Rivista Italiana di Paleontologia e Stratigrafia | volume 106 | numero 2 | pagine 141-156 | Luglio 2000

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

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

Received February 8, 2000; accepted May 5, 2000

Key-words: Noriaster barberoi, Echinodermata, Asteroidea, Poraniidae, Norian, Triassic, Taxonomy, Systematics, Phylogeny, Palaeoecology.

Riassunto. Noriaster barberoi gen. n. sp. n. è descritta sulla base di un singolo esemplare proveniente dal Calcare di Zorzino (Norico, Triassico Superiore) dell'Italia settentrionale. *Noriaster barberoi* gen. n. sp.n. è ascritta 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 *Trichasteropsis*, 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 divergenti e pochi sono i caratteri derivati utilizzabili per ricostruire 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 comparsa 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 *Trichasteropsis* 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.

Zusammenfassung. Noriaster barberoi gen. et sp. n. beruht auf einem einzigen Exemplar aus dem Zorzinokalk (Trias, Nor) von Norditalien. Als ein Vertreter der heute noch lebenden Poraniidae (Valvatida; Echinodermata) ist *N. barberoi* der älteste Beleg einer Familie, die sonst erst ab dem Jura oder später bekannt ist, und die erste solche Art aus der Trias. Paläozoische Arten mit engen Beziehungen zu Krongruppen-Familien liegen nicht vor. *Noriaster* und die wenig ältere triassische Gattung *Trichasteropsis* aus dem Germanischen Muschelkalk belegen, dass die Diversifizierung der Krongruppen-Asteroiden spätestens während Mittel- und Obertrias in Gang gekommen war.

Die Stammesgeschichte der Krongruppen-Asteroiden ist kompliziert, weil heutige Familien morphologisch zu unterschiedlich sind. Außerdem zeigen sie vergleichsweise wenige zweifelsfreie Merkmale, die klar auf phylogenetische Beziehung und Abfolge hinweisen. Die Familienzuordnung von *Noriaster* wird durch eine neue kladistische Analyse begründet.

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, 1301 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, encrinus@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 allocthonous. 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 fragmented 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 *Noriaster barberoi* 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, 1909; 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. *Noriaster 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 *Astropecten*; 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 know 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.

Wöhrmann (1889) assigned terminal ossicles from the Carnian Raibl Formation of the Bavarian Alps to *Astropecten*. Ossicular form is suggestive of that of astropectinids, although at the current 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 forcipulates (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 forcipulates (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 Astropectinidae (Paxillosida), which is sometimes suggested to be a basal surviving crown-group asteroid taxon (e.g., Mortensen, 1922; Gale, 1987). Of course a Triassic astropectinoid 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 valvatidans are epifaunal marine invertebrates found from intertidal habitats to deep ocean settings and from the arctic to the antarctic. Although some valvatidans 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 paxillosidans (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*. Prying apart of bivalve prey, famous in asteriids 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 Calcare di Zorzino 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, D; 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

