A NEW, EARLY CROWN-GROUP ASTEROID (ECHINODERMATA) FROM THE NORIAN (TRIASSIC) OF NORTHERN ITALY

DANIEL B. BLAKE 1, ANDREA TINTORI 2, & HANS HAGDORN 3

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Riassunto. Noriaster barberoi gen. n. sp. n. è descritta sulla base di un singolo esemplare proveniente dal Calcare di Zorzino (Norian, Triassico Superiore) dell'Italia settentrionale. Noriaster barberoi gen. n. sp. n. è allocrita agli attuali Poraniidae (Valvatida; Echinodermata) e rappresenta la più antica specie appartenente a una famiglia tutt’ora esistente e l’unica del Triassico. Finora nessuna specie paleozoica è stata ritenuta affine a famiglie considerabili come crown-groups. Noriaster gen. n. e Trichtasteropsis, rinvenuto nel Muschelkalk tedesco, indicano che la diversificazione del crown-group degli asteroidi era già in corso almeno nel Triassico Medio-Superiore. La filogenesi dei crown-groups degli asteroidi è problematica in quanto le attuali famiglie sono morfologicamente diversi e pochi sono i caratteri derivati utilizzabili per ricostituire i reali rapporti di parentela.

Comunque una nuova analisi cladistica conferma l’attribuzione di Noriaster gen. n. ai Poraniidae e, per uno studioso di asteroidi attuali, la comparazione di un Noriaster gen. n. vivente non sarebbe sorprendente vista la sua ‘normalità’.

Da un punto di vista morfologico-funzionale, Noriaster gen. n. fa ritenere che gli attuali modi di vita degli asteroidi si siano originati rapidamente durante la diversificazione triassica.

Abstract. Noriaster barberoi gen. et sp. n. is based on a single specimen from the Calcare di Zorzino (Norian, Triassic) of northern Italy. A member of the surviving Poraniidae (Valvatida; Echinodermata), N. barberoi is the oldest-known species assignable to a Jurassic and younger family and the first such species known from the Triassic. No Paleozoic species with close affinities with crown-group families has been recognized. Noriaster and the slightly older Triassic genus Trichtasteropsis from the Muschelkalk of Germany together indicate that the diversification of crown-group asteroids was well underway at least by Middle and Late Triassic time.

Phylogeny of crown-group asteroids is problematic because extant familial-level taxa are morphologically divergent, and they exhibit comparatively few uncontested characters that clearly indicate phylogenetic affinities and sequence. Familial assignment of Noriaster is supported by a new cladistic analysis.

To the student of living asteroids, the appearance of a living Noriaster would be remarkable only because it would seem so commonplace. To the extent that form correlates with function, Noriaster suggests that modern asteroid life modes emerged quite promptly during the Mesozoic asteroid diversification.


Für den Bearbeiter heutiger Asteroiden wäre das Auftreten eines lebenden Noriaster nur deshalb bemerkenswert weil dieser so alltäglich wäre. Hinsichtlich der Tatsache, dass Form und Funktion sich entsprechen, lässt Noriaster darauf schließen, dass sich Lebensweisen heutiger Asteroiden während der mesozoischen Asteroiden-Diversifikation ziemlich schnell entwickelten.

Introduction.

During the past 30 years, several localities in the Norian Zorzino Limestone (Calcare di Zorzino) of the Lombardian Prealps have yielded abundant, well-preserved fossils. Studies to date have focused on the comparatively abundant vertebrates, with the description and interpretation of about 20 fish and 15 reptile species. Several other fishes await description, but their condition has dictated a long preparation period. The vertebrate fauna is important for interpretation of both fishes and reptiles because it encompasses the first major neopterygian radiation and it includes the oldest-known flying reptiles. In addition to the vertebrates, coprolites, terrestrial plants, and invertebrates have been collected. The invertebrates include corals, a single brachiopod

1 - Department of Geology, University of Illinois at Urbana-Champaign, 1305 W. Green St., Urbana, IL 61801, USA; dblake@uiuc.edu
2 - Dipartimento di Scienze della Terra, Università degli Studi, Via Mangiagalli 34, 20133 Milano, Italy; Andrea.Tintori@unimi.it
3 - Muschelkalkmuseum, Schloßstraße 11, 7118 Ingelfingen, Germany; encerinus@t-online.de
specimen, and diverse echinoderms (echinoids, ophiuroids, crinoids, and a single asteroid, which is treated here); both taxon types and overall diversity clearly indicate a marine origin. Rare gastropods and much more common bivalves (Tintori, 1995) and crustaceans (Pinna, 1974; Garassino & Teruzzi, 1993) give a final touch to the benthic fauna, which as a whole is rather rich in individuals but poor in species, in this contrasting with the variety of fishes (Tintori, 1998). Several tiny terrestrial reptiles (Renesto, 1994a, b, 1995) indicate the presence of adjacent small islands.

With this paper we begin the description of the echinoderms of the Zorzino Limestone, which, like the fishes, indicate important milestones in the history of their phylum.

Geologic Setting and Fossil Preservation.

The Zorzino Limestone (Norian, Triassic) is one of a number of limestone bodies located in northern Italy that are inferred to have been deposited in localized marine basins associated with early Mesozoic rifting (Renesto & Tintori, 1995). The basins opened within a huge and very thick carbonate platform, the Dolomia Principale Formation, that extended over all of the western margin of the Tethys. Because of the widespread very shallow-water environments, connections between the basins and the open sea were only through tidal channels, which explains the limited benthic fauna. On the other hand, the relatively restricted environment allowed diversification of a largely endemic vertebrate fauna including both marine and terrestrial species. Surface waters were well oxygenated, which allowed nekton to thrive. Conditions at the margins of the basins were favorable for life (Tintori, 1995).

Inference of anoxic bottom conditions in the Zorzino basins is based in part on presence of numerous taxonomically diverse nektic fish, aquatic and terrestrial reptiles, and benthic invertebrates that are preserved almost always fully articulated. Thin lamination of the rock yielding the fossils provides further evidence of an undisturbed bottom at the center of the basins. Thus, all the fossils preserved in the fossiliferous levels of the Zorzino Limestone must be considered as allochthonous. They allow reconstruction of life assemblages of both superficial waters and benthic settings at the edges of the basins, as well as those of the nearby islands. Unfortunately, any invertebrate fossils of the margin carbonates were destroyed by carbonate platform dolomitization.

