Anatomy of the Spherical, Valvatid Starfish *Podosphaeraster* (Echinodermata; Asteroidea) with Comments on the Affinities of the Genus

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Abstract—The plate arrangement of *Podosphaeraster* includes a dorsal apical system comprising a centrodorsal plate and abutting interradial and radial plates. Marginal plates are not recognisable. *Podosphaeraster* differs from *Sphaeraster* mainly by a reduction in plate number, from over 100 to 10 ventrally and from 38 to 10–12 dorsally. The digestive system of *Podosphaeraster* is highly specialised. The cardiac stomach is very reduced, there is no well-defined pyloric complex and there are no true rectal caeca but a rectal canal from the pyloric floor to the anus. Histologically the digestive system is similar to other asteroids. *Podosphaeraster* is known from the North Atlantic and the western Pacific regions. *Sphaeraster* is known from Jurassic beds in southern Germany, France and Spain.

Introduction

The unusual spherical starfish *Podosphaeraster polyplax* was originally described by Clark and Wright (1962) from a single specimen collected either by H. M. S. EGERIA or H. M. S. PENGUIN during a survey of Macclesfield Bank, South China Sea, in the late 1800s. Bell (1894) had originally reported on the echinoderms collected during the survey, but had missed the significance of the specimen, considering it a juvenile form, possibly a new species, of the large Indo-Pacific cushion-star *Culcita*. Clark and Wright recognised the importance of the specimen and commented on its relationship to the Jurassic and Cretaceous starfish family Sphaerasteridae. A second, somewhat damaged, specimen from Loyalty Islands was similarly reported by Bell (1899) as *Culcita* sp. This specimen was similarly identified as *P. polyplax* by Clark and Rowe (1971).

Since *P. polyplax* was described, two new species of *Podosphaeraster* have been recognised from north Atlantic waters off the Bay of Biscay: first, *P. thalassae*

Cherbonnier, 1970, from two small complete specimens; secondly, *P. crassus* Cherbonnier, 1974, from some ventral fragments. Cherbonnier (1974) also reported a total of five specimens of *P. thalassae* collected on expeditions to the Bay of Biscay area between 1968 and 1972. A third new species, *P. pulvinatus*, collected off the Island of Guam, north Pacific, has been described by Rowe and Nichols (1981). They considered that the Loyalty Islands specimen of Bell (1899) belongs to this new species, and they have tabulated all known records of *Podosphaeraster* collected to the present time. The external morphology of *Podosphaeraster* is described in the present paper, based on all the known species. The internal anatomy of *Podosphaeraster polyplax* is described in detail. For this latter purpose, two of the specimens of *P. polyplax* from the collection in The Australian Museum, Sydney, have been partly or completely dissected and examined for gross internal structure and by histological sectioning.

External Morphology

The test is composed of polygonal (usually hexagonal) plates between which the papulae emerge (Fig. 1). The plates all bear bullet-shaped spines, which are sometimes restricted to a ring round the periphery of the plate, or there may be one or

