	1

Shell thin, white, inflated, fragile; left valve slightly larger than right and overlapping posterior dorsal margin; umbo rounded, incurved, anteriorly directed and nearly central in position; no surface ornamentation, shell markings consist of irregular concentric growth lines; posterior dorsal margin straight, sloping ventrally to the more or less evenly rounded posterior margin; dorsal anterior margin concave, meeting the relatively straight vertical anterior margin in a well-defined rounded angle; ventral margin moderately curved. Hinge, without teeth; lithodesma short and broad. Specimens range in size from 0.95 mm to 1.7 mm total length.

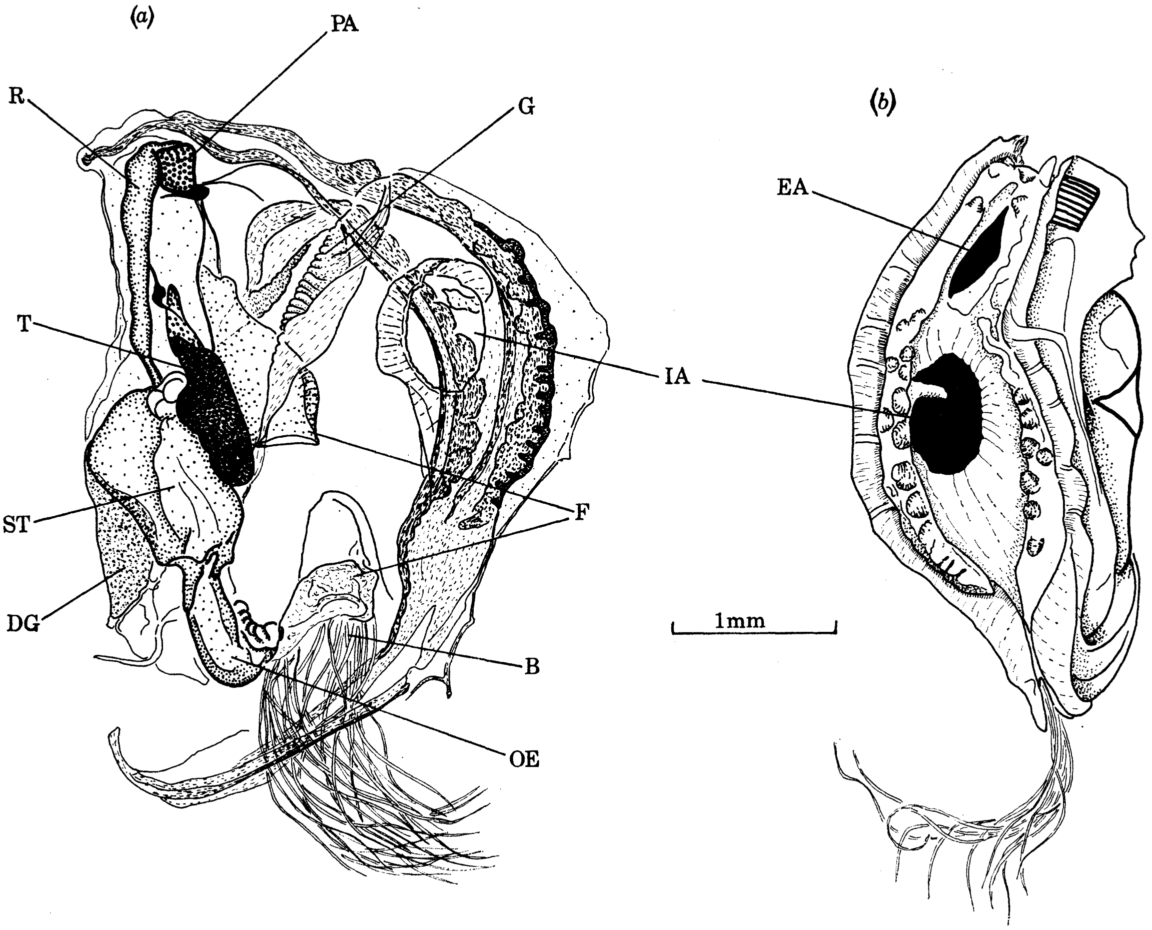

Figure 94. *Policordia jeffreysi.* (*a*) Lateral view of whole mount to show anatomy, note that the specimen is very distorted and that the foot (F) is broken in two; (*b*) posterior view of apertures of the same specimen.

The mantle of *P. insolita* is less modified than that of any other verticordiid examined. Only two pairs of radial mantle glands are present, one on each side at the dorsal and ventral limit of the inhalent aperture. The inhalent and exhalent apertures are not siphonate, nor are they surrounded by tentacles. The periphery of the inhalent aperture is slightly thickened and with a row of small rounded papillae that look similar to those of the tentacles of other verticordiid species. There is no inhalent valve. The pallial musculature is not well developed and the adductor muscles are very small. The oval posterior adductor muscle is particularly small in cross-section, being about one quarter the area of the crescent shaped anterior muscle.

The much reduced gills consist of the inner demibranchs only. These have a relatively broad descending lamella which hangs vertically from the axis, and a narrow ascending lamella lying in the horizontal plane. A marginal groove is present at the junction of the lamellae, interfilamentar connexions being restricted to the region of the groove and to the inner margin of the ascending lamella. Posterior to the foot the margins of the ascending lamellae are joined together by ciliary junctions and the gill axes lie close together. Thus, the hypobranchial cavity in this region resembles a conical basket, circular in cross-section and almost entirely surrounded by gill filaments (figure 95*c*). The gill filaments are few in number, each demibranch comprising 14–18 filaments. The gill axis is unusual in that it lies close to the dorsal margin of the body, whereas in most other verticordiid species the axis runs horizontally across the centre of the body. There are very few muscle fibres in the gill of *P. insolita*.

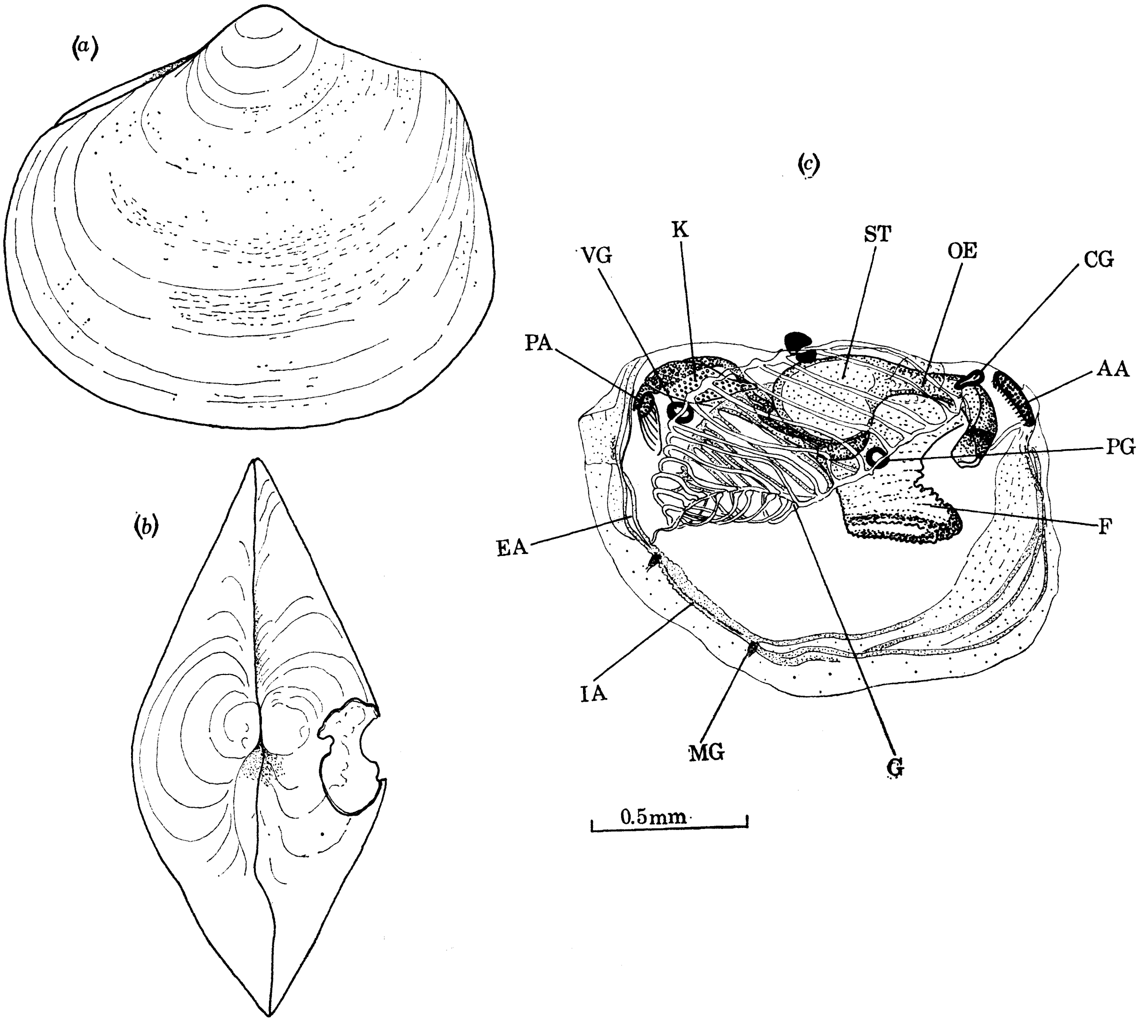

FIGURE 95. *Policordia insolita*. (*a*) Lateral view of right valve; (*b*) dorsal view of shell; (*c*) lateral view of whole mount to show details of soft part anatomy.

The upper (anterior) lips are broad and together with the rudiments of the palps form a posteriorly directed hood over the mouth. The lower (posterior) lips are little developed and fuse laterally with the anterior palps forming a short oral groove. No palp ridges are present, but judging from the folding of the palp margins of preserved specimens, the hood is capable of considerable extension. The inner surfaces of the palps and lips are heavily ciliated, the outer surface of the central region of the lips has tissue connexion with the anterior margin of the mantle.

The gut follows a course similar to that described in *L. abyssicola*, however the histology and internal morphology differ considerably from this species. The oesophagus is cylindrical with no marked internal ridges and no surrounding layer of thick muscle. The cells lining the oesophagus bear long cilia. The stomach differs from *L. abyssicola* in that it is only partly lined with scleroprotein which is not thrown into deep ridges and convolutions (figure 96*a*), only the dorsal, ventral and left sides of the stomach which are lined with a gastric shield which bears one mid-dorsal tooth and a thickened area to the left perimeter of the style sac. Beneath the cuticle the regular cuboid cells are filled with golden granules, typical of gastric shield epithelia. The right side of the stomach consists of a layer of tall cells which contain a few granules and are ciliated. Externally no dorsal hood can be seen, but serial sections show that there is a pit in the thickness of the dorsal epithelium to the right of the tooth which may represent the rudiment of the dorsal hood. The ciliated surface has a few ill defined grooves on the right side. The surrounding muscle layer, which is a feature of the stomach of other verticordiids, is extremely tenuous in *Policordia insolita*. The combined mid gut and style sac is small and arises from a mid-ventral point and that the sac-like stomach extends beyond the level of the mid gut aperture. The style sac is lined with typical cuboidal ciliated cells. The course of the hind gut is posterior and then dorsal before expanding to form a chamber immediately anterior to the posterior adductor and from which a short narrow rectal region passes over the mid dorsal surface of the posterior adductor muscle terminating at the anus.

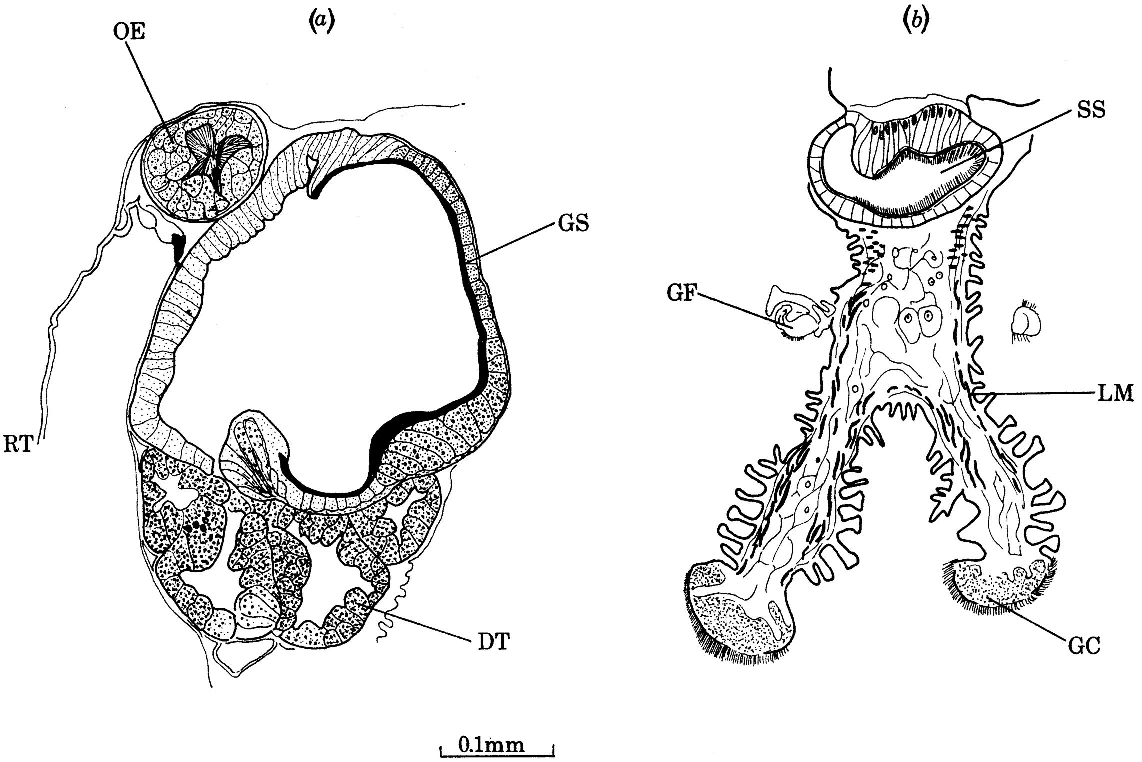

FIGURE 96. *Policordia insolita.* (*a*) Oblique, transverse section through stomach, oesophagus and digestive gland; (*b*) oblique, transverse section through foot and combined mid gut and style sac.

The digestive diverticula are lateral and ventral to the anterior part of the stomach. The digestive ducts are very short and open ventrally close to the junction of oesophagus with stomach. On each side close to the origin of the ducts there is a branch of the diverticula that extends dorsally and posteriorly level with the top of the stomach.

