ORGANISM–SEDIMENT RELATIONSHIPS IN SILURIAN MARINE ENVIRONMENTS

by C. E. BRETT

ABSTRACT. Organisms played major roles as producers and modifiers of sediments in many Silurian marine environments. Pelmatozoan skeletal debris formed extensive shoals and banks in many high-energy, tropical environments; algae, bryozoans, tabulate corals, and stromatoporoids were the major skeletal contributors to reefal buildups common in mid and late Silurian subtropical shelves. Articulate brachiopods and lesser numbers of ostracodes, trilobites, and molluscs formed extensive, although relatively thin (5–15 cm), shell beds in shallow shelf facies; pelagic, cephalopod limestones characterized the circum-Gondwana region. Skeletal hard substrates and hardgrounds supported relatively complex epifaunal suspension-feeding communities. The apparent scarcity of endolithic sponges and bivalves indicates that rates of hard substrate bioerosion were far below those of post-Palaeozoic times. Substrate selection, spatial competition, and polarity of cryptic versus exposed subcommunities are clearly evident, for the first time, in Ordovician to latest Silurian hard substrate communities. Unconsolidated sediments displayed a wide variety of characteristic trace and body fossil associations that were, to some degree, substrate controlled. Sand and silt substrates supported a low diversity of shelly organisms but preserved abundant traces, ranging from *Skolithos* and *Arthrophycus*-dominated nearshore sediments to offshore diverse ichnofacies. Some Silurian nearshore sediments display bioturbation up to 1m deep and contain very few epifaunal organisms, suggesting destabilization of substrates. However, biogenic disturbance of offshore, soft substrates remained relatively restricted in the Silurian with infauna extending only about 10–15 cm into the sediment. Silurian epifaunal organisms displayed varied morphological adaptations to soft substrates, including 'snowshoe' and 'iceberg' strategies, as well as attachment to other organisms. Taphonomic feedback, mediated by storm depositional processes, led to variably complex shelly communities in offshore, level-bottom areas. Low, intermediate, and high-level suspension feeding tiers existed, with some pelmatozoans attaining levels of over 1m above the substrate. In shallow carbonate shelves, sediment baffling and binding were induced by thickets of pelmatozoans, ramose bryozoans, and corals. Stromatolites were confined largely to hypersaline or low-oxygen inner shelf environments, presumably due to disruption of algal mats by grazers in normal marine settings. However, many offshore bioherms are partially thrombolitic. Hence, algal binding facilitated the development of coral-stromatoporoid bioherms in many high energy shelf settings. Bioherms, in turn, provided niches for numerous secondary inhabitants. Substrate appears to have been a critical determinant of local patch community development within generalized Silurian habitats. However, at the broader level of biofacies, bathymetric and sedimentological (deposition rates, turbidity) features played more dominant roles in controlling distribution patterns.

ONE of the most exciting and challenging areas of palaeoecology is the elucidation of interactions between physical environments and modes of life in ancient organisms. The relationship of organisms and sediments is a complex one involving numerous feedback loops. On the one hand, organisms are significant producers and modifiers of sediments, and on the other hand, sediments comprise the substrates upon and within which benthic organisms dwell. In some Silurian environments, particularly carbonate platforms, organisms were the primary producers of sediments, both as biologically standardized sedimentary particles and as organic buildups such as reefs, biostromes, and shell beds. Marine animals also played a critical role in modifying sediments by producing faecal pellets, agglutinating fine-grained sediments into silt and fine sand-size particles, and by the sorting and churning action associated with bioturbation. Cyanobacteria, algae, and certain animals (corals, sponges, bryozoans, pelmatozoans) baffled or bound fine-grained sediments in place, greatly changing the local properties of the sea floor. Other organisms produced fine-grained sediments out of larger grains by their bioerosive functions.

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Silurian organisms filled all of these roles as sedimentological agents, although not to the same extent as recent organisms. For example, the production of skeletal debris by echinoderms may have matched that typical of modern carbonate shelves, where algae and corals are the primary sediment producers (e.g. Lowenstam 1957). On the other hand, Silurian brachiopods did not commonly form massive shell beds of the sort produced by molluscs in some post-Palaeozoic shelf environments. Also, Silurian organisms were much less significant in producing pelagic sediments than are nannoplankton, foraminiferans, and radiolarians in modern seas. Rates of both bioturbation and bioerosion appear to have been much lower in the Silurian than in modern marine ecosystems, largely because of the subsequent evolution of deep-burrowing bivalves and other organisms as well as bioeroding sponges, echinoids, and bivalves. Silurian reefs were produced largely by the baffling and binding guilds of organisms, whereas modern reefs are somewhat more dominated by framework constructors, among them mostly scleractinian corals.

Substrate is recognized widely as one of the key parameters that control the distribution of modern organisms and the same was undoubtedly so in the Palaeozoic (see West 1977; Boucot 1981 for detailed treatment). The field of substrate/organism interactions is particularly well suited for palaeoecological study, as substrate is the one environmental parameter that may be preserved directly in the geological record as sedimentary rocks. Many organisms require hard or at least firm substrates for initial attachment and in some cases for subsequent growth. Others require soft, fluid substrates for burrowing or furrowing in search of food and dwelling sites. A complex interaction exists between skeletonized organisms and substrates, sometimes referred to as taphonomic feedback (Kidwell and Jablonski 1983). The buildup of skeletal debris on the sea floor has a positive effect in providing substrates for epifaunal communities. However, the development of pavements of shells may also inhibit infaunal organisms and some epifaunal scavenging and furrowing animals. Conversely, strong bioturbation of substrates may destabilize the sediment/water interface producing a fluid 'floc' zone (Rhoads 1974), which is unfavourable to the settlement and/or further growth of epifaunal organisms and may also produce high turbidity which clogs filtration systems of suspension-feeding organisms. Such trophic group amensalism was undoubtedly less significant in the Silurian than in later Palaeozoic and particularly in post-Palaeozoic times, owing to the absence of deep burrowing infaunal organisms in most offshore environments – the 'biological bulldozing' factor (Thayer 1983). Nonetheless, trophic group amensalism (Rhoads 1974) probably did have some importance in controlling distribution of organisms on soft substrates.

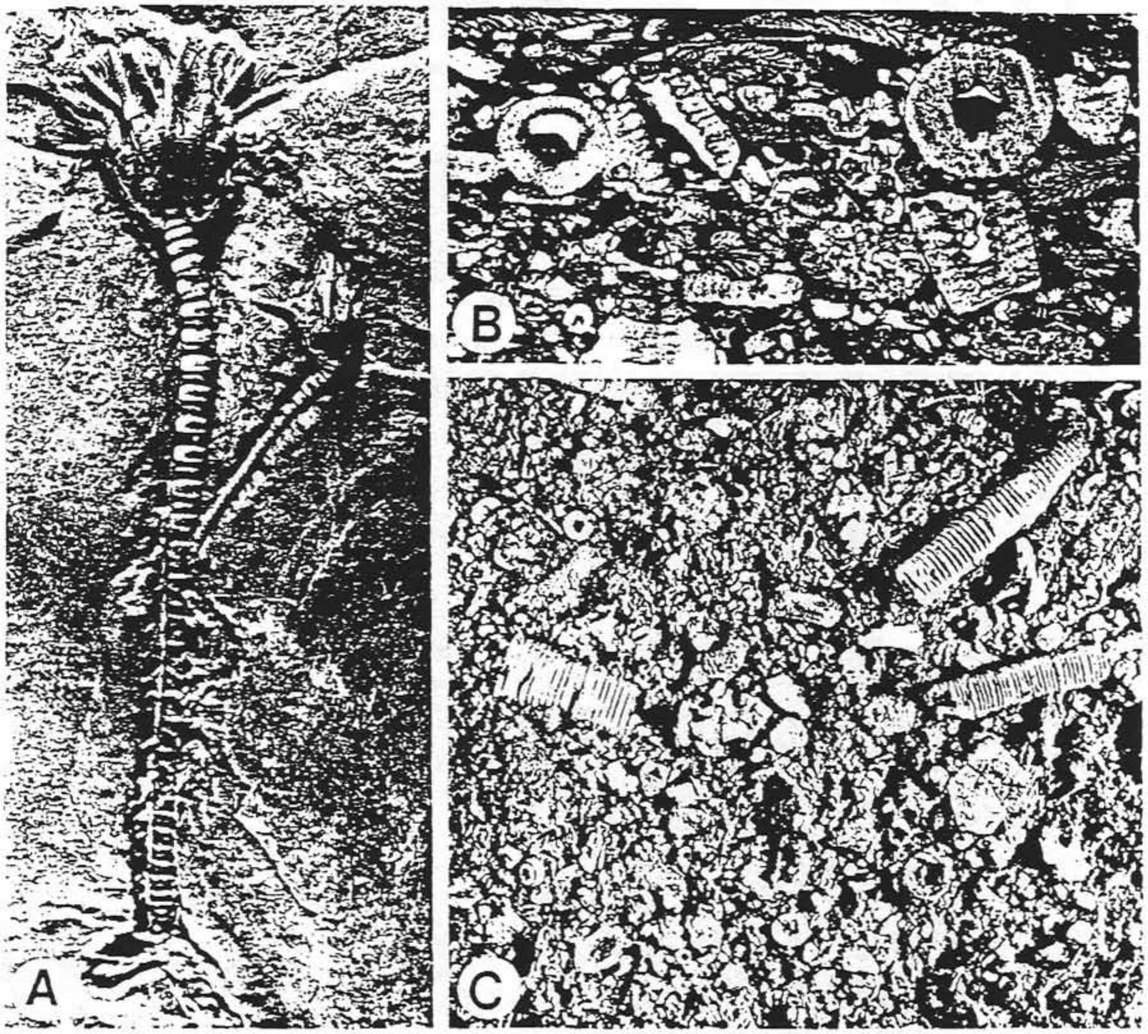
Again, uniformitarianism partially fails as a guide for interpreting Silurian organism/substrate relationships. Many strategies very common among extant marine animals, such as deep infaunal suspension feeding and vagrant predatory and grazing modes of life, were relatively rare or absent in the Silurian. Conversely, some of the most abundant strategies of Silurian organisms such as soft substrate reclining, inferred for many brachiopods and other organisms, appear to be much scarcer in modern communities. Undoubtedly, evolutionary escalation (*sensu* Vermeij 1987) in terms of predation, competition, and substrate interactions has played an important role in altering Palaeozoic-type communities to modern forms.