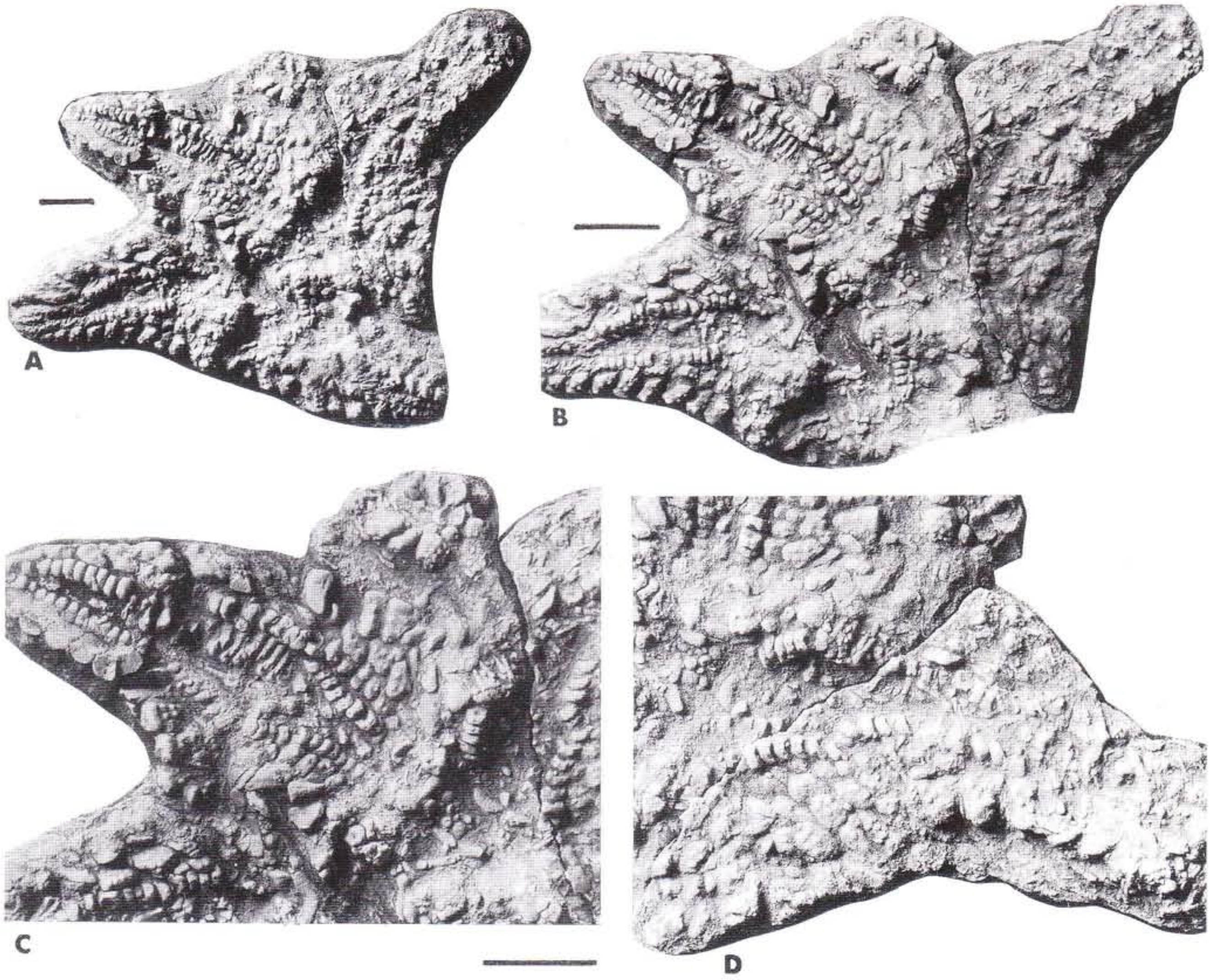


Fig. 1 - A-D, *Noriaster barberoi* n. gen. et sp. The holotype (the single-known specimen, MPUM 8420 from the Zorzino Limestone of Endenna-Zogno) at different magnifications and directions of lighting; scale 3 mm. Ventral aspect. See Fig. 4 for comparative diagrams.

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* 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 Asteroidea 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.

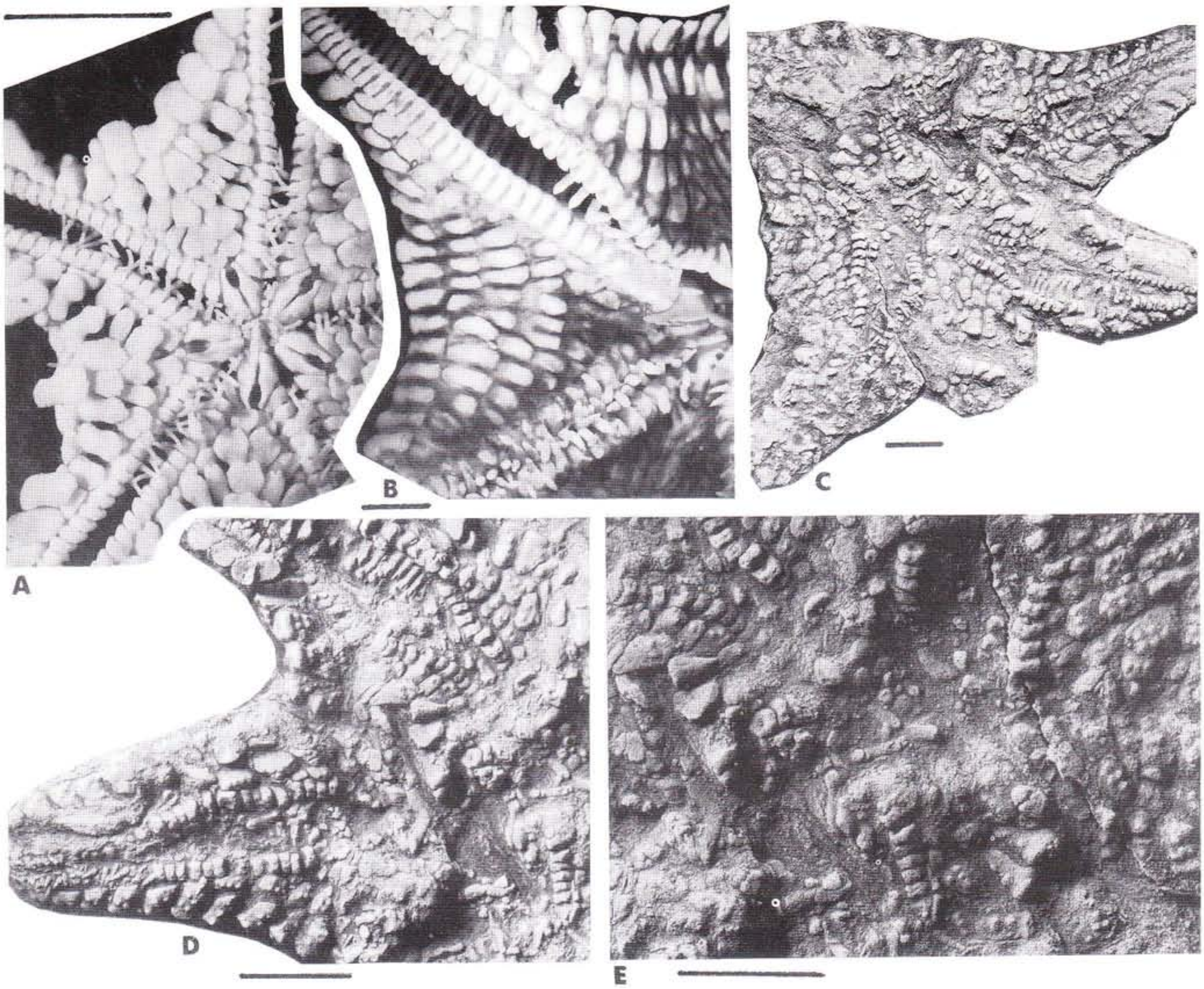


Fig. 2 - A, *Marginaster pectinatus* Perrier in ventral view, USNM E12462, 00 18 N, 044 17 N; B, *Porania pulvillus* Verrill in ventral view, USNM E46649, North Atlantic Ocean. C-E, *Noriaster barberoi* n. gen. et sp. (the holotype, MPUM 8420 from the Zorzino Limestone of Endenna-Zogno, at different magnifications and directions of lighting). Ventral views. Scale 3 mm. Note arrangement of actinal ossicles and their somewhat irregular configuration; also the complex, somewhat irregular arrangement of abactinals in *M. pectinatus*. See Fig. 4 for comparative diagrams.

