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Aspects of life mode among Ordovician asteroids: Implications of new specimens from Baltica

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A new genus and species of Asteroidea (Echinodermata), *Estoniaster maennili*, is described from the Upper Ordovician (Caradocian) of Estonia; it is similar to the western European genus *Platanaster* and the North American *Lanthanaster* and an as yet unpublished new genus. Specimens of *Urasterella?* sp. and *Cnemidactis* sp. are recognized from the Middle Ordovician of northwest Russia; although similar to known species, incomplete preservation precludes more precise taxonomic assessment. Asteroids are important in many existing marine communities, and in spite of a meager fossil record, diversity suggests they were important in the early Paleozoic as well. Some debate has centered on arm flexibility in early asteroids, which bears on their roles in their communities. Parallels in ambulacral series arrangement between Ordovician and extant species and presence of an ambulacral furrow indicate similar broad ranges of motion and therefore potentially parallel ecologic roles. Many factors might have contributed to the differences between ancient and extant ambulacral articulation, including changes in positioning of a part of the water vascular system, changes in predation and bioturbation pressures, and taphonomic events that obscure skeletal details.

Key words: Echinodermata, Asteroidea, functional morphology, Ordovician, Baltica.

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Introduction

The fossil record of asterozoans is meager. Because of body arrangement, these organisms are readily destroyed taphonomically; however, the morphological diversity of early asterozoans (documented in part by fossils recorded here) suggests presence of a varied but largely unknown fauna (Blake 2000). Not surprisingly, reports of comparatively early asteroids from Baltica are few (e.g., Franzen 1979; Kutscher 2004; Rozhnov 2004; Hansen et al. 2005). Both the Platanasteridae and the Urasterellidae are important Paleozoic taxa, yet they are poorly understood in large part because of the poor preservation of much of the limited available material. New partially disarticulated specimens provide basis for reinterpretation of aspects of both systematics and behavior.

At present, there is considerable interest in changes through time in such ecological interactions as predation and bioturbation (e.g., Aronson and Blake 2001; Kowalewski et al. 2005; Aberhan et al. 2006; Madin et al. 2006). Much of this work focuses on shell crushing, durophagous organisms, whereas durophagy is unknown among asteroids of all ages; nevertheless, the role of asteroids is important to comprehensive reconstruction of Phanerozoic benthic marine ecosystem evolution.

Sepkoski (1984) classified stelleroids as a taxon of the

Paleozoic fauna. Asteroids (as well as ophiuroids and polychaetes) were described by Aronson and Blake (2001) as slow-moving predators of a Paleozoic functional grade. Gale (1987) and Shackleton (2005) argued that Ordovician asteroids were inflexible and limited to quiet environments; such inferences might suggest that Ordovician species had not attained or at least fully attained the predatory abilities ascribed to a Paleozoic grade, which raises questions on the functional organization of early Paleozoic communities. Data from the new specimens support inferences of Schuchert (1915) and Spencer (1918) on structural arrangement and broad behavioral complexity attained by early asteroids; it is concluded that early asteroids were not restricted to quiet environments and that they were flexible and hence available as potential early Paleozoic predators.

Institutional abbreviations.—PIN, Paleontological Institute RAS, Moscow, Russia; SM, Sedgwick Museum of Geology, University of Cambridge, UK; UI, Department of Geology, University of Illinois, Urbana, USA; USMN, United States National Museum (Smithsonian Institution), Washington, DC, USA.

Other abbreviations.—IM, inferomarginal ossicle; MAO, mouth-angle ossicle; SM, superomarginal ossicle.

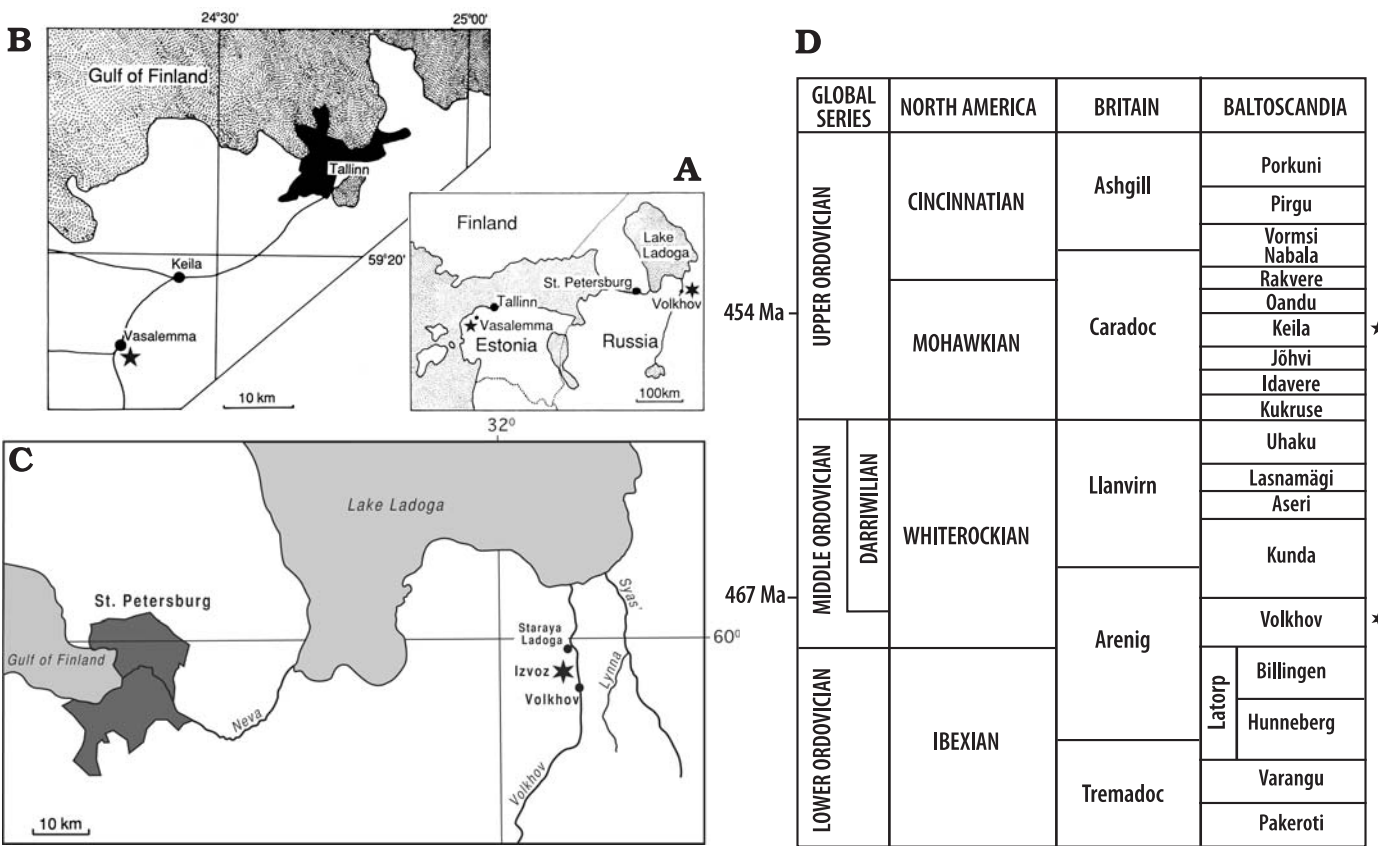


Fig. 1. Geographic and stratigraphic settings of the new fossils. **A**. Regional geography; specimens of *Estoniaster maennili* gen. et sp. nov. found near Vasalemma, Estonia; those of Urasterellidae found near Volkhov, Russia. **B**. Local geography in the region of Vasalemma, Estonia, discovery site for the described specimens of *Estoniaster maennili*. **C**. Local geography in the region of Volkhov, Russia, discovery site for the described specimens of Urasterellidae. **D**. Ordovician correlation chart, data from Webby et al. (2004). Asterisks mark positions of new fossils.

Geological setting

The fossil asteroids described here were collected from rocks of the Volkhov regional stage (Middle Ordovician, Upper Arenigian) near St. Petersburg, northwest Russia, and from the Keila regional stage (Upper Ordovician, Caradocian) near Tallin, Estonia (Fig. 1).

The Volkhov sediments were deposited in a cold-water setting (Dronov 1997, 2001). Both biohermal and interbiohermal intervals are present; the asteroids were collected from the interbiohermal facies. The Volkhov bioherms are mud-mounds whose framework appears to have been formed by sponges, bacteria, and algae (Fedorov 2003). The dead portions of the bioherms formed a convoluted sea floor topography accumulating under complex hydrodynamic conditions with apparent abundant nutrients that supported a rich, diverse biota. Small re-entrants developed in dead portions of the bioherms; these sites, protected from waves, were rapidly filled with sediment, which protected and preserved various echinoderms, brachiopods, bryozoans and trilobites. Among echinoderms, most common are the eocrinoids *Rhipidocystis*

and *Paracryptocrinites*, various inadunate crinoids, peritocrinid crinoids, the rhombiferan *Echinoencrinites*, and astero-cystid diploporitans. The asteroids themselves appear to have inhabited soft- and semi-soft substrates, perhaps feeding on an organic-rich sediment surface. Although more complete fragments are only rarely encountered, disarticulated ossicles are found with some frequency, suggesting that asteroids were not rare.