In this paper, I explore the two sides of organism–sediment interaction as it relates specifically to Silurian marine environments. Data are synthesized from a variety of disparate sources, although I cannot claim to be comprehensive. Information on organism/sediment relationships should be of considerable importance not only to palaeoecologists and sedimentologists in their attempts to understand ancient depositional environments, but also to palaeobiologists in seeking answers to broader-scale evolutionary questions of adaptation and interaction amongst ancient organisms.

SEDIMENT PRODUCTION AND MODIFICATION BY SILURIAN ORGANISMS

Organisms as sediment formers

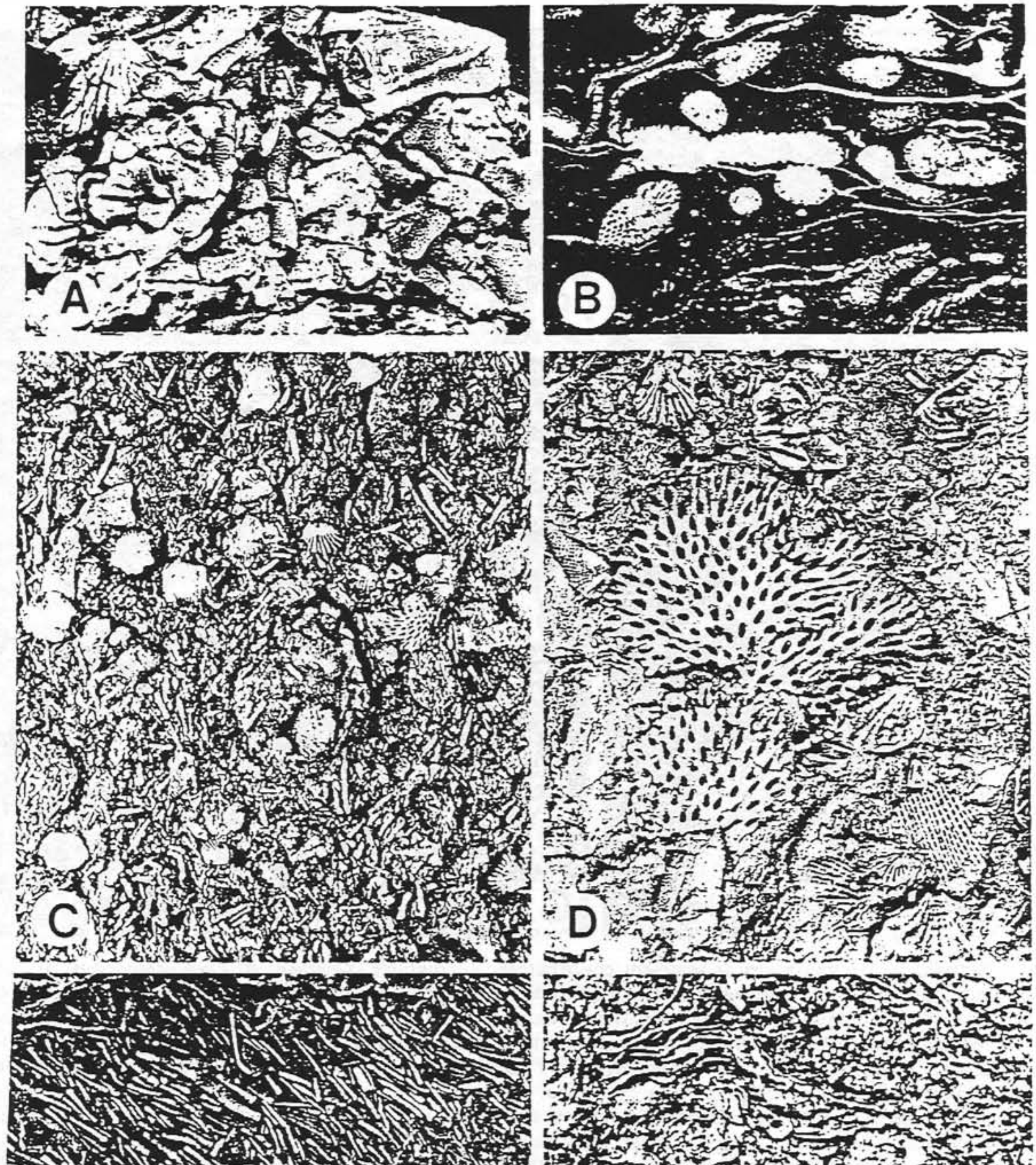
Organisms played major roles as producers and modifiers of sediments in many Silurian marine environments. Pelmatozoan echinoderms, bryozoans, brachiopods, corals, and stromatoporoids all



TEXT-FIG. 1. Pelmatozoans as sediment contributors. *A*, complete specimens of *Eucalyptocrinites*, one of the most abundant and widespread genera of Silurian crinoids; note dendritic holdfast, robust column, and crown; each of these components yielded persistent skeletal ossicles; also note attachment of juvenile to adult crinoid; the gregarious nature of pelmatozoans aided in the formation of local thickets of crinoids; Wenlock, Rochester Shale, Orleans Co., NY; photo courtesy of S. T. LoDuca, × 1·25. *B*, polished section of crinoidal packstone (biomicrite) showing numerous large cylindrical pelmatozoan columnals and plates, and admixed bryozoans; note geopetal mud filling in lumen of columns, and partial winnowing of muds in grain interstices; Wenlock, Irondequoit Limestone, Niagara Gorge, Niagara Co., NY, × 3·0. *C*, surface of weathered crinoidal grainstone showing robust pluricolumnals, plates, and partly articulated thecae of crinoids and rhombiferans; Wenlock, Gasport Limestone, Grimsby, Ontario, Canada, × 1·0.

contributed significant quantities of skeletal debris, particularly in subtropical, shallow platform areas (Text-figs 1–7).