The terrestrial vertebrate beds lack recognized scour surfaces and sediment textures that could demonstrate mode of transport of the fossils to their final burial site. Rare possible turbiditic horizons from the basin margins occur, which usually are rich only in fragmental bivalve shell debris (Tintori, 1995).

About twenty-five years of collecting has yielded a very small number of echinoids, crinoids, ophiuroids, and a single asteroid representing Noraster barberoi n. gen. n. sp. n. The asteroid fossil was preserved with the ventral surface exposed; its body is collapsed and the skeleton partially disarticulated. It is a difficult fossil in that it only incompletely exposes important features. Other echinoderms known from the Zorzino Limestone are less seriously disrupted (Blake et al., 1999a) and their study is in progress.

Triassic asteroids and the diversification of crown-group asteroids.

The Triassic history of asteroids is almost unknown (Tab. 1). This is unfortunate because post-Triassic asteroids all belong to the crown group whereas nearly all known Paleozoic species belong to the stem group. Paleozoic asteroids were both taxonomically and functionally diverse (e.g., Schöndorf, 1929; Spencer, 1914-1940; Schuchert, 1915; Blake & Guensburg, 1994). Recent asteroid families begin to appear in significant numbers in the fossil record of the Jurassic (e.g., Hess, 1972; Blake, 1984, 1990). Most familiar among Triassic asteroids is Trichasteropsis, from the Middle Triassic Muschelkalk of Germany. Most known specimens represent T. weissmanni (Münster, 1843), although poorly known and fragmentary material suggests presence of additional species and even genera (Blake, unpublished). Taxonomic position of Trichasteropsis has not received comprehensive modern treatment.

1. Noraster barberoi, gen. et sp. n., Norian, Italy
2. Trichasteropsis, most specimens assignable to T. weissmanni but other species are present; Anisian and Ladinian, Germany; many references
3. terminal ossicles assigned to Asteropecten; Raibl Formation, Carnian, Germany; Wöhrmann (1889)
4. terminal ossicle, early Carnian, Hungary; Bather (1909)
5. isolated ossicles of different types, possibly assignable to recent families; St. Cassian Formation, lower Carnian, Italy; Zardini (1973)
6. poorly preserved body fossil, now lost; Norian, China; Yang (1982)
7. undescribed terminal ossicles similar to those of Quenstedt (1876); Carnian, China; repository Muschelkalk Museum

Tab. 1 - Summary of known fossil Triassic asteroid occurrences.

Zardini (1973) illustrated remarkably well-preserved isolated ossicles from the Upper Triassic of northern Italy. Gale (1987) assigned these ossicles to
two living families, the Goniasteridae and Asteriidae, whereas Blake (1987, 1989) followed a more conservative approach in suggesting that although the ossicles of Zardini (1973) are similar to those of certain post-Triassic asteroids, available data were insufficient for more precise taxonomic assessment. Yang (1982) reported a poorly preserved Norian specimen from western China, which unfortunately has been lost (Yang Zunyi, personal comm. to DBB, 1998). Published illustrations suggest presence of a small disk and long, columnar arms; this is a configuration found in diverse stem- and crown-group asteroids. Taxonomic and phylogenetic positions of the Chinese specimen must remain uncertain.

Wöhmann (1889) assigned terminal ossicles from the Carnian Raibl Formation of the Bavarian Alps to Astropecten. Ossicular form is suggestive of that of astrocotomids, although at the present state of knowledge, few terminals are diagnostic. From Hungary, Bather (1909) described a single terminal ossicle from rocks of age similar to those bearing Trichasteropsis. The age of several terminals (unpublished) discovered by Hagdorn in China (Sichuan) is also Carnian. The single specimen of Noriaster barberoi n. gen. and sp. is a new addition to this very scanty record (even Trichasteropsis is a rare fossil).

Systematists studying recent asteroids (e.g., W. K. Fisher, 1911) have recognized that the forcupulites (e.g. Asteriidae) are readily separated from representatives of the remainder of the class; the two have been treated as representing a deep-seated phylogenetic branching in crown-group asteroids (Blake, 1987). Trichasteropsis has been aligned with the forcupulites (Blake, 1987; Blake et al., 1999b) whereas Noriaster gen. n. belongs to the Valvatida, an order assigned to the second branch. Neither Triassic genus indicates close affinities with the Astrocotomidae (Paxillosida), which is sometimes suggested to be a basal surviving crown-group asteroid taxon (e.g., Mortensen, 1922; Gale, 1987). Of course a Triassic astrocotomid might await discovery. Regardless of phylogenetic interpretations, the known Triassic fossils indicate that crown-group asteroid diversification was underway by the Middle and Late Triassic, although the sister taxon of the post-Paleozoic diversification is unknown.

Palaeoecology.

Remarkable about ancient Noriaster (Fig. 1A-D; 2C-E; 3B-F) is how unremarkable it is, and to the extent form correlates with habit, life mode of Noriaster is unlikely to have been any more unusual than its appearance. Living valvatanid are epifaunal marine invertebrates found from intertidal habitats to deep ocean settings and from the arctic to the antarctic. Although some valvatanids are feeding specialists, most tend to be generalists, taking a variety of small prey and detrital feeding at the surface (e.g., Sloan, 1980). Many recent valvatanid (e.g. Astropecten, Luidia) are capable of burying themselves to shallow depths in particulate substrates; these asteroids have well-developed radial furrows or “fascioles” that are absent from Noriaster. Prey ing apart of bivalve prey, famous in asteroids such as Asterias, is absent from most asteroid groups including the Valvatida.

The few known late Paleozoic asteroids, in contrast with Noriaster, are distinctive in form (although perhaps some were functionally similar). After major extinctions at the end of the Paleozoic, modern asteroid form and behavior seemingly were established early in the Mesozoic.

The Norian Calcarea of Zorzin documents a diversification of durophagous fishes, although the record of benthic organisms is limited (Tintori, 1998). The skeleton of Noriaster is quite robust, although any linkage of asteroid form to predation pressure is conjectural.

Terminology.

