Paleoecology and Taphonomy of an Edrioasteroid-Dominated Hardground Association from Tentaculitid Limestones in the Early Devonian of New York: A Paleozoic Rocky Peritidal Community

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The taphonomy, sedimentology, and paleoecology of a rare peritidal hardground in the Lower Devonian (Lochkovian) Thacher Limestone Member of the Manlius Formation in east-central New York State provides insights into sediment dynamics and modes of life of ancient hard substrate-inhabiting organisms. The hardground occurs near the top of a shallowing-upward carbonate cycle, slightly below desiccation-cracked micritic ribbon limestones. The hard surface developed on a partially exhumed tentaculitid pavement and overlying pelletal calcisiltite; the hardground has a relief of about 2–3 cm and is overlain by a thin siliciclastic mud layer. Tentative correlation of the hardground across a lateral distance of about 35 km perpendicular to depositional strike suggests a very subdued topographic profile for this region and development of an extensive peritidal hardground pavement. Tentaculites gyracanthus *occurs in a dense pavement of strongly bimodally aligned shells with an ENE to WSW orientation, parallel to the inferred paleoshoreline. Some specimens also occur vertically embedded, suggesting possible life orientations within firm substrates. The presence of pits around the apertures of these shells suggests scouring effects around the shells burrowed into the substrate. Upper portions of the irregular hardground surface were preferentially colonized by an undescribed small postibulinid edrioasteroid, which may have lived somewhat like acorn barnacles on wave-swept rock platforms. The latter shows a population structure with few juveniles. Although fauna within the Thacher limestone includes leperditian ostracodes, ramose and encrusting bryozoans,* Howellella vanuxemi *brachiopods, and rare pterioid bivalves, the hardground community is rather limited. This low-diversity assemblage represents an unusual edrioasteroid-dominated hardground community type that persisted from at least Early Ordovician to Late Devonian in peritidal hardgrounds and rockgrounds.*

INTRODUCTION

Shallow, peritidal hard-substrate communities are widely studied along modern rocky shorelines, but are generally poorly preserved in the ancient geologic record (Johnson 1987; 1988 a, b). What were the analogs of barnacle-encrusted rocky shores in the Paleozoic? Hardgrounds are sysnsedimentarily lithified carbonate sea floors cemented by precipitation of carbonate cements in the primary pore spaces (Wilson and Palmer, 1992). Exposure of these cemented surfaces by storms or current activity may provide a hard substrate on an otherwise soft, muddy bottom, allowing for the colonization and establishment of encrusting communities.

There are several recorded occurrences of echinoderm-dominated hardground communities in the fossil record (e.g., Brett and Liddell, 1978; Fürsich, 1979; Waddington, 1980; Brett et al; 1983; Guensburg, 1984, 1988; Brett and Brookfield, 1984; Brett, 1988; Meyer, 1990; Guensburg and Sprinkle, 1992; Sumrall et al., 2000; Sumrall, 2001). The preservation of these communities occurred by catastrophic burial or obrution (Brett and Seilacher, 1991; Wilson and Palmer, 1992), providing, in essence, a snapshot of the hard seafloor community. In some instances it is possible to discern community composition, succession, and species interactions, as well as other ecological patterns, primarily because the fauna is preserved in situ.

Hardgrounds are common during certain intervals of geologic time, probably associated with widespread marine transgressions and the development of major carbonate platforms. They apparently are associated with certain climatic regimes, particularly during greenhouse times and with relatively high levels of carbon dioxide and low Mg/Ca ratios in seawater, so-called calcite oceans (Wilkinson et al., 1982; Stanley and Hardie, 1998; Wilson et al., 1992). For various reasons that are still poorly understood, certain intervals of geologic time, even during greenhouse times, provide fewer examples of hardgrounds than others. Notably, these include the Silurian to Early Devonian interval. Hence, discovery and documentation of hardgrounds and their biotas from these intervals form a significant contribution to the understanding of these interesting marine hard-substrate environments through geologic time.

In this paper, a somewhat unusual hardground is described from the Early Devonian (Lochkovian) of eastern New York State, with a fauna dominated by *Tentaculites* and a new small edrioasteroid. This is one of the relatively few occurrences of Early Devonian hardgrounds, it is a rare example of a peritidal hardground, and it provides an important comparative example for this portion of the middle Paleozoic.

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LOCALITY AND METHODS

The hardground described here was collected (in 1997) from the lower Thacher Member of the Manlius Formation (Lower Devonian, Lochkovian Stage) in the Mohawk River Valley. The majority of the material was derived from a small roadcut on Kilts Road just southeast of its junction with county route 34; about 1 km east of the village of Sharon Springs, Schoharie County, New York (Sharon Springs 7.5' Quadrangle; Fig. 1). Subsequently (in 2001) a second occurrence of a similar, and possibly the same, edrioasteroid-bearing hardground was discovered in a small roadcut on NY Route 443 northwest of the bridge over Fox Creek, 0.5 km southeast of Gallupville, Schoharie County, New York (Gallupville 7.5' Quadrangle; Fig. 1). This locality is approximately 35 km SE of Sharon Springs, suggesting the persistence of at least the identical facies, if not the same hardground over a substantial area.

The Sharon Springs site was recognized and collected initially by Bruce Bell in the early 1970s and is briefly mentioned by Fisher (1979). Bell reposited a large quantity of edrioasteroid-encrusted slabs in the New York State Museum, and this collection supplements our field studies. Thomas Whiteley and Gerald Kloc re-located and excavated the hardground horizon at the Sharon Springs site in 1997. In all, an area of about 2.4 m² was uncovered. The limestone was marked in several places with north orientations using a Brunton compass. During the collection process, the slab was removed as several dozen smaller pieces, which were reassembled in the laboratory to reform a single large slab. This slab represents a single bedding plane measuring about 140 cm by 170 cm. The slab was cleaned with a dry brush, and washed gently with mild soap solution to remove a thin clay shale that locally adhered to the hardground.

In order to document edrioasteroid size frequency, specific distribution patterns, and tentaculitid orientation on the slab, a chalk line was used to create a 10 cm x 10 cm grid work on the fossiliferous region of the hardground surface (Fig. 2). Each of the fossiliferous quadrants (~185) was assessed for faunal elements. Edrioasteroids were located, counted, and their average diameter recorded. The angle of orientation of the apex of the conical skeleton of *Tentaculites gyracanthus* Hall relative to the north azimuth was measured to denote angle direction. Topography of the hardground (e.g., elevated knobs, low depressions), approximate relief, and other taphonomic and sedimentary features were noted and recorded in the appropriate quadrant (see Fig. 2).

For statistical purposes, the measured azimuths of *Tentaculites* were grouped into approximately five-degree increments (e.g., 0°–4.9°, 5.0°–9.9°, etc.) and were entered into a Microsoft Excel spread sheet for calculation of descriptive statistics. The strength of orientation (r value) was calculated by using the following formula:

$$r = (x^2 + y^2)/2$$

where $x^2 = (\Sigma\,|\cos\theta|)/N$ and $y^2 = (\Sigma\,|\sin\theta|)/N$, and N = the number of measured angles. An r value close to one, indicates cohesiveness or unity in the orientation (i.e., a strongly preferred orientation), whereas an r value close to zero suggests no preferred orientation.

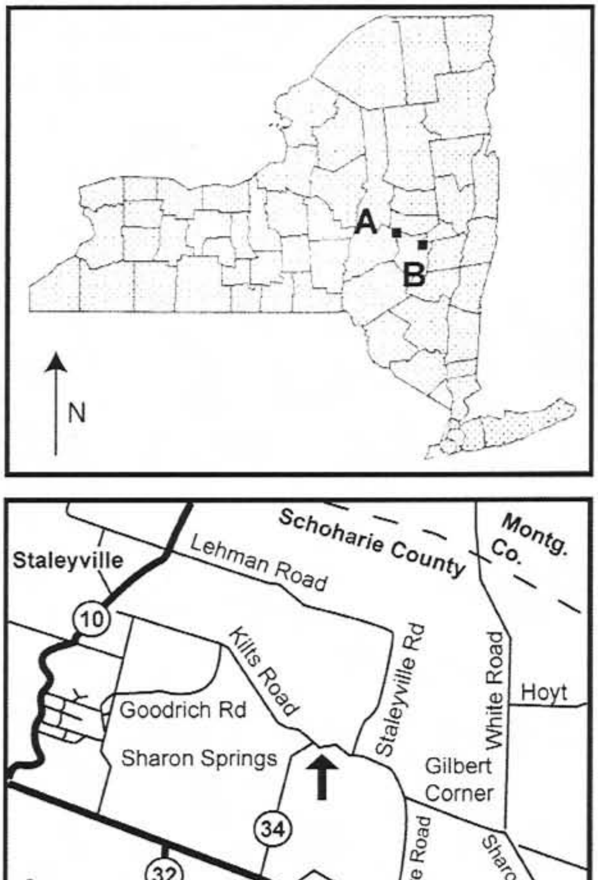


FIGURE 1—Location map of the study area. Inset map shows general location of outcrop localities in east central New York State. (A, B) Detailed maps showing: (A) portions of the Sharon Springs 7.5' quadrangle; (B) Gallupville 7.5' quadrangle. Exposures of the hardground discussed herein indicated by arrows.