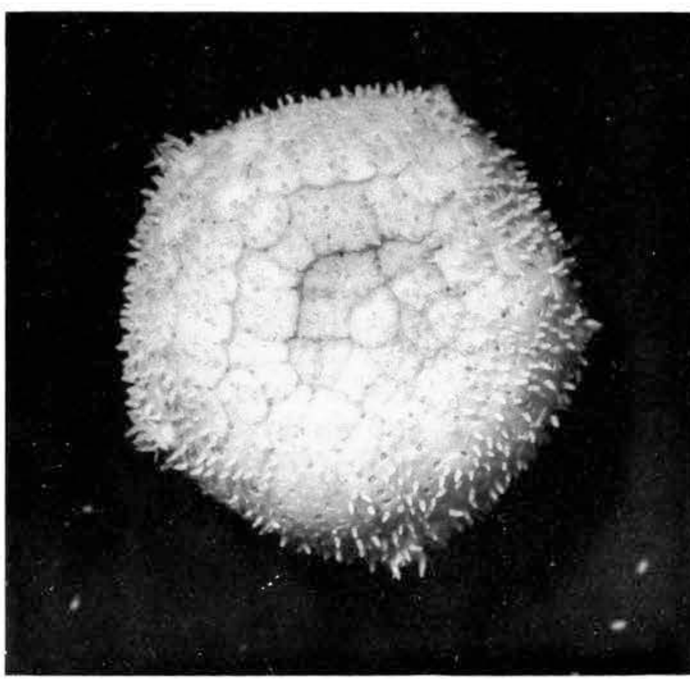

Fig. 1. Aboral view of *Podosphaeraster polyplax* (AM J11721, part), 15.0 mm diameter. A diagram of the apical system of this specimen is given in Fig. 2, A.

more spines within the periphery as well. Five grooved ambulacra, each with two rows of tube-feet, radiate from the ventral mouth and terminate just dorsal to the ambitus. The ambulacral grooves are lined by adambulacral plates, each of which bears furrow spines contributing to an arch over the groove, and subambulacral spines or granules on the flat surface of each plate.

The arrangement of the test plates is distinctive when compared with other starfishes. Dorsally, there is an apical system consisting of a variable arrangement of plates (Figs. 1; 2, A to D). There is a large centrodorsal plate, surrounded in the simplest arrangement by five interradials which touch the centrodorsal and laterally each other, forming a ring. In each distal angle between adjacent interradials is a small, often triangular, radial plate. This system is somewhat reminiscent in appearance of the apical arrangement of certain regular echinoids with exsert radial ('ocular') plates, though this is not to imply any homology.

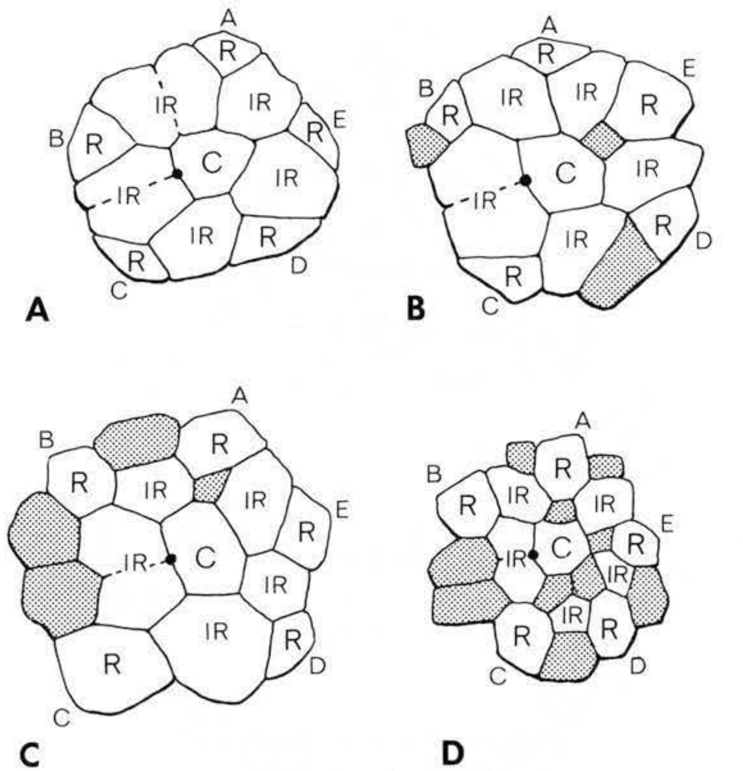

Fig. 2. The variation in plate arrangement of the apical system of *Podosphaeraster polyplax*. A, Loyalty Island specimen (AM J11721, part), diameter 15.0 mm. B, Loyalty Island specimen (AM J11721, part), diameter 9.5 mm. C, Arafura Sea specimen (AM J11720), diameter 11.5 mm. D, South China Sea specimen (BM [NH] 1894.7.3.1 holotype), diameter 12.0 mm. C = centrodorsal plate; R = radial plates; IR = interradial plates; stippled = additional plates; A-E = radii, on Carpenter's notation.