Terminology largely follows that of Spencer & Wright (1966). These authors used oral for the entire lower surface, but this usage can be confused with the restricted area around the mouth; dorsal and ventral are used here. Accessory ossicles are the spines(Fig. 3C, F), spinelets, granules and pedicellariae that occur in abundance on most asteroids. Accessory ossicles rest on and are supported by more or less enlarged primary ossicles, which can overlap one another but do not form a covering layer over other ossicular types. Three major groups of primary ossicles build the non-ambulacral body wall of the asteroid. Commonly most distinctive and occurring at the edge of the body are a double row of marginals, the superomarginals (Fig. 3A, B; 4A, B) above and the inferomarginals (Fig. 1B, C; 2A, D; 4B, D) below. Abactinals are dorsal to the marginal series. A variety of descriptive terms are applied to these ossicles; see discussion of character 13, Appendix. Carinals form a differentiated, unpaired mid-arm abactinal series. Actinals lie between the marginals and the ambulacral column. Actinals (Fig. 1A-D; 2A-D; 3F; 4C-D) are arranged in more or less regular rows, and their pattern can be useful in taxonomic and phylogenetic inference; those ossicles immediately adjacent to the oral frame are referred to as suboral. The ambulacral skeleton includes the adambulacrals, which line the margins of the furrows, and the ambulacrals, which rest on the adambulacrals (Fig. 1A-D; 2A-E; 3C, E, F; 4C-D).

Adradial is directed toward the arm axis, and abradial is away from the arm axis. Proximal is toward the
Fig. 1 - A-D, Noriaster barberai n. gen. et sp. The holotype (the single-known specimen, MPUM 8425 from the Zorzino Limestone of Enden-na-Zogno) at different magnifications and directions of lighting; scale 3 mm. Ventral aspect. See Fig. 4 for comparative diagrams.

disk axis (the dorsal-ventral pole through the center of the mouth); distal is away from this axis. Length is approximately parallel to the arm longitudinal axis, width is approximately perpendicular to length in a horizontal plane, and height (low, high) is perpendicular in a vertical plane. Some ossicular rows curve from arm to arm across the disk, and orientation of equivalent ossicular surfaces gradually changes. For uniformity, all ossicles are described relative to axes of a medial or distal ossicle.

Systematic Palaeontology

Class Asteroidae de Blainville, 1830
Subclass Neoasteroidea Gale, 1987

Spencer & Wright (1966) separated most Paleozoic from post-Paleozoic asteroids at the subordinal level, but they extended surviving orders from an inferred Ordovician diversification. Both Blake (1987) and Gale (1987) separated all known Paleozoic from post-Paleozoic asteroids at the ordinal level. Gale (1987) provided formal recognition in proposing the subclass "Neoasteroidea" for post-Paleozoic asteroids. Blake (1987, in press 2000) suggested that crucial apomorphies for recognition of crown-group asteroids are offset (rather than paired) arrangement of ambulacrals and adambulacrals and the presence of dorsal podial pores. Based on these characters, Calliasterella americana Kesling and Strimple, 1966, (Carboniferous) qualifies as a member of the crown group (see Blake & Guensburg, 1988) and the term Neoasteroidea is used here in this sense. Both offset ambulacral-adambulacral articulation and dorsal podial pores appear to offer plausible adaptive advantages (Blake in press 2000), and both might be expected to have originated more than once; at present, these characters provide only working crown-group synapomorphies.
Among crown-group asteroids, evolution of ambulacral and adambulacral morphology appears to have been conservative. For example, ambulacrals and adambulacrals of *Noriaster* are broadly similar to those of the Pedicellasteridae (Forcipulataceae), Goniasteridae (Valvatacea), and Echinasteridae (Spinulosacea), suggesting significant plesiomorphic expression (although each possesses synapomorphicies). Certain of the plesiomorphies are apomorphic relative to the *Calliasterella* level of organization. Added work is needed on these complex ossicles before specific phylogenetic patterns will emerge.

Assignment of *Noriaster* to the Valvatida is based on overall body shape; presence of a stout, angular body margin formed by the marginals; presence of block-like marginals; and ambulacral and adambulacral configuration.

Family Poraniidae Perrier, 1894

Among genera assigned to the Poraniidae *sensu* Spencer & Wright (1966), Hotchkiss & Clark (1976) recognized two groups based on the arrangement of ossicles of the actinal interbrachial area. In the restricted family Poraniidae (Fig. 2A, B; 3A), the longest row of actinal ossicles is adjacent to the inferomarginals whereas in the Asteropseidae (which these authors separated from the Poraniidae), it is the shortest actinal row that adjoins the inferomarginals. *Asteropsis, Dermasterias,*
and *Petricia* were assigned to the Asteropseidae. Unfortunately, Hotchkiss & Clark (1976) did not include diagnoses for the two families, but Clark & Courtman-Stock (1976) provided a comprehensive descriptive diagnosis that forms the basis for that below.

**Diagnosis.** Body form pentagonal or short-rayed stellate, flat or slightly convex below, well arched above, often cushion-like with the dorsal body wall more or less thickened. Abactinal ossicles generally obscured or concealed in the body wall; ossicles rounded or oblong, forming a loose reticulum or reduced and disassociated during growth, even lost altogether in large specimens of a few species. Marginals enlarged relative to ossicles of immediately adjacent series but typically inconspicuous and embedded, especially the superomarginals; superomarginals erect on inferomarginals. If any external armament is present, it is generally only one series of skin-covered spinelets or small spines fringing the line

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**Fig. 3** - A. *Marginaster pecinatus* Perrier in dorsal view; B-F. *Noriaaster barberoi* n. gen. et sp. (the holotype, MPUM 8420 from the Zorzino Limestone of Endenna-Zagno, at different magnifications and directions of lighting). B, D in dorsal view; C, E, F in ventral view. Scale 3 mm. See Fig. 4 for comparative diagrams.

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**Fig. 4** - *Noriaaster barberoi* n. gen. et sp., ossicular diagrams taken from photographs. A, dorsal view of arm tip; B, dorsal view of arm extending to interbrachial position; C, ventral view of most of one arm; D, ventral view of portions of three interbrachia and two arms centered on disrupted mouth area. Most ossicles are partially obscured by sediment and accessory ossicular debris; many ossicular boundaries are unclear. Many ossicles are broken and both external and internal (i.e. interossicular contact and body cavity) faces are exposed. Preservation of abactinal ossicles is particularly problematic and identity of some uncertain. Comparisons: 4A with 3D; 4B with 3B; 4C with 1A, B and 2C, note position of ambulacral "A"; 4D with 1A-C and 2C-E. Key: A, ambulacral; B, abactinal interbrachials; C, carinals; D, distal actinals; I, inferomarginals; L, lateral abactinal longitudinal series; M, ambulacrales; O, possible oral actinal; P, proximal actinals; S, superomarginals; T, terminal.
New Triassic asteroid (Echinodermata)
of junction between abactinal and actinal areas, but large spine bases can occur. Actinal areas large, longest row and largest ossicles are adjacent to inferomarginals, arrangement of rows and outlines of individual ossicles typically somewhat irregular. Plating typically reduced or obscured by the thick skin, which is marked by parallel channels at right angles to the furrows. Actinal papulacae lacking. Adambulacral ossicles usually with only one or two furrow spines and one or two subambulacral spines, rarely more, all sheathed in thick skin. No pedicellariae.