The Caradocian, Keila, sediments were deposited in a tropical setting. Again, both biohermal and interbiohermal intervals are recognized, with the asteroids coming from marly limestone that occur between the large, well-formed mud-mound bioherms. The biohermal framework organisms were algae, bryozoans, and echinoderms, including the tube-like edrioasteroid *Cyathocystis*, whose adjoining skeletons supported the structure. The rhombiferan *Hemicosmites* appears to have been an important contributor to the inter-biohermal facies, which consists of skeletal debris and terrigenous muds. These sediments supported a greater species diversity than did the Volkhov setting, although this fauna was dominated by comparatively few species. Asteroids are only rarely found, these in the quiet-water carbonate clay deposits.

Terminology for asteroids

Terminological usage follows that of Spencer and Wright (1966) and Blake and Hagdorn (2003). Not all ossicular types recognized among asteroids are preserved in the present material. Those that are include the *ambulacral* and *adambulacral series*, which arise at the proximal side of the unpaired *terminal* at the distal tip of the arm and extend proximally to the mouth frame, which includes the *mouth angle ossicles* (MAO) and adjacent *circumorals*. A more or less distinctive single or double *marginal series* (*inferomarginals* and *superomarginals*) marks the edge of the body of most asteroids and separates *abactinal ossicles* of the dorsal surface from the *actinal ossicles* found between the marginals and the adambulacrals. A differentiated *primary circlet* of abactinals is found near the dorsal center of the disk of most asteroids, and a usually unpaired *carinal series* commonly occurs along the dorsal midline of the arm. The *madreporite* connects the water vascular system to the environment. *Accessory ossicles*, *spines*, *spinelets*, and *granules* variously invest ossicles of the *primary series*.

Systematic paleontology

Class Asteroidea de Blainville, 1830

Order Platysterida Spencer, 1951

Family Palasteriscidae Gregory, 1900; emended Blake (in press)

Discussion.—Content in addition to *Estoniaster* includes *Palasteriscus* Stürtz, 1886; *Platanaster* Spencer, 1919; *Lanthanaster* Branstrator, 1972; and new genus A, Blake (in press). *Uranaster kinahani* Baily, 1878, and new genus B, Blake (in press) are tentatively included.

Genus *Estoniaster* nov.

Type species: *Estoniaster maennili* gen. et sp. nov., Ordovician, Estonia.

Derivation of the name: The name honors the national origin of the type material.

Diagnosis.—As for species.

Estoniaster maennili sp. nov.

Fig. 2.

Derivation of the name: The name in honor of the memory of the Estonian paleontologist and student of echinoderms, Ralf M. Maennil, 1924–1990.

Type material: Holotype PIN 4125/766; paratypes PIN 4125/767 and PIN 4125/768.

Type locality: Collected in the working Vasalemma Quarry, a limestone quarry about 1 km southeast of the railway station of the village of Vasalemma, near the town of Keila, near Tallinn, northern Estonia.

Type horizon: Upper Ordovician (Caradocian, upper part of the *Didymograptus multidentatus* Zone).

Material.—Holotype PIN 4125/766, a relatively complete specimen consisting of the disk and the proximal intervals of all arms. The abactinal skeleton is partially recrystallized and

form of many ossicles is unclear. Because PIN 4125/766 is relatively complete, paratypes PIN 4125/767 and PIN 4125/768 appear derived from one or two additional individuals.

Diagnosis.—*Estoniaster* differs from other representatives of the family in the presence of a large, domed madreporite near the body margin; presence of two well-defined marginal series in which the superomarginals are fusiform and at least some bear a single enlarged accessory; inferomarginals lack enlarged spines.

Discussion.—Abactinal ossicles are small in palasteriscids and prone to alteration; nevertheless those of *Estoniaster* are most like those of new genus A (Blake in press) in being relatively short, robust, with a broad base; those of *Lanthanaster* are delicate with a broad base. Abactinals of *Platanaster* are slender with a small base; those of *Palasteriscus* are more robust than those of *Platanaster* but more delicate than those of *Estoniaster*; data are very limited for both new genus B (Blake in press) and *U. kinahani* but those of both appear not to be clearly paxilliform, those of the former perhaps somewhat flattened and the latter more robust. *Estoniaster* differs from *Lanthanaster*, *Platanaster*, and *Palasteriscus* in the presence of two well-defined series of marginal ossicles. The fusiform, accessory-bearing superomarginals are unlike the more paxilliform superomarginals of new genus A (Blake in press) and *Uranaster kinahani*, the superomarginal series not well defined in *U. kinahani*. The madreporite is ventral in *Palasteriscus* and perhaps *Lanthanaster* but not recognized in new genus A (Blake in press) and *U. kinahani*. Disk form suggests *Estoniaster* has at most few actinal ossicles, unlike new genus A (Blake in press) and *Uranaster kinahani*. Adambulacrals are nearly equidimensional in *Estoniaster* and *U. kinahani* but appear a little wider than long in *Lanthanaster* and new genus B (Blake in press) and they are very wide in the other three genera. The ventral mouth frame expression of only new genus B (Blake in press) includes shovel-like mouth angle ossicles partially enclosed by proximal adambulacrals. *Estoniaster* appears similar to *Lanthanaster* and *U. kinahani* in body whereas arms are broad in *Platanaster* and *Jurgiaster* and columnar in *Palasteriscus*. New genus B (Blake in press) has long, tapered arms.

Description; form.—Five-armed palasteriscid; disk, although collapsed, appears small but larger than juncture of arms; presence of adambulacrals with overlapping marginals indicate absence of actinals at approximate midarm position; incomplete longest preserved arm (PIN 4125/766) approx. 18 mm. Abactinal abundance suggests some arching of profile in life.

Abactinals.—Abactinals (Fig. 2A₅–A₇) small, robust, paxilliform, appearing to vary somewhat in size and form locally. Bases enlarged, faceted; column robust, crown more or less expanded. Abactinals probably aligned in series inclined to the arm axis. Primary circlet, carinals not recognized.

Madreporite.—Madreporite (Fig. 2A₁, A₅, A₆) dorsal, near marginal frame; ovate, long axis apparently radially oriented; madreporite 3.75 mm long, reconstructed width approx. 3 mm; surface sharply domed, grooving radiating from central area.