In all specimens so far examined, one plate, the interradial lying between radii B and C (on Carpenter's system of notation), is radially cleft, and the anus lies where this furrow meets the centrodorsal. However, in the largest known specimen of *P. polyplax* (AM J11721, part), which has been dissected, a similar furrow was also present on interradial AB.

Since in *P. polyplax* the apical system may contain additional plates, a convenient starting point in the description of these plates is the situation in the relatively undivided system of the specimens of *P. pulvinatus* from Guam (B.P.B.M. W2813, Fig. 3) and from Loyalty Islands (B.M. [N.H.] 1898.8.8.109) and in the holotype, at least, of *P. thalassae* from the N. Atlantic (Cherbonnier, 1970). Here, there are no plates additional to the simplified condition described above. In the smallest specimen of *P. polyplax* from Loyalty Islands (AM J11721, part, Fig. 2, B) there is a small additional plate on each of the interradii BC and CD, and another

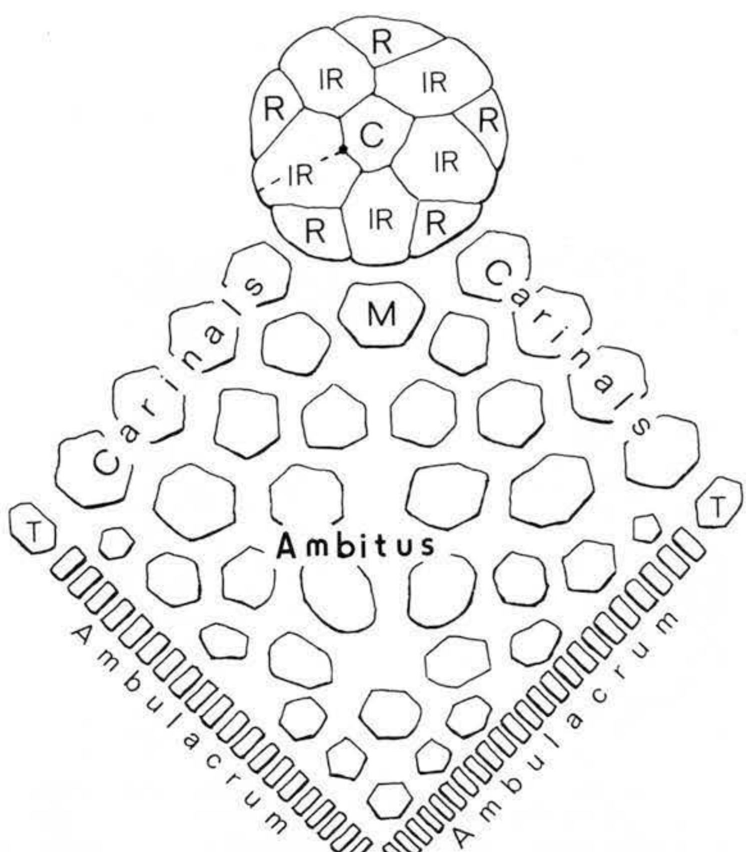

Fig. 3. Diagrammatic plate arrangement of *Podosphaeraster pulvinatus* from Guam, (BPBM W2813, holotype), diameter 21.5 mm. C = centrodorsal plate; R = radial plates; IR = interradial plates; M = madreporite; T = terminal plates.

lying along radius E, between the radial and centrodorsal plates. In each of the specimens so far described the outline of the apical system is easily delimited, and is roughly circular.

In the specimen of *P. polyplax* from the Arafura Sea (AM J11720, Fig. 2, C), it is more difficult to delimit the outline of the apical system. This may be due to the presence of a number of extra plates at the periphery which we here include within the system. On our interpretation, therefore, there is one extra plate in interradius AB and two in interradius BC, as well as an additional small plate lying along radius A between the centrodorsal and the radial.