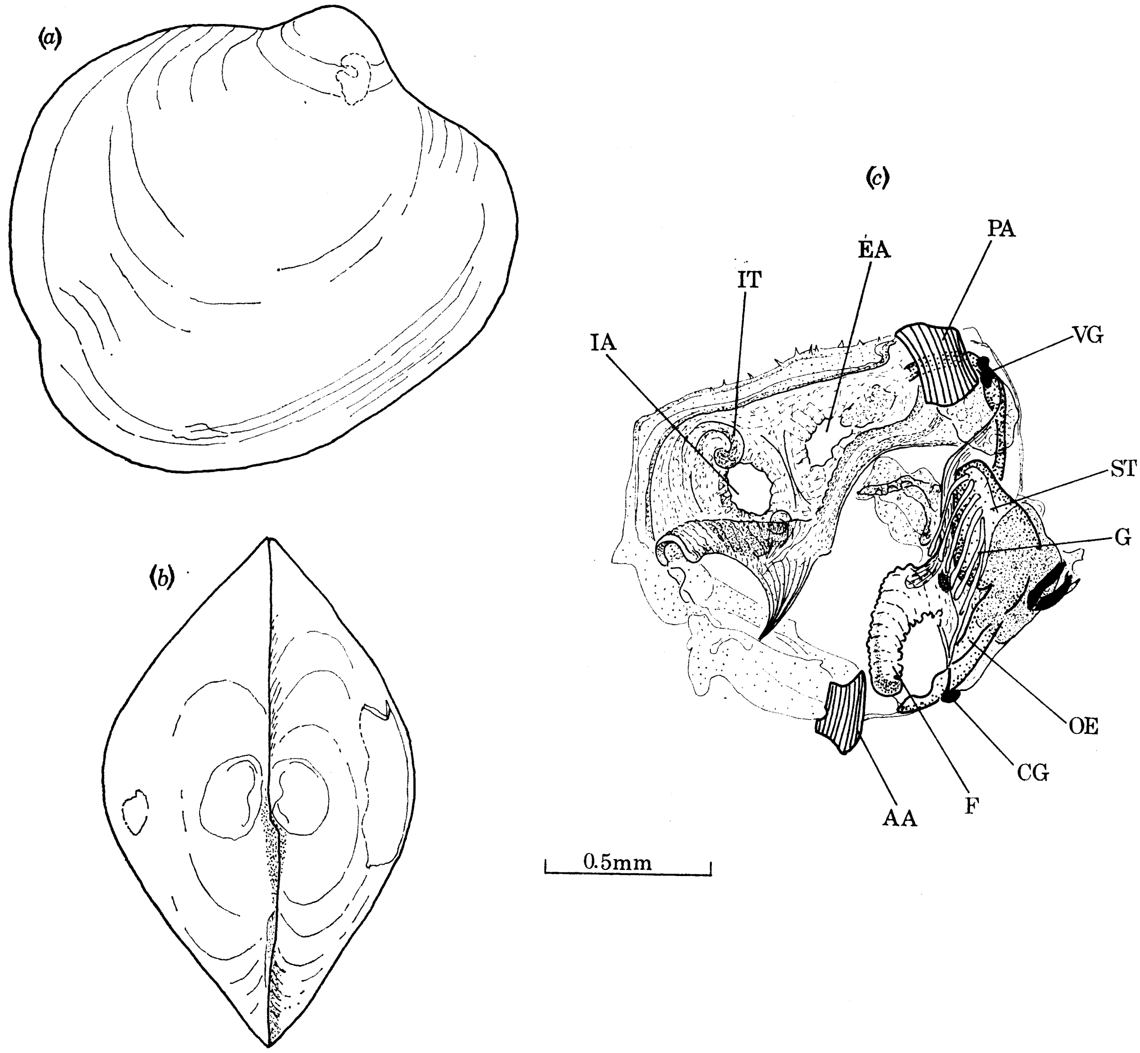

FIGURE 97. *Policordia laevis.* (*a*) Lateral view of right valve of shell; (*b*) dorsal view of shell; (*c*) lateral view of whole mount to show details of the soft part morphology.

The kidney is remarkably simple for a verticordiid, comprising of two small simple undivided sacs, one on each side of the hind gut above the visceral ganglion. These do not extend forward lateral to the stomach as in the case of many other species.

The anteriorly directed foot is relatively broad, as compared with the more cylindrical foot of most other verticordiids. It is deeply divided along the length of the sole, the groove presumably being homologous with the byssus groove of other species. No specimens have byssus threads, nor is there a central byssus gland at the posterior limit of the groove, nor are there gland cells internal to the deepest part of the groove. Instead, gland cells staining densely with acid fuchsin and similar in appearance to byssus gland cells of other species, are present peripherally along the length of each half sole immediately below the ciliated epithelium of the foot (figure 96*b*). There is no indication that these glands form a byssus but they may be adhesive. The foot is well supplied with muscles and is reminiscent of the divided foot of the Protobranchia. This, possibly, together with the lack of siphons, suggests that *P. insolita*, in contrast to other verticordiids, may be mobile. The ganglia are well developed and are subequal in size.

No specimens have developed gonads, and it seems likely that these are young of the species. Because of this, it may be that certain structures, such as tentacles and mantle glands, are not fully developed.

Policordia laevis n.sp. (figure 97)

Material: Holotype: M.C.Z. 272763

						no. of specimens
Atlantis II	20. ii. 67	sta. 167	07° 58.0′ S, 34° 17.0′ W 07° 50.0′ S	943–1007 m	E.S.	1

Shell, fragile, white, inflated, without ornamentation; left valve very slightly overlapping right dorsally and posterior to umbos; umbos large, inwardly directed and anterior; posterior margin of shell rounded and dorso-ventrally, broad; anterior margin, rounded, short; posterior dorsal margin convex, anterior dorsal margin deeply concave. No hinge teeth; lithodesma relatively large and broad. Irregular growth lines are present and these indicate that this specimen has been damaged some time before collection. The specimen measures 1.6 mm total length.

It was possible to extract the body from the shell (figure 97*c*). Although this was badly distorted, it revealed that *P. laevis* is similar in many respects to *P. insolita*. It differs in that the inhalent aperture is flanked on either side by an inwardly curled tentacle, which is minutely papillate. There are no tentacles adjacent to the exhalent aperture. The muscular lobe of the mantle is broad, well developed, but not extended as siphons; otherwise the mantle is similar to *P. insolita* and other relatively unspecialized species. The adductor muscles are moderately well developed, the posterior being much larger than the visceral ganglion, the latter not being greatly developed.

Other morphological features, namely, the gills, palp, lips and gut are basically the same as described in the preceding species. The foot of *P. laevis* is somewhat more elongate and vermiform with the byssal groove not so marked as it is in *P. insolita*. The specimen is without gonads.

Laevicordia horrida n.sp. (figures 98–100)

Material: Holotype: M.C.Z. 272761

						no. of specimens
Atlantis II	21. viii. 64	sta. 64	38° 46′ N, 70° 06′ W	2886 m	E.S.	2
Atlantis II	24. viii. 64	sta. 72	38° 16′ N, 71° 47′ W	2864 m	E.S.	1
Chain	29. vii. 65	sta. 76	39° 38′ N, 67° 57.8′ W	2862 m	E.S.	4

Shell white, small, fragile, globular, with very prominent slightly incurved umbos, anteriorly directed over a large, moderately defined lunule; shell slightly inequivalve, valve margins anterior and posterior to umbo, sinuous; left valve slightly overlapping right. Shells change somewhat in outline with increasing size, young specimens somewhat rectangular; posterior dorsal margin slopes upwards; older shells more rounded, especially posterior at limit of dorsal margin; posterior margin remains very broad; anterior margin of all specimens falls steeply from umbo; umbo large, anterior, incurved.

Shell ornamented with a dense covering of pointed spinules which, in small specimens, are

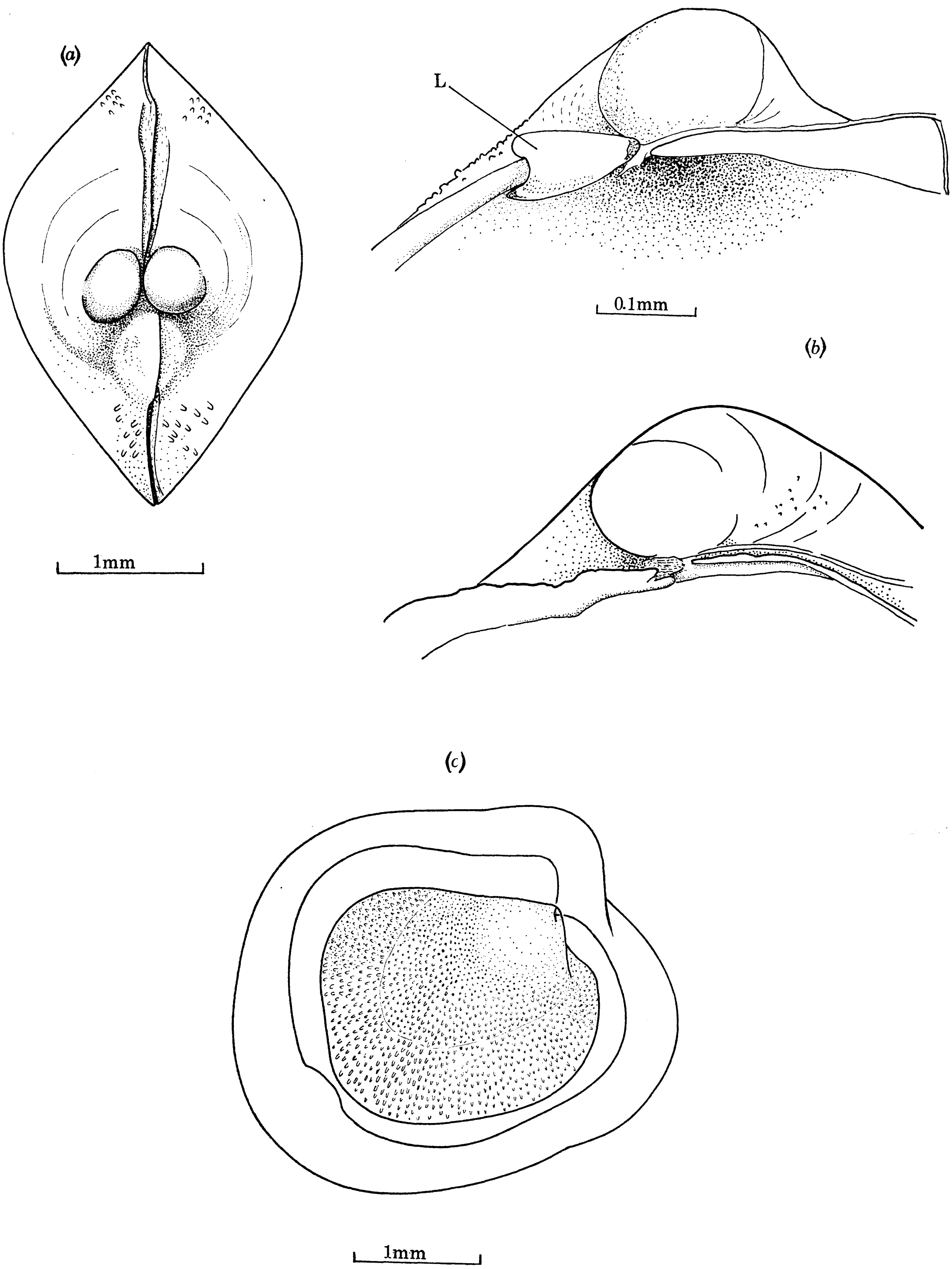

Figure 98. *Laevicordia horrida*. (*a*) Dorsal view of shell; (*b*) hinge region of left and right valves; (*c*) lateral view of right valve of three shells (two in outline) to show the degree of variation in shape.

not arranged in well-defined radiating rows, although the direction the pustules point follows the general generating curvature of the shell. In older specimens there is a tendency for the pustules to become more regular in their distribution although not to the extent of forming radiating rows. Occasional irregular concentric growth lines. Fine sediment usually adheres to the surface of the shell. Most shells have a well-defined, large, larval shell (0.47 mm total length). Hinge simple, with an ill-defined cardinal tooth on right valve below umbo; lithodesma posterior to tooth, relatively stout, broad, with an indented posterior margin; ligament similar to that of *L. abyssicola*. Specimens vary in length from 1.6 mm to 3.2 mm.

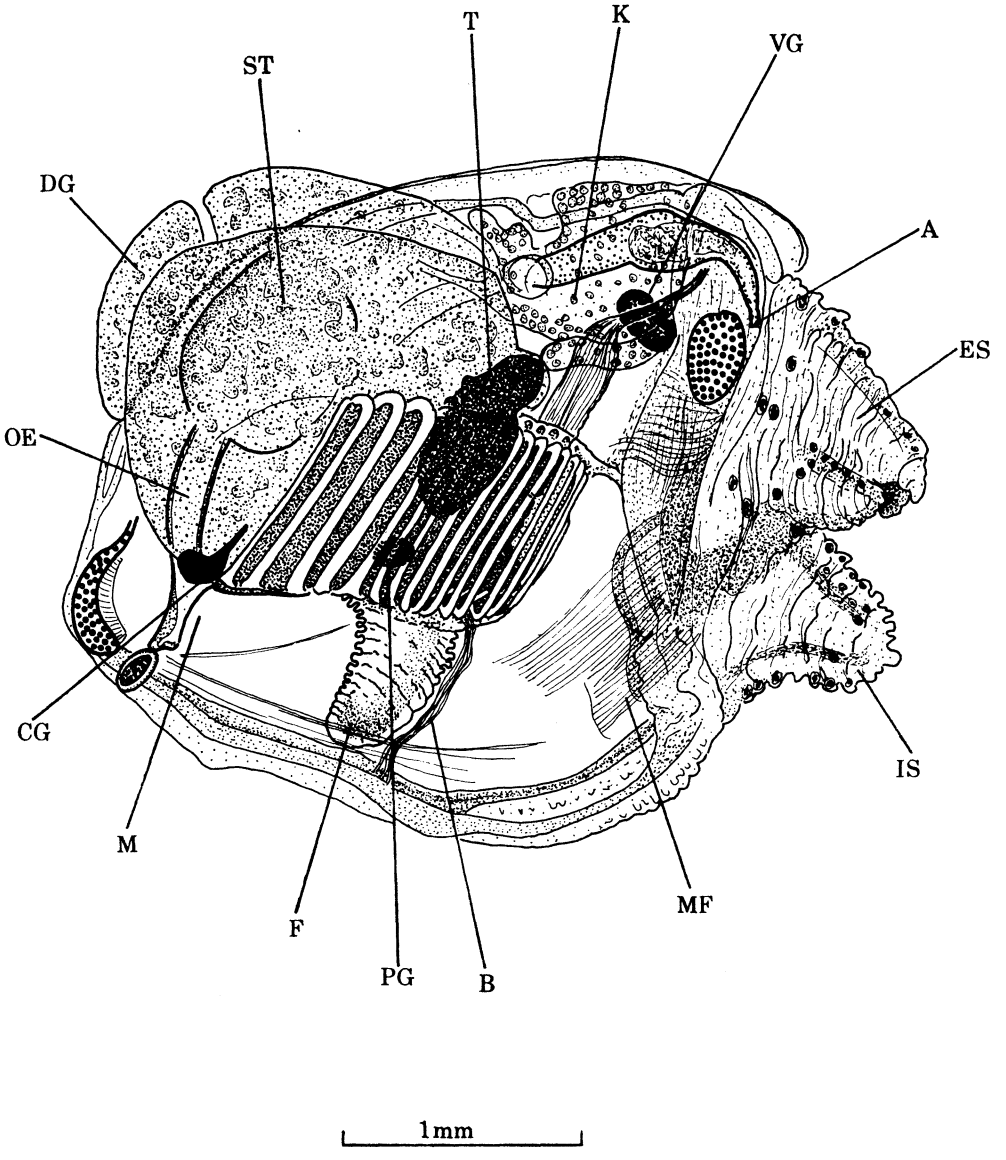

FIGURE 99. *Laevicordia horrida*. Lateral view of whole mount to show details of the soft part morphology.