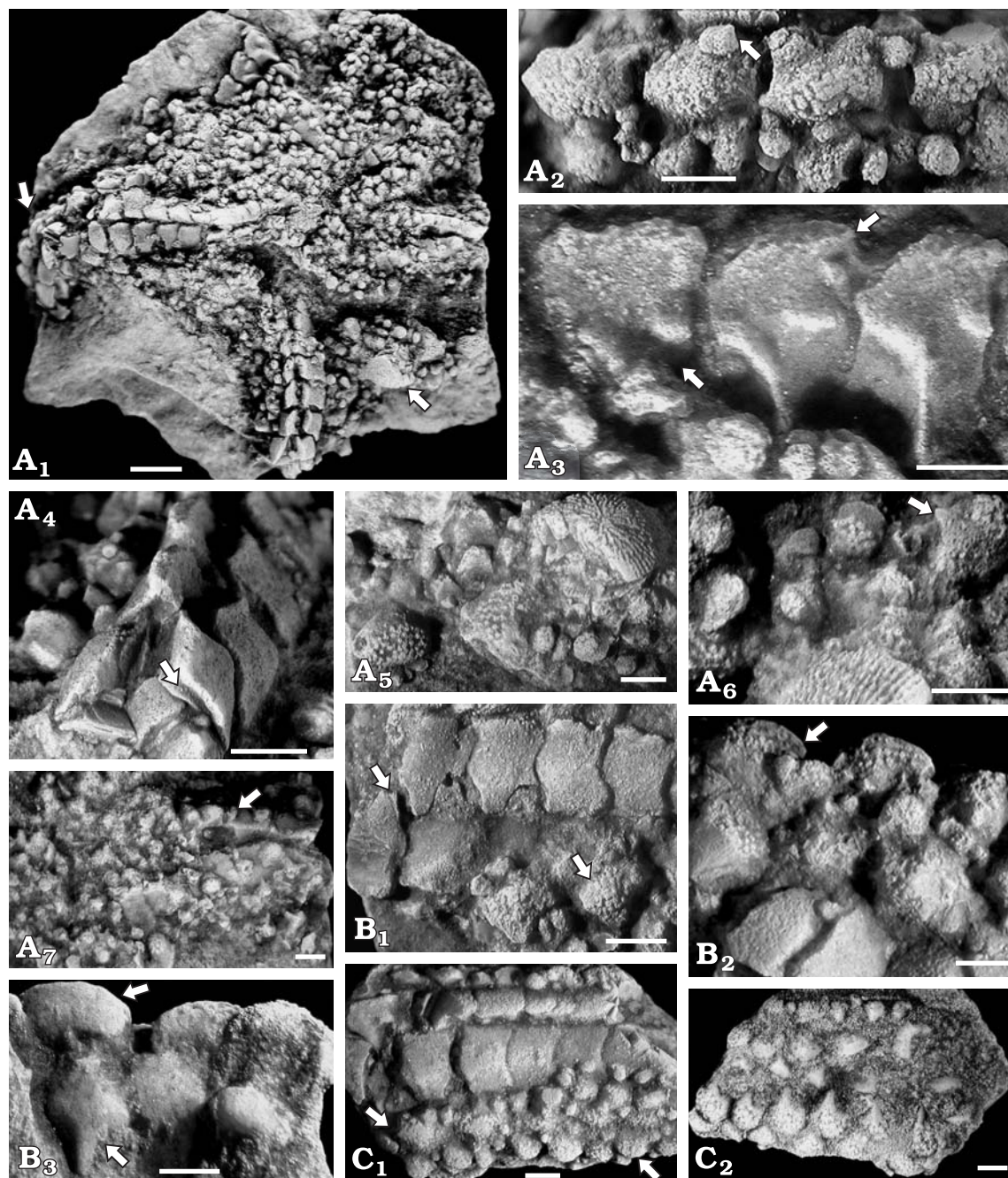


Fig. 2. Palastericid asteroid *Estoniaster maennili* gen. et sp. nov. from Keila (Upper Ordovician) of northern Estonia. **A.** PIN 4125/766; A₁, entire specimen, dorsal view; large transverse paired ossicles are ambulacrals in life orientation (i.e., vaulted); left arrow identifies position of A₂; lower right arrow indicates the madreporite; A₂, four superomarginals above, medial two with apparent spine remnants (arrow); paxilliform ossicles below SMs are intermarginals; A₃, ambulacral series located top center of A₁, left arrow points to transverse canal with the radial canal beyond, base of arrow rests in podial basin of next-distal ambulacrum; gracile cross-furrow articular structures (upper right arrow); A₄, slightly disrupted ambulacrals; contact between subsequent ambulacrals is sinuous, with transverse interambulacral articular structures (arrow); A₅, madreporite (upper right) with two superomarginals (lower left) and paxillae (lower right); A₆, paxillae, arrow points to basal flange that separates papillary? re-entrants; to the left of the arrow is a paxilla with pustules for accessory spinelets; madreporite partially illustrated below; A₇, upper surface, distal right, arrow points to right branch of ambulacrals of buccal slit. **B.** PIN 4125/767; B₁, ambulacrals (above) and adambulacrals (below), the latter pushed against the ambulacrals and offset from the paired life position; left arrow points to nose of adambulacral and adambulacral-ambulacral facet; a skeletal gap is lateral to the nose. Re-entrants of two left ambulacrals suggest podial pores, these re-entrants lacking from ambulacrals at right; right arrow points to a superomarginal; B₂, two partially exposed inferomarginals, dorsal view (arrow points to left IM); two ambulacrals below; B₃, ventral view; upper arrow is an inferomarginal, lower arrow at a nose of an adambulacral; **C.** PIN 4125/768; C₁, dorsal view, ambulacrals (above), those to left suggest podial pores, putative pores absent to right; superomarginals (left arrow), intermarginals (right arrow) with inferomarginals barely visible at lower edge, scattered paxillae above superomarginals; C₂, ventral view, inferomarginals along lower margin, adambulacrals above these with nose directed toward axial furrow. Scale bars: A₁, 3 mm; all others, 1 mm.

Marginal identification.—Marginals are poorly exposed, and the two marginal series (supero- and inferomarginal) are not exposed together. Inferomarginals are recognized based on similarities in form and position to those of other platyasteriscids. Enlarged fusiform dorsal ossicles (PIN 4125/766) are superomarginals (Fig. 2A₂, A₅, also C₁), these separated from the disk margin by smaller paxilliform ossicles, which are therefore intermarginals (Fig. 2C₁). In PIN 4125/768, the arm edge is preserved and positioning suggests ossicles of all three series.

Marginal description.—Superomarginals fusiform, elongate parallel to arm axis. Length at midarm approx. 1.5 mm, width approx. 1.0 mm. Exposed surface pustulate, arched; enlarged spines present. Lateral (i.e., adradial, abradial) margins irregularly faceted for contact with intermarginals, abactinals; distal termini sunken for articular tissues. One superomarginal preserved adjacent to madreporite appears enlarged, curvature suggests it abutted madreporite in life.

Inferomarginals (Fig. 2B₂, B₃) tabulate, thickened. IMs from approximately midarm position at least 2.75 mm in breadth, overlapped by adambulacrals; length approximately 1.5 mm. Ventral surfaces weakly arched; adradial portion of ventral face notched for overlapping adambulacrals. Abradial ossicular edge rounded; abradial portion of ossicle exposed dorsally, pustulate. Adradial portion of dorsal surface flattened where marginals abut intermarginals. Side faces ridged for intermarginal articulation. Abradial edge of ossicles pustulate but enlarged spine bases not present.

Intermarginals.—Intermarginals (Fig. 2C₁, below ambulacrals) similar to abactinals; rows few distally on arms.

Actinals.—No actinals identified; size of collapsed specimen suggests disk small and therefore at most only few actinals.

Adambulacrals.—Adambulacrals and ambulacrals paired; adambulacral width at marginals approx. 2 mm, length approx. 1.5 mm. Adambulacrals (Fig. 2B₁, B₃, C₂) rectangular, wider than long, arched, pustulate, enlarged spine bases not recognized. Adambulacral nose prominent, near-medial; ossicular curvature and ambulacral form suggest presence of skeletal gap. Abradial end of ossicle broadly rounded; ventral surface weakly arched. Dorsal surface (Fig. 2B₁) smooth, transverse profile concave.

Ambulacrals.—Ambulacrals (Fig. 2A₁, A₃, A₄, A₇, B₁, C₁) rectangular, slightly wider than long. Cross-furrow articular structures gracile; ambulacral channel broad, concave, radial canal not distinct. Transverse ridge robust, T-shaped, breached by well-developed distal groove for transverse water canal; abradial end of ridge weakly flared for contact with adambulacrals; ambulacral abutting or only weakly overlapping adambulacral (Fig. 2B₁). Podial basin broad, approximately shared between successive ambulacrals. Dorsal ambulacral outline problematic: re-entrant in few ossicles suggests podial passageway (Fig. 2B₁, C₁). Abradial end of ambulacral appears straight thus allowing space for skeletal gap adjacent to adambulacral nose, this edge only weakly recurved to partially enclose podial basin. Contact between

successive ambulacrals with abactinal edge of more proximal ambulacral weakly overlapping more distal ambulacral; contact weakly sinuous. Articular structures consisting of marginal ridge and central depression (Fig. 2A₄). Dorsal surface weakly undulating, adradial end of ossicle weakly raised, surface arched medially; abradial edge upright.

Mouth frame.—Mouth frame region obscured by debris.

Discussion.—The adambulacral and ambulacral series are displaced relative to one another in Fig. 2B₁, thereby superficially appearing offset rather than paired. The left arrow in the figure identifies the articular nose of the adambulacral, and the adjacent ambulacral has been partially pushed between the successive adambulacrals; its adambulacral articular facet now lies adjacent to the next adambulacral to the right. The prominent nose is also visible in Fig. 2C₂. Ambulacral-adambulacral positioning is not well exposed in the present specimen, but it is both well preserved and well exposed in specimens of the very similar new genus A (Blake in press).

A re-entrant present in the dorsal outline of a few ambulacrals (Fig. 2B₁, C₁) suggests a podial pore similar to those suggested in a Devonian specimen of *Promopalaeaster*? (Haude 1995). Exposure for both Haude's and the present specimen is poor. If the gaps indeed are podial in both the new species and in the *Promopalaeaster*? of Haude (1995) then transfer of ampullae to the arm interior occurred in at least two asteroid lineages. Further, podial pore presence between only some ossicles indicates that transfer did not occur in a single evolutionary step in either lineage. Finally, available specimens are sufficient to demonstrate transfer of only a few ampullae, not of all, as found in post-Paleozoic asteroids.

Suborder Uractinina Spencer and Wright, 1966

Remarks.—Spencer and Wright (1966) assigned the suborder Uractinina to the order Forcipulatida, which includes exclusively post-Paleozoic, crown-group suborders. A major extinction and rediversification event took place in asteroid evolution during the Paleozoic–Mesozoic transition (Blake 1987; Gale 1987; Blake and Hagdorn 2003); Paleozoic taxa lacking the ambulacral-adambulacral arrangement of post-Paleozoic taxa should not be assigned to crown-group orders, but widely accepted ordinal concepts for the Paleozoic fauna are not available (e.g., Shackleton 2005).

Family Urasterellidae Schuchert, 1914

= Cnemidactinidae Spencer, 1918: 155

Description.—Five-armed asteroids; disk small, formed by juncture of elongate, parallel-sided arms; interbranchial arcs angular, arms cylindrical, dorsal midline can be angular, marginals obscured by adambulacrals in ventral view. Madreporite where recognized small, dorsal.

Abactinal ossicles small, usually paxilliform; arm ossicles not radially symmetrical but rather with column near adradial edge; ossicle overlapping next (more adradial) abactinal. Where paxilliform, column expanding gradually to terminus; base more or less shield-like, flanged for papillary? reentrants,

terminus bearing spine or spinelet tuft. Abactinals can lack a column, rather bear many pustules. Arm abactinals arranged in both longitudinal and transverse intersecting rows. Carinal series at least usually present; carinal ossicular form similar to that of lateral abactinals but ossicles radially symmetrical except for lateral flanges; ossicles can be enlarged, stout, elongate, forming spine-like row; carinal series can be partially offset, forming a double series. Differentiated series lateral to carinal series present in some species. Primary circlet present, ossicles weakly enlarged, radially symmetrical, similar to carinals; more than 10 ossicles usually present in primary circlet; abactinals within circlet can be numerous, can be regularly arranged (i.e., in a ring); centrale recognized in some species. Additional disk abactinals can be present beyond circlet, these generally similar to arm abactinals.

Madreporite where recognized generally small, abutting primary circlet.

Marginals in a single series, weakly to moderately enlarged relative to abactinals, ranging from similar to abactinals to robust, rectangular, subpaxilliform; accessories similar to those of abactinals.

Single axillary at least usually if not always present; size small to large, dorsal-ventrally elongate, shield-like; typically abutting MAO frame proximally, marginal series laterally, abactinals dorsally. Actinals absent.