Pelmatozoan echinoderms (crinoids and stemmed blastozoans) have justly been termed the '*Halimeda* of the Paleozoic' (Lowenstam 1957). Volumetrically, pelmatozoans contributed the greatest proportion of skeletal debris to the formation of Silurian carbonates. A survey of about 100 fossiliferous carbonate samples from the Great Lakes area of North America reveals that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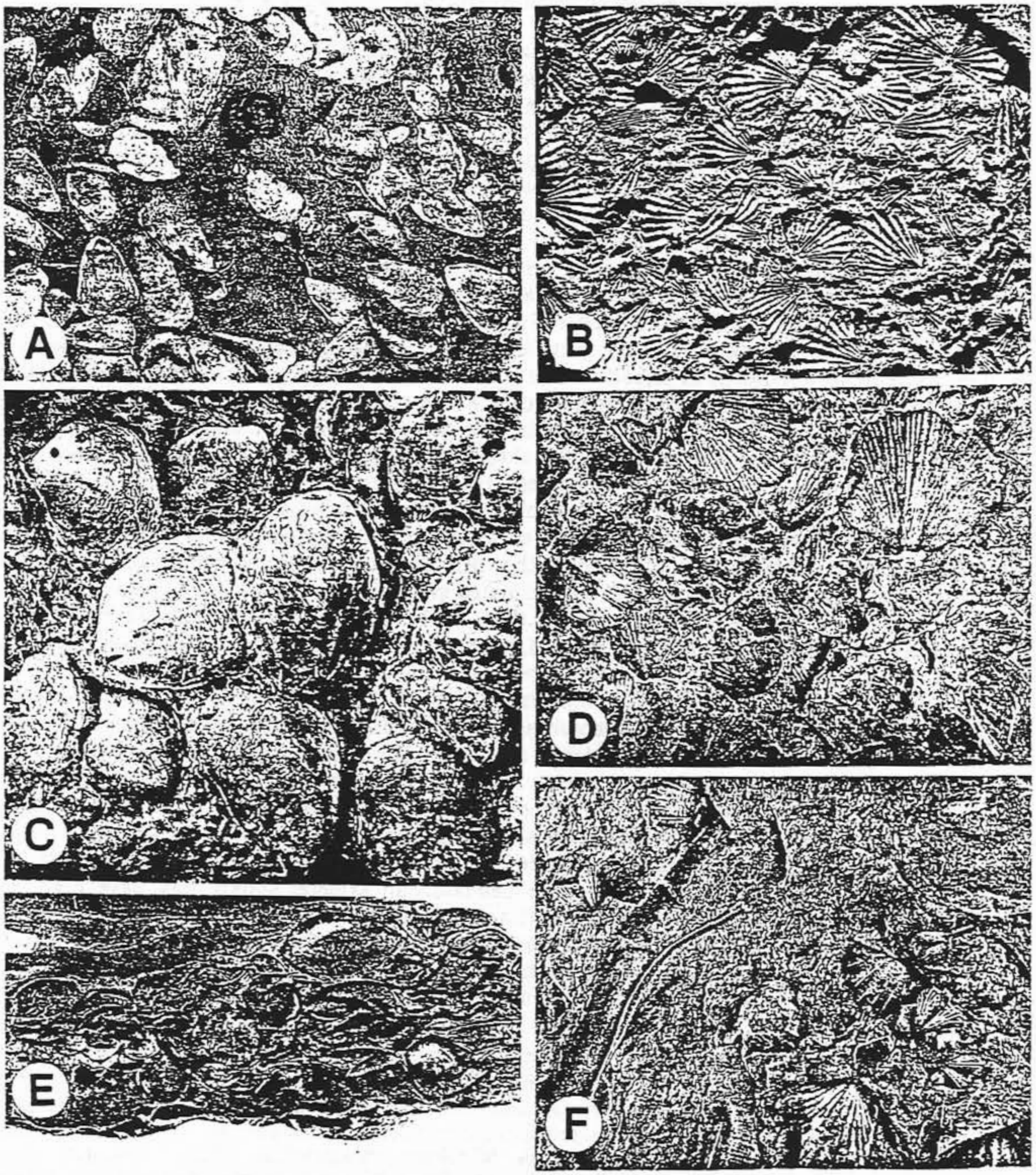
approximately 90 % are composed predominantly of pelmatozoan (~ 30–80 %) wacke-, pack- and grainstones. In particular, the columns of pelmatozoans, which in the Silurian ranged to over a metre in length and were typically 5–10 mm in diameter, disarticulated relatively rapidly upon death to form resistant sedimentary particles (Text-fig. 1). The pluricolumnals and individual ossicles that constitute crinoid stems form a major and probably underestimated fraction of many sediments. Macurda and Meyer (1983) estimated that an average cubic metre of crinoidal limestone represents remains of about 15,000 crinoids. As such, some Silurian 'encrinites', which may range up to tens of metres in thickness and span hundreds of square kilometres obviously represent the remains of vast numbers (about 10^{16}) of individual crinoids and cystoids. Even in many wackestones the proportion of echinoderm skeletal debris may range upward to 20 or 30 % of rock volume.

Crinoid columnals, composed of relatively large single crystals of high magnesian calcite, are among the most durable of all skeletal particles in terms of mechanical breakdown. Geochemically, they are relatively resistant to dissolution as a result of their large crystal size and their apparent rapid recrystallization from high magnesian calcite to the more stable low magnesian calcite phase. Seilacher (1982) proposed a 'maturity index' for skeletal sediments: aragonitic shells < calcitic shells < echinoderm ossicles < phosphatic skeletons. This gradient implies that pelmatozoan ossicles are among the last bioclasts to disintegrate as sediments are progressively reworked. The net result is that the more robust pelmatozoan columnals may form lag deposits, commonly with minor enrichments of other geochemically stable allochems such as glauconitic grains and phosphatic nodules and steinkerns. It should be noted that pelmatozoan thecal and arm/brachiole plates are almost invariably underrepresented in amalgamated grainstone accumulations, presumably because their relatively thin, fragile nature causes them to be fragmented and abraded rapidly. They ultimately form unrecognizable, fine-grained, mud- and silt-size sediment which may be winnowed out from high-energy, grain-supported deposits.

Columnals are also 'biologically standardized' particles (Seilacher 1973). Their cylindrical nature causes accumulations of crinoid pluricolumnals to form relatively unstable, shifting sand or gravel blankets, perhaps comparable with barren oolite shoals observed in the Bahamas (Purdy 1964). This, of course, begs the important question as to the source areas of pelmatozoan skeletal shoals. Most Silurian pelmatozoans were, themselves, adapted to semipermanent attachment on hard or firm substrates (Brett 1981, 1984). Hence, shifting pelmatozoan sands would not have provided adequate attachment substrates for later generations of most pelmatozoans. The paradox has at least three potential solutions. First, some pelmatozoan skeletal shoals may have been partly allochthonous. Aigner (1985) proposed that amalgamated crinoidal packstones and grainstones commonly accumulated as skeletal shoals landward of the life sites of the crinoids themselves. In the case of the Triassic Muschelkalk, small bioherms and hardgrounds just offshore of the skeletal shoals probably represented 'rooting grounds' for *Encrinus* and other crinoids (Hagdorn 1985).

TEXT-FIG. 2. Bryozoans as constituents of Silurian sediments. *A*, fossiliferous mudstone intercalated with intact fragile, ramose bryozoans (*Cheilotrypa*), as well as brachiopods and the theca of a pelmatozoan (*Stephanocrinus*, upper right): bryozoan–pelmatozoan thickets were important contributors of offshore biostromal sediments: Wenlock, Rochester Shale, Middleport, Niagara Co., NY. × 1·5. *B*, thin section of similar bryozoan-rich mudstone showing cross-section of spar-filled ramose bryozoans, as well as foliaceous and fenestrate bryozoans and brachiopods, Wenlock, Rochester Shale, Niagara Gorge, Niagara Co., NY. × 3·0. *C*, slab of argillaceous packstone comprised of small twig-like bryozoans (*Helopora fragilis*), sheet-like bifoliates (*Phaenopora*), rhynchonellid (*Stegerhynchus*) and orthid (*Resserella*) brachiopods: Lower Llandovery, Cabot Head Shale, Hamilton, Ontario. × 1·0. *D*, bryozoan-rich packstone with abundant lacey bryozoans (*Phylloporina*, at centre, and *Fenestella*) and brachiopods (*Plectatrypa*); Rochester Shale, Niagara Gorge, Niagara Co., NY. × 1·5. *E*, slab of red sandy packstone composed of current-aligned *Helopora* bryozoans: Lower Llandovery, Grimsby Formation, Hamilton, Ontario, × 0·8. *F*, field photograph of weathered surface of small bioherm showing foliaceous fistuliporoid bryozoan which served to bind sediments in place: note ingrown specimens of *Favosites*: Wenlock, Gasport Limestone, Lockport, Niagara Co., NY, × 0·5.



