AN ANATOMICALLY BIZARRE, FLUID-FEEDING, GALEOMMATOIDEAN BIVALVE: *DRACULAMYA POROBRANCHIATA GEN. ET SP. NOV.* (MOLLUSCA: BIVALVIA)

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Abstract   For the first time we propose ectoparasitism, by piercing and fluid-feeding in the Bivalvia. Draculamya porobranchiata gen. et sp. nov. *is described and the anatomy reveals a number of functional adaptations related to the feeding mode. Primary among these is a puncturing organ situated at the anterior end of the byssus groove. The ctenidia are reduced to a series of ciliated pores set ventrally within a suspensory membrane and the labial palps are not present, indicating that suspension feeding cannot take place. The alimentary tract is highly modified; the oesophageal musculature is in the form of a suction pump. The fore stomach is greatly expanded, lacking sorting ridges and is presumed to store large volumes of ingested fluid. The central cavity of the stomach is poorly defined with a small gastric shield and style sac while the openings to the digestive diverticula are wide. The ovary is situated in the mantle and foreign sperm are stored in paired ctenidial seminal receptacles. No males were found. There are left and right pericardia and their failure to fuse as in other bivalves prevent the development of a heart. Oxygenation of the blood probably occurs across the thin walls separating the mantle cavity and the proportionally very large blood sinuses.*

   Comparisons are made with Kurtiella tumidula (=Mysella verrilli) *the only other described galeommatoid with a suctorial habit.*

Key words   Draculamya porobranchiata, *Galeommatoidea, functional morphology, systematics, ectoparasitism, fluid-feeding,* Kurtiella tumidula

INTRODUCTION

In preparation of a web based identification guide to the marine bivalves found around the British Isles (Oliver *et al.*, 2010) a collection from the Porcupine Seabight and Abyssal Plain, held by the National Oceanographic Centre Southampton, was examined. This material had been examined by Olabarria (2005) and her paper cited numerous taxa identified to genus only. Samples labelled as "*Cetoconcha* sp." were of immediate interest as the overall appearance was galeommatoid but the ctenidia, which could be seen through the shell, consisted not of filaments but as a series of pores and therefore superficially septibranch. Furthermore the labial palps were not evident. Jørgen Lützen was invited to join the investigation and his semi-thin (2 μm) sections revealed a number of other unusual characters including an accessory organ in the foot. The primary aim of this paper is to describe the functional morphology of this enigmatic bivalve and to make comparisons with other galeomma-

toids, specially *Kurtiella tumidula* (Jeffreys 1866) (= *Mysella verrilli* Dall 1899), which has a reduced ctenidium and no labial palps (Allen, 2000).

Although mistakenly identified as *Cetoconcha*, the Porcupine shell had been seen previously, and as early as 1882, when Jeffreys identified it as *Lasaea pumila* S.V. Wood. This species was first described from the Coralline Crag, a shallow water, Pliocene formation and the relationship between the fossil and living taxa requires resolution. The first part of this paper is concerned with the taxonomy and nomenclature following on from the conclusions of Aartsen & Carrozza (1997).

Abbreviations used in the text: sh shell; spm specimen; v valve; NMW.Z National Museum of Wales, Zoology; BM(NH) Natural History Museum London; NOC National Oceanographic Centre London.

Abbreviations used in the figures: aa anterior adductor muscle; ab amorphous body; al anterior lateral tooth; amt anterior marginal tooth; arp anterior retractor pedis muscle; bc buccal cavity; bg 1 byssus gland (the byssus-producing part); bg 2 byssus gland (major part); bgr byssus groove;

bs blood sinus; by byssus; c cardinal tooth; cc 'central chamber'; cce cylindrical ciliated epithelium; cds cavity left from dissolved shell; ct ctenidium; ctp ctenidial pore; cu cuticle; dd digestive diverticula; dvs dorso-ventral septum; ea exhalant aperture; em embryos; f foot; fst fore stomach; gs gastric shield; hg hindgut; hs 'heart sinus'; ia inhalant aperture; ibc infrabrianchial chamber; ilj interlamellar junction; k kidney; la larvae; m mantle; mf mantle fold; mo mouth opening; mrw muscular ring wall in oesophagus; mu muscle fibre; mua muscular apparatus; mu-fst muscles supplying fore stomach; oe oesophagus; oeb oesophageal 'bristles'; oep oesophageal suction pump; ov ovary; p periostracum; pa posterior adductor muscle; pb proboscis; pc pericardium; pg pedal ganglion; pl posterior lateral tooth; pmt posterior marginal tooth; po puncturing organ; prp posterior protractor pedis muscle; re rectum; rs receptaculum seminis; rs 1 receptaculum seminis (terminal blind part); rs 2 receptaculum seminis (middle part); rt rejectory tract; sbc suprabranchial chamber; seg subepithelial gland cells; sm suspensory membrane (ctenidium); sp sperm cells; ss style sac; te testis.

Systematics

Galeommatoidea
Montacutidae
***Draculamya* gen. nov.**

Type species Draculamya porobranchiata this paper.

Definition Shell small, ovoid, RV with a single cardinal peg and single anterior and posterior laterals; LV without a cardinal peg and with single anterior and posterior laterals as extensions of the shell margin. Ligament internal on a deeply sunken, posteriorly directed resilifer. Ctenidium comprises a series of ciliated pores. Labial palps absent. Mouth, small on a domed cushion of tissue, oesophagus with pumping musculature. Foot with a byssus and a puncturing organ.

Etymology Draculamya the "Dracula Clam" named for its inferred feeding habit of ingesting body fluid following a puncture made by the accessory foot organ.

Affinities The shell (Fig. 1A) is very similar to that of the fossil taxon *Kellia pumila* Sowerby 1844 (Fig. 1B), which was cited as the type species of *Mancikellia* Dall 1899. Aartsen & Carrozza (1997) discussed the status of *Mancikellia* and concluded that it was a replacement name for *Zoe* Monterosato 1878 but that Monterosato's concept of *K. pumila* was different from that of S.V. Wood. Consequently Aartsen & Carrozza redescribed Monterosato's species under the name *Mancikellia divae* Aartsen & Carrozza (Fig. 1C–E). They concluded that *Kellia pumila* was not congeneric with *M. divae* but declined from commenting further.

Mancikellia divae and *K. pumila* co-occur in the Coralline Crag and we have examined such shells along with a recently collected shell in the Sykes collection in the Natural History Museum, London. The rimmed protoconch of *Mancikellia* is distinctive (Fig. 1D) as are the hinge sockets situated medially of the lateral teeth (Fig. 1D). Both characters are absent in *K. pumila* and we agree with Aartsen & Carrozza (1997) that *K. pumila* should not be placed in *Mancikellia*.

The hinge arrangement of *Draculamya* is much simpler than that of *Kellia* or *Lasaea* and the anatomy is unique. Consequently we choose to erect a new genus based on both shell and anatomy. The placement of *K. pumila* in this new genus can only be based on shell characters as we can never know the anatomy. The total dependence on shell characters to define taxa will come under increasing doubt with the addition of anatomical and molecular data. An analogous situation occurs in the genus *Kurtiella,* which remains defined by the hinge alone (Gofas & Salas, 2008). However, *K. tumidula* has a highly modified buccal anatomy and lacks labial palps, and is thus remarkably different from the type of the genus, *K. bidentata* (Montagu 1803) and not typical of the genus as a whole.

The shell morphology and especially the reproductive anatomy show affinity with the galeommatoids and the Montacutidae in particular. The galeommatoids are in need of review using molecular methods and we are aware that the placement of *Draculamya* in the Montacutidae is tentative.

***Draculamya porobranchiata* sp. nov.**

Lasaea pumila S.V. Wood – Jeffreys, 1882: 699–700 *in part*
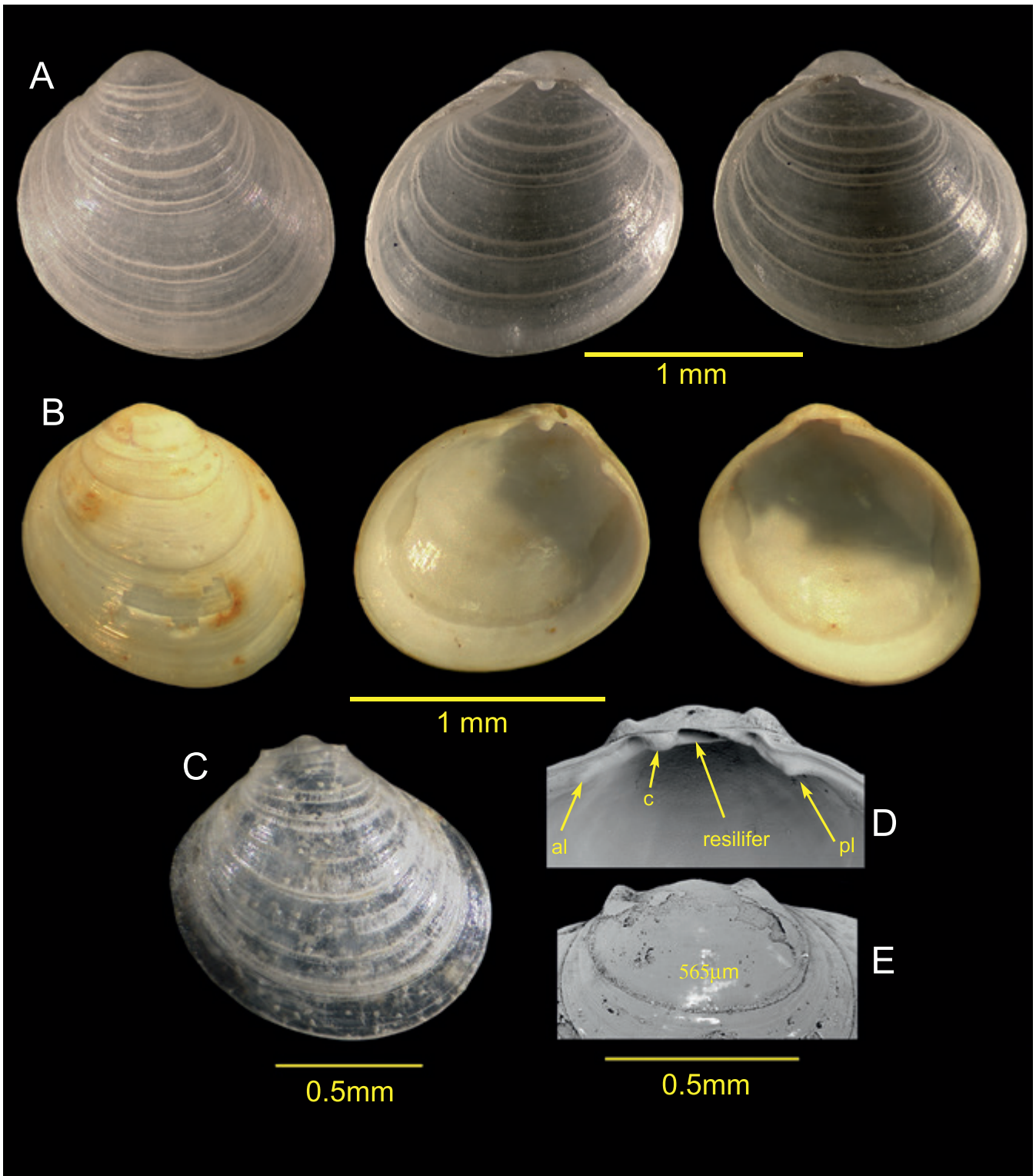
Figure 1A   *Draculamya porobranchiata*. Holotype, NMW.Z. 2011.001.1. Porcupine Bight.
Figure 1B   *Draculamya pumila*. Lectotype, BM(NH) L.4593.1, Coralline Crag, Sutton.
Figure 1C–E   *Mancikellia divae*. **C** external view of RV of Recent shell from Sicily, Sykes coll., BM(NH). **D** scanning electron micrograph of RV hinge of fossil shell from Coralline Crag, Sutton. **E** external view of B showing prodissoconch dimensions.

Lasaea pumila Wood – Friele, 1886: 37, pl. 12, fig. 13a, b

Lasaea pumila S. Wood – Locard, 1898: 299

Mancikellia pumila (S.V. Wood 1850) – Smith & Heppell, 1991: 66 *in part*

Holotype (Fig. 1A) 1 dry shell, Porcupine Sea Bight, RRS Challenger, IOS Cruise 514, Station 51420#4, 51°37.9'N 12°59.5'W to 51°37.5'N 12°59.6'W, 1279–1287 m, 2.iv.1982. NMW.Z.2011.001.1.

Paratypes Porcupine Sea Bight, RRS Challenger, IOS Cruise 514, All wet preserved. 8 spm, as *Kelliella* sp2, Station 51403#1, 51°37.7'N 12°59.8'W to 51°36.6'N 13°00.0'W, 1292–1314 m, 24.iii.1982. NOC, Southampton. 45 spm, as *Axinodon* sp1 & 1 spm, as *Thyasira inflata*, Station 51403#5, 51°37.8'N 12°58.9'W to 51°37.3'N 12°59.0'W, 1289–1297 m, 26.iii.1982. NMW.Z.2011.001.2 & NOC, Southampton. 10 spm, as *Kelliella* sp1, 1 spm, as *Mysella verrilli*, & 2 spm, as *Cetoconcha* sp1, Station 51420#1, 51°37.3'N 12°58.6'W to 51°36.9'N 12°58.6'W, 1326–1328 m, 2.iv.1982. NOC, Southampton. 28 spm, as *Cetoconcha* sp1, & 2 spm as *Kelliella* sp1, Station 51420#3, 51°38.3'N 12°58.9'W to 51°38.0'N 12°59.0'W, 1293–1298 m, 2.iv.1982. NOC, Southampton. 34 spm as *Cetoconcha* sp1, Station 51420#4, 51°37.9'N 12°59.5'W to 51°37.5'N 12°59.6'W, 1279–1287 m, 2.iv.1982. NMW.Z.2011.001.3.

