On the genus *Podosphaeraster* A. M. Clark & Wright
(Echinodermata, Asteroidea),
with description of a new species from the North Atlantic

by F. W. E. Rowe

Abstract. — *Podosphaeraster gustavei* nov. sp. is described. A comparative discussion is given of the anatomy of the species of the genus. The genus *Podosphaeraster*, considered ancient, arose between the late Cretaceous and the early Tertiary period and was probably, formerly pan-Tethyan. Its present day, apparent disjunct, distribution has been due to vicarient events. This interpretation permits the occurrence of the genus in the Indian Ocean to be predicted. *Podosphaeraster crassus* Cherbonnier is synonymised with *Nymphaster arenatus* and is placed in the Goniasteridae.

Résumé. — *Podosphaeraster gustavei* nov. sp. est décrite. L'anatomie des diverses espèces du genre est discutée de façon comparative. Le genre *Podosphaeraster*, considéré comme ancien, est sans doute apparu entre la fin du Crétacé et le début du Tertiaire, et appartenait probablement à l'ancienne Téthys. Sa distribution actuelle, apparemment disjointe, résulterait d'un processus vicariant. Cette interprétation permet de supposer la présence de ce genre dans l'océan Indien. *Podosphaeraster crassus* Cherbonnier est synonyme de *Nymphaster arenatus* et est placée parmi les Goniasteridae.

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Introduction

The genus *Podosphaeraster* Clark and Wright, 1962, was described for an unusual, spherical sea-star *P. polyplax* Clark and Wright, collected from the South China Sea in the latter part of the 19th century. Since *polyplax* was described, three new species have been recognised : *P. thalassae* Cherbonnier, 1970, from the North-east Atlantic, *P. crassus* Cherbonnier, 1974, also from the North-east Atlantic ; *P. pulvinatus* Rowe and Nichols, 1980, from the West Pacific. Cherbonnier (1974) also recorded five further specimens of *P. thalassae* from the North-east Atlantic. Rowe and Nichols (1980) recorded *P. polyplax* from the Arafura Sea and the south-west Pacific and summarised records of known specimens. Rowe *et al.* (1982) gave a detailed account of the anatomy of the genus and its affinities with the Jurassic-Cretaceous genus *Sphaeraster* Quenstedt. Their study was based on material of *P. polyplax* and *pulvinatus* which they had examined, and relevant information drawn from Cherbonnier's (1970, 1974) works. None of Cherbonnier's material was examined.

During an overseas study visit to the Muséum national d'Histoire naturelle of Paris, in 1981 the present author examined the existing material of *Podosphaeraster* housed in that Institution. This comprised six specimens identified by Dr. CHERBONNIER as *P. thalassae* and the fragment (holotype) representing *P. crassus*. The present author was convinced that only the original material of *thalassae*, that is the holotype and paratype, represented that species, the four other specimens (five were actually recorded by CHERBONNIER, 1974) representing a new species. He also considered that the fragment of *P. crassus* did not possess characteristic structures necessary for its inclusion in the genus *Podosphaeraster*. All this material was therefore, returned to the Australian Museum for formal re-examination and redescription.

This paper, records the results of the re-examination of that material, together with a reassessment of *Podosphaeraster* and a discussion of the distribution and probable ancient history of the genus.

SYSTEMATIC ACCOUNT

A. — **Podosphaeraster gustavei** nov. sp.
(Pl. I, A-F ; text-fig. 1)

MATERIAL : 44°11′8″ N, 8°40′6″ W (" Thalassa " stn. Y428), 500 m, 4.ix.1972 ; 1 specimen (holotype : MNHN n° EcAs 4653). 44°11′8″ N, 8°40′4″ W (" Thalassa ", stn. 434), 500-540 m, 13.x.1970 ; 1 specimen (paratype : MNHN n° EcAs 4654). 44°07′1″ N, 4°43′8″ W (" Thalassa ", stn. X349), 615 m, 12.ix.1971 ; 1 specimen (paratype : MNHN n° EcAs 4652). 39°22′S″-31°54′4″ N (" Jean-Charcot "-Biacores, stn. 117), 500-520 m, 21.x.1971 ; 1 specimen (paratype : MNHN n° EcAs 4650).

DIAGNOSIS : A species of *Podosphaeraster* of maximum known size hd = 14 mm ; cushion-shaped to spherical, hd/vd = 1.5-1.1 ; apical system regular, simple ; carinal row of abutting flat plates, extending between the radial plate of apical system and the terminal plate of the ambulacrum ; terminal plate losing perforation with growth ; recorded from the North-east Atlantic Ocean, 500-615 m.

ETYMOLOGY : The species is named for Dr. Gustave CHERBONNIER.

DESCRIPTION OF THE HOLOTYPE

The holotype has a horizontal diameter (hd) of 9.5 mm and is pentagonal in horizontal cross-section. The vertical diameter (vd) is 6.2 mm, so that the ratio hd/vd is 1.5, giving the animal a cushion-like shape (pl. I, A). The test comprises abutting, usually hexagonal plates. The plates are textured with low, glassy bumps.

The apical system is pentagono-stellate, 3.6 mm diameter. It is simple, comprising a central-dorsal plate surrounded by five interradials, which themselves abut laterally. In each distal angle, between adjacent interradials is a wedge-shaped radial plate, which is more or less equal in size to an uncleft interradial. The interradial plate in interradius BC

is radially cleft and is the largest of the five plates. The anus lies in the suture between the central-dorsal plate and cleft interradial (pl. I, B).