TEXT-FIG. 3. Brachiopod shell beds across an environmental gradient. Views of typical brachiopod assemblages representing nearshore (BA-1) to offshore (BA-4) benthic assemblages. *A*, bedding plane in reddish sandstone, displaying numerous disarticulated valves of *Lingula* (BA-1); note phosphatic gastropod in centre of view; lower Llandovery, Grimsby Sandstone, Niagara Gorge, Niagara Co., NY, × 1·0. *B*, coquinoid brachiopod grainstone ('pearly bed') composed almost entirely of *Eocoelia intermedia* (BA-2); middle Llandovery, Lower Sodus Shale, Rochester, Monroe Co., NY, × 1·5. *C*, biostromal packstone composed mainly of large robust shells of *Pentamerus oblongus* (BA-3); middle Llandovery, Reynales Limestone, Rochester, Monroe Co., NY, × 0·5. *D*, dolomicrite slab covered with large valves of *Costistricklandia*, cf. *C. gaspiensis* (BA-4);

Aigner argued that during storms, low-density crinoid ossicles would commonly be transported shoreward up to a few kilometres and accumulate as skeletal sandbanks. This model may apply to some Silurian crinoid grainstone bodies. In other cases, small patches of stabilized micritic sediments, microbioherms, apparently developed within crinoidal grain shoals, but ultimately were mainly destroyed by storm wave reworking. For example, in the Silurian crinoidal carbonates of New York, small remnants of algal(?)-bryozoan and pelmatozoan holdfast mounds are found within beds of winnowed grainstones (Brett 1985). Presumably, the small boundstone masses developed in sheltered 'pockets' within the crinoidal shoals (e.g. in the troughs between relatively stable sandwaves). These stabilized ares would then have provided local sources for additional pelmatozoan debris. Finally, it is possible that a few taxa of abundant pelmatozoans, such as periechocrinids, were able to colonize skeletal shoals directly because of their possession of flexible, adjustable cirri on the column. Robust cirriferous columns of such crinoids may be common in some grainstone deposits.

Other contributors to carbonate shoal sediments include pentamerid brachiopods, stromatoporoids, tabulate corals (Text-figs 7, 22), and, in a few areas, dasycladacean algae, such as cyclocrinitids. Shoal-like accumulations of stromatoporoid debris have been reported from the Silurian of Siberia (Nestor 1984). Stromatoporoids, tabulates, and colonial rugosans, together with binding algae, were the major contributors to Silurian bioherms (see below).

In slightly deeper, quieter carbonate shelves below wave base, ramose and fenestrate bryozoans appear to have been codominant with pelmatozoans. A smaller, but significant proportion of Silurian limestones represent bryozoan wacke- and packstones (Text-fig. 2). Bryozoan thickets apparently grew preferentially in relatively shallow, agitated waters which were well below normal wave base, but frequently affected by storms. In some areas, a 'bryozoan belt' appears to have been formed just seaward of echinoderm shoals, and, in fact, bryozoan thickets provided important rooting grounds for diverse pelmatozoans, especially cystoids. Bryozoans are probably second after pelmatozoans as overall sediment producers in the Silurian (Brood 1984). It is interesting to note that bryozoans form mounds and thickets in cooler water areas today (e.g. south of the Great Barrier Reef), where they replace stony corals in a manner possibly analogous to their Silurian replacement of corals and crinoids in deeper water (P. Copper pers. comm. 1989).

Pelmatozoans, bryozoans, and corals were most significant as sediment producers in shallow, probably subtropical carbonate shelves. Elsewhere, in many siliciclastic-dominated shallow water shelves, other groups of organisms were of greater importance. Brachiopods were the primary 'shellfish' of most Silurian muddy to silty substrate, shallow water areas. Together with lesser amounts of trilobites, ostracode, and molluscan debris, brachiopod shells are the main contributor to thin shell pavements and beds (Text-figs 3, 4). In restricted, sometimes hypersaline shallow marine to peritidal environments, bivalves, ostracodes, especially leperditians, and occasionally gastropods or tentaculitids formed thin, but densely packed skeletal accumulations (Text-fig. 4).

Most Silurian shell beds appear to have undergone some degree of concentration, perhaps by storm waves or currents (see below). Silurian shell beds are mainly thin (< 5–10 cm, rarely exceeded 20 cm), in contrast to the often massive encrinites. Indeed, brachiopod shells, with the exception of pentamerids (Text-fig. 3*C*), do not appear to form major skeletal shoals. Kidwell (1988) has recently contrasted the general style of Palaeozoic shell beds with those of later Mesozoic and Cenozoic times. She notes the general thinness of Palaeozoic shell beds in contrast to molluscan accumulations

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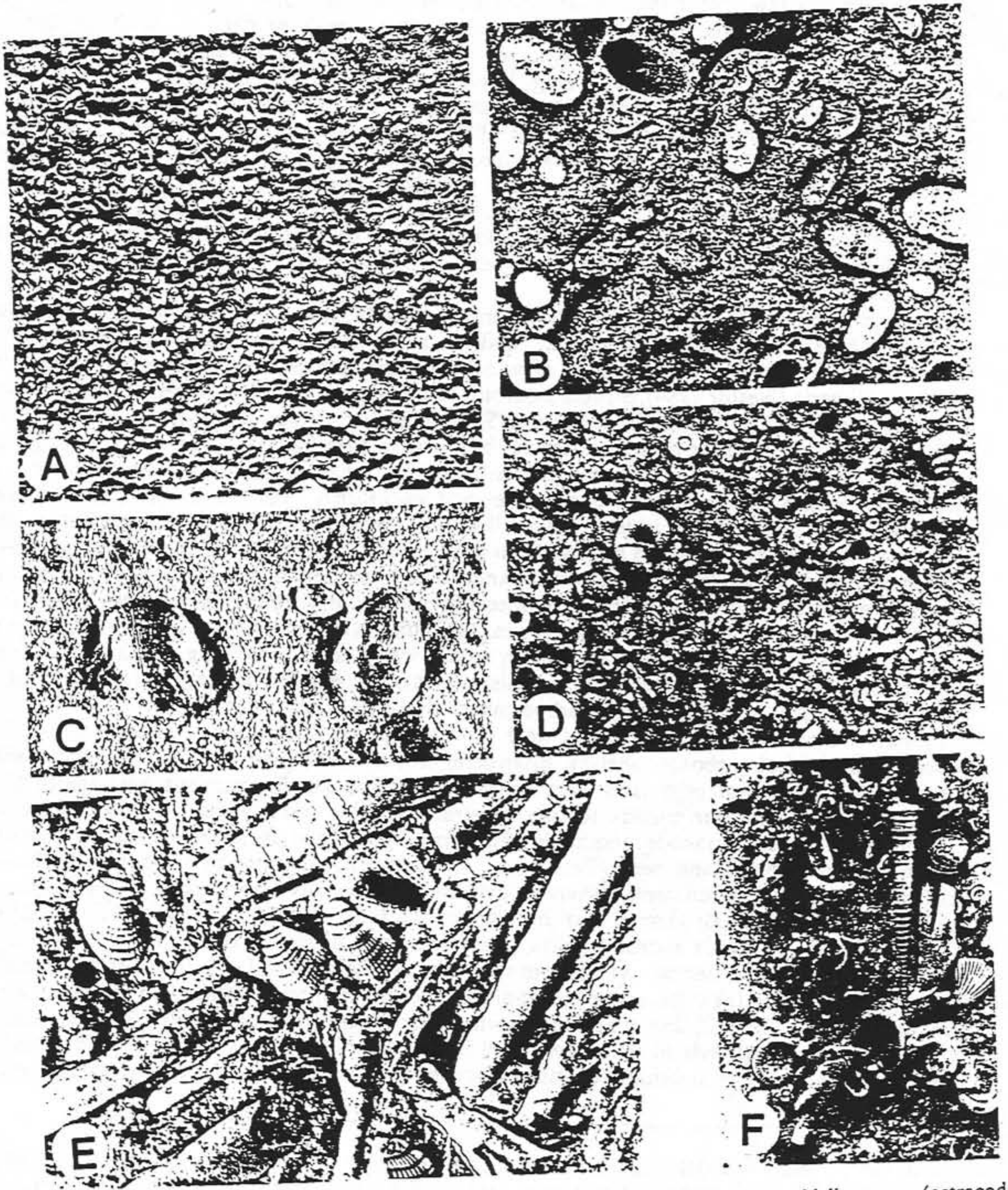
lowest Wenlock, Rockway Dolostone, St Catharines, Ontario, × 0·5. *E*, polished lateral surface of graded bed of coquinoid limestone composed of articulated shells of *Eoplectodonta transversalis* and *Atrypa reticularis* (note geopetal fill on specimens in lower right); sharp-based bed graded upward into laminated siltstone represents a tempestite or storm layer; this biofacies is assignable to BA-4; uppermost Llandovery, Williamson Shale, Alton, Wayne Co., NY, × 2. *F*, calcareous mudstone containing abundant and diverse brachiopods of the *Dicoelosia* (BA-4 to 5) biofacies; included are *D. biloba*, *E. transversalis*, and rhynchonellids; Wenlock, Rochester Shale, Rochester, Monroe Co., NY, × 2.