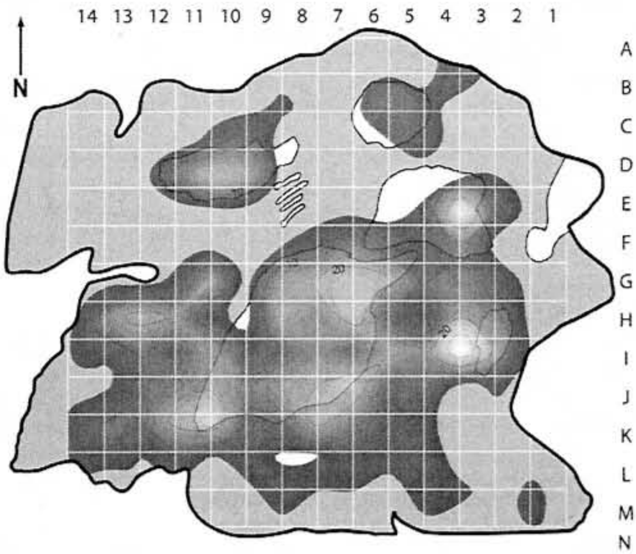


FIGURE 2—Schematic drawing of the hardground slab with contoured edrioasteroid distribution overlay. The schematic underlay shows outline of the hardground. Irregularly shaped patterns within outline indicate raised regions of the hardground surface; dark-gray areas represent the lower tentaculitid pavement. The graduated gray overlay shows the contoured edrioasteroid frequency distribution. Major contour lines are drawn at multiples of 10 individuals per increment. Grid dimensions used to count edrioasteroid frequency were drawn at 10 cm x 10 cm square. Note highest densities of edrioasteroids occur on elevated portions of the hardground surface as opposed to the lower pavement.

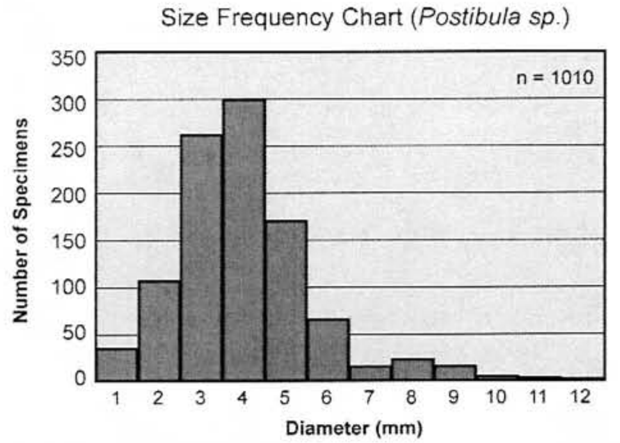


FIGURE 3—Edrioasteroid size frequency histogram based on 1010 specimens. Average edrioasteroid diameter is between 3 and 4 mm. Some small (1 mm) specimens are represented, as are a few very large specimens (up to 12 mm). It is possible that 2 cohorts are represented, with an elder cohort represented by specimens in the 7–10 mm range, and a younger cohort in the 1–5 mm size range.

Edrioasteroid diameters were measured to the nearest millimeter. The number of edrioasteroids in each size range was counted and plotted graphically, using Excel, to show the size frequency distribution (Fig. 3). In order to document the spatial distribution of edrioasteroids on the hardground surface, the total number of edrioasteroids per quadrant was recorded and provided an x, y coordinate location. These spatial data, along with the number of edrioasteroid occurrences, were used to generate a contour map using the software program Surfer® (2002, Rockware®, Golden, CO). The coordinate data were gridded within the software program using the nearest neighbor calculation method and plotted (Fig. 2).

STRATIGRAPHY AND GEOLOGIC SETTING

The hardground-bearing lower submember of the Thacher Member (Manlius Formation) is the lowest unit of the Lower Devonian Helderberg Group (Fig. 4). While there has been some controversy as to the exact age of the Thacher Member (see Matteson et al., 1996; Ebert et al., 2001), most workers accept that this unit lies slightly above the Silurian–Devonian boundary (Rickard and Zenger, 1964), making it earliest Devonian (Lochkovian) in age.

The Thacher Member in central and eastern New York State is comprised mainly of thinly bedded micritic ribbon limestone facies, primarily calcisiltites. This unit previously was termed the Tentaculite Limestone (Hall, 1839), because it contains prolific numbers of *Tentaculites gyracanthus*.

The Thacher Member represents the initial portion of a marine transgression, superimposed on the final phase (Tutelo phase) of the Tippecanoe Megasequence (Sloss, 1963). The interval is about 16 meters (52 feet) thick in its type section area, near Albany, NY, but thins to about 10.7 meters (35 feet) near Sharon Springs (Rickard and Zenger, 1964). The Thacher Member conformably overlies fine-grained dolostones of the Rondout Formation (Silurian, Pridolian), but is unconformably overlain by crinoidal grainstones and packstones of the Lower Devonian Coeymans Formation (Rickard and Zenger, 1964).

The Thacher Member is divisible into two distinctive units. The lower submember in the Richfield Springs area (west of Sharon Springs) measures about 8 m (25 feet) thick and thins in the direction of Gallupville. Throughout this region, the lower Thacher consists mainly of fine-grained calcilutite (micrite) to calcisiltite beds that range from 2.5 to 9 cm thick. Toward its top, this unit exhibits mudcracks, ripple marks, rip-up clasts, and very small-scale cross bedding. A low-diversity, high-dominance fauna consists mainly of *Tentaculites gyracanthus*, the large ostracode *Hermanina alta*, the brachiopod *Howellella vanuxemi*, small pterioid bivalves, and a few bryozoan fragments.

The upper submember measures about 3 m (10 feet) thick. The base of this interval contains a 2.4 meter-thick stromatoporoid biostrome with a great abundance of *Syringostroma barretti*, providing some relief to the contact with the lower Thacher unit. This portion of the upper section is slightly coarser, more argillaceous, and thicker bedded than the underlying unit. This section is overlain by thinner bedded limestones of variable thickness (also called waterlimes in older literature) and is capped by another section of stromatoporoid biostromes forming the top of the Thacher Limestone (Rickard, 1962) (see Fig. 4).

Facies relationships and depositional environments of the Lower Devonian Helderberg Group in eastern New York, and to a lesser extent in Pennsylvania, have been discussed in detail by a number of previous workers (Rick-

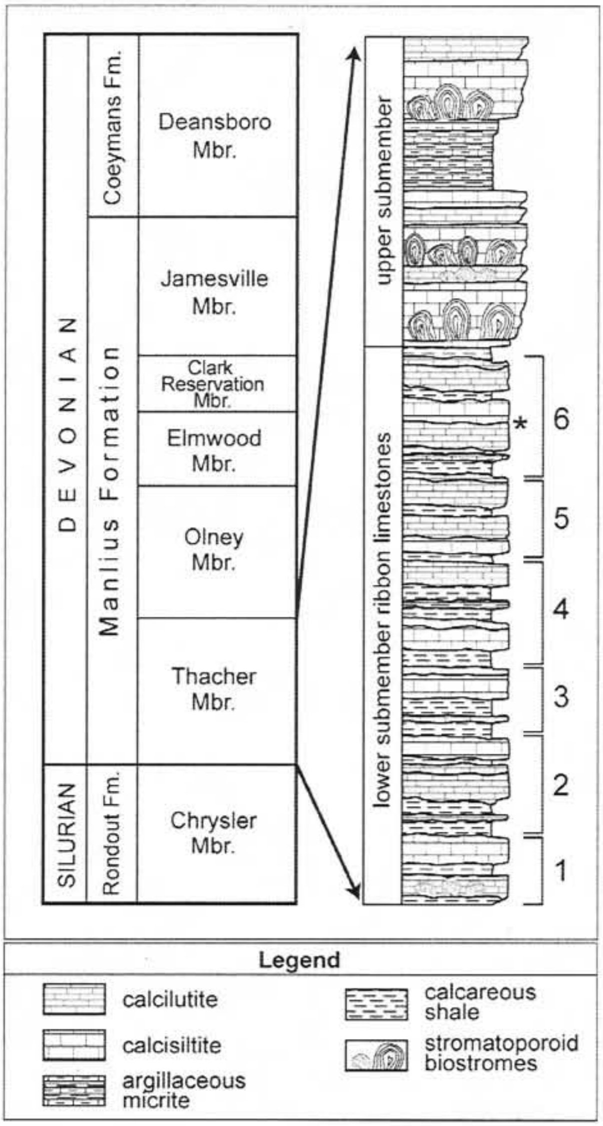


FIGURE 4—Generalized stratigraphy of the Lower Devonian Helderberg Group in eastern New York (not drawn to scale). Inset shows details of stratigraphy of the Thacher Member, including small-scale cycles (PACs of Goodwin and Anderson, 1985); asterisk marks the approximate position of the Sharon Springs-Gallupville hardground.