Remarks. Because cladistic analyses at the generic and species levels for the Valvataida sensu Blake (1987) are unavailable, this is a traditional, descriptive diagnosis rather than a summary of synapomorphies. Aspects of the reticulated dorsal arrangement, marginal form and orientation, and actinal form and arrangement will provide synapomorphies whereas most other traits are likely to prove plesiomorphic.

Most living poraniids exhibit thick dermal tissues and correlated reduction of accessory ossicles, a pattern present as early as the Middle Jurassic Sphaeraster jurassicus (Hess, 1972). Nevertheless, tissues of a number of recent species of Porania and Poraniomorpha are not particularly robust, and the prominent spine bases and possible superomarginal granules of Noriaster also suggest comparatively limited tissue development.

Genus Noriaster n. gen.

Type species: Noriaster barberoi, sp. n.

Derivatio nominis. Noriaster was collected from Norian rocks, which is important because it currently is the oldest-known representative of a major branch of crown-group asteroids.

Diagnosis. Poraniid with robust marginals, the inferomarginals enlarged, peg-like, transversely elongate with flattened adradial and abradial surfaces. Inferomarginals are abruptly truncated abradially, and the terminus is swollen. The ventral ossicular surface bears one or two rows of two to four disjunct, robust pustules.

Actinals arranged in two or three rows (quality of preservation of the single specimen does not allow unequivocal recognition of a third [suboral] series). The largest ossicles are in the distal-actinal series, the proximal-actinal series is intermediate in size, and the row is intermediate in length. The suboral series, if it is present, consists of few, comparatively small ossicles. Enlarged interbrachial ossicles present in at least the distal-actinal row. Actinals disk-like and imbricated, irregular in outline; ossicles of the distal-actinal series particularly irregular. Actinal ossicles bear pustules similar to those of the inferomarginals but those of the actinals not arranged in an apparent regular pattern.

Noriaster barberoi sp. n.

Fig. 1A-1D; 2C-E; 3B-F; 4A-D

1999a unidentified asteroid, Blake et al., pp. 35-38
1999b unidentified asteroid, Blake et al., p. A43

Derivatio nominis. The species is named for the late Mr. Carlo Barbero, who found the specimen and provided much valuable help to A. Tintori during many field seasons.

Horizon and locality. The holotype was collected from the uppermost part of the Zorzino Limestone. Pollen dating places the fossil-bearing horizon near to the boundary between the Middle and Late Norian. Endenna site (Zogno, Bergamo, Italy). Holotype. The only-known specimen, Paleontological Museum Università degli Studi di Milano. MPUM 8420.

Diagnosis. As for the genus.

Description.

Overall form (Fig. 1A, B). Five-armed asteroid with rounded interbrachia and short, rather bluntly rounded arm tips. Specimen arm radius approximately 60 mm, disk radius approximately 30 mm.

Remarks. The specimen is collapsed, incomplete, distorted, and many ossicles have been displaced; radii values, particularly that of the the disk, are likely to be inaccurate. The marginal frame provided an abrupt, angular edge to the body, and the known abactinal ossicles suggest that the dorsal surface was low, arched, and firm in life. Overall appearance probably was broadly similar to that of species of Porania and Poraniomorpha, see e.g. Clark & Downey (1992).

Abactinals (Fig. 3B, D). Carinals stout, peg-like, subpaxillate to tabular; mid-arm carinals approximately 0.75 mm in diameter, probably with granulate crowns. Remainder of abactinals probably bar-shaped to ovate, varied in size, probably arranged in irregular(?) longitudinal and transverse series.

Remarks. The dorsal surface is known only from two very small fragments, of which only one exhibits a portion of the disk. Ossicular form and arrangement is not certain.

Madreporite. Unknown

Marginals. Marginals developed in two series, both reaching the arm tip; ossicles evenly gradational in size. Four marginal pairs in 3.5 mm at the arm tip. Ossicles of the two series paired to weakly offset, corresponding with one another in approximate size and form; arm tip robust. Marginals bearing robust pustules; closely arranged granules retained on one superomarginal.

Distal superomarginals (Fig. 3B, D; compare to 3A) tabular, upright, abutted laterally at the tip but less tightly abutted proximally by the fourth of fifth marginal proximal to the tip. On ossicles toward the interbrachial position, the outer face becomes broadly arched and rounded in proximal-distal profile. Dorsal-ventral profile of superomarginals is somewhat angular.
Distal inferomarginals (Fig. 2D) perhaps not as tall as superomarginals and the proximal-distal profile of these ossicles is less rounded. Proximal inferomarginals (Fig. 3F) transversely elongate, ossicular axis inclined to arm axis. Ossicles up to about 1.33 mm wide, 0.75 mm long. Ventral surface broad, ventral face arched, bearing one or two rows of two to four disjunct, prominent, uniform pustules; pustules of the two rows offset. Abradial (lateral) face low, slightly arched so that the ossicle appears bluntly truncated; outer face with medial pustules of uncertain number, but few. Junction edge of abradial and ventral faces angular with elevated junction ridge, extended above face surfaces. Differentiated pustules developed on some junction ridges. Side faces concave, profile concave as viewed ventrally; in life, side faces presumably supported well-developed connective tissues. The juncture between the side face and the actinal face is angular to somewhat rounded. Abradial face flattened, surface not depressed for soft tissues, face junctures with adjacent faces angular. Distal inferomarginals abutted adambulacrals whereas more proximal inferomarginals abutted distal-actinal ossicles. Pustules present at lateral-ventral edges of some inferomarginals.

Remarks. Eleven inferomarginals are preserved on one side of one relatively complete arm, and arm shape suggests several more were present in life. As preserved, the ossicles have been pulled apart but articulating features indicate that the inferomarginals were closely arranged in life. The inferomarginal pustules are similar in form to those of the adambulacrals and the actinals; preserved spines therefore suggest a rather uniform pattern of short but robust spines. The smaller pustules, as well as presence of possible granules, suggest an additional rather uniform accessory series.