TEXT-FIG. 4. Ostracodes and molluscs as sedimentary constituents. *A*, thin coquinoid limestone (ostracodal packstone), composed almost entirely of single valves of palaeocopid ostracodes; Ludlow, McKenzie Formation, Holidaysburg, Blair Co., Pennsylvania, × 3. *B*, bedding plane of reddish sandstone with an abundance of mainly convex-upward valves of a leperditian ostracode; lower Llandovery, Grimsby Sandstone, Niagara Gorge, Niagara Co., NY, × 3. *C*, bedding plane in reddish sandstone displaying valves of pterioid and modiomorphoid bivalves; lower Llandovery, Grimsby Sandstone, Niagara Gorge, Niagara Co., NY, × 0·75. *D*, thin sandy limestone composed of *Heiopora* bryozoans, crinoid ossicles and an abundance of high spired of later times, often several metres thick. She speculates that brachiopods were subject to more rapid fragmentation than certain thicker-shelled bivalves; hence their preservation is often all or none, i.e. either complete, intact and unabraded shells or unrecognizable abraded fragments.

A distinctive shelly facies that characterized the Bohemian and related circum-Gondwana region during later Silurian times is the so-called *Orthoceras* limestone facies (Text-fig. 4*E*). These carbonates are dominated by closely packed and commonly current oriented shells of orthoconic nautiloids, together with small epifaunal bivalves that apparently used the nautiloid shells as substrates (Kříž 1984). The exact conditions that favoured development of these peculiar pelagic limestones are uncertain. However, they appear to include relatively sediment-starved conditions in deeper portions of poorly oxygenated continental margins, and cooler climatic belts associated with the Silurian high latitude areas. Preservation of aragonitic shells may perhaps be favoured by elevated levels of dissolved bicarbonate brought on by sulphate reduction within the sediments. Furthermore, cephalopod shell accumulations were undiluted by other bioclasts.

In still deeper, typically dysaerobic outer shelf to basinal environments of the Silurian, shelly faunas were largely absent (see Boucot, this volume). The organic skeletons of graptolites were common in many offshore muds but were volumetrically insignificant as sedimentary particles. Pelagic sediments, dominated by foraminiferan or radiolarian oozes were apparently absent or rare in the Silurian offshore areas.

Biogenic buildups

Stromatolites. Layered algal boundstones or stromatolites, so characteristic of shallow carbonate shelves from early Proterozoic times to the early Palaeozoic, experienced a sharp decline in most normal marine environments in about the Middle Ordovician (see Kennard and James 1986). This decline of shallow water stromatolites has been attributed commonly to the evolutionary expansion of grazing and burrowing organisms which tended to disrupt algal mats and prevented binding of sediments (Garratt 1970). Most Silurian nearshore carbonates display a lack of stromatolites, but under peculiar, restricted conditions algal buildups are abundant. For example, stromatolites and cryptalgal laminites are very well developed in hypersaline peritidal settings such as in the Salina Group of the North American Appalachian Basin and midcontinent areas. Stromatolites are similarly common in nearshore McKenzie-Lockport shaly limestone facies of the central Appalachians (Text-figs 5, 6). In the second case, stromatolites are associated with dark and apparently dysaerobic shale facies representing restricted lagoonal to tidal flat settings. Apparently, in these cases, environmental stresses of elevated salinity and/or diminished oxygenation excluded grazing organisms and enabled stromatolites to flourish. It is notable that these stromatolitic carbonates are also associated with features such as flat-pebble conglomerates (Text-fig. 5*B*, *C*) which, again, typify early Palaeozoic shelves but undergo radical reduction in the early Ordovician coincident with the decline of stromatolites (Sepkoski 1982). The reduction of flat-pebble conglomerates apparently coincides with an increase in bioturbation which prevented early cementation and/or algal binding of thin carbonate storm layers from which flat pebbles were commonly derived. Apparently, stress factors that permitted stromatolite growth in some areas also favoured the reappearance of the 'anachronistic' facies.

Bioherms. During the early Silurian (Llandovery A to C_5), reefs were small, uncommon, and restricted to a few areas such as Manitoulin Island, Anticosti Island, the Baltic, and portions of China (Copper 1988); apparently the paucity of reefs during this interval reflects the lag phase