The inner mantle lobes are fused to form both inhalent (IS) and exhalent siphons, the siphon being separate (figures 99, 100*b*) and capable of complete retraction within the shell. From their highly convoluted appearance in the preserved specimens, it seems certain that they are capable of considerable extension. In the retracted state the tips of the siphons are bent towards each other so that the apertures appear to be hooded. The exhalent aperture is protected by a short, broad, median finger-like process projecting from the dorsal side of the aperture. There is no obvious comparable process on the median ventral border of the inhalent siphon, however the lateral walls appear to be extended. The morphology suggests that these siphons may have evolved by fusion of peripheral tentacles or flaps such as are found in other verticordiids.

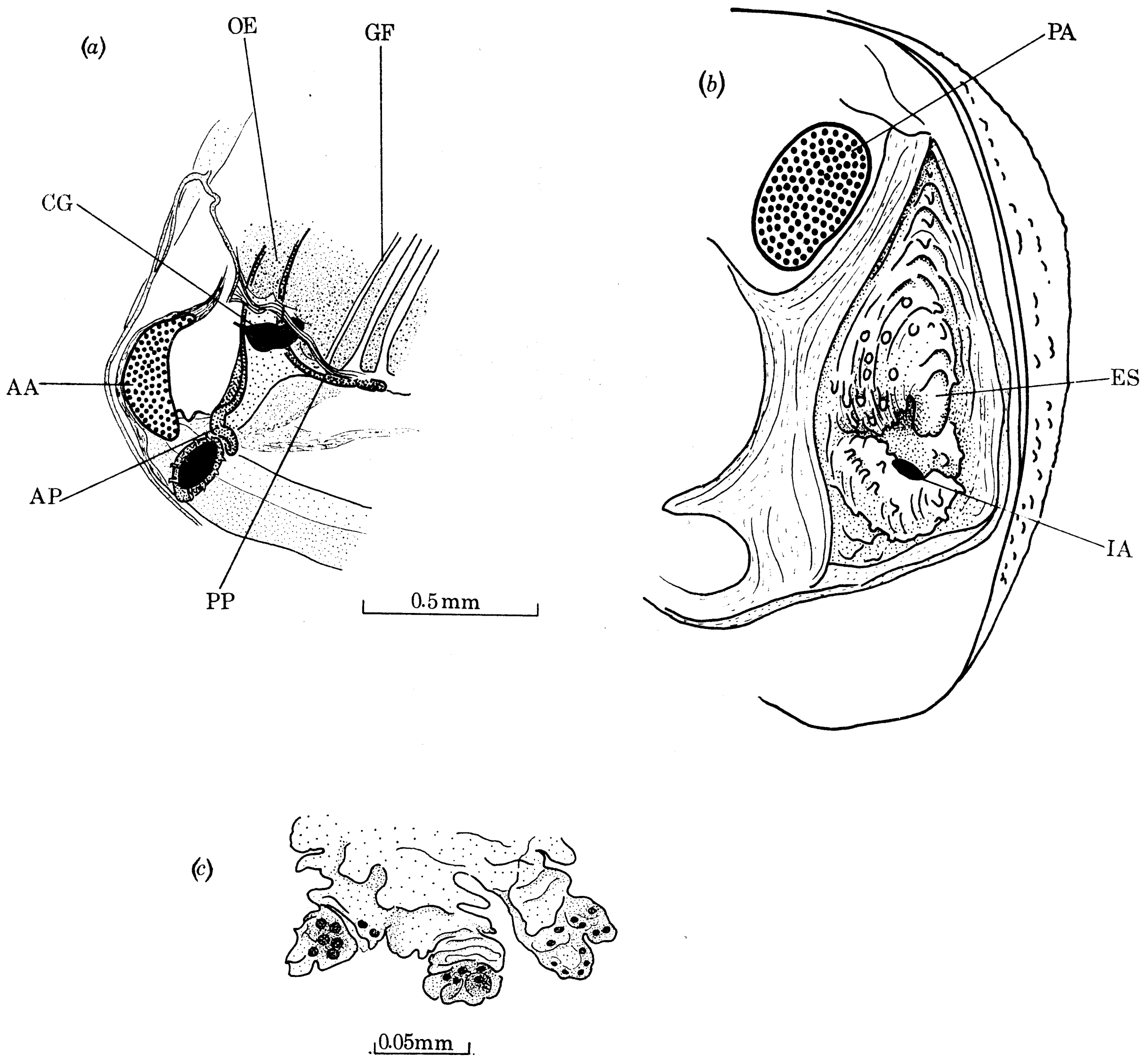

FIGURE 100. *Laevicordia horrida*. (*a*) Detail of the region of the mouth in lateral view. The oval object below the anterior lip (AP) is the skeleton of a micro-organism; (*b*) detail of the siphonal region; (*c*) enlargement of the papillae at the distal end of the inhalent siphon.

Laterally there is a broad, but thin, lamina of retractor muscles extending from the siphons into the mantle, those of the inhalent being longer than those of the exhalent siphon (figure 99). These retractors are continued within the siphons as a series of longitudinal muscle bundles lying between the epidermal layers. Externally the siphons are richly supplied with rounded papillae giving a warty appearance. The terminal cells of the papillae are secretory (figure 100*c*). There appears to be no regular arrangement of the papillae. The middle sensory fold of the mantle edge is not papillate except over a short distance where mantle fusion of the inner muscular layer divides the inhalent region from the pedal gape. Here, there is a long region of fusion and as a result the pedal gape for the most part is anteriorly directed. There are no multicellular radial mantle glands but a dense area of gland cells is present on the mantle to the inside of the base of the siphons and on either side of the fused region, posterior to the pedal gape. The adductor muscles are small, the posterior is oval in cross-section, the anterior is crescent shaped. There is a valve to the inside of the inhalent aperture but this is less well defined than that in other verticordiids such as *Lyonsiella abyssicola*.

The gills are much broader than those of other verticordiids presumably reflecting the difference in morphology of the inhalent aperture. They comprise the inner demibranchs alone. The individual filaments of the descending lamella of the demibranch are relatively long, thus the lamella lies vertically with the mantle cavity. The ascending filaments are much shorter, particularly those that are most anterior. Those of the posterior part of the lamella are longer and extend diagonally and posteriorly in the horizontal plane around the posterior part of the body, where by means of a ciliary junction they join with those of the other side. There is a well-defined groove along the ventral margin of the gill. Posteriorly the gill is attached to the septum between the siphons. Hyaline cells are present adjacent to the posterior adductor muscles and are very similar to those described earlier (p. 431). The mouth is a short, broad, posteriorly directed funnel. The lips are not well developed in comparison with other verticordiids, the lower lips are restricted to a narrow, mid-central rim, spanning the tips of the anterior gill filaments on each side, the upper lip lies close to the anterior adductor muscle and is attached to the mantle epithelium of this region (figure 100*a*). It is somewhat more extended than the lower with a few lateral cells that are probably homologous to palp tissue. The short oesophagus passes dorsally where it enters a large globular stomach. Because of the very extensive dorsal and lateral covering of digestive gland, stained whole mounts show little detail of the stomach. Ventrally, there is a very short combined mid gut and style sac and the rectal portion of the hind gut is expanded anterior to the posterior adductor muscle. Sections indicate that the stomach is similar to those described earlier, with a complete scleroprotein lining except for a ventral area between the openings to the mid gut, digestive gland and oesophagus which are in close proximity to each other. The style sac is lined with typical, dense, even cilia. The foot is relatively small, with a functional byssus gland similar to that described for other species. The three main paired ganglia are well defined with the visceral being the largest while the cerebral is relatively larger than in other verticordiids described in this paper. The kidney is broad, but does not penetrate far forward (figure 99). *Laevicordia horrida* is hermaphrodite, the testis lying close to the posterior ventro-lateral wall of the stomach, the ovary overlying the postero-dorsal wall of the stomach. The ova are large and relatively few in number.

Halicardia flexuosa (Verrill & Smith 1881)

Material from:

						no. of specimens
Atlantis II	16. v. 68	sta. 189	23° 00′ S, 12° 45′ E	1007–1014 m	E.S.	1

The single specimen consists of a complete shell together with the remains of the body enclosing a large and extensively damaged nematode. The shell details confirm but in no way add to earlier descriptions (see appendix for references). The anatomy of this genus has been described by Nakazima (1967) and does not greatly differ from that of *L. abyssicola*.

DISCUSSION

One conclusion, above all others, to be drawn from the present studies is that this, the least known of all bivalve families, provides a link between the filter feeding Eulamellibranchia and the carnivorous Poromyacea. It illustrates how the septibranch stomach may have been derived as well as the septibranch gill, possession of both being essential to the evolution of the carnivorous habit in bivalves. In addition, these studies also show that the family is highly specialized in ways peculiar to itself.

In its most extreme form the verticordiid is sessile, anchored by a few fine byssus threads, with a fan of spreading papillate adhesive tentacles surrounding the inhalent and exhalent apertures and lying at the surface of the sediment. The mantle cavity below might be regarded as an atrium, an extension of the buccal funnel, the latter being formed largely by the considerable enlargement of the lips. The gills, much reduced, become conveyer belts passing captured organisms to the mouth.

While the taxonomy and shell characters of the genera within the family Verticordiidae have been the subject of much early debate (see p. 402 *et seq.*), it is possible to refer species to seven genera on the basis of the form of the hinge and shell ornamentation and species described in this study are classified in this way. Unfortunately, studies on the anatomy of these genera in no way emphasize the division based on shell morphology, rather the reverse, and have shown a number of unusual features common to all the genera. These are: radial mantle glands and adhesive feeding tentacles around the apertures; greatly enlarged lips; greatly reduced gills and palps; muscular wall to oesophagus and stomach; persistence of the combined mid gut and style sac; enlarged kidney with an associated lacunal system.

The fragile inequivalve shell, the weak hinge line with few or no teeth and the presence of a lithodesma, are features characteristic of the Anomalodesmacea.

The majority of species have a trapezoidal shell outline, the shell itself being inflated. However there are exceptions, some (e.g. *P. laevis*) being rounded, others (e.g. *L. compressa*) being elongate and compressed. In general the shape of the shell may be correlated with the great development of the posterior apertures, the inhalent aperture occupying much of the posterior and ventral margins, and also with the shallow burrowing habit and the functional advantage in that the trumpet-shaped posteriorly directed mouth lies relatively close to the inhalent aperture.

Radial mantle glands appear to be unique to this family. They do not occur in *Laevicordia horrida*, a species without radial ornamentation, but conversely they are not universally present in species with rays (e.g. *L. subquadrata*). While in some species they appear to be associated with raised radiating lines (e.g. *L. formosa*), in others they are not so related. Close examination of the glands shows little more than a densely staining column of cells with a duct or ducts leading to an opening or openings on the middle lobe of the mantle. Usually sections show a haemocoelic space between the column of gland cells and the adjacent mantle tissue. They always occur in the region of the pedal gape and may extend to a point opposite the dorsal limit of the exhalent aperture. Their number varies from 2 to 30 or 40, depending on the species, and their number may increase with increasing size of the animal. The function of the glands is almost certainly to supply an adhesive fluid and most verticordiids are characteristically coated with a layer of adhering fine sediment. The secretion probably plays an important part in the ability of the verticordiid to remain at the surface of very floccular fine sediments. In this they may be assisted by the spreading of very fine byssus threads, although these are relatively few in number. We have no evidence that these are attached to large particles of sediment, the threads are tufted at their distal extremity and do not have adhesive disks common to attached bivalves such as *Mytilus*. In no specimen were they adhering to any material. Again, not all species of verticordiids have a functional byssus gland at the adult stage.

Adhesive secretions also play a major part in the collection of food. The inhalent region is well supplied with glandular papillae which are usually borne on fringing tentacles. Survival of the verticordiids in terms of protection and food gathering probably depends largely on their cryptic habit and in this the secretions of radial mantle glands and papillae are of paramount importance. The inhalent tentacles are much more papillate than those around the exhalent aperture. The tentacles vary in number in the different species. Normally there is a single tentacle dorsal to the exhalent aperture with one or two additional pairs lateral to the aperture. There are usually greater numbers of inhalent tentacles, the number varying from 4 to 15 pairs. While the exhalent tentacles are finger-like, the inhalent tentacles may branch in an arborescent fashion. Frequently branching is restricted to a single pair of lateral arms at the base of the tentacle and in the same plane as the mantle edge. The tentacle may be flattened and club-shaped, e.g. *P. papyracea* (figure 91). The tentacles like the shell are covered with a fine layer of adhering particles but the tips of the papillae with their complement of gland cells, each with its own duct, extend to the surface of this layer. The tentacles in *L. abyssicola*, and probably in all other species, extend across the surface layer of the abyssal sediment in life and passively wait for organisms to brush against them and to adhere to them. The musculature of the tentacles varies from species to species, but commonly it comprises of central longitudinal retractors with two or more associated longitudinal haemocoeles – presumably the tentacles extend by hydrostatic pressure. In addition there are peripheral longitudinal muscles at the base of the tentacle. These are frequently asymmetrically developed, those on the aperture side being larger. There is a good nerve supply to the tentacles (figure 11) and the visceral ganglia are particularly large and well developed in most species of the family.

The tentacles with adhering food contract and move inwards into the inhalent aperture where they are wiped clean by the constriction of the inhalent aperture and valve – when the latter is present. Both apertures and valve are rimmed with circular muscles. The valve is found in many species and is an extension of the inner wall of the inhalent aperture. It may be asymmetrically developed with the dorsal (*L. abyssicola*) or ventral (*L. formosa*) side extended. At their simplest the margins of the inhalent aperture are minutely papillate, e.g. *P. insolita*, exceptionally the lateral margins are produced as broad flaps, e.g. *L. fragilis*, and in *Laevicordia horrida* they are joined to form a siphon. The exhalent aperture may also be flanked by lateral flaps, e.g. *P. densicostata*, but more frequently is siphonate, e.g. *L. subquadrata*.

Stomach contents indicate that the captured food consists of copepods, some 2 mm in length or less, and smaller radiolarian skeletons, etc. Little or no fine material is present in the stomach even in species with least developed inhalent tentacles. The captured material must either be passed down the gills or fall directly into the buccal funnel.

In all verticordiids the gills are reduced in size but within the family a trend can be seen towards even smaller size. With the exception of a few laterally compressed species such as *L. compressa*, in which at least one demibranch lies in the vertical plane, the gills of verticordiids lie in the horizontal plane, the filaments being very short and few in number. Interfilamentar junctions occur at the margins of the demibranchs and at the junction of descending and ascending lamellae. However, Ridewood (1903) in his description of the gill of *L. acuticostata*, a larger species than those described here, reports that there are multiple rows of interfilamentar junctions. Undoubtedly the simplicity of most verticordiid gills may be in part a reflection of the size of the specimens. The gill axis and the marginal groove of the inner demibranch form ciliated channels to the mouth. In cross-section the gill filaments are typical of most eulamellibranchs except that the lateral cilia are far removed from the latero-frontals. The frontal cells of many species are very large and regular in their arrangement.