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 (Forcipulatacea), Goniasteridae (Valvatacea), and Echinasteridae (Spinulosacea), suggesting significant plesiomorphic expression (although each possesses synapomorphies). 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.

Superorder Valvatacea McKnight, 1975

Order Valvatida Perrier, 1884

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*,

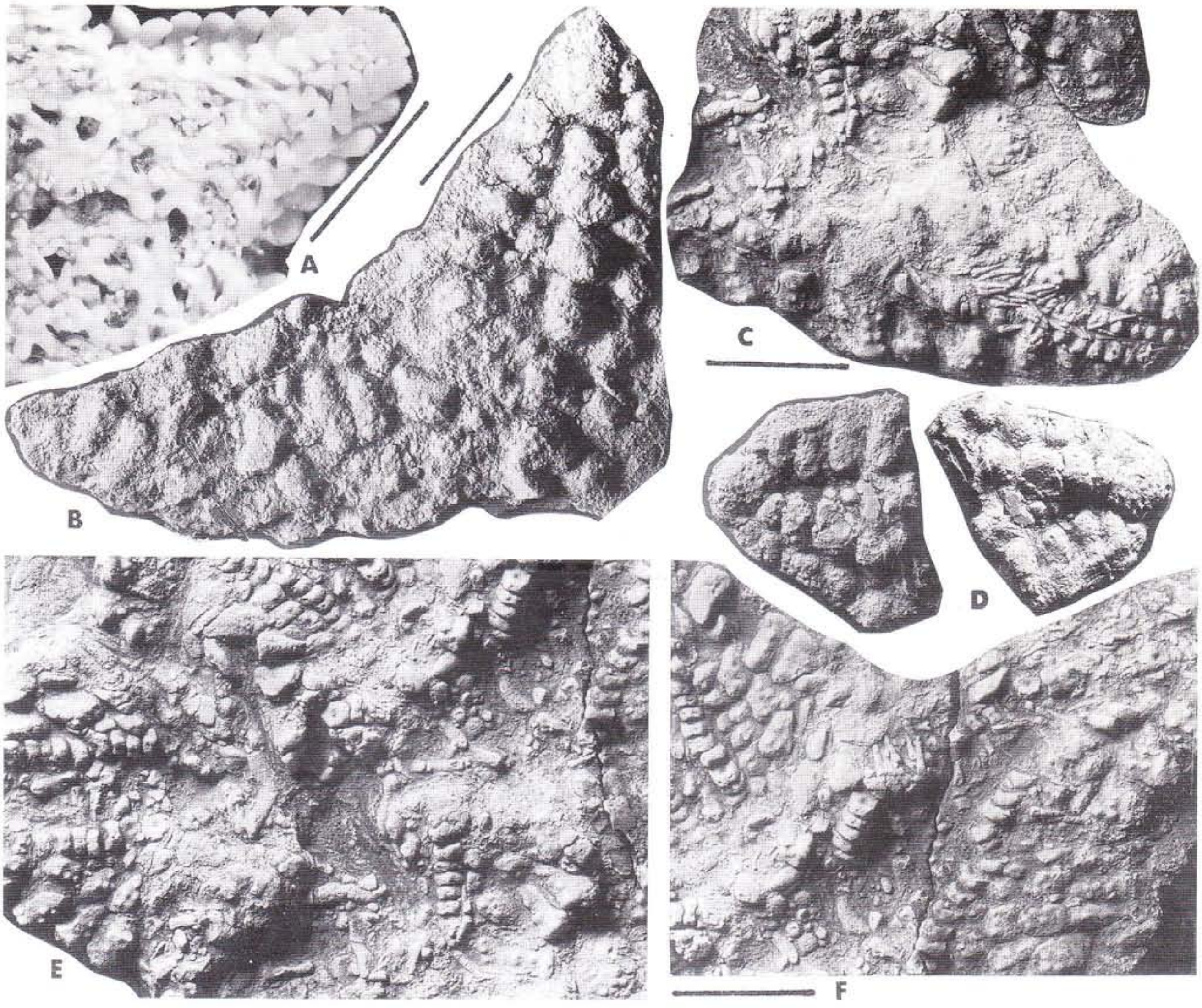
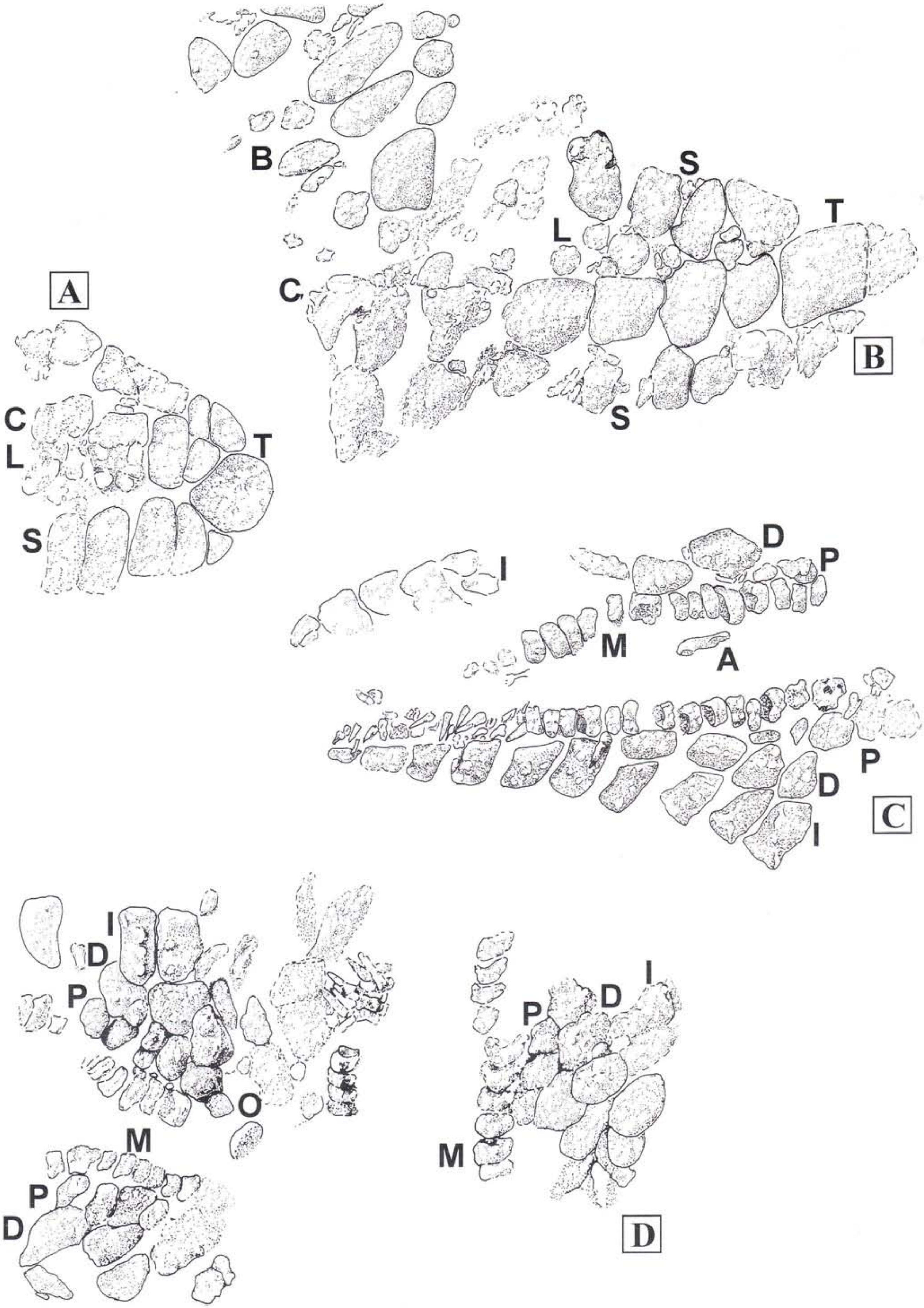