Actinals (Fig. 1A-G; 2D; E; 3F; compare to 2A, B). Actinals arranged in two or three rows. The distal-actinal row (i.e., adjacent to the marginals) is longest but it terminates well before the arm tip; ossicles of the distal-actinal row are the largest actinals. The proximal-actinal row ossicles are of intermediate size. Suboral ossicles appear to have been present, perhaps in a more or less linear series. Suboral row, if differentiated as a linear series, is the shortest of the three, the ossicles are the smallest, and arrangement probably was somewhat irregular. Somewhat enlarged interbranchial ossicles probably were developed, especially in the distal-actinal row. Correspondence of ossicles about at the mid-arm position is as follows: two or three marginals correspond to three distal-laterals; these abut five proximal actinals; these abut eight adambulacrals. Ossicles of the successive series are not precisely aligned and transverse fascicles-like furrows are not developed (although furrowing could have been restricted to soft tissues). Actinals are of irregular outline, relatively tall (and therefore robust). Actinal ossicles weakly imbricated. Actinal outer faces are weakly arched, bear pustules similar to those of inferomarginals, but perhaps smaller.

Mouth frame ossicles. Unknown.

Ambulacrals (especially Fig. 3E). Ambulacral body (i.e. abradial end of the ossicle) length at about 0.5 mm, each ossicle overlapping proximally by means of distinct triangular flanges. Ambulacral cross-furrow articulate structures (facets and tissue depressions) are robust. Mid-ossicular waist is narrow and rounded for podial passageway to arm interior. Skeletal stereom strongly developed in transverse ridges at waist area (unfound in the living Ganeriidae). Abradial, flanges for tissues linking ambulacrals to adambulacrals are subdued and similar to one another and therefore the abradial end of the ossicle as viewed dorsally is bilateral. Ambulacral-adambulacral articular edge oriented at about 450 to the ossicular axis, indicating a deep furrow in the living animal. Width of approximately mid-arm ambulacrals between the edge of the adambulacrals and the arm mid-line is approximately 1.5 mm.

Remarks. Ambulacral form is somewhat plesiomorphic but characteristic of valvatidans.

Adambulacrals (Especially Fig. 3F). About 6 adambulacrals per 2 mm from proximal or proximally on arm nearly to arm tip. Adambulacrals squared in side-face outline, 0.6 mm high and wide. Tissue depression occupying most of side face; depression bordered by narrow, rounded, ridges. Dorsal adambulacral end arched distally, forming a short flange to overlap the next distal adambulacral. Outer face bearing two relatively large pustules, which form a figure-8 face outline. Abradial (proximal) face flat rather than prominent (i.e. the furrow edge would appear flattened rather than digitate for prominence partially separating sequential tube feet). Ossicular width approximately equal to width of ambulacral-adambulacral articular flange (i.e., adambulacral not expanded adradially beyond edge of ambulacral as is true of many Paleozoic species). Dorsal surface of adambulacral with narrow transverse tissue de-pressions for ambulacral-adambulacral articulating ossicles. Preserved (distal) spines approximately 0.75 mm in length, circular in cross section, expanded basally then tapering gradually to narrowed tip; no indication of differentiation between furrow spines and subambulacral spines.

Remarks. Adambulacral form, like that of the ambulacrals, is somewhat plesiomorphic but typical of crown-group Valvatida.

Terminal (Fig 3D). Length approximately 1.5 mm, maximum width approximately 1.33 mm at about mid-ossicle. Ossicular surface somewhat domed. In dorsal view, terminal rounded distally, proximal-lateral sides straight, abutting superomarginals. Exposed surface pustulose, pustules in an open arrangement, about five across widest portion of ossicle.
Comparisons. Recent which few iae have found, characterize those recent ossicular surface can be formed in Fig. 1s0 D. closly based l"loriaster Pedicellariae. Pedicellariae actinals (1996) Notoml.otida; Spencer rozona; S:Spinulosa; Others: Fo=Forcipulatida; affiliations after Phylogenetic hypothesis, on marginal they are absenr are therefore no expect rhemes or spines of unknown form of the paxillosidan-benthopectinid suborder to this family. Genera of the Paxillosida sensu Blake (1987) cluster together and form a sister branch of the Benthopectinidae. The gonasterid genera form a sister to the paxillosidan-benthopectinid branch, but the Valvatida sensu Blake (1987) is not monophyletic.

Asteroïd form is varied, yet recurring themes include plan-view outline, the size of the marginals relative to other body wall ossicles, and presence or absence of protected passageways over the body surface for water currents. Passageway types include the furrows or "fascioles" found between marginals and actinal ossicles as well as the passageways between paxillosform abactinal ossicles. Enlarged spines are more characteristic of passageway-bearing forms, and pedicellariae are more likely to be slender and spine-like in these taxa. Taxa lacking passageways tend toward a more closely fitted skeleton with granular rather than spine-like accessories; pedicellariae are flattened and blade-like. In some taxa (e.g.,

**Remarks.** The terminal is similar to those described by Wöhmann (1889) under the name Astropecten pickleri; however, divergent asteroid groups bear similar terminal ossicles and therefore the similarity is of unknown significance.

Pedicellariae. Pedicellariae of different types help characterize those recent asteroid taxa in which they are found, but they are absent from recent Poranidae, and there seems to be no reason to expect them in Noriaster. Pedicellariae formed of simple spines mounted on an ossicular surface can be difficult to recognize in fossils, especially so in specimens such as that of Noriaster in which few spines are preserved. Some pedicellariae types have distinctive attachment surfaces on primary ossicles, but these alone were not recognized. Alveolar pedicellariae (i.e., those mounted in a pit) can be distinctive, but Breton (1996) suggested that these originated later than the Triassic, and they are unknown in the Poranidae.

**Phylogenetic Analysis.**

Phylogenetic treatment is discussed in the appendix. Results (Figs. 5-7) are equivocal in part but nevertheless they suggest generalizations. Most important is the strong linkage of Noriaster to the hitherto Jurassic (Hess, 1972) to Holocene Poranidae, allowing assignment of Noriaster to this family. Genera of the Paxillosida sensu Blake (1987) cluster together and form a sister branch of the Benthopectinidae. The gonasterid genera form a sister to the paxillosidan-benthopectinid branch, but the Valvatida sensu Blake (1987) is not monophyletic.