Adambulacrals robust to short and plate-like; wide; arched, weakly to strongly overlapping in the distal direction. Adambulacrals bearing large ventral depressions for longitudinal articular tissues, medial transverse articular facets, and dorsal depressions for articular tissues (or water vascular system storage). Outer face bearing transverse series of spine or spinelet bases, bases can be differentiated by size, form.

Ambulacrals more or less slab-like; broad, high, fairly short; paired or nearly so across furrow; dorsal surface rather flat to ridged; cross-furrow articular structures and longitudinal articular structures gracile to moderately robust; ambulacrals strongly overlapping adambulacrals; muscular facets or water vascular pocket present along ventral abradial edge. Furrow for radial canal quite narrow, transverse ridge well developed, podial pores absent, ampullar basin narrow, apparently equally shared between subsequent ossicles. Skeletal gaps absent.

Near-oral adambulacrals not abruptly differentiated in size relative to more distal ossicles; proximal adambulacrals appearing capable of forming facultative adoral carina in at least some taxa. Mouth angle ossicular pair little enlarged relative to adjacent adambulacrals; MAO pair robust, broad, keel-like, each ossicle triangular in outline, outer surfaces rounded; accessory bases, accessories similar to those of adambulacrals but probably more robust. Internal MAO anatomy poorly known but broadly similar to that of other asteroids: oral tip short, blunt; circumoral and first adambulacral articular surfaces well developed. Circumorals poorly known, probably generally little differentiated from proximal ambulacrals but can be narrow or elongate and possibly consisting of fused second and third (i.e., after MAO) ambulacrals; circumoral

cross-furrow tissue depressions well-developed. Odontophore data unavailable.

Content.—*Urasterella* McCoy, 1854; *Salteraster* Stürtz, 1893; *Cnemidactis* Spencer, 1918; *Ulrichaster* Spencer, 1950; *Stiberaster* Blake and Guensburg, 1993.

Discussion.—An apomorphy-based diagnosis of the Urasterellidae is not attempted here because of the still-tentative nature of the systematics of Paleozoic asteroids. Spencer and Wright (1966) recognized many Paleozoic families differentiated on comparatively few characters. Shackleton (2005) treated the Urasterellidae and the Palasteriscidae as subfamilies of the Palasteriscidae Gregory, 1900. This author's diagnosis (Shackleton 2005: 97) of the Urasterellinae included positioning of the inferomarginals and cross-sectional shape of the ambulacrals as well as character loss based on cladistic analysis. More extended description is provided here because the still incompletely understood early asterozoan fauna suggests continuing revisionary work can be expected.

Genus *Cnemidactis* Spencer, 1918

Type species: *Cnemidactis girvanensis* (Schuchert, 1914); Upper Ordovician, Girvan, Scotland.

Cnemidactis sp.

Fig. 3.

Geological horizon: Middle Ordovician (upper part of the Volkhov regional stage or the lower part of the Kunda regional stage, Upper Arenig).

Material.—PIN 4125/769 No disk elements are available. Arm fragment 31 mm in length, 7 mm in breadth proximally, 5 mm in breadth distally, exposed in ventral view. A slightly shorter fragment of a more distal? arm interval is adjacent to the larger fragment. The ventral surface of the second fragment is also exposed. Preservation is quite good, but only ambulacrals, adambulacrals, and a single series of apparent marginals immediately adjacent to the adambulacrals are exposed. Ossicular form indicates a single species and size and close positioning suggest but do not prove a single individual. Specimens were collected at an abandoned limestone quarry located on the left side of the Volkhov River to the south of the village of Izvoz, northwestern Russia (St-Petersburg region). In this quarry, a clay limestone spans the upper part of the Volkhov regional stage and the lower part of the Kunda regional stage, both Upper Arenig; scattered ossicles have been found only in the Upper Volkhov portion of the interval, and it is likely the more complete fragments were collected from this portion of the section as well.

Description.—Arms elongate, cylindrical; disk unknown.

Abactinals, marginals.—Marginals in a single series (Fig. 3B, F, G), these above and abutting adambulacrals. Ossicles dorsal to enlarged marginals disrupted but not enlarged nor differentiated as to suggest a second marginal series. Marginals alternate with adambulacrals, resting in re-entrants formed by successive adambulacrals. Marginals approximately 2 mm in breadth. Marginals robust, closely abutted, paxilliform; column short, base robust, angular, sides of bases extend between

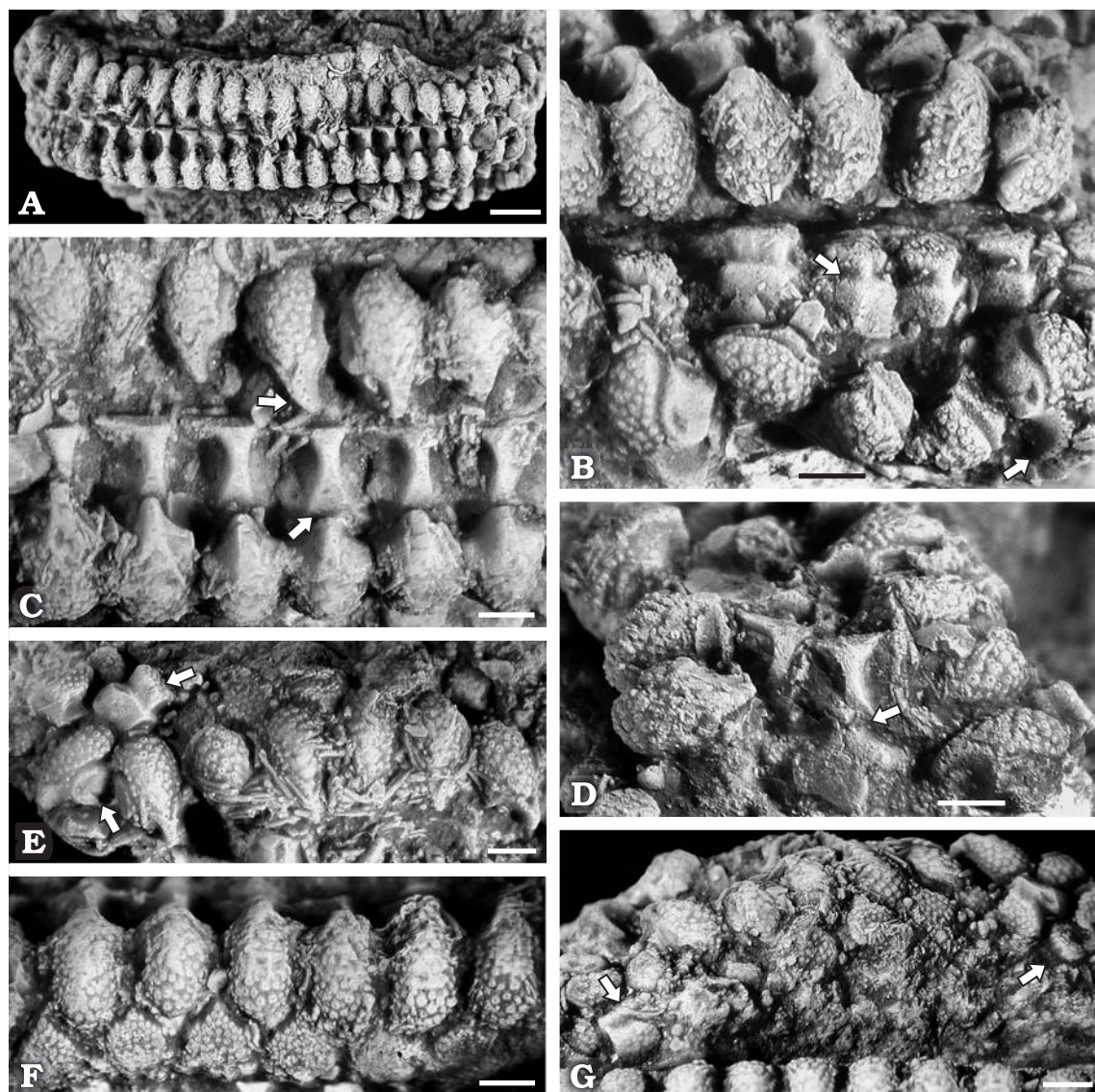


Fig. 3. Urasterellid asteroid *Cnemidactis* sp., PIN 4125/769, Middle Ordovician, Volkov, Russia. **A.** Entire specimen, ventral view. **B.** Lower right portion of A, rotated; adambulacral series at top with nose directed upward and overlapping ambulacra; taphonomically displaced marginal series in middle showing lateral facets (below), central waist (upper arrow), and crown. Adambulacra of the second fragment are below, scale is to right of an adambulacral nose, lower arrow points to nose of rotated adambulacral; robust interadambulacral articular surfaces at lower left. **C.** Right portion of A; ambulacra medial, series of spine pustules on nose of adambulacra (upper arrow), two spines have fallen into the basin below the arrow; triangular articular surface of ambulacral (lower arrow) is equivalent to that illustrated by Spencer (1918; Fig. 6A herein), articular flanges also visible on adjacent ambulacra. **D.** Displaced ambulacra medially, with adambulacra; triangular articular surface on ambulacral (arrow). **E.** Marginal in lateral view (upper arrow), and adambulacral series, the lower arrow at inter-adambulacral articular surfaces. **F.** Adambulacral series above, marginal series below, these fitted between successive adambulacra, the relationship indicating *Cnemidactis*. **G.** Ossicles from second fragment, lower center of A; series of disrupted marginals (arrows), abactinals below right marginal. Adambulacra are above marginals; edge of adambulacral series of primary fragment is below. Scale bars: A, 3 mm; all others, 1 mm.

adambulacra, sides flattened forming angular ossicular margin. Exposed surface of marginals flat to weakly convex, closely pustulate. Spinelets small, fine, uniform, cylindrical, scattered along adambulacral-marginal boundary, spinelets might be derived from either or both ossicular types. Two incompletely exposed ossicles similar to but smaller than marginals appear to be abactinals (Fig. 3G).