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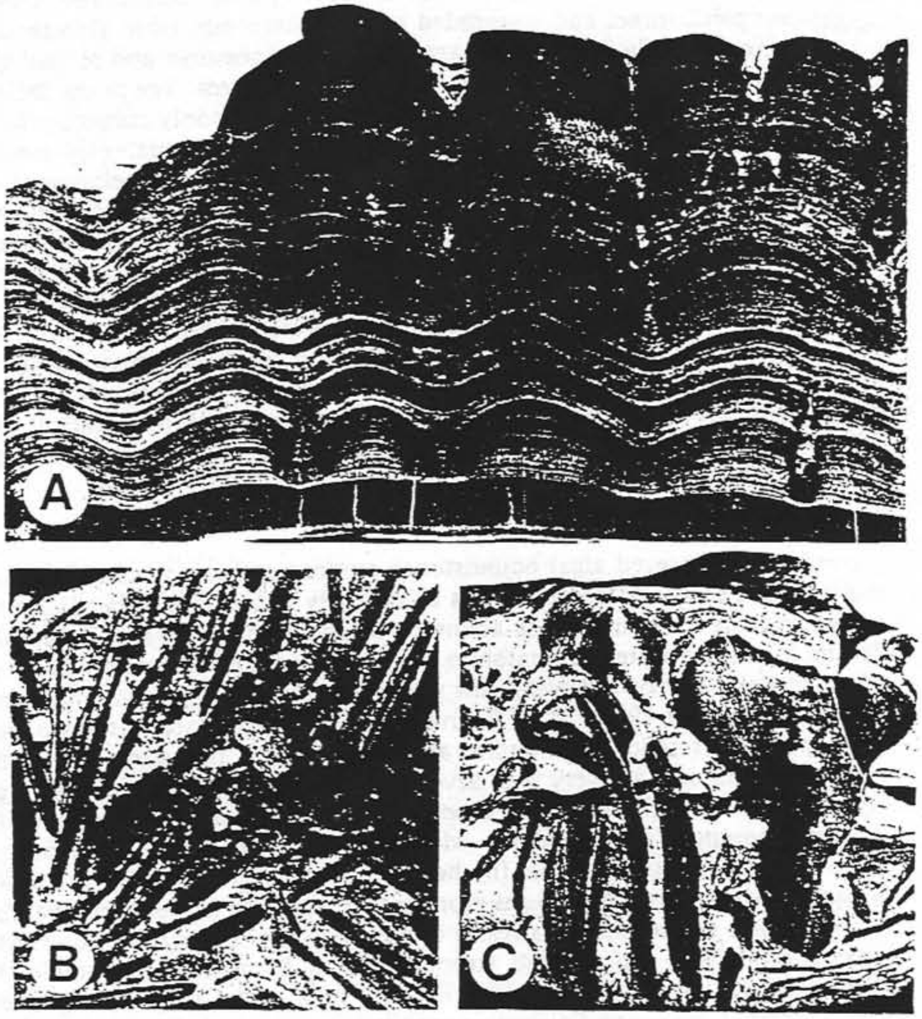
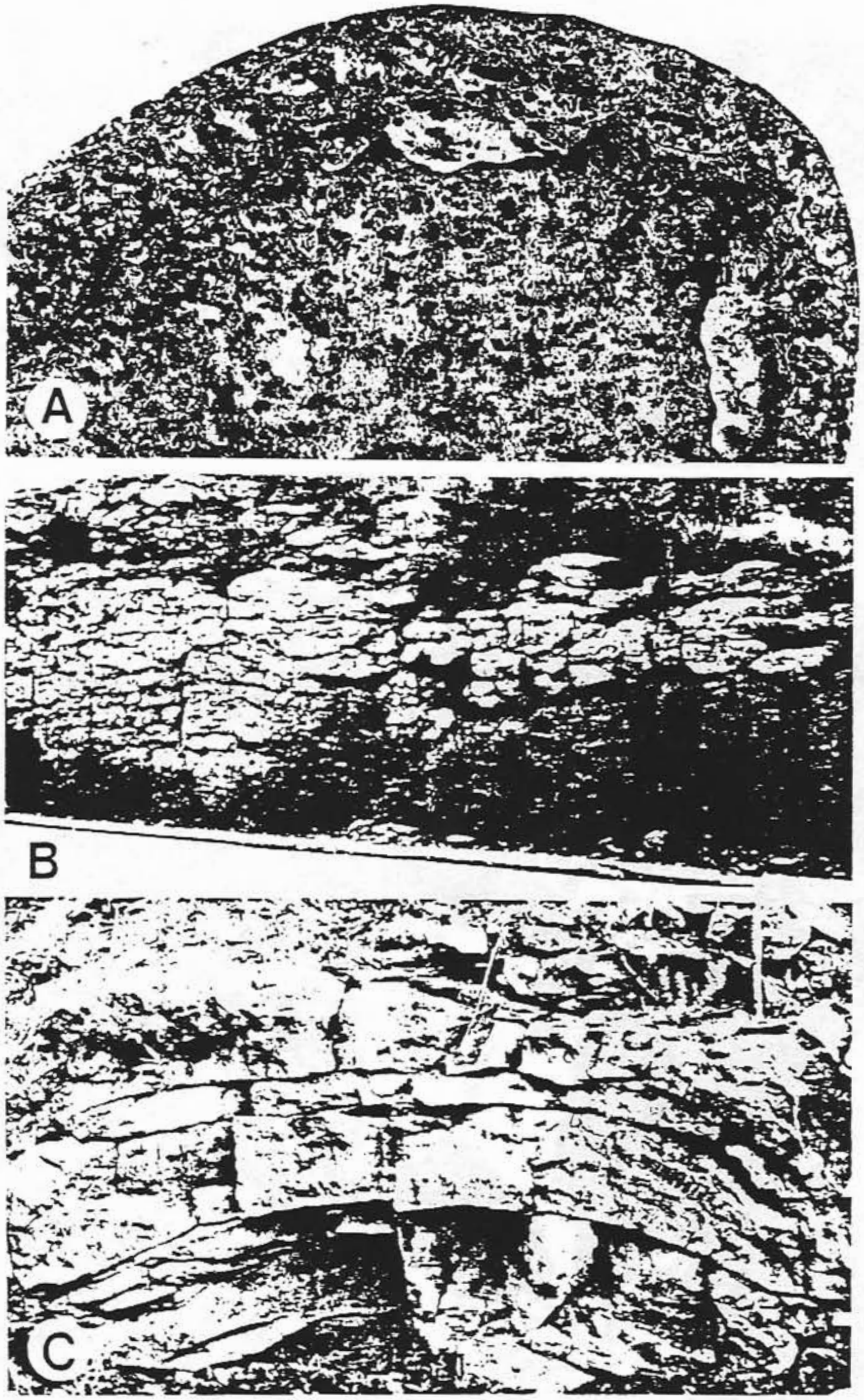
gastropods: lower Llandovery, Power Glen Formation, Niagara Gorge, Niagara Co., NY, × 2. *E*, cephalopod limestone containing numerous specimens of the bivalve *Cardiola gibbosa* and the cephalopod *Protobactrites styloideum*: lower Ludlow, Prague Basin, Bohemia: photo from Kříž (1984), × 1. *F*, thin limestone composed of ostracodes, trilobite fragments, crinoid ossicles and *Tentaculites* sp.: Wenlock, Rochester Shale, Lockport, Niagara Co., NY, × 3.



TEXT-FIG. 5. Silurian stromatolites and associated microfacies. *A*, polished slab through LLH–SH type stromatolite; note digitate projections on upper surface; × 0·5. *B*, oolitic edgewise conglomerate from runnel between stromatolitic heads; note imbricated thin, flat clasts of laminated (cryptalgalaminite) calcisiltite probably derived from nearby stromatolitic mud; × 0·75. *C*, edgewise conglomerate serving as a substrate for laminated (LLH) stromatolitic crusts; × 0·75. All slabs from Ludlow, Sconondoa Formation, Sconondoa Creek, Madison Co., NY.