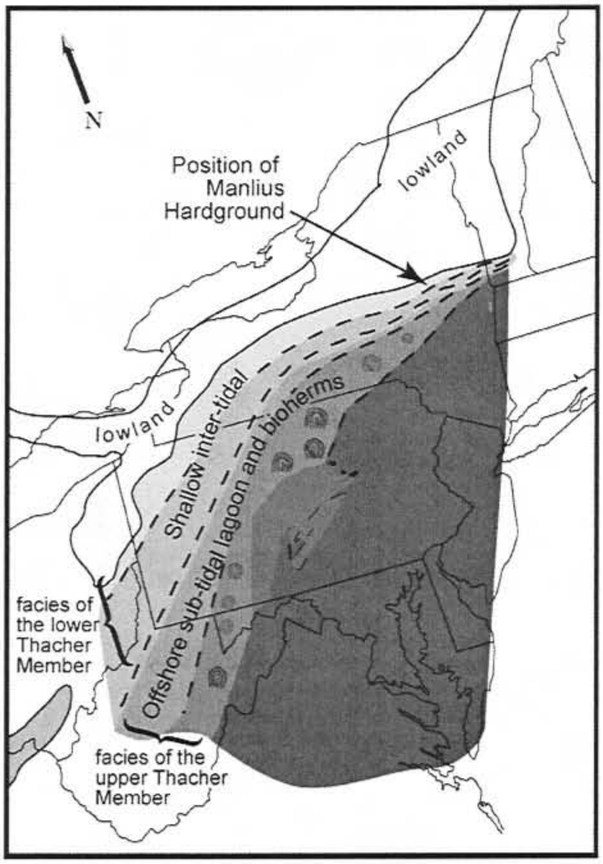


FIGURE 5—Paleogeographic reconstruction of the Appalachian foreland basin during earliest Devonian (Lochkovian) time. Arrow denotes approximate position of the Manlius hardground site; north arrow indicates modern geographic north. Inferred facies belts of the Thacher Limestone are labeled. Dashed lines show approximate contours of basin, deepening to the southeast. Figure modified from Anderson (1971).

ard, 1962; Rickard and Zenger, 1964; Laporte, 1969; Anderson and Goodwin, 1980; Anderson et al., 1984; Goodwin and Anderson, 1985; Goodwin et al., 1986; Ebert et al., 2001). Previous paleogeographic reconstructions for the Helderberg basin (Fig. 5) show a northeast to southwest trending depocenter lying to the southeast of the study region (the southern Hudson Valley to central Pennsylvania area) bordered to the northwest by carbonate ramps, which led into extensive tidal flats. Hardground-bearing strata formed in proximity to this northwestern paleoshoreline.

Rickard (1962) provided a detailed survey of Helderberg stratigraphy and established important aspects of facies inter-relationships, particularly in the lower Manlius Formation. Notably, he was able to establish that lower Helderberg units display a gradual westward change from offshore skeletal packstone and grainstone facies (Coeymans/Kalkberg formations) into mudstone to wackestone facies of the Manlius Formation to the northwest.

The Helderberg Group forms the type example of the low-high-low (x, y, z) energy profile typical for carbonate ramps (Laporte, 1969). The Manlius Formation, as a whole, was deposited during the initial phases of a larger scale (third order) transgression associated with the lower of two large-scale cycles in the Helderberg Group. In this context, the Manlius records a low-energy inner shelf (z zone in the model of Irwin, 1965).

The Manlius Formation comprises several distinct facies that suggest deposition in a peritidal environmental complex. The most offshore Manlius facies are thin-to-medium bedded skeletal packstones to wackestones that represent storm-generated graded beds derived from adjacent shoal facies to the southeast (Coeymans facies). These skeletal limestones, usually dominated by crinoid hash, form a transition between typical Coeymans skeletal pack- and grainstone facies and the most proximal, typically thick-bedded limestones commonly containing stromatoporoid bioherms. Rickard (1962) and others have interpreted these bioherms as inner lagoonal mounds.

The stromatoporoid facies in turn appear to be replaced laterally in the onshore direction, and vertically in shallowing-upward successions by ribbon limestones. These facies typically are platy, sparsely fossiliferous, laminated micrites and calcisiltites. Included in these dark blue-gray, fine-grained calcisiltites are a number of hardgrounds. Insights into the depositional environment and paleogeography are provided by the unique faunal and taphonomic features of these beds.

The ribbon limestones pass laterally westward (and also vertically upward) into still thinner-bedded, typically shaly and somewhat dolomitic cryptalgal laminates (i.e., micritic limestones with crinkly or wavy laminations probably of microbial origin) with well-developed desiccation cracks and fenestral fabrics (birds eye structures). Laporte (1969) interpreted the ribbon limestones to represent a low-energy, inner-lagoonal to tidal-flat succession. The source of the fine-grained sediment, which make up most of the Manlius Formation, is uncertain, but is considered to be an offshore carbonate factory, probably associated with shallow-water conditions represented by winnowed skeletal carbonates in portions of the Coeymans Formation. Shoreward transport of pelletal carbonate mud apparently took place during fair-weather conditions (Laporte, 1967, 1969). Although the limestones are relatively clean, they are interbedded with thin, shaly to slightly bentonitic partings. The argillaceous content increases into the most proximal mud-cracked facies, suggesting that low-relief land northwest of the study area supplied a very minor amount of siliciclastic sediment to the peritidal region.

The Helderberg Group is divisible into small-scale cyclic packages, some of which seem to be widespread, that show general tendency to shallow upward from flooding surfaces (see Fig. 4). Indeed, this unit has become a classic reference section for the study of small-scale, shallowing-upward successions in carbonates. Anderson and Goodwin (1980) and Goodwin and Anderson (1985) recognized a series of about five to six 1–3 meter thick, shallowing-upward cycles, which they termed punctuated aggradational cycles (PACs), within the lower Thacher Member. These intervals have been correlated over wide areas in central to eastern New York State and central Pennsylvania. Each cycle is bounded at its top by an abrupt flooding surface and follows a roughly upward-shallowing pattern. Goodwin and Anderson (1985) argued that these cycles represent widespread sea level rises, on the order of a few meters of water depth, followed by a widespread aggradation of the bottom. Given the unusual conditions under which the Sharon Springs hardground formed, coupled with its stratigraphic position (see below), it is reasonable to assume that the Gallupville hardground maybe coeval. Thus the apparently widespread character of the hardground reported herein may favor Goodwin and Anderson's (1985) allocyclic mechanism for producing the upward-shallowing packages.

The hardground interval recovered from the Sharon Springs locality lies approximately 1 m from the top of the lower division of the Thacher Member. Moreover, the hardground at Gallupville lies in approximately the same stratigraphic position (i.e., slightly below a stromatoporoid biostrome). The occurrence of beds showing polygonal desiccation cracks a few centimeters above the hardground suggests that this sediment was deposited in very shallow water, probably an inner lagoonal to outer tidal-flat setting. As for the Gallupville locality, the hardground-bearing interval is followed within a meter by a biostromal stromatoporoid bed that appears to represent somewhat deeper lagoonal conditions. Hence, there is some indication that these hardgrounds formed during periods of relatively slow sedimentation near the cap of a shallowing-upward cycle.

HARDGROUND MORPHOLOGY

The Manlius hardground is the uppermost of three to four closely stacked layers of micritic, bluish-gray, pelletal limestone (calcisiltite–wackestone). Each of these distinct layers is separated from the one above by a very thin argillaceous parting. Such bedding planes show abundant, very small-scale bioturbation (1–2 mm wide by 10–20 mm long burrows) identifiable as *Chondrites* and *Planolites*. The sharpness of these burrows, which are typically cast on the base of the next overlying bed, suggests that the mud separating the limestone layers had undergone a minor amount of consolidation, forming firmgrounds prior to the deposition of the next overlying unit. Alternatively, erosional scouring immediately preceding the deposition of the pelletal limestones may have resulted in the breaching of soft-sediment layers and exposure of burrows produced in semi-consolidated sediment. However, only the upper layer displays evidence of a genuine hardground condition.

The hardground itself is developed on varied lithologies in a graded bed at the top of the succession. The hardground-bearing bed is not separated from the one below it by an argillaceous parting, rather the beds seem to have been amalgamated. However, polished cross-sections show an abundance of tentaculitids and other fossil debris, which form a line of separation between the two beds. This debris is sharply overlain by a 5–7 mm pelletal calcisiltite-calcisiltite bed on which much of the hardground is developed. The tentaculitid pavement may represent a period of winnowing prior to a sedimentation event that deposited carbonate silts and mud.

The hardground shows a relief of about 1–2 cm. Small furrow-like structures (Fig. 6A) up to 3 cm wide and 5–15 cm long were cut downward in places through the calcisiltite layer prior to lithification. In certain areas, the surface of the calcisiltite displays cracks or fractures (Fig. 6B). The upper layer of the calcisiltite generally is sparsely fossiliferous, but in a few areas tentaculitids apparently were buried within this layer as well. It is notable that certain tentaculitid specimens have been breached open, indicating a period of abrasion of the calcisiltite following at least partial induration that anchored the skeletons in place. In places, the calcisiltite layer was removed completely and the hardground was developed along the more planar surface of the tentaculitid layer (Fig. 6C). In these areas, the tentaculitid skeletons are densely packed, virtually edge-to-edge, and display a very strong, visually evident, preferred orientation, roughly northeast to southwest (Fig. 6D) (see below).