Ambulacra.—Ambulacral (Fig. 3A, C, D) ossicles nearly paired across arm axis; local offset might be taphonomic. Ambulacra approximately square in outline; longitudinal

canal deep, consisting of narrow axial canal bordered by a sloping surface formed by adradial margin of transverse ridge. Transverse ridge sharp, J-shaped, adradial flange (the base of the “J”) robust, transverse canal crosses ridge distally. Podial basin broad, complete, no indication of podial pore; contact between successive ossicles sinuous, approximately medial in basin, abradial flange of more distal basin extending over distal rim of the more proximal basin. Abradial end of ambulacral weakly overlaps adambulacral. Abactinal surface of the ambulacra unknown.

Adambulacrals.—Twenty-one adambulacrals (Fig. 3A–G) present along 31 mm fragment; ossicular width approx. 3.5 mm. Adambulacrals upright in arm, wide, approximately rectangular in outline, abradial margin rounded; nose prominent, abutting abradial base of ambulacral. Sides of nose rounded, forming podial walls. Outer face weakly arched, with numerous similar, closely spaced pustules; pustules along proximal, distal margins of adambulacrals slightly smaller than uniform pustules over remainder of surface. Actinal surface of nose massive, pustules not clearly developed. Ossicular side faces (Fig. 3E) with elliptical inter-adambulacral articulation surfaces consisting of a marginal rim enclosing a depressed surface. Fine spinelets remain near adambulacrals, marginals.

Other ossicular types not exposed.

Remarks.—Assignment to *Cnemidactis* is based on presence of interdigitated adambulacrals and marginals, the marginals quite robust rather than truly paxilliform, and the presence of a uniform series of small spine bases on both ossicular types (Spencer 1918). The comparatively small marginals of *Cnemidactis* sp. are unlike those of the type (Spencer 1918: pl. 13: 2) but perhaps suggestive of those of *C. osloensis* Hansen, Bruton, and Jacobsen, 2005; because of absence of data on the mouth frame of the present specimen, no species assignment is made. Another occurrence of *Cnemidactis* is cited by Blake and Guensburg (1993).

Urasterella McCoy, 1854

= *Roemeraster* Stürtz, 1886

= *Phillipsaster* Spencer, 1950

Type species: *Uraster ruthveni* Forbes, 1848, Upper Silurian, England.

Diagnosis.—Urasterellid with generally small, paxilliform abactinals; carinal series, primary circlet differentiated but generally weakly so (where dorsal surface is known). Marginals in a single series, similar but not identical in number to adjacent abactinals and adambulacrals; marginals paxilliform, ranging among species from little differentiated from abactinals to robust; lateral edges of marginals not closely fitted between adambulacrals; accessories present. Axillary small (where recognized), extended to MAO. Adambulacrals thin to quite robust; upright, overlapping distally; adambulacral spines robust. Disk appearing to be able to contract to allow proximal adambulacrals to form facultative adoral carina; mouth angle ossicles little enlarged; torus small.

Remarks.—Publication data for *Urasterella* are variously given in the literature; data here taken from a copy in the library at the University of Illinois, Urbana-Champaign. McCoy (1854: 59) noted that the name *Urasterella* existed earlier but in manuscript form.

Because of a meager fossil record and the poor preservation of the type material of most recognized species, generic concepts within the Urasterellidae, including that of *Urasterella*, are difficult. Useful sources for *Urasterella* include Schuchert (1914, 1915), Spencer (1918, 1950), Spencer and Wright (1966), and Shackleton (2005). Among proposed

Urasterella-like genera, *Roemeraster* Stürtz, 1886, is Devonian, the remainder are Ordovician. Schuchert (1914, 1915) synonymized *Roemeraster* and *Salteraster* with *Urasterella*; Spencer and Wright (1966) retained *Salteraster* as well as *Phillipsaster* Spencer, 1950, and *Ulrichaster*. Separation of genera made use of presence of a well-defined carinal series in *Salteraster* and a double series in *Ulrichaster* as well as size and form of the dorsal surface of the arm. Shackleton (2005) was unable to obtain data on the midarm of *Urasterella ruthveni* Forbes, 1848, the type species, and she synonymized *Salteraster*, *Phillipsaster*, and *Ulrichaster* with *Urasterella* in part because of lack of information on the dorsal surface; other presumed generic differences were attributed to taphonomic effects.

A cast of a type of *U. ruthveni*, SM A-5497a, the type species, was available. The specimen shows the ventral surface with abradial edges of the abactinal series. This specimen, and others representing other species, suggest the presence of facultative adoral carina, this based on subtle differences in ossicular positioning around the mouth frame. Spencer (1918) concluded that superomarginals are not present in *Urasterella*, although these were recognized by Schuchert (1915); superomarginals were not identified in any of the specimens available to DBB.

Although *Salteraster* was separated largely based on presence of a carinal series, Shackleton (2005) found presence of such a series to be equivocal in the type species, *S. asperrimus* (Salter, 1857). Casts of the type were available to DBB, who believes the carinal series can be recognized. Abactinal ossicles of specimens of *Urasterella* available for the current study each overlap the next abactinal toward the arm midline. The arrangement would appear to all but dictate some form of differentiation of arm midline ossicles, the midline functionally analogous to a ridgepole in a gable roof. Spencer and Wright (1966) characterize *Urasterella* as having flat arms, which appears to be true of specimens of *U. ruthveni* illustrated by Spencer (1918: pl. 9). Flat arms would seem to lessen the need for a ridgepole; nevertheless, a carinal series appears to be present. Illustration of the type species of *Salteraster* appears to have an adoral carina (Spencer and Wright 1966: fig. 64.4b) although this specimen is sharply distorted in a manner that might have squeezed the ossicles together. To the extent discerned on the poorly preserved specimens, morphology of ossicular systems is quite similar but both genera are tentatively retained here based on Spencer and Wright's conclusion that the arms are comparatively flat, and presumably few rows of abactinals between the carinals and the marginals in the type species of *U. ruthveni*.

The types of *Ulrichaster ulrichi* (Schuchert, 1915) were available, and although the ventral surface is unavailable except in a small specimen assigned to the species by Schuchert (1915), carinals are slightly enlarged, radially symmetrical, and developed in an offset series that appears to be original rather than taphonomic; a double series would appear to be a rather minor variant of the ridgepole specialization, but it is distinctive, and therefore this genus is also retained here.