Asteroid form is varied, yet recurring themes include plan-view outline, the size of the marginals relative to other body wall ossicles, and presence or absence of protected passageways over the body surface for water currents. Passageway types include the furrows or "fascioles" found between marginals and actinal ossicles as well as the passageways between paxillosform abactinal ossicles. Enlarged spines are more characteristic of passageway-bearing forms, and pedicellariae are more likely to be slender and spine-like in these taxa. Taxa lacking passageways tend toward a more closely fitted skeleton with granular rather than spine-like accessories; pedicellariae are flattened and blade-like. In some taxa (e.g.,

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Fig. 5 - Phylogenetic hypothesis, see text for explanation. Key to affiliations after Fisher, 1911: F = Forcipulatida; P = Phanerozoa; S = Spinulosida; Others: Fo = Forcipulatida; No = Notomyotida; Pa = Paxillosida; Sp = Spinulosida; Va = Valvatida. Notomyotida is a suborder of Valvatida sensu Spencer & Wright.

Fig. 6 - Phylogenetic hypothesis, see text for explanation. Key to affiliations after Fisher, 1911: F = Forcipulatida; P = Phanerozoa; S = Spinulosida; Others: Fo = Forcipulatida; No = Notomyotida; Pa = Paxillosida; Sp = Spinulosida; Va = Valvatida. Notomyotida is a suborder of Valvatida sensu Spencer & Wright.
Poraniidae), accessory and even primary ossicles are reduced, and a thickened dermal skeleton is present.

Unifying morphological themes appear to provide the vehicle for homeomorphy, and they contribute to uncertainty of phylogenetic interpretation. For example, does the grouping here of Dermasterias and Petricia with the Poraniidae reflect affinities or only presence in both thickened dermal tissues? Hotchkiss & Clark (1976) assigned Asteropsis as well as Dermasterias and Petricia to their Asteropsideidae (see Appendix), yet the ambulacral column ossicular morphology of Asteropsis suggests its affinities lie with the Orestereidae. Perhaps linkage of Dermasterias and Petricia to the Poraniidae sensu Hotchkiss & Clark only reflects thickening of tissues combined with yet unidentified but correlated characters.

Because of uncertainties, molecular and morphological analyses seeking to determine relationships must sample broadly at the species and generic levels. For these reasons, the classification of Blake (1987) is retained here in spite of somewhat inconsistent cladistic results.

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REFERENCES


Müller O. F. (1776) - Zoologische Darücke Pocormodium, seu Animalium Daniae et Norvegiae indigenarum, etc. 282 pp., Havniae.


Quenstedt F. A. (1874-1876) - Petrefactenkunde Deutschlands; Echinoderm (Asteriden und Echinochen), pt. 1, v. 4, pp. 1-742, Fues's Verlag, Leipzig.


Schöndorf F. (1959) - Paläozoische Seesterne Deutschlands. I.


Zardini R. (1973) - Fossili di Cortina; arenite degli echinodermi cossiani, Trias medio superiore della regione dolomitica attorno a Cortina d'Ampezzo, pp. 1-29, Foto Ghezina, Cortina d'Ampezzo.

**APPENDIX**

**CLADISTIC ANALYSIS**

**Background.**

Two crown-group asteroid branches were recognized by Blake (1987), the Forcipulatacea forming one branch and the Valvatacea and Spinososaca forming the second. This arrangement echoes the perspective of Fisher (1911, p. 251).

Initially, evaluations included representation of both major surviving branches, along with both *Noraster* and *Triasteropsis*. First cladistic analyses clearly separated traditional forcipulataceans and *Triasteropsis* from the remainder of the crown-group. *Noraster* is included here as an outgroup taxon but other forcipulataceans were deleted, along with characters that proved invariant among the non-forcipulatacean taxa.

**Taxon Selection.**

Within the Spinososaca plus Valvatacea, taxon selection sought to be both broadly comprehensive and to sample basal groups sensu Blake (1987). Emphasis is on taxa at least superficially similar to *Noraster*.

For the Valvataida sensu Blake (1987), *Pseudarchaster*, *Antibrachia*, *Mediaster*, and *Archaster* were selected because of their likely basal position within the Gonastideridae and because of general similarities with *Noraster* and extant poraniids. *Antibrachia* was specifically selected because it, like many living poraniids, has thickened dermal tissues, and *Archaster* was selected because it is a homeomorph of *Asteropecten*. *Cycethra* and *Asterina* were selected because of the close affinities between their respective families (Ganeriidae and Asterinidae) and the Poraniidae sensu Blake (1987). Hotchkiss & Clark (1976) separated the family Poraniidae from the family Asteroidea based on the arrangement of the ventral surface ossicles. *Petricia* and *Demasterias* represent the Asteroidea. They are of particular interest because they share the heavy dermal tissues typical of most poraniids. Other important valvaturaean families, e.g., Oreasteridae, Acanthasteridae, Ophiidiasteridae, and Mithrodidiidae are derived and very different from members of the Poraniidae. *Porania palpilla* (O.F. Müller, 1776), the type species of the Poraniidae, is one selected representative of this family. The second, *Marginaster*, was chosen because dermal tissues are limited in this genus, as they appear to have been in *Noraster*. Known Marginaster specimens are small, and Clark
& Downey (1992) suggested that Marginaster might represent the immature of another genus, but this possibility is not an impediment to its use here, which is to indicate breadth of form with a small sample rather than to contribute to a familial phylogeny.

For the Paxillosida sensu Blake (1987), Astreopetiaceae and Luididae were selected because of their enduring appearance in phylogenetic reconstructions. A generalized Astreopetidae was based on such taxa as Pliasteraster and Telphaster but not the specialized, e.g., Dyastera. The Radiasteridae, important in the phylogeny of Blake (1987), was coded here based on both Radiaster and the Cretaceous genus Betoasteria Blake and Reid. The Porellanoasteridae exhibits distinctive apomorphies, but it is included because the ventral ossicular arrangement is similar to that of the Poraniidae. The Benthopectinidae is included as the third order of the Valvatida sensu Blake (1987). *Hirouitsa* represents the Spinulosida and Solaster the Valatida. The Spinulosida sensu Blake (1987) includes only the Echinasteridae whereas the Valatida includes a number of families that are apparently derived from a Solasteridae-like ancestry.