In the holotype of *P. polyplax* (B.M. [N.H.] 1894.7.3.1, Fig. 2, D) the situation appears to us to be somewhat similar to that in the specimen from Arafura Sea. Here, there are again extra peripheral plates, one in interradius AB, two in BC, one in CD, one in DE and one in EA; there are also extra plates along radii A, C, D and E. In this specimen the situation is so complex that it is not easy to be certain of the identity of the primary interradials CD and DE.

The arrangement of the remaining skeletal plates (excluding the furrow plates) shows little variation (Fig. 3). Dorsally there is a row of four plates, here called carinals, extending along each dorsal radius from the radial plates of the apical system down to the terminal plates of the ambulacra. In *P. thalassae* radii A, D and E have only three midradial plates and a small nodule, while radii B and C have the more usual four carinals.

In the triangular area of each interradius formed between the carinals of adjacent radii and the ambitus are three rows of plates. In the Loyalty Islands and Guam specimens these are formed of three plates at the apex of the triangle and two rows of four plates ambitally, whereas in the Arafura Sea and China Sea specimens there are usually two plates radially aligned on either side of a single larger plate in the first row. The middle plate in this top row in interradius CD bears the madreporite.

Below the level of the ambitus is a row of six to eight plates across each interradius. The two central plates of this row are more oval and obliquely aligned than the others of the row. Below this row is a ventral interradial triangle comprising four, three, two and one plates. There is no variation in the disposition of these plates in the specimens studied.

Neither supero- nor inferomarginal plates can be distinguished in any of the specimens examined.

Comparison of the Skeletal Plates of *Podosphaeraster* and *Sphaeraster*

The reconstruction of the Jurassic *Sphaeraster 'punctatus'* (in Schondorf, 1906) is based on at least three species which may not even be congeneric, according to Clark and Wright (1962), hence the specific name here placed in parenthesis. This may be significant in the interpretation of the position of structures in Schondorf's reconstruction, for instance, the difficulty in distinguishing the infero- and superomarginal rows of plates in *Podosphaeraster*, as opposed to Schondorf's interpretation of the row of larger marginal plates in *Sphaeraster* as superomarginals. Also, the position of the madreporite piercing a plate in *Podosphaeraster* does not compare with its interplate position in *S. 'punctatus'*.

Comparing the dorsal plate arrangement of *S. 'punctatus'* and *P. polyplax* by means of exploded diagrams, Clark and Wright (1962) indicate some extra intercalary plates in *P. polyplax*. Taking the reconstruction of *S. 'punctatus'* as a whole, however, another explanation is possible, based on the evolutionary reduction of the number of plates. In the much larger *S. 'punctatus'* there are nine carinal plates per radius and ten marginals at the ambitus. In the enclosed interradial triangle are eight tangential rows of plates, increasing in number of plates per row from one to nine (no row of seven plates) from apex to ambitus. The main difference between *Sphaeraster* and *Podosphaeraster* can therefore be seen in terms of a straight reduction in number of plates, from about 38 to 10 or 12 dorsally, and from over 100 to 10 ventrally (excluding the marginal row in *S. 'punctatus'*). This reduction in number of plates is accompanied by a reduction in size: *S. 'punctatus'* is approximately 100 mm horizontal diameter and 90 mm vertical diameter, while the maximum size for *P. pulvinatus* is 21.5 mm (HD) $\times$ 12 mm (VD), and for *P. thalassae* 8.5 mm (HD) $\times$ 7.4 mm (VD); the estimated horizontal diameter of *P. crassus*, known only from disarticulated plates, is 50–70 mm.

There is a small depression (in two plates on the Arafura Sea specimen a perforation) in the upper surface of each terminal plate of each ambulacrum, and a perforated plate occurs in a similar position on *S. 'punctatus'*. The most likely explanation of this structure is that it marks the position of the terminal tentacle of the water-vascular canal.

Internal Anatomy of *Podosphaeraster polyplax*

The inner wall of the test is reinforced in each interradial midline by a calcite ridge (Fig. 4, C). Each ridge arches away from the internal test wall, particularly towards the oral side of the body; they correspond to the interradial columns of a more conventional asteroid. The ambulacral plates also form reinforcing ridges internally (Fig. 4, D), but these ridges extend only from the oral region to just above the ambitus.