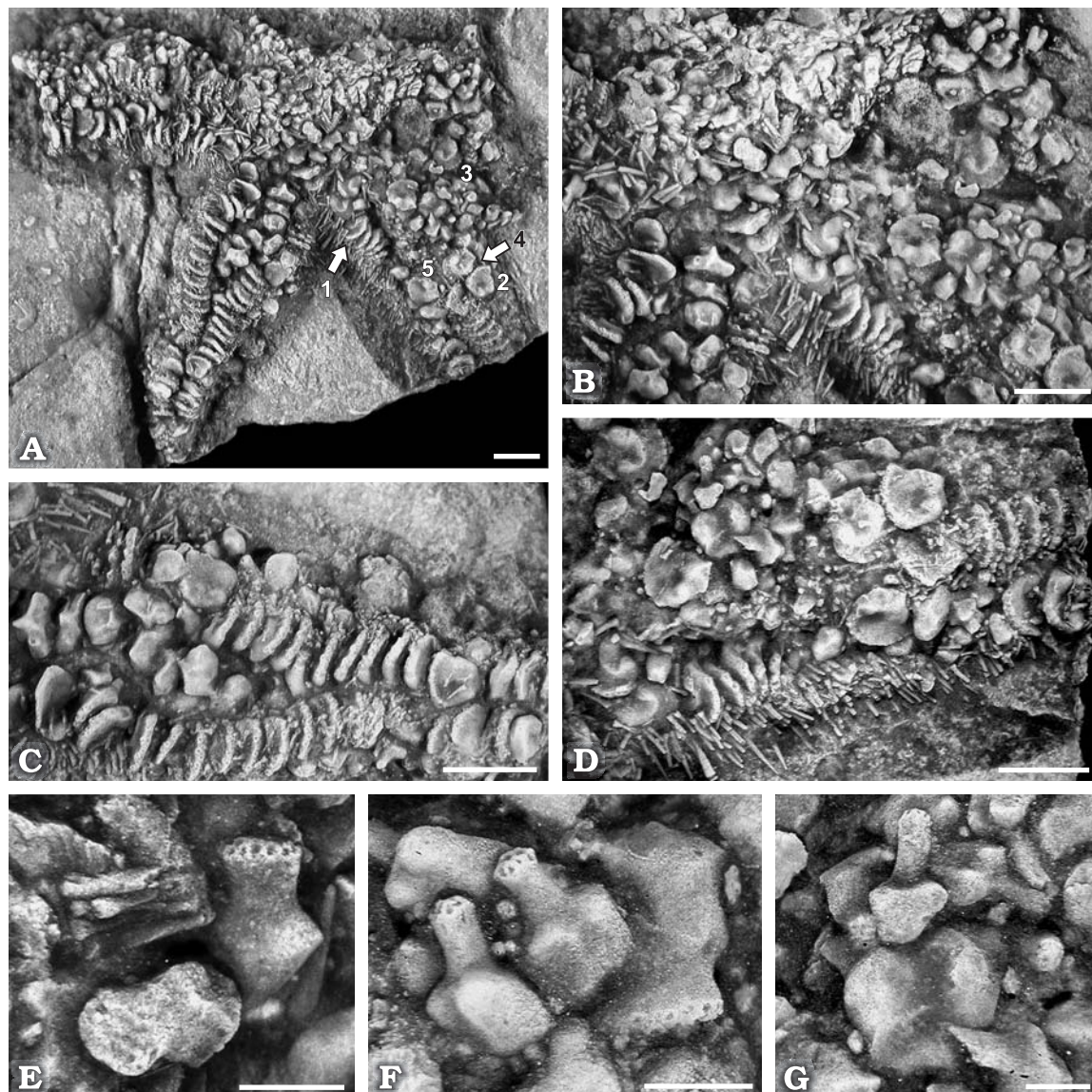


Fig. 4. *Urasterella?* sp., PIN 4125/770, Middle Ordovician, Volkov, Russia. **A.** Entire specimen, ventral view; numbers identify ossicles of Fig. 5C. **B.** Disk region oriented as A, many displaced adambulacrals, spines above and to the left of the scale bar. **C.** Lower left arm of A, disk, interbranchial angle to left. **D.** Lower right arm of A, disk to left. **E.** Two abactinals, lateral view; crowns showing accessory depressions. **F.** Two abactinals to left, abactinal or possible inferomarginal to right. **G.** Two abactinals, above, adambulacrals below; ossicles toward upper left of same approximate orientation as in D. Scale bars: A–D, 3 mm; E–G, 1 mm.

Spencer (1918) separated *Cnemidactis* based largely on the nature of accessories, form of the marginals and adambulacrals, the relationships between these two ossicles, and presence of a large torus. The cladistic analysis of Shackleton (2005) placed *Cnemidactis* adjacent to *Urasterella*, and she assigned the genus to the Urasterellinae. Shackleton (2005) recognized *Stiberaster* as the sister group to her Palasteriscinae plus Urasterellinae, and it is here assigned to the Urasterellidae.

Urasterella? sp.

Figs. 4, 5C.

Material.—PIN 4125/770. A single specimen exposed in ventral view, consisting of one complete arm and the disk with the

remaining four arms more or less incomplete. The specimen is collapsed and partially dissociated. Disk center to arm tip = 23 mm, collapsed disk radius about 5 mm. Specimens collected at the same quarry and horizon as *Cnemidactis* sp.

Description.—Five-armed asteroid; arms probably long, slender; disk small.

Abactinals and marginals.—Few lateral and dorsal ossicles are exposed; these broadly paxilliform, bases robust, columns distinct, columns expanding toward their tip, tips with deep apparent accessory pits (Fig. 4E–G); no accessories exposed. Paxilliform ossicles closest to adambulacrals with bases enlarged relative to those of adjacent abactinals, therefore those adjacent to adambulacrals probably are marginals.

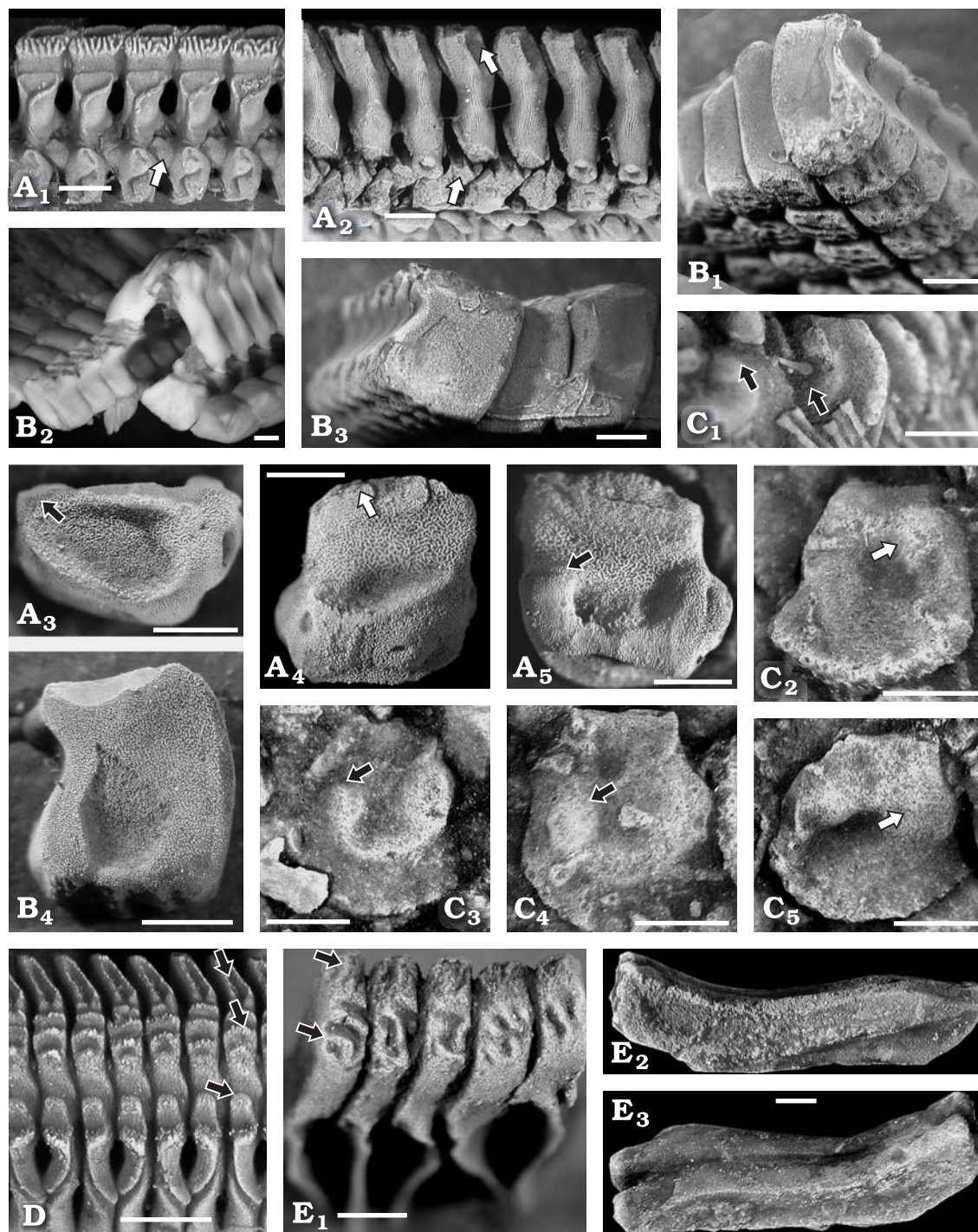


Fig. 5. Ambulacral series details in Ordovician and extant asteroids, see text for further discussion. **A.** Family Echinasteridae, *Echinaster* sp., extant, Florida (USA), scale bars A_1 , A_2 , 1 mm; A_3 – A_5 , 0.5 mm. A_1 , furrow view of ambulacrals and adambulacrals, proximal right; adambulacrals are angled (arrow) in the distal direction; cross-furrow tissue grooves (at top) overlie vertical articular plates and grooves, which in turn overlie flattened, ovate, lower cross-furrow tissue grooves; A_2 , inclined dorsal view of ambulacrals and adambulacrals, proximal left, longitudinal tissue groove (upper arrow) and angled adambulacrals (lower arrow); A_3 , proximal view of a right adambulacral, furrow right (see A_1); view direction approximately corresponding to C_1 , except the latter is rotated to the horizontal; black arrow identifies corresponding horizontal U-shaped contact bars in A_3 , A_5 , C_1 , C_3 , C_4 ; A_4 , ventral-distal view, white arrow identifies corresponding interadambulacral contact facets above muscle depression in A_4 , C_2 , C_5 ; A_5 , dorsal-proximal view of adambulacral. **B.** Family Goniasteridae, *Peltaster placenta* Verrill, 1899, Atlantic Ocean, extant, scale bars, 1 mm. B_1 , inclined ventral-distal furrow view of adambulacrals and adjacent actinal ossicles showing closely abutted adambulacrals with broad, flat interadambulacral contact surfaces in an extant asteroid; B_2 , inclined proximal-dorsal view of ambulacral series with vaulted ambulacrals, compare A_1 , A_4 , C_1 ; B_3 , proximal view, adambulacral to left, compare to B_4 , with tightly abutted actinal ossicles to right; B_4 , distal view of adambulacral, furrow left; large, flat abutment surface encloses tissue depression. **C.** Family Urasterellidae, *Urasterella?* sp., Ordovician, Russia, PIN 4125/770, scale bars, 1 mm; C_1 , proximal view, ventral right, of adambulacral series with interadambulacral bar (arrow), approximately corresponding to that of *Echinaster* sp., A_3 ; C_2 , C_5 , distal views corresponding to A_4 ; C_3 , C_4 , proximal views →

Adambulacrals.—Adambulacrals (Fig. 4A–D) coin-like, large, approximately eight ossicles in 5 mm interval, width approximately 2 mm. Adambulacrals wide, overall profile convex, abactinal margin arched distally. Medial proximal-face articular ridge U-shaped, separating interadambulacral articular surfaces below from adambulacral-ambulacral surfaces above. Distal face concave with prominent articular facets near abactinal abradial and adradial corners. Outer face narrow, bearing an irregular series of ten or more ring-like pustules of uniform morphology, these varying in size. Many spines preserved near adambulacrals, these robust, pointed, cylindrical to slightly flattened, of varying length but with no clear indication of any differentiation (e.g., bimodality).