Fig. 3 - A, *Marginaster pectinatus* Perrier in dorsal view; B-F, *Noriaster barberoi* n. gen. et sp. (the holotype, MPUM 8420 from the Zorzino Limestone of Endenna-Zogno, at different magnifications and directions of lighting). B, D in dorsal view; C, E, F in ventral view. Scale 3 mm. See Fig. 4 for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

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

Fig. 4 - *Noriaster 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 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 adambulacrals; O? possible oral actinal; P proximal actinals; S superomarginals; T terminal.


B
S
L
T
C
A
C
L
T
S
B
S
D
I
P
M
A
P
D
C
I
I
D
P
O
M
P
D
I
D
P
M
D

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 papulae 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 Valvatida 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 *Sphaeriaster 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 ridges 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. Adradial 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 articular 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-C; 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 interbrachial 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 fasciole-like skeletal furrows are not developed (although furrowing could have been restricted to soft tissues). Actinals are of irregular outline, relatively tall (and therefore robust). Actinals 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. adradial end of the ossicle) length at least 0.5 mm, each ossicle overlapping proximally by means of distinct triangular flanges. Ambulacral cross-furrow articular 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 (a pattern found in the living Ganeriidae). Abradially, 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 midline is approximately 1.0 mm.

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

Adambulacrals (Especially Fig. 3F). About 6 adambulacrals per 2 mm from proximal or proximal-medially 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 edge 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. Adradial (proximal) face flat rather than prominent (i. e. the furrow edge would appear flattened rather than digitate for prominences partially separating sequential tubefeet). 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 adambulacral-ambulacral articular tissues. 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.