It is well known (Allen & Sanders 1966, 1973; Sanders & Allen 1973; Allen 1971, 1973) that the respiratory surfaces of deep-sea bivalves are much reduced in comparison with shelf species, the oxygen requirements of the small abyssal species (few are greater than 5 mm total length) can probably be met by diffusion through their extensive epithelial surfaces. However, gills maintain an essential circulation within the mantle cavity and thus they are never so reduced or modified that there is no flow of water across them.

A series of stages can be assembled which illustrate an evolutionary sequence in the reduction of the gill from a hypothetical condition with two complete demibranchs on each side of the body. All verticordiids show some reduction of the outer demibranch and none of the species examined had an ascending lamella to the outer demibranch. Furthermore, in most of these species the descending lamella of the outer demibranch was present only posterior to the foot. Similarly the ascending lamella of the inner demibranch is much reduced although usually present, the filaments of the inner demibranch usually being much shorter posteriorly where they lie adjacent to the outer demibranch when this is present.

The gills in most species have a great depth of axis and well developed peripheral membrane attachments to body and mantle (figure 13). The gill axis is usually attached at the junction of body and mantle and in species with both demibranchs present the region may be fenestrated posterior in the kidney so that the hypobranchial cavities above each demibranch are united (figure 22). Apart from a small region posterior to the foot where ascending lamellae of the inner demibranchs are usually joined by a fused ciliary junction peripherally, the gills are joined to mantle, body and to each other by a tissue membrane. Sections indicate that the membranes are derived from the dorsal surface of the tips of the filaments and the marginal interfilamentar connexions. The membranes may be very extensive and the hypobranchial space large. Longitudinal axial muscles are well developed in many species (figure 60) and in some cases longitudinal muscles were noted below the abfrontal surface of the filament.

A species possessing only an inner demibranch consisting of the descending lamella of say 12 filaments, with well-developed membranes, e.g. *L. frielei*, must be considered to be close to the septibranch condition in general and the poromyacean condition in particular. The longitudinal axial muscles of the verticordiid may well be homologous with the outer septal muscles of the cuspidariid. However the verticordiid membrane is so tenuous and with so little muscle as to make consideration of homologies difficult at this stage and we would wish to defer detailed consideration of the evolutionary relationships of the septibranch septum until the publication of the complementary study on the Cuspidaridae and Poromyacidae of the abyssal Atlantic. However, it seems clear that the septibranch condition can be derived from the verticordiid gill.

In most species the mouth is posteriorly directed and trumpet-shaped. The funnel is formed by the enlargement of the anterior lips and sometimes, but not always, by similar enlargement of the posterior lips. The palps are greatly reduced forming a fringe approximately 6 cells deep at the lateral rim of the lip. Thus there are no sorting ridges of the type seen in other eulamellibranchs. There is one exception in the case of *L. compressa*, which still retains small palps which have five typical sorting ridges on the inner face of the anterior palps and not more than three on the posterior palps. As will be discussed below, the three laterally compressed species – *L. fragilis*, *L. formosa* and *L. compressa* – have anomalodesmacean features, the palps of *L. compressa* add support to the conclusion that the verticordiids (and septibranchs) can be derived from the eulamellibranchs and the Anomalodesmacea in particular. The inner face of the typical verticordiid buccal funnel is heavily ciliated and ridged, the ridges being a continuation of those on the oesophagus. It is doubtful whether there is any sorting in the region of the mouth. However, the presence of a ciliated tract to the inside of the inner mantle fold, together with the dense concentration of mucous cells on the mantle to the inside of the inhalent aperture, would indicate that rejection of material can occur and that pseudofaeces may be formed.

In one species, *L. formosa*, the buccal region is greatly modified, the central part of the lips having fused to form a hollow sac ventral to the mouth. The sac has an opening on each side from fluted lateral extensions of the lips which connect with the gills. Dall (1895) reports a somewhat similar condition in *Euciroa pacifica*. In this species the modification is less profound, with paired lateral sacs forming a buccal cavity but with the mouth central and with anterior and posterior lips on either side. The lateral sacs appear to be formed from the anterior (dorsal) palps which are adnate on the posterior face of the sacs. In addition Dall (1895) describes a central 'lappett' posterior to the mouth, but out with the buccal cavity, which is probably homologous to the tongue in *L. formosa* but which is now incorporated into the roof of the buccal sac. The only function that can be ascribed to the buccal sac is that it supplies an additional digestive facility. Evolution of additional digestive structures is well known in abyssal bivalves (Allen & Sanders 1966), these being advantageous when much of the food consists of refractile proteins. In this connexion it should be noted that the stomach in *L. formosa* is smaller than most other verticordiids examined and without an enlarged ridged sac like extension posterior to the mid gut and style sac opening. No food remains were seen in this stomach of specimens of *L. formosa*. However, in the closely related *L. compressa* food remains are relatively small in size comprising of the skeletons of unicellular organisms.

The verticordiid gut is remarkably similar to that of the septibranch families Cuspidariidae and Poromyidae. All are characterized by a muscular oesophagus and stomach, much reduced style sac leading to a short hind gut. The oesophagus is lined with a heavily ciliated epithelium. It is capable of considerable distension and food is presumably passed to the stomach by both muscular and ciliary action, the passage of bulky and often spiny organisms being lubricated by the product of the large numbers of mucus-secreting cells. The stomach is extremely large and in most species lined with scleroprotein. In most species examined it is little different from that of *Cuspidaria* (Yonge 1928; Purchon 1956; and personal observations) ciliation being restricted to a narrow region of the floor of the stomach between the opening to the mid gut and the oesophagus with short lateral extensions to the apertures to the digestive ducts. However, in the genus *Policordia* there is additional ciliation. In *P. atlantica* a dorsal ciliated tract extends from the oesophagus to the posterior extension of the stomach. This tract is also present in *P. densicostata* and *P. gemma* although in these species it is much more restricted, only extending a very short distance beyond the oesophageal entrance. In *P. insolita* the right side of the stomach is also ciliated with a few longitudinal grooves. This is also true for *L. fragilis*. In these species there is a tooth on the dorsal side of the cuticular lining which must be homologous with that present on the gastric shield of eulamellibranchs, in fact there is no reason for not supposing that the cuticular lining is homologous with the gastric shield (GS) of other bivalves. Unless a small pit close to the tooth in *P. insolita* can be very doubtfully homologized with the dorsal hood, no species possesses this structure. It must be noted that those species with ciliation on the dorsal and right side of the stomach do not have such a pronounced posterior extension.

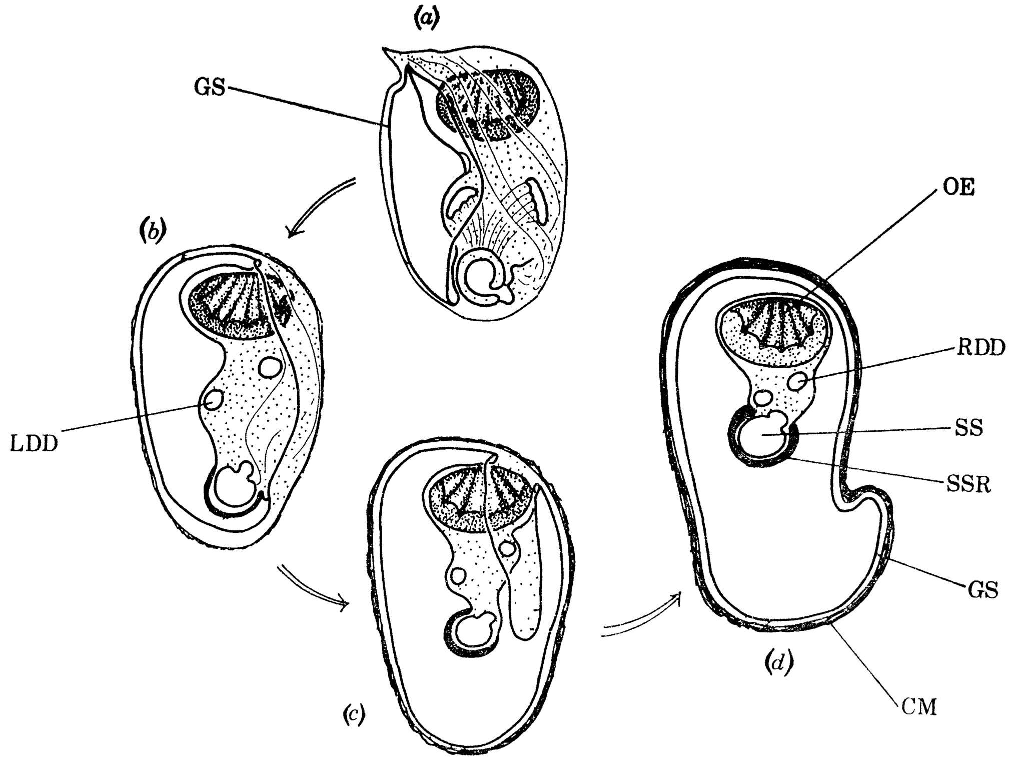

FIGURE 101. Diagram to illustrate the probable sequence of events in the evolution of the verticordiid stomach; (*a*) *Lyonsia*; (*b*) *Policordia insolita*; (*c*) *Policordia densicostata*; (*d*) *Lyonsiella abyssicola*. Stippled areas are ciliated.

Purchon (1956, 1958, 1960, 1963) from his extensive studies on the bivalve stomach recognized five different morphologies and then used this observation as the basis for a new classification of the bivalvia in which the Protobranchia and Septibranchia (Gastroproteia and Gastrodeuteia) were separated, as the Oligosyringia, from the remainder of the bivalves which he grouped together as the Polysyringia. The Polysyringia (Filibranchia + Eulamellibranchia) were divided into three groups, the Gastrotriteia, Gastrotetrartika and Gastropempta. Purchon (1956, 1963) argues that the Septibranchia could not have arisen from the Eulamellibranchia and that the Protobranchia and Septibranchia are closely related. This study on the Verticordiidae shows that, apart from the alimentary canal, they are eulamellibranch bivalves. Thus they have typical lamellibranch gills, byssus gland, non-divided foot, do not have a large statocyst dorsal to the pedal ganglion and do not have palp proboscides (one species, *L. compressa*, has typical palp ridges). Nevertheless, most species have a stomach which conforms to the description of Gastrodeuteia and, at first sight, the exceptional species with a ciliated right wall to the stomach (*P. insolita* and *L. fragilis*) are reminiscent of the condition of nuculoid protobranch bivalves (Purchon 1956). Furthermore, it has been shown (Allen & Sanders 1969) that the protobranch *Nucinella* has a stomach somewhat similar to the septibranch in that it is almost entirely lined with scleroprotein and which might be regarded as primitive. However, the stomach of *Nucinella* differs from that described here in that the exit to the intestine is posterior and that the style sac is ill defined. The Verticordiidae are characterized by a short ventral style sac which secretes a crystalline style identical to that of Lamellibranchia and not the soft particulate structure seen in nuculoid Protobranchia.

Because of the similarities of the Verticordiidae with the eulamellibranchs in general and the Anomalodesmacea in particular, further consideration has been given to possible derivation of the verticordiid stomach from that of the latter group (figure 101). There is much confusion in recent accounts as to the homologies and the naming of the parts of the 'Polysyringian' stomach (Graham 1949; Owen 1953; Allen 1954; Purchon 1958, 1960; Reid 1965). However, Reid (1965) gives a description of the common features of this stomach which is useful to this discussion. Thus, the oesophagus opens antero-ventrally; the apertures of the mid gut and style sac are posterior; digestive ducts open from the left and right walls; dorsally and to the left the stomach is lined with a gastric shield; antero-dorsally, and usually to the left, there is a broad opening to the blind conical outgrowth, the dorsal hood; two ridges, the minor and major typhlosoles, lead from the right and left side of the stomach to the midgut; a ciliated acceptance tract from the dorsal hood to the right of the minor typhlosole; a ciliated posterior sorting area between the latter tract and the right duct of the digestive diverticula.

It must be emphasized that the number of digestive ducts and the extent of the sorting areas in the lamellibranch bivalve is related to the size of the species. Thus small eulamellibranch genera such as *Thyasira* or *Montecuta* (Allen 1958; Purchon 1958) have two ducts and small sorting areas with few or no ciliated ridges. Consideration of the above list shows that the stomach of *L. fragilis* or *P. insolita* comply but for the lack of a dorsal hood and that the style sac and mid gut leave ventrally. We can see no reason why they cannot be derived from a simple gastrotetrartikan stomach. Note that in *L. fragilis* and *P. insolita* the muscles of the stomach wall are little developed. Further support is gained from a comparison with the stomach of the anomalodesmacean *Lyonsia californica* (Narchi 1968), for it is significant that in this species the style sac and mid gut are ventral, that the gastric shield is large, that there are only two openings to the digestive diverticula close to the oesophagus, and ciliary sorting surfaces are relatively simple considering that this is a relatively large species (> 20 mm total length).

In the evolution of the typical verticordiid stomach from the Anomalodesmacean condition, the following events would have occurred; the dorsal hood was lost, the stomach enlarged posteriorly, the gastric shield extended posteriorly and to the right side and the muscles of the wall of the stomach hypertrophied.

The digestive diverticula of the Verticordiidae are unusual in two respects; one, that the ducts are extremely short and two, that the tubules are not in the form of small, discrete, spherical units but are in a lobulated mass with interconnecting branches with a voluminous lumen. Nevertheless the tubule cells are no different from those of other lamellibranchs.

The hind gut is typically short, but is unusual in that the rectal region between the heart and the posterior adductor is inflated in all but one of two species. Most specimens have a mass of loosely aggregated material within the rectum. It seems possible that this may be retained here for further digestive processing, being reminiscent of the condition in other abyssal lamellibranchs such as *Abra profundorum* (Allen & Sanders 1966).

Other morphological features of note are the extensive kidney present in many species, and the unusual associated lacunal system for which we are unable to suggest any function.

Like the Anomalodesmacea in general, the Verticordiidae are hermaphrodite and produce relatively few, large, eggs. Of the species examined in this study, *V. triangularis* with approximately 100 eggs present in a specimen 3.6 mm total length, had the largest number of eggs, most other species have less than 50. Prodissoconch measurements show that the larval shell measures 0.20–0.25 mm in most specimens. This would indicate that any planktonic phase must be very short. Indeed it would be difficult to sustain a long planktonic life at great depths, nor do plankton investigations being carried out at the same stations as those of the benthic programme indicate that larvae of deep sea bivalves reach the upper layers. Nevertheless some species have a wide distribution, for example *L. abyssicola*, our most common species, is present on both sides of the Atlantic and from arctic to equatorial latitudes. Other species with equally widespread distributions are *L. subquadrata*, *L. formosa*, *V. triangularis* and *P. gemma*. Thus, although larval life is probably short there is evidence of gene flow or a very slow rate of change. The Verticordiidae, while a characteristic family of abyssal depths, is not common in our samples which contain 18 species and 333 specimens from more than 300 stations. Of these, *V. triangularis*, *A. abyssicola* and *Policordia gemma* account for 231 of the specimens. There is evidence (Sanders & Allen 1973; Allen & Sanders 1966, 1969, 1973) that the abyssal bivalve fauna is ancient and that speciation may have occurred over a great period of time, the *Policordia gemma/densicostata/atlantica* complex indicates that it is still proceeding. However the generic and specific differences are not great and our studies, together with those of Nakazima (1967) on *Halicardia nipponesis* show that the morphology is circumscribed. Generic differences based on shell characters are slight, and this study shows that these are in no way emphasized by differences in anatomy – rather the reverse. To take an extreme example – *E. pacifica* and *L. formosa* have similar highly specialized buccal structures possessed by no other species so far described, but on shell characters alone the two species fall into different genera, yet on consideration of shell characters alone it would be difficult to maintain the distinction between *Euciroa* and *Verticordia*. It is a matter of debate whether the differences warrant generic separation except that on practical grounds it may be useful to retain the divisions based on shell characters.