A carinal row of four plates extends along each dorsal radius, abutting proximally with the radial plate of the apical system and distally with the terminal plate. In the interradial triangle, between adjacent carinal rows and the ambitus, are three horizontal rows of plates. At the apex of the triangle is the proximal row of three plates, below which are two rows, a middle and distal row, each of four plates. The central two plates of the middle row are elongate-oval, rather than hexagonal, and very slightly obliquely aligned. The madreporite is prominent and occurs on the middle plate of the proximal row in inter-radius CD. The centre of the plate is raised with the madreporic pore being surrounded by four subequal nodules.

In the actinal interradial triangle, between adjacent ambulacra and below the ambitus, are five horizontal rows of plates. The distalmost row of six plates extends between the terminal plate of each ambulacrum. The two central plates of this row are the smallest and are slightly obliquely aligned. Together they approximate in size to the adjacent plate on each side in the row. The outer plate at each end of this row, and adjacent to the terminal plate, is relatively large. Proximal to this row of plates are four rows of plates, of four, three, two and, in the proximal position adjacent to the oral plates, one plate.

The terminal plates are more or less hemispherical in outline. Three of these plates (radii B, C, D) possess a slight to deep actinal channel in the order of B-D respectively. The terminal plate in radius E possesses a large perforation. However, the actinal surface of the plate, under the perforation, seems to be breaking down in a way that appears to be leading to the opening (or loss) of the perforation (see p. 315). The terminal plate in radius A possesses a small perforation (text-fig. 1).
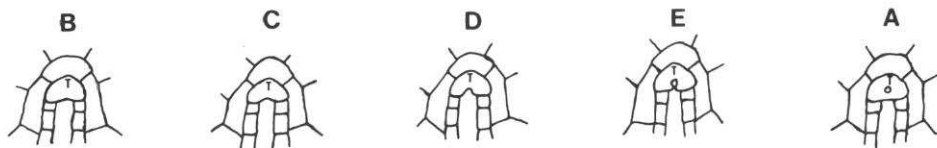

Fig. 1. — *Podosphaeraster gustavei* nov. sp., holotype, EcAs 4653 : terminal plates (T) in ambulacra A-E.

Marginal plates have not been formally distinguished (see p. 315-316).

The ambulacral furrows bear two rows of tube-feet. The tube feet do not possess spicules. The adambulacral grooves are lined by fourteen adambulacral plates on each side. Each plate bears two or three furrow spines on the adradial edge. On the flat surface of the plate two subambulacral spines (up to 700 μm long) stand more or less at right angles to the furrow.

Each oral plate bears three furrow spines and two or three subambulacral spines.

Four to eight bullet-shaped granules occur spaced on the abactinal and actinal plates. The abactinal granules are shorter (270-380 μm) than the actinal granules (360-450 μm).

Papulae occur singly at the angles between the abactinal and actinal plates, except the proximalmost two rows of one and two actinal plates.

NOTE ON THE PARATYPES

The smallest paratype (EcAs 4650) (pl. I, E) measures hd = 5.6 mm, vd = 4.5 mm, hd/vd = 1.28. In the proximal row of plates of the abactinal, interradial triangle, the first and third plates are much smaller than the middle plate in that row. Each of the terminal plates of the ambulacrum possesses a central perforation. The ambulacrum comprises ten pairs of adambulacral plates. Papulae do not occur between the plates of the apical system or between plates of the three proximal rows of the actinal triangle.

Paratype EcAs 4654 measures hd = 7.1 mm, vd = 6.0 mm, hd/vd = 1.18 (pl. I, C). Three of the terminal plates (radii A, B, D) are perforate whilst two (radii C, E) are not. The ambulacrum comprises fifteen pairs of adambulacral plates. Papulae occur actinally from between the third and fourth rows of plates.

The largest paratype (EcAs 4652) measures hd = 14 mm, vd = 12.7 mm, hd/vd = 1.1 and is the most spherical of the four specimens (pl. I, F). The apical system has a diameter of 6.2 mm, with plates in interradii AB and EA each having a transverse cleft. Otherwise the plates of the apical system are unmodified. In the proximal row of abactinal, interradial plates the three plates are more or less similar in size. The test plates are textured with glassy bumps between which run slight furrows. There are twenty pairs of adambulacral plates, each bearing three furrow spines and two subambulacral spines. None of the terminal plates is perforate.

INTERNAL ANATOMY

Two paratypes (EcAs 4654 and EcAs 4652) were partly dissected in order to examine the internal anatomy for comparison with *P. polyplax* (ROWE *et al.*, 1982). The general anatomy is similar to that described by ROWE *et al.* (1982) for *P. polyplax* and does not require description (pl. I, C, D, F). However, the rectum is quite different in *gustavei* being produced into five pouch-like structures, one lying in each interradius between adjacent pairs of radial pyloric caecae (pl. I, C). Each rectal pouch is plicate internally. Subsequent examination of the smallest specimen of *P. polyplax* (AM J11721) has shown poorly developed rectal caecae which are absent in large specimens (see p. 318). Both specimens of *gustavei* examined were female, with developing oocytes in the paired, lobate gonads (pl. I, D). In the smaller specimen (EcAs 4654) the oocytes measured up to about 135 μm diameter, whilst in the largest specimen examined (EcAs 4652) the oocytes were larger, up to 230 μm diameter. Each pair of gonads contains an estimated 200-400 oocytes This indicates a probable perenniel, low productive effort with the development of moderately large eggs and non-planktotrophic (FAUCHALD, 1983) possibly demersal (PEARSE, 1969) larvae. Although histological evidence shows the gonoduct to be dorsally directed, the position of the gonopore has not been determined. This is due to conservative dissection in order not to significantly damage the specimen. Retrieval of additional specimens will allow further investigation by dissection.

