RESTRICTION OF THE FAMILY PORANIIDAE, *SENSU* SPENCER & WRIGHT, 1966 (ECHINODERMATA: ASTEROIDEA)

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SYNOPSIS

The amalgamation of two families of asteroids under the name Poraniidae in the Asterozoa section of the *Treatise on invertebrate paleontology* by Spencer & Wright (1966) is here rejected on the basis of the fundamentally different arrangement of the actinal plates in the two groups of genera concerned.

INTRODUCTION

THE initiative for this note and the observation on which it is based came from one of us (F. H. C. H.), the history of the problem being dealt with by the other. The specimens used to illustrate it were specially prepared (by treatment with KOH followed by glycerine to increase the transparency of the normally opaque skin and reveal the skeleton) by Mr R. H. Harris of the Histology and Preservation Section of the Zoology Department, British Museum (Natural History), and photographed to emphasize further the skeletal structure by Mr P. A. Richens of the Photographic Unit of the Museum, to whom we are indebted.

HISTORY

In 1840 three nominal genera of stellate, thick-skinned asteroids were described :

(1) *Asterope* Müller & Troschel (1840a) with type *Asterias carinifera* Lamarck, 1816, by monotypy, renamed *Asteropsis* by the same authors (1840b) several months later (without explanation but presumably because they had found the first name preoccupied) ;

(2) *Gymnasteria* Gray for *G. spinosa* and *G. inermis* spp. nov. ; and

(3) *Porania* Gray for '*Asterias gibbosa* Leach', said to be Leach 1817 but probably from an MS catalogue of the British Museum collections. (This is not the same species as *Asterias gibbosa* Pennant, 1777, which Gray gives as *Asterina gibbosa* on the next page.) Gray's paper was published in December, 1840 and post-dated both of Müller & Troschel's (see Fisher, 1908).

In their main work, the *System der Asteriden* in 1842, Müller and Troschel cited both *Gymnasteria* and *Porania* as synonyms of *Asteropsis*. They included in the genus *A. carinifera* (Lamarck), *Asteropsis ctenacantha* sp. nov. (referred to the synonymy of *Porania pulvillus* (O. F. Müller) by Perrier, 1875), *Asterias pulvillus*

O. F. Müller, 1788, with synonym *Porania gibbosa* Gray, and *Asterias vernicina* Lamarck, 1816; also in a postscript Gray's *Gymnasteria spinosa* and *G. inermis*, which they thought to be conspecific at least with each other.

After study of Gray's types of *G. spinosa* and *G. inermis* in the British Museum collections, Perrier (1875 : 285) referred both to the synonymy of *Asterias carinifera* Lamarck. This should automatically have relegated *Gymnasteria* Gray where it belongs in the synonymy of *Asteropsis* Müller & Troschel. Although Perrier was aware of Müller & Troschel's usage of *Asteropsis* in 1840 before Gray's of *Gymnasteria* (see 1875 : 9-10), for some reason he retained the name *Gymnasteria* for *A. carinifera* and at the same time improperly emended *Asteropsis* to include only *Asterias vernicina* Lamarck, ineligible as type-species since not included in 1840. Since he simultaneously synonymized *Petricia punctata* Gray, 1847, the type species of *Petricia* Gray, with *A. vernicina*, this move dispensed with a valid generic name while perpetuating at the same time an invalid one.

Unfortunately Sladen was apparently unaware that Müller & Troschel had used *Asteropsis* already in 1840 and perpetuated Perrier's errors until they were pointed out by Fisher (1908 and 1911 : 247, 248) when he noted that *Asterope* Müller & Troschel, 1840 is not invalidated by *Asterope Philippi*, 1840, having been published at least two months earlier. He therefore referred *Gymnasteria* Gray to the synonymy of *Asterope*, rejected *Asteropsis* as superfluous and revived *Petricia* Gray from synonymy.