The verticordiids clearly bridge the gap between anomalodesmacean genera such as *Lyonsia* and *Thracia* and the septibranch genera *Poromya* and *Cuspidaria*. The evolution of gill and stomach within the family shows how the septibranch condition evolved. Although the stomach is gastrodeuteian the gill structure of the Verticordiidae precludes their inclusion in a group Septibranchia. Thus we would support their inclusion together with the Cuspidaridae and Poromyidae in a Suborder Poromyoidea of the Order Anomalodesmacea, the word 'septibranch' being retained as a non-taxonomic descriptive term.

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REFERENCES

Adams, A. 1862 On some new species of acephalous Mollusca from the Sea of Japan. *Ann. Mag. nat. Hist.* Ser. 3, **9**, 223–230.

Adams, A. & Reeve, L. 1848 *The zoology of the voyage of H.M.S.* 'Samarang' (*Mollusca*), London.

Adams, H. & Adams, A. 1853–8 *The genera of recent Mollusca arranged according to their organization*, vols. 1, 11. London.

Allen, J. A. 1954 On the structure and adaptations of *Pandora inaequivalvis* and *P. pinna*. *Q. Jl microsc. Sci.* **95**, 473–482.

Allen, J. A. 1958 On the basic form and adaptations to habitab in the Lucinacea (Eulamellibranchia). *Phil. Trans. R. Soc. Lond.* B **241**, 421–484.

Allen, J. A. 1960 The ligament of the Lucinacea (Eulamellibranchia). *Q. Jl microsc. Sci.* **101**, 25–36.

Allen, J. A. 1961 The British species of *Thracia*. *J. mar. biol. Ass. U.K.* **41**, 723–735.

Allen, J. A. 1971 Evolution and functional morphology of the deep water protobranch bivalves of the Atlantic. *Proc. Joint Oceanogr. Assembly* (Tokyo 1970), 251–253.

Allen, J. A. 1973 The adaptations of the bivalves of the Atlantic abyssal plain. *Proc. Challenger Soc.* **4** (in press).

Allen, J. A. & Sanders, H. L. 1966 Adaptations to abyssal life as shown by the bivalve, *Abra profundorum* (Smith). *Deep-sea Res.* **13**, 1175–1184.

Allen, J. A. & Sanders, H. L. 1969 *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. *Malacologia* **7**, 381–396.

Allen, J. A. & Sanders, H. L. 1973 Studies on deep sea Protobranchia. The families Siliculidae and Lametilidae. *Bull. Mus. comp. Zool. Harv.* **145**, 263–310.

Appelius, F. L. 1870 Cataloge delle conchiglie fossili del Livornese desunte *Bull. malac. ital.* Anno III, 177–178.

Chenu, J. C. 1842–54 *Illustrations conchyliologigues on descriptions et figures de lorikes les coquilles vivantes et fossiles, suivant le système de Lamark.* Paris.

Clarke, A. H., Jr. 1962 Annotated list and bibliography of the abyssal marine molluscs of the world. *Bull. natn. Mus. Can.* **181**, 1–114.

da Costa, O. G. 1850 *Paleontologia del regno di Napoli*, vol. **13**, Naples.

Dall, W. H. 1878 Preliminary note on mollusks of the 'Blake' Expedition. *Bull. Mus. comp. Zool. Harv.* **5**, 55–64.

Dall, W. H. 1881 Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, 1877–79, by the U.S. Coast Survey Steamer, 'Blake'. XV. Preliminary report on the Mollusca. *Bull. Mus. comp. Zool. Harv.* **9**, 33–144.

Dall, W. H. 1886 Report on the Mollusca. Part I. Brachiopoda and Pelecypoda. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80) by the U.S. Coast Survey Steamer 'Blake'. *Bull. Mus. comp. Zool. Harv.* **12**, 171–318.

Dall, W. H. 1889*a* A preliminary catalogue of the shell bearing marine mollusks and Brachiopoda of the south eastern coast of the United States, with illustrations of many species. *Bull. U.S. natn. Mus.* **37**, 1–221.

Dall, W. H. 1889*b* Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Scientific results of explorations by the U.S. Fish Commission Steamer 'Albatross', no. 7. *Proc. U.S. natn. Mus.* **12**, 219–362.

Dall, W. H. 1892 Contributions to the Tertiary fauna of Florida, with special reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Tertiary mollusks of Florida. Part II. Streptodont and other gastropods included. *Trans. Wagner free Inst. Inst. Sci. Philad.* **3**, 201–473.

Dall, W. H. 1895 Report on Mollusca and Brachiopoda dredged in deep water, chiefly near the Hawaiian islands, with illustrations of hitherto unfigured species from north-west America. *Proc. U.S. natn. Mus.* **17**, 675–733.

Dall, W. H. 1900 Contributions to the Tertiary fauna of Florida with especial reference to the silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including, in many cases, a complete revision of the generic groups treated and of their American Tertiary species. Part V. Teleodesmacea: *Solen* to *Diplodonta*. *Trans. Wagner free Inst. Sci. Philad.* **3**, 949–1218.

Dall, W. H. 1903 Contributions to the Tertiary fauna of Florida with especial reference to the silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases, a complete revision of the generic groups treated and of their American Tertiary species. Part VI. Concluding the work. *Trans. Wagner free Inst. Sci. Philad.* **3**, 1219–1654.

Dall, W. H. 1913 Diagnoses of new shells from the Pacific Ocean. *Proc. U.S. natn. Mus.* **45**, 587–597.

Dall, W. H., Bartsch, P. & Rehder, H. A. 1938 A manual of the recent and fossil marine pelecypod mollusks of the Hawaiian islands. *Bull. Bernice P. Bishop Mus.* **153**, 1–233.

Dautzenberg, P. 1927 Mollusques provenant des Campagnes scientifiques du Prince Albert ler de Monaco dans L'Océan Atlantique et dans le Golfe de Gascogne. *Résult. Camp. scient. Prince Albert* 1. **72**, 1–400.

Deshayes, G. P. 1856–65 Description des animaux sans vertèbres découverts dans le bassin de Paris pour servir de supplement à la description de coquilles fossiles des environs de Paris comprenant une revue générale de toutes les espèces actuellement connues, vol. 1. Paris.

Fischer, P. 1860 Note sur les genres *Hippagus* et *Verticordia*. *J. Conch. Paris*, ser. 2, **4**, 295–300.

Fischer, P. 1862 Nouvelle note sur le genre *Verticordia*. *J. Conch. Paris.*, ser. 3, **2**, 378–381.

Friele, H. 1879 Catalog der auf der norwegischen Nordmeer expedition bei Spitzbergen gefunden mollusken. *Jb. dt. malakozool. Ges.* **6**, 264–286.

Friele, H. 1886 Mollusca II. *Norw. North-Atlant. Exped.* 1876–78. *Zool.* 1–44.

Graham, A. 1949 The molluscan stomach. *Trans. R. Soc. Edinb.* **61**, 737–778.

Gray, J. E. 1840 *Synopsis of the contents of the British Museum* (42nd ed.). London.

Gray, J. E. 1842 *Synopsis of the contents of the British Museum* (44th ed.). London.

Hedley, C. 1904 Studies on Australian Mollusca. Part VIII. *Proc. linn. Soc. N.S. Wales.* **29**, 182–212.

Heilprin 1882 Remarks on the molluscan genera *Hippagus*, *Verticordia* and *Pecchiolia*. *Proc. Acad. nat. Sci. Philad.* 423–428.

Iredale, T. 1924 Results from Roy Bell's Molluscan collections. *Proc. linn. Soc. N.S. Wales.* **49**, 179–278.

Iredale, T. 1930 More notes on the marine mollusca of New South Wales. *Rec. Austr. Mus.* **17**, 384–407.

Jeffreys, G. 1876 New and peculiar Mollusca of the *Kellia*, *Lucina*, *Cyprina* and *Corbula* families procured in the 'Valorous' Expedition. *Ann. Mag. nat. Hist.* Ser. 4, **18**, 490–499.

Jeffreys, G. 1878 On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1868–1870. (Part I.) *Proc. zool. Soc. Lond.* 393–416.

Jeffreys, G. 1881 On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1868–70. (Part IV.) *Proc. zool. Soc. Lond.* 922–925.

Kobelt, W. 1888 *Prodromus Faunae Molluscorum testaceorum maria europaea inhabitatum.* Nurnberg.

Knudsen, J. 1967 The deep sea Bivalvia. *Scient. Rep. John Murray Exped.* **11**, 235–343.

Knudsen, J. 1970 The systematics and biology of abyssal and hadal bivalvia. *Galathea Rep.* **11**, 7–241.

Lea, I. 1833 *Contributions to geology.* Philadelphia.

Locard, A. 1898 Mollusques Testaces. 2. *Exped. Sci. Travailleur 'Talisman'.* 1–515.

Meneghini, G. 1851 *Considerazioni sulla Geologia Stratigrafische della Toscana.*

Mörch, O. A. L. 1861 Beitrage zur Molluskenfauna Central-Amerikais. *Malak. Bl.* **7**, 170–213.

Nakazima, M. 1967 Some observations on the soft part of *Halicardia nipponensis* Okutani. *Venus* **25**, 147–158.

Narchi, W. 1968 The functional morphology of *Lysonia californica* Conrad, 1837 (Bivalvia). *Veliger* **10**, 305–313.

Newall, N. D. 1965 Classification of the Bivalvia. *Am. Mus. Novit.* **2206**, 1–25.

d'Orbigny, A. 1845 In: Sagra, R. de la, *Histoire physique, politique et naturelle de l'ile de Cuba*; *Mollusques.* Paris.

Owen, G. 1953 On the biology of *Glossus humanus* (L.) (*Isocardia cor* Lam.). *J. mar. biol. Ass. U.K.* **32**, 85–106.

Owen, G. 1970 The fine structure of the digestive tubules of the marine bivalve *Cardium edule*. *Phil. Trans. R. Soc. Lond.* B **258**, 245–260.

Paetel, F. 1875 *Catalog der Conchylien Sammlung von F. Paetel. Nebst Uebersicht des angewandten Systems.* Berlin.

Pecchioli, 1852 Notice sur un nouveau genre de bivalve fossile des *terrains sub-apennins*. *Rev. Mag. Zool.* **12**, 577.

Pelseneer, P. 1888*a* Report on the anatomy of the deep sea Mollusca collected by H.M.S. 'Challenger' in the years 1873–76. *Rep. scient. Res. Challenger* **27**, 1–42.

Pelseneer, P. 1888*b* Les pélècypodes (ou lamellibranches) sans branchies. *C. r. hebd. Séanc. Acad. Sci. Paris.* 1029–1031.

Pelseneer, P. 1911 Les lamellibranches de l'Expedition du Siboga. Partie Anatomique. *Siboga Exped.* **71**, 1–125.

Philippi, R. A. 1844 *Enumeratio Molluscorum Siciliae cum viventium, tum in tellure tertiaria fossilium quae in itinere suo observavit auctor*, vol. **2**. Naples.

Por, F. D. 1969 Deep-sea Cerviniidae (Copepoda: Harpacticoida) from the western Indian Ocean, collected with R/v 'Anton Brunn' in 1964. *Smithsonian Contr. Zool.* **29**, 1–60.

Purchon, R. D. 1956 The stomach of the Protobranchia and Septibranchia. *Proc. zool. Soc. Lond.* **127**, 511–525.

Purchon, R. D. 1958 The stomach in the Eulamellibranchia: stomach type IV. *Proc. zool. Soc. Lond.* **131**, 487–525.

Purchon, R. D. 1960 The stomach in the Eulamellibranchia: stomach types IV and V. *Proc. zool. Soc. Lond.* **135**, 431–489.

Purchon, R. D. 1963 Phylogenetic classification of the Bivalvia, with special reference to the Septibranchia. *Proc. malacol. Soc. Lond.* **35**, 71–80.

Reid, R. G. B. 1965 The structure and function of the stomach in bivalve molluscs. *J. Zool.* **147**, 156–184.

Reid, R. G. B. 1966 Digestive tract enzymes in the bivalves *Lima hians* Gmelin and *Mya arenaria* L. *Comp. biochem. Physiol.* **17**, 417–433.

Ridewood, W. G. 1903 On the structure of the gills of the Lamellibranchia. *Phil. Trans. R. Soc. Lond.* B **195**, 147–284.

Sanders, H. L. & Allen, J. A. 1973 Studies on deep sea Protobranchia (Bivalvia); Prologue and the Pristiglomidae. *Bull. Mus. comp. Zool. Harv.* **145**, 237–262.

Sanders, H. L. & Hessler, R. R. 1969 Ecology of the deep sea benthos. *Science, N.Y.* **163**, 1419–1424.

Sanders, H. L., Hessler, R. R. & Hampson, G. 1965 An introduction to the study of deep sea benthic faunal assemblages along the Gay Head–Bermuda transect. *Deep-sea Res.* **12**, 845–867.

Sars, G. O. 1872 On some remarkable forms of animal life from the great deeps off the Norwegian coast. *University prog. 1st half year, Christiania*, 1869, 1–82.

Sars, M. 1868 Fortsatte Benaerkninger over det dyriske Livs Udbredning i Havets Dybder. *Forh. Vidensk Selsk. Krist.* (1867), 246–275.

Schumacher, C. F. 1817 *Essai d'un nouvean système des habitations des vers testacés.* Copenhagen.

Seguenza, G. 1876 Cenne intorno alle Verticordie fossilii del Plioceno Italiano. *Rc. R. Accad. Sci. fis. mat. Napoli* **15**, 104–115.

Seguenza, M. 1860 Du genre *Verticordia* Searles Wood. *J. Conch. Paris* ser. 2, **8**, 286–295.

Smith, E. A. 1885 Report on the Lamellibranchiata collected by H.M.S. 'Challenger' during the years 1873–76. *Rep. scient. Res. Challenger* **13**, 1–341.

Smith, E. A. 1889 Mollusca. Report of a deep sea trawling cruise off the south west coast of Ireland under the direction of Rev. W. Spotswood Green, M.A., F.R.G.S. *Ann. Mag. nat. Hist.* ser. 4, **6**, 420–425.

Soot-Ryen, T. 1966 Revision of the pelecypods from the Michael Sars North Atlantic deep sea expedition 1910 with notes on the family Verticordiidae and other interesting species. *Sarsia* **24**, 1–31.

Sowerby, J. 1844 *The mineral conchology of Great Britain*, vol. 7, London: Sowerby.