REMARKS

Re-examination of, and comparison between, the holotype and paratype of *P. thalassae* and the specimens of *P. gustavei* described herein shows that the new species differs from the sympatric *thalassae* in its larger size and more particularly in the arrangement and shape of the plates in the carinal row. In the holotype of *thalassae*, which measures hd = 8.5 mm, the carinal plate adjacent to the radial plate of the apical system has become small and convex (nodular) and is separated from the next plate in the carinal row by the contiguity of plates of the proximal rows of adjacent interradii, at least in radii A, D and E. In the smaller paratype of *thalassae*, hd = 6.0 mm, the separation of these small nodular plates from others in the carinal row has not occurred. However, the shape and size of these plates affords a distinctive difference. The loss of the perforation in the terminal plates of *thalassae* (each terminal plate of the paratype is perforate but *none* is perforate in the holotype) occurs before the animal reaches hd = 8.5 mm, whereas some of these plates remain perforate in *gustavei* even at hd = 9.5 mm. Finally, although the largest known specimen of *gustavei* is more or less spherical (hd/vd = 1.1) (pl. I, F), smaller animals appear to grow through a more cushion-shaped form (hd/vd = 1.18-1.5) (pl. I, A). Insufficient material of *thalassae* does not permit a direct comparison of this feature to be made. However, the small paratype of *thalassae* is somewhat flatter (hd/vd = 1.2) than the larger holotype (hd/vd = 1.15), which might suggest a similar growth pattern.

P. gustavei is easily distinguished from the Pacific species *P. polyplax* by the complexity of the apical system in *polyplax*. Differences of the rectal region occur but may not be important taxonomically (JANGOUX, 1982). Re-examination of the Australian Museum material of *P. polyplax* has confirmed that the terminal plates remain perforate even in the largest specimen known (hd = 15 mm).

P. gustavei is distinguished from *P. pulvinatus* by its small size, its shape and fewer granules on the test plates. The internal anatomy of *pulvinatus* is not known but the terminal plates of the large holotype (hd = 21.5 mm) are reported perforate by ROWE and NICHOLS (1980).

P. crassus is removed, herein, from the genus *Podosphaeraster* and placed in the synonymy of the goniasterid species *Nymphaster arenatus*.

B. — THE STATUS OF *Podosphaeraster crassus* Cherbonnier, 1974

Nymphaster arenatus (Perrier)

(Pl. I, G-I)

Pentagonaster arenatus Perrier, 1884 : 236, pl. vii, figs. 3-4.
Nymphaster arenatus : MORTENSEN, 1927 : 84, fig. 8 ; DOWNEY, 1973 : 58, pl. 22, figs. C, D.
Podosphaeraster crassus Cherbonnier, 1974 : 1731.

MATERIAL : 47°39′8″ N, 8°05′3″ W (" Jean-Charcot ", stn. 16), 1 120-900 m, 5.xii.1968 ; 1 specimen (holotype of *Podosphaeraster crassus* : MNHN n° EcAs 4651).

REMARKS

CHERBONNIER (1974) gave a detailed description of a triangular, actinal fragment (12.4 mm long) of a sea-star, believing it to represent a portion of a new, relatively large species (50-70 mm hd) of *Podosphaeraster*. Two features of particular interest described by CHERBONNIER (1974) were the presence of perforated, denticulate bars in the tube feet and his interpretation of a perforated actinal plate as possibly representing an unusually actinally placed madreporite. ROWE and NICHOLS (1980), while describing *P. pulvinatus*, commented on these features in distinguishing *P. crassus*. They suggested that *crassus* might be separated from the other species in *Podosphaeraster* at a generic, if not familial level. However, not having examined CHERBONNIER's material, they declined to comment further.

An examination of the fragmentary type material (pl. I, G-I) has now convinced the present author that CHERBONNIER was incorrect in assigning the species, *crassus*, to the genus *Podosphaeraster*. It represents, instead a proximal oral fragment of a goniasterid. The evidence for the assertion lies in the presence of bars in the tube-feet (a goniasterid feature ; see ROWE, 1977) ; the complexity and arrangement of the adambulacral armature ; the imbricating, rather than abutting, actinal plates ; the absence of actinal papulae between the plates. Most significantly, the absence of the internal mid-interradial calcite ridge, present in all other species of *Podosphaeraster*, precludes the inclusion of *crassus* in that genus (pl. I, G). Finally, CHERBONNIER was mistaken in describing a perforation in one of the actinal plates. He correctly represents the arrangement of granules on the plate (CHERBONNIER, 1974, fig. 2c) but the plate is *not* perforated. It appears that minor damage has occurred, such as the loss of one or two granules and that a circlet of new, small granules is in the process of developing to replace this loss (pl. I, H-I).