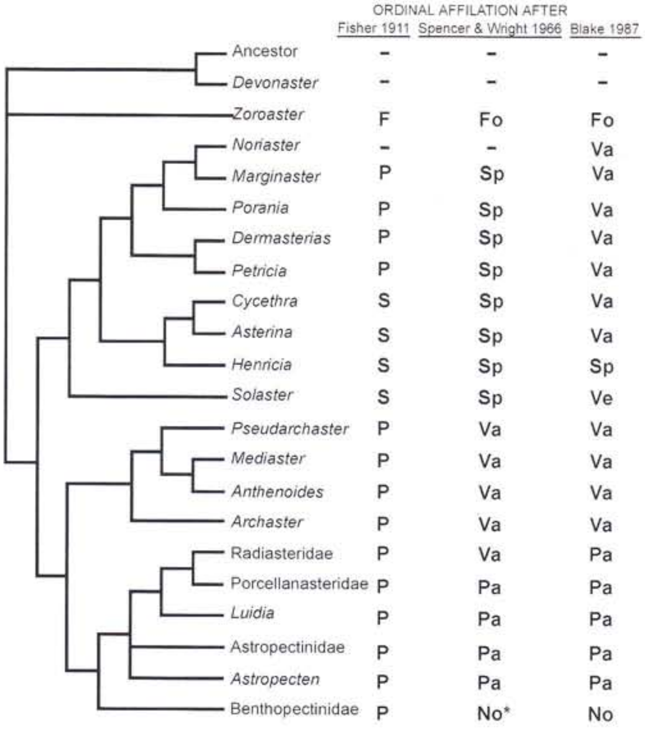


Fig. 5 - Phylogenetic hypothesis, see text for explanation. Key to affiliations after Fisher, 1911: F=Forcipulatida; P=Phanerozona; S=Spinulosa; Others: Fo=Forcipulatida; No=Notomyotida; Pa=Paxillosida; Sp=Spinulosida; Va=Valvatida * Notomyotida is a suborder of Valvatida sensu Spencer & Wright.

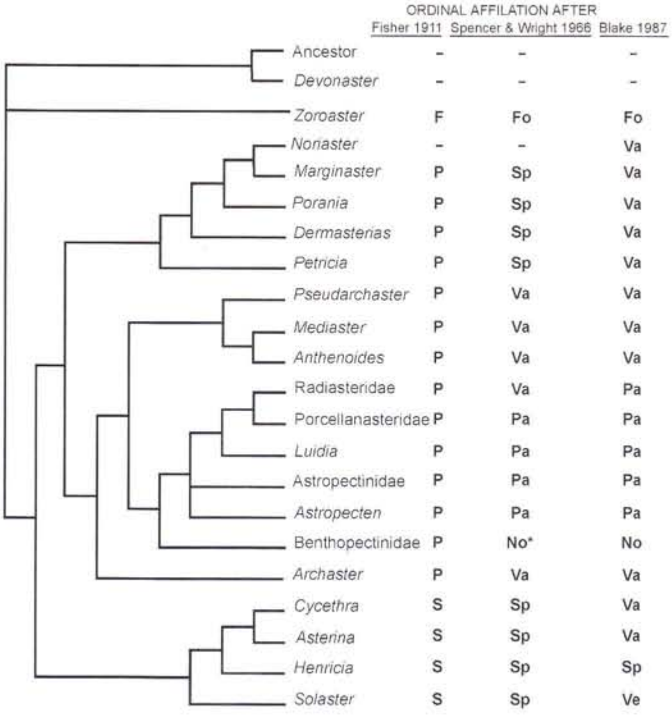


Fig. 6 - Phylogenetic hypothesis, see text for explanation. Key to affiliations after Fisher, 1911: F=Forcipulatida; P=Phanerozona; S=Spinulosa; Others: Fo=Forcipulatida; No=Notomyotida; Pa=Paxillosida; Sp=Spinulosida; Va=Valvatida * Notomyotida is a suborder of Valvatida sensu Spencer & Wright.

Remarks. The terminal is similar to those described by Wöhrmann (1889) under the name *Astropecten pichleri*; 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 Poraniidae, 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 also 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 Poraniidae.

Comparisons.

Noriaster can be distinguished from other poraniids based on marginal form and accessory development. A closely arranged actinal pattern with differentiated medial actinals might be distinctive as well, although recent forms are incompletely documented.

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 Poraniidae, allowing assignment of *Noriaster* to this family. Genera of the Paxillosida *sensu* Blake (1987) cluster together and form a sister branch of the Benthopectindae. The goniasterid 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 paxilliform 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.,

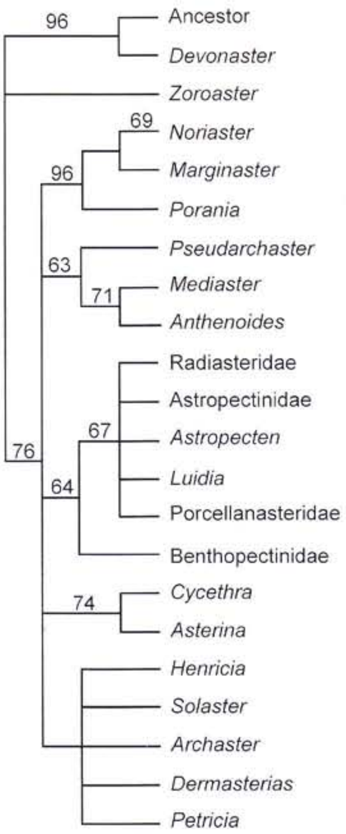


Fig. 7 - Bootstrap analysis of data set for figure 5, see text for explanation.

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 of thickened dermal tissues? Hotchkiss & Clark (1976) assigned *Asteropsis* as well as *Dermasterias* and *Petricia* to their Asteropseidae (see Appendix), yet the ambulacral column ossicular morphology of *Asteropsis* suggests its affinities lie with the Oreasteridae. Perhaps linkage of *Dermasterias* and *Petricia* to the Poraniidae *sensu* Hotchkiss & Clark only reflects thickening of tissues combined with as 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.

Acknowledgments.

DBB travel and research was supported by a US National Science Foundation grant, INT-9815164. We thank Drs. G. Breton, H. Hess, and F. H. C. Hotchkiss for valuable review comments and Ms C. Ahearn and the authorities of the US National Museum for the loan of specimens.