The coelomic cavity is lined by a thin perivisceral membrane. This cavity is incompletely divided into five partitions by the interradial mesenteries which extend from the interradial columns for about half the distance of the central axis of the body (Fig. 4, A). Each interradial mesentery is closely associated with a gonad and supports it aborally (Fig. 4, A, B and C). The studied specimen is a female with relatively little-developed gonads containing growing oocytes (Fig. 5, D).

Four polian vesicles arise from the water-vascular ring in four interradii; in the fifth interradius the stone canal arises and courses through the interradial mesentery to the madreporite near the apical system. The ambulacral ampullae are non-

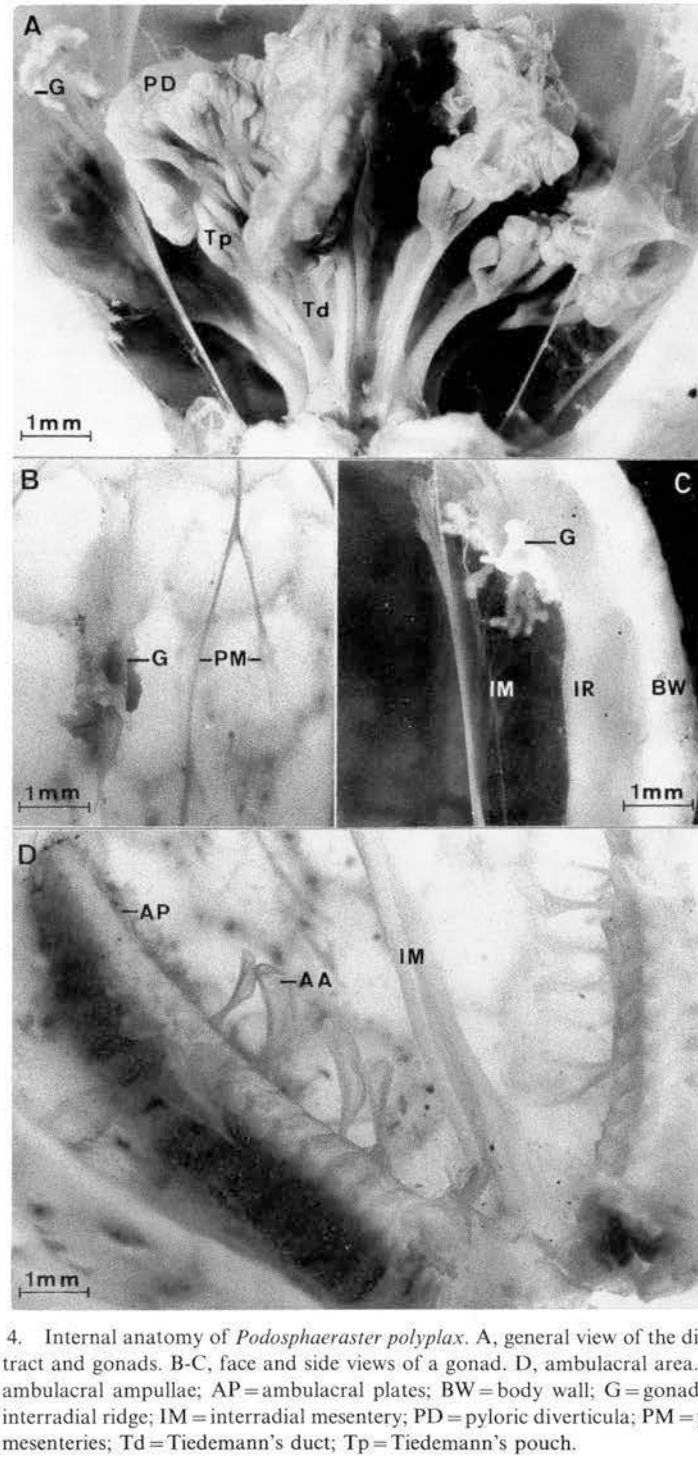

Fig. 4. Internal anatomy of *Podosphaeraster polyplax*. A, general view of the digestive tract and gonads. B-C, face and side views of a gonad. D, ambulacral area. AA = ambulacral ampullae; AP = ambulacral plates; BW = body wall; G = gonad; IR = interradial ridge; IM = interradial mesentery; PD = pyloric diverticula; PM = pyloric mesenteries; Td = Tiedemann's duct; Tp = Tiedemann's pouch.