The arrangement of the plates, granulation and adambulacral armature suggested to the present author that the fragment represents part of a specimen of *Nymphaster*. The species *N. arenatus* (Perrier) is known from the same area and depth as that from which *Podosphaeraster crassus* was collected. In fact, *N. arenatus* is wide-spread in the North Atlantic (MORTENSEN, 1927 ; DOWNEY, 1973). Following a request by the author, Miss A. M. CLARK, (British Museum (Natural History), London), compared a photograph of *P. crassus* with specimens of *Nymphaster arenatus* (Perrier) ; *Ceremaster granulatus* (O. F. Müller) ; *Plinthaster dentatus* (Perrier) ; *Pseudarchaster parelii* (Düben & Koren) and *Sphaerodiscus placenta* (Müller & Troschel) and thought the author correct in his assessment (A. M. CLARK, pers. comm.). After directly comparing *P. crassus* with a similar section of *N. arenatus* sent to the author by Miss CLARK, he is now convinced that, despite the fewer furrow spines present (5 in *crassus* as opposed to 6-9 in *N. arenatus*), the best course to follow is to consider *Podosphaeraster crassus* a synonym of *Nymphaster arenatus* and formally commit it herein. It is considered that it would be impossible to recognise any whole animal collected as that representative of the likely complete form of *P. crassus*, a species founded on such an inadequate and broken fragment.

STRUCTURE, AFFINITIES AND DISTRIBUTION
OF THE GENUS *PODOSPHAERASTER*

Despite the recent discovery and description of the genus from the relatively few (12) known specimens representing the four nominal species of *Podosphaeraster*, a good deal of interest has been shown in this sea-star (CLARK and WRIGHT, 1962 ; CHERBONNIER, 1970, 1974 ; ROWE and NICHOLS, 1980 ; ROWE *et al.*, 1981 ; JANGOUX, 1982).   The present study of this enigmatic asteroid has further high-lighted perplexing features both from the point of view of explaining evolutionary development of, and relationships between, the known species.

Firstly, there appears to be a progressive loss of the perforation of the terminal plate of the ambulacrum, with growth of the animal, in both of the Atlantic species.   The apparent progressive opening of the actinal (ventral) surface of the five terminal plates in the holotype of *P. gustavei*, which is intermediate in size in the series of specimens described (see p. 311), shows this phenomenon most clearly (text-fig. 1).   Even in the only two known specimens of *thalassae* pores are present in the smaller specimen but absent from the larger.   In both of the Pacific species the terminal plates remain perforate in the known material, with the holotype of *pulvinatus* at least 50 % larger than the known Atlantic specimens.   The significance of possessing a pore in the terminal plate, which is presumably occupied by the sensory, terminal tentacle of the water vascular system, is unknown, but such a pore is known to occur in a few, widely related extant species (*Caymanostella* spp., *Tosia queenslandensis, Pentagonaster crassimanus, P. duebeni, Stichaster striatus, S. australis*).

The report of the occurrence of a perforation in the terminal plate of the fossil *Sphaeraster 'punctatus'* (ROWE *et al.*, 1982) was made in error.

The early, post metamorphic skeletal development of only a few extant asteroid species has been described (see KOMATSU, 1975 ; OGURO *et al.*, 1976 ; KOMATSU *et al.*, 1979).   However, one of the most detailed accounts still remains that of FEWKES (1888).   It appears that the terminal plates, which are the first to be laid down at metamorphosis, are cap-shaped, each with an actinal (ventral) channel which is occupied by the terminal tentacle.   It would appear likely, therefore, that the pore which perforates the terminal plates of those asteroid species listed above, is developed by the actinal closure of that channel.   If this is the case then what is occurring in *Podosphaeraster*, at least, is that the Atlantic species are exhibiting what appears to be a secondary opening of the actinal channel of the terminal plate with growth.   The significance of this development is difficult to determine on the present evidence, other than to speculate a redundant evolutionary experiment.

Secondly, the adopted practise of describing the arrangement of abactinal and actinal plates in *Podosphaeraster*, with the exception of the radially aligned carinal plates and the apical system, has been in horizontal order (CLARK and WRIGHT, 1962 ; ROWE and NICHOLS, 1980 ; ROWE *et al.*, 1982 and herein) instead of longitudinal order as in other asteroids.   The position of marginal plates therefore has not been determined (ROWE *et al.*,

1982). The occurrence of marginal plates in asteroids is varied and may comprise a single row, a double row, which may or may not have equal numbers of plates, or marginals which may be restricted along the arms (SPENCER and WRIGHT, 1966). Within the family Sphaerasteridae, as currently understood, the fossil genus *Sphaeraster* has been reconstructed as a dome-shaped animal with a flattened or slightly concave actinal surface, at the rim of which a row of superomarginal plates and a row of smaller but of equal number, inferomarginals occur (SCHONDORF, 1906). *Valettaster* Lambert has been compared in shape with *Sphaeraster*, though a reconstruction has not been published (SPENCER & WRIGHT, 1966). It seems to the present author that in *Podosphaeraster*, imposition of the spherical shape on such a rigid test structure might well necessitate major realignment of plates. This would include the probable separation of the superomarginal and inferomarginal plates from each other, at least interradially, and the necessary addition of intermarginal plates. Spherical shape may not be the only reason for such a realignment of the marginal region since intermarginal plates are known to occur in a number of regularly stellate, but high-disced, asteroids. These however, have a more flexible skeleton, the primary plates being supported by internal connecting rods. ROWE (1977) has suggested ecological pressures for the arrangement of reduced number of marginals, extensive intermarginal plating and extension of papulae from the abactinal surface in the family Asterodiscididae.