Stoliczka, F. 1870–1 The Pelecypoda, with a review of all known genera of this class, fossil and recent. *Mem. Geol. Surv. India, Paleont. Indica. Cretaceous Fauna* 3.

Thiele, J. 1912 Die Antarktischen Schneken und Muscheln. *Dt. Südpol-Exped.* **13**, 232–233.

Thiele, J. 1935 *Handbuch der systematischen weichtierkunde*, vol. 2, *Classis Bivalvia.* Jena: von Gustav Fischer.

Thiele, J. & Jaeckel, S. 1931 Muscheln der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped.* 'Valdivia' **21**, 1–110.

Tryon, G. W. 1882 *Structural and systematic conchology: an introduction to the study of the Mollusca*, vol. 1. Philadelphia.

Verrill, A. E. 1880 Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part II. Mollusca, with notes on Annelida, Echinodermata, etc., collected by the United States Fish Commission. *Proc. U.S. natn. Mus.* **3**, 356–409.

Verrill, A. E. 1881 Notice of the remarkable marine fauna occupying the outer banks of the southern coast of New England. no. 2. *Am. J. Sci.* **22**, 292–303.

Verrill, A. E. 1882*a* Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England, no. 7, and some additions to the fauna of Vineyard Sound. *Am. J. Sci.*, ser. 24, **3**, 360–371.

Verrill, A. E. 1882*b* Catalogue of marine Mollusca added to the fauna of New England region during the past ten years. *Trans. Conn. Acad. Arts Sci.* **5**, 447–587.

Verrill, A. E. 1884 Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep sea species with notes on others previously recorded. *Trans. Conn. Acad. Arts Sci.* **6**, 139–294.

Verrill, A. E. 1885 Third catalogue of Mollusca recently added to the fauna of New England. *Trans. Conn. Acad. Arts Sci.* **6**, 395–452.

Verrill, A. E. & Bush, K. J. 1898 Revision of the deep water mollusca of the Atlantic coast of North America with descriptions of new genera and species. Part 1; Bivalvia. *Proc. U.S. natn. Mus.* **20**, 777–901.

Vokes, H. E. 1967 Genera of the Bivalvia: a systematic and bibliographic catalogue. *Bull. Am. Paleont.* **51**, 111–394.

Woodward, S. P. 1851–6 *A manual of the Mollusca; or, a rudimentary treatise of recent and fossil shells.* London: John Weak.

Woodward, S. P. 1868 *A manual of the Mollusca; or, a rudimentary treatise of recent and fossil shells*, 2nd ed. London.

Yonge, C. M. 1928 Structure and function of the organs of feeding and digestion in the Septibranchs *Cuspidaria* and *Poromya*. *Phil. Trans. R. Soc. Lond.* B **216**, 221–263.

Appendix. List of recent species of the family Verticordiidae

(This list does not include the new species described in this paper.)

Euciroa aethiopica Thiele & Jaekel 1931

1931 *Euciroa aethiopica* Thiele & Jaekel, *Wiss. Ergebn. dt. Tiefsee-Exped.* 'Valdivia' **21**, p. 90, pl. V, fig. 129.

Euciroa crassa Thiele & Jaekel 1931

1931 *Euciroa crassa* Thiele & Jaekel, *Wiss. Ergebn. dt. Tiefsee-Exped.* 'Valdivia' **21**, pp. 90, 91, pl. V, fig. 130.

1952 *Euciroa cistagemma* Kuroda, *Venus* **17**, p. 14, pl. 1, figs. 16–18.

1958 *Euciroa cistagemma* Habe, *Publs Seto mar. biol. Lab.* **6**(3) p. 277, pl. 13, fig. 9.

1961 *Euciroa cistagemma* Habe, *Coloured illustrations of the shells of Japan* **2**, p. 145, pl. 65, fig. 8.

1964 *Euciroa cistagemma* Habe, *Shells of the Western Pacific in colour* **2**, p. 213, pl. 65, fig. 8.

1967 *Euciroa crassa* Knudsen, *Scient. Rep. John Murray Exped.* **11**(3), p. 300, fig. 28A, pl. 3, fig. 3.

Euciroa eburnea Wood-Mason & Alcock 1891

1891 *Verticordia (Euciroa) eburnea* Wood-Mason & Alcock, *Ann. Mag. nat. Hist.* p. 447, figs. 14*a–d.*

1894 *Euciroa (Verticordia) eburnea* Dall, *Proc. U.S. natn. Mus.* **17**, p. 687.

1894 *Verticordia optima* Sowerby, *Proc. malac. Soc. Lond.* **1**, p. 39, pl. 5, fig. 3.

1897 *Verticordia (Euciroa) eburnea* Alcock & Anderson, Illustrations of the zoology of the Royal Indian Marine surveying steamer 'Investigator'. *Mollusca* **1**, pl. 4, figs 1*a–e.*

1904 *Euciroa eburnea* E. A. Smith, *Ann. Mag. nat. Hist.* **14**(7), p. 8.

1931 *Euciroa eburnea* Thiele & Jaeckel, *Wiss, Ergebn. dt. Tiefsee – Exped.* 'Valdivia' p. 89, pl. 5, fig. 128.

1940 *Euciroa eburnea* Winckworth, *Proc. malac. Soc. Lond.* **24**, p. 28.

1967 *Euciroa eburnea* Knudsen, *Scient. Rep. John Murray Exped.* **11**(3), p. 301, figs 28B–D, 29; pl. 3, figs 6, 7.

Euciroa elegantissima Dall 1881

1878 *Euciroa elegantissima* Dall, *Bull. Mus. comp. Zool. Harv.* **5**, pp. 61, 62.

1881 *Verticordia (Euciroa) elegantissima* Dall, *Bull. Mus. comp. Zool. Harv.* **9**, pp. 106, 107.

1894 *Euciroa elegantissima* Dall, *Proc. U.S. natn. Mus.* **17**, pp. 687, 688.

1952 *Euciroa (Verticordia) elegantissima* Kuroda, *Venus* **17**, p. 11.

Euciroa millegemmata Kuroda & Habe 1952

1952 *Euciroa millegemmata* Kuroda, *Venus* **17**, p. 14, pl. 1, figs 12–15.

1967 *Euciroa millegemmata* Knudsen, *Scient. Rep. John Murray Exped.* **11**(3), p. 303.

Euciroa pacifica Dall 1894

1894 *Euciroa pacifica* Dall, Bartsch & Rheder, *Bull. Bernice P. Bishop Mus.* **153**, p. 219, pl. 57, figs 1–4.

1967 *Euciroa pacifica* Knudsen, *Scient. Rep. John Murray Exped.* **11**(3), p. 303.

Euciroa rostrata Thiele & Jaekel 1931

1931 *Euciroa (Acreuciroa) rostrata* Thiele & Jaekel, *Wiss. Ergebn. dt. Tiefsee Exped.* 'Valdivia', p. 91, pl. V, fig. 132.

1935 *Euciroa (Acreuciroa) rostrata* Thiele, *Handbach der Systematischen weichtierkunde* **2**, p. 945, fig. 863.

1952 *Euciroa teramachii* Kuroda, *Venus* **17**, p. 15, figs 19–20.

1959 *Euciroa (Acreuciroa) teramachii* Kira, *Coloured illustrations of the shells of Japan* p. 165, pl. 62, fig. 9.

1962 *Euciroa (Acreuciroa) teramachii* Kira, *Shells of the Western Pacific in colour* p. 182, pl. 63, fig. 9.

1967 *Euciroa rostrata* Knudsen, *Scient. Rep. John Murray Exped.* **11**(3), pp. 303–304.

Euciroa spinosa Thiele & Jaekel 1931

1931 *Euciroa spinosa* Thiele & Jaekel, *Wiss. Ergebn. dt. Tiefsee Exped.* 'Valdivia' p. 249, pl. V, fig. 131.

Halicardia flexuosa (Verrill & Smith 1881)

1881 *Mytilimeria flexuosa* Verrill, *Am. J. Sci.* **21**, p. 302.

1882 *Mytilimeria flexuosa* Verrill, *Trans. conn. Acad. Arts Sci.* **5**, p. 567, p. 58, fig. 38.

1884 *Mytilimeria flexuosa* Verrill, *Trans. conn. Acad. Arts Sci.* **6**, p. 258.

1886 *Verticordia flexuosa* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, p. 286.

1894 *Halicardia flexuosa* Dall, *Proc. U.S. natn. Mus.* p. 697, pl. XXIII, figs 1, 3, 5, 6, pl. XXIV, fig. 3.

1898 *Mytilimeria flexuosa* Locard, *Exped. Sci. Travailleur Talisman* **2**, p. 210, pl. X, figs. 14–17.

1931 *Mytilimeria flexuosa* Grieg, *Rep. Scient. Results Michael Sars N. atlantic deep sea Exped.* 1910, p. 4.

1935 *Halicardia flexuosa* Thiele, *Handbuch der systematischen weichtierkunde* **2**, p. 944.

1937 *Halicardia flexuosa* Tomlin, *Ann. S. Afr. Mus.* **32**(2), p. 23–24.

1966 *Halicardia flexuosa* Soot Ryen, *Sarsia* **24**, p. 17, pl. 1(7), pl. 3 (36, 39) and figs 11, 12.

Halicardia gouldi Dall, Bartsch & Rheder 1938

1938 *Halicardia gouldi* Dall, Bartsch & Rheder, *Bull. Bernice P. Bishop. Mus.* p. 218, pl. 56, figs 1–4.

1962 *Halicardia gouldi* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **32**, p. 32.

1966 *Halicardia gouldi* Soot-Ryen, *Sarsia* **24**, p. 17.

Halicardia nipponensis Okutani 1957

1957 *Halicardia nipponensis* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **17**, p. 28, pl. 1, figs 2, 3, 6, 7.

1961 *Halicardia nipponensis* Habe, *Coloured illustrations of the shells of Japan* **11**. Osaka: Hoikusha.

1962 *Halicardia nipponensis* Shikama, *Sci. Rep. Yokohama natn. Univ.* **8**, Ser. 11, p. 54, pl. 3, figs 8*a–c*.

1962 *Halicardia* (*Halicardia*) *nipponensis* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **32**, p. 31, pl. II, fig. 3, pl. IV, fig. 13.

1964 *Halicardia nipponensis* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **46**, p. 9.

1966 *Halicardia nipponensis* Soot Ryen, *Sarsia* **24**, p. 17.

1967 *Halicardia nipponensis* Nakazima, *Venus* **25**(3, 4), p. 147–158.

1968 *Halicardia nipponensis* Okatani, *Bull. Tokai, reg. Fish. Res. Lab.* **56**, p. 17.

Halicardia saharica (Locard 1898)

1898 *Mytilimeria saharica* Locard, *Exped. Sci. Travailleur Talisman* p. 213, pl. X, figs 29–31.

Halicardissa perplicata Dall 1889

1889 *Verticordia perplicata* Dall, *Proc. U.S. natn. Mus.* **12**(773), p. 278, pl. 8, fig. 1.

1913 *Halicardissa perplicata* Dall, *Proc. U.S. natn. Mus.* **45**, p. 594.

1935 *Halicardissa perplicata* Thiele, *Handbuch der systematischen weichtierkunde* **2**, p. 944.

1966 *Halicardissa perplicata* Soot-Ryen, *Sarsia* **24**, p. 17.

Laevicordia abscissa (Pelseneer 1911)

1911 *Lyonsiella abscissa* Pelseneer, *Siboga exped.* **53**, pp. 76–77, pl. XXV, figs 4, 56.

1966 *Laevicordia abscissa* Soot-Ryen, *Sarsia* **24**, p. 25.

Laevicordia compressa (Locard 1898)
1898 *Mytilimeria compressa* Locard, *Exped. Sci. Travailleur Talisman* **2**, p. 211, pl. X, figs 18–21.

Laevicordia pacifica (Dall 1908)
1908 *Lyonsiella pacifica* Dall, *Bull. Mus. comp. Zool. Harv.* **43**, p. 428.
1962 *Lyonsiella pacifica* Clarke, *Bull. natn. Mus. Can. No.* **181**, p. 69.
1966 *Laevicordia pacifica* Soot-Ryen, *Sarsia* **24**, p. 24.

Lyonsiella abyssicola (G. O. Sars 1872)
1868 *Lyonsiella abyssicola* M. Sars, *Forh. Vidensk. Selsk Krist.* pp. 257, 434.
1872 *Pecchiolia abyssicola* G. O. Sars, *University program for the 1st half year. Christiania* 1869; p. 25, pl. 3, fig. 21–43.
1879 *Lyonsiella abyssicola* Friele, *Jahrb. Malac. Gesellsch.* **6**, p. 268.
1880 *Lyonsiella abyssicola* Verrill, *Proc. U.S. natn. Mus.* **3**, p. 396.
1881 *Pecchiolia abyssicola* Jeffreys, *Proc. zool. Soc. Lond.* p. 931.
1882*b* *Pecchiolia abyssicola* Verrill, *Trans. Conn. Acad. Arts Sci.* **5**, p. 565.
1882 *Lyonsiella abyssicola* Tryon, *Struct. a. Syst. Conch.* **1**, p. 146.
1884 *Pecchiolia abyssicola* Verrill, *Trans. Conn. Acad. Arts Sci.* **6**, p. 278.
1888 *Lyonsiella abyssicola* Pelseneer, *Challenger Rep.* **27**(74), p. 1030.
1888 *Pecchiolia abyssicola* Kobelt, *Prodromus*, p. 322.
1889*a* *Lyonsiella abyssicola* Dall, *Bull. U.S. natn. Mus.* **37**, p. 277.
1893 *Lyonsiella abyssicola* Norman, *Ann. Mag. nat. Hist.* **6**, ser. 12, p. 344.
1894 *Lyonsiella abyssicola* Dall, *Proc. U.S. natn. Mus.* **17**, p. 705.
1897 *Lyonsiella abyssicola* Dautzenberg & Fischer, *Mém. Soc. zool. Fr.* p. 228.
1901 *Lyonsiella abyssicola* Friele & Grieg, *The Norwegian North-Atlantic Exped.* **6**, 1876–78.
1927 *Lyonsiella abyssicola* Dautzenberg, *Résult. Camp. Scient. Prince Albert* 1, **70**, p. 349.
1958 *Lyonsiella abyssicola* Ocklemann, *Meddt. Grønland* **122**, p. 158.
1962 *Lyonsiella abyssicola* Clarke, *Bull. natn. Mus. Can. No.* **181**, p. 68.
1966 *Lyonsiella abyssicola* Soot-Ryen, *Sarsia* **24**, p. 25, pl. 3, fig. 31.

Lyonsiella agulhasensis Thiele & Jaekel 1931
1931 *Lyonsiella agulhasensis* Thiele & Jaekel, *Wiss. Ergebn. dt. Tiefsee-Exped.* 'Valdivia' p. 92, pl. V, fig. 133.
1966 *Thracidora agulhasensis* Soot-Ryen, *Sarsia* **24**, p. 26.

Lyonsiella fischeri (Jeffreys 1880*b*)
1880*b* *Mytilimeria fischeri* Jeffreys, *Rep. Brit. Ass. Sci.* p. 383.
1898 *Mytilimeria fischeria* Locard, *Exped. Sci. Travailleur Talisman* **2**, p. 212, pl. X, figs 22–28.