As for the family position of these genera, in 1875 Perrier included *Porania*, *Asteropsis* (emended), *Dermasterias* nov. and *Gymnasteria* at the end of the Goniasteridae, following them with the Asterinidae and implying some affinity with the latter family. In 1879 Viguiier referred the first three genera to the Asterinidae. However, in 1884 Perrier divided the families of asteroids into named orders, placing the Asterinidae in the order Spinulosae but establishing a new family Gymnasteriadae in the order Valvulatae (p. 165) (although on p. 154 he lists a family Asteropsidae in the order Valvatae !). Included in the Gymnasteriadae were *Gymnasteria*, *Porania*, *Asteropsis*, *Dermasterias* and *Marginaster* gen. nov. In the Challenger report, Sladen (1889 : 355-356) adopted Gymnasteriidae (with corrected spelling) and added *Tylaster* and *Poraniomorpha*, both of Danielssen & Koren, 1881, also *Rhegaster* Sladen, 1883 and *Lasiaster* gen. nov. ; he commented on the affinity of some of these with the Asterinidae.

After discovery of the echinasterid which he called *Poraniopsis*, Perrier in 1891 (pp. 107, 163) removed *Porania* from the Gymnasteriidae to the Asterinidae, adjacent to the Echinasteridae in the order Spinulosae. He made no mention in the discussion of *Porania* that it should be referred to a family of its own but in 1894 (p. 163) took this action, though citing 'Poraniidae Perrier, 1891'. This is more puzzling because in his preliminary discussion on classification in the 1894 *Travailleur* and *Talisman* report he makes not the slightest mention of Poraniidae and indeed lists *Marginaster pentagonus* (the only relevant species collected by these vessels) under the family Pentagonasteridae (i.e. Goniasteridae) on p. 30. On p. 163 he placed Poraniidae in the Spinulosae and included in it *Porania*, *Tylaster*, *Poraniomorpha*, *Marginaster*, *Rhegaster* and *Lasiaster*. This would leave only *Gymnasteria*, *Asteropsis* and

Dermasterias in the family Gymnasteriidae, which is listed on p. 327 under the order Valvata [sic]).

Having in 1908 renamed as Asteropidae Perrier's Gymnasteriidae, in 1911 Fisher referred *Porania* and its relatives to the Asteropidae. Verrill (1914 : 304) expressed doubt about this because of affinity of *Porania* with the Asterinidae and in 1919 Fisher separated them again, though removing also *Dermasterias* to the Poraniidae, leaving only *Asterope* and *Petricia* in the Asteropidae.

In the years following, several new nominal genera were added to the Poraniidae, while others were synonymized. Mortensen (1933 : 249) included under the heading Asteropidae *Tylaster meridionalis* and '*Cryaster*' *brachyactis* (both more closely related to *Porania* than to *Asterope*) ; then Fisher (1940 : 136) named a new genus *Spoladaster* for *C. brachyactis*, again giving the family as Asteropidae (while on p. 154 he deals separately with the family Poraniidae) a treatment also followed by A. M. Clark in 1952. H. L. Clark (1946 : 109) also evidently considered that Poraniidae and Asteropidae can be kept distinct. However, Madsen (1959 : 153) refers to *Porania* under Asteropidae, order Spinulosa.

Spencer & Wright (1966 : U69) in the *Treatise on invertebrate paleontology* again unite the two groups of genera but under the name Poraniidae Perrier, 1894, in the order Spinulosida. They also show that *Asterope* Müller & Troschel is after all invalid, being preoccupied by *Asterope* Hübner, 1819, an insect, and must be replaced by *Asteropsis* (a fact noted independently by A. M. Clark in 1967).

TAXONOMY

Clearly with so much anomalous treatment it is time that this problem was re-examined by further study of the skeleton obscured beneath the thick skin of these asteroids. The use of X-radiography by Dons (1936, 1938) and Madsen (1959) has revealed the extent of reduction of the skeleton in some species related to *Porania* and even more to *Poraniomorpha* but it is comparison between the better-calcified *Porania* itself and *Asteropsis* that is needed.