The site of development of marginal plates is from each side of the terminal plate of each arm (FEWKES, 1888). The marginal plates extend into the interbranchial arch where the apex of the arch is formed by the contact of the first developed marginals from adjacent arms. In the case of *Podosphaeraster* species there are two interradially placed,
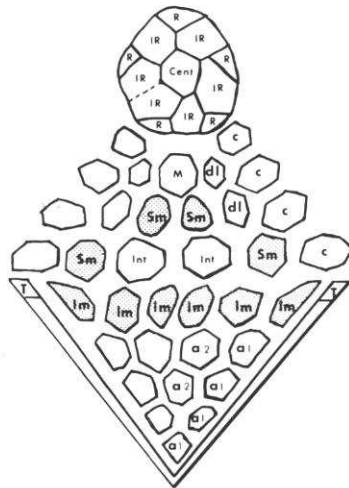

FIG. 2. — Diagrammatic representation of proposed plate arrangement of *Podosphaeraster* : Cent = central-dorsal plate ; R = radial plates ; IR = secondary interradial plates ; C = carinal plates ; dl = proposed abactinal-lateral plates ; M = madreporic plate (primary interradial plate) ; Sm = proposed superomarginal plates ; Int = proposed intermarginal plates ; Im = proposed inferomarginal plates ; a1 = first row, proposed actinolateral plates ; a2 = second row, proposed actinolateral plates ; T = terminal plate at tip of ambulacra.

lozenge-shaped plates in both the horizontal middle row of abactinal plates and the outer-most row of actinal plates which lie immediately below the ambitus (ROWE & NICHOLS, 1981 ; ROWE *et al.*, 1982 ; herein). If these were considered to be the first marginals then an arrangement of marginal plates could be suggested which incorporate two, additional, intermarginal plates to "fill the gap" between the arching supero- and inferomarginal rows (text-fig. 2). The remaining plates in the ventral interambulacral region may then be regarded as actinal-lateral plates forming two chevrons (text-fig. 2). Such an arrangement of actinal plates is recognised in other asteroids including the goniasterid *Tosia* and oreaste-rid *Culcita*.

To interpret the remaining abactinal plates requires comparative comment about the development of the disc region. The first ten plates to develop at metamorphosis are five radial (= terminal) plates followed by the five primary interradials. A central-dorsal plate is then formed (FEWKES, 1888). The radial (= terminal) plates move out along the arm as the median dorsal (or carinal) and other plates develop just proximal to each of the termi-nal plates. That the primary interradial plates do not move very far from the central-dorsal plate is obvious in many asteroids. Despite the described alternative developments of the madreporite, either incorporated by a primary interradial plate or resulting from the fusion of the separately developed madreporic plate with a primary interradial plate (OGURO *et al.*, 1976) the location of the primary interradials can be detected in each interradius by reference to the position of the madreporite. Development of plates of the disc occurs within this ring as the asteroid expands with growth. In *Podosphaeraster* the madreporic pore is simple and centrally placed in the madreporic plate. The other four primary inter-radials can be distinguished clearly in each of the other interradii. Within the circlet of primary interradials is a ring of five interradials, around the central dorsal plate. These may be considered as secondary interradials having arisen later than the primary plates. It is difficult to determine whether the radials, of the apical system, as defined by ROWE & NICHOLS (1981) ; ROWE *et al.* (1982) ; herein, have arisen from the disc region or represent the first dorsal carinal plates, which would have arisen proximal to the terminal plate. The size of these radial plates might suggest the latter.

CLARK and WRIGHT (1962, fig. 3b) have described the occurrence of a few irregular plates around the central-dorsal plate in the holotype of *P. polyplax*. It seems to the pre-sent author that these represent the development of extra radial and interradial plates. There is a partial ring of four secondary radial plates abutting with the central-dorsal. These occur in radii A, C, D and E. Alternating with these, in each of interradii BC, CD and DE, at least, is a small interradial plate, which may represent either some divi-sion of the adjacent secondary interradial plates or the partial development of tertiary inter-radial plates in the apical region. Such development does appear variable in *polyplax* with the extreme condition being exhibited in the holotype (see ROWE *et al.*, 1982, fig. 2). The development of secondary radial, apical (or disc) plates does not occur in any of the other species of *Podosphaeraster* with the exception of the transverse clefts occurring in three of the secondary interradials in one of the specimens of *gustavei* (see p. 312).

Following this line of reasoning, it is possible to find the equivalent of conventional asteroid abactinal-lateral plates. These are the remaining interradial abactinal plates of the proximal horizontal row, that are on either side of the madreporite, and the outermost two plates of the middle horizontal row (text-fig. 2). Although extra apical plates do not

appear to occur in *Sphaeraster*, the abactinal interradial plates might similarly be interpreted in longitudinal, abactinal-lateral fashion (see CLARK and WRIGHT, 1962, fig. 3).