Ambulacrals, other ossicular types.—No other ossicular type can be identified with certainty.

Remarks.—The fossil is incompletely preserved and exposed, but overall form and the form of the marginals and adambulacrals are in accord with those of *Urasterella*; both adambulacrals and marginals appear broadly similar to those of *U. grandis* and *U. pulchella* (Billings, 1857). The rather delicate adambulacrals of *Urasterella?* sp. are unlike those of *U. ruthveni*, *U. thraivensis* Spencer, 1918, *Cnemidactis*, *Salteraster*, and *Stiberaster*. *Ulrichaster* shares abactinals of broadly similar size and form, and adambulacrals of a small syntype (USNM 60612B) suggest a similar form, but ventral characters of a larger specimen are unavailable for this genus, and the dorsal surface is unavailable in the fossil.

Arm flexibility in Ordovician asteroids

Background.—Asteroids today are abundant in a wide variety of marine benthic environments and over a broad range of depths. Most are epifaunal on both soft and firm substrates, although some are infaunal. Dietary habits are varied but many are voracious predators (Jangoux 1982). The limited fossil record suggests taphonomic constraint rather than geologically recent diversification; it is likely that asteroids were significant and diverse in ancient communities. Understanding of community evolution requires delineation, as possible, of changes in ecologic roles through time of these important organisms.

In recent years, some debate has accompanied interpretation of arm flexibility of early asteroids, and arm flexibility bears on ecologic potential. Schuchert (1915) included *Urasterella* among the “Cryptozonia” (i.e., asteroids with re-

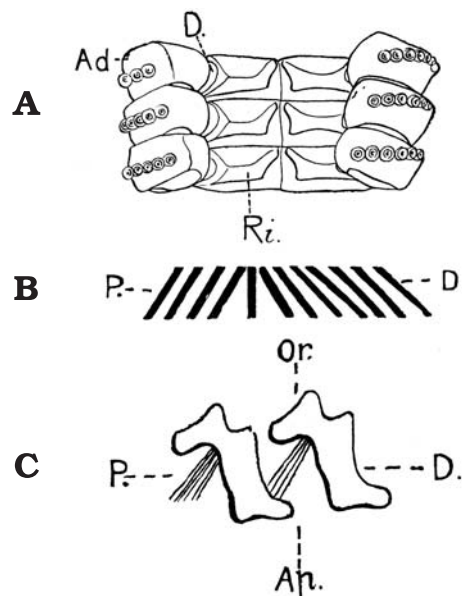


Fig. 6. Original illustration of *Urasterella thraivensis*; figures 83–85 from Spencer (1918) reproduced courtesy *Palaeontographical Society* illustrating ambulacral details. **A.** Ambulacrals and adambulacrals. **B.** Diagram of adambulacrals in lateral view. Spencer (1918) thought adambulacral orientation changed along the length of the arm. **C.** Spencer (1918) reconstructed inclined muscle strands between adambulacrals, see text. Abbreviations: Ad, adambulacrals; Ap, apical (dorsal in usage here) surface; D (on A), depression for muscle between ambulacral and adambulacral; D (on B and C), distal; P, proximal; Or, oral surface; Ri, transverse ridge separating successive podial basins.

duced marginals); he thought that cryptozonians had multiple phanerozonian (i.e., asteroids with enlarged marginals) sources, and that “even greater flexibility appears to be the main stimulus” (Schuchert 1915: 32) for cryptozonian evolution. Spencer (1918: 127) argued that arm length and ambulacral articulation structure suggested “a wriggling form of life” for *Urasterella*. This author interpreted a depression on the ambulacral as indicating presence of a muscle linking the ambulacral with its paired adambulacral, and he reconstructed longitudinal musculature extending between successive adambulacrals (Fig. 6). Fell (1963) envisioned the phylogenetic transition from somasteroids to asteroids as including a transition from a facultatively erect ambulacral furrow to one that is permanently erect. Although he does not explicitly state that early asteroid arms were flexible, it is the view of the writers that such an interpretation is implicit in his treatment. Spencer and Wright (1966: U25) noted existence of a specimen of *Salteraster* (variously interpreted as a synonym of *Urasterella*) in the feeding position of the Aste-

corresponding to A₅. **D.** Family Asteriidae, *Asterias* sp., scale bar, 1 mm, extant, north Atlantic Ocean, furrow view of ambulacral series, proximal left; upper arrow identifies corresponding superior cross-furrow tissue depressions in both *Asterias* and *Promopalaeaster* (E₁); second arrow in both identifies cross-furrow articular facets and grooves. Lowest arrow identifies inferior cross-furrow tissue facet; corresponding surfaces in *Promopalaeaster* are broad enough to support tissues but no facet is clearly differentiated. Dark semi-elliptical areas below are for podia; compare A₁. **E.** Family Promopalaeasteridae, *Promopalaeaster*, Ordovician, eastern United States, UI X-6461, scale bars, 1 mm. E₁, furrow view, arrows correspond to those in D; E₂ and E₃, opposite sides of two ambulacrals, partial dorsal views, both surfaces depressed (for tissues?) and rimmed; also contact surfaces; E₂, furrow left, proximal? view, podial basin is triangular area to lower right; E₃, furrow right, inclined abactinal distal? view.

riidae Gray, 1840, an interpretation that demonstrates that these authors accepted presence of arm mobility as well as a complicated predatory capability on a par with that found among living asteroids. Spencer and Wright (1966) further appear to suggest similarity of behavior in assigning all Paleozoic asteroids, including those of the Ordovician, to diverse extant ordinal groups.

In contrast, Gale (1987: 129) argued "All known Lower Palaeozoic asteroids lacked musculature between the ambulacral groove ossicles, and thus were rather inflexible animals, incapable of complex arm movements." He concluded that these asteroids lived on unconsolidated substrates, feeding by swallowing sediment using the proximal tube feet. Shackleton (2005) reaffirmed the conclusions of Gale (1987), finding the skeleton of early asteroids to be "brick-like" and "amuscular" (Shackleton 2005: 60). For Ordovician asteroids, she further added that "Life position was dominantly epifaunal on soft substrates, in relatively calm conditions."

New Ordovician fossils and extant analogies.—Partially dissociated fossilized asteroids such as those reported here can expose internal details unavailable among more intact specimens, and internal details can be profitably compared to those of extant equivalents. Arrangement of ambulacral furrow ossicles is complex in all asteroids. Each adambulacral is linked to lateral (abradial) ossicles (e.g., marginals, actinals), and in almost all known Paleozoic asteroids, each adambulacral is paired with and abuts a single ambulacral (Fig. 3C) whereas in all known post-Paleozoic asteroids, the arrangement is offset such that a single ambulacral abuts a pair of adambulacrals (Fig. 5A₁, A₂). Adambulacral ossicular form among species ranges from strongly arched and overlapping to nearly upright in the furrow. Interpretation is further complicated by orientation changes during life activities and preservation in varying attitudes. These complexities are only partially illustrated and described in photographic material here.

In summary, corresponding articular structures can be recognized in ambulacral-furrow ossicles of all ages, and correspondence is particularly striking for the adambulacrals. In both ancient and extant species, prominent transverse articular facets mark the contact between successive adambulacral ossicles (Fig. 5A–C); these facets lie dorsal to depressions for longitudinal tissues (presumably muscles) and ventral to linkages between ambulacrals and adambulacrals. In specimens treated here, these linkages are most clearly developed in *Urasterella* sp., and they can also be clearly seen in adambulacral ossicles illustrated by Kutscher (2004: fig. 1A, B). Adambulacrals and ambulacrals of *Cnemidactis* sp. are similar in shape to those illustrated by Spencer (Fig. 6A), and they have apparent muscle depressions (Fig. 3C) similar to those recognized by this author. Ambulacrals are not exposed in the present specimen of *Urasterella*? sp.

Spencer (1918: 159) noted the "tight firmly-fitting ambulacralia almost give one the impression of bricks set in mortar" in his *Cnemidactis*, and he later concluded about the genus (Spencer 1918: 162): "the closely set ambulacralia, suggest that the arm had but little power of lateral or vertical

movement"; yet he also noted without comment (Spencer 1918: 158) that "displaced adambulacralia show ... concavities for the insertion of the interambulacral muscles"; muscles that must be articular. Not only the adambulacral articular sites, but also overlapping ambulacral flanges can be seen on the present specimen (Fig. 3B–E). Presence of articular structures in *Cnemidactis* and its basic similarity to *Urasterella* indicate mobility in spite of the apparent ability of the former genus to contract (as indicated by Spencer 1918), perhaps under the duress of the death event.

Broad, flat contact surfaces as well as enlarged medial muscle depressions are found among extant asteroids (e.g., *Peltaster placenta* Verrill, 1899: fig. 5B). *Peltaster*, with a large disk and broad arms, presumably lacks the flexibility found in asteroids with slender arms; however, this genus shows that abutted, even brick-like ossicular surfaces are not per se demonstrators of inflexibility.

Spencer (1918) reconstructed interambulacral muscles (Fig. 6C) and ambulacral-adambulacral muscle facets (Fig. 6A) in a species of *Urasterella*. He suggested that adambulacral orientation changed along the length of the arm of *Urasterella* (Fig. 6B); the writers have seen no specimen that supports the Fig. 6B reconstruction, and we find orientation change to be unlikely given requisite ontogenetic changes and functional shifts such reorientation would require. Perhaps the Spencer (1918) reconstruction derives from differential taphonomic displacement of ossicles such as that illustrated here (Fig. 4A). Spencer's (1918) interpretation, if correct, would only add to overall complexity of early asteroid motion and function, hence his reconstruction does not challenge the thrust of interpretations here.