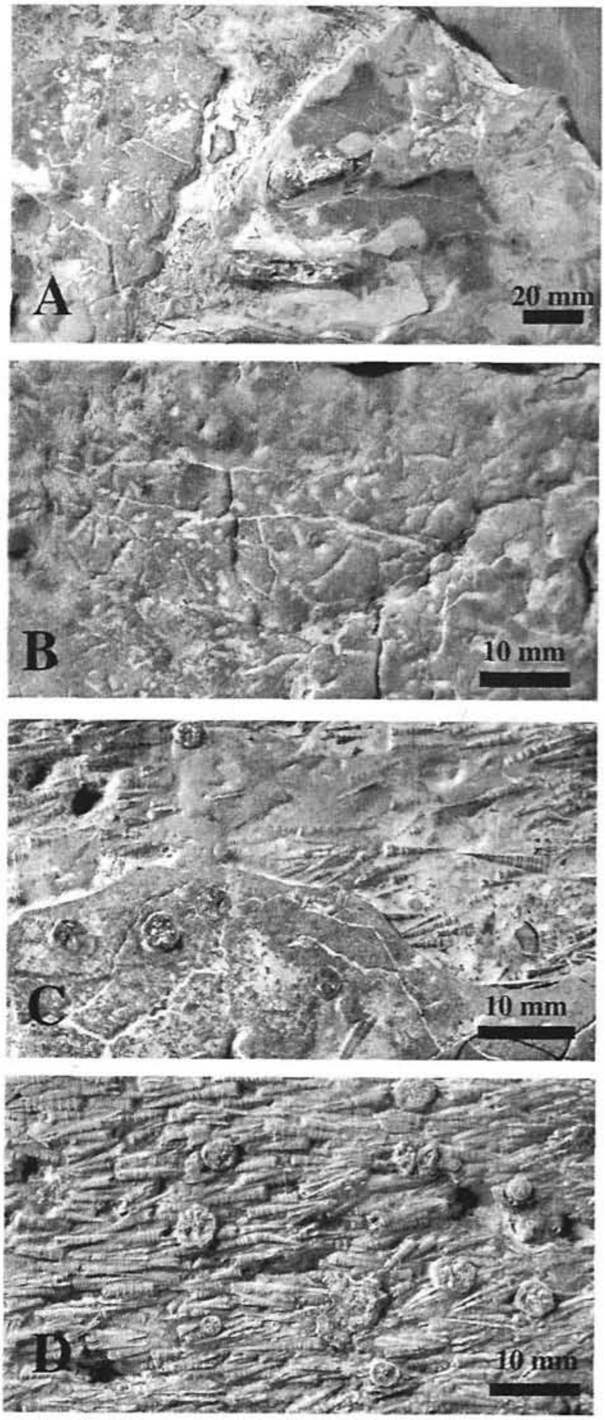


FIGURE 6—Morphological features of the Manlius hardground surface; Thacher Member, Sharon Springs, NY. (A) Note slight ledge at edge of high area to left of center; also note low areas with *Tentaculites* and grooves (erosionally enlarged burrows?) in center of view. (B) Section of hardground showing *Chondrites* burrows and collapsed portions of the upper calcisiltite bed. (C) Portion of elevated calcisiltite hardground in lower half of view shows attached postibulinid edrioasteroids; low-relief area in upper portion of view shows pavement of aligned *Tentaculites* where calcisiltite has been eroded; also note single small edrioasteroid attached to *Tentaculites*-bearing bedding plane. (D) View of lower surface of hardground with edrioasteroids attached to bimodally aligned *Tentaculites*.

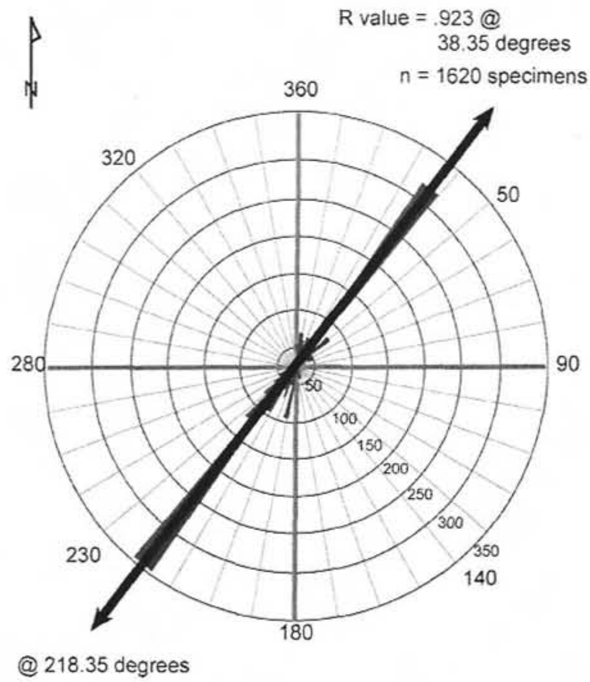


FIGURE 7—Rose diagram of azimuths of *Tentaculites gyracanthus* shells from the Manlius hardground. Mean vector is indicated by arrows and statistical z-values are given. Note nearly perfect bimodal distribution of *Tentaculites*.

HARDGROUND FAUNA

The fauna of the Manlius hardground in both localities has a very low diversity, being almost exclusively dominated by a single undescribed species of postibulinid edrioasteroid. In addition, a single small zoarium of an unidentified trepostome bryozoan ($\sim$1 cm diameter) was observed. Associated ramose bryozoans may have been attached, but no holdfasts of either bryozoans or crinoids were observed. A few ill-defined small pits occur on the surface, but surprisingly no recognizable borings such as *Trypanites* were noted. Possible in situ tentaculitids (see below) may have been part of a predecessor firmground stage in the development of this surface, but obviously are not bored into the hardground. Thus, in contrast to most described hardground faunas, this assemblage is almost exclusively echinoderm dominated and virtually lacks bryozoans and borings.

TAPHONOMY

Tentaculitids

Detailed measurements of the azimuths of 1620 *Tentaculites* specimens on the lower portions of the hardground show a very strong bimodal orientation (Fig. 7). In one quadrant alone, a count of nearly 500 specimens revealed that virtually equal numbers were oriented with apical ends northeast (243 specimens) and southwest (242 specimens). The strongly bimodal alignment calculated at NNE to SSW (r = 0.92 at $\sim 38^\circ$ and 218°) is parallel with the inferred NE–SW trending paleoshoreline of the Early Devonian sea (Anderson, 1971; Brett, 1999). The strongly bi-

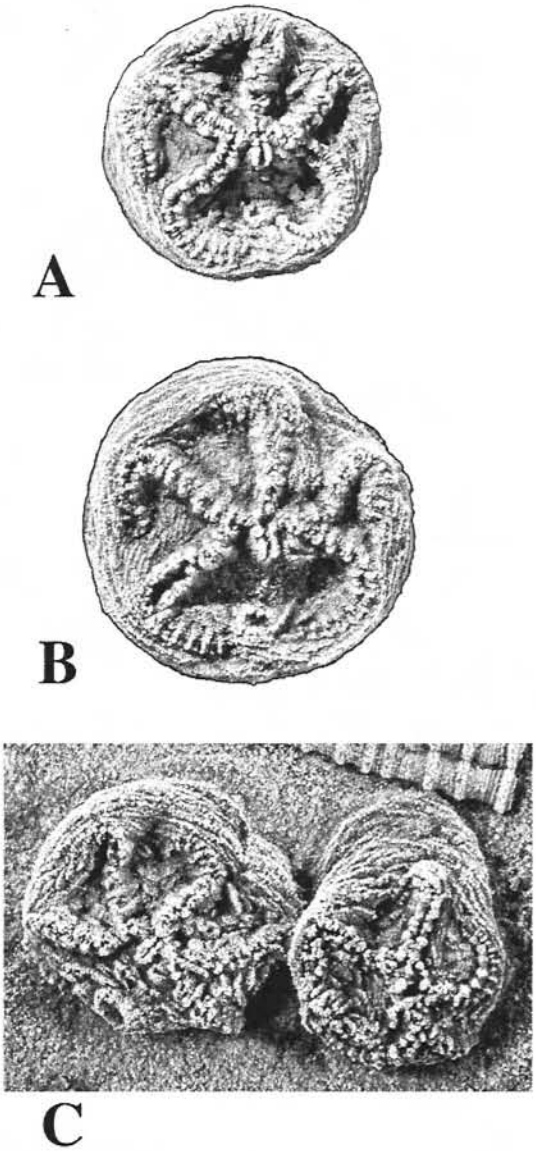


FIGURE 8—Enlarged images of several specimens of the postibulinid edrioasteroid, all ×8. (A) Edrioasteroid in contracted posture showing gaped cover plates. (B) Very large edrioasteroid preserved in contracted posture with gaped cover plates and open anal pyramid. (C) Two specimens preserved in extended posture with peripheral rim and pedunculate zone showing near bottom.

modal pattern suggests an oscillatory current oriented at 90° to these measured angles. This would imply southeast to northwest wave or tidal action, which is normal to the Early Devonian paleoshoreline.