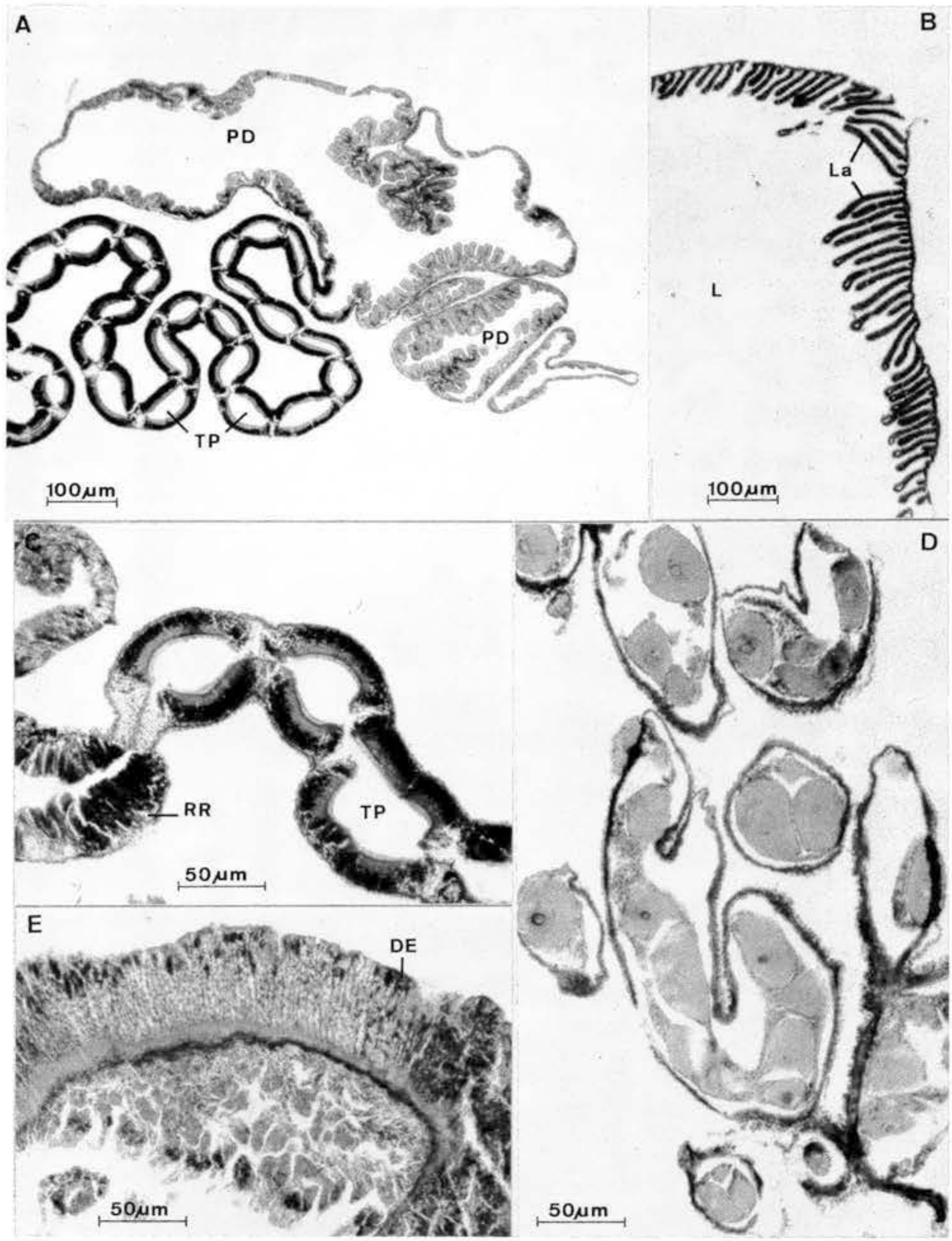

Fig. 5. General histology of some organ systems of *Podosphaeraster polyplax* (AM J11721, part). A and C, radial digestive structures. B, rectal canal. D, ovary. E, ventral part of stomach. DE = digestive epithelium; L = digestive lumen; La = rectal lamellae; PD = pyloric diverticulum; RR = radial reservoir; TP = Tiedemann's pouch.

bifurcated (Fig. 4, D).

The digestive system of *P. polyplax* is highly specialized and rather different from those of most other asteroid families. The cardiac stomach is very reduced, reaching about the same diameter as the peristomial membrane (Fig. 4, A). Five small radial cardiac pouches occur. The stomach retractor system is inconspicuous, being limited in each radius to two short strands joining the lateral parts of the cardiac pouches to those of the first ambulacral plate. The pyloric digestive structures are unusual and rather different from