REFERENCES

Bather F. A. (1909) - Triassic Echinoderms of Bakony. *Result. wissenschaft. Erfor. Balatonsees*, v. 1, n. 1, pp. 1-288.

Blake D. B. (1978) - The taxonomic position of the modern sea star *Cistina* Gray, 1840. *Proc. biol. Soc. Wash.*, v. 91, n. 1, pp. 234-241, Washington.

Blake D. B. (1983) - Some biological controls on the distribution of shallow-water sea-stars. *Bull. Mar. Sci.*, v. 33, n. 3, pp. 703-712.

Blake D. B. (1984) - The Benthopectinidae (Asteroidea: Echinodermata) of the Jurassic of Switzerland. *Eclogae geol. Helv.*, v. 77, n. 3, pp. 631-647, Basel.

Blake D. B. (1987) - A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata). *Journ. Nat. Hist.*, v. 21, n. 2, pp. 481-528.

Blake D. B. (1989) - Asteroidea: functional morphology, classification and phylogeny. In M. Jangoux M. & J. M. Lawrence J. M. (eds.) - *Echinoderm Studies*, v. 3., p. 179-233, A. A. Balkema, Rotterdam.

Blake D. B. (1990) - Hettangian Asteriidae (Echinodermata: Asteroidea) from southern Germany: taxonomy, phylogeny and life habits. *Paläont. Zeit.*, v. 64, n. 1/2, pp. 103-123, Berlin.

Blake D. B. (in press, 2000) - The class Asteroidea (Echinodermata): Fossils and the base of the crown group. *Am. Zool.*, Lawrence.

Blake D. B. & Guensburg T. E. (1988) - The water vascular system and functional morphology of Paleozoic asteroids. *Lethaia*, v. 21, n. 3, pp. 189-206, Oslo.

Blake D. B. & Guensburg T. E. (1994) - Predation by the Ordovician asteroid Promopalaeaster on a pelecypod. *Lethaia*, v. 27, n. 3, pp. 235-239, Oslo.

Blake, D. B., Hagdorn H. & Tintori A. (1999a) - Echinoderm taphonomy of the Zorzino Limestone (Norian, Late Triassic). In S. Renesto (ed.), Third Int. Symp. Lith. Limestones. *Riv. Mus. Civ. Sci. Nat. "E. Caffi"*, v. 20 (supp.), pp. 35-38, Bergamo.

Blake D. B. Hagdorn H. & Tintori A. (1999b) - A new asteroid (Echinodermata) from the Triassic Calcare di Zorzino of Northern Italy (abstract). *Geol. Soc. Am. Abs. Prog.*, v. 31, n. 7, p. 43, Boulder.

Breton G. (1996)- Les pédicellaires alvéolaires sont-ils arrivés chez les Goniasteridae (Echinodermata: Asteroidea) au Crétacé par voie ´pid´mique? *Bull. Soc. zool. Fr.*, 121 (1), pp. 87-92.

Clark A. M. & Courtman-Stock J. (1976) - The Echinoderms of Southern Africa. *Brit. Mus. Nat. Hist. Pub.* n. 776, pp. 1-277, London.

Clark, A. M. & Downey M. E. (1992) - Starfishes of the Atlantic. Chapman and Hall, v. of 794 p., London.

Fisher W. K. (1911) - Asteroidea of the North Pacific and adjacent waters. *Bull. U. S. Nat. Mus.*, v. 76, pp. 1-420, Washington.

Gale A. S. (1987) - Phylogeny and classification of the Asteroidea. *Zool. Journ. Linn. Soc.*, v. 89, n. 2, pp. 107-132, London.

Garassino A. & Teruzzi G. (1993) - A new decapod crustacea assemblage from the Upper Triassic of Lombardy (N. Italy). *Paleontologia Lombarda*, n.s., v. 1, 27 pp., Milano.

Hess H. (1972) - Eine Echinodermen-Fauna aus dem mittleren Dogger des Aargauer Juras. *Abh. Schweiz. Paläont. Ges.*, v. 92, pp. 1-87, Basel.

Hotchkiss F. H. C. & Clark A. M. (1976) - Restriction of the family Poraniidae, sensu Spencer and Wright, 1966 (Echinodermata: Asteroidea). *Bull. Brit. Mus. Nat. Hist. (Zool.)*, v. 30, n. 6, pp. 263-268, London.

Kesling R. V. & Strimple H. V. (1966) - *Calliasterella americana*, a new starfish from the Pennsylvanian of Illinois. *Journ. Paleont*, v. 40, n. 5, pp. 1157-1166, Boulder.

Mortensen Th. (1922) - Echinoderm larvae and their bearing on evolution. *Nature*, v. 110, pp. 806-807, London.

Müller O. F. (1776) - Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum, etc. 282 pp., Havniae.

Münster G. von. (1843) - *Asterias weissmanni. Beiträge Petrefactenkunde*, v. 6, p. 78, Bayreuth.

Pinna G. (1974) - I Crostacei della fauna Triassica di Cene in Val Seriana (Bergamo). *At. Soc. It. Sc. Nat.*, v. 21, pp. 7-33, Milano.

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

Renesto S. (1994a) - *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of Northern Italy. *J. Vert. Paleont.*, v. 14, n. 1, pp. 38-52, Lawrence.

Renesto S. (1994b) - A new Prolacertiform reptile from the Late Triassic of Northern Italy. *Riv. It. Paleont. Strat.*, v. 100, n. 2, pp. 285-306, Milano.

Renesto S. (1995) - A sphenodontid from the Norian (Late Triassic) of Lombardy (Northern Italy): A preliminary note. *Modern Geology*, v. 20, pp. 149-158, Malaysia.