In contrast to the lower cemented surface, the upper encrusted surface of the hardground shows much lower concentrations of tentaculitids, but in this case, they generally are oriented with apex end pointing in the same direction, especially in close proximity to the bases of raised regions of the hardground. This observation suggests that these specimens were oriented by unidirectional currents that were focused and directed around the base of elevated surfaces. As such, these tentaculitids were subject to a different orientation process, which potentially was related to the initial phases of the final obrution event.

Edrioasteroids

As noted, the hardground shows a large number of small postibulinid edrioasteroids belonging to a new genus and species (Fig. 8 A–C). Most edrioasteroid thecae are intact, although some of the larger individuals show some evidence of incipient disarticulation. Small individuals are almost perfectly intact and some even appear relatively inflated. Upon death and burial the thecae underwent post-mortem collapse, which pressed the upper surface downward against the hardground. This thecal collapse enhances the elevated appearance of the ambulacra and oral area (see Fig. 8C) because the floor plates and oral frame plates are thicker than the interambulacral plating. Coupled with the tall cover plates of postibulinid edrioasteroids, this compaction preserved specimens with high ambulacra and low interambulacra.

Unlike other postibulinids (Bell, 1976 a, b; Bell and Petersen, 1976; Sumrall et al., 2000), specimens of this edrioasteroid have a clavate theca that in the extended position has a bulbous oral surface and a thick tapering pedunculate zone that attached to a somewhat smaller peripheral rim. This design is convergent on the Discocystinae and easily distinguished by the nature of the pedunculate zone plating (Sumrall, 1996). Most specimens are preserved with the thecae in the retracted position while the edge of the pedunculate zone forms the edge of the thecae somewhat reminiscent of *Torquerisediscus kypsi* specimens described by Sumrall (2001). Several specimens are preserved with the thecae slightly extended and the oral surface shifted to the side, and in these specimens, a portion of the peripheral rim and a side view of the pedunculate zone are evident (Fig. 8C).

Most unusual in the preservation of these edrioasteroids is the nature of the ambulacral cover plates, hydropore, and periproct. Most edrioasteroids are preserved with the cover plates completely closed along the peradial suture (Sumrall, 1996). The cover plates rarely are collapsed into the food groove (Sumrall and Bowsher, 1996; Sumrall, 2001). In nearly every specimen of this edrioasteroid, the cover plates either are gaped or folded open with one or more proximal sets of cover plates folded back onto the interambulacra, exposing the interior surface of the cover plates. Most specimens also are preserved with the hydro-gonopore and periproct open. These open, delicate structures likely are not a response to stress. Arguably, edrioasteroid response to stress would be to close all of the thecal openings tightly, thus explaining the more common condition of tightly closed thecal openings. The shifting of the plates covering the thecal openings must have happened after death of the animals. Either the edrioasteroids were killed and had a brief period of decay followed rapidly by burial in mud, or they were killed and buried in a single event and contraction of connective tissues opened the plates covering the thecal orifices.

PALEOBIOLOGY

Tentaculitids

Because tentaculitids are a group of annulated conical shelled organisms of uncertain affinities, their exact mode

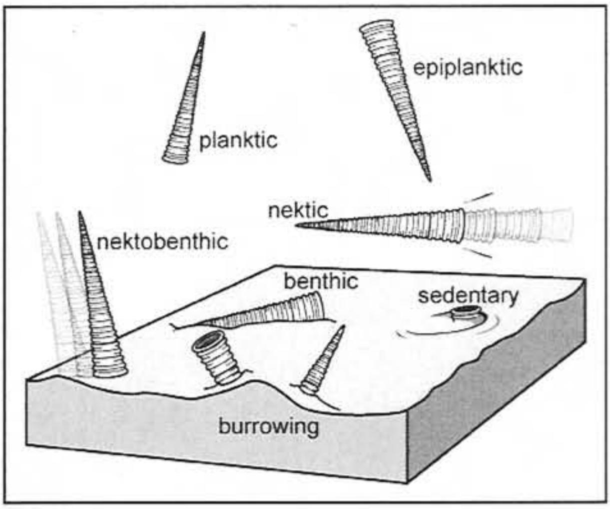


FIGURE 9—Postulated modes of life for *Tentaculites*. Several specimens on the Manlius hardground suggest a sedentary life mode for these enigmatic organisms. Modified from Fisher, 1971.

of life remains enigmatic. They have been interpreted to have been either pelagic, benthic scavengers, or sedentary filter feeding organisms (Fisher, 1966; Fig. 9). Clearly most specimens from the Manlius hardground are reworked and current-aligned skeletons (Fig. 10A, B). However, a few individuals are preserved in possible life position. These are represented by specimens in which the conical shell is oriented vertically with the aperture directed upward and elevated slightly above the surface of the calcisiltite (Fig. 10C, D). Typically, the aperture in these specimens is elevated slightly above a semicircular depression, which is only slightly larger than the tentaculitid test. The depression could have been produced by currents flowing around the tentaculitids or by movements of the animals' appendages. These specimens could represent individuals that burrowed into the firm carbonate silt prior to its complete cementation. If so, then the preferred mode of life may have been as a sedentary, suspension-feeding organism. This unorthodox interpretation has been suggested previously by Fisher (1966). The alternate interpretation of these specimens is that they were washed into borings or other openings in the hardground, but this interpretation seems unlikely given the number of vertically oriented specimens.

Edrioasteroids

The distribution pattern of edrioasteroids indicates that these echinoderms were capable of colonizing both the lower exposed areas of the tentaculitid surface and the raised, indurated calcisiltite patches. It is readily apparent from the contoured frequency of occurrence for each 10 cm^2 quadrant (Fig. 2) that the edrioasteroids were not evenly distributed across the hardground surface (see also Table 1 for counts). Rather, they were patchy and more commonly settled on the elevated portions of the hardground. The highest densities of specimens (31 to 37 individuals per square decimeter) occur on the elevated regions of the hardground. Much lower densities, comprising much smaller individuals, occur on the lower surfaces.

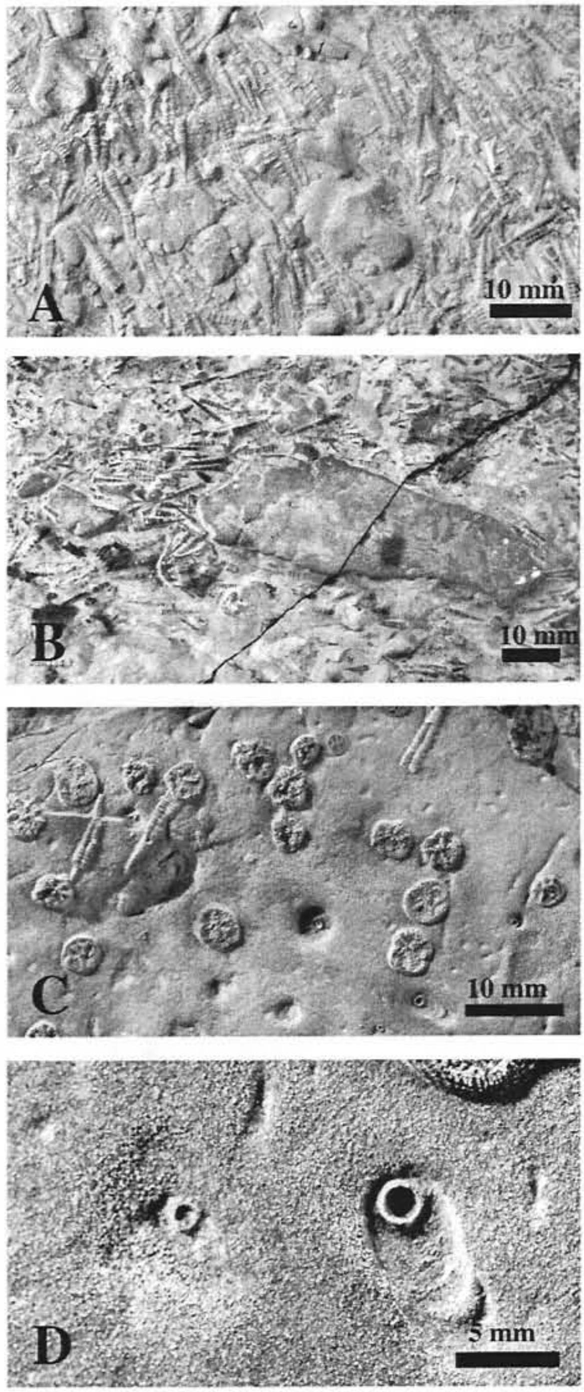


FIGURE 10—Fauna of Manlius hardground. (A) Pavement of bimodally aligned *Tentaculites gyracanthus*; also note fragments of ramose bryozoans. (B) Portion of the slab surface showing densely packed *Tentaculites* and a brachiopod (*Howellella vanuxemi*) located just left of center; also note small clast of cemented calcisiltite, probably derived from erosion of the hardground. (C) Hardground surface showing numerous articulated postibulinid edrioasteroids; also note shallow pits, which are concentric on vertically oriented *Tentaculites*. (D) Enlargement of two vertically oriented *Tentaculites* specimens (rings) showing small scour pits around them. Note that in this image, a comparison between horizontal free-lying tentaculitids (oriented bimodally) and elongated scour pits around vertical specimens suggests different current processes affected the hardground (oscillating and unidirectional).