TEXT-FIG. 6. Silurian bioherms. *A*, small thrombolitic bioherm; note dark clotted micrite, with numerous bound in gastropod shells (*Murchisonia*?), and infiltrated geopetal sediment; the porous structure of thrombolites may result from partial disruption of algal structure by burrowing organisms such as the gastropods shown here; Wenlock, McKenzie Formation, Millerstown, Juniata Co., Pennsylvania. × 1. *B*, bioherm composed of thrombolitic (?) micrites with abundant favositids and stromatoporoids; note overlap of right-hand margin of mound over bedded, argillaceous dolostone; Wenlock, Lockport Dolostone, Pekin, Niagara Co., NY; bushes give scale. *C*, stromatolitic bioherms; digitate stromatolitic fabric is superimposed on larger-scale (note hammer) domal mounds; Ludlow, upper Lockport Group, Robert Moses Power Plant, Niagara Co., NY.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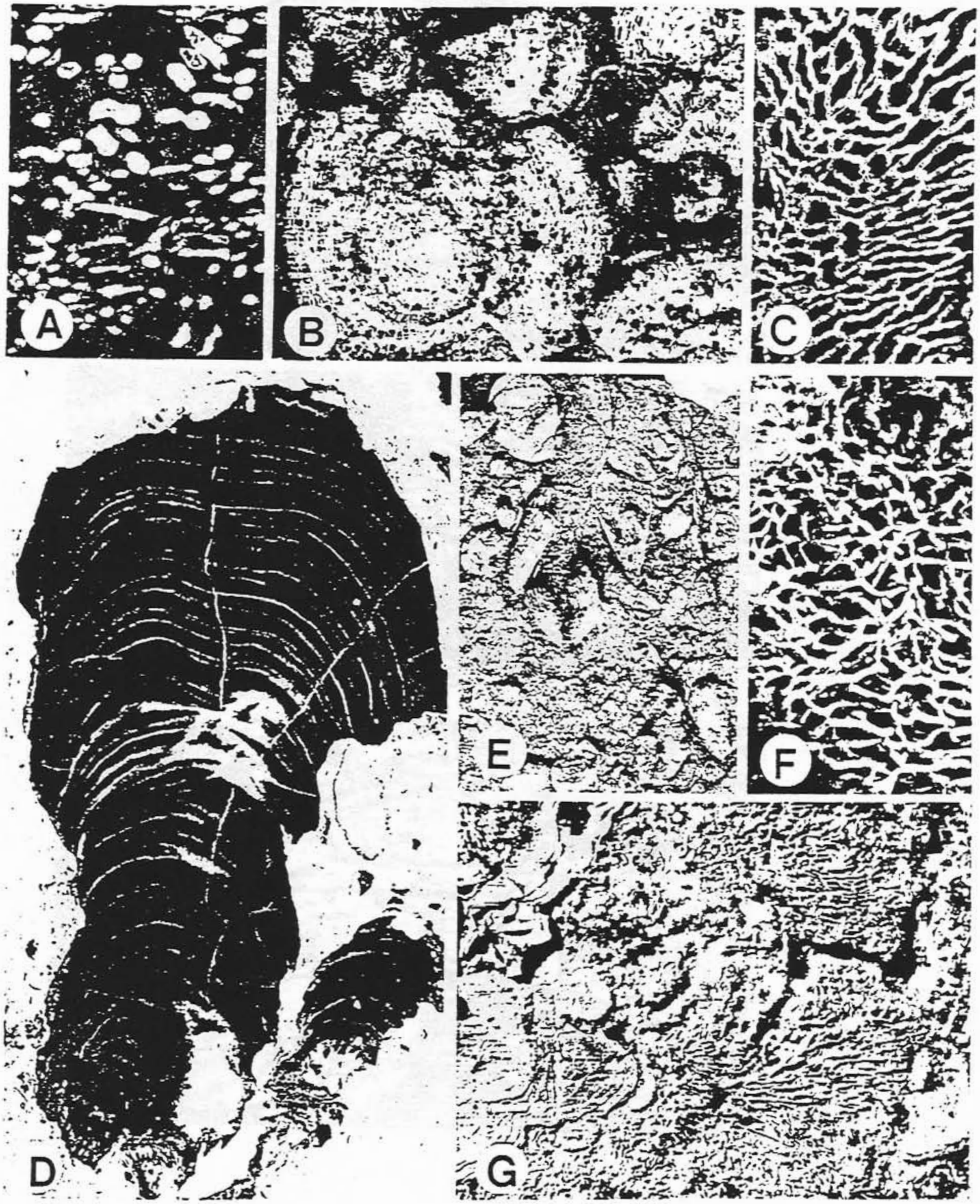
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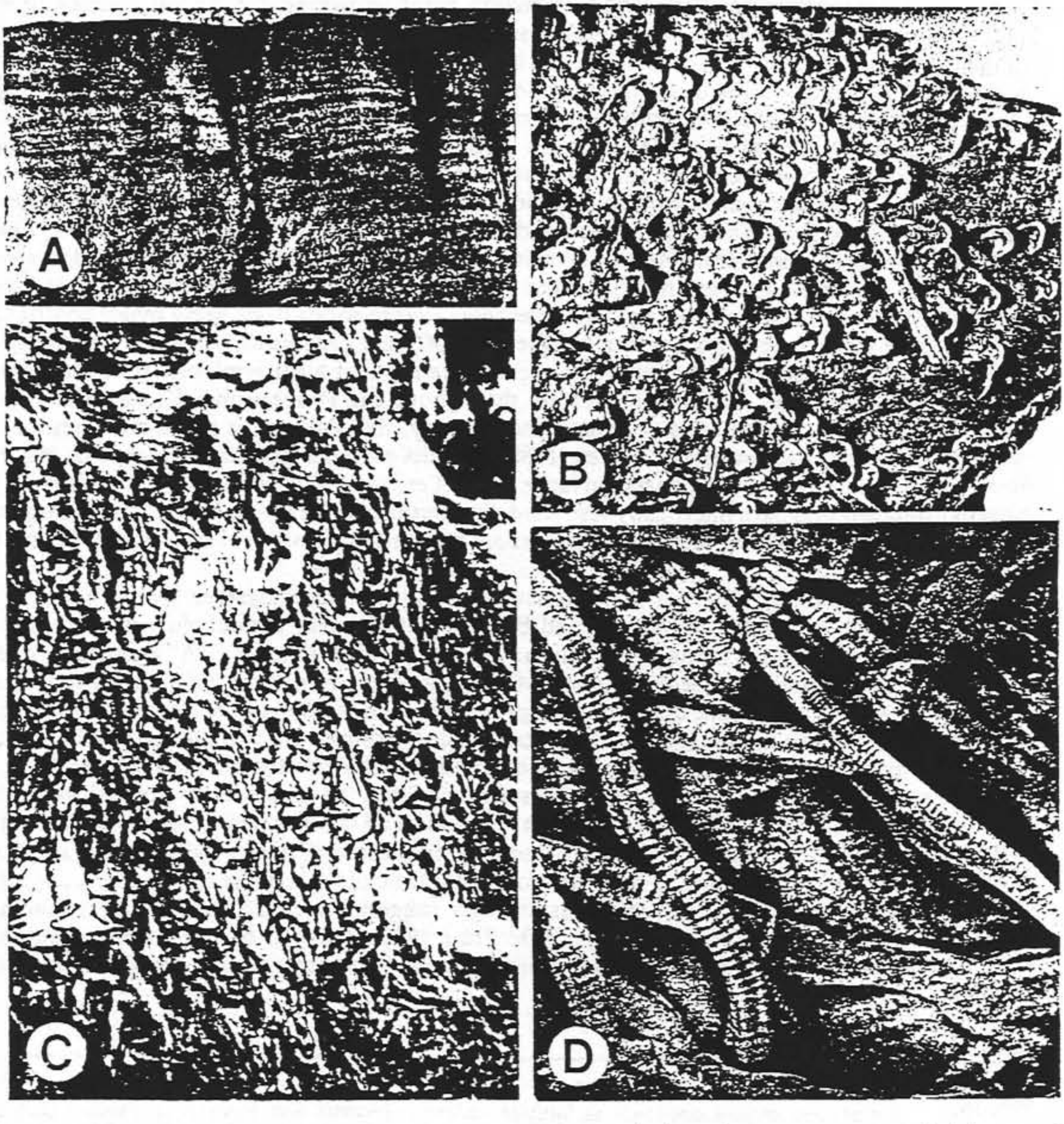
following the great terminal Ordovician extinction event. However, the medial Silurian to early Upper Devonian (Llandovery C_6 to Frasnian) stands out as one of the major reef-building intervals of the Palaeozoic. Copper (1988) refers to this interval as the second of six major evolutionary reef faunas, with bioherms during this time being dominated by stromatoporoids, tabulates, and rugose corals (Text-figs 6, 7). Massive bioherms, as much as tens of metres high and several kilometres wide, are especially typical of the late Silurian platform areas in Arctic North America, the Urals and the Baltic region (see Copper and Brunton, this volume, for review).

Fagerstrom (1988) recognizes five major guilds of reefal organisms: *constructors*, *bafflers*, *binders*, *destroyers*, and *dwellers*. The constructor guild in the Silurian mainly comprised massive, domal, and hemispherical stromatoporoids plus favositid, halysitid, and heliolitid tabulates, and to a much lesser extent, rugose corals (Text-fig. 7; Copper 1988). Coates and Oliver (1973) suggest that the lack of an edge zone, and relatively slow growth prevented rugose corals from being major contributors to Palaeozoic reefs. It remains unclear whether any of these organisms possessed endosymbiotic zooxanthellae, although Cowen (1988) has argued recently that algal symbiosis is of fundamental importance to most reef building organisms throughout the Phanerozoic. Coates and Jackson (1987) have inferred, on the basis of skeletal morphology, that Palaeozoic reefal tabulates, but not rugosans, possessed zooxanthellae. Cowen (1988) provides evidence that stromatoporoids may have possessed zooxanthellae as well, based on large areas of exposed thin tissue, rapid growth rates, and biogeographically and bathymetrically restricted distributions. Both favositids and stromatoporoids may display growth banding that suggests seasonal fluctuations in skeletal secretion of hermatypic organisms.

However, the bulk of Silurian reef frameworks was not held together by members of the constructor guild, but rather by binders and bafflers. Bafflers were undoubtedly important in the initial stages of Silurian mound formation. Philcox (1970) stressed the significant role of pelmatozoans in causing local sedimentation of mounds which formed the early successional stages of Silurian reefs; numerous thicket-forming organisms such as fasciculate corals, ramose bryozoans, sponges (bafflers in the Gaspe sponge-algal mounds) and stromatoporoids also probably produced low-energy pockets that served as traps for fine-grained carbonate sediments (text-fig. 7).

Binding of sediments within bioherms was accomplished by crustose bryozoans, particularly fistuliporoids (Cuffey 1971; Text-fig. 2*F*), and a few corals and laminar stromatoporoids (Text-fig. 7) as well as, possibly, the dendritic holdfasts of some pelmatozoans (Crowley 1973; Hewitt and Cuffey 1985; Gibson *et al.* 1988). It should be underscored that the clotted textures seen in many apparently 'structureless' micrites of Silurian mounds strongly suggest the critical role of algal binding in stabilizing these bioherms (see Crowley 1973; Pratt 1982; Text-fig. 6). Sediment-clotting algae evidently were capable of producing wave-resistant mounds, which typically show sediment-filled, undercut cavities.