Renesto S. & Tintori A. (1995) - Functional morphology and mode of life of the Late Triassic placodont *Psephoderma alpinum* Meyer from the Calcare di Zorzino (Lombardy, n Italy). *Riv. It. Paleont. Strat.*, v. 101, pp. 37-48, Milano.

Schöndorf F. (1909) - Paläozoische Seesterne Deutschlands. I. Die echten Asteriden der Rheinischen Grauwacke. *Palaeontographica*, v. 65, n. 2, pp. 37-112, Stuttgart.

Schuchert C. (1915) - Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea. *Bull. U. S. Nat. Mus.*, v. 88, pp. 1-312, Washington.

Sloan N. A. (1980) - Aspects of the feeding biology of asteroids. In Barnes M. (ed.) - *Ocean. Mar. Biol. An. Rev.*, v. 18, pp. 57-124.

Spencer W. K. (1914-1940) - British Palaeozoic Asterozoa. *Palaeont. Soc. Lon. Mem.*, pp. 1-540, London.

Spencer W. K. & Wright C. W. (1966) - Asterozoans. In Moore R. C. (ed.) - Treatise on Invertebrate Paleontology, Pt. U, Echinodermata-3, U4-U107, *Geol. Soc. Am. & Univ. Kansas Press*, Lawrence.

Swofford D.L. (1996) - Phylogenetic Analysis Using Parsimony (and Other Methods), version 4.0. Sinauer Associates, Sunderland, Massachusetts.

Tintori A. (1995) - Biomechanical fragmentation in shell-beds from the Late Triassic of the Lombardian Basin (Northern Italy). Preliminary report. *Riv. It. Paleont. Strat.*, v. 101, pp. 371-380, Milano.

Tintori A. (1998) - Fish diversity in the marine Norian (Late Triassic) of Northern Italy: the first Neopterygian radiation. *It. Journ. Zool.*, v. 65, suppl., pp. 193-198, Napoli.

Wöhrmann S. (1889) - Die Fauna der sogenannten Cardita-und Raibler-Schichten in den Nordtiroler und bayerischen Alpen. *Jb. K. K. geol. Reichsanst.*, v. 39, pp. 181-258.

Worthen A. H. & Miller S. A. (1883) - Class Echinodermata, p. 327-338. In: *Geology and Palaeontology, Geological Survey of Illinois*, v. 7, 373 p., Illinois State Printing, Springfield.

Yang Z. (1982) - Noric asteroid of Late Triassic from Suri Hill, Dingri, Xizand, *Monograph on Mount Xixla Bangma Scientific Expedition*, 1964, p. 349. Peking Science Press.

Zardini R. (1973) - Fossili di Cortina; atlante degli echinodermi cassiani. Trias medio superiore della regione dolomitica attorno a Cortina d'Ampezzo, pp. 1 - 29, Foto Ghedina, 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 Spinulosacea forming the second. This arrangement echoes the perspective of Fisher (1911, p. 251).

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

Taxon Selection.

Within the Spinulosacea 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 *Noriaster*.

For the Valvatida *sensu* Blake (1987), *Pseudarchaster*, *Anthenoides*, *Mediaster*, and *Archaster* were selected because of their likely basal position within the Goniasteridae and because of general similarities with *Noriaster* and extant poraniids. *Anthenoides* was specifically selected because it, like many living poraniids, has thickened dermal tissues, and *Archaster* was selected because it is a homeomorph of *Astropecten*. *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 Asteropseidae based on the arrangement of the ventral surface ossicles. *Petricia* and *Dermasterias* represent the Asteropseidae. They are of particular interest because they share the heavy dermal tissues typical of most poraniids. Other important valvatidan families, e.g., Oreasteridae, Acanthasteridae, Ophidiasteridae, and Mithrodiidae are derived and very different from members of the Poraniidae. *Porania pulvillus* (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 *Noriaster*. 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), *Astropecten* and *Luidia* were selected because of their enduring appearance in phylogenetic reconstructions. A generalized Astropectinidae was based on such taxa as *Plutonaster* and *Tethyaster* but not the specialized, e. g. *Dytaster*. The Radiasteridae, important in the phylogeny of Blake (1987), was coded here based on both *Radiaster* and the Cretaceous genus *Betelgeusia* Blake and Reid. The Porcellanasteridae exhibits distinctive aporphies, 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 Valvatacea *sensu* Blake (1987). *Henricia* represents the Spinulosida and *Solaster* the Velatida. The Spinulosida *sensu* Blake (1987) includes only the Echinasteridae whereas the Velatida includes a number of families that are apparently derived from a solasterid-like ancestry.

Outgroup selection.

Blake (in press 2000) argued that two apomorphies of crown-group asteroids are presence of offset positioning of adambulacrals and ambulacrals and presence of dorsal podial pores between successive ambulacrals. Neither feature is found in an undescribed Ordovician species from the Wah Wah Formation of Utah, nor in the lower Paleozoic genera *Salteraster* 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. Marginal expression was deemed too uncertain for "ancestor" value assignment.

Devonaster 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-adambulacral positioning; these are *Calliasterella americana* Kesling and Strimple, 1966, and *Compsaster formosus* Worthen and Miller, 1883. In preliminary analyses, both grouped with the forcipulatacean branch, and therefore they were not included here. Finally, recent *Zoroaster* was included in the outgroup.

Character selection.