SCHONDORF (1906) compared the form of the madreporite of *Sphaeraster* '*punctatus*' particularly with that of *Tosia australis* (as *Astrogonium astrologorum*). Examination of *Tosia* shows that the madreporic sieve occurs prominently on the abradial edge of the madreporic plate (i.e. primary interradial plate) and is part of that plate. Because of its size, the abactinal lateral plates immediately distal to it accommodate in shape so that externally, without dissociating the individual plates, the sieve appears to be a separate entity which is interplate in position. SCHONDORF (1906) suggested that the madreporite of *Sphaeraster* may either be a modified interradial plate or be independant of the other skeletal plates and occurring between them. ROWE *et al.* (1982) supported the latter hypothesis. It seems to the present author that despite his recent support, given with other authors, for that view, it is more likely that the madreporite forms part of the interradial plate and is not therefore interplate in position or unusual in any way. SCHONDORF's first hypothesis is therefore supported here. The main differences between the madreporites of *Sphaeraster* and *Podosphaeraster* lie in the position of the pore on the plate and the complexity of the sieve indicated as occurring in *Sphaeraster* by SCHONDORF (1906).

Thirdly, judging from the measurements of the known species, with the exception of *P. pulvinatus*, which remains markedly cushion-shaped, each of the other species appears to grow through a somewhat more flattened form before becoming more or less spherical.

Fourthly, the prominent development of rectal caecae in the Atlantic species, *gustavei*, is difficult to explain. Examination of two paratypes of *gustavei* shows that simple, pouch-like rectal caecae in the smaller specimen (hd = 7.1 mm) (pl. I, C) are more prominently developed than in the larger specimen (vd = 14.0 mm). This would tend to indicate a diminution of the importance of the organ as the animal matures and grows. ROWE *et al.* (1982), after the dissection and examination of two specimens of *P. polyplax* (hd = 11.5 mm ; hd = 15.0 mm) assumed the absence of rectal caecae, describing a long rectal canal. Like rectal caecae in other asteroids, however, the rectal canal of *Podosphaeraster* possesses numerous internal epithelial lamellae. Unlike other asteroids, however, no muscular layer is present in the rectal wall. Histological examination has shown that the muscle layer is similarly absent from the rectal caecae of *P. gustavei*.

Following the partial dissection of the third and smallest specimen of *P. polyplax* (hd = 9.5 mm), which is held in the Australian Museum collections (AM J11721), rectal caecae, albeit poorly developed, have been found. Since these pouch-like outpushings are absent from the larger specimens of *P. polyplax* (ROWE *et al.*, 1982), it can only be inferred that, unlike *P. gustavei*, the necessity for caecal pouches totally diminishes with growth. Without further information, at least relating the evolution of relative feeding habits, the significance of this development cannot be determined. It is unfortunate that the internal anatomy of neither *P. pulvinatus* nor *P. thalassae* can be compared until new, suitably preserved, material is recovered. The known material has either been dried or insufficiently well preserved for dissection. It is, however, interesting to note that in his survey of digestive systems JANGOUX (1982) considers the rectal caecae to be the most inconsistently developed organ in asteroids, even at intraspecific level.

Finally, the apparent, disjunct distribution of *Podosphaeraster*, in the West Pacific and North-eastern Atlantic Oceans (text-fig. 3) suggests that the genus must have reached the
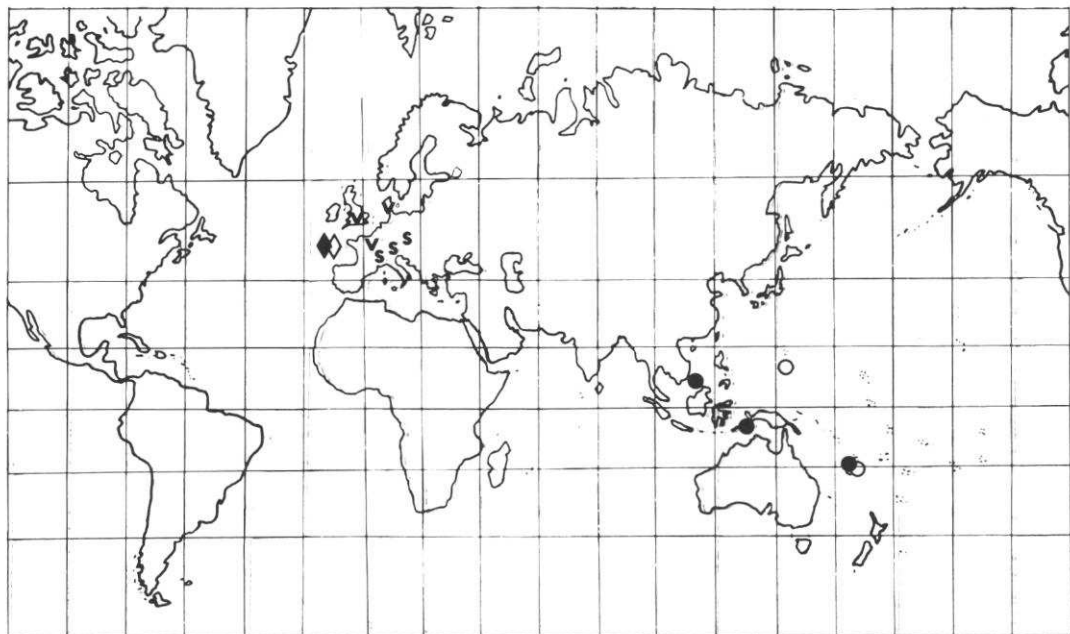
FIG. 3. — Distribution of *Sphaeraster* (S) : *Valetaster* (V) and *Podosphaeraster* spp. *P. gustavei* (◊), *P. thalassae* (♦), *P. polyplax* (●), *P. pulvinatus* (○).