**Outgroup selection.**

Blake (in press 2000) argued that two apomorphies of crown-group asteroids are presence of offset positioning of ambulacral and ambulacral and presence of dorsal podial pores between successive ambulacra. Neither feature is found in an undescribed Ordovician species from the Wah Wah Formation of Utah, nor in the lower Paleozoic genera Salasteraster and Hudsonaster. Information is incomplete for these taxa; therefore, an “ancestor” was recognized through a combination of traits from the three. Coding of the “ancestor” used common expression for all three if available, or common expression for two and an unknown. Other characters, such as presence of cylindrical spinelets and absence of pedicellariae, were based on typical Paleozoic occurrence. Morphological expression was deemed too uncertain for “ancestor” value assignment.

*Devaster* is included because it has lateral (rather than dorsal) podial pores, which suggested an organization intermediate between that of “ancestor” and the crown group. Only two Paleozoic species are known to the author that might have both dorsal podial pores and offset ambulacral-ambulacral positioning; these are *Callasterella americana* Kesling and Strimple, 1966, and *Compassaster formosus* Worthen and Miller, 1883. In preliminary analyses, both grouped with the forcipulate branch, and therefore they were not included here. Finally, recent *Zoraster* was included in the outgroup.

**Character selection.**

The goal of the present analysis is the determination of the position of *Noraster* relative to surviving crown-group asteroids; it is not intended to fully evaluate relationships among selected taxa nor to reevaluate earlier phylogenetic hypotheses. Emphasis was placed on those characters that appear to have fairly broad taxonomic distribution. Features that differ significantly among closely related genera, e.g., morphology of the marginals, was de-emphasized.

Development of characters began with Blake (1987); treatment differed from that study in that only hard part characters are included here in order to code fossil forms as completely as possible. Unlike the earlier study, no attempt was made to generalize across family-level taxa. Many recent families were not treated because of the restricted scope of the study.

**Analysis.**

The data set was evaluated using PAUP4.0b4a (Swofford, 1996). All characters were unordered and all characters were weighted equally. Five trees of equal length were recovered, with a consistency index of 0.4194 and a retention index of 0.6170. Two examples are provided (Figs. 5, 6). The five equal-length trees differ in positioning of *Dermasterias* and *Petrichia* relative to the Poraniidae, the two occurring either as a sister branch to the Poraniidae (Fig. 5) or as a comb-branch (Fig. 6). Trees further differ in the position of the Astreopetidae relative to Astreopetidae and the remainder of the Paxillosida (whether as a tricotomy or as a sequence beginning with the Asteriidae).

Bootstrap analysis (Fig. 7) showed strong support for the Poraniidae grouping and weaker support for the Paxillosida, Goniasteridae, and Asterinidae (*Asterina*) and Goniasteridae (*Cycletheca*). The somewhat weakly supported output results in part from taxon selection; for example, *Archaster*, *Dermasterias*, and the Porellanoasteridae were specifically included to challenge groupings in various ways, see taxon selection above. Consistency indices of individual characters are generally low; the limited fossil record, as well as molecular analyses, suggest both comparatively rapid diversification of crown-group asteroids and pervasive homoplasies.

The hypothesis of Fig. 5 approximates the grouping of Fisher (1911), suggesting perhaps both this author’s recognition of enduring taxonomic concerns as well as the need for phylogenetic analyses at the generic and species levels.

**CHARACTER LISTING**

| 1 | Disk small, interbrachial angles acute |
| 2 | Disk enlarged, interbrachial angles usually more or less rounded |
| 3 | Body profile more or less flattened; disk not arched nor arms rounded |
| 4 | Disk arched and arms more or less rounded, cardinal ridge expressed or not |
| 5 | Madreporite large, generally offset toward the disk margin |
| 6 | Madreporite small, near calcylinal ring |
| 7 | Papulae arranged in small re-entrants between abactinal ossicular digitations |
| 8 | Papulae multiple and in fields |
| 9 | Papulae usually dorsal to superomarginals, rarely between marginals |
| 10 | Papulae extending ventral to the inferomarginals |
| 11 | Actinals aligned 1:1 with ambulacral |
| 12 | Actinals not aligned 1:1 with ambulacral |
| 13 | Actinostome present |
| 14 | Actinostome lacking |
| 15 | An actinostome is a sunken mouth region, and it is typical of e.g. asteroids |
| 16 | Ambulacra protected by skeleton, dermal tissue |
| 17 | Ambulacra not protected by skeleton, dermal tissue |
| 18 | A protected ambulacral furrow is typical of *Valvatida sensu* Blake (1987); see Blake (1983) |
| 19 | Dermal tissues significantly thickened |
| 20 | Dermal tissues not significantly thickened |
| 21 | Much thickened body-wall tissues are typical of poraniids and also found in certain ganeriids |
| 22 | Arm margins prolonged internal toward the mouth |
| 23 | Disk margin arched, interbrachial septum distinct from arms calcified or not |
| 24 | Marginals abut oral frame, disk absent |
| 25 | *Viguié* (1879) observed that mode of disk formation is distinctive between the forcipulate groups and the remainder of the recent asteroids. Most Paleozoic forms lack a clearly differentiated disk (state 2), although one can occur |
| 26 | Interbrachial septum uncalcified |
| 27 | Interbrachial septum calcified either as a near-oral column or a more or less complete wall |
12 0 Superambulacrals present, can be reduced
  1 Superambulacrals absent
13 0 Form of the actinal ossicles
  0 Paxillae
  1 Metapaxillae
  2 Pseudopaxillae
  3 Disks, more or less angular in vertical cross section
  4 Crosses and bars

Variation in ossicular morphology among recent asteroids indicates widespread homoplasy and dorsal ossicular type recognition is somewhat arbitrary. Paxillae have a slender cylindrical column that is orthogonal to a small, weakly digitate, elliptical, or subcircular base; crown enlarged or not; paxillae are more or less uniform within a species. Metapaxillae have a short, almost granular column orthogonal to a comparatively enlarged base of different outlines; crown rarely enlarged; uniform to somewhat varied within a taxon. Pseudopaxillae have an elongate column inclined to a typically prominently digitate base; crown typically enlarged; somewhat varied within a taxon. Disks are tubular and abraded or rather weakly overlapping laterally. Crosses and bars are somewhat irregular, digitate, overlapping ossicles in which the larger ossicles in a species typically are cross-shaped and linked to both lateral and longitudinal series, commonly with a central raised area supporting one or more accessories.