The goal of the present analysis is the determination of the position of *Noriaster* 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 *Petricia* relative to the Poraniidae, the two occurring either as a sister branch to the Poraniidae (Fig. 5) or as a comb-sequence (Fig. 6). Trees further differ in the position of the Astropectinidae relative to Astropecten and the remainder of the Paxillosida (whether as a tricotomy or as a sequence beginning with the *Astropectinidae*).

Bootstrap analysis (Fig. 7) showed strong support for the Poraniidae grouping and weaker support for the Paxillosida, Goniasteridae, and Asterinidae (*Asterina*) and Ganeriidae (*Cycethra*). The somewhat weakly supported output results in part from taxon selection; for example, *Archaster*, *Dermasterias*, and the Porcellanasteridae 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 homoplasy.

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 0 Disk small, interbrachial angles acute
  1 Disk enlarged, interbrachial angles usually more or less rounded
2 0 Body profile more or less flattened; disk not arched nor arms rounded
  1 Disk arched and arms more or less rounded, carinal ridge expressed or not
3 0 Madreporite large, generally offset toward the disk margin
  1 Madreporite small, near calycinal ring
4 0 Papulae arranged in small re-entrants between abactinal ossicular digitations
  1 Papulae multiple and in fields
5 0 Papulae usually dorsal to superomarginals, rarely between marginals
  1 Papulae extending ventral the to inferomarginals
6 0 Actinals aligned 1:1 with adambulacrals
  1 Actinals not aligned 1:1 with adambulacrals
7 0 Actinostome present
  1 Actinostome lacking

An actinostome is a sunken mouth region, and it is typical of e.g. asteriids

8 0 Ambulacra protected by skeleton, dermal tissue
  1 Ambulacra not protected by skeleton, dermal tissue

A protected ambulacral furrow is typical of Valvatida *sensu* Blake (1987); see Blake (1983)

9 0 Dermal tissues significantly thickened
  1 Dermal tissues not significantly thickened

Much thickened body-wall tissues are typical of poraniids and also found in certain ganeriids

10 0 Arm margins prolonged internal toward the mouth
  1 Disk margin arced, interbrachial septum distinct from arms calcified or not
  2 Marginals abut oral frame, disk absent

Viguier (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.

11 0 Interbrachial septum uncalcified
  1 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 Form of the abactinal ossicles
 0 Paxillae
 1 Metapaxilla
 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 to 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 tabular and abutted 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. 4c, 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 ossicles
21 0 Marginals of two series differ in size; or only a single marginal series
 1 Superomarginals erect on transversely elongate distinctive inferomarginals
22 0 Distal marginals not more or less enlarged.
 1 Distal marginals more or less enlarged
23 0 Marginal fascioles absent
 1 Marginal fascioles present

Marginal fascioles 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 adambulacrals
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 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 Podial pores lacking
 1 Lateral podial pores present
 2 Dorsal podial pores present
30 0 Tube feet arranged in two rows
 1 Tube feet in four rows proximally with rows reflected only in adambulacrals
 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 Zoroasteridae.

31 0 Ambulacrals not foreshortened
 1 Ambulacrals moderately foreshortened
 2 Ambulacrals strongly foreshortened, 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 articular surfaces not inclined and imbricated
 1 Adradial, longitudinal amb-amb articular surfaces inclined and imbricated

Articular structures linking ambulacral bodies of successive ambulacrals

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

Wing-like processes at the abradial ends of ambulacral ossicles

35 0 Lateral facets not developed (ambs abut adambs 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 a flattened, and at least in some, rimmed and ventrally directed surface

36 0 Dorsal abradial 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 stereom of ambulacral not of transverse, hyaline rods
 1 Dorsal stereom 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 subambulacral
1 Furrow accessories differentiated from subambulacrals

Adambulacral furrow accessories are those immediately adjacent to the furrow and the tubefeet; 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 interbrachia
2 Adoral carina well-developed throughout taxon

The term "adoral 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 adambulacral

44 0 Mouth angle ossicle not sharply truncated proximally
1 Mouth angle ossicle sharply truncated proximally

45 0 First adambulacral overlaps lateral face of mouth angle ossicle
1 First adambulacral abuts distal side of mouth angle ossicle

46 0 Lacking pedicellariae with little-differentiated spinelike 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

ancestor	01100111120130011990000033220000000000000000000010
Devonaster	01000111100130011110002100101000000000000000000920
Zoroaster	01101101101030001010000101002210001001201211100110
Noriaster	11990199119149000101101100112001101111200999999919
Marginaster	11110111011140000101101100112001101111200000000010
Porania	11110111011140000101101100102001101111200000000000
Pseudarchaster	10100110110100111101001212002001011101211000011020
Mediaster	10100010110030111101001211000001001101201000001020
Anthenoides	10100110010130111101001211000001001101211000001020
Radiasteridae	11000011110001111100011221002000012001210000000010
Astropectinidae	10000111110001111101011221002000012001211000010011
Astropecten	00000111110001111101111221002000012001211000010011
Luidia	00000011110001111101012221002000012001211000010021
Porcellanasteridae	00000011110001111101011110102000002001210000000011
Cycethra	11110011111010111100001221002001101111211000000020
Asterina	11110011111010111111001221002001101111211000000020
Benthopectinidae	00000111110100111101000221002001011001211000010011
Henricia	01111111111010111110000021002001102011210000000010
Sölaster	11101111110120111110001221002001101001210000000010
Archaster	00100110111100011101110021002001111001210000001010
Dermasterias	11110110011030101100001211102011101001200000001000
Petricia	11110110011131001100001212102001101001210000000000

Tab. 2 - Data set for cladistic analysis. "9" = unknown.