TABLE 1—Numerical counts of edrioasteroid specimens within the most fossiliferous region of the hardground. Note 10 cm × 10 cm sampling grid. Quadrants were labeled initially using alpha-numeric coordinate system. Subsequently all data were converted to x, y coordinates for use in computer-assisted analysis (presented in the overlay of Figure 2).

North

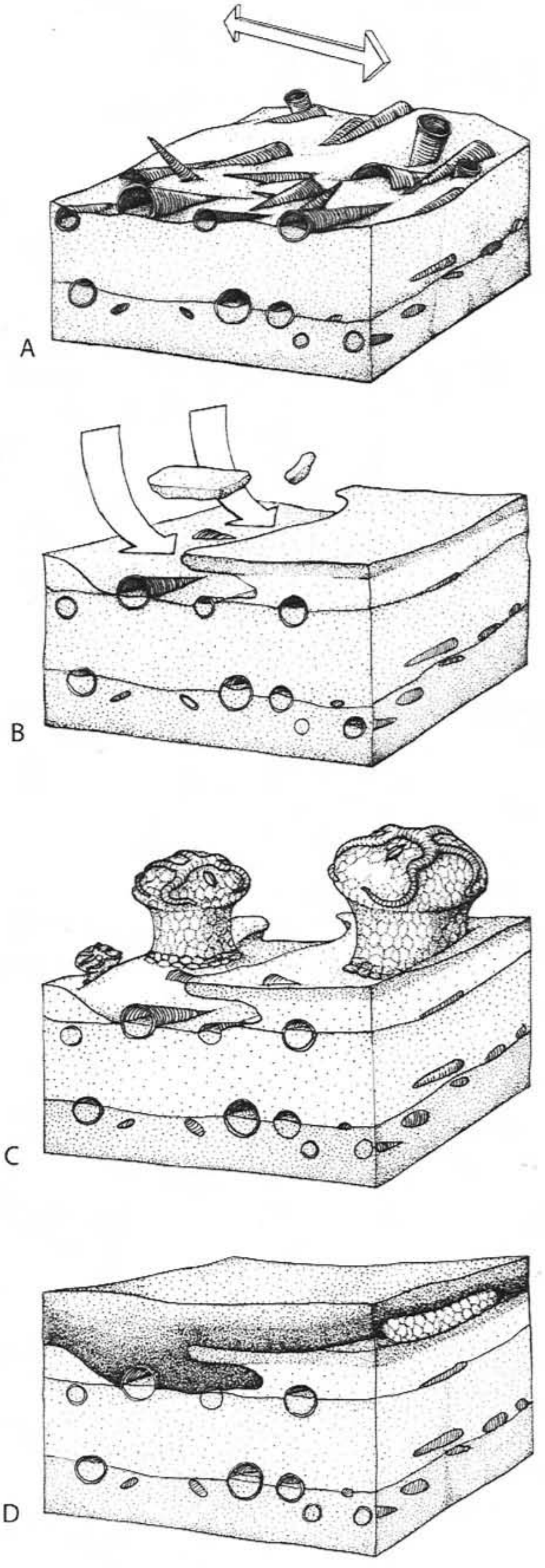
		14	13	12	11	10	9	8	7	6	5	4	3	2	1		
												6	2				A
							3			11	4						B
					3	8				2	4	1					C
				7	20	17							2				D
											3	31	7				E
							2	5	14	6	3	12					F
				3	18		16	20	24	20	10	15	6				G
		15	23	19	4		19	14	24	9	2	23	11				H
		10	12	9	19	5	18	14	8	21	17	37	18	1			I
		5	12	14	19	12	17	20	26	9	11		3				J
		12	11	22	27	9	10	23	14	6	3						K
		13	2	7	2	6	1	2	3	4	5						L
					1		6	2	2		4	3		3			M
														2			N
TOTALS:		55	60	81	113	57	92	100	115	88	66	128	49	6	0	0	1010

Furthermore, there does not appear to have been any preferential orientation of the thecae of the edrioasteroids on the surface. Measurements of the orientations of the thecae relative to the position of the anal vent show a high degree of scatter and virtually all angles occur with equal facility.

The edrioasteroids apparently were buried alive, or very shortly after death, and thus represent a census sample of the living community at the time of their death. As such, one might anticipate a right-skewed size frequency distribution as seen in other studied localities (Kammer et al., 1987; Meyer, 1990; but see Sumrall, 2001 for an example of spat-fall accumulations). However, in this case study there is an anomalously low number of juveniles (see Fig. 3). Relatively few specimens smaller than two mm in diameter are present. Collection and cleaning methods probably did not selectively remove juveniles from the sample. The small number of juveniles in the population may reflect either seasonal recruitment, as influenced by environmental conditions, or burial early in the reproductive season, such that only a few of the earliest offspring had settled and cemented. In any case, successive cohorts of individuals greater than 4 mm in diameter show the expected decrease in population size through time.

SEQUENCE OF EVENTS IN HARDGROUND FORMATION

The basic development of hardground features can be summarized in the following steps. A period of relatively prolonged sediment starvation, probably representing several decades or centuries, allowed the accumulation of tentaculitid skeletons (Fig. 11A). Causes of the cessation of sedimentation are uncertain, but may involve the aggradation of sediments to near sea level, the beginning of sea-level rise following a shallowing episode, or both. The tentaculitid skeletons may have undergone periods of exhumation and burial that resulted in their dense concentration. These conical skeletons were strongly affected by oscillatory currents, which aligned them in an almost perfectly bimodal fashion on this pavement. The northeast-southwest direction of lineation suggests that these skele-



tons were aligned parallel to the shoreline of the basin. If one assumes that this represents a strand-line accumulation, then the skeletal lineation would represent the strike of the paleo-shore line of approximately N 38°E. However, the apparently extensive nature of this pavement, across some 35 km roughly perpendicular to depositional strike, implies a very low gradient shoreline with extensive peritidal flats.

The pavement of tentaculitid skeletons was buried by 6–8 mm of carbonate silt (Fig. 11B). This represents an episode of deposition in which pelletal carbonates were transported in a shoreward direction and deposited rapidly. Following this series of events, the region experienced a period of minimal sedimentation, during which cements began to develop in the interstices of the carbonate pellets forming an indurated firmground. Presumably this partial cementation took place slightly below the sediment-water interface, associated with sulfate reduction and the build up of bicarbonate ions within the sediment (Wilson and Palmer, 1992). Some of the cementation could have resulted from early meteoric diagenesis during periods of exposure. The exact timing of the induration of the tentaculitid pavement is unclear, but it appears to have preceded the induration of the overlying calcisiltite layer. The embedment of tentaculitids in vertical burrows may have occurred at this stage, prior to full cementation.

During a second period of prolonged sediment starvation, the loose surficial sediment plus portions of the upper carbonate silt layer were exhumed and scoured away. Some of the erosion occurred after a period of induration. Some fragments and collapsed ledges of the calcisiltite layer are found on the surface, which suggests that the upper few centimeters of that layer were cemented, while a thin zone of non-cemented sediment existed below this crust, but above the tentaculitid pavement. Burrowing may have contributed to some exhumation of the firm carbonate silt, as suggested by the groove-like features cut into its surface. Erosion undercut the crust of the upper calcisiltite. Subsequently, scouring removed some major portions of the upper surface, forming indurated clasts of the calcisiltite and exposing portions of the older tentaculitid pavement (Fig. 11C). Hence, erosion produced a composite hardground, composed of two distinctive lithified layers, still separated by a thin zone of less-indurated sediment. This exhumed surface had a micro-topography with a relief of less than 2 cm between the tentaculitid pavement and the more elevated patches and knobs composed of calcisiltite.

The exhumed irregular surface then was colonized by two or more generations of postibulinid edrioasteroids (Fig. 11D). Evidently, the tentaculitid pavement was cemented, as indicated by the encrustation of a few edrioasteroids directly on this surface. Unlike most subtidal hard-

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FIGURE 11—Block diagrams illustrating reconstructions of various stages in the development of Manlius hardground. (A) Accumulation of *Tentaculites* shells and their alignment by oscillatory currents. (B) Erosion and partial exhumation of previously buried *Tentaculites* pavement; note erosive undercutting of partially-cemented calcisiltite. (C) Colonization of hardground by edrioasteroids. (D) Final rapid burial of hardground by siliciclastic muds.

grounds, there are very few bryozoans or *Trypanites* on this surface. This suggests that the surface might have had a veneer of some other material on it, such as sediment or stromatolitic microbial films, which prevented many organisms from actually settling. However, the postibulinid edrioasteroids were capable of encrusting both the smooth (preferred) surface of the hardened calcisiltite and the rough surface of the tentaculitid pavement. New tentaculitid individuals accumulated in low spots on the hardground surface. This may further indicate a period of condensation associated with the exposure of the hardground. More than one generation of edrioasteroids was present at the time of final burial.