TEXT-FIG. 7. Corals and stromatoporoids as Silurian sediment formers and binders. *A*, ramose cladoporid tabulate corals surrounded by dark, petroliferous dolomicrite; Ludlow, Lockport Dolostone, Penfield, Monroe Co., NY, × 1. *B*, biostromal packstones composed of numerous spheroidal *Favosites* cf. *F. niagarensis* in dark dolomicrite; Ludlow, Lockport Group, Red Creek near Williamson, Wayne Co., NY, × 1·25. *C*, *Halysites* sp. with burrowed dolomitic mud matrix; Lockport Group, western NY (precise locality unknown), × 0·6. *D*, elongate stromatoporoid showing pronounced latilaminae suggesting periodic growth; such large stromatoporoids from a major framework component of larger Silurian bioherms; lower Ludlow, Lockport Group, Brockport, Monroe Co., NY, × 0·5. *E*, slab of biostromal dolostone containing numerous specimens of the solitary rugose coral *Enterolasma* sp. together with atrypid brachiopods; small rugose corals are important accessories of Silurian bioherms and biostromes; Wenlock?, Lockport Group, Joy, Wayne Co., NY, × 0·75. *F*, fasciculate tabulate coral *Syringopora* sp.; such thicket-type corals aided in biohermal buildups by baffling and binding sediment; Lockport Group, western NY (precise locality unknown), × 0·75. *G*, weathered surface of small bioherm showing *in situ* stromatoporoids, favositids, and thickets of cladoporid tabulates; Wenlock, Gasport Limestone, Lockport, Niagara Co., NY, × 0·25.



TEXT-FIG. 8. Silurian nearshore trace fossil assemblages. *A*, lateral view of *Monocraterion*, vertical burrows in laminated red Tuscarora Sandstone; western Maryland (precise location unknown), × 0·75. *B*, undersurface of sandstone slab showing hypichnial casts of current-aligned *Rhizocorallium*-like trace; lower Llandovery, Kodak Sandstone, Webster, Monroe Co., NY, × 0·5. *C*, lateral view of weathered reddish sandstone ledge displaying vertical *spreiten* of trace fossil *Daedalus*; individual *spreiten* extend for over 70 cm vertically; lower Llandovery, Grimsby Sandstone, Rochester, Monroe Co., NY, × 0·2. *D*, undersurface of red sandstone slab, showing hypichnial casts of *Arthrophycus*; note typical annulated vermicular burrows of this common trace fossil; lower Llandovery, Grimsby Sandstone, Rochester, Monroe Co., NY, × 0·5.

In turn, Silurian bioherms or reefs provided niches for diverse associations of reef dwellers; of these, pelmatozoans were among the more significant (Text-figs 7, 24). These crinoids and cystoids commonly rooted directly to the surfaces of bioherms (Brett 1985). Brachiopods are not particularly dominant in most bioherms but include a few pentamerids and the nestling lingulids seen in some coral heads (Newall 1970; Richards and Dyson-Cobb 1976) as notable exceptions. Most Silurian bioherms also harbour specialized trilobites such as illaenids and some lichids that may have preferentially occupied sheltered depressions on mound surfaces (Fortey 1975; Mikulic 1980). Nautiloid cephalopods were also very common in these pockets on the bioherms and may have dwelled preferentially on or near the surfaces of the reefs (Text-fig. 24).

The destroyer (recycler) guild in the Silurian appears to have been rather limited. Boring clionids, bivalves, rasping echinoids, the teleost fishes, which are major destroyers of reef rock today, were either rare or absent. Consequently, reef building may have proceeded at different rates than in the modern cases and preservation may have been favoured. It should be noted that the so-called 'destroyer' guild might better be termed 'recyclers' as these organisms recycle nutrients and may actually enhance the growth of reefs.

Silurian reefs produced some substantial topographical features on otherwise flat sea floors, ranging upwards to hundreds of metres above the bottom. As such, they also created their own microenvironments. Moreover, they were sediment 'factories', producing local inclined flank deposits of reef-derived debris, particularly crinoid columnals (Shaver and Sunderman 1989).

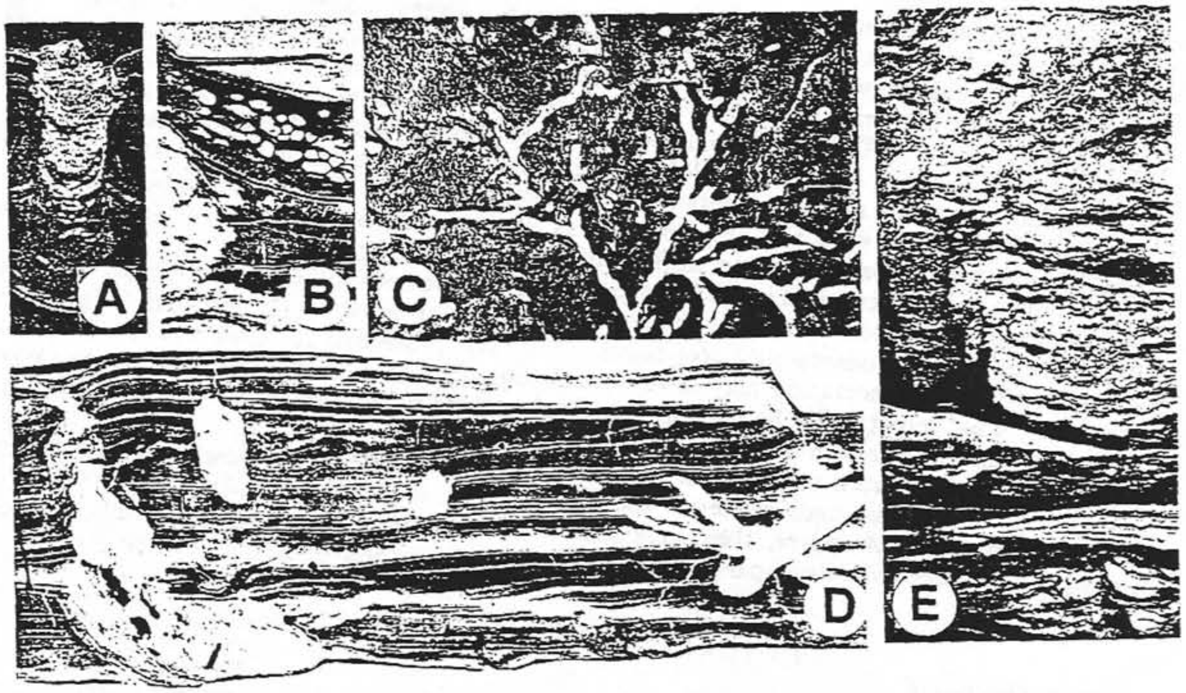
BIOTURBATION IN THE SILURIAN

Silurian ichnofacies

In addition to skeletal production and biodeposition, Silurian organisms modified existing sediments through their burrowing activities. Distinctive suites of trace fossils (ichnofacies) typify differing grades of substrata during the Silurian. Similar ichnofacies were developed in siliciclastic and carbonate substrate (Narbonne 1984; Pemberton and Risk 1982). Silurian nearshore, medium to coarse sands, were colonized primarily by deep-burrowing suspension feeders that produced simple vertical tubes (*Skolithos*, *Monocraterion*; Text-fig. 8*A*). In contrast, shallow-water (tidal flat) fine, muddy sands supported a low-diversity association of sediment feeders, which produced highly distinctive trace fossil associations (*Arthrophycus-Daedalus*: see Pemberton and Risk 1982; Text-fig. 8*B–D*), typically associated with lingulid brachiopods, small bivalves and eurypterids. Offshore mixed mud and sand substrates hosted diverse sediment-mining and furrowing organisms (e.g. varied worms and trilobites) and these yielded abundant traces such as *Planolites*, *Cruziana*, and *Rusophycus* (Text-fig. 21*C*). Shallow shelf carbonates commonly also display *Thalassinoides*-like burrow galleries (Text-fig. 10*A*). Deeper water muds and silts were characterized by complex mining traces such as *Chondrites* and *Teichichnus* (Text-fig. 9) commonly associated with abundant body fossils of strophomenid brachiopods, small, shallow-burrowing nuculid and endobyssate bivalves, gastropods, and pelmatozoans. A *Zoophycos* ichnofacies was rarely developed in the Silurian (but see Text-fig. 10*B*). Finally, some Silurian deeper water mudstone-shale facies yield grazing traces belonging to the *