north Atlantic prior to the final separation of the Indo-west Pacific segment of the Tethyan seaway from the Atlantic Ocean (and the Mediterranean Sea) in the mid-Tertiary period. Despite the absence of fossil representatives of *Podosphaeraster*, this suggests the genus to be relatively old and to have appeared at least in the early Tertiary if not as early as the late Cretaceous period. If *Podosphaeraster* is a direct descendent of *Sphaeraster*, and probably also related to *Valettaster*, as suggested by CLARK and WRIGHT (1962), then the occurrence of these Jurassic-Cretaceous genera in western Europe and southern England (SPENCER, 1913) (text-fig. 3) would, to some extent, support that conclusion. Certainly a number of equally wide-spread extant asteroid genera are considered, supported by fossil evidence and assuming correct taxonomy, to be just as ancient (SPENCER and WRIGHT, 1966). The present distribution of the species of *Podosphaeraster* is more likely to have been achieved from a pan-Tethyan genus. Events subsequent to the Cretaceous period, including plate movements, resulting in altered seaways and ocean current systems, and the varied effects of climatic and tectonic changes in sea levels, with their consequential effect on the emergence and submergence of continental shelves, would have contributed to the isolation of representatives of the genus in the Atlantic and Pacific Oceans. It is most likely, however, that *Podosphaeraster* will be found to occur at least in the Indian Ocean, if not also in the Mediterranean Sea. An argument relating such geological events to the present-day distribution of stalked crinoids in the Atlantic, Indian and West Pacific Oceans has been advanced by ROUX (1979, 1980*a*, 1980*b*, 1980*c*, 1981).

The paucity of material available at the present time would indicate the rarity of

Podosphaeraster and almost certainly does not reflect either the total number of species or the entire distribution of the currently recognised nominal species. Interestingly the presently known depth ranges of the Atlantic species (500-615 m) are greater than those from the Pacific species (72-125 m, *polyplax* ; 244-324 m, *pulvinatus*), indicating that at least *polyplax* occurs on the continental shelf rather than the continental slope. In this latter case distribution may have been affected since major parts of the China and Arafura Seas, from each area of which *polyplax* has been recorded, would have been emergent during Pleistocene glacial periods (WISE and SCHOPF, 1981 ; WOODWARD, 1983).

Histological sections of the gonads of both *P. gustavei* and *P. polyplax*, examined herein, shows interesting features. Firstly all specimens dissected (2 of *gustavei* ; 3 of *polyplax*) are female. Unless sex change occurs then, to date, no male specimens, at least of these two species, have been collected. In neither species are the gonads large or ramifying (*P. gustavei*, pl. I, D ; *P. polyplax*, ROWE *et al.*, 1982, fig. 4). An estimate of oocyte number per animal based on examination of sections indicates low fecundity with the five pairs of gonads containing probably no more than some 1 000-2 000 oocytes in *gustavei* or about 3-4 000 in *polyplax*. The size of oocytes in *gustavei* ranges up to 235 μm but oocytes of a comparable developmental stage range only to 100 μm in *polyplax*. This in itself would indicate different reproductive strategies in the two species.

It has been suggested (p. 312) that *gustavei* may develop a demersal larva. On the other hand, the distribution of *polyplax*, in depths which extends its range not more than half way across the continental shelf, would indicate a planktotrophic (whether feeding or non-feeding) larval development. This would be necessary since the known geographic distribution requires the traverse of a number of deep troughs and basins (FAIRBRIDGE, 1966). Such interspecific (even intraspecific) differences in types of larval development in benthic marine invertebrates are not unusual (MILEIKOVSKY, 1971). Further, MILEIKOVSKY (1971) also notes that whereas the vast majority of species inhabiting shallow shelf areas develop by means of planktotrophic larval stages, those from higher latitudes and those occurring on the slope and deeper in low temperature regimes tend to replace pelagic development. Such might also explain the differences in reproductive strategies between the tropical, shallow-water species *P. polyplax* from the East Indies and West Pacific, and deeper-water species *P. gustavei* from the North-east Atlantic.

Whereas water current patterns within the East Indian Archipelago (LAFOND, 1966) might well be cited as the means of present day distribution of *P. polyplax* between the China and Arafura Seas, presuming in this case a planktotrophic larva, the distribution of *polyplax* in the Loyalty Islands raises the perplexing question of the geographical origin of that species. Prevailing wind and ocean currents move westward towards the East Indian Archipelago and South-west toward the Loyalty Islands. This might support a western Pacific origin with westward spread to the East Indies (LADD, 1960). Conversely, CHAPRONIERE (1980), considering foraminiferan distributions in the Australasian region, concluded foraminiferans probably reached New Zealand by way of the Louisade Archipelago and Rennen Ridge to New Caledonia and thence via the Norfolk Ridge to New Zealand, probably in Miocene times. It is possible such a route may have been taken by *Podosphaeraster polyplax* to reach the Loyalty Islands.

Until further material is available for study a detailed analysis of geographical origins and distributions of the species of *Podosphaeraster* is not justified.

In conclusion, the discussion presented above has set out to try to understand and redescribe the arrangement of the test plates and other features of *Podosphaeraster*. This is achieved through deduction from the known, early, post-metamorphic development of some other asteroids. This thesis might, therefore, be considered speculative in view of the paucity of material of *Podosphaeraster* available, and therefore open to discursive question. For this reason, therefore, the description of a new species in this paper is based on the conventional format of CLARK and WRIGHT (1962).