The last event to affect the hardground was a pulse of rapid burial by silty, terrigenous muds. This burial may have resulted from the backwash of a storm surge that eroded sediment from the upper parts of the tidal flat. The sediment accumulated rapidly enough so that the edrioasteroids were buried intact with relatively little evidence of decay (Fig. 11E). Perhaps the most remarkable feature of this occurrence is the apparent correlation of this burial event for over 35 km perpendicular to shoreline. This and similarly widespread obrution deposits (Brett and Seilacher, 1991) suggest that mud blankets may be distributed very rapidly and broadly following certain storm events.

COMPARISON WITH OTHER HARDGROUNDS

Most hardgrounds described in previous literature, at least for the early to mid-Paleozoic, occur in shallow offshore-shelf environments (Wilson and Palmer, 1992). Most commonly, they seem to have been associated with the outer margins of skeletal shoals. In such areas rapid transport and deposition of skeletal sand and gravel resulted in the development of episodic layers, which then became cemented. These offshore shoal-margin hardgrounds, described by Fürsich (1979), Brett and Brookfield (1984), Brookfield and Brett (1988), and others, seem to be the normal situation. In contrast, the Manlius hardgrounds were developed in a peritidal facies. These fine-grained sediments were deposited in inner-lagoonal to lower tidal-flat settings. As such, they may have been subjected to rare exposure.

The faunal assemblage associated with this hardground is quite different from those described in most early to middle Paleozoic hardground faunas. Whereas the latter tend to be dominated by the boring *Trypanites*, various encrusting and mound-shaped bryozoans, and annelid tubes, this hardground shows an almost monospecific assemblage of edrioasteroids. Edrioasteroids occur on many of the more offshore marine hardgrounds, but in such cases they generally are less common than bryozoans and *Trypanites*.

The assemblage of leperditian ostracodes, small pterioid bivalves, a few species of brachiopods, and abundant tentaculitids suggests a very nearshore (BA inner 2 to 1 of Boucot, 1975) assemblage. Relatively few hardgrounds are known from BA 1 and 2 assemblages. However, rockgrounds representing ancient rocky shoreline assemblages have been discussed in some detail by Johnson (1987, 1988a, b), Johnson & Rong (1989), and Johnson and Baarli (1999). Rocky shoreline assemblages through time have been dominated by just a few taxa of highly eurytopic or tolerant organisms, such as acorn barnacles in the present day. Edrioasteroids have not been reported previously on rocky shoreline assemblages, although there is an undescribed occurrence in the Lower Pennsylvanian of Oklahoma. However, nearshore hardgrounds more nearly comparable to those described herein for the Lower Devonian Manlius Formation have been observed through a fairly long time range. The oldest of these hardgrounds developed in the Lower Ordovician Fillmore and the Middle Ordovician Kanosh Formations in Utah and Nevada. These hardground faunas include both edrioasteroids and pelmatozoan holdfasts, and developed on micritic mound facies or on skeletal grainstones and flat pebble conglomerates (Guensburg and Sprinkle, 1992; Wilson and Palmer, 1990; Wilson et al., 1992).

Two undescribed Silurian peritidal hardgrounds also are known. Desiccation-cracked calcareous green mudstones in the mid-Silurian (Aeronian) Wingfield Formation, near Cabot Head, Ontario have yielded rare undescribed edrioasteroids, apparently pyrgocystids, in association with firmgrounds or hardgrounds containing abundant leperditian ostracodes and tentaculitids. The most nearly comparable situation occurs in the mid-Silurian (Ludlow) Mackenzie Formation (Lockport Group) in central Pennsylvania. Thin-bedded platy limestones alternating with shales show rich assemblages of a few rhynchonellid brachiopods, pterioid bivalves, leperditian ostracodes (*Hermanina*), and tentaculitids. Platter-like hardgrounds that developed in this facies are well exposed at Castanea, Pennsylvania and have yielded an assemblage of a few *Trypanites* borings and a number of undescribed hemicystitid edrioasteroids. These are comparable in size to the edrioasteroids seen on the Manlius hardground and appear to represent a similar depositional setting. Leperditian- and tentaculitid-rich, hard- and firmground surfaces also are known from the Upper Silurian Lockport Group in New York and the Keyser Formation of Pennsylvania. However, to date they have not yielded any edrioasteroids.

Finally, a high-density assemblage of three species of edrioasteroids occurs in the Upper Devonian Shell Rock limestone in east-central Iowa (Koch and Strimple, 1968). These edrioasteroids, associated with attached short-stalked rhombiferan cystoids, also inhabited a shallow-water, nearshore rocky platform and may represent somewhat similar environments.

Hence, monospecific edrioasteroid populations associated with near shore shallow-water hardgrounds of BA 1 and 2 are known from at least Middle Ordovician to Late Devonian time and perhaps persisted into the Pennsylvanian. These persistent low-diversity communities were probably relatively resilient to environmental change. The edrioasteroids may have occupied a niche somewhat similar to acorn barnacles in modern rocky intertidal settings. Because of their ability to close their ambulacral plates, these organisms probably were effective in sealing off their body during times of stress, possibly including temporary periods of exposure. In addition, they also were cemented firmly and streamlined against dislodgement by tidal currents or waves, which demonstrably swept these rocky settings. Their patchy distribution through time may represent nothing more than a taphonomic bias against preservation in near-shore environments.

SUMMARY

An Early Devonian hardground as described herein provides a detailed case study of a peritidal hard substrate community. The hardground evidently formed due to partial erosion of a relatively firm pelletal mud that had been deposited above a cemented, wave-aligned tentaculitid layer. Strong bimodally aligned *Tentaculites* suggest that these communities may have occupied a position close to a strand line of the Early Devonian sea. The life mode of the tentaculitids remains uncertain. However, evidence of possible in situ specimens surrounded by scour pits suggests that these animals may have lived as sedentary suspension feeders, with the shells oriented vertically (apex downward) within firm sediments. A population of edrioasteroids preserved in situ on the hardground shows characteristics of variable recruitment through an annual cycle. These organisms inhabited a nearshore, wave- or tidal-swept environment where they encrusted the irregularly sculptured hardground—a mode of life perhaps analogous to living acorn barnacles. If present correlations are correct, this hard pavement extended for at least 35 km perpendicular to depositional strike, implying an extremely low gradient peritidal zone. This environment was subjected to oscillatory currents, probably associated with minor tidal currents, and potentially to limited subaerial exposure. Moreover, the final burial of the edrioasteroid community would represent a rapid and widespread mud-blanketing event.

This hardground community is representative of a persistent low-diversity nearshore assemblage that includes leperditian ostracodes, tentaculitids, a few species of articulate brachiopods, and edrioasteroids. This general community type persisted for approximately 80 to 100 million years between the Early Ordovician and the Late Devonian.

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REFERENCES

ANDERSON, E.J., 1971, The interpretation of calcarenite paleoenvironments: the Coeymans Formation, Lower Devonian of New York: Guidebook for Eastern Section Society of Economic Paleontologists and Mineralogists Field Conference: Temple University, Philadelphia, 67 p.

ANDERSON, E.J., and GOODWIN, P.W., 1980, Application of the PAC hypothesis to limestones of the Helderberg Group: Guidebook for Eastern Section Society of Economic Paleontologists and Mineralogists Field Conference, 32p.

ANDERSON, A.J., GOODWIN, P.W., and SOBIESKI, T.H., 1984, Episodic accumulation and the origin of formation boundaries in the Helderberg Group of New York State: Geology, v. 12, p. 120–123.

BELL, B.M., 1976a, Phylogenetic implications of ontogenetic development in the Class Edrioasteroidea (Echinodermata): Journal of Paleontology, v. 50, p. 1001–1019.

BELL, B.M., 1976b, A Study of North American Edrioasteroidea: New York State Museum Memoir 21, 446 p.

BELL, B.M., and PETERSEN, M.S., 1976, An edrioasteroid from the Guilmette Formation at Wendover, Utah–Nevada: Journal of Paleontology: v. 50, p. 577–589.

BOUCOT, A.J., 1975, Evolution and Extinction Rate Controls: Elsevier, New York, 427 p.

BRETT, C.E., 1988, Paleoecology and evolution of marine hard substrate communities: an overview: PALAIOS, v. 3, p. 374–378.

BRETT, C.E., 1999, Lower Devonian Manlius/Coeymans Formation of central New York, USA: *in* Hess, H., Ausich, W.I., Brett, C.E., and Simms, M.J., eds., Fossil Crinoids: Cambridge University Press, Cambridge, p. 103–110.