Other material examined 4 v, as *Lasaea pumila*, West of the Hebrides, Lousy Bank, RRS Challenger stn. ES250, 59°43'N 12°33"W, 1270 m, leg. I.J. Killeen, NMW.Z.2011.002.1. "From illustration" as *Lasaea pumila*, Northern Norway, Vestfjord, Vøringen Station 192, 69° 46'N 16° 15'E, 1187 m, 7.vii.1877.

Dimensions Ten specimens from station 51420#4:

| Length mm	Height mm	Tumidity mm	Larvae
1.5	1.41	0.89	X
1.5	1.48	0.96	X
1.7	1.5	1.01	
1.7	1.5	1.01	X
1.7	1.5	1.1	
1.85	1.7	1.1	
1.85	1.7	1.1	
1.93	1.63	1.1	X
1.93	1.78	1.1	X
2.1	1.85	1.18	

Description Shell (Figs 1A, 2A–L) minute rarely exceeding 2 mm in length. Equivalve. Tumid. Thin but robust. Slightly inequilateral, beaks slightly behind the midline. Outline subcircular, slightly oblique and expanded anteriorly, all margins rounded. The anterior dorsal margin slightly longer than posterior dorsal. Sculpture of comarginal lines and growth stops of varying intensity, some prominently lined, some apparently smooth. Periostracum obscure but minutely lirate, most obvious on the lateral margins (Fig. 2B). Hinge (Fig. 2F–J) relatively strong; RV with a single cardinal peg and single anterior and posterior laterals; LV lacking cardinal teeth, with single anterior and posterior lateral teeth as extensions of the shell edge. Ligament (Fig. 2H) internal on a shallow resilifer set obliquely between the cardinal tooth and the posterior laterals. Prodissoconch (Fig. 2K–L) large, 470–500 mm in diameter, initially with radial microsculpture. Muscle scars obscure in fresh shells but adductor scars similar in size; the anterior situated more towards the anterior ventral margin than the posterior is to the posterior ventral margin.

Reproduction direct, brooding. Ctenidium as a series of ciliated pores (Fig. 5A). Seminal receptacles present (Fig. 6B). Labial palps absent (Fig. 7B). Oesophagus surrounded by a heavy ring of muscle sheath. Anterior stomach greatly expanded, lacking sorting ridges (Fig. 7C). Foot byssate (Fig. 5D) and with a puncturing organ in the form of a bulb bearing a terminal spike that projects from a cavity on the anterior sole (Fig. 6B).

Etymology The specific name "*porobranchiata*" refers to the pore structure of the ctenidium.

Distribution Verified records from the Northeast Atlantic from 69°N to 44°N at bathyal depths of 1100 m to 1350 m. All verified records from the Mediterranean have proved to be of *Mancikellia divae*.

Habitat Habitat data are available only for the Porcupine Bight. All specimens were collected from a very narrow bathymetric zone between 1279 m and 1328 m. The bottom here is dominated by the siliceous sponge *Pheronema carpenteri* and lies within the "*Holtenia* ground" so frequently mentioned by Wyville-Thomson (1873).
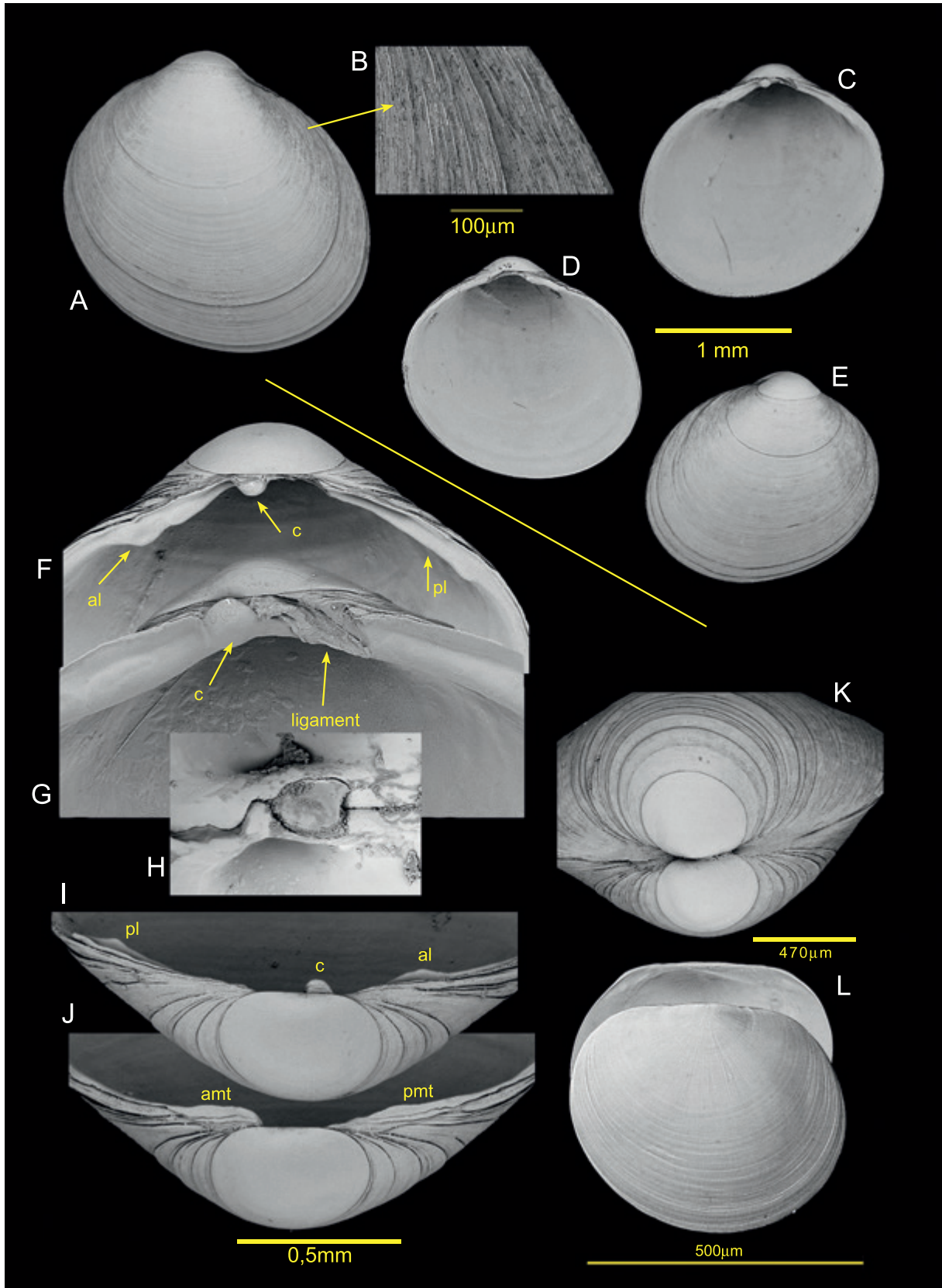
Figure 2 *Draculamya porobranchiata*. Scanning electron micrographs of the shell. **A** external of RV. **B** periostracum. **C** internal of RV. **D** internal of LV. **E** external of LV. **F** detail of RV hinge. **G** as F but valve tilted to view beneath beak. **H** internal of joined valves showing ligament in situ. **I, J** tilted dorsal views of the hinge plate RV & LV. **K** dorsal view showing prodissoconch. **L** shell of fully developed larval stage.
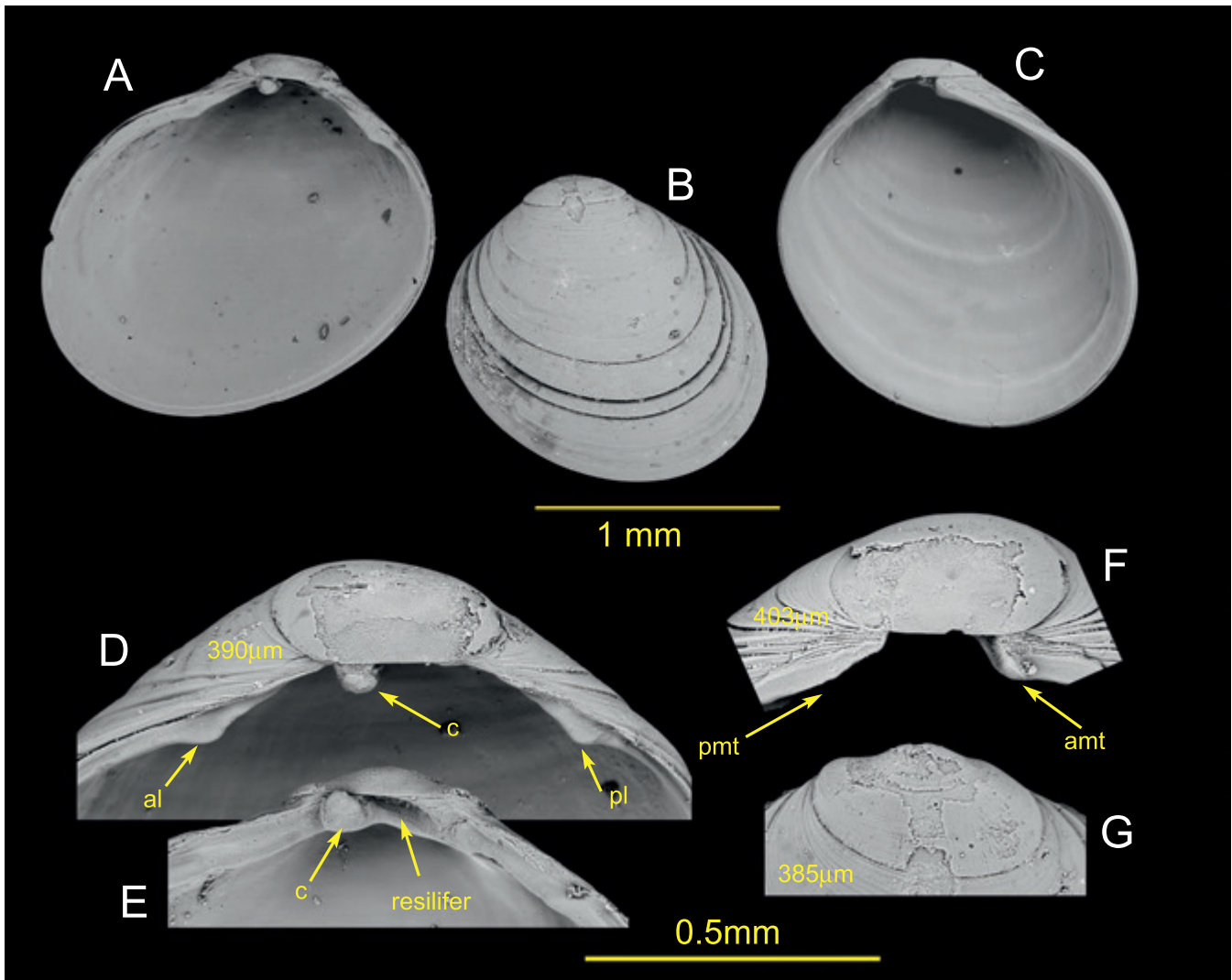
Figure 3   *Draculamya pumila*. Scanning electron micrographs of the shell. **A** internal of RV. **B** external of RV. **C** internal of LV. **D** detail of RV hinge. **E** as D but valve tilted to view beneath beak. **F** detail of LV hinge. **G**, dorsal view showing prodissoconch.

Rice *et al.* (1990) and Bett & Rice (1992) noted that the macrobenthos diversity of this sponge ground is very high with many taxa associated with the sponge, notably the ophuroid *Ophiactis abyssicola*, the crab *Dorynchus*, pectinid bivalves, polychaetes and sipunculans. The spicule-rich sediment was also diverse with large numbers of holothurians especially *Ypsilotheria talismani*. Echinoderms and sipunculans are frequent hosts of galeommatoids but *Draculamya* could not be directly associated with any.

Comparisons   The shell of *D. porobranchiata* is very similar to that of the Pliocene fossil *Kellia pumila* (Figs 1B, 3A–G) and this name has been consist-ently applied to the Recent form. Comparisons with many shells of *K. pumila* from the type locality at Sutton in the Coralline Crag revealed the following differences. *Kellia pumila* is more obliquely oval in outline and there is a distinct marginal groove most prominent on the dorsal lateral edges. The prodissoconch is smaller rang-ing from 380–410 μm as opposed to 470–500 μm in *D. porobranchiata*. Given the similarity in shells *Kellia pumila* is herein transferred to *Draculamya* and a re-description and lectotype designation are given below.

The ecological setting of *D. pumila* is rather dif-ferent with the Coralline Crag deposits consid-ered to be laid down in shallow water of around

50 m (Williams *et al.*, 2009). Although traditionally regarded as being laid down in a warm phase there is conflicting evidence from molluscan data of a much cooler setting (Williams *et al.*, 2009), but there seems to be no suggestion that the setting was a bathyal one. The possibility of *D. pumila* and *D. porobranchiata* being synonymous is therefore remote.

Draculamya pumila (J. de C. Sowerby 1844)

Montacuta pumila Wood 1840: 247
Kellia pumila Wood in J. de C Sowerby 1844: pl. 637, fig. 3
Kellia pumila Wood in J de C Sowerby 1846: 60
Kellia pumila Wood 1851: 124, pl. 12, fig. 15
Lasaea pumila Wood 1851 – Aartsen & Carrozza, 1997: 28–29, figs 1–4

Type material   Lectotype (Fig. 1B); Herein designated, 1 complete shell, Coralline Crag at Sutton. S.V. Wood Coll. BM(NH) L.4593.1.

Paralectotypes   As lectotype, 3v on SEM stub + 1 sh & 34 whole valves on one card with other fragments. BM(NH) L.4593. 2, 3.

Other material examined   3 sh + 16 v with other fragments on one card. Coralline Crag at Sutton. Robert Bell Coll. BM(NH) L.7319.

Type locality   Coralline Crag Formation at Sutton, Suffolk, England.

Description   Shell (Figs 1B, 3A–G) minute rarely exceeding 1.5 mm in length. Equivalve. Tumid. Thin but robust. Slightly inequilateral, beaks slightly behind the midline. Outline ovate, oblique and expanded anteriorly, all margins rounded but anterior slope less rounded than posterior. Sculpture of comarginal lines and growth stops. Hinge (Fig. 3D–F) relatively strong; RV with a single cardinal peg and single anterior and posterior laterals; LV lacking cardinal teeth, with single anterior and posterior lateral teeth as extensions of the shell edge. Inner margin with a distinct groove most developed on the lateral edges. Ligament internal on a shallow resilifer set obliquely between the cardinal tooth and the posterior laterals. Prodissoconch large, 385–410 mm in diameter (Fig. 3F–G). Adductor scars similar in size, pallial entire, distinct.

FUNCTIONAL MORPHOLOGY OF *DRACULAMYA POROBRANCHIATA*

Material and methods   No observations were performed on living *D. porobranchiata.* All specimens were fixed in formaldehyde and stored in 70% ethanol and were therefore not suitable for transmission electron microscopy. Gross anatomy was examined after dissolution of the shell and removal of the periostracum with subsequent staining in methylene blue. Some were similarly prepared but not stained and were critically point dried and mounted for scanning electron microscopy. Nine specimens were prepared for semi-thin sectioning. These had a shell length (SL) ranging from 1.3 to ca. 1.75 mm, were decalcified in Bouin's fluid and embedded in araldite. They were cut into transverse (N=4), sagittal (N=4) and horizontal (N=1) 2 µm-thick serial sections that were stained with toluidine blue.

A 2.0 mm long specimen of *Kurtiella tumidula* collected from 1380–1480 m in the Porcupine Bight preserved in formaldehyde was similarly (transversely) sectioned and stained as above. Section series from earlier studies of other araldite-embedded galeommatoidean species including *Epilepton clarkiae*, *Mysella moelleri*, *M. gregaria*, *Koreamya arcuata*, and *Arthritica bifurca* were studied for comparison.

Gross anatomy   Following the removal of the shell, the following gross features were observed. The adductor muscles are relatively small, the anterior in a more ventral position (Fig. 4A). The ctenidial pores are visible in an almost horizontal series rather close to the ventral margin as are the suspensory membranes to which they are attached Fig. 4B–D). Antero-ventrally the dorso-ventral septum is visible forming a veil over the mouth region (Fig. 4D). Antero-dorsally is a large opaque oval region which is the voluminous fore stomach (Fig. 4A). Posterior to this are the more dense digestive diverticula and posterior again lies the suprabranchial chamber which was often laden with developing ova (Fig. 4A) or with mature larvae (Fig. 4E). The toe of the foot is prominent and the mouth opening on a dome of tissue is situated close to the ventral side of the anterior adductor muscle (Fig. 4C–D).

Mantle, mantle folds and mantle cavity   The inner left and right mantle folds are fused for only
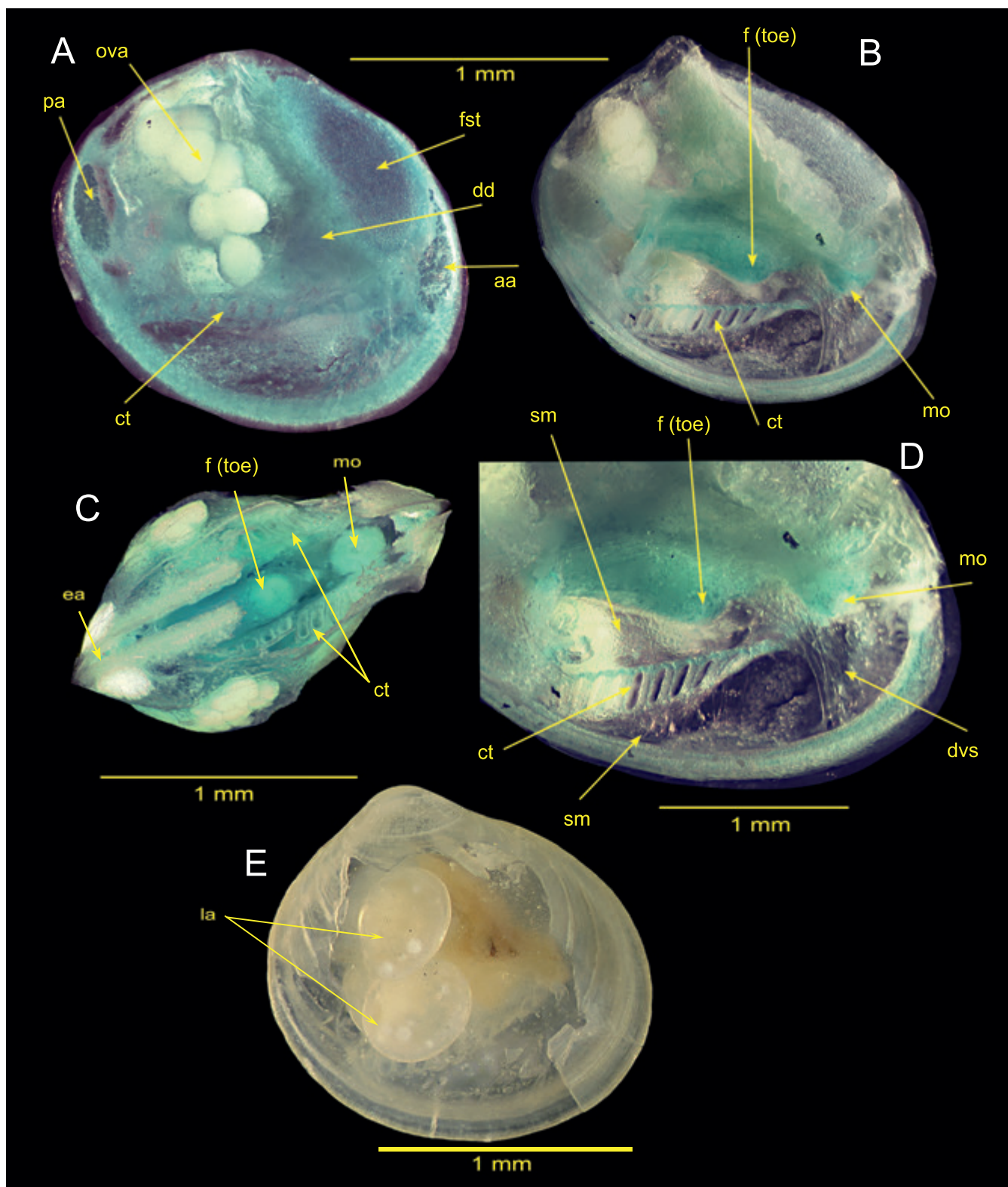
Figure 4 *Draculamya porobranchiata*. Gross anatomy after staining with methylene blue. **A** from the right side after removal of shell and periostracum. **B** as A but with mantle removed. **C** ventral view. **D** detail of anterior ventral region. E Broken shell revealing mature larval stages in brood chamber.

a short distance posteriorly, separating a large anterior inhalant/pedal/byssal aperture from a small exhalant aperture; no siphons are present (Fig. 4C). The inner (muscular) mantle fold is only slightly more prominent than the middle (sensory) fold and contains scattered radial muscles (Fig. 6A). All along its course the epithelium is non-ciliated and bears a thin cuticle. A rejection tract is absent. The middle fold is neither ciliated nor cuticularised. In some sections its free edge seems to bear very small papillae, but they may rather be simple irregularities. Both folds contain a few and scattered unicellular glands.

The gills divide the mantle cavity into supra- and infra-branchial chambers (Fig. 8C), both of which are lined with a non-ciliated squamous epithelium. On each side of the mouth, the dorsal parts of the infrabranchial chambers become cut off from the rest of the mantle cavity by a dorso-ventral septum (Fig. 4B, D). Each septum issues from the front part of the gill bases, runs in an antero-lateral direction and fuse with the inner mantle wall of the respective side just above the inner mantle fold (Fig. 6A). Besides many subepithelial gland cells, the septum contains a layer of muscle fibres which attach to the shell diametrically opposite to the mouth.

Along the entire length of the infrabranchial chamber the ventral part of the pallial wall contains numerous sub-epithelial glandular cells (Fig. 6A). A pair of large groups of similar, but deeper lying, cells occurs in the dorsal wall below the anterior adductor and level with the mouth region. The fine granules of all the subepithelial gland cells stain intensely with toluidine blue. The hypobranchial gland is located on the inner wall of the hindmost part of the suprabranchial cavity between the ventral margin of the pallial parts of the ovary and the mantle folds and extends almost back to the pallial fusion. The close-set glandular cells are columnar, 30–35 μm tall, with basal nuclei and a cytoplasm laden with minute granules.

A pallial blood sinus occupies most of the interior of the mantle (Fig. 9A, B). It is most extensively developed dorsally where the mantle borders on the suprabranchial chamber.

Foot   The foot is comparatively slender, laterally compressed and provided with many longitudinal folds (Fig. 5B, D). It has apparently no creeping sole. The epithelia of the lateral and ventral surfaces of the foot are non-ciliated except for the mid-ventral byssal groove and the byssus cavity. The rather deep mid-ventral byssus groove starts in a non-ciliated depression in the first fourth of the foot, level with the pedal ganglia. The depression contains the puncturing apparatus, a unique organ not found in any other bivalve. The following part of the byssus groove is ciliated and terminates in the relatively small byssus gland (Fig. 6B), which in cross sections of the foot is seen to be divided into two symmetrical halves, both heavily ciliated. A single, very slender byssus thread emanated from the gland in three bivalves and reached at least to the shell margin. The most conspicuous gland complex of the foot occupies the dorsal part of the foot's interior for more than three-fourths of its length. The gland cells stain strongly with toluidine blue and discharge their secretion by way of long, sinuous and slender ducts into the lateral parts of both the byssus gland and byssus groove.

The puncturing organ (Figs 5E, 6B, 7A, C, 9B) is onion-shaped with a pointed tip, but the shape varies according to the state of muscular contraction. Except for the organ's terminal, slender third, which is lined by small columnar epithelial cells, its interior is provided with a heavy intrinsic musculature most of which consists of circular fibres arranged around a small blood sinus running along the organ's long axis. Many, smaller extrinsic muscles run from the base of the organ to the immediate surroundings of the foot. They obviously function in turning the axis of the structure somewhat in various directions. Lengthening and shortening of the puncturing organ probably comes about when the intrinsic muscle fibres contract, respectively relax, around the central blood sinus. When retracted into its hollow, the organ becomes thicker (110 μm) and shorter (125 μm), and its tip does not reach to the opening. When stretched out, it was seen to project at least 40 μm out of its opening while at the same time its terminal part becomes more elongate (90 μm) and awl-shaped. The surface of the whole structure is unciliated, and lined with a thin cuticle. The pointed tip has a small pore leading into a group of a few (glandular?) cells with elongate nuclei (Fig. 7A).

Muscles   The anterior and posterior adductor muscles are of equal size and show no obvious subdivisions.
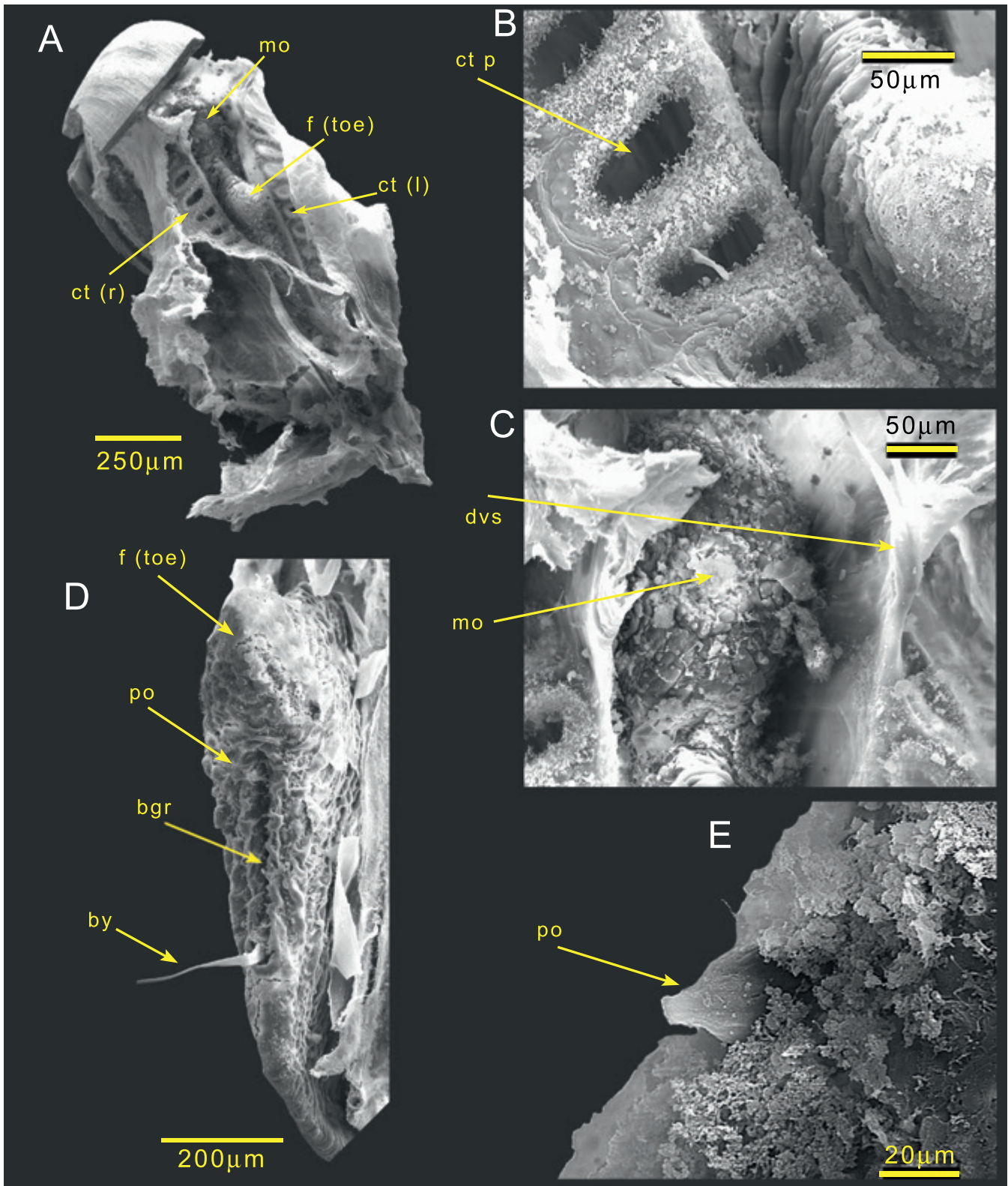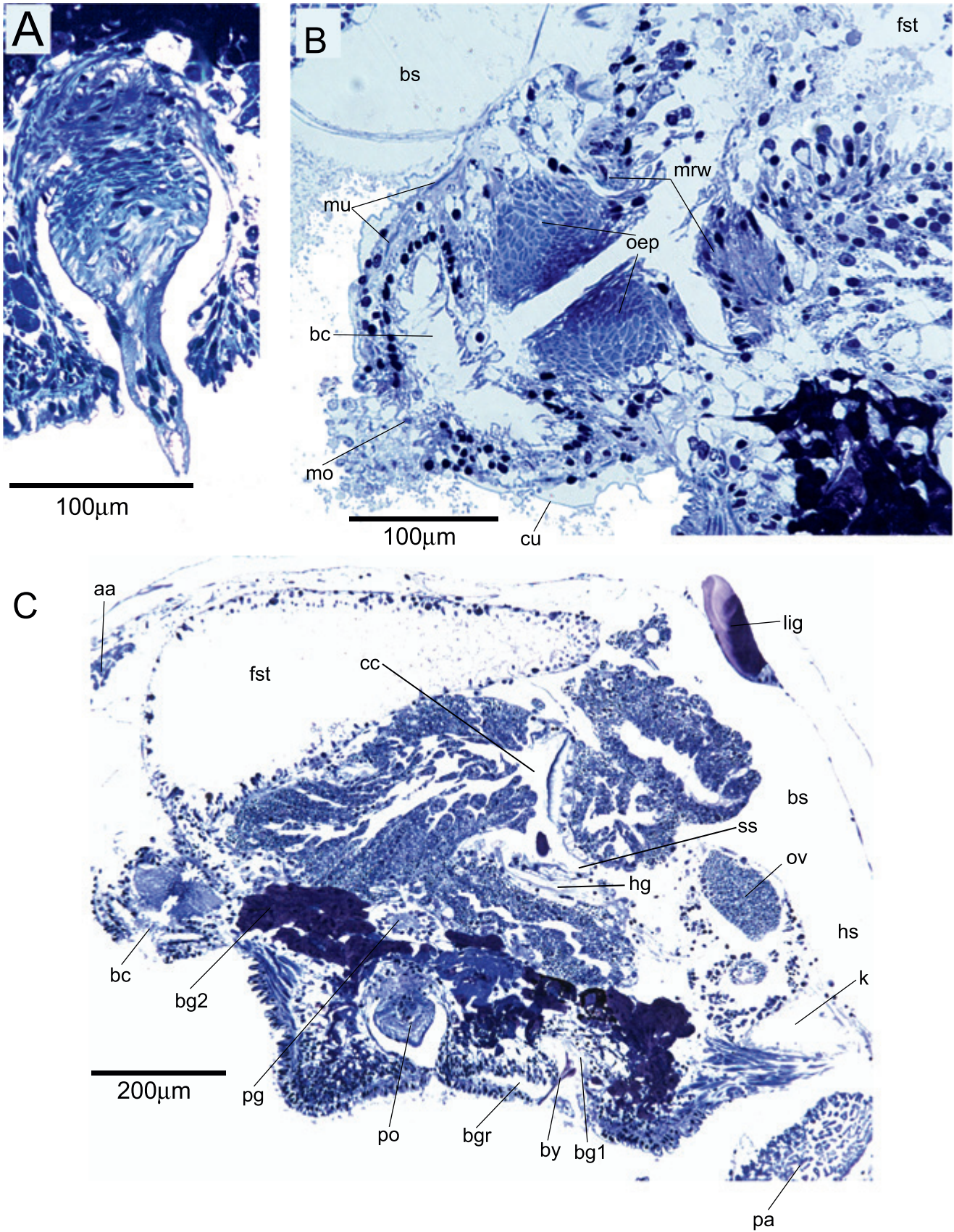
Figure 5 *Draculamya porobranchiata*. Scanning electron micrographs of soft parts following critical point drying. **A** whole specimen ventral view. **B** detail of the ctenidial pores. **C** detail of the buccal region. **D** view of the sole of the foot. **E** Lateral view showing the puncturing organ protruding from the foot.
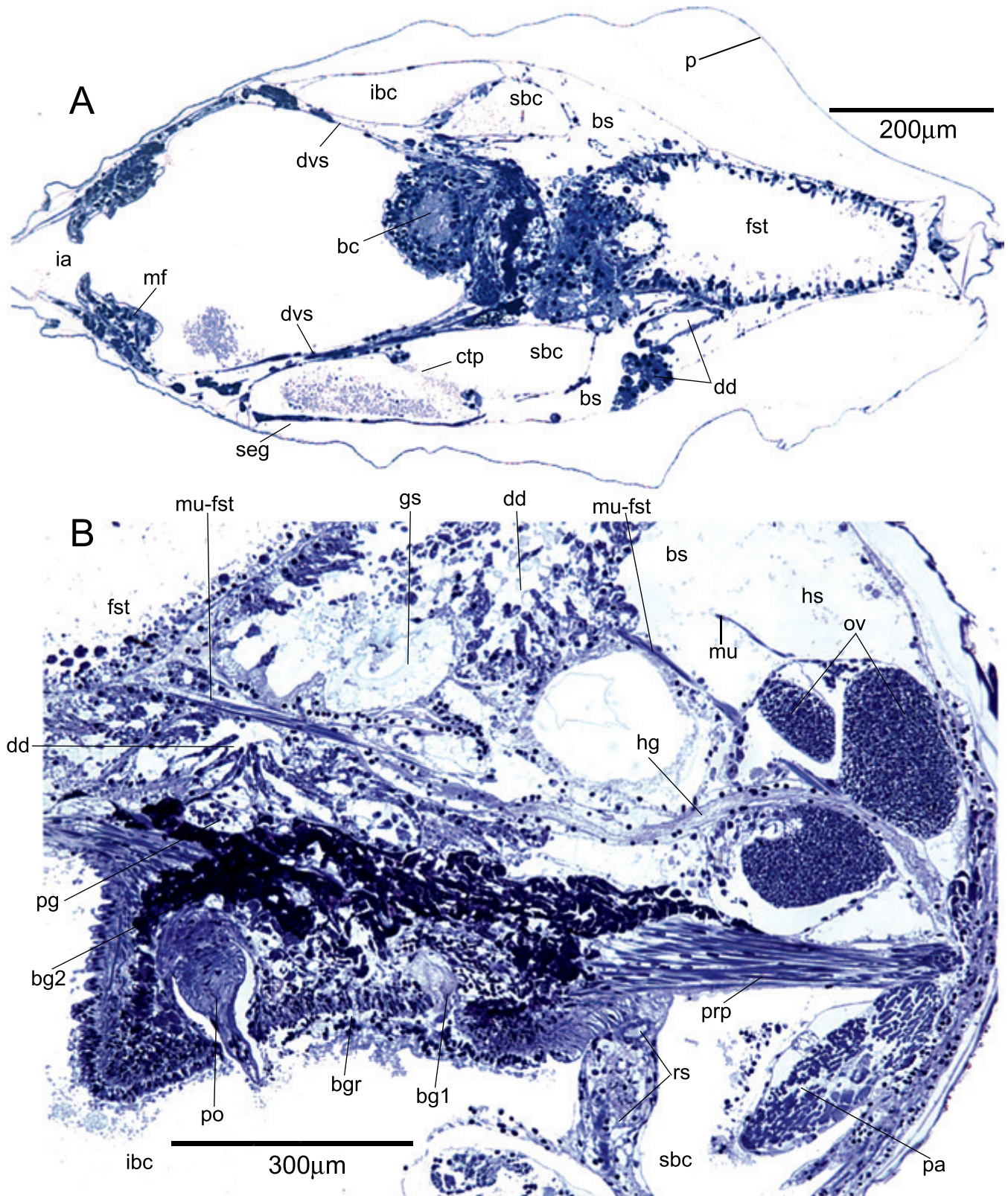
Figure 6 *Draculamya porobranchiata*. Toluidine blue-stained 2-μm thick transverse (**A**) and sagittal (**B**) sections.

The anterior paired retractor pedis muscle is inserted on the shell immediately dorsal to the adductor scars. Most of its fibres terminate behind and lateral to the oesophageal region, while others either continue to the anterior part of the foot or merge with the posterior retractor

Figure 7 *Draculamya porobranchiata.* Toluidine blue-stained 2-μm thick sections. **A** longitudinal section through puncturing organ. **B** sagittal section through mouth and oesophagus. **C** sagittal section through visceral mass and foot.

pedis muscle. The latter muscle is very powerful and has a ventral division which terminates in the hind part of the foot near the byssus gland (Fig. 6B). It is divided into two along its posterior course (Fig. 9B). The major part of the muscle proceeds forwards to separate the digestive gland and the pedal ganglia from the gland complex of the foot. However, paired minor branches of the muscle run in among the digestive diverticula to spread upon the antero-ventral wall of the fore stomach (Fig. 6B). Paired series of slender muscles issue from the posterior pallial wall of the 'heart sinus' (see later) immediately lateral to where the posterior pedal muscles attach. These muscles have a more or less parallel course, traverse a large median blood sinus and split up into many smaller muscles before they attach to the postero-ventral wall of the fore stomach (Fig. 6B). A pair of short muscles connecting the antero-lateral wall of the fore stomach with the pallial epithelium originates near the attachments of the anterior adductor.

Two very weak protractor pedis muscles are inserted on the shell just below the anterior adductor. Some of the fibres of these muscles attach to the front wall of the fore stomach.

*Alimentary tract* No remains whatsoever of labial palps could be detected in any of the studied specimens.

For most of its length, the alimentary tract has a structure that is most unusual for a galeommatoidean bivalve. The mouth opening is a small pore, situated on a domed cushion of tissue and leading into a hemispherical and thin-walled buccal cavity (Figs 4C, 7B, C). The exterior epithelium produces a continuous, fairly thick, light-staining cuticle while each of the epithelial cells lining the interior of the cavity has individual cuticular appointed excrescences. The latter are especially long and even tooth-like all around the entrance to the oesophagus. A few radiating muscle cells are sandwiched between the two epithelia. In a few specimens the wall of the buccal cavity had contracted, resulting in a widening of the mouth opening. The oesophagus is short (120 µm) and for most of its length (75–80 µm) supplied with a 40–50 µm thick and prominent circular musculature, and interiorly covered with a thin squamous non-ciliated epithelium (Fig. 7B). Posterior to the muscle apparatus and separated from it by a short circular groove is a thin ring wall, partially composed of radiating fibres, that marks the transition to the stomach.

The stomach is divided into two distinctly separated parts, a large dorsal fore stomach and a ventral cavity that contains some of the attributes of a normal bivalve stomach while at the same time forming part of the digestive diverticula. The fore stomach communicates with the ventral cavity via a broad opening in its mid ventral wall. The fore stomach, into which the oesophagus leads directly, is a very spacious, elongated sac. It is situated dorsally in the visceral mass and extends back to near the middle of the body; in some specimens almost to the level of the ligament (Figs 4A, 6A, 7C). In horizontal sections the fore stomach is seen to be broadest anteriorly, and to taper regularly backwards. The total length and maximum height of the fore stomach in a 1.7 mm long female is 650 µm and 240 µm respectively. In another female the total length measured 760 µm and maximum height and width 300 and 350 µm, respectively. The dorsal wall of the fore stomach is tethered to the pallial epithelium by many short connective tissue fibres. The many muscles which attach to the fore stomach have been mentioned earlier.

The fore stomach is lined with a gastric epithelium which is partly glandular. The most conspicuous cell type is evenly scattered all over the interior wall. These cells have a basal oval nucleus and an apical conical, ca. 12 µm long portion. In some areas of the stomach, especially anteriorly or around its mid ventral opening, they become clavate or even drop-shaped and finally release most of their contents into the gastric cavity as spherical droplets laden with minute faintly staining granules. Otherwise the gastric epithelium consists of many cuboidal to squamous non-ciliated and non-glandular cells. A very thin muscle sheet invests the exterior walls of the fore stomach.

Ventrally the fore stomach opens into the large cavity which, for want of a better term, we have called the 'central' chamber and into which the digestive diverticula empty by way of wide paired lateral and one large ventral opening (Figs 7C, 8A, C). Moreover, the anterior and lateral walls of the chamber are histologically indistinguishable from the digestive diverticula. Only along a narrow, median, 80–120 µm broad, strip on the dorsal and posterior walls, does the central chamber possesses some of the
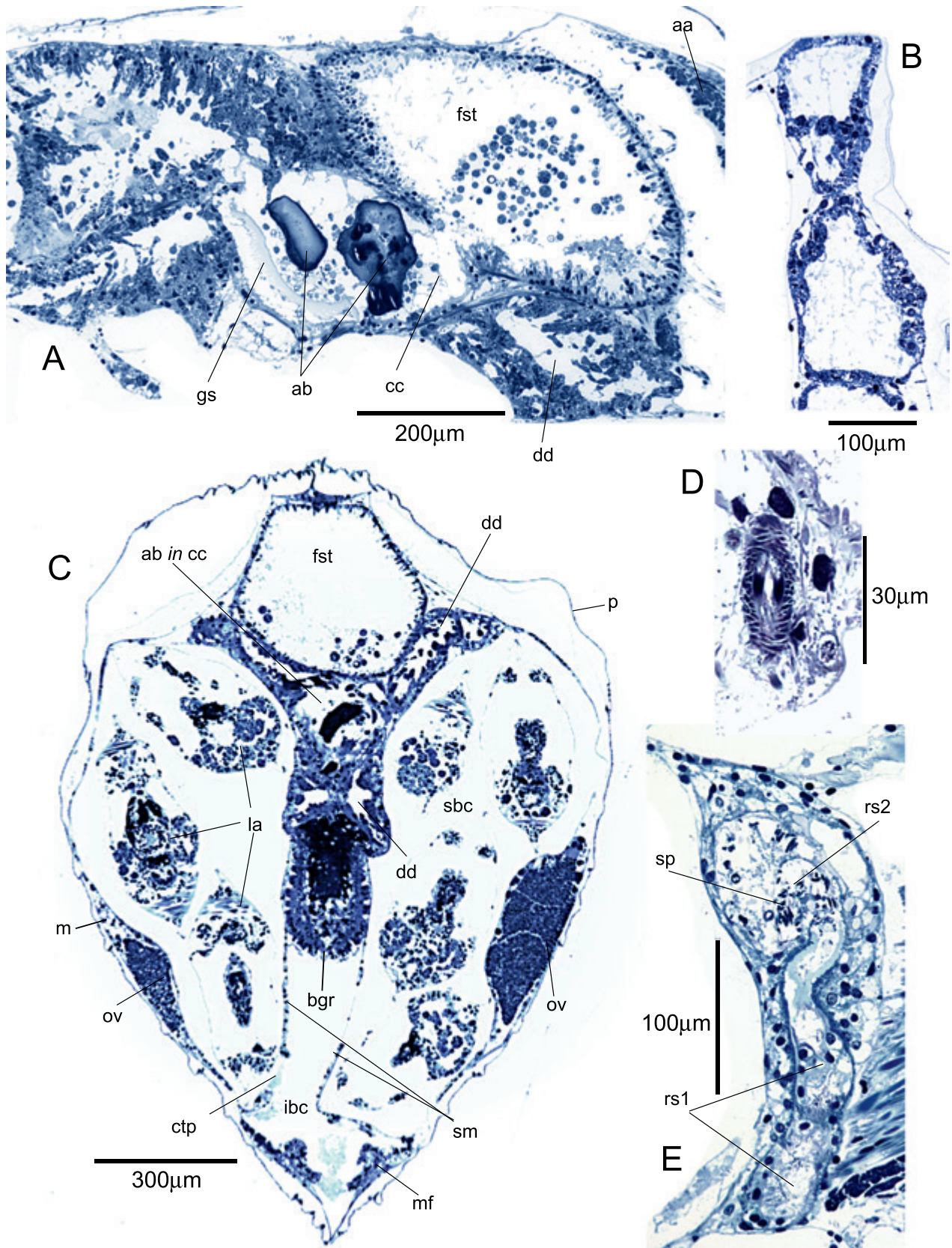
Figure 8 *Draculamya porobranchiata*. Toluidine blue-stained 2-µm thick sections. **A** sagittal section through fore stomach, 'central cavity' and part of the digestive diverticula. **B** digestive diverticula in a resting state. **C** transverse section of entire body in front of hinge. **D** transverse section of distal part of receptaculum seminis. **E** longitudinal section through receptaculum seminis.

characteristics of a true bivalve stomach. Its roof, extending backwards from the opening to the fore stomach, is lined by a ciliated cuboidal epithelium. The posterior wall of the central chamber is clothed by a glandular epithelium which produces a prominent, up to 15 μm thick gastric shield, which in many specimens seem to have the shape of a forwardly open, wide but incomplete funnel. A short style sac lined by a uniform ciliated cuboidal epithelium, opens into the narrow part of funnel-shaped shield (Fig. 7C). The style it produces is elongate, up to 185 μm long and 25 μm broad and may project far into the cavity of the chamber, but in some specimens is difficult to identify. An opening very close to that of the style sac leads into the mid gut, which without forming any loops, continues backwards directly into the hindgut and rectum (Fig. 6B). The rectum passes over the kidney, through the 'heart blood sinus' (see later) and over the posterior adductor muscle to finally open by way of the anus. Throughout its length, the mid gut is very slender, has a narrow lumen without a typhlosole, and is lined by a richly ciliated cuboidal epithelium. Pellets were never found in the intestine or rectum. Both are probably only engaged in fluid transport.

The digestive diverticula comprise two lateral parts, which are placed between the fore stomach, the roof of the suprabranchial chamber and those parts of the ovary which lie in the mantle (Fig. 8C). Each of them extends backwards along the side of the fore stomach to near the hinge. Another unpaired portion extends from the central chamber in a ventral direction towards the foot (Fig. 7C). All diverticula are simple, large-lumened sacs and are lined by a single type of digestive cells that are sometimes irregularly cuboidal and up to 30–40 μm high. Other such cells may be elongate, clavate, or drop-shaped and, protruding far into the cavity of the diverticula or the central chamber, may reach a length of 100 μm or more. Irrespective of their shape, the digestive cells have a ca. 8 μm large basal nucleus with a small distinct nucleolus and a cytoplasm containing a multitude of inclusions of many sizes which stain strongly with toluidine blue. These cells are hardly glandular by nature, as the secretory droplets which sometimes do occur in the central chamber are reminiscent of those produced in the fore stomach and have most likely

originated there. No ciliation occurred anywhere in the digestive diverticula and the pyramidal cells of other bivalves, could not be identified.

The digestive diverticula varied enormously in volume in specimens of the same size. In three specimens, they had not only decreased in extension to a fraction of the size seen in the other bivalves, but the individual cells had shrunk to a height of only 5–15 μm (Fig. 8B).

No remnants whatsoever of ingested organisms were found in any of the stomach parts or digestive diverticula of the nine sectioned specimens. In two specimens, part of the fore stomach contained a clotted substance. A few, but very large, amorphous acellular bodies that stained intensely with toluidine blue invariably occurred within the larger cavities of the digestive gland, the central chamber or, exceptionally, in the fore stomach (Figs 8A, C, 9A). Because of their size and yellowish brown colour, they could sometimes be seen from outside through the semi-transparent shell of whole animals.

The ctenidia and seminal receptacles   Only the inner demibranch is present. This has been reduced in that the normal filament array is absent and replaced by a single row of gill slits pores (Figs 5A, B, 8C). The traditional gill filaments have been reduced to short bridges separating neighbouring gill pores, but they are still supported by skeletal rods. The pores are oval in outline and measure 60–65 μm in length (parallel with the transverse plane of the body and gill) and 30–35 μm across. The number of pores per gill, counted from serial sections in a few female specimens, was 9 or 10.

The ctenidial axis has been dislocated from its usual dorsal position in the mantle to a line that runs more or less along the ventral margin of the part of the ovary, which is included within the mantle (Fig. 8C). This may be connected with the unusual intrusion of the ovary into the mantle. The gill pores lie in a suspensory membrane that issues from the gill axis and connects to the sides of the foot along a line where the glandular and muscular interior meets the digestive diverticula (Figs 4D, 8C). Afferent and efferent branchial veins could not be identified. The membrane consists of two epithelia of non-ciliated and exceedingly thin and flattened cells arranged back to back and has an average thickness of ca. 3 μm. The suspensory membrane
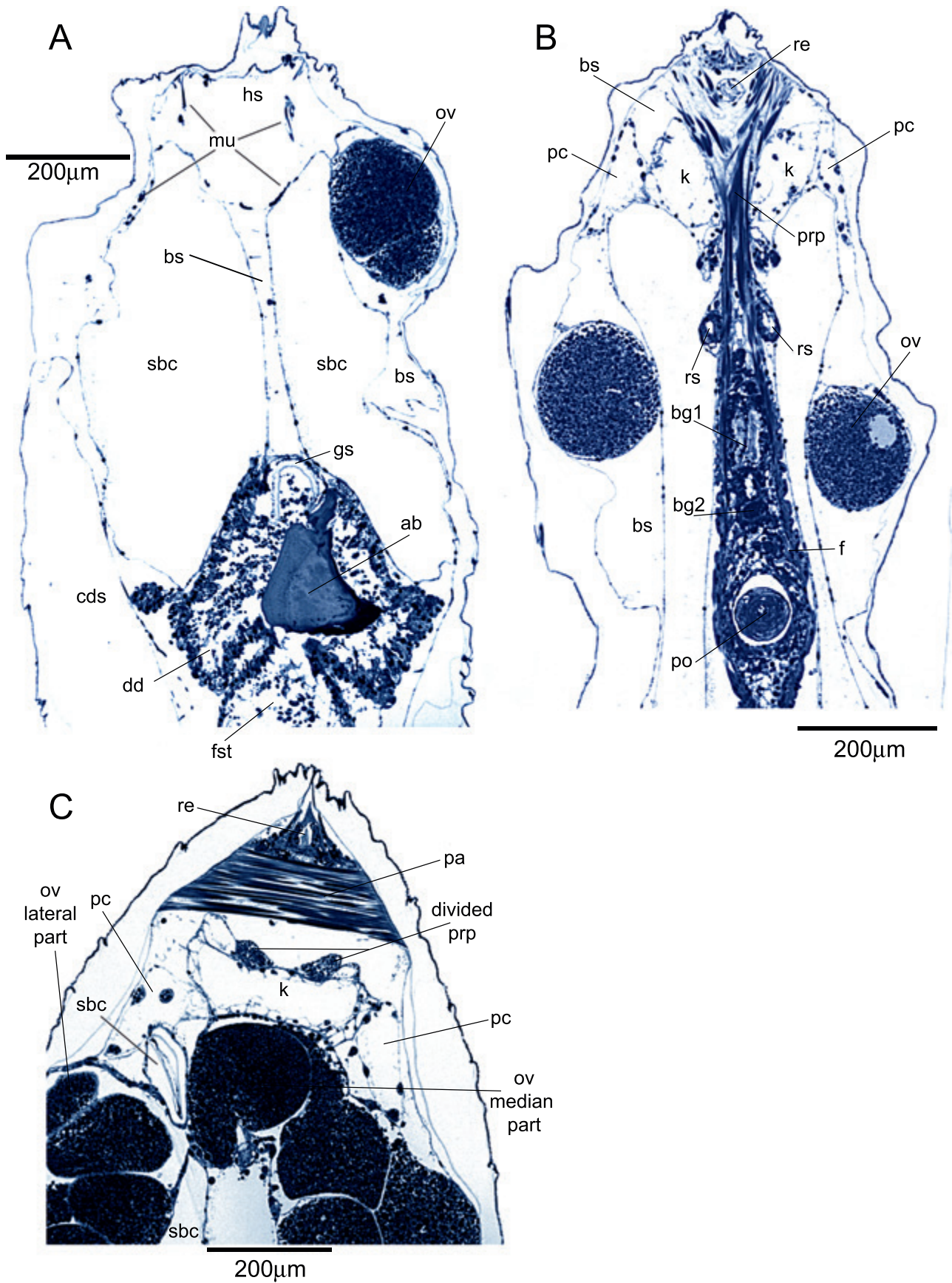
Figure 9 *Draculamya porobranchiata*. Toluidine blue-stained 2-µm thick sections. **A, B** horizontal sections at the level of the stomach (**A**) and the foot (**B**). **C** transverse section of posterior dorsal part of body.

bulges down into the mantle cavity with the row of gill pores forming the bottom of the bag. The spacious suprabranchial chamber above each gill serves as a brood pouch. No muscle cells are present either in the membranes or around the gill pores. Because of the simple structure of the gill, there are neither interfilamentary nor interlamellar junctions. Each gill pore is richly provided with cilia. Most of them clearly correspond to the lateral cilia of a normal gill slit, but whether frontal and laterofrontal cilia are present, is difficult to tell. A ciliated food groove along the line of gill pores is definitely absent.

Behind the last gill pore, the suspensory membrane of each gill swells along its edge to a thickening that contains a seminal receptacle (Figs 6B, 9B). Each receptacle consists of a slightly sinuous tube. The terminal parts of the two seminal receptacles lie dorsally in that part of the suspensory membrane closest to the foot and not far from each other. From there, each tube takes a ventro-lateral course to end where the membranes fuse, first with one another behind the foot and next with the muscular bridge separating the inhalant/pedal and exhalant apertures.

Each seminal receptacle is divided into three parts (Fig. 8D, E). The terminal portion of the receptacle is lined with a cuboidal vacuolated epithelium and has a minute lumen. At the blind end the epithelium appears ciliated in some specimens. The next, or middle part, is more spacious and barrel-shaped, ca. 50 μm in diameter, and provided with a low epithelium. This is where the majority of the unoriented sperm are found lying in a finely granular substance. Their number was always moderate, except for one non-ovigerous bivalve, in which the spherical middle part was crowded with sperm. From the middle portion a rather long and very narrow duct surrounded by a fine circular musculature (Fig. 8D) leads to the small pore which opens on the bridge separating the inhalant and exhalant apertures. A study of section series of several specimens confirmed that the receptacles open onto the infrabranchial, not the suprabranchial surface of the bridge.

No sperm sacs, spermatophores or any other containers with sperm were found in the gills or at the orifice of the seminal receptacles.

The female reproductive organs All of the sectioned specimens were females. The ovary is very voluminous in females about to spawn their eggs. The major part consists of paired lateral portions placed dorsally in the posterior two-thirds of the mantle, which causes it to bulge into the brood pouch (Fig. 8C). The two portions are united with a minor, median one, located behind the level of the visceral ganglion and hinge (Fig. 9C). In females with large ova still in the ovaries, it was impossible to locate the genital openings, but in a female that had quite recently spawned its eggs the oviducts were wide open. Each formed a short, non-ciliated canal which opened dorsally into the posterior part of the brood pouch. Most likely, the oviducts are temporary structures that form only at the time of spawning by fusion of the ovarian wall with the brood pouch. In ovaries with mature ova, small previtellogenic oocytes of the second generation were few and scattered, although always quite numerous in the unpaired median portion. In individual ovaries, all the oocytes were at the same stage of development and about the same size. In specimens with apparently full-grown and not crowded and compressed oocytes, they were spherical, filled with yolk and measured 310–320 μm in diameter. The number of such oocytes calculated from sections of two specimens were 9 and 10. Eight spherical blastulas of another female measured ca. 350 μm across. This female had extremely shrunken ovaries and an ovarian wall with many minute oogonia or oocytes having a dark-staining nucleus and with almost no cytoplasm.

A few sperm cells occurred in the unpaired portion of the ovary of a 1.5 mm long female with large ovarian ova. The sperm cells are elongate, ca. 8.5 μm long and of a uniform diameter of ca. 1 μm. Length and diameter compared well to that of the sperm cells found in the seminal receptacles.

The embryos of a single brood were seen to develop synchronously in all six brooding females indicating that the ova are spawned and fertilized simultaneously. The number of embryos or larvae in the brood pouch in four females counted from the section series was 6, 8, 11, and 15, while a single dissected female contained 14 larvae. Three of the nine sectioned bivalves were non-ovigerous.

The development of *D. porobranchiata* is modified because of the large amount of yolk in the ovum and the suppression of a free-swimming

veliger larva. Embryonic development is direct and the young are released as miniature adults. The SL of the most advanced shelled larvae in two females is 420–430 µm, and in a third one 470 µm. The general lay-out of the anatomy of oldest larvae reflects that of the adult in most respects. Development of the nervous system and kidney is precocious and all the major muscles are present. The number of gill pores, still devoid of cilia, is small, three or four. The digestive diverticula, two lateral and one mid-ventral, still containing a few large yolk granules, are well-developed hollow sacs and the gastric shield recognizable where the sacs meet. The fore stomach is a small vesicle with a simple epithelium, while the short oesophagus is surrounded by a relatively thick circular musculature. While the byssus gland (without a byssus) could be identified, not even a rudiment of the puncturing organ had developed.

Nervous system and sense organs We identified the three major pairs of ganglia, the cerebro-pleural, pedal and visceral. The pedal ganglia (Fig. 6B) lie very close together and the statoliths they contain are spherical.

SEM showed what might represent a sense organ placed in the midline at the frontal base of the foot and shortly behind the mouth. It consists of an accumulation of what appears to be long, slender cells radiating in all directions. However, it was difficult to identify and study the organ on the sections.

Pericardium, kidney, and circulatory system There are two, left and right, pericardial cavities, which do not intercommunicate. They are located within the mantle immediately under the shell and are squeezed in between the kidney, the ovaries and the suprabranchial chambers. Far posteriorly each of them borders upon the large 'heart blood sinus' (see below). The epithelium of the pericardial cavities consists of typical squamous podocytes, the large rounded nuclei of which protrude into the lumen (Fig. 9B, C). The reno-pericardial ducts are extremely small, short and lined by a few squamous ciliated cells.

The kidney (Fig. 9B, C) consists of two paired sacs located within the mantle, ventral to the ovaries, but fuse immediately behind the visceral ganglia to form a single large unpaired sac.

This kidney sac lies between the posterior pedal retractor muscles (ventrally) and the median part of the ovary, the suprabranchial chambers, and the paired pericardial sacs (dorsally). The kidney sacs are slightly subdivided by a few septa and invested with cuboidal epithelial cells with small basal nuclei and a vacuolated cytoplasm. No solid excretory concretions were ever present in the cells or in the kidney's lumen. The contents of the kidney are excreted by way of paired and heavily ciliated nephroducts, which open dorsally in the suprabranchial cavity.

A normal bivalve heart consisting of paired auricles discharging into a single median ventricle is absent in *D. porobranchiata.* In its place a spacious blood sinus, or 'heart sinus', lies beyond the pallial epithelium and between the unpaired parts of kidney and gonad and the posterior pedal retractors (Figs 6B, 9A). Having passed above the gonad and kidney, the rectum traverses the 'heart sinus'. Anteriorly the sinus communicates with another and much larger median blood sinus (Fig. 9A), which extends forward to embrace the digestive diverticula, all sides of the fore stomach, and further on to the anterior adductor. In a bivalve with a normal heart, this sinus would correspond to the anterior aorta. The communication between the two sinuses is wide in the dorso-ventral plane, but constricted in the horizontal plane. The series of muscles that issue from the posterior pallial wall of the 'heart sinus' and passes through the median sinus to attach to the posterior wall of the fore stomach have been mentioned earlier. At a level behind the fore stomach the large median sinus communicates with paired pallial sinuses, which lie in the mantle and surround the lateral parts of the ovary (Fig. 9A, B). Posteriorly the pallial sinuses open into the left and right sides of the 'heart sinus'.

For most of its course, the median blood sinus is enclosed between the extremely flattened epithelia of the right and left suprabranchial chambers, while the pallial sinuses lie between the mantle epithelium and the epithelia of both suprabranchial chambers. The connective tissue walls of the sinuses are so thin and applied so intimately to the epithelia of the suprabranchial chambers that it is almost impossible to separate one from another. All of the sinuses contain scattered connective tissue fibres and smaller muscles.

DISCUSSION

Mantle and mantle cavity   The middle, mantle fold in many galeommatoideans is often reflected for a shorter or longer distance over the surface of the shell. In the present species, however, this fold is so moderate in size that it can hardly be expanded beyond the shell margins.

The paired muscular septa spanning the front part of the infra-brachial chamber are novel structures that have no equivalents in any other galeommatoidean. About their possible role in the species' food uptake, see later.

Muscles   The anterior and posterior retractor pedis muscles have the same general course as in other galeommatoideans, but it is remarkable that many of the fibres of the anterior retractor pedis muscle terminate in the oesophageal region. The course of the protractor pedis muscles in several species has been investigated by Deroux (1961) and was found to be inserted on the shell either dorsal or ventral to the anterior adductor, or in such a way that it splits the adductor into two unequal halves. Since the course of this muscle might have systematic implications (Jespersen *et al.*, 2007) it is worth noting that other species in which the protractor muscle is inserted as in *D. porobranchiata* include such diverse species as *Kellia suborbicularis*, *Bornia corbuloides*, *Lasaea rubra*, and *Kurtiella bidentata* (Deroux, 1961; Oldfield, 1961).

The fore stomach of *D. porobranchiata* is supplied with a number of muscles that may pull it forwards or backwards or, if they contract in concert, may aid in expanding it. Some of these muscles are derivatives of existing ones (the protractor and the posterior retractor pedis muscles), while others are independent of them. However, similar muscles have not been discovered in other galeommatoideans, or at least have remained undescribed. Most likely, they are novel structures that have arisen in connection with the transformation of the original galeommatoidean stomach which has taken place in *D. porobranchiata*.

The puncturing organ   Nothing similar to the puncturing organ has been described in any other bivalve and we are unable to explain how it has originated. Its position, within a depression at the head of the byssus groove, might suggest that it evolved as a specialization of the byssus apparatus, although not of the glands producing the byssus. However that may be, we are convinced that it has evolved in tandem with the radical transformation of the structures involved in feeding (gills, labial palps and gut).

Alimentary tract and feeding   The vast majority of the Bivalvia feed using the ctenidia and/or palps as the primary feeding organs. These feeding structures enable a wide range of feeding types, primarily suspension feeding, some deposit feeding and for a few, carnivory. The galeommatoideans are suspension filter feeders, although in some this is supplemented by 'pedal sweep feeding' (Reid *et al.*, 1992). A few species are claimed to be parasitic. Malard (1904) suspected the galeommatoidean *Devonia perrieri* to lead a parasitic mode of life by sucking the tissue of its synaptid host into the opening of the byssus gland, a belief that has never met with approval (Ohshima, 1931). To date the only reliable evidence of parasitism in any bivalve is provided by Allen (2000), in the galeommatoidean *Kurtiella tumidula (= verrilli)*, to be discussed later.

In the galeommatoideans the mouth is a simple fissure level with the surrounding surface, or placed at the tip of a small snout as in for instance *Epilepton clarkiae* (Jespersen *et al.*, 2007) and *Koreamya arcuata* (Lützen *et al.*, 2009). It leads into a tubular, heavily ciliated oesophagus (Pérès, 1937; Oldfield, 1961; Narchi 1966). The mouth in the present species is a circular pore at the end of a hemispherical buccal cavity, the interior wall of which is lined with a cuticularised armature of unknown hardness and dubious function. The oesophagus is non-ciliated throughout and lined with a flattened epithelium surrounded by a heavy circular muscle sheath, such as occurs in no other known galeommatoidean (except for *Kurtiella tumidula*, see later), but which strikingly resembles the oesophageal suction pump of the Septibranchia.

In many galeommatoideans, the boundary between the oesophagus and the stomach is marked by a constriction (Pérès, 1937 and Lützen, personal observations). If, as we believe, this corresponds to the muscular ring wall in *Draculamya*, the fore stomach is a derivation from the bivalve stomach rather than from the hind part of the oesophagus. While its strange structure has no equivalent in other galeomma-

toideans, it obviously functions in storing large volumes of food, and in all probability liquid food, as particulate matter or solid objects of any size were never found within it.

The galeommatoidean stomach belongs to type 4 according to the classification of Purchon (1958). What in the 'central chamber' is leftover from this stomach type are a gastric shield and a style sac which opens very close to, but separate from, the orifice of the midgut. All complex structures engaged in handling particulate matter such as a dorsal hood, sorting fields of ciliated ridges and grooves and a typhlosole flanking an intestinal groove, have disappeared. The many small orifices of the digestive diverticula into the stomach have been replaced by three enormous openings that have virtually obliterated the normally sharp boundary between them and the stomach. The *Draculamya* stomach is strictly bilaterally symmetrical in contrast to the normal bivalve stomach, or rather it may have retained the perfect original symmetry of the larval stomach as seen in *Lasaea rubra* (see Oldfield, 1964). It is worth noticing that the stomach in the predatory Septibranchia has also evolved a bilateral symmetry (Purchon, 1956) although it differs in most other respects from that of *Draculamya*.

The architecture of the digestive diverticula in *D. porobranchiata* has also distanced itself from the system of ciliated primary and secondary ducts ending in masses of blind acini in the filter-feeding bivalves. In stead they have turned into large-lumened sacs with a single type of cells that are often enlarged and protrude far into the cavity. Combined with the total absence of a ciliation, this means that an orderly circulation of the contents through the diverticula has been abandoned.

The strongly reduced gills, the absence of labial palps, and the simple structure of the stomach is evidence that *Draculamya* is incapable of taking up, sorting and handling particulate matter. Similarly, a predatory mode of feeding can be excluded since there are no structures that could catch or, except for the muscular oesophagus, perhaps crush any prey. This is supported in that remnants of foreign organisms or faecal pellets were never found in any parts of the alimentary tract. Clearly, the structure of the alimentary tract of *Draculamya* is well adapted to take up, store and digest liquid food. The fluid, whether blood or coelomic fluid, may be pumped by oesophageal peristalsis into the spacious fore stomach and stored there until its later transfer to the 'central chamber' and the digestive diverticula. If the secretion, produced by some of the gland cells in the fore stomach, contains enzymes, some extracellular breakdown of the fluid food may take place here. Other enzymes are probably released from the crystalline style, together with the gastric shield the only remnant left of a normal bivalve stomach. The liquid food containing coelomocytes or haemocytes and dissolved organic solutes, whether subjected to a prior extracellular digestion or not, then enters the digestive cells by endocytosis as in other bivalves to be intercellularly digested. Morton (1956) demonstrated that the histology of the digestive diverticula of the intertidal galeommatoidean *Lasaea rubra* undergo a cycle that depends on the time of feeding. After a meal the digestive cells become loaded with ingested material and bulge into the lumen in a way resembling the state of the cells in most (six) of the sectioned *D. porobranchiata*. The diverticula in the remaining three specimens obviously represented a resting state prior to the next intake of food.

It is possible that the buccal cavity wall of *Draculamya* can be contracted so much that the cuticular excrescences, radula-like, may grate minute pieces off the skin of a host for ingestion. However, normal food uptake must, in some way, involve the action of the puncturing organ, since no other conceivable function than that of piercing the skin of a host can be assigned to it. As a holdfast organ it is less suited than the already existing byssus and a role as a weapon of defence is even less likely as the normal and effective reaction in bivalves to disturbances is closing the shell. We therefore imagine that it is used to stab and puncture the surface of a thin-skinned host to get access to the body fluid or blood after which the wall of the buccal cavity is closely applied to the wound whereupon oesophageal suction begins. Because of the position of the mouth within the shell and with limits to how much the valves can open, we find it probable that only minor body parts such as tentacles or filamentous gills of a host can be taken into the mantle cavity to be fed upon. However, the muscles of the septa in the anterior part of the mantle cavity most likely aid in drawing the mouth closer towards the shell margins.

In bivalves, ingested material is conveyed through the gut by ciliary action. In *D. porobranchiata,* the only ciliated part of the alimentary tract worth mentioning is the intestine, and transport elsewhere results mostly from muscular activity. Liquid food is pumped by the oesophageal ring muscles into the fore stomach, combined perhaps by an increase in its volume caused by contraction of the many minor muscles attaching to it. The fine exterior muscle layer, which invests the fore stomach, may assist in emptying its content into the 'central chamber'. Once arrived here, the food becomes slowly reduced by absorption into the digestive cells while surplus fluid is removed through the intestine. The amorphous bodies in the 'central chamber' and digestive diverticula are probably insoluble by-products of digestion, which instead of being voided, slowly accumulate in the gut throughout the life of the bivalve.

Reproduction   The gonad of galeommatoideans, irrespective of the sex, is placed in the posterior part of the visceral mass. Apart from *D. porobranchiata*, in only two other galeommatoidean species (of *Peregrinamor*) are the major parts located within the mantle (Shôji, 1938; Kato & Itani, 2000) while only minor parts of the gonad (ovary) are placed in the visceral mass.

All nine sectioned specimens (SL 1.3 to 1.75 mm) were females. The sperm cells in the ovary of a single non-ovigerous female (SL 1.5 mm) were probably left over from an earlier male phase. This is the only, but nevertheless plausible, indication that the species is a protandrous consecutive hermaphrodite. No specimens less than 1.3 mm SL occurred in the sample, perhaps because they were either not collected by the gear used on account of their small size, or were ignored when the material was later sorted out. It is to be expected that the males are in a size-group less than 1.3 mm in SL. In the three specimens with advanced larvae, there were large oocytes in the ovary, suggesting that the species is iteroparous, producing a succession of batches.

Incubating the ova within the suprabranchial brood chamber occurs in all galeommatoideans. Direct development in this group involves the substitution of the velum by a large cephalic mass, which serves as a storage of yolk. The cephalic mass in *Lasaea rubra* (Montagu) appears in post-gastrulas and disappears when the yolk has been consumed shortly before the larvae are released from the parent (Oldfield, 1964). As the few known developmental stages of *D. porobranchiata* only comprise blastulas, early and late gastrulas plus nearly fully formed juveniles, we do not know if a cephalic mass occurs in this species in the stages in between.

The SL of the prodissoconch measured on the adult shell (470–500 μm) compares to the size (470 μm) of the oldest of the brooded larvae. Although a few yolk granules were still left, the organs and systems of these larvae were nearly in the adult condition. It is expected that when they have reached their maximum size, they are able to start feeding soon after they are released. Because of the absence of the puncturing organ, the diet of the juveniles presumably differs from that of the adults. *D. porobranchiata* occurred only at dredge stations characterized by the glass-sponge *Pheronema carpenteri* and not at similar depths where the sponge was absent, suggests that it is dependent on one or more host species belonging to the fauna associated with *Pheronema*. Provided the spatial distribution of the host is restricted, a non-planktonic development in *D. porobranchiata* may be advantageous since it minimizes the risk of the larvae being swept away from a habitat where conditions are favourable for their further growth and development.

Most galeommatoideans produce relatively small (80–110 μm) eggs (various sources) and release the larvae as planktotrophic free-swimming veligers. A few species, however, are known to brood much larger, 300–400μm, ova that develop directly into non-planktonic larvae, which are released in a benthic crawling stage. Direct development among the Galeommatoidea is presumably most frequent in polar regions and known to occur in three arctic and two antarctic species (Zelaya & Ituarte, 2002; Petersen & Lützen, 2008), but may also take place at lower latitudes (Oldfield, 1964; Gage, 1979; Beauchamp, 1986; Morton, 1992; Iwasaki, 1996; Jespersen & Lützen, 2009). Larval development in deep-sea galeommatoideans is known only in *Kurtiella tumidula* from the Atlantic Ocean at 485–2178 m, which has planktonic larvae (Allen, 2000, as *Mysella verrilli*). *Draculamya porobranchiata* is the only known example of a deep-sea galeommatoidean in which the very large eggs are brooded and developed to a non-planktonic crawling stage. It is, therefore, an exception to the general trend that deep-sea

bivalves are predominantly non-brooders, which produce lecithotrophic eggs that develop into short-lived planktonic larvae (Ockelmann, 1965).

The seminal receptacles in *D. porobranchiata* cannot be derived from any of the various types of receptacles as yet known in other galeommatoideans. By far the most common type consists of paired pouches in the wall of the visceral mass, which open close to the genital apertures. In *Mysella sovaliki* MacGinitie 1959 the saccular receptacle is placed in the reduced outer demibranch (Petersen & Lützen, 2008). In a few other species, the receptacle is placed in the inner demibranch as in *D. porobranchiata*, but instead of the paired tubular receptacles of that species consists of an unpaired, open ciliated furrow along the two fused ascending lamellae (Lützen *et al.*, 2009). Irrespective of its structure, all these receptacles open into the suprabranchial chamber ensuring that the sperm, when released, have direct access to the spawned oocytes. *D. porobranchiata* is exceptional so far in that the receptacles open into the infrabranchial chamber. However, in a species that does not feed by filter feeding, such an arrangement is not necessarily disadvantageous. When sperm are released from the receptacles through peristalsis of the circular musculature enveloping the terminal duct, they are probably not being retained when sucked in through the nearest gill pores but pass unimpeded into the suprabranchial brooding chamber. The small number of stored sperm and a certain loss during passage of the gill is probably acceptable because of the moderate number of oocytes to be fertilized.

Ctenidia   The outer demibranch in many species of the Galeommatoidea is reduced or has been lost entirely (Passos *et al.,* 2005) something that has probably occurred independently in different groups (Ponder, 1971). In some species, the ascending lamella of the remaining inner demibranch has also undergone a certain reduction in length as compared to the descending one, but in only one species, *Mysella charcoti* (Lamy 1906), has it been completely lost (Passos *et al.,* 2005). The reduction has gone even further in the present species, in that the gill slits have been shortened to oval pores while the rest of the ctenidium has turned into suspensory membranes. There is no way to decide whether the single file of pores in *D. porobranchiata* represents the gills slits of the descending or the ascending lamella.

The role of the ctenidia in *D. porobranchiata* is discussed below.

Kidney, pericardium, circulatory system, and respiration   The heart-kidney complex of *L. porobranchiata* shows both resemblances and significant dissimilarities with that of other galeommatoideans. The pericardial cavity of the adult galeommatoideans have been described in several species and consists, as in other bivalves, of a single unpaired vesicle which surrounds the rectum and the heart (White, 1942; Oldfield, 1961; Narchi, 1966). The heart consists of left and right thin-walled auricles, each of which opens by way of an auriculo-ventricular valve into a median, tubular and more muscular ventricle, which is traversed by the rectum. The kidneys are paired sacs that fuse somewhere along their length in the midline. They communicate with the pericardium through two ciliated reno-pericardial ducts and discharge into the suprabranchial chamber by way of paired ciliated nephroducts. The kidney in *D. porobranchiata* conforms to this general model, although the reno-pericardial ducts are very much shorter than in other species (Oldfield, 1961; Rotvit *et al.*, 2007).

The absence of a heart in *D. porobranchiata* is probably related to the unusual paired condition of the pericardial cavities. In other bivalves, including the galeommatoidean *Lasaea rubra,* the pericardium arises from paired rudiments that later fuse, grow up dorsally to surround the rectum and fuse in the midline, forming a complete vesicle with outer and inner walls pierced by the rectum (Ziegler, 1885; Okada, 1939; Oldfield, 1964). The inner walls of this vesicle develops to form a cast upon which muscle cells later arise and arrange themselves to form the musculature of ventricle and auricles. The two apparently histologically normal pericardia in *D. porobranchiata* have probably arisen from such paired embryonic sacs, but have failed to fuse into a single vesicular pericardium. The failure of this has prevented the normal development of a heart.

In bivalves the ctenidial vessels form an essential part of the blood system, through which most of the blood circulates. If the extremely thin and membranous ctenidia of *D. porobranchiata* are at all vascularised, only a trickle of blood passes through them, and their respiratory role is

probably entirely negligible. This means that the water of the supra- and infrabranchial chambers are nearly equally rich in oxygen. Conditions for an easy gas exchange across the very thin combined walls of the large median and pallial blood sinuses and the suprabranchial cavity are therefore optimal and this is probably where the blood becomes oxygenated. We imagine that the major, and presumably only, role of the gill pores is to generate a steady flow of seawater into the suprabranchial chamber. In the absence of a heart and one-way valves in *D. porobranchiata,* it is difficult to envisage that the blood circulates unidirectionally. The many muscles to the fore stomach may pull it forward or backward or expand it and thus displace the blood masses which surround it, just as opening and closing the shell is likely to redistribute the blood in several of the sinuses. The large diameter of the blood sinuses and the resulting low resistance makes it easier to generate a flow through them.

Comparison with Kurtiella tumidula   This species deserves special attention because Allen (2000), basing himself on dissections and serial sections, concluded that it is probably a suctorial ectoparasite and if so the first one described among the Galeommatoidea. Possibly because of poor preservation, some of his observations were incomplete and our study of a single well-preserved specimen (see the following section and Figs 10 and 11) has shown that some of his conclusions are not tenable.

Contrary to *D. porobranchiata*, the mouth of *K. tumidula* lies at the end of a short proboscis (Figs 10B, 11A) and the alleged longitudinal musculature, the very reason why Allen believed the species to be suctorial, is hardly identifiable in our specimen. Overlooked by Allen however, at the base of the proboscis there is a short oesophageal suction pump reminiscent of that in *D. porobranchiata*, with the important difference that the lining epithelium in *K. tumidula* produces a covering of tooth-like excrescences (Fig. 11B). Perhaps, this muscular apparatus is used not only to inhale food, but also to masticate it. The stomach and digestive diverticula of *K. tumidula* are rather typical of a galeommatoid (Purchon, 1958), and show no similarity to the highly specialized stomach and aberrant digestive diverticula in *Draculamya*.

The ctenidia (inner demibranchs) of *K. tumidula*, on the other hand, could be conceived to represent an evolutionary stage leading to the condition in *Draculamya*. Among galeommatoid bivalves, a conspicuous non-respiratory membrane is known only in these two species. That the descendent respiratory area is much larger than the ascendant one in *K. tumidula,* combined with the fact that in *Mysella charcoti* the ascendant area has been lost (Passos *et al.*, 2005), could be taken to mean that the single series of gill pores in *Draculamya* represent that of the descendent lamella.

Apart from serving as a brood pouch, the only other ctenidial function in *K. tumidula* is respiration. In contrast to *D. porobranchiata*, heart-mediated circulation is of the ordinary bivalve type. It is significant that the visceral mass and mantle in *K. tumidula* are very solid (massive) and almost completely devoid of the extensive blood lacunae which in *Draculamya* serve for the uptake and distribution of oxygen.

Contrary to the rule in galeommatoideans, in which the gonads are placed in the visceral mass, a considerable part of them in *K. tumidula* (ovary and testis, Fig. 11D, E) and *D. porobranchiata* (ovary) lie in the mantle. It may also be significant that the paired seminal receptacles in both species are located in the posterior most part of the ctenidia, a location not shared by any other galeommatoid.

The two species differ with respect to the pericardium and heart, which in *K. tumidula* are normal, while in *D. porobranchiata* they are respectively reduced and entirely lost. The most significant difference between the two species, however, is that the muscular puncturing organ of *D. porobranchiata* is absent in *K. tumidula*.

The absence of labial palps, in both species, and the consequent loss of connection between the mouth and the gills strongly indicates that suspension feeding can no longer take place, and is further supported by the reduced nature of the gills. In *Draculamya* there is ample evidence that the food is fluid and that this fluid is accessed actively. In *K. tumidula* fluid-feeding is not so well supported and it is suggested here that surface particulate matter could be taken up by the short proboscis and further processed by the oesophagus and sorting structures retained by the stomach. Without a puncturing organ, access to body fluids is likely to be problematic
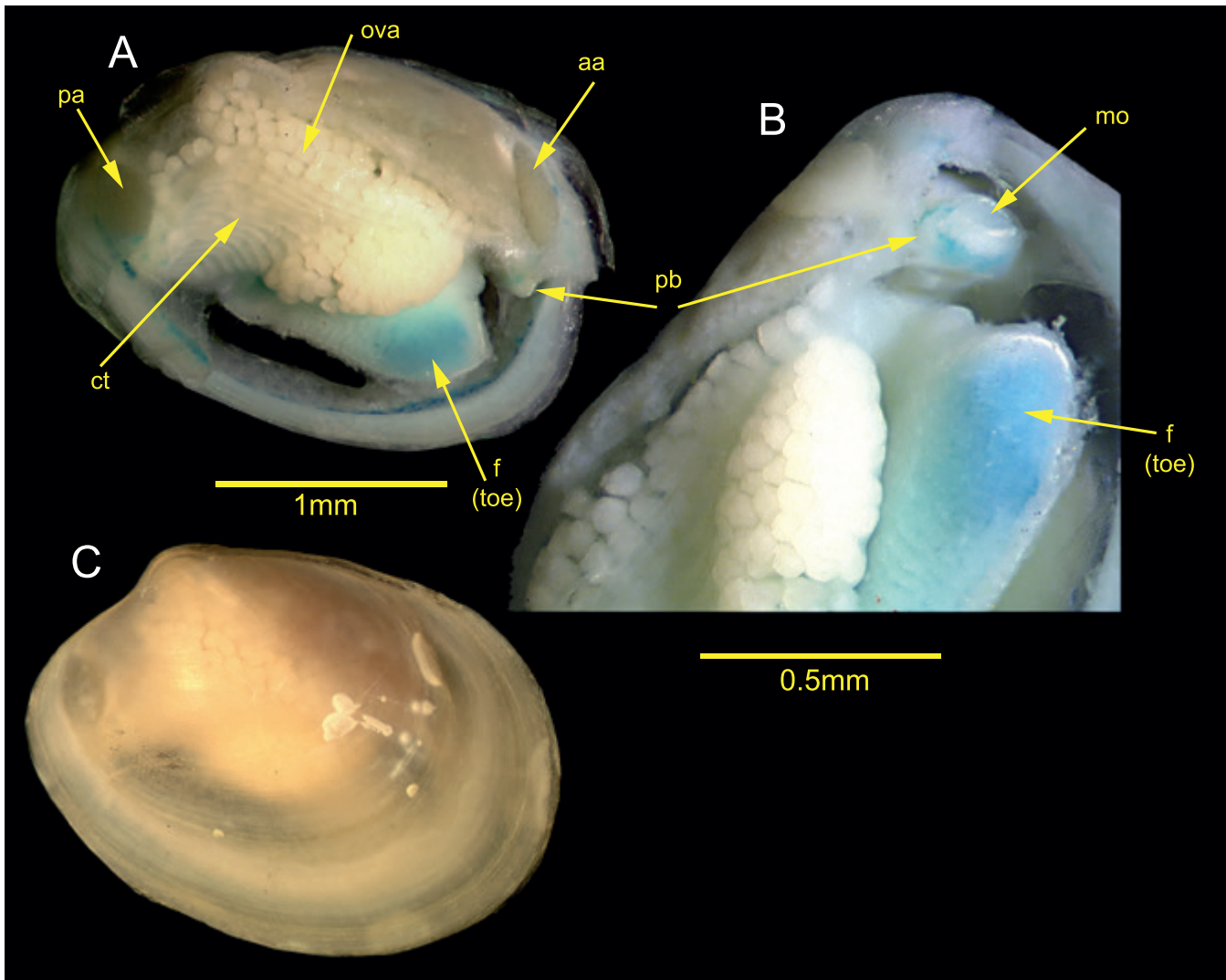
Figure 10   *Kurtiella tumidula*, Porcupine Bight. **A** gross anatomy after removal of right valve and partially stained with methylene blue. **B** oblique view of anterior to show proboscis. **C** whole specimen from the right side.

but when attached to its host *K. tumidula* could remove surface cells or detritus.

KURTIELLA TUMIDULA (JEFFREYS 1866), AMENDED DESCRIPTION

Alimentary tract   The mouth is placed terminally on a ca. 160 µm long proboscis (Fig. 10A, B). The first part of the oesophagus is lined by a tall cylindrical and ciliated epithelium with the nuclei placed near the middle of cells (Fig. 11A). Surrounding the epithelium there is a relatively thin connective tissue with scattered mucous cells that probably discharge on to the snout's surface, which is lined by a thin squamous epithelium.

Longitudinal muscle fibres running along the length of the snout, as described and illustrated by Allen, could not be identified. Behind the base of the snout the ciliated part of the oesophagus passes ventral to the anterior adductor muscle and continues into a short, ca. 55 µm long, well-defined muscular apparatus which was not noted by Allen. Internally it is lined by a cuboidal epithelium, which produces many solid excrescences or teeth that are apically split up into small bristles. Surrounding these there is a compact (40–50 µm) thick sheath of circular muscle fibres. Presumably, the whole apparatus is used to masticate ingested food.

As described by Allen (2000), the next (and last) part of oesophagus is deeply longitudinally grooved with broad ridges in between (Fig. 11D).
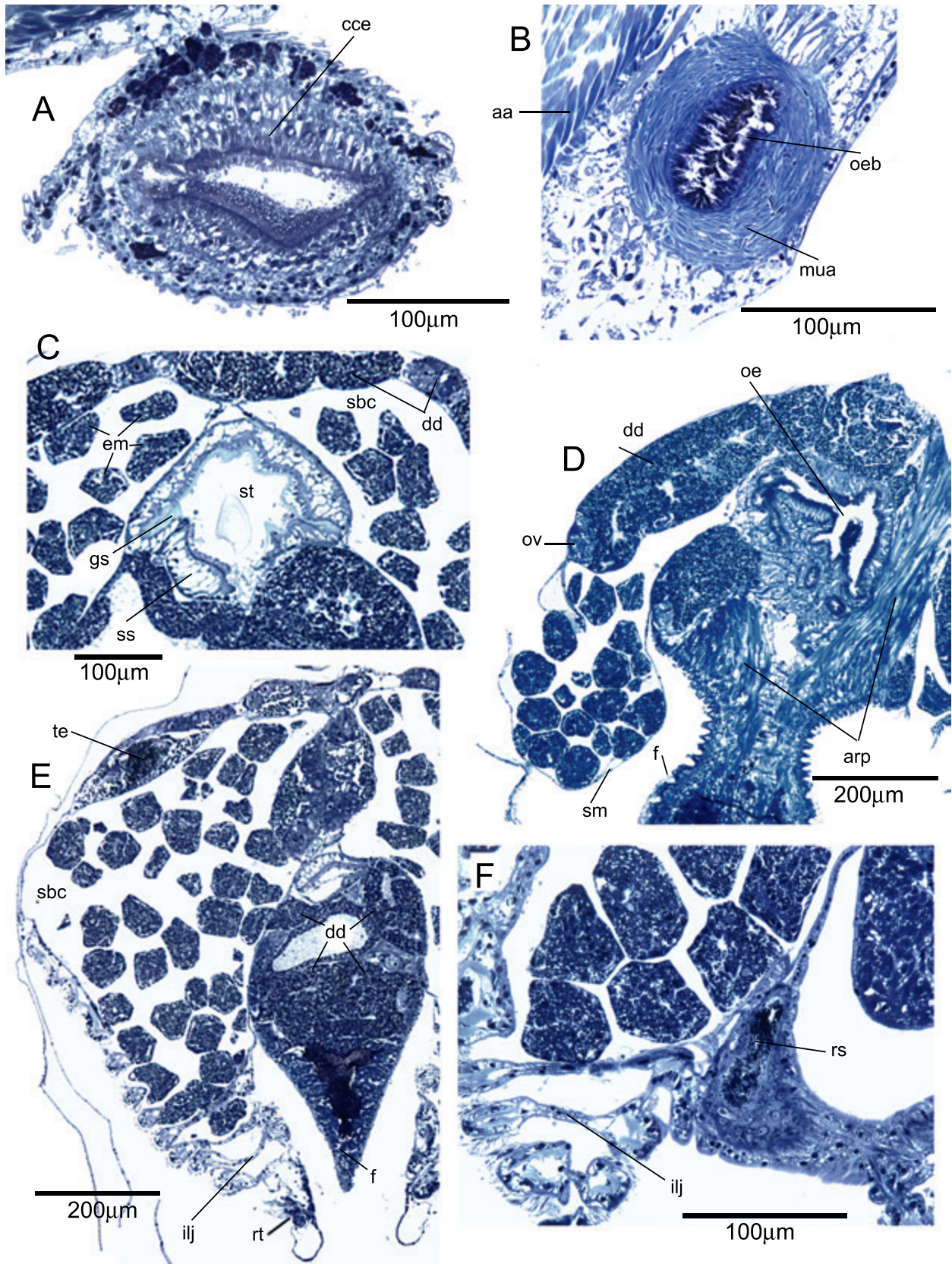
Figure 11 *Kurtiella tumidula.* Toluidine blue-stained 2-µm thick sections. **A, B** cross sections through base of proboscis and muscular apparatus. **C–F** transverse sections through the stomach region (**C**), the body at the oesophageal level (**D**), the body at a more posterior level (**E**) and the lower part of a ctenidium with the receptaculum seminis (**F**).

The profusely ciliated epithelium is tall to cuboidal, depending on whether it forms the ridges or the grooves. Posteriorly and ventrally, some of the grooves become isolated from the main lumen to form a small number of ciliated blind crypts.

Posteriorly the oesophagus leads into the stomach, (Fig. 11C) which, especially anteriorly, has irregularly folded walls lined by very large and short-ciliated cells with a light cytoplasm. The digestive diverticula are very prominent, surround the stomach and occupy not only the dorsal half of the visceral mass but also much of the mantle. They discharge by way of many ducts into the lateral and ventral part of the stomach (Fig. 11C, D). A locally thick gastric shield lines most of the posterior part of the stomach. The style sac forms a simple cone, opens widely into the hind part of the stomach and is directed posteriorly. The hindgut is confluent with the style sac and when leaving it dives in among the digestive diverticula to proceed almost without looping backwards to continue into the rectum. All along its length it is ciliated and of small diameter.

Ctenidia, brood pouch and seminal receptacle The absence of labial palps is confirmed. The ctenidia are represented by the inner demibranch only. Allen (2000) described and illustrated a small outer demibranch in some specimens with an SL < 2.0 mm, which may explain its absence in the present specimen. Each inner demibranch consists of a descending and an ascending lamella with respectively 12–13 and 3–4 almost horizontal gill filaments (Fig. 11D, E). Anteriorly the filaments are absent and both lamellae are represented by an extremely thin non-respiratory membrane consisting of two non-ciliated epithelia arranged back to back (Figs 10A, 11D). It is estimated that this membrane occupies half of the area of the ctenidium. Perfect transverse sections of the gill filament show a single tract of relatively short cilia on the frontal surface and a pair of lateral tracts of longer cilia. No latero-frontal cilia could be identified. There is a ciliated groove along the ventral margins of the ctenidium's respiratory part (Fig. 11E), which may be a rejectory tract, as it does not continue forwards to the mouth. A few interlamellar junctions span the space ventrally between the two respiratory lamellae (Fig. 11E, F). The demibranchs of the two sides are united behind the foot, but the series here is too imperfect to study the posterior part of the gills more closely.

The suprabranchial chamber of both demibranchs serves as a brood pouch and in the only available specimen was filled with rather early embryos with an average diameter of ca. 80 µm (Figs 10A, 11C–F). Allen found larvae in a single bivalve and that they were located outside the ctenidia. Most probably, the delicate non-respiratory membrane, which he does not mention occurring in any of his specimens, was overlooked or, as on one side of our specimen, had ruptured and emptied its contents into the infrabranchial chamber.

A pair of seminal receptacles is located in a thickening in the lower part of the narrow suspensory membrane, which connects the ascending gill lamella with the visceral mass (Fig. 11F). The surrounding walls consist of a relatively tall, unciliated epithelium with a compact cytoplasm and spherical nuclei. The 30×85 µm large lumen is packed with unoriented sperm. Because of a hiatus in the section series, only one of the receptacles could be studied and how and where the sperm are discharged (whether to the supra- or infrabranchial chamber) could not be decided.

Gonads, kidney, pericardium etc. The specimen is a hermaphrodite. The ovary contains young oocytes located in many narrow ovarian tubules distributed among the digestive diverticula in the visceral mass and mantle (Fig. 11D). The testis is rather compact with portions in the posterior parts of each mantle half (Fig. 11E) which communicate with a single voluminous space in the hind part of the visceral mass. While spermatogenesis chiefly occurs in the mantle, ripe sperm had accumulated in the visceral part. Allen (2000) interpreted the latter as the enlarged parts of two vasa deferentia storing mature sperm, but we suggest that the structure is unpaired and represents the posterior part of the testis in which sperm is often deposited in species of galeommatoids. The sperm have long flagella. The sperm heads are rod-shaped, slender and of uniform diameter and ca. 6 µm long. We were not able to locate the genital ducts and their openings.

The kidney is a voluminous sac that is imperfectly subdivided by a number of septa. At each side the kidney has a flat forwardly directed branch, which lies close to the abfrontal part of

the descending gill lamellae. Allen claimed that the descending gill lamella is attached to the posterior margin of a flattened leaf-like gonadal extension of the visceral mass. This tallies with our observation except that the leaf-like extension is made up of the kidney, not gonadal tissue, and the attachment is only apparent, not real. The pericardium is a spacious vesicle and the heart possesses a normal structure consisting of a ventricle penetrated by the rectum and two auricles.

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