14 0 Primary ring ossicles detectable at least at some stage of life
  1 Primary ring ossicles not detected at any stage
15 0 Carinal series present
  1 Carinal series absent
16 0 Lateral abactinal longitudinal series (Fig. 4e, 4d, "L") present, slightly separated from or abutting carinal series
  1 Lateral longitudinal series absent
17 0 Transverse abactinal series present
  1 Transverse series absent

The abactinal field is more or less irregular in some taxa, and recognition of longitudinal and transverse series can be somewhat arbitrary.

18 0 One marginal rows
  1 Two marginal rows

Recognition of marginal rows follows criteria established by Blake (1978); the most important is that marginal series arise proximal to the terminal. Pattern is difficult to establish for many Paleozoic taxa.

19 0 Marginals significantly enlarged relative to ossicles of adjacent series
  1 Marginals not significantly enlarged relative to ossicles of adjacent series
20 0 Marginal form similar to ossicles of adjacent series
  1 Marginals dissimilar from ossicles of adjacent series
21 0 Marginals of two series differ in size; or only a single marginal series
  1 Superomal marginals erect on transversely elongate distinctive interomal marginals
22 0 Distal marginals not more or less enlarged.
  1 Distal marginals more or less enlarged
23 0 Marginal fascicles absent
  1 Marginal fascicles present

Marginal fascicles are the transversely oriented, spinelet-bearing channels found e.g., in most members of the Astropectinidae.

24 0 Actinals absent to few
  1 Longest actinal row adjacent to marginals
  2 Longest actinal row adjacent to ambulacrals
25 0 Actinal size generally increases from furrow toward marginals
  1 Size generally decreases from furrows to marginals
  2 Size more or less uniform from furrow to marginals
  3 Actinals absent to few
26 0 Actinals near mouth frame more irregular in arrangement than those near interbrachial edge
  1 Actinal arrangement more or less regular throughout ventral disk

2 0 Actinals near interbrachial edge more irregular in arrangement
  3 Actinals absent to few
27 0 Actinal outlines more or less regular although ossicular size can vary
  1 Actinal outlines more or less irregular
  2 Actinals absent to few
28 0 No interbrachial actinals differentiated in form or size from other interbrachials
  1 Enlarged interbrachial actinals differentiated from other interbrachials
  2 Actinals absent to few
29 0 Podal pores lacking
  1 Lateral podal pores present
  2 Dorsal podal pores present
30 0 Tube feet arranged in two rows
  1 Tube feet in four rows proximally with rows reflected only in ambulacrals
  2 Tube feet in four rows proximally with rows reflected in both ambulacrals and adambulacrals
  3 Tube feet in four rows throughout the arm with rows reflected weakly if at all in adambulacrals

In asteroids with four rows of tube feet, adambulacrals immediately adjacent to the tube foot have a flattened furrow surface whereas (alternate) adambulacrals adjacent to mid-furrow tube feet can have a more or less prominent, angular furrow profile extended toward the arm axis. The condition is most obvious in the Zoarctasteridae.

31 0 Ambulacrals not lengthened
  1 Ambulacrals moderately lengthened
  2 Ambulacrals strongly lengthened, flattened, upright
32 0 Ambulacral body outline rectangular
  1 Ambulacral body outline triangular

The ambulacral body is the adradial extremity of the ossicle, the outline as viewed dorsally.

33 0 Adradial, longitudinal amb-amb articulation surfaces not inclined and imbricated
  1 Adradial, longitudinal amb-amb articulation surfaces inclined and imbricated

Articular structures linking ambulacral bodies of successive ambulacrals

34 0 Aboral flanges for amb-adamb muscles similar, approximately bilateral
  1 Such flanges not similar and bilateral

Wing-like processes at the aboral ends of ambulacral ossicles

35 0 Lateral facets not developed (amb not adamb at flat, ventral surface in paired arrangement of most Paleozoic species
  1 Amb/adamb articular facets bilaterally symmetrical and facets are linked by a ridge extended between facets
  2 Amb/adamb articular facets not bilaterally symmetrical and facets not linked by a linear ridge

In Paleozoic species lacking an alternate ambulacral-adambulacral arrangement, the contact between ossicles is flattened, and at least in some, rimmed and ventrally directed surface

36 0 Dorsal aboral end of ambulacral not enlarged, rounded, angled to ossicular axis
  1 End of ambulacral enlarged, rounded, knee-shaped and angled to ossicular axis
37 0 Dorsal stome of ambulacral not of transverse, hyaline rods
  1 Dorsal stome of ambulacral of transverse, hyaline rods
38 0 Ambulacrals/ambulacrals paired
  1 Ambulacrals/adambulacrals offset
39 0 Adambulacrals upright and laterally abutted
  1 Adambulacrals imbricated in the proximal direction
  2 Adambulacrals imbricated in the distal direction
40 0 Adambulacral side faces similar, dominated by longitudinal muscle depressions
  1 Side faces dissimilar, not dominated by longitudinal muscle depressions
41 0 Furrow accessories (spines, spinelets) not differentiated from subambulacrals
1 Furrow accessories differentiated from subambulacrals
Adambular furrow accessories are those immediately adjacent to the furrow and the tubelets in many asteroids, those of the abradial portion of the ossicle are variously differentiated (e.g., size, form, arrangement) and these are the "subambulacrals"
42 0 Adoral carina lacking
1 Adoral carina developed in some specimens or only some inter-brachials
The term "oral carina" is used for the ridge distal to the mouth angle ossicles formed by adambulacrals abutting across the interbrachial surface.
43 0 Mouth angle ossicle robust, triangular in outline
1 Mouth angle ossicle intermediate, narrowed, keel-like
2 Mouth angle ossicle small, similar in size to adjacent adambulacrals
44 0 Mouth angle ossicle not sharply truncated proximally
1 Mouth angle ossicle sharply truncated proximally
45 0 First adambular overlaps lateral face of mouth angle ossicle
1 First adambular abuts distal side of mouth angle ossicle
46 0 Lacking pedicellariae with little-differentiated spine-like blades
1 Such pedicellariae present
47 0 Lacking pedicellariae with broadened blades and anchoring pits in the primary ossicle
1 Such pedicellariae present
48 0 Lacking three-element uncrossed pedunculate pedicellariae
1 Such pedicellariae present
49 0 Small accessory ossicles absent from above the ambitus
1 Acute, pointed or cylindrical spinelets dominate above the ambitus
2 Granules dominate above the ambitus
50 0 Spines or other enlarged accessories absent above the ambitus
1 Spines or other enlarged accessories can occur above the ambitus