Lyonsiella formosa (Jeffreys 1881)
1881 *Lyonsia formosa* Jeffreys, *Proc. zool. Soc. Lond.* p. 930, pl. LXX, fig. 1.
1882 *Lyonsia formosa* Jeffreys, *Proc. zool. Soc. Lond.* p. 686.
1885 *Lyonsia formosa* Smith, *Challenger Rep. Zool.* **13**, p. 72, pl. VI, figs 3–3*b*.
1889 *Lyonsia formosa* Dautzenberg, *Contr. faune malac. Accres* p. 89.
1898 *Lyonsia formosa* Locard, *Exped. Sci. Travailleur Talisman* **2**, p. 218.
1962 *Lyonsia formosa* Clarke, *Bull. natn. Mus. Can. No.* **181**, p. 68.

Lyonsiella galatheae (Knudsen 1970)
1970 *Laevicordia galatheae* Knudsen, *Galathea Rep.* II, p. 128, figs 85, 86.

Lyonsiella magnifica Dall 1913
1913 *Lyonsiella magnifica* Dall, *Proc. U.S. natn. Mus.* **45**, p. 595, fig. ibid 66, pl. 23, fig. 2.
1966 *Lyonsiella magnifica* Soot-Ryen, *Sarsia* **24**, p. 25, pl. 3(35).

Lyonsiella media Okutani 1962
1962 *Lyonsiella media* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **32**.
1966 *Lyonsiella media* Soot-Ryen, *Sarsia* **24**, p. 21.
1968 *Lyonsiella media* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **56**, p. 17.

Lyonsiella parva Okutani 1962
1962 *Lyonsiella parva* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **32**, p. 29, pl. III, fig. 7.
1966 *Lyonsiella parva* Soot-Ryen, *Sarsia* **24**, p. 21.
1966 *Lyonsiella parva* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **46**, p. 9.
1968 *Lyonsiella parva* Okutani, *Bull. Tokai reg. Fish. Res. Lab.* **56**, p. 17.

Lyonsiella planulata Thiele 1912
1912 *Lyonsiella planulata* Thiele, *Deutsche Südpolar Exp.* 1901–1903, **13**, *Zoologie* **5**, pp. 232–233, pl. 18, fig. 25.
1951 *Lyonsiella planulata* Soot-Ryen, *Det. Norske, Videnskaps-Akademi i Oslo*, **3**(32), p. 22.
1966 *Lyonsiella planulata* Soot-Ryen, *Sarsia* **24**, p. 25, pl. 3(33).

Lyonsiella quadrata Hedley 1907
1907 *Lyonsiella quadrata* Hedley, *Rec. Aust. Mus.* **6**, pp. 302–303, pl. 56, figs 31, 33.
1930 *Proagorina quadrata* Iredale, *Rec. Aust. Mus.* **17**, p. 388.
1966 *Lyonsiella quadrata* Soot-Ryen, *Sarsia* **24**, p. 25, pl. 3, fig. 32.

Lyonsiella smidti (Smith 1885)
1885 *Lyonsiella jeffreysi* Smith, *Challenger Rep. Zool.* **13**, p. 73, pl. 25, figs 1–16.
1886 *Lyonsiella smidti* Friele, *Den. Norske Nordhaus. Exped.* 1876–1878, **16**, Zool. p. 38, pl. XII, figs 15, 16.
1897 *Lyonsiella jeffreysi* Dautzenberg & Fischer, *Mém. Soc. zool. Fr.* **10**, p. 228.
1927 *Lyonsiella smithi* Dautzenberg, *Résalt. Camp. scient. Prince Albert*, **70**, p. 348.
1932 *Lyonsiella smithi* Prashad, *Siboga-Exped.* **53***c*, 1, p. 325, pl. VII, figs 25, 26.
1962 *Lyonsiella smithi* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Laevicordia smidti* Soot-Ryen, *Sarsia* **24**, p. 24, pl. 2, fig. 27.
1970 *Laevicordia smidti* Knudsen, *Galathea Rep.* **2**, p. 129.

Lyonsiella subquadrata (Jeffreys 1881)
1881 *Pecchiolia subquadrata* Jeffreys, *Proc. zool. Soc. Lond.* p. 932, pl. 70, fig. 3.
1888 *Pecchiolia subquadrata* Kobelt, *Prodromus* p. 323.
1889 *Verticordia subquadrata* Smith, *Ann. Mag. nat. Hist.* **6**, ser. 4, p. 423.
1897 *Lyonsiella subquadrata* Dautzenberg & Fischer, *Mém. Soc. zool. Fr.* p. 228.
1898 *Lyonsiella subquadrata* Verrill & Bush, *Proc. U.S. natn. Mus.* **20**, p. 817, pl. LXXXVII, fig. 3.
1927 *Lyonsiella subquadrata* Dautzenberg, *Résalt Camp. Scient. Prince Albert* 1, **70**, p. 349.
1934 *Lyonsiella subquadrata* Johnson, *Proc. Boston Soc. nat. Hist.* **40**, p. 32.

1962 *Lyonsiella subquadrata* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Lyonsiella subquadrata* Soot-Ryen, *Sarsia* **24**, p. 25, pl. 3, fig. 34.

Policordia alaskana (Dall 1894)
1894 *Lyonsiella alaskana* Dall, *Proc. U.S. natn. Mus.* **17**, p. 703, pl. XXV, fig. 2.
1921 *Lyonsiella alaskana* Dall, *Bull. U.S. natn. Mus.* **112**, p. 28.
1924 *Lyonsiella alaskana* Oldroyd, *The marine shells of the west coast of North America* **1**, p. 97.
1960 *Lyonsiella alaskana* Clarke, *Breviora* **119**, p. 12.
1961 *Verticordia* Wolff, *Galathea Rep.* **5**, p. 150.
1962 *Lyonsiella alaskana* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1963 *Lyonsiella alaskana* Clarke, *Bull. natn. Mus. Can.* **185**, p. 103.
1966 *Policordia alaskana* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2, fig. 20.
1968 *Lyonsiella alaskana* Boss *et al. Bull. U.S. natn. Mus.* **287**, p. 16.
1970 *Policordia cf. alaskana* Knudsen, *Galathea Rep.* **2**, pp. 129–130, figs 87, 88.

Policordia cordata (Verrill & Bush 1898)
1898 *Lyonsiella cordata* Verrill & Bush, *Proc. U.S. natn. Mus.* **20**, p. 818, pl. XCV, figs 7, 8.
1934 *Lyonsiella cordata* Johnson, *Proc. Boston Soc. nat. Hist.* **40**(1), p. 36.
1962 *Lyonsiella cordata* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Policordia cordata* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2, fig. 23.

Policordia densicostata (Locard 1898)
1898 *Verticordia densicostata* Locard, *Exp. Sci. Travailleur Talisman* **2**, pp. 202–204, pl. 10, figs 5–8.
1962 *Verticordia densicostata* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Policordia densicostata* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2(22).

Policordia diomedea Dall, Bartsch & Rehder 1938
1938 *Policordia diomedea* Dall, Bartsch & Rehder, *Bull. Bernice P. Bishop, Mus.* p. 217, pl. 56, figs 5–8.

Policordia gemma (Verrill 1880)
†1876 *Verticordia insculpta* Seguenza, *Rend. Accad. Napoli* **15**, p. 110.
1880 *Lyonsiella gemma* Verrill, *Proc. U.S. natn. Mus.* III, p. 396.
1881 *Pecchiolia insculpta* Jeffreys, *Proc. zool. Soc. Lond.* p. 932, pl. LXX, fig. 4.
1882*a* *Pecchiolia gemma* Verrill, *Am. J. Sci.* **24**, ser. 3, p. 365.
1882*b* *Pecchiolia gemma* Verrill, *Trans. Conn. Acad. Arts Sci.* **5**, p. 565.
1884 *Pecchiolia gemma* Verrill, *Trans. Conn. Acad. Arts Sci.* **6**, p. 258, pl. XXX, figs 7, 8.
1885 *Lyonsiella gemma* Smith, *Challenger Rep.* **13**, p. 166.
1886 *Lyonsiella insculpta* Dall, *Bull. Mus. comp. Zool.* **12**, p. 288.
1888 *Pecchiolia insculpta* Kobelt, *Prodromus* p. 323.
1889 *Pecchiolia gemma* Smith, *Ann. Mag. nat. Hist.* **6**(24), ser. 4, p. 423.
1889 *Verticordia insculpta* Dautzenberg, *Contr. faune malac. Acores* p. 88.
1892 *Verticordia insculpta* Locard, *Les coquilles marines des cotes de France*, p. 132, Paris.
1898 *Verticordia insculpta* Locard, *Exped. Sci. Travailleur Talisman* **2**, p. 206.
1927 *Verticordia insculpta* Dautzenberg, *Résalt. Camp. Sci. Prince Albert* 1, p. 347.

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† Fossil.

1931 *Lyonsiella insculpta* Grieg, *Rep. Sci. Results Michael Sars N. Atlantic deep sea Exped.* 1910, **5**, p. 4.
1962 *Verticordia insculpta* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1962 *Lyonsiella gemma* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Policordia gemma* Soot-Ryen, *Sarsia* **24**, pp. 22, 23, fig. 13, pl. 1, figs 8, 9, 10, pl. 2 figs 24, 25.

Policordia grandis (Smith 1885)
1885 *Lyonsiella grandis* Smith, *Challenger Rep.* **13**, p. 74, pl. 25, figs 3, 36.
1962 *Lyonsiella grandis* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Policordia grandis* Soot-Ryen, *Sarsia* **24**, p. 20, pl. 2(17).

Policordia jeffreysi (Friele 1879)
1879 *Lyonsiella jeffreysi* Friele, *Jahr. Deutsch, Malakozool. Gesellsch.* **6**, p. 269.
Friele, *Norwegian North Atlantic Exped.* **16**, pl. 12, figs 15, 16.
1901 *Lyonsiella jeffreysi* Friele, *Norwegian North Atlantic Exped.* Mollusca III.
1946 *Lyonsiella jeffreysi* Gorbunov, *Dreifuiushchaia Ekspeditsiia Glavseomorputi na ledokol nom parokhodi* 'G. Sedov.' 1937–40 g.g. Trudy 3.
1958 *Lyonsiella jeffreysi* Ockelmann, *Medd. Grønland* **122**, p. 159.
1962 *Lyonsiella jeffreysi* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1963 *Lyonsiella jeffreysi* Clarke, *Bull. natn. Mus. Can.* **185**, p. 103.
1966 *Policordia jeffreysi* Soot-Ryen, *Sarsia* **24**, p. 20, pl. 2(16).

Policordia lisbetae Knudsen 1970
1970 *Policordia lisbetae* Knudsen, *Galathea Rep.* **2**, p. 132, figs 89, 90.

Policordia murrayi (Knudsen 1967)
1967 *Lyonsiella murrayi* Knudsen, *Scient. Rep. John Murray Exped.* **11**, pp. 297, 298, figs 26, 27.

Policordia papyracea (Smith 1885)
1885 *Lyonsiella papyracea* Smith, *Challenger Rep.* **13**, pp. 73–74, pl. 25, figs 2, 2*b*.
1894 *Lyonsiella papyracea* Dall, *Proc. U.S. natn. Mus.* **17**, p. 703.
1962 *Lyonsiella papyracea* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1966 *Policordia papyracea* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2(19).

Policordia pilula (Pelseneer 1911)
1911 *Lyonsiella pilula* Pelseneer (Prashad 1932), *Siboga Exped.* **53**, pp. 76–77, and **53***a*, p. 325, pl. 7, figs 23, 24.
1962 *Lyonsiella pilula* Okutani, *Bull. Tokai reg. Fish Res. Lab.* **32**, p. 28.
1966 *Policordia pilula* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2(14).

Policordia radiata (Dall 1889)
1889*a* *Lyonsiella radiata* Dall, *Bull. U.S. natn. Mus.* **37**, p. 442.
1889*b* *Lyonsiella radiata* Dall, *Proc. U.S. natn. Mus.* **12**, pp. 276–277, pl. 8, fig. 7.
1966 *Policordia radiata* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2(15).

Policordia uschakovi (Gorbunov 1946)
1946 *Lyonsiella uschakovi* Gorbunov, *Trudy ek.* **3**, Expedition Sedov 1937–1940, pp. 321–322, pl. 1, figs 4*a*, *c*.

1962 *Lyonsiella uschakovi* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1963 *Lyonsiella uschakovi* Clarke, *Bull. natn. Mus. Can.* **185**, p. 103.
1966 *Lyonsiella uschakovi* Soot-Ryen, *Sarsia* **24**, p. 21, pl. 2(21).

Verticordia affinis Thiele & Jaekel 1931
1931 *Verticordia affinis* Thiele & Jaekel, *Wiss. Ergelon. dt. Deutsch en Tiefsee Exped.* 'Valdivia' **1**, p. 247, pl. V, fig. 127.

Verticordia angulata (Jeffreys 1881)
1881 *Pecchiolia angulata* Jeffreys, *Proc. zool. Soc. Lond.* p. 933, pl. LXX, fig. 6.
1897 *Pecchiolia angulata* Dautzenberg & Fischer, *Mem. Soc. zool. Fr.* **10**, p. 228.
1898 *Verticordia angulata* Locard. *Exped. Sci. Travailleur Talisman* **2**, p. 207.

Verticordia australiensis Smith 1885
1885 *Verticordia australiensis* Smith, *Challenger Rep.* **13**, p. 167, pl. XXV, fig. 6(66).
1907 *Verticordia australiensis* Hedley, *Rec. Aust. Mus.* **6**, p. 303, pl. XVI, figs 38, 39.

Verticordia axinoides Seguenza 1876
1876 *Verticordia axinoides* Seguenza, *Acad. Sc. fis. math.* p. 111.

Verticordia carinifera Locard 1898
1898 *Verticordia carinifera* Locard, *Exped. Sci. Travailleur Talisman* **2**, p. 208, pl. X, fig. 9–13.
1962 *Verticordia carinifera* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.

Verticordia crebrilirata Prashad 1932
1932 *Verticordia* (*Verticordia*) *crebrilirata* Prashad. *Siboga Exped.* **53***c*, p. 324, pl.VII, figs 19, 20.

Verticordia cuneata Kuroda 1952
1952 *Verticordia* (*Vertambitus*) *cuneata* Kuroda, *Venus* **17**, p. 8, pl. 1, figs 1–3.

Verticordia expansa Prashad 1932
1932 *Verticordia expansa* Prashad, *Siboga exped.* **55***c*, p. 324, pl. VII, figs 21, 22.

Verticordia fischeriana Dall 1881
1881 *Verticordia fischeriana* Dall, *Bull. Mus. comp. Zool. Harv.* **9**, p. 106, pl. 11, figs 4*a*, *b*.
1886 *Verticordia* (*Haliris*) *fischeriana* *Bull. Mus. comp. Zool. Harv.* **12**(6), p. 291, pl. 11, figs 4*a*, *b*.

Verticordia granulata Seguenza 1860
†1860 *Verticordia granulata* Seguenza, *J. Conch. Paris* **8**, p. 293, pl. 10, fig. 2*f–h*.
†1876 *Verticordia trapezoidea* Seguenza, *Acad. Sci. fis. emath.* p. 7.
1881 *Pecchiolia granulata* Jeffreys, *Proc. zool. Soc. Lond.* p. 933.
1886 *Haliris granulata* Dall, *Bull. Mus. comp. Zool. Harv.* **12**(6), p. 287.
1898 *Verticordia granulata* Locard, *Exped. Sci. Travailleur* 'Talisman' **2**, p. 209.