The zoogeographic discussion set out above has taken the pragmatic approach that neither dispersal from a "centre of origin" (e.g. BRIGGS, 1981) nor even present-day long-distance dispersal (e.g. DANA, 1975 ; SCHELTEMA, 1979) can account for the current known distribution of *Podosphaeraster*. Rather the inclusion of information from a number of disciplines including vicarient factors such as tectonic and climatic events ; consequent alteration of the course of oceanic currents leading to the present, distributionally controlling current patterns ; as well as reproductive strategies and larval behaviour is required in determining the ultimate reasons for the varied distributions of marine invertebrate species (McCoy and HECK, 1983).

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PLATE I

A, B. — *Podosphaeraster gustavei* nov. sp., holotype, EcAs 4653, hd = 9.5 mm : A, lateral view ; B, apical system.

C, D. — *P. gustavei* nov. sp., paratype, EcAs 4654, hd = 7.1 mm : C, partially dissected to show rectal caecae (rc) ; D, internal view of actinal radius and interradius, gonad (g), interradial ridge (ir), ambulacrum (a).

E. — *P. gustavei* nov. sp., paratype, EcAs 4650, hd = 5.6 mm : abactinal view.

F. — *P. gustavei* nov. sp., paratype, EcAs 4652, hd = 14.0 mm : lateral view (partially dissected).

G, H, I. — *Podosphaeraster crassus* Cherbonnier (= *Nymphaster arenatus* (Perrier)), holotype, EcAs 4651, 12.4 mm long : G, internal ; H, external ; I, damaged plate (arrowed).
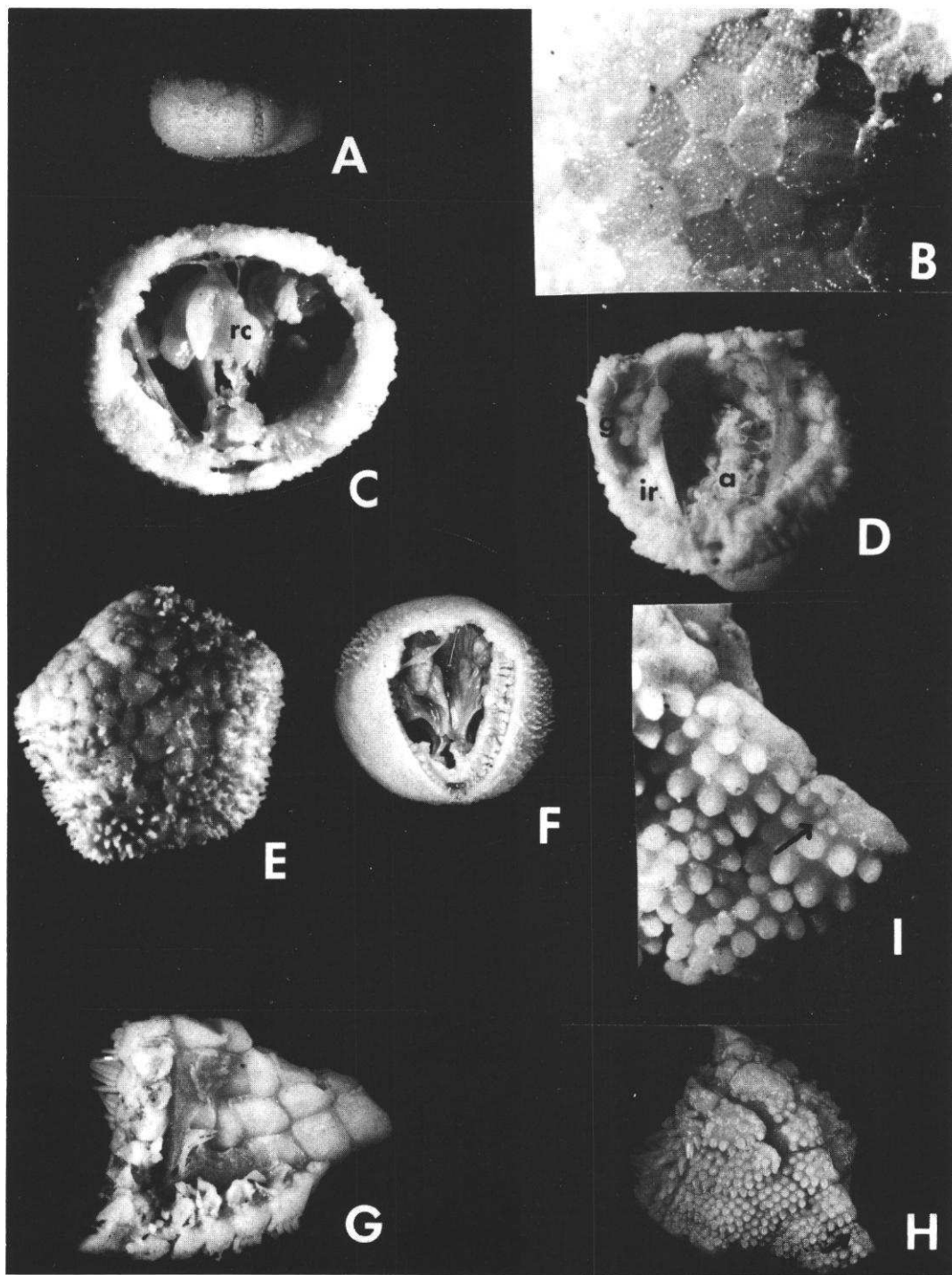
PLATE I