Examination revealed that there are two fundamentally different arrangements of the plates in the triangular actinal intermediate areas under each side of the arm among the genera of Poraniidae *sensu* Spencer & Wright. In *Porania* itself and also *Poraniomorpha* and *Tylaster*, for instance, the arrangement consists of rows of actinal plates running parallel to the inferomarginals, the zone of plate addition is adjacent to the adambulacrals and the shortest row is in the proximal part of the interradial area near the oral plates (Pl. 1). Conversely, in *Asteropsis*, *Dermasterias* and *Petricia* the arrangement consists of rows of plates running parallel to the adambulacrals, the zone of addition is adjacent to the inferomarginals and the shortest row adjoins the interradial inferomarginals in the distal part of the interradial area (Pl. 2 ; Pl. 3). The second pattern is the usual one in the families of the order Valvatida (e.g. Goniasteridae and Oreasteridae) as well as in some Spinulosida (e.g. Asterinidae).

It is therefore possible to divide the genera concerned into two distinct groups. In the cases where the actinal plates are either few and irregular (e.g. the diminutive species referred to *Marginaster**) or extremely reduced (e.g. *Spoladaster* and *Tylaster*)

* Which I think may all prove to be based on juveniles of other Poraniid genera. A. M. C.

by resorption in adults, the pattern can be estimated by the locus of plate formation, judged by the sizes of the plates or the positions of the surviving plates when the older ones have been resorbed.

The two groups of genera are as follows :

PORANIIDAE Perrier, 1894

Porania Gray, 1840
Chondraster Verrill, 1895
Marginaster Perrier, 1881
Poraniella Verrill, 1914
Poraniomorpha Danielssen & Koren, 1881
Poranisca Verrill, 1914
Pseudoporania Dons, 1936
Sphaeriaster Dons, 1939
Spoladaster Fisher, 1940
Tylaster Danielssen & Koren, 1881

ASTEROPSEIDAE* Hotchkiss & Clark, 1976

Asteropsis Müller & Troschel, 1840
Dermasterias Perrier, 1875
Petricia Gray, 1847

The Triassic genus *Trichasteropsis* Eck, 1879 (illustrated by Spencer & Wright, 1966, fig. 43.3a-c) has poraniid actinal growth gradients and should be transferred to the Poraniidae from the Palasterinidae (order Paxillosida).

Concerning the Ordovician somasteroid *Chinianaster levyi* Thor, Spencer's reconstruction of this (1951, fig. 7 ; Spencer & Wright, 1966, fig. 39.4) shows poraniid-

Fig. 1.

Fig. 2.

FIG. 1. Diagram showing orientation and polarity of growth gradients as observed by Fell.

FIG. 2. Diagram showing orientation and polarity of growth gradients observed in Poraniidae.

* This family name is based on *Asteropsis* Müller & Troschel, 1840b, which is the earliest available name to replace *Asterope* Müller & Troschel, 1840a, and is a senior subjective synonym of *Gymnasteria* Gray, (Dec.), 1840 (see Müller & Troschel, 1842 : 65). *Asteropsidae* Perrier (1884:154) is not valid under Article 55 of the Code because he excluded the type-species, *A. carinifera* Lamarck, from the type-genus, *Asteropsis*. *Gymnasteriidae* (as *Gymnasteriadae*) Perrier (1884:165), based on the junior synonym, though adopted by some nineteenth century authors, has not been used for nearly 70 years and may be considered to have lost all claims to validity under Article 40. The inserted 'e' in *Asteropseidae* derives from the genitive singular root *Asteropse-*. We are indebted to Dr R. V. Melville for help with this nomenclatorial problem.

like growth gradients, the shortest longitudinal series adjoining the ambulacra proximally. This contrasts with Fell's 'inferred appearance' of the same species (1963, fig. 11D), where minor differences in the sutures result in an asteropseid arrangement, conforming with his theories on the phylogeny of asteroids (Fig. 1). If Spencer is proved correct, then Fell's growth gradient argument for crinoid ancestry of the Asterozoa is seriously undermined.

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