BRETT, C.E., and BROOKFIELD, M.E., 1984, Morphology, faunas and genesis of Ordovician hardgrounds from southern Ontario, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 46, p. 233–290.

BRETT, C.E., and LIDDELL, W.D., 1978, Preservation and paleoecology of a Middle Ordovician hardground community: Paleobiology, v. 4, p. 329–348.

BRETT, C.E, LIDDELL, W.D., and DERSTLER, K.L., 1983, Late Cambrian hard substrate communities from Montana/Wyoming: the oldest known hardground encrusters: Lethaia, v. 16, p. 281–289.

BRETT, C.E., and SEILACHER, A., 1991, Fossil Lagerstaetten; a taphonomic consequence of event sedimentation: *in* Gerhard, E., Ricken, W., and Seilacher, A., eds., Cycles and Events in Stratigraphy: Springer-Verlag, New York, p. 283–297.

BROOKFIELD M.E., and BRETT, C.E., 1988, Paleoenvironments of the Mid-Ordovician (Upper Caradocian) Trenton limestones of southern Ontario, Canada: storm deposition on a shoal-basin shelf model: Sedimentary Geology, v. 57, p. 75–105.

EBERT, J.R., MATESON, D.K., and NATEL, E.M., 2001, Early Acadian tectonism and Pridoli–Lochkovian eustasy in the Helderberg Group of New York State: Abstracts of the 15th International Senckenberg Conference, Frankfurt, Germany, p. 34.

FISHER, D.C., 1966, Small conical shells of uncertain affinities: *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology: Geological Society of America, Boulder, p. W98–W143.

FISHER, D.W., 1979, Devonian stratigraphy and paleoecology in the Cherry Valley, New York region: *in* Friedman, G.M., ed., New York State Geological Association Annual Meeting Guidebook 51: New York State Geological Survey, Albany, p. 20–46.

FISHER, D.W., 1980, Bedrock Geology of the Central Mohawk Valley, New York: Map and chart series (New York State Geological Survey), no. 33, 44 p.

FÜRSICH, F.T., 1979, Genesis, environments, and ecology of Jurassic hardgrounds: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 158, p. 1–63.

GOODWIN, P.W., and ANDERSON, E.J., 1985, Punctuated aggradational cycles: a general hypothesis of episodic stratigraphic accumulation: Journal of Geology, v. 93, p. 515–533.

GOODWIN, P.W., ANDERSON, E.J., GOODMAN, W.M., and SARAKA, L.J., 1986, Punctuated aggradational cycles: implications for stratigraphic analysis: Palaeoceanography, v. 1, p. 417–429.

GUENSBURG, T.E., 1984, Echinodermata of the Middle Ordovician Lebanon Limestone, central Tennessee: Bulletins of American Paleontology, v. 86, p. 1–100.

GUENSBURG, T.E., 1988, Systematics, functional morphology, and life modes of Late Ordovician edrioasteroids, Orchard Creek Shale, southern Illinois: Journal of Paleontology, v. 62, p. 110–126.

GUENSBURG, T.E., and SPRINKLE, J., 1992, Rise of echinoderms in the Paleozoic evolutionary fauna: significance of paleoenvironmental controls: Geology, v. 20, p. 407–410

HALL, J., 1839, Third annual report of the fourth geological district of the State of New York: New York Geological Survey Annual Report, v. 3, p. 287–319.

IRWIN, M.L., 1965, General theory of epeiric clear water sedimentation: American Association of Petroleum Geologists Bulletin, v. 49, p. 445–459.

JOHNSON, M.E., 1987, Encrusting corals on a latest Ordovician to earliest Silurian rocky shore southwest Hudson Bay, Manitoba, Canada: Geology, v. 15, p. 15–17.

JOHNSON, M.E., 1988a, Hunting for ancient rocky shores: Journal of Geological Education, v. 36, p. 147–154.

JOHNSON, M.E., 1988b, Why are ancient rocky shores so uncommon?: Journal of Geology, v. 96, p. 469–480.

JOHNSON, M.E., and BAARLI, B.G., 1999, Diversification of rocky-shore biotas through geologic time: Geobios, v. 32, p. 257–273.

JOHNSON, M.E., and RONG, J.Y., 1989, Middle to Late Ordovician rocky bottoms and rocky shores from the Manitoulin Island area, Ontario: Canadian Journal of Earth Science, v. 26, p. 642–653.

KAMMER, T.W., TISSUE, E.C., and WILSON, M.A., 1987, *Neoisorophusella*, a new edrioasteroid genus from the Upper Mississippian of the Eastern United States: Journal of Paleontology, v. 61, p. 1033–1042.

KOCH, D.L., and STRIMPLE, H.L., 1968, A new Devonian cystoid attached to a discontinuity surface: Iowa Geological Survey Report of Investigations, v. 5, p. 1–49.

LAPORTE, L.F., 1967, Carbonate deposition near mean sea-level and resultant facies mosaic: Manlius Formation (lower-Devonian) of New York State: American Association of Petroleum Geologists Bulletin, v. 51, p. 73–101.

LAPORTE, L.F., 1969, Recognition of a transgressive carbonate sequence within an epeiric sea: Helderberg Group (Lower Devonian) of New York State: *in* Friedman, G.M., ed., Depositional Environments in Carbonate Rocks: Society of Economic Paleontologists and Mineralogists Special Publication 14, Tulsa, Oklahoma, p. 98–119.

MATTESON, D.K., NATEL, E.M., and EBERT, J.R., 1996, Extending the stratigraphic range of a distinctive Silurian community: a Pridolian annelid and dasycladacean algae dominated biota from the upper Thacher Member, Manlius Formation (Helderberg Group) of New York: Second International Symposium on the Silurian System Abstracts, Rochester, NY, p. 74A

MEYER, D.L., 1990, Population paleoecology and comparative taphonomy of two edrioasteroid (Echinodermata) pavements: Upper Ordovician of Kentucky and Ohio: Historical Biology, v. 4, p. 155–178.

RICKARD, L.V., 1962, Late Cayugan (Upper Silurian) and Helderbergian (Lower Devonian) stratigraphy in New York State: New York State Museum and Science Service Bulletin, v. 386, 157 p.

RICKARD, L.V., and ZENGER, D.H., 1964, Stratigraphy and Paleontology of the Richfield Springs and Cooperstown Quadrangles, New York: New York State Museum and Science Service Bulletin 369, 101p.

SLOSS, L.L., 1963, Sequences in the cratonic interior of North America: Geological Society of America Bulletin, v. 74, p. 93–114.

STANLEY, S.M., and HARDIE, L.A., 1998, Secular oscillations in carbonate mineralogy of reef-building and sediment-producing organisms driven by tectonically forced shifts in sea water chemistry: Palaeogeography, Palaeoclimatology, Palaeoecology v. 144, p. 3–19.

SUMRALL, C.D., 1996, Late Paleozoic edrioasteroids from the North American mid-continent: Journal of Paleontology, v. 70, p. 960–985.

SUMRALL, C.D., 1999, Spatfall accumulations and differential taphonomy of edrioasteroids in the Mississippian Borden Formation of northern Kentucky: Geological Society of America Abstracts with Programs, v. 32, p. A–421.

SUMRALL, C.D., 2001, Paleoecology and taphonomy of two new edrioasteroids from a Mississippian hardground in Kentucky: Journal of Paleontology, v. 75, p. 136–146.

SUMRALL, C.D., and BOWSHER, A.L., 1996, *Giganticlavus*, a new genus of Pennsylvanian edrioasteroid from North America: Journal of Paleontology, v. 70 p. 986–993.

SUMRALL, C.D., GARBISCH, J., and POPE, J.P., 2000, The systematics of postibullinid edrioasteroids: Journal of Paleontology, v. 74, p. 72–83.

WADDINGTON, J.B, 1980, A soft substrate community with edrioasteroids from the Verulam Formation (Middle Ordovician) at Gamebridge: Canadian Journal of Earth Sciences, v. 17, p. 674–679.

WILKINSON, B.H., BRETT, C.E., JANECKE, S.U., 1982, Low-magnesium calcite marine cement in Middle Ordovician hardgrounds from Kirkfield, Ontario: Journal of Sedimentary Petrology, v. 52, p. 47–57.

WILSON, M.A., and PALMER, T.J., 1990, A review of evolutionary trends in carbonate hardground communities: The Paleontological Society Special Publication, v. 5, p. 137–152.

WILSON, M.A., and PALMER, T.J., 1992, Hardgrounds and Hardground Faunas: University of Wales, Aberystwyth Institute of Earth Studies Publication v. 9, Aberystwyth, p. 1–131.

WILSON, M.A., FINTON, C.D., GUENSBURG, T.E., KAUFMAN, L.E., and PALMER, T.J., 1992, The development of an Early Ordovician hardground community in response to rapid sea-floor calcite precipitation: Lethaia, v. 25, p. 19–34.

ZAR, J.H., 1999, Biostatistical Analysis, 4th edition: Prentice Hall, Upper Saddle River, 929 p.

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