those of other valvatid asteroids (Anderson, 1978; Jangoux, 1982). There is no well-defined pyloric complex in *P. polyplax*; the digestive structures forming the branches of that complex in other valvatids are here integrated within each pyloric caecum, giving five pairs of unusual pyloric appendages (Figs. 4, A; 6). The central part of these appendages consists of a conspicuous Tiedemann's pouch surrounded along its entire length by an elongated radial reservoir; the pyloric diverticula are located distally while the pyloric folds surround the Tiedemann's duct proximally. There are no true rectal caeca, but there is a long rectal canal which connects the pyloric floor to the anus.

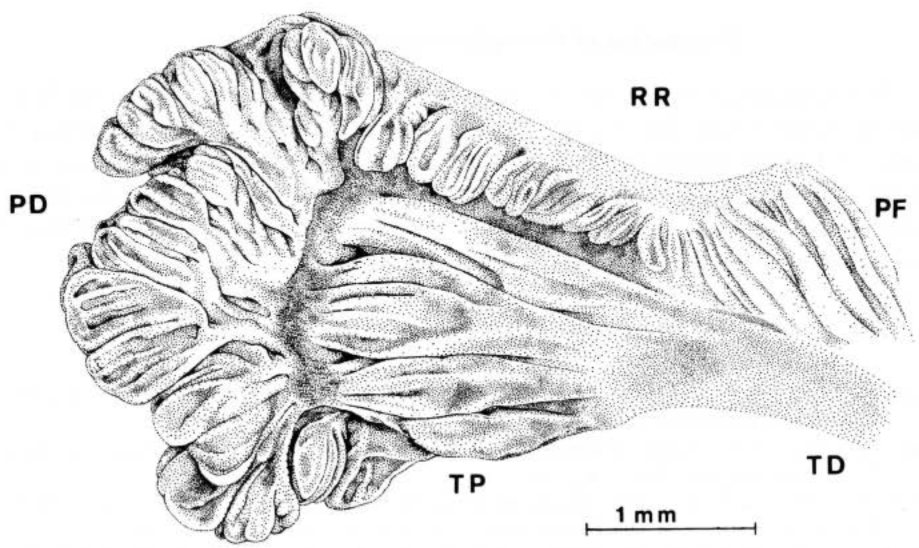

Fig. 6. Lateral view of the radial pyloric structure of *Podosphaeraster polyplax*. PD = pyloric diverticula; PF = pyloric folds; RR = radial reservoir; TD = Tiedemann's duct; TP = Tiedemann's pouch.