Promopalaeaster Schuchert, 1914 (Late Ordovician) further documents diversity among Ordovician asteroids. In *Promopalaeaster*, ambulacral articular cross-furrow plates and superior muscle grooves are robust (Fig. 5E₁) and similar to those of extant *Asterias* Linnaeus, 1758 (Fig. 5D). *Echinaster* Müller and Troschel, 1840 (Fig. 5A₁) and *Asterias* sp. exhibit attachment points for inferior muscles; although a broad inferior surface is present in *Promopalaeaster*, muscle attachment points are at most subtle. Some form of opposing musculature must have existed (otherwise, the furrow once open would have been fixed), and the fact that attachment is not obvious exemplifies the difficulties encountered in interpreting function in ancient asteroids. Sides of ambulacrals of *Promopalaeaster* are rounded and grooved for flexure (Fig. 5E₂, E₃) with subtle facets and tissue? depressions.

In *Promopalaeaster*, ambulacral superior cross-furrow muscle surfaces as well as articular surfaces of the adambulacrals consist of ridges and grooves, as opposed to the rather featureless pits typical of extant asteroids (Fig. 5D, E₁, upper arrow). Significance of these differences is not known, but functional nuance is suggested.

Discussion.—The first recorded phase of asteroid evolution took place during Ordovician times, with faunal associates and in ecologic settings (e.g., Vermeij 1987) that were different from those pervasive during the radiation of the crown

group. With these important potential constraints in mind, it is argued here that range of body flexibility among early asteroids was comparable to that seen within the extant fauna. This conclusion, supported by the arguments below, is in accord with views of earlier authors and in contrast with more recent suggestions of Gale (1987) and of Shackleton (2005).

(1) The same ossicular systems with the same essential articular arrangements and patterns of ossicular addition are found in Ordovician and extant asteroids; to argue that lower Paleozoic asteroids lacked musculature between the ambulacral series ossicles or that arms were amuscular is to argue that natural selection first evolved a basic skeletal arrangement, then devised articular tissues to put the skeletal arrangement into motion. We find this supposition to be implausible.

(2) Adambulacral ossicle articular arrangements are remarkably similar between Ordovician and extant asteroids (Fig. 5), but many (not all, e.g., Fig. 5E) Ordovician ambulacral articular structures are gracile as compared to those of extant species. In all known post-Paleozoic species, passageways between ambulacrals locate the ampullae in the interior of the arm, above the ambulacrals (e.g., Fig. 5A₁), whereas in almost all Paleozoic species, podia and any ampullae were restricted to external basins (e.g., Fig. 2A₁, B₁, C₁). The water vascular system is intimately associated with ambulacral ossicles but only peripherally so with the adambulacrals; it is reasonable that ambulacral morphology and articular arrangements would be more strongly affected than those of the adambulacrals by retreat of ampullae to the arm interior. Space and functional demands of external positioning logically affects furrow closure and other aspects of arm motion, but it does not dictate inflexibility.

Possible partial transfer of ampullae to the arm interior, tentatively suggested here for *Estoniaster* and by Haude (1995) for *Promopalaeaster*, hints at the functional value of ampullar positioning. Blake (2000) interpreted other aspects of positioning.

(3) *Promopalaeaster* is of particular interest because of an Ordovician specimen of this genus discovered wrapped about a bivalve in the feeding posture typical of extant asteroiids (Blake and Guensburg 1994). Not only did the *Promopalaeaster* assume this complicated feeding posture, but it is also asteroiid-like in many aspects of morphology, leading Branstrator (1975) to assign it to an extant suborder. The fossil occurrence demonstrates complex behavior attained by asteroids early in their history. Although both Gale and Donovan (1992) and Shackleton (2005) were skeptical of the significance of this specimen, they offer no alternative explanation for its genesis; indeed the specimen led Donovan (1999: 589) to conclude that it provides “near-irrevocable support for the views of Blake and Guensburg.”

Promopalaeaster ranges into the Devonian (Haude 1995); other genera similar in overall form and general articular arrangement and therefore perhaps life modes include Devonian *Jaekelaster*, Stürtz, 1899, and Carboniferous *Compsaster* Worthen and Miller, 1883.

Spencer and Wright (1966: U25–U26) also reported a specimen of *Salteraster* in a position indicating active predatory behavior. Shackleton (2005) assigned *Promopalaeaster* and *Urasterella* (includes *Salteraster* in her usage) to well-separated positions within asteroids, the former to a near-basal plesion, the latter to a relatively derived position within her Palasteriscidae. If Shackleton’s phylogenetic hypothesis is accepted and Spencer and Wright (1966) are correct in their interpretation of their *Salteraster* specimen, then active, predatory behavior must be near-basal in asteroid diversification, and this behavior has endured.

(4) An analysis of the functional significance of the ambulacral furrow in *Echinaster* by O’Neil (1990) provides a free-standing (i.e., independent of other lines of consideration) argument in favor of arm flexibility in all asteroids; and further, that arm flexibility, as a function, originated with the class Asteroidea because furrow presence, as a morphological expression, is a recognized apomorphy of the class Asteroidea. Both *Promopalaeaster* and *Urasterella* are similar to *Echinaster* in overall arrangement, sharing a small disk, long, cylindrical arms with an ambulacral furrow, and a skeleton of comparatively small, similar ossicles. O’Neil (1990: 149) pointed out that “There is no a priori reason why a starfish should have an ambulacral groove” and that instead a cylindrical arm would allow greater volume for soft organ systems. O’Neil (1990) argued that although organisms generally avoid torsional stress, experimental approaches in *Echinaster* demonstrated that presence of an ambulacral furrow reduces resistance to stress relative to a corresponding cylindrical construction by approximately two orders of magnitude; further, ossicles are placed as to minimize torsional stiffness. She concluded that a major function of the ambulacral groove “is the reduction of torsional stiffness of the ray” (O’Neil 1990: 149), which allows flexibility.

Torsional stiffness based on cylindrical arms would be desirable if early asteroid organization sought rigidity, yet presence of an ambulacral furrow is an asteroid apomorphy (Spencer and Wright 1966; Blake 2000; Shackleton 2005). Regardless of articular faceting, the arguments of O’Neil indicate that furrow presence onto itself indicates flexibility, with all its functional implications. This flexibility is a basal, class-level property.

(5) Gale and Donovan (1992) and Shackleton (2005) suggested that asteroids were inhabitants of relatively quiescent environments. Higher energy environments are not conducive to asteroid preservation and therefore the argument relies in part on negative evidence. Nevertheless, Kolata (1973: 54) reported a fairly large asteroid from the Guttenberg Formation “on the crest of a megaripple in dolomitized biocalcarenite.” The surface extended over many tens of square meters (personal observation of DBB) and the specimen is not altered as to suggest transport. Guensburg (1992) reconstructed a urasterellid in a hardground habitat; the asteroid is associated with a diverse fauna that included stemmed, suspension-feeding echinoderms. The environment was interpreted as a storm-dominated cratonic platform with paleodepths as subtidal but

averaging only a few meters. This author's environmental interpretations were based on sedimentary structures and presence of both coarse lithologies and abundant calcareous algae. These two occurrences demonstrate that Ordovician asteroids were not restricted to quiet settings; early asteroid organization included articular specializations adequate to deal with these active environments.

(6) The notion of evolutionary escalation through time (Vermeij 1987) is useful in interpreting asteroids both as predators and prey (Blake 1983, 1990; Aronson and Blake 2001). Refinement of articular arrangements through time might reflect no more than evolutionary escalation, but it need not begin with an absence of mobility.

(7) Similarly, demands associated with increased bioturbation and substrate instability in the Mesozoic could have stimulated refinement of existing articular structures.

(8) Taphonomic constraints are important in comparing articular structures through time. Asterozoans have a meager fossil record, and the skeletally robust are inevitably more likely to endure. For example, the unique Early Devonian asteroid fauna of the German Hunsrück Slate (Lehmann 1957) is dominated by large, comparatively delicate species whereas robust, small asteroids are found in the stratigraphically adjacent sandy facies (e.g., Schöndorf 1910). The Hunsrück fauna is post-Ordovician and therefore its applicability to Ordovician diversity could be debated, nevertheless the large and delicate Hunsrück asteroids indicate the uncertainty encountered in relying on negative evidence. Finally, for taphonomic reasons, many better preserved asterozoan fossils are found in fine clastic sediments, which, during compaction, are squeezed together, closing and obscuring articular details.

Conclusions

Behavior of ancient asteroids is difficult to determine. As is true of other organisms, few specifics of morphology are correlated with single behavioral traits. Ordovician and extant ecosystems placed and place different constraints on all groups of organisms. For taphonomic reasons, the fossil record of asteroids is scanty and biased.

Nevertheless, skeletons of early asteroids have not been demonstrated to be brick-like and amuscular and therefore incapable of complex arm movements; instead, complex articular structures equivalent to those of extant species, together with presence of an ambulacral furrow, indicate significant arm flexibility and thus a broad behavioral potential. Ordovician asteroids are morphologically diverse, and they have been collected from low-energy to comparatively high-energy sedimentary settings, thus suggesting their importance in different ecologic environments. It is concluded that life modes among Ordovician asteroids was varied, and that modes included such complexities as asteriid-like predation.

Aberhan et al. (2006) evaluated important changes in marine benthic ecosystems during the Mesozoic, noting that

predatory asteroid diversification during the Jurassic might have been significant. A parallel hypothesis favored here is that the diversification of Ordovician asteroids was similarly important to Ordovician community evolution.

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