Verticordia granulifera (Verrill 1885)
1885 *Pecchiolia granulifera* Verrill, *Trans. Conn. Acad. Arts Sci.* **6**, p. 434, 448.
1886 *Verticordia granifera* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, p. 286.

† Fossil.

1889 *Verticordia granulifera* Dall, *Bull. U.S. natn. Mus.* **37**, p. 66.
Verticordia granulifera Verrill & Bush, *Proc. U.S. natn. Mus.* **20**, p. 816, pl. LXXXVII, fig. 2; XCV, figs 2, 3, 4.
1934 *Verticordia granulifera* Johnson, *Proc. Boston Soc. nat. Hist.* **40**, p. 35.
1962 *Verticordia granulifera* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.
1962 *Lyonsiella granulifera* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.

Verticordia guineensis Thiele & Jaekel 1931
1931 *Verticordia guineensis* Thiel & Jaekel, *Wiss. Ergebn. dt. Deutschen Tiefsee Exped.* 'Valdivia' **21**, p. 88, pl. V, fig. 125.
1962 *Verticordia guineensis* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.

Verticordia japonica Adams 1862
†1844 *Verticordia acuticostata* Philippi, *Enum. Moll. Sicil.* **11**, p. 42, pl. XIV, fig. 19*a–c*.
†1844 *Verticordia cardiiformis* J. Sowerby, *Man. Conch.* **7**, p. 67, pl. DCXXXIX.
†1850 *Hippagus verticordius* S. Wood, *Monogr. Crag. Moll.* 2, p. 150, pl. XII, fig. 18.
†1860 *Verticordia acuticostata* Seguenza, J. *Conch. Paris* **8**, p. 286.
1862 *Verticordia japonica* Adams, *Ann. Mag. Nat. Hist.*, ser. 3, **9**, p. 224.
†1862 *Verticordia deshayesiana* Fischer, *J. Conch. Paris* **10**, p. 35, pl. V, figs 10, 11.
1873 *Verticordia acuticostata* Wyville-Thomson, *Depths of the sea*, p. 464.
1877 *Verticordia acuticostata* Hidalgo, *Mol. mar. Esp. Catal. Gen.* p. 139.
1881 *Verticordia acuticostata* Dall, *Bull. Mus. comp. Zool. Harv.* **9**, p. 105.
1881 *Pecchiolia acuticostata* Jeffreys, *Proc. zool. Soc. Lond.* p. 933.
1882 *Verticordia japonica* Tryon, *Struct. a. syst. Conch.* **1**, p. 196.
1885 *Verticordia deshayesiana* Smith, *Challenger Rep.* **13**, p. 165.
1886 *Verticordia acuticostata* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, pp. 285–288.
1887 *Verticordia acuticostata* Fischer, *Manuel de conch.* p. 1161.
1888 *Pecchiolia acuticostata* Kobelt, *Prodromus* p. 322.
1889*a* *Verticordia acuticostata* Dall, *Proc. U.S. natn. Mus.* **12**, p. 277.
1889*b* *Verticordia acuticostata* Dall, *Bull. Mus. comp. Zool. Harv.* **18**, p. 446.
1889 *Verticordia* (*Pecchiolia*) *acuticostata* Dautzenberg, *Cont. Faune malac. Acores C* Sc. 1, p. 88.
1894 *Verticordia acuticostata* Dall, *Proc. U.S. natn. Mus.* **17**, p. 688.
1897 *Verticordia acuticostata* Dautzenberg & Fischer, *Mém. Soc. Zool. Fr.* **10**, p. 226.
1898 *Verticordia acuticostata* Locard, *Exped. Sci. Travailleur* 'Talisman' **2**, p. 204.
1899 *Verticordia acuticostata* Locard. *Coq. mar. an large descotes de France*, p. 131.
1927 *Verticordia acuticostata* Dautzenberg, *Résalt. Camp. Scient. Prince Albert* 1, **70**, p. 346.
1931 *Verticordia deshayesiana* Thiele & Jaekel, *Wiss. Ergebn. dt. Deutschen Tiefsee Exped.* **1**, pt 2, p. 246.
1934 *Verticordia acuticostata* *Proc. Boston Soc. nat. Hist.* **40**(1), p. 35.
1952 *Verticordia* (*Spinosipella*) *japonica* Kuroda, *Venus* **17**, pp. 8, 11, figs 10, 11.
1962 *Verticordia acuticostata* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.

Verticordia inornata Thiele & Jaekel 1931
1931 *Verticordia inornata* Thiele & Jaekel, *Wiss. Ergebn. dt. Deutschen Tiefsee Exped.* 'Valdivia' **21**, p. 245, pl. V, fig. 124.

† Fossil

Verticordia lamothei Dautzenberg & Fischer 1897

1897 *Verticordia lamothei* Dautzenberg & Fischer, *Mém. Soc. Zool. Fr.* **10**, p. 227, pl. VII, figs 13, 14, 15, 16.

1898 *Verticordia lamothei* Dautzenberg, Fischer & Locard, *Exped. Sci. Travailleur* 'Talisman' **2**, p. 205.

1899 *Verticordia lamothei* Locard, *Coq. mar. au large des cotes de France* p. 132.

1927 *Verticordia lamothei* Dautzenberg, *Résalt. Camp. Scient. Prince Albert* 1, **70**, p. 347, pl. IX, figs 15, 16, 17, 18.

1931 *Verticordia lamothei* Thiele & Jaekel, *Wiss. Ergebn. dt. Deutschen Tiefsee Exped.* 'Valdivia' **21**, p. 245.

Verticordia makiyamai Habe 1952

1952 *Verticordia (Haliris) makiyamai* Habe, *Venus* **17**, figs 8, 9.

Verticordia multicostata Adams 1862

1862 *Verticordia multicostata* Adams, *Ann. Mag. nat. Hist.* **9**, p. 224.

1862 *Verticordia multicostata* Fischer, *J. Conch. Paris* **2**, ser. 3, p. 379.

1885 *Verticordia multicostata* Smith, *Challenger Rep.* **13**, p. 165.

1952 *Verticordia (Haliris) multicostata* Kuroda, *Venus* **17**, p. 9, pl. 1, figs 4, 5.

Verticordia ornata (d'Orbigny 1846)

1846 *Trigonulina ornata* d'Orbigny, *Moll. Cuba* **2**, p. 292.

1850 *Hippagus novemcostatus* Adams & Reeve, *Voy Samarang Zöol.* p. 76, pl. XXIV, fig. 1.

1862 *Trigonulina ornata* Chenu. Man. *Conch.* **2**, p. 169, fig. 843.

1862 *Verticordia ornata* Fischer, *J. Conch., Paris* **10**, p. 380.

1881 *Verticordia ornata* Dall, *Bull. Mus. comp. Zool. Harv.* **9**, p. 105.

1884 *Verticordia caelata* Verrill, *Trans. conn. Acad. Arts Sci.* pl. XXX, figs 9, 9*a*.

1885 *Verticordia caelata* Smith, *Challenger Rep.* **13**.

1886 *Verticordia (Trigonulina) ornata* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, p. 286.

Verticordia perversa Dall 1886

1886 *Verticordia perversa* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, p. 289.

1889*a* *Verticordia perversa* Dall, *Bull. U.S. natn. Mus.* **37**, pl. XXXIX, fig. 4.

Verticordia pygmaea Kuroda 1952

1952 *Verticordia (Haliris) pygmaea* Kuroda, *Venus* **17**, p. 10, pl. 1, figs 617.

Verticordia quadrata Smith 1885

1885 *Verticordia quadrata* Smith, *Challenger Rep.* **13**, p. 169, pl. XXV, figs 8, 8*b*.

1888 *Pecchiolia quadrata* Kobelt, *Prodromus* p. 324.

1962 *Verticordia quadrata* Clarke, *Bull. natn. Mus. Can.* **181**, p. 69.

Verticordia seguenzae Dall 1886

1886 *Verticordia seguenzae* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, p. 290.

Verticordia setosa (Hedley 1905)

1905 *Verticordia rhomboidea* Hedley, *Trans. N.Z. Inst.* **38**, pp. 72, 73, pl. 11, figs 12, 13, 14.

1907 *Haliris setosa* Hedley, *Rec. Aust. Mus.* **6**, p. 303.

Verticordia tenerrima Thiele & Jaekel 1931

1931 *Verticordia tenerrima* Thiele & Jaekel, *Wiss. Ergebn. dt. Deutschen Tiefsee Exped.* 'Valdivia' **21**, p. 246, pl. V, fig. 126.

Verticordia transversa Locard 1898

1898 *Verticordia transversa* Locard, *Exped. Sci. Travailleur* 'Talisman' **2**, p. 201, pl. X, figs 1–4.

1962 *Verticordia transversa* Clarke, *Bull. natn. Mus.* Can. **181**, p. 70.

Verticordia triangularis Locard 1898

1898 *Verticordia triangularis* Locard, *Exped. Sci. Travailleur* 'Talisman' **2**, p. 207, pl. XI, figs 1–5.

1962 *Verticordia triangularis* Clarke, *Bull. natn. Mus. Can.* **181**, p. 70.

Verticordia vadosa Hedley 1907

1907 *Verticordia vadosa* Hedley, *Rec. Aust. Mus.* **6**, p. 303, pl. LVI, figs 34, 35, 36, 37.

Verticordia woodi Smith 1885

1885 *Verticordia woodi* Smith, *Challenger Rep.* **13**, p. 168, pl. XXV, figs 7, 7*b*.

1886 *Verticordia woodi* Dall, *Bull. Mus. comp. Zool. Harv.* **12**, p. 289.

1934 *Verticordia woodi* Johnson, *Proc. Boston Soc. nat. Hist.* **40**, p. 36.

1962 *Verticordia woodi* Clarke, *Bull. natn. Mus. Can.* **181**, p. 70.

ADDITIONAL RECORDS

						no. of specimens
			Lyonsiella perplexa (p. 437)			
Atlantis II	28. iii. 71	sta. 264	36° 12.7′ S, 52° 42.7′ W	2041–2048 m	E.S.*	83
Knorr	25. ii. 72	sta. 288	11° 02.2′ N, 55° 05.5′ W	4417–4429 m	E.S.	8
			Lyonsiella frielei (p. 440)			
Knorr	25. ii. 72	sta. 288	11° 02.2′ N, 55° 05.5′ W	4417–4429 m	E.S.	1
			Lyonsiella fragilis (p. 456)			
Atlantis II	11. iii. 71	sta. 236	36° 27.0′ S, 53° 32.3′ W	497–518 m	E.S.	2
	11. iii. 71	sta. 237	36° 32.6′ S, 53° 23.0′ W	993–1011 m	E.S.	4
	11. iii. 71	sta. 239	36° 49.0′ S, 53° 15.4′ W	1661–1679 m	E.S.	1
			Verticordia triangularis (p. 460)			
Knorr	3. iii. 72	sta. 307	12° 34′ 4 N, 59° 09.2′ W	3862–3835 m	E.S.	2
			Verticordia quadrata (p. 472)			
Atlantis II	27. iii. 71	sta. 262	36° 05.2′ S, 52° 17.9′ W	2440–2480 m	E.S.	1
Knorr	24. ii. 72	sta. 287	13° 16.0′ N, 56° 53.1′ W	4980–4832 m	E.S.	1
			Policordia jeffreysi (p. 500)			
Knorr	25. ii. 72	sta. 288	11° 02.2′ N, 55° 05.5′ W	4417–4429 m	E.S.	2

* ES, Epibenthic Sledge Haul.

Key to the lettering on the text figures

A	anus
AA	anterior adductor muscle
AI	inhalent aperture
ANT	anterior
AP	anterior lip
AS	aperture side
B	byssus
BC	buccal cavity
BG	byssus gland
BGR	byssus groove
BR	buccal region
BRM	pedal retractor muscle
BS	blood sinus
CE	ciliated epithelium
CF	fused ciliary junction
CG	cerebral ganglion
CIG	ciliated groove
CL	cuticular lining
CLM	central longitudinal muscles
CM	circular muscle
COB	circumoesophageal ciliated band
CT	ciliated tract
CNT	connective tissue
D	duct
DD	digestive duct
DG	digestive diverticula
DL	descending lamella
DT	digestive tubule
E	oesophagus
EA	exhalent aperture
EP	epithelial papilla
ES	exhalent siphon
ET	exhalent tentacle
F	foot
FC	frontal cilia
FL	fluted lateral lip
FM	fused mantle
FO	food organism
G	gill
GA	gill axis
GC	gland cell(s)
GF	gill filament
GL	granular lacunal 'cell'
GS	gastric shield
GT	glandular tissue
H	heart
HBC	hypobranchial cavity
HC	haemocoele
HGT	hind gut
IA	inhalent aperture
ICM	inner circular muscle
ID	inner demibranch
IFL	lateral flap
IL	inner lobe
IS	inhalent siphon
IT	inhalent tentacle
IV	inhalent valve
K	kidney
KC	kidney cells
KD	kidney duct
L	lithodesma
LC	lateral cilia
LDD	left digestive diet
LFC	latero-frontal cilia
LI	inner layer of ligament
LM	longitudinal muscle
LO	outer layer of ligament
M	mouth
MA	mantle connectives
MB	membrane
MC	mucous cells
MF	muscle fibres
MG	radial mantle gland
MGR	marginal groove
MGT	mid gut
ML	middle lobe
MN	mantle
MM	membrane
MS	mantle shelf
MZ	muscle blocks
N	nerve
NGL	non-granular lacunal 'cell'
OCM	outer circular muscle
OD	outer demibranch
OE	oesophagus
OR	oesophageal ridge
OL	outer lobe
OT	outer tentacle
OV	ovary
OVT	lacunal tissue
P	periostracum
PA	posterior adductor muscle
PE	periostracum
PG	pedal ganglion
PGR	periostracal groove
PGP	pedal gape
PL	palp
PM	pallial muscle
PME	papillate mantle edge
PN	pallial nerve
PP	posterior lip
R	rectum
RAM	radiating muscle
RDD	right digestive duct
RM	retractor muscle
RT	right
S	style
SA	adhering sediment
SC	secretory epithelial cells
SEC	specialized epithelial cells
SH	shell
SK	skeletal support
SMB	small muscle blocks
SP	space
SPT	septum
SS	style sac
SSR	style sac rim
ST	stomach
STR	stomach ridges
T	testis
TC	thickened cuticle
TMF	transverse muscle
TN	tentacular nerve
TO	tongue
VAD	aperture of testis duct
VG	visceral ganglion

Scanning e.m. photographs of: (*a*) ***Lyonsiella abyssicola***, left valve (magn. × 22); (*b*) ***Verticordia triangularis***, shell spinules (magn. × 785); (*c*) ***Policordia gemma***, left valve (magn. × 40); (*d*) ***Policordia atlantica***, left valve (magn. × 60); (*e*) ***P. gemma***, a raised radiating line on the shell surface (magn. × 785); (*f*) ***P. atlantica***, a sunk radiating line on the shell surface (magn. × 785).