The general histology of the digestive system of *P. polyplax* has been tentatively investigated in spite of a rather inappropriate fixative method. The gross digestive histology corresponds to that of other asteroids (Jangoux, 1982). The ventral part of the cardiac stomach shows numerous mucous cells in its digestive epithelium and its muscular layer is strongly developed (Fig. 5, E). Tiedemann's pouches and

Tiedemann's ducts are lined by heavily flagellated cells, the muscular layer of these structures being well developed. The Tiedemann's pouches of *P. polyplax* are very similar to those of *Henricia sanguinolenta* (Anderson, 1960), i.e., they have internal partitions produced by peculiar seam-cells which divide the pouches into several tubular conduits running from the Tiedemann's duct to the pyloric diverticula (Fig. 5, A, C). The pyloric diverticula are histologically similar to those of other asteroids, and the inner cavity of the radial reservoirs is lined by numerous mucous cells. The rectal canal resembles the rectal caeca in having numerous epithelial lamellae, but differs in having almost no muscular layer.

The digestive system of *P. polyplax* shows a conspicuous development of the Tiedemann's organs (ducts and pouches), together with a strong reduction of the cardiac stomach. Tiedemann's organs are known to be capable of pumping food into the digestive tract; they also act to augment the efficiency of water circulation inside the digestive tract (Jangoux, 1982). According to its digestive organization one may presume that *P. polyplax* is a microphagous asteroid feeding on deposit particulate matter (epibenthic film).

Distribution of *Podosphaeraster* and *Sphaeraster*

Podosphaeraster is now known to occur off the Bay of Biscay in the North Atlantic, South China Sea, Arafura Sea, off Guam in the North Pacific and in the vicinity of Loyalty Islands in the southwest Pacific. The Jurassic fossil *Sphaeraster* is known from southern Germany, France and Spain. The ecology of the Recent *Podosphaeraster* is not known, beyond a statement by Cherbonnier (1970) that *P. thalassae* appears to have been taken from rough ground.

References Cited

Anderson, J. M. 1960. Histological studies on the digestive system of a starfish, *Henricia*, with notes on Tiedemann's pouches in starfishes. Biol. Bull. 119: 371–398.

Anderson, J. M. 1978. Studies on functional morphology in the digestive system of *Oreaster reticulatus* (L) (Asteroidea). Biol. Bull. 154: 1–14.

Bell, F. J. 1894. On the echinoderms collected during the voyage of H.M.S. 'Penguin' and by H.M.S. 'Egeria', when surveying Macclesfield Bank. Proc. zool. Soc. Lond. 1894: 392–413.

Bell, F. J. 1899. Report on echinoderms (other than holothurians) collected by Dr. Willey. Pages 135–140. *In* A. Willey (ed.), Zoological Results based on material from New Guinea, New Britain, Loyalty Islands and elsewhere, collected 1895–7. Part II. London.

Cherbonnier, G. 1970. *Podosphaeraster thalassae*, nov. sp., espèce actuelle d'Astérie de la famille jurassique des Sphaerasteridae. C. r. Acad. Sci. Paris (D) 271: 203–206.

Cherbonnier, G. 1974. *Podosphaeraster crassus* nov. sp., espèce actuelle d'Astérie de la famille jurassique des Sphaerasteridae. C. r. Acad. Sci. Paris (D) 278: 1731–1733.

Clark, A. M., and C. W. Wright. 1962. A new genus and species of recent starfishes belonging to the aberrant family Sphaerasteridae, with notes on the possible origin and affinities of the family. Ann. Mag. nat. Hist. 13 (5): 243–251.

Clark, A. M., and F. W. E. Rowe. 1971. Monograph of shallow-water Indo-west Pacific echinoderms. London. 238 p.

Jangoux, M. 1982. Digestive systems: Asteroidea. Pages 235–272. *In* M. Jangoux and J. M. Lawrence (eds.), Echinoderm Nutrition. Balkema Publ., Rotterdam.

Rowe, F. W. E., and D. Nichols. 1981. A new species of *Podosphaeraster* Clark & Wright, 1962 (Echinodermata: Asteroidea) from the Pacific. Micronesica 16 (2): 289–295.

Schondorf, F. 1906. Die organisation und systematische stellung der sphaeriden. Arch. biont. 1: 245–306.