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The functional morphology of *Penicillus philippinensis* (Anomalodesmata: Clavagelloidea: Penicillidae) and the evolution of an unique muscular system in the Bivalvia

Brian Morton
Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.
e-mail: *prof_bsmorton@hotmail.com*

Abstract – The Indo-West Pacific watering pot shell *Penicillus philippinensis* (Penicillidae) is essentially amyarian, that is, the posterior adductor and pedal retractor muscles are lost, their anterior equivalents vestigial. In addition to a small group of pallial retractor muscles arising from the pallial line, as is typical of other penicillids, this bivalve is connected to its adventitious tube dorso-laterally by a saddle-shaped array of papillae that previses the more elaborate system in the southern Australian *Kendrickiana veitchi*. That species and *P. philippinensis* also differ from other penicillids in that their siphons are capable of only limited retraction into the tube. Their extension in both species is largely by hydraulic means, the complex pallial musculature acting antagonistically with extensive blood-filled haemocoels. *P. philippinensis* can also be separated from other penicillids by a number of anatomical characters. For example, some taxa such as *K. veitchi* and *Nipponoclava gigantea* (but not *Foegia novaezelandiae*) have vestigial posterior pedal retractor muscles and associated pericardial proprioreceptors but *P. philippinensis* does not. Like other penicillids, however, *P. philippinensis* has a muscular pedal disc whereas *K. veitchi* does not. A trend in the Penicillidae towards even greater specialization for life inside an adventitious tube has arguably culminated in the unique muscular system of *K. veitchi*. *P. philippinensis* indicates how this may have been achieved.

INTRODUCTION

The Anomalodesmata comprises one sixth of all bivalve families (Harper *et al.* 2000) and these, as currently defined, have been discussed by Morton (2003a) and were last reviewed by Morton (1981, 1985a). Most anomalodesmatans are 'rare'; most are also aberrant and many are quite bizarre, compared with the generality of Bivalvia. Pojeta and Sohl (1987: 1) referred to the Late Cretaceous *Ascaulocardium armatum* (Morton, 1833) as "the ultimate variation on the bivalve paradigm". *A. armatum* is a member of the Clavagelloidea, that is, the watering pot shells, which arguably contain the most aberrant of all bivalves and these are currently being examined in some detail by this author to reveal an adaptive radiation not hitherto wholly appreciated (Morton 2002a, b, 2003b, 2004a, b, c).

Representatives of the endobenthic tube-dwelling Clavagelloidea (Penicillidae) are characterised by the loss of the posterior adductor muscle and, sometimes, the anterior, for example, *Kendrickiana veitchi* (Smith, 1971), and either loss or great reduction of the pedal retractor muscles. *Foegia novaezelandiae* (Bruguière, 1789), for example, is amyarian (Morton 2004a). Such a loss of musculature has had powerful implications for the mode of life of these animals. This is because, in their absence and with shell valves immovably fused horizontally into the fabric of the adventitious tube, all movements of the body with respect to siphonal extension and retraction, in particular, have to be achieved by the hydraulic pumping into and out of the mantle cavity of supernatant and interstitial water by contractions and relaxations of a muscular pedal disc. This structure acts as a pump to generate the necessary internal hydraulic pressures in the mantle cavity (Purchon 1960) that, in turn, exert equivalent pressures within the blood vascular system, that is, in the complex pallial haemocoels (Morton 1984a, 2002a).

Initially, it was thought that water was pumped out of the watering pot and into the sediment to effect either reburial following disinterment or deeper burrowing (Purchon 1960; Savazzi 1999). It is now known that the principal function of the pedal disc is to pump interstitial water *into* the mantle cavity (Morton 2002a, 2004a). There are other adaptations to a tube-dwelling mode of life, notably with regard to the development of unique, paired pericardial proprioreceptors that monitor body tonus, possibly either to avoid over-filling of the capacious rectum, as may be the case in

Brechites vaginiferus (Lamarck, 1818) (Morton 2002a) or, more generally, to enable the body as a whole to be maintained in a state of ambient tonicity, as in *Kendrickiana veitchi* (Morton, 2004b). Strangely, however, such receptors have hitherto only been identified in epibenthic, cemented clavagelloids, for example, *Humphreyia strangei* (A. Adams, 1852) and *Dianadema multangularis* (Tate, 1887) (Morton 2002b, 2003b), and where they are associated with what are probably the surviving vestiges of posterior pedal retractor muscles. They are absent in the endobenthic *Brechites vaginiferus* and *Foegia novaezelandiae,* where such muscles are vestigial and lost, respectively (Morton, 2002a, 2004a). In *Kendrickiana veitchi* and *Nipponoclava gigantea* Sowerby, 1888, the vestigial posterior pedal retractors form a simple union with the visceral ganglia and possibly function as tonus proprioreceptors (Morton 2004b, c).

The watering pot shells of the Clavagelloidea have long been of interest because of their distinctive structure and figure prominently in early malacological texts (Bruguière 1789; Chenu 1843; Reeve 1860) and were similarly objects of great scientific interest in the 19th century (Owen 1835; Gray 1847, 1858a; Lacaze-Duthiers 1870, 1883). More recently, a number of clavagelloids have been described in greater detail, for example, species of *Clavagella* (Soliman 1971; Morton 1984b), *Bryopa* (Appukuttan 1974; Savazzi 2000) and *Dianadema* (Morton 2003b) (Clavagellidae), and *Brechites* (Purchon 1956, 1960; Morton 1984a, 2002a), *Humphreyia, Foegia, Kendrickiana* and *Nipponoclava* (Morton 1984a, 2002b, 2004a, b, c) (Penicillidae). In addition, Harper and Morton (2004) have described how the penicillid adventitious tube is formed and thereby greatly clarified our understanding of how these unusual animals have been able to adopt their distinctive tube-dwelling lives. Recently, intact specimens of a species of *Penicillus* were obtained from the collections of the Museum of Comparative Zoology, The Agassiz Museum, Harvard University, and will be described below.

The anatomy of species of *Penicillus* Bruguière, 1789 have been investigated by Lacaze-Duthiers (1870, 1883), that is, *P.* (as *Aspergillum*) *javanum* Chenu, 1843 (= *P. philippinensis* Bruguière, 1789), *P.* (as *Aspergillum*) *dichotomum* Chenu, 1843 (= *P. penis* [Linnaeus, 1758]) and Purchon (1956, 1960), that is, *P.* (as *Brechites*) *penis*. Such studies were, however, undertaken with no knowledge of the anatomy of any other penicillid genus and thus of the full spectrum of clavagelloid adaptive radiation. Further, the studies were undertaken in the absence of histological information so that important anatomical details remained undescribed. As a consequence, currently published classifications, for example, Smith (1998), place all tube dwelling anomalodesmatans in one family – the Clavagellidae Orbigny, 1844. It has been demonstrated, however, that the Clavagelloidea comprises two families – the Clavagellidae and Penicillidae Bruguière, 1789 – that show remarkable convergent adaptations to a tube-dwelling life (Morton 2004a, b, c).

This paper provides a description of a representative of one of the last genera (*Penicillus*) to be studied in the light of a better appreciation of the superfamily as a whole, building on the earlier work of Lacaze-Duthiers and Purchon (see above). This study has resulted in a more complete interpretation of the adaptive radiation of the Clavagelloidea, including an understanding of how the unique muscular system of *Kendrickiana veitchi* evolved (Morton 2004b).

MATERIALS AND METHODS

What follows is a description of two preserved specimens of *Penicillus philippinensis* from the collections of the Agassiz Museum, Harvard University (Reg. No. MCZ 1744) and which were collected by H. Cuming from an unknown locality. One specimen was dissected; the entire second specimen was subjected to routine histological procedures and 6 μm transverse sections of the entire animal were cut. Every tenth section was stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome. In addition, tubes of putative *P. philippinensis* in the collections of the Western Australian Museum were examined and are also reported upon herein.

TAXONOMY

According to Keen and Smith (1969), the type species of the genus *Penicillus* Bruguière, 1789 is *P. javanus* Bruguière, 1789 (= *Serpula penis* Linnaeus, 1758). Smith (1976), in his revision of the extant Clavagelloidea, concluded that *Penicillus* was a subgenus of *Brechites* Guettard, 1770. Keen and Smith (1969) considered this latter genus name to be a nonbinomial synonym of *Penicillus.* Morton (1984a, 2002a), however, considered *Brechites* to be sufficiently different from *Penicillus* to warrant its separation at the generic level. According to Smith (1976) *Penicillus* comprises two species, that is, the type *P. penis,* and *P. philippinensis.* Chenu (1843) and Reeve (1860) illustrated and described a large number of penicillids, many collected by H. Cuming, and which Smith (1976) and Lamprell and Healy (1998) further considered to be synonyms of either *P. philippinensis* or *P. penis.*

Morton (2004c) showed that *Nipponoclava gigantea* and other penicillids, for example, *Foegia novaezelandiae* and *Kendrickiana veitchi* (Morton, 2004a, b), differ from *Penicillus philippinensis* in terms of adductor and pedal retractor muscle arrangements. The taxonomic arrangement followed herein, therefore, is that the name *Brechites* should be restricted to its type species, that is, *Aspergillum vaginiferum* Lamarck, 1818 and that *Penicillus* (Bruguière, 1789) should be returned to its original, full generic ranking.

Identity of the species herein considered

The species herein under investigation is considered to be *Penicillus philippinensis,* as noted above. The two studied specimens were part of a larger lot of 12 preserved individuals held in the collections of the Museum of Comparative Zoology, Harvard University (MCZ). The label of the lot reads only 'Coll. H. Cuming. Ex. J. G. Anthony, 15 Dec. 1863'. It seems possible that the specimens of *P. philippinensis* in MCZ were collected by Cuming and eventually either sold to or exchanged with American shells in the collections of J. G. Anthony.

Cuming made extensive collections in Southeast Asia including the Philippines, Indonesia and Singapore. The holotype of *Penicillus philippinensis* is a specimen collected by Cuming with the type locality as 'Saint Nicolas, Zebu Island, Philippines'. Smith (1976) provides a map of the distribution of *P. philippinensis* and shows it to range throughout the Philippines, the eastern islands of Indonesia and the eastern half of the South China Sea and from southern Western Australia (Rottnest Island) across northern Australia to central Queensland. Smith (1976) also provides a map of the distribution of *P. penis.* It is described therein as ranging from the Arabian Gulf, the east coast of Africa, across the Indian Ocean to the Andaman Sea, West Malaysia, Thailand, the western islands of Indonesia and East Malaysia, and the western half of the South China Sea and Singapore (Purchon 1956, 1960). *Penicillus penis* is not known to occur in Australia and it appears therefore that the distributions of the two species are mainly contiguous except for some overlap only in waters of central Southeast Asia. Moreover, only specimens of *P. penis* have been recorded from Singapore and, therefore, the specimens herein under consideration very probably would have come from either the Philippines or Java, Indonesia (from where they are illustrated, as *P. javanum,* by Dharma [1992, plate 26, fig 19]) and, hence, confirming their identity as *P. philippinensis.*

HABITAT NOTES

Apart from the above description of the distribution of *Penicillus philippinensis,* there is little other information on it hitherto available except for details of the Australian and other material reported upon by Smith (1971). He cites specimens from off Pratas Island in the South China Sea in 88 fathoms (160 m), the southeast coast of Tawi Tawi in 18 fathoms (33 m) and one in the United States National Museum from an unknown location and a depth of 100 fathoms (183 m). In the collections of the Western Australian Museum, Perth (WAM), there are a number of specimens of *P. philippinensis* (as *P. strangulatus* [Chenu, 1843]). These were collected from Onslow/Broome (WAM Reg. No. 194-71), Gunn Point, east of Darwin (WAM Reg. No. S10849), Torres Strait, Queensland (WAM Reg. No. S15949) and Cape York, Queensland (WAM Reg. No. 600-69) and thus fit into the distribution described by Smith (1976). I have collected one empty tube of *P. philippinensis* from an intertidal sand flat at Dampier, northwestern Western Australia (own collection).

RESULTS

Anatomy

The adventitious tube

The adventitious tubes of specimens of *Penicillus philippinensis* in the collections of the MCZ, range in length from 66 –96 mm and in greatest width from 7 – 12 mm. Those in the collections of the WAM range in total length from 80 – 150 mm and in greatest width from 7 – 16 mm. One such adventitious tube is illustrated in Figure 1. The tube is chalky white with only a light covering of sand and other particles along the central part of its shaft. From the watering pot, the tube tapers posteriorly, except that it bulges anterior to and more strongly posterior from the true shell valves (Figure 1A). This is unlike the situation in the congeneric *P. penis,* that tapers smoothly from anterior to posterior (Smith 1971, 1976, figs 21–25). The posterior bulge in *P. philippinensis* houses the main body of the animal, the anterior one the pedal disc. Anteriorly, there is a circular "watering pot". This is seen from the posterior aspect in Figure 1B. Its rim comprises a continuous radiating flange of fused tubules, some of which branch dichotomously (Figure 1F). The central convex element of the watering pot also possesses tubules and there is a central dorso-ventrally aligned pedal gape. Few sand grains and other debris attach to the anterior region of the tube and watering pot. The shaft of the tube containing the siphons accounts for approximately three-quarters of its total length and it ends posteriorly at an 8-shaped siphonal opening (Figure 1C). The adventitious tube is not covered with sand grains posteriorly, suggesting that it projects above the sediment, and shows signs of either growth or repair. In the illustrated specimen, there are two growth/repair increments located close together in the posteriorly naked element of the tube (Figure 1D). Antero-ventrally, as in *Brechites vaginiferus* (Morton 2002a), there is a

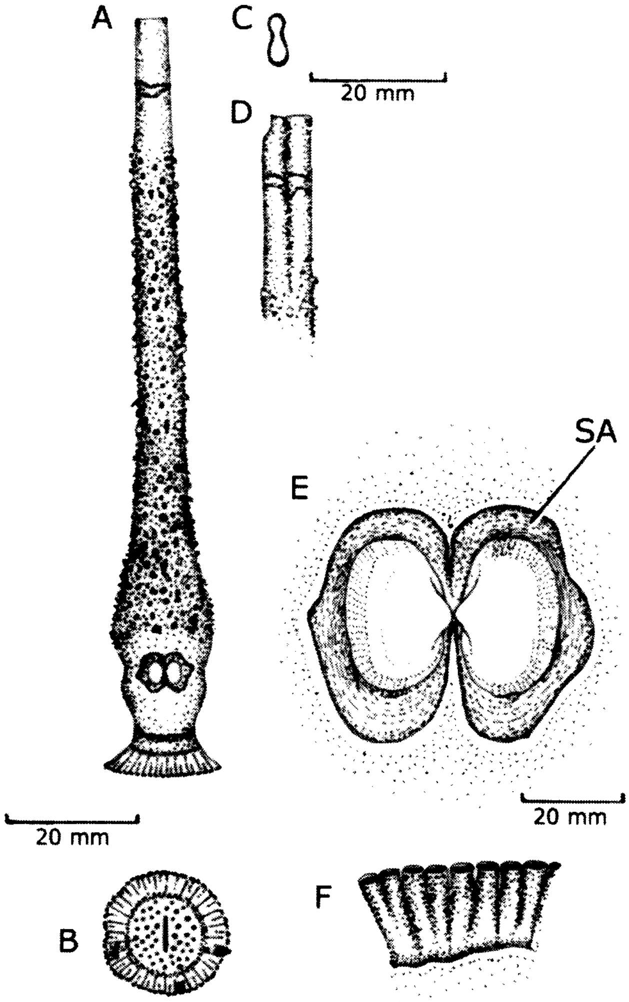

Figure 1 *Penicillus philippinensis.* The adventitious tube as seen from A, the dorsal; B, the anterior and C, the posterior aspects. D is a more detailed view of the posterior siphonal end showing growth/repair increments. E shows the true shell valves and surrounding saddle (SA) in more detail and F, the tubules of the watering pot rim.

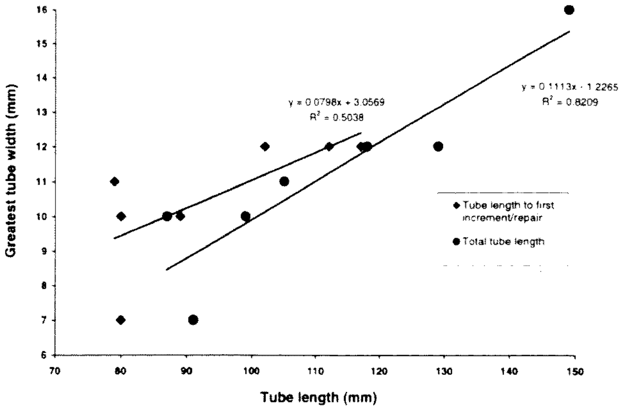

Figure 2 *Penicillus philippinensis.* The relationships between adventitious tube width and total length (●) and length to the first growth (or repair) increment (◆).

"line" separating tube from watering pot, although Harper and Morton (2004) do not believe this to have any significance in terms of tube manufacture and its provenance remains obscure. Where the covering of sand and other particles is eroded from it (Figure 1A), the chalky nature of the tube is more obvious and is covered in a delicate, light-brown periostracum.

Some of the tubes of *Penicillus philippinensis* in the collections of the WAM have a series of either growth or repair increments, as illustrated in Figures 1A and D. Two of these had breaks and repairs just above the watering pot, but in most individuals these were located posteriorly and ranged in number from one to eight and in such cases it is unclear whether these are repairs or growth increments (or both). It seems likely, however, that the posterior extensions represent damage and repair events but which, in the longer term, also keep the siphonal apertures above the habitat of accretive sand.

The greatest adventitious tube width plotted against (i), total tube length and (ii), tube length to the first break and repair are illustrated in Figure 2. Both are, albeit weak, straight-line relationships that parallel each other approximately. Thus, (i), there is a positive correlation between tube length and width, (ii), tube repairs (or a growth increment) occur at approximately half the maximum tube length and (iii), there is no positive correlation between break length (or increment addition) and tube width. This suggests, as has been proposed and similarly illustrated for other endobenthic penicillids, for example, *Brechites vaginiferus, Foegia novaezelandiae* and *Kendrickiana veitchi* (Morton 2002a, 2004a, b), that the main structure of the tube is probably produced only once, as argued by Harper and Morton (2004), but can be added to posteriorly as either repair or growth increments.

The shell valves

Harper and Morton (2004, fig. 3) describe and illustrate the true shell valves of a specimen of *Penicillus pulchrum* (Reeve, 1860, species 13) (= *P. penis*) (Smith 1976). The shell valves of *P. philippinensis* are illustrated in Figure 1A in relation to the adventitious tube and in greater detail in Figure 1E. As in all clavagelloids, except *Nipponoclava gigantea* (Morton 2004c), the valves are about 3.5 mm long and 3.0 mm high and are equivalve and inequilateral, that is, anteriorly foreshortened and posteriorly elongate. There is a light pattern of radial striae and periostracal spinules as first described for *Lyonsia hyalina* Conrad, 1848 by Prezant (1979a, 1981). Similar spicules have been reported upon for some representatives of the Laternulidae (Aller 1974; Carter and Aller 1975), Pholadomyidae,

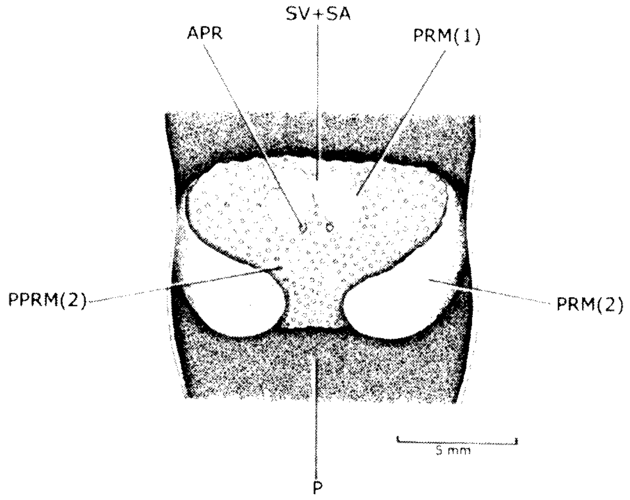

Figure 3 *Penicillus philippinensis*. An internal view of the adventitious tube showing the 'saddle' of calcareous material secreted beneath the periostracum and its various muscle impressions. For abbreviations see the Appendix.

Parilimyidae, Poromyidae, Thraciidae, Verticordiidae and Lyonsiellidae (Morton 1985, 2003a). The shell valves of *P. philippinensis*, indeed of all clavagelloids, however, resemble those of representatives of the Lyonsiidae which Dreyer, Steiner and Harper (2003) have shown genetically to be a sister taxon. Where the outer aragonitic layer has been eroded away, the true shell of *P. philippinensis* is seen to be nacreous, as in all other penicillids so far described (Taylor *et al.* 1973). The two valves are aligned horizontally and surrounded by and united with a "saddle" of shell material that has been secreted subsequently and is characterized by a weak sculpture of irregular concentric growth lines.

As in other penicillids, the shell and saddle of *Penicillus philippinensis* are hidden internally within the fabric of the adventitious tube by a similarly saddle-shaped coating of aragonite secreted by the dorsal surface of the mantle. In *P. philippinensis*, the shell valve and saddle impressions are indistinct (Figure 3) in this internal sheet of secondarily secreted tube material. Similarly, the impressions of the two bean-shaped pallial lines, identifying pallial retractor muscle attachments, and anterior pedal retractor scars are difficult to identify. The internally secreted saddle is, however, distinctly isolated from the remainder of the adventitious tube by the surrounding sheet of periostracum that defines its circumference. Thus, the internal saddle (Figure 1E, SA) is secreted beneath the periostracum and serves the principal function of similar concretions in other penicillids, for example *Brechites vaginiferus* (Morton 2002a), of binding the shell, external saddle and tube elements into a structurally stronger whole. Unlike these other penicillids, however, dorsally and laterally, just anterior to the position of the true shell and pallial line with pallial retractor muscles, the saddle concretion is lightly dimpled. As will be discussed, this is reminiscent of the internal tube structure of *Kendrickiana veitchi* (Morton 2004b). As noted above, the periostracal sheet that covers the body of the animal, including the siphons and the pedal disc, arises from the circumference of the internal saddle-shaped concretion. Because of the concretion, however, the correspondingly saddle-shaped area of mantle beneath it is not covered in periostracum and, as will be described, is dotted with small papillae.

Internal anatomy

The anatomy of an individual of *Penicillus philippinensis* that has been removed from its tube is illustrated in Figure 4. In dorsal view (Figure 4A), the pericardium and its contained organs is the most obvious structure. There is a single ventricle that has paired lateral auricles. The rectum is enclosed by the ventricle of the heart and passes posteriorly over the paired kidneys. Anterior to the pericardium, there is a pair of tiny anterior pedal retractor muscles located on the antero-dorsal edges of the left and right blocks of pallial retractor muscles. Purchon (1956, 1960) did not identify anterior pedal retractor muscles in *P.* (as *Brechites*) *penis*. As in *Brechites vaginiferus, Foegia novaezelandiae* (Morton 2002a, 2004a) and *P. penis*

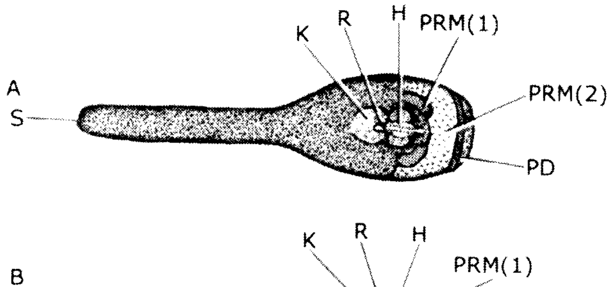

Figure 4 *Penicillus philippinensis*. Views of an intact individual, as seen from A, the dorsal; B, right lateral and C, ventral aspects. For abbreviations see the Appendix.

(Purchon 1956), however, there are no posterior pedal retractor muscles.

The pericardium of *Penicillus philippinensis* is surrounded, except posteriorly, by the saddle-shaped array of papillae, the tip of each of which is located in the dimples or slight impressions in the surface of the internal calcareous concretion of the adventitious tube above it. These will be described in detail but are also illustrated in right lateral view in Figure 4B, and wherein the pedal disc is also seen to be positioned anterior to the saddle of papillae. The circular pedal disc with its dorso-ventrally aligned pedal gape is seen from the ventral view in Figure 4C. As in *Kendrickiana veitchi* and *Nipponoclava gigantea*, but unlike *B. vaginiferus* and *F. novaezelandiae*, *P. philippinensis* has a fourth pallial aperture located just posterior to the ends of the saddle of papillae. Lacaze-Duthiers (1883) also described *P.* (as *Aspergillum*) *dichotomum* Chenu, 1843 (= *P. philippinensis*) as possessing a fourth pallial aperture, whereas *P.* (as *Brechites*) *penis* does not (Purchon 1956, 1960). The entire body of *P. philippinensis* is covered in periostracum, except for the saddle-shaped area of papillate mantle beneath the overlying calcareous concretion. In Figure 4 also the periostracum has been removed from the pedal disc to show the papillae on its outer surface.

The organs of the mantle cavity

The organs of the mantle cavity of *Penicillus philippinensis* are shown from the right lateral aspect in Figure 5. From the antero-ventral surface of the visceral mass arises a small round-ended foot that is aligned approximately with the gape of the pedal disc. The visceral mass is also pointed posteriorly and contains paired dorsal ovaries and ventral testes. The ctenidia are long, as in *P. penis* (Purchon 1956), and extend into the apices of the siphons as in *Foegia novaezelandiae* (Morton 2004a). Each ctenidium comprises a complete inner demibranch and the ascending limb only of the outer demibranch. This is typical of all known, non-septibranch anomalodesmatans (Morton 1981, 1985) and is of the Type E of Atkins (1936, 1937a). There are thus ciliary acceptance tracts in the ctenidial axes and in the ventral marginal food grooves of the inner demibranchs. The ctenidia are, however, very short dorso-ventrally and link up anteriorly with relatively large labial palps in a junction described by Stasek (1963) as Category III. All labial palps possess transverse ridges on their inner faces and thus effect sorting of any particles collected and transported to them by the ctenidia. The proximal oral grooves are long and the outer lip of the mouth overarches the inner.

The siphons

The siphons of *Penicillus philippinensis* are illustrated from the posterior aspect in Figure 6. The exhalant siphon comprises a simple unornamented cone while the aperture of the inhalant siphon is fringed by eight small papillae. Surrounding the two siphons is a ring of fourteen papillae, eight around the exhalant and six around the inhalant. The periostracum extends up to the apices of the siphonal openings but does not cover them. As in *Nipponoclava gigantea* (Morton 2004c), but unlike other penicillids, including *P. penis* (Purchon 1956, 1960), the siphonal periostracum is not camouflaged by adhering sand grains and other debris.

The siphons are illustrated in transverse section in Figure 7A. The 14 siphonal nerves that connect up with the encircling siphonal papillae are shown, as is the general distribution of the siphon glands that characterise the siphonal apices of most

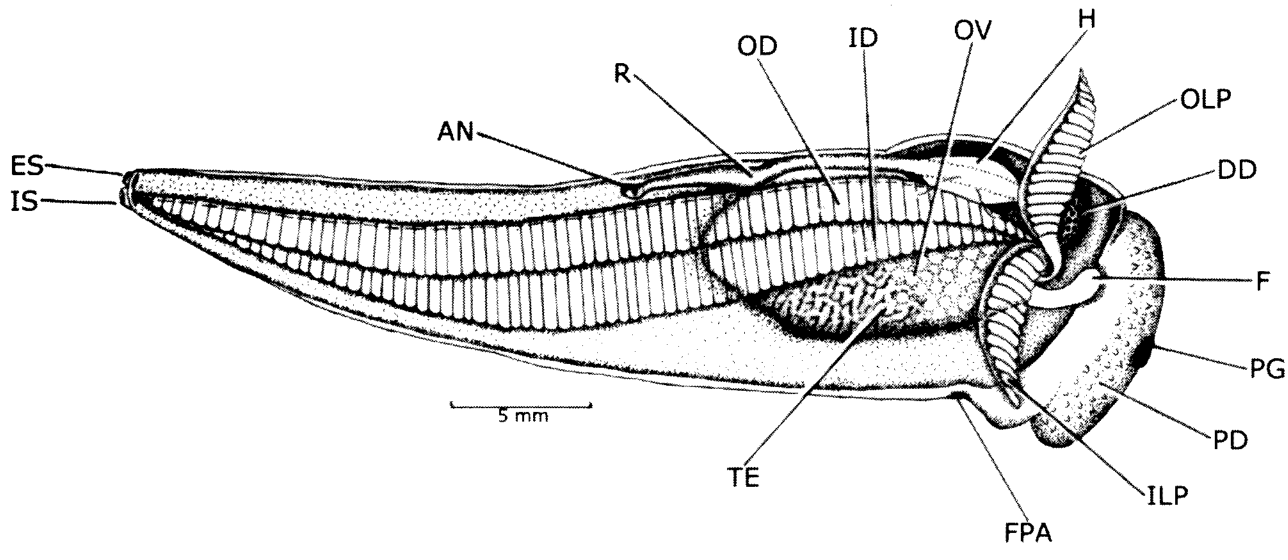

Figure 5 *Penicillus philippinensis*. The organs of the mantle cavity, as seen from the right side. For abbreviations see the Appendix.

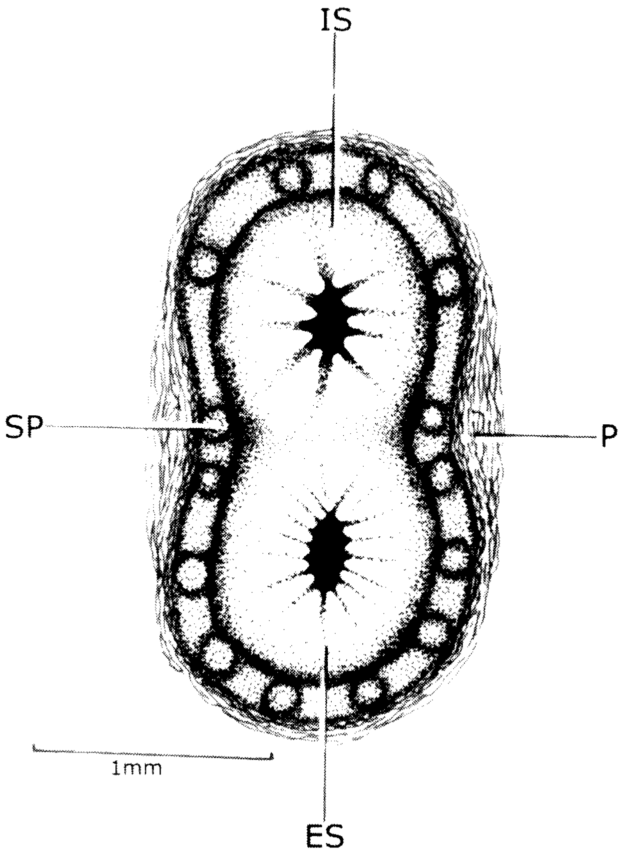

Figure 6 *Penicillus philippinensis.* The siphons as seen from the posterior aspect. For abbreviations see the Appendix.

penicillids. Unlike other penicillids, but as in *Nipponoclava gigantea* (Morton 2004c), there are no radial mantle glands in the apices of the siphons. Such glands were first described by Prezant (1979b) for *Lyonsia hyalina* and were believed to produce a sticky secretion binding sand grains and other debris to the siphons and shell to camouflage them. The absence of such glands in both *P. philippinensis* and *Nipponoclava gigantea* (Morton 2004c) probably explains the absence of debris attached to the siphonal periostracum of these species. The siphonal wall is shown in greater detail in Figure 7B. Internal to the inner epithelium is a haemocoelomic area that also contains the red staining (in Masson's trichrome) siphonal glands, illustrated in greater detail for *N. gigantea* (Morton 2004c). The outer epithelium is connected to the body of the siphonal wall by bundles of transverse muscle fibres. Internal to this are twice repeated layers of circular and longitudinal muscles. Beneath the outer epithelium is another haemocoelomic area cross- connected to the internal muscle layers by bundles of transverse fibres. The two layers of longitudinal muscles in the siphonal walls are cross–connected by bundles of oblique muscles. The outer epithelium is covered by periostracum comprising two layers, that is, a thick inner layer which stains blue in Masson's trichrome and is therefore probably mucoid and a thinner (~ 2 μm) outer layer which stains red and is therefore proteinaceous.

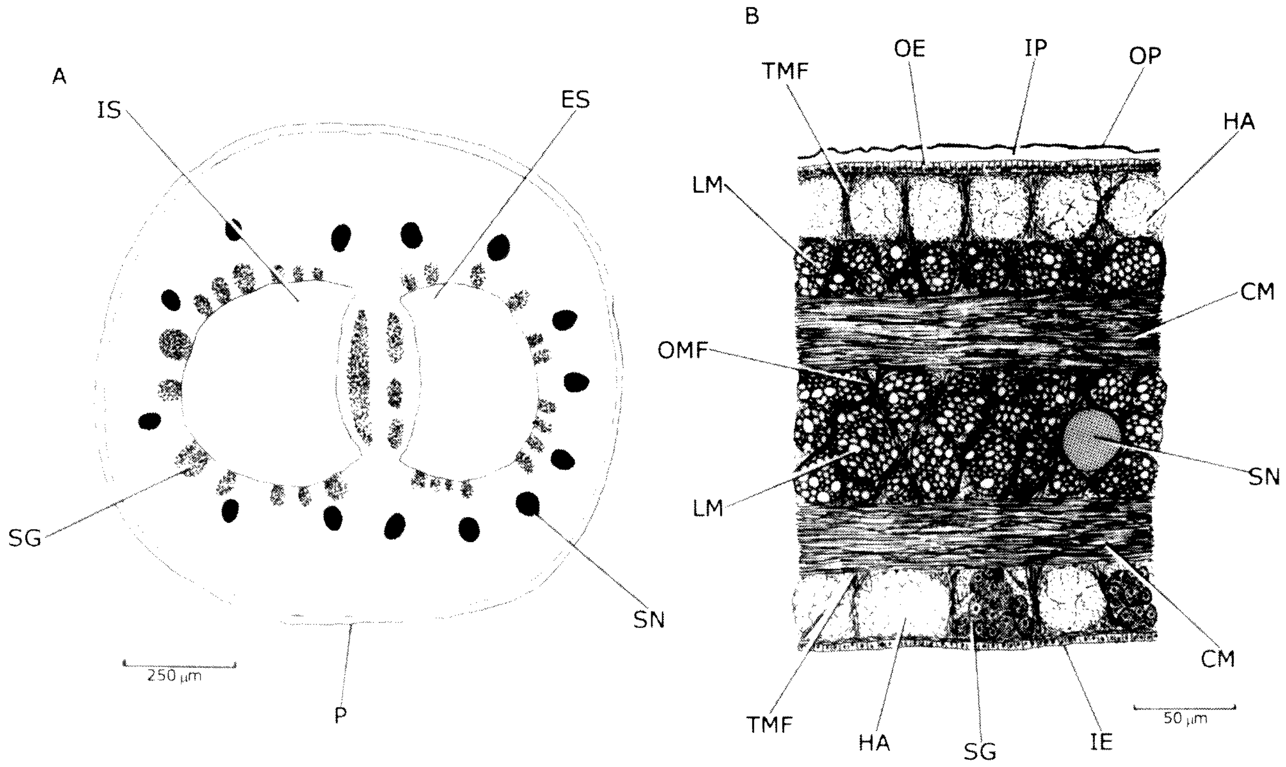

Figure 7 *Penicillus philippinensis.* A, A diagrammatic illustration of a transverse section through the siphons at their tips and B, a detail of a transverse section through the siphonal wall. For abbreviations see the Appendix.

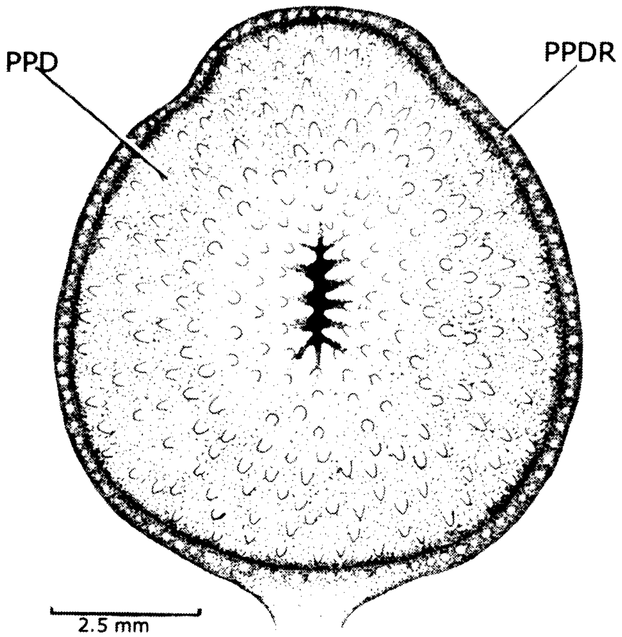

Figure 8 *Penicillus philippinensis*. The pedal disc as seen from the anterior aspect. For abbreviations see the Appendix.

The pedal disc

The highly muscular pedal disc of *Penicillus philippinensis* is illustrated from the posterior aspect in Figure 8. The periostracum covering it has been removed to show the epithelium of the disc dotted with small papillae. Similarly, the circumference of the disc is defined by a papillate, raised rim. In the centre of the disc is a dorso-ventrally aligned pedal gape. In *Foegia novaezelandiae*, the periostracum covering the pedal disc is covered in an agglomeration of inorganic and organic debris and rod-shaped bacteria (Morton 2004a): this has not been observed in *P. philippinensis*.

The ventral mantle margin

The mid-ventral mantle margin of *Penicillus philippinensis* is illustrated in transverse section in Figure 9. Mantle fusion is extensive and involves inner and middle mantle folds and the inner surfaces only of the outer mantle folds, Type C of Yonge (1982). Virtually the entire surface of the mantle is therefore covered in periostracum. The periostracum arises from left and right periostracal grooves, located just below the point of attachment of the pallial retractor muscles onto the tube. The ventral mantle margin largely comprises a haemocoel but there are additional bundles of longitudinal muscles that will assist in siphonal retraction.

The papillate pallial saddle and musculature

The structure of the pallial saddle in *Penicillus philippinensis* is illustrated in dorsal view in Figure 10. It abuts the pallial line and hence its pallial retractor muscles and the dorsal visceral mass posteriorly and the rim of the pedal disc anteriorly. It extends laterally, to the left and right, around the mantle (Figure 4). It is not covered in periostracum and, although covered in small papillae, is transparent enough to identify the fine strands of the vestigial anterior adductor muscle, also identified in *P. penis* (Purchon 1956, 1960). Two

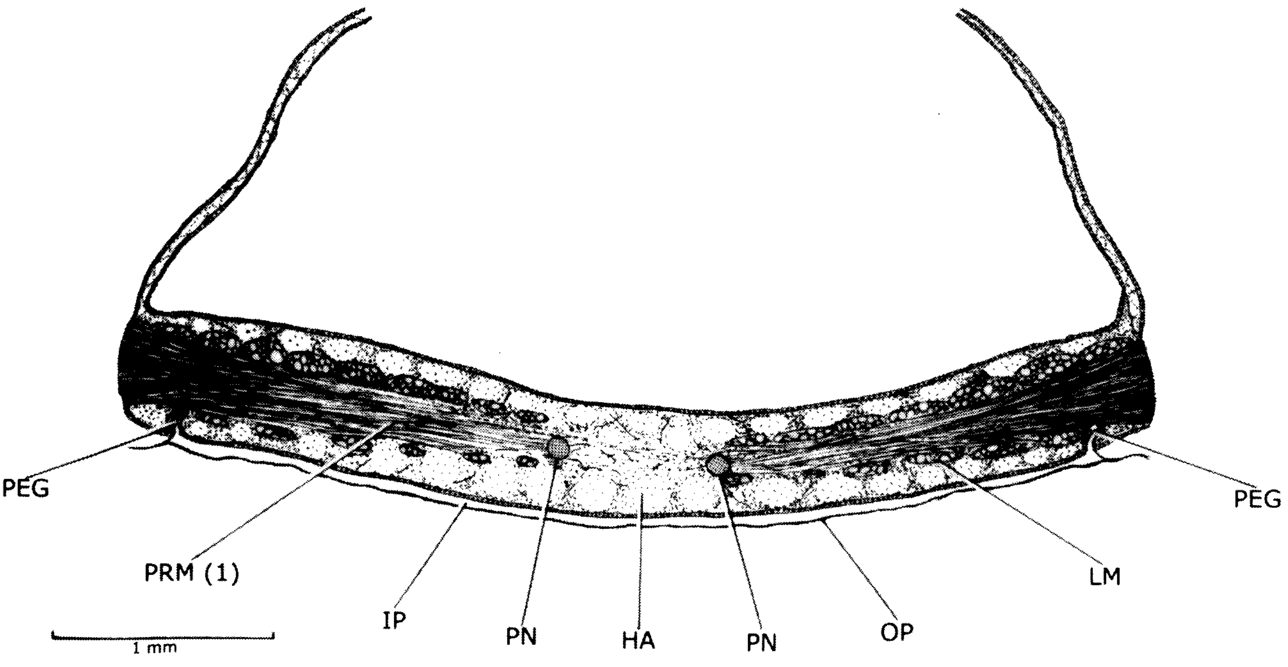

Figure 9 *Penicillus philippinensis*. A transverse section through the mid-ventral mantle margin. For abbreviations see the Appendix.

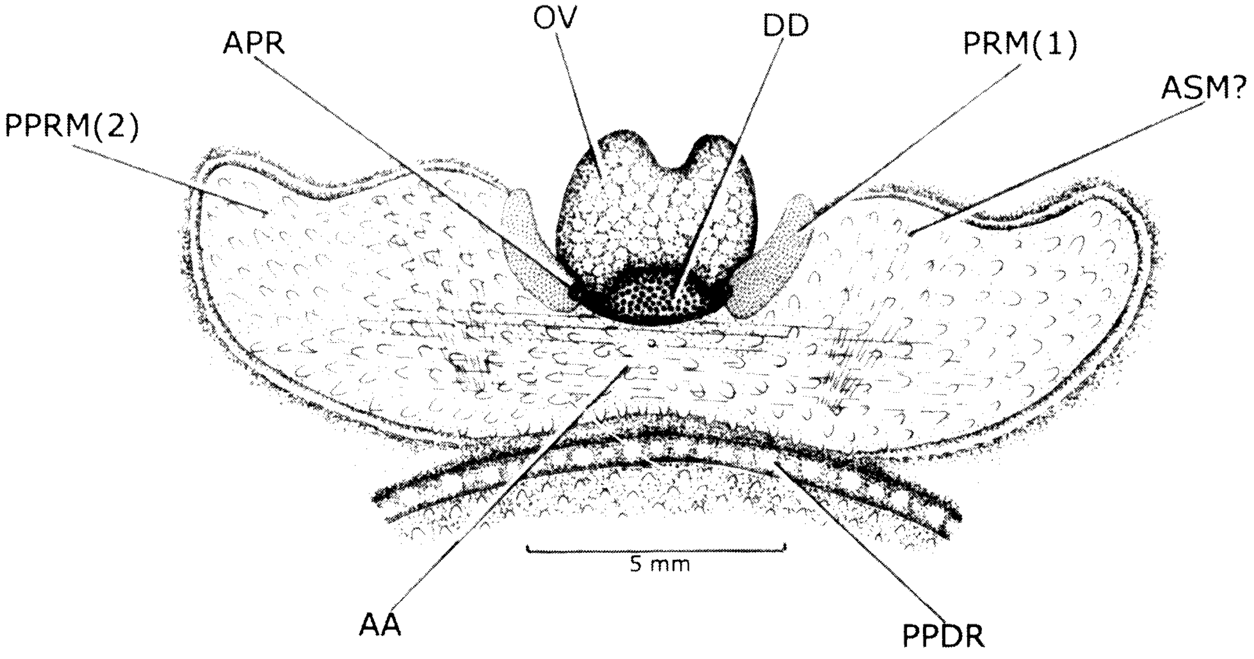

Figure 10 *Penicillus philippinensis*. The true pallial retractor muscles and saddle-shaped array of pallial papillae as seen from the dorsal aspect and somewhat spread out. For abbreviations see the Appendix.

small muscles, herein termed accessory suspensory muscles as they function like those of greater definability seen in *Kendrickiana veitchi* (Morton 2004b), serve to attach the antero-dorsal region of the visceral mass to the adventitious tube. Purchon (1956, 1960) did not identify such muscles in *P. penis*.

The mantle margin of *Penicillus philippinensis* at the pallial saddle is illustrated in transverse section in Figure 11. As with the mantle margin further posteriorly (Figure 9), mid ventrally there are large haemocoelomic spaces, (fewer) longitudinal muscle fibres and both left and right pallial retractor muscles. However, here, the lateral areas of the mantle are thickened and are traversed from the inner mantle epithelium to the outer by discrete muscle blocks interspersed by haemocoelomic spaces. These must be responsible for contraction of

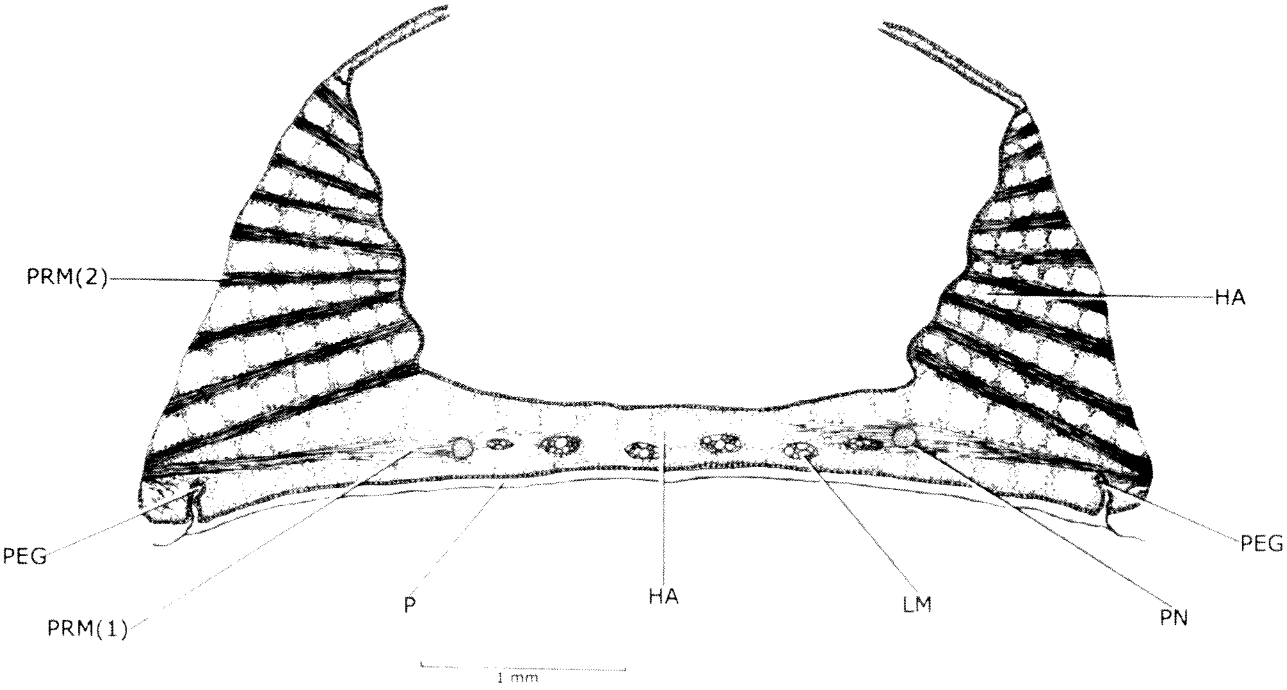

Figure 11 *Penicillus philippinensis*. A transverse section through the antero-ventral mantle margin showing the true pallial retractor muscles and the muscles of the saddle-shaped array of pallial papillae. For abbreviations see the Appendix.

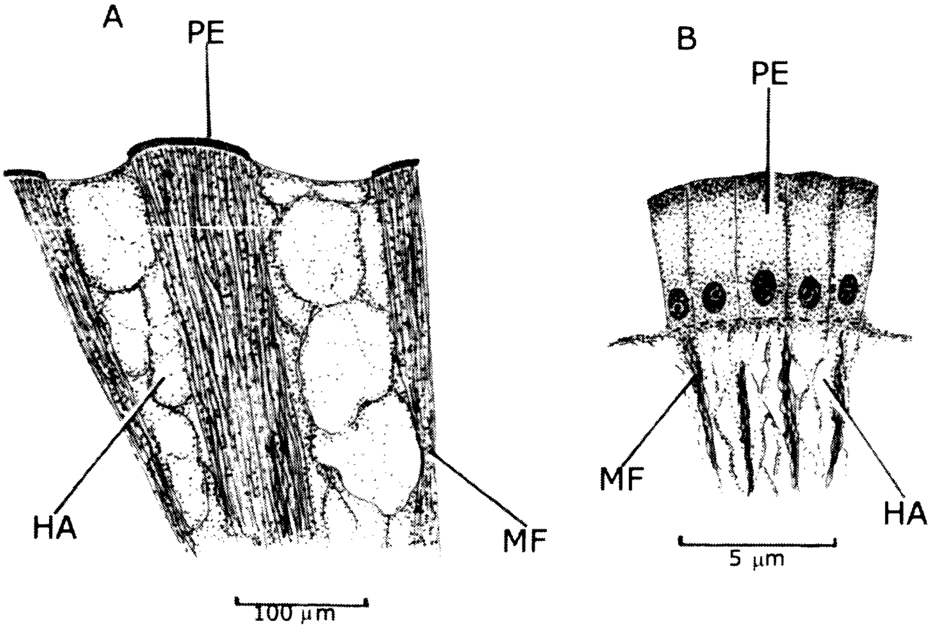

Figure 12 *Penicillus philippinensis*. Transverse sections through the points of attachment of the papillae of the saddle-shaped array of pallial retractor muscles to the adventitious tube at two different levels of magnification. For abbreviations see the Appendix.

the mantle inwards and upwards, as in *Kendrickiana veitchi* (Morton 2004b).

Points of attachment of the pallial saddle papillae to the calcareous area of the adventitious tube of *Penicillus philippinensis* are shown in greater detail in Figure 12A. Each muscle unit, separated from its neighbours by haemocoelomic spaces, ends in a small swelling, identified as a small papillae, on the outer surface of the saddle. Closer inspection of the attachment point shows that the muscles are not attached directly to the tube but form a union with the basement membrane of a group of epithelial cells some 5 µm tall (Figure 12B). This is unlike the situation seen in *Kendrickiana veitchi* where the much larger equivalent papillae are attached directly to the tube by papilla muscles (Morton 2004b).

The remnants of the true musculature of *Penicillus philippinensis* are illustrated in Figure 13 in a transverse section through the dorsal visceral mass. Above it is the delicate, vestigial anterior adductor muscle and flanking it are the paired remnants of the anterior pedal retractor muscles. Also seen in Figure 13 are antero-dorsally located

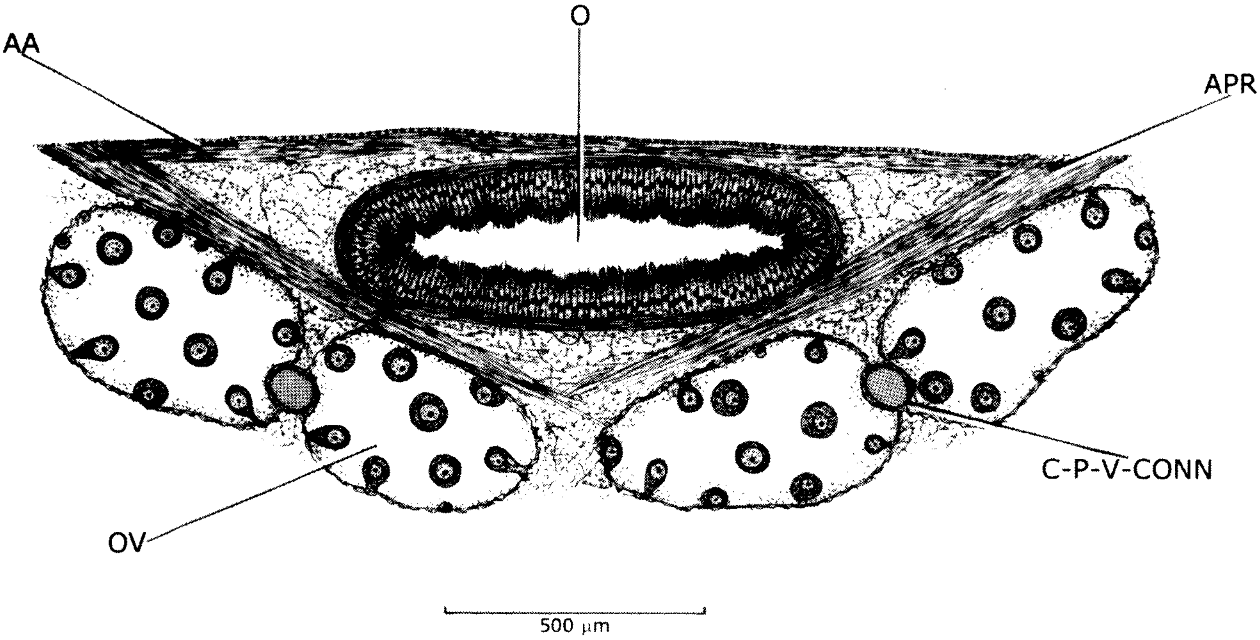

Figure 13 *Penicillus philippinensis*. A transverse section through the oesophagus also showing the vestigial anterior adductor and pedal retractor muscles. For abbreviations see the Appendix.

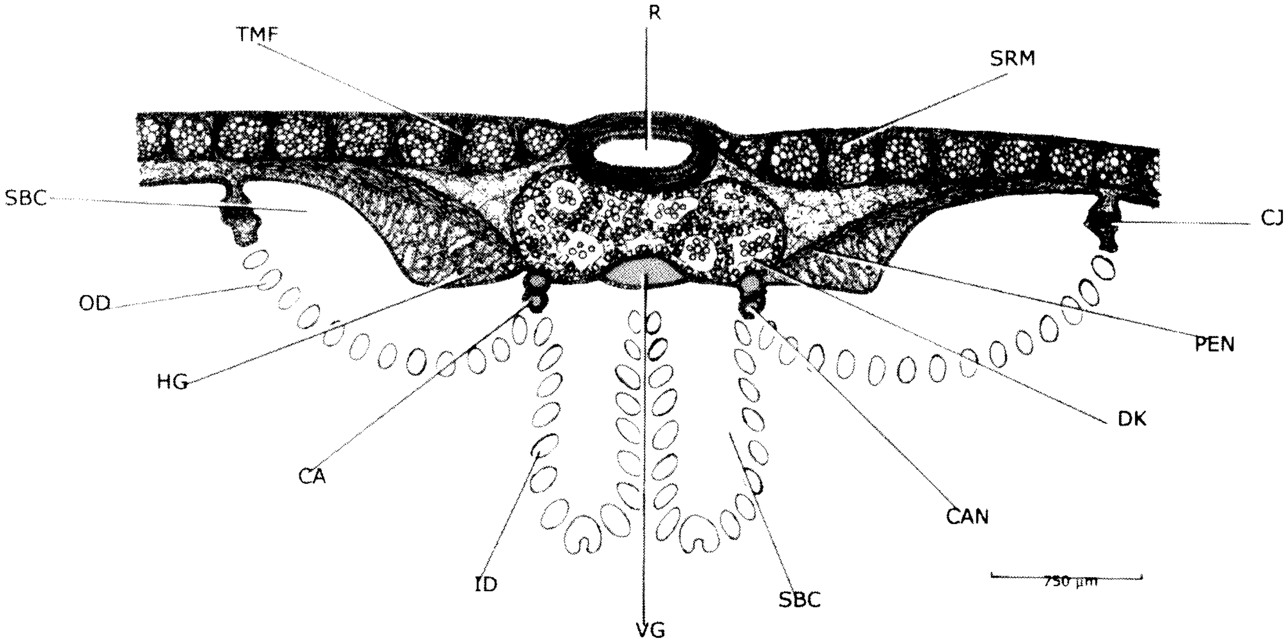

Figure 14 *Penicillus philippinensis*. A transverse section through the rectum, kidneys, hypobranchial glands and visceral ganglia. For abbreviations see the Appendix.

ovaries. The paired testes are located postero-ventrally in the visceral mass.

The pericardium and kidneys

The pericardium of *Penicillus philippinensis* is illustrated in right lateral view in Figure 5. The ventricle of the contained heart surrounds the rectum. The auricles lie above the supra-branchial chamber of the outer demibranch. In transverse section (Figure 14), the rectum comprises a simple tube that possesses a thick muscular coat. In the dorsal mantle, to the left and right of the rectum, are the dorsal elements of the longitudinal muscles of the siphonal retractors. Beneath the pericardium are the posterior elements of the kidneys. In this section, only the tubules of the distal limbs are present. The paired kidneys do, however, comprise paired ciliated proximal limbs that open into the supra-branchial chamber at renal apertures. The surrounding distal limbs comprise tubules made up of epithelial cells some 8 µm tall and which are mostly vacuolated. Within some cells and densely occupying the tubule lumina are spherical kidney concretions approximately 10 µm in diameter and which stain blue in Masson's trichrome but have a lighter core.

The supra-branchial chamber of the outer demibranch is lined dorsally by a hypobranchial gland typical of all penicillids and illustrated in detail for *Nipponoclava gigantea* by Morton (2004c). Beneath the posterior edges of the kidneys lie the visceral ganglia with nerves extending into the mantle and ctenidial axes. The outer demibranch attaches to the mantle at a cuticular junction like that described by Atkins (1937b).

The visceral ganglia

The visceral ganglia of *Penicillus philippinensis* are illustrated from beneath in Figure 15. They lie

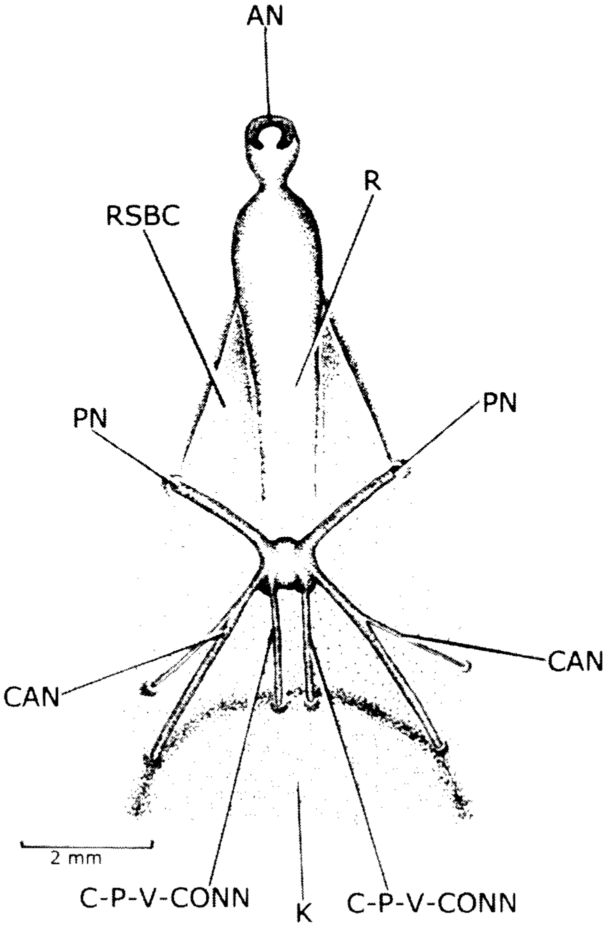

Figure 15 *Penicillus philippinensis*. A ventral view of the visceral ganglia and associated nerves. For abbreviations see the Appendix.

between the kidneys anteriorly and rectum, the latter extending into the supra-branchial chamber posteriorly. The paired ganglia are connected to the cerebro-pleural ganglia anteriorly by cerebro-pleural visceral connectives that pass anteriorly into the kidneys. From the posterior ends of the ganglia arise the posterior pallial nerves that posteriorly divide and extend into the siphons. From the anterior lateral edges of the ganglia arise nerves that divide into two components and make connection with the ctenidia at the ctenidial axes.

The statocysts

The statocysts of *Penicillus philippinensis* are located in close proximity to the dorso-lateral edges of the pedal ganglia (Figure 16). But one is

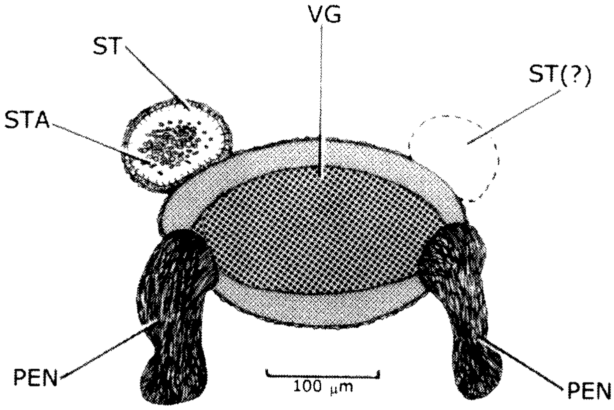

Figure 16 *Penicillus philippinensis.* A transverse section through the right statocyst and pedal ganglia. For abbreviations see the Appendix.

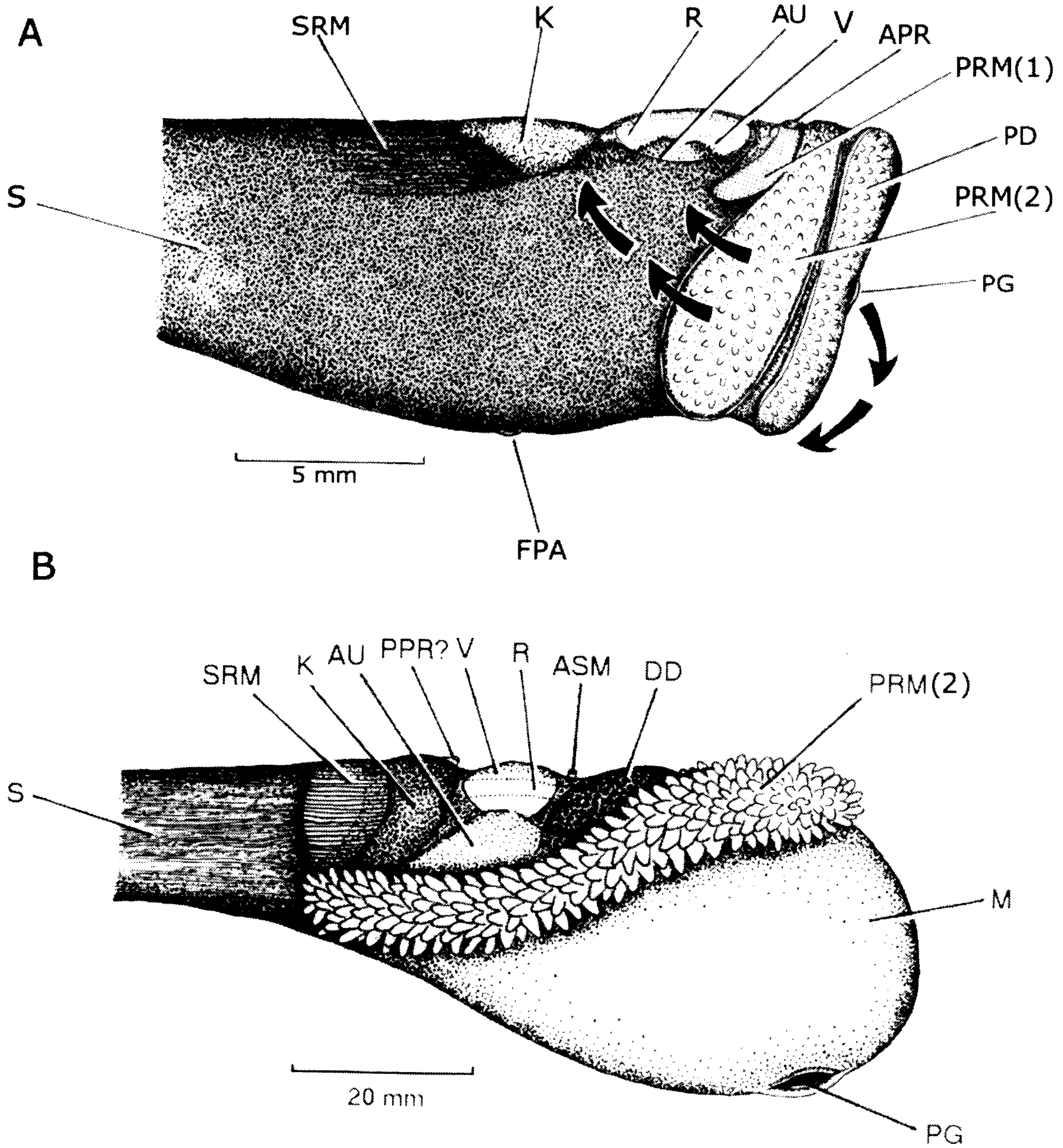

Figure 17 *Penicillus philippinensis.* A, The anterior end of an individual showing how the postero-dorsal movement of the papillate pallial retractor muscles and pedal disc would essentially recreate the situation seen in B, *Kendrickiana veitchi* (redrawn after Morton 2004a). For abbreviations see the Appendix.

illustrated because only one in ten sections of the specimen was saved thus losing the second statocyst. The statocysts are Type B_3 of Morton (1985b) as are those of all other penicillids described to date. Each statocyst thus possesses a large number of small crystalline statoconia of about equal size and there is not one dominant statolith as in other statocyst types (Morton 1985b).

DISCUSSION

Penicillus philippinensis can be separated from *P. penis* on the basis of the form of the adventitious tube which is curved in the former and straight in the latter, and by the presence of anterior pedal retractor muscles and a fourth pallial aperture (Purchon 1956, 1960; this study). Of all known penicillids, however, *P. philippinensis* (Figure 17A) is structurally most similar to *Kendrickiana veitchi* (Morton 2004b) (Figure 17B). This similarity relates to the occurrence in both, respectively, of a saddle- or horseshoe-shaped array of muscular papillae, that connects each animal to its adventitious tube dorso-laterally. No other clavagelloid possesses such an array of muscular pallial papillae. The situation in *K. veitchi* seems to have evolved from an ancestral condition similar to that in *P. philippinensis* by the rotation dorsally of the papillate area of mantle and the movement of the pedal gape to a more antero-ventral, as opposed to a more anterior, position (Figure 17). This scenario may also account for the radial symmetry of the watering pot of *P. philippinensis* and the asymmetrical one of *K. veitchi*. There are, moreover, other differences between the two. In many ways the simple, tiny papillae of *P. philippinensis* foreshadow the situation seen in *K. veitchi*. That is, the papillae of the latter are large and have a deep muscular attachment within pits in the adventitious tube, whereas in the former they are slightly attached, *via* the intermediary of an epithelium, to the calcareous concretion covering the interior surface of the tube beneath and anterior to the positions of the true shell valves. *Kendrickiana veitchi* also possesses a distinct pair of accessory suspensory muscles, attaching the visceral mass dorsally to the adventitious tube. There is a similar but much smaller, less distinct, pair of such muscles in *P. philippinensis*. Conversely, *P. philippinensis* possesses an, albeit small, pallial line on the tube (with pallial retractor muscles), whereas *K. veitchi* does not. Purchon (1956, 1960) described neither dorsal saddle papillae nor suspensory muscles for *P. penis*.

This study of *Penicillus philippinensis* completes a personal series of papers on the structure of the adventitious tubes and anatomical characteristics of representatives of the known genera of the Penicillidae, that is, *Brechites vaginiferus*, *Humphreyia strangei*, *Foegia novaezelandiae*, *Kendrickiana veitchi* and *Nipponoclava gigantea* (Morton 1984a, 2002a, b, 2004a, b, c). Such characteristics are compared and summarized in Table 1. Morton (2006) has published a similar table for representatives of the extant genera of the Clavagellidae, that is, *Dacosta australis* (Sowerby, 1829), *Bryopa aligamenta* (Morton, 2005), *Dianadema multangularis* and *Stirpulina ramosa* Dunker, 1882. All representatives of the Penicillidae are characterized by having both shell valves incorporated into the structure of the adventitious tube, unlike representatives of the Clavagellidae where only the left valve is – the right being free within the crypt (*Dacosta, Bryopa*) or tube (*Dianadema, Stirpulina*). *Humphreyia strangei* is easily distinguished from all other penicillids by being cemented epibenthically. Representatives of all other genera are endobenthic and occupy vertically oriented adventitious tubes. Representatives of the five endobenthic genera are separable in terms of the details of the tube structure, for example whether the shell valves are clearly visible (*Brechites, Penicillus, Nipponoclava*) or covered by concretions (*Foegia, Kendrickiana*). They are also separable in terms of anatomical details. For example, although all have lost their posterior adductor muscles, a vestigial anterior muscle is present in both *Penicillus* and *Nipponoclava*. Similarly, remnant anterior pedal retractor muscles are present only in *Brechites, Penicillus* and *Nipponoclava* whereas remnant posterior pedal retractor muscles are present only in *Humphreyia, Kendrickiana* and *Nipponoclava* facilitating the development in these genera only of pericardial proprioreceptors. Similarly a fourth pallial aperture is present only in the juvenile of *Humphreyia* and in *Nipponoclava*, while only *Penicillus* and *Nipponoclava* do not possess radial mantle glands at the siphonal tips.

Notwithstanding such differences of detail, all penicillids are united in the possession of Type C pallial fusions (Yonge 1982), Type E ctenidia (Atkins 1936, 1937a), a Type 3 ctenidial labial palp junction (Stasek 1963) and statocysts of Type B_3 (Morton 1985b). Such characters are also common to representatives of the Clavagellidae (Morton 2006) suggesting a common ancestry, albeit with radiation of the two families in the Mesozoic (Clavagellidae) and Cenozoic (Penicillidae) (Morton 2006).

Gray (1858b), Lamy 1923, Smith (1978) and Morton (1984a, 2002a), among others, have speculated upon the formation of the clavagelloid adventitious tube. All authors agree that the structure is produced but once although it may be added to posteriorly to effect growth and repair. Harper and Morton (2004) described how in *Brechites vaginiferus* the sequential secretion of

Table 1 A comparison of shell, adventitious tube and internal anatomical characters of *Brechites* and its allies (Penicilloidea: Penicillidae)

Character	*Brechites*	*Humphreyia*	*Penicillus*	*Foegia*	*Kendrickiana*	*Nipponoclava*
Shell	Juvenile + saddle	Juvenile + saddle	Juvenile + saddle	Juvenile + saddle	Juvenile + saddle	Post-juvenile + saddle
Shell	Both valves united with adventitious tube	Both valves united with adventitious tube	Both valves united with adventitious tube	Both valves united with adventitious tube	Both valves united with adventitious tube	Both valves united with adventitious tube
Ligament	External	External	External	External	External	External
Lithodesma	Unknown	Present	Unknown	Unknown	Unknown	Unknown
Periostracum	Two layers	Two layers	Two layers	Two layers	Two layers	Two layers
Shell microstructure	Prismatic outer layer Inner sheet nacre	Prismatic outer layer Inner sheet nacre	Prismatic outer layer Inner sheet nacre	Prismatic outer layer Inner sheet nacre	Prismatic outer layer Inner sheet nacre	Prismatic outer layer Inner sheet nacre
Adventitious tube	Present	Present	Present	Present	Present	Present
Adventitious tube	Free / cemented	Cemented	Free	Free	Free	Free
Watering pot	Present	Present	Present	Present	Present	Present
Anterior tubules	Present	Present but occluded	Present	Present	Present	Present
Juvenile	Juvenile metamorphosis	Juvenile metamorphosis	Juvenile metamorphosis	Juvenile metamorphosis	Juvenile metamorphosis	Juvenile metamorphosis
Anterior adductor muscles	Unknown	Present	Unknown	Unknown	Unknown	Present
Posterior adductor muscle	Unknown	Present	Unknown	Unknown	Unknown	Present
Anterior pedal retractor muscles	Unknown	Absent	Unknown	Unknown	Unknown	Present
Posterior pedal retractor muscles	Unknown	Absent	Unknown	Unknown	Unknown	Present
Pallial sinus	Unknown	Absent		Unknown		Present
Adult						
Anterior adductor muscle	Absent	Absent	Present	Absent	Absent	Present
Posterior adductor muscle	Absent	Absent	Absent	Absent	Absent	Absent
Anterior pedal retractor muscles	Present	Absent	Present	Absent	Absent	Present
Posterior pedal retractor muscles	Absent	Present	Absent	Absent	Present	Present
Pedal disc	Present	Present	Present	Present	Absent	Present
Pericardial proprioreceptors	Absent	Present	Absent	Absent	Present	Present
Rectum	Passes above kidneys	Passes above kidneys	Passes above kidneys	Passes above kidneys	Passes above kidneys	Passes above kidneys
Suspensory muscles	Absent	Absent	Present	Absent	Present	Absent
U-shaped papillae	Absent	Absent	Present	Absent	Present	Absent
Ctenidial ciliation	Type E	Type E	Type E	Type E	Type E	Type E
Ctenidial/labial palp junction	Category 3	Category 3	Category 3	Category 3	Category 3	Category C
Pallial fusion	Type C	Type C	Type C	Type C	Type C	Type C
Fourth pallial aperture	Present	Present (only in the juvenile)	Present	Present	Absent	Present
Pedal gape	Present	Partially occluded	Present	Present	Present	Present
Pedal disc glands	Present	Absent	Absent	Absent	Absent	Present
Radial mantle glands	Present	Present	Absent	Present	Present	Absent
Siphonal sense organs	Present	Present	Absent	Absent	Absent	Present
Statocysts	Type B_3	Type B_3	Type B_3	Unknown	Type B_3	Type B_3

periostracum, calcium carbonate and another layer of periostracum form the adventitious tube against the template of the burrow wall. The tube of *Penicillus philippinensis* is probably secreted in the same manner and, like all other penicillids, is probably produced but once.

Savazzi (1982) has described the general adaptations to life in a clavagelloid adventitious tube. The function of the tube has also been speculated upon. Purchon (1956, 1960) thought that water was pumped out of the watering pot into the sediment to liquefy the sediments and thereby effect reburial following disinterment. Savazzi (1999) inferred an ability to rebury on the basis of a reconstruction of the growth process of anomalous individuals of *Brechites*. Notwithstanding, Morton (2002a) showed that *B. vaginiferus* could not rebury and that interstitial water was pumped *into* the mantle cavity *via* the watering pot. Such an activity may have a number of functions, as described for *Foegia novaezelandiae* by Morton (2004a). One is to effect siphonal extension, following their withdrawal, by the hydraulic forces generated inside the mantle cavity and *via* pallial haemocoels pumping blood into the siphonal walls. Morton (2004a) further suggested for *F. novaezelandiae* that the tube also fulfils other functions of the true shell. That is, it functions as an exoskeleton which acts antagonistically to the hydraulically-generated forces in the mantle and body to effect the movement into and out of the mantle cavity of water from both the sea above and the interstitial spaces at the end of the burrow. The same structures and the forces they collectively engender essentially act to maintain the body in a state of optimal tonus.

Penicillus philippinensis and *Kendrickiana veitchi* are different from all other known penicillids, for example, *Brechites vaginiferus, Foegia novaezelandiae, Nipponoclava gigantea* (Morton 2002a, 2004a, b) and *P. penis* (Purchon 1956, 1960) in the possession by the former two species of the saddle- or horseshoe-shaped array of muscular mantle papillae. This can be considered to represent a neomorph, that is, a secondarily derived structure replacing the pumping function of either the lost (*K. veitchi*) or vestigial (*P. philippinensis*) adductor and pallial retractor muscles but further serving to attach the animal to its tube and no longer the shell valves. As such, the papillae do not serve to close the shell valves, since these structures are tiny and immovably fused into the fabric of the adventitious tube, but re-create another function, that is, to generate the forces which effect the exchange of mantle fluids with the water column above and interstitial waters in the burrow below. How this is achieved has been illustrated and described for *K. veitchi* by Morton (2004b). It is suggested here that the same forces are generated by the saddle-shaped array of pallial papillae seen in *P. philippinensis.*

The siphons of *Kendrickiana veitchi* are poorly muscularised and cannot be contracted deeply into the adventitious tube (Morton 2004b) unlike in *Brechites vaginiferus, Foegia novaezelandiae* and *Nipponoclava gigantea* (Morton 2002a; 2004a, c). Strangely, the siphons of *Penicillus philippinensis* are well muscularised but the two specimens studied were not retracted deeply into their tubes. This species may be anatomically and functionally intermediate between *B. vaginiferus* and *F. novaezelandiae,* both of which exchange fluids in the mantle cavity using a pedal disc (a structure which *P. philippinensis* also possesses), and the muscularised mantle papillae of *K. veitchi* with no pedal disc. In these two groups of species, therefore, there are two quite different 'pumps' that create the hydraulic forces in the mantle cavity necessary to effect siphonal extension, the exchange of fluids between the supernatant water above and that of the burrow, respiration, the collection of particulate food and the discharge of pseudofaeces and faeces.

The pressures generated in the mantle cavity by contraction of the muscular mantle papillae (or pedal disc) must act, in turn, on the haemocoelomic blood vascular system to achieve movements of, for example, the foot but, especially, the siphons. In the case of *Penicillus philippinensis* and *Kendrickana veitchi*, the blood vessels and pallial haemocoels are huge in comparison with those of other penicillids, for example, *Brechites vaginiferus, Foegia novaezelandiae* and *Nipponoclava gigantea* (Morton 2002a, 2004a, b).

In many other respects *Penicillus philippinensis* is a typical penicillid, for example, with regard to the presence of a distinct pair of pallial retractor muscles attached to a pallial line on the tube, as in *Brechites vaginiferus, Foegia novaezelandiae, Kendrickiana veitchi* and *Nipponoclava gigantea* (Morton 2002a, 2004a, b, c) and to the structures of the mantle cavity, that is, the siphons, ctenidia and labial palps. Commensurate upon the earliest loss of the adductor and pedal retractor muscles with the adoption of a tube-dwelling mode of life, however, natural selection has resulted in the evolution of a new 'adductor muscle' system, that is, a heavily muscularised pedal disc pump. This structure characterizes many representatives of the endobenthic Penicillidae, for example, *B. vaginiferus* and *F. novaezelandiae,* and even the epibenthic cemented *Humphreyia strangei* (Morton 2002b). Possibly because of some inherent inefficiency in this system, however, natural selection has acted further to, essentially, re-create a yet more elaborate replacement for the lost adductor muscle system, that is, the horseshoe-shaped array of muscular mantle papillae in *K. veitchi. P. philippinensis* seems, in the possession of a pallial line and functional pallial retractor muscles, a pedal disc but also a saddle-shaped array of muscular mantle papillae, to be representative of an intermediate state between these two kinds of pumps, thereby giving us an invaluable insight into how the unique muscular system of *K. veitchi* may have evolved.

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APPENDIX

AA	Anterior adductor muscle
AN	Anus
APR	Anterior pedal retractor muscle (or impression)
ASM?	Anterior suspensory muscle?
AU	Auricle
CA	Ctenidial axis
CAN	Ctenidial axis nerve
CJ	Cuticular junction
CM	Circular muscle layer
C-P-V-CONN	Cerebro-pleural visceral connective
DD	Digestive diverticula
DK	Distal limb of the kidney
ES	Exhalant siphon
F	Foot
FPA	Fourth pallial aperture
H	Heart
HA	Haemocoel
HG	Hypobranchial gland
ID	Inner demibranch
IE	Inner epithelium
ILP	Inner labial palp
IP	Inner layer of periostracum
IS	Inhalant siphon
K	Kidney
LM	Longitudinal muscle
M	Mantle
MF	Muscle fibres
O	Oesophagus
OD	Outer demibranch
OE	Outer epithelium
OLP	Outer labial palp
OMF	Oblique muscle fibres
OP	Outer layer of periostracum
OV	Ovary
P	Periostracum
PD	Pedal disc
PE	Papilla epithelium
PEG	Periostracal groove
PEN	Pedal nerve
PG	Pedal gape
PN	Pallial nerve
PPD	Papilla of pedal disc
PPDR	Papilla of pedal disc rim
PPR	Posterior pedal retractor muscle
PRM(1)	Pallial retractor muscle (or impression)
PRM(2)	Papillate pallial retractor muscle (or impression)
PPRM(2)	Papilla of pallial retractor muscle (or impression)
R	Rectum
RSBC	Roof of the supra-branchial chamber
S	Siphons
SA	Shell saddle (or impression)
SBC	Supra-branchial chamber
SG	Siphonal gland
SN	Siphonal nerve
SP	Siphonal papilla
SRM	Siphonal retractor muscles
ST	Statocyst
STA	Statoconia
SV	Shell valve (or impression)
TE	Testes
TMF	Transverse muscle fibres
V	Ventricle
VG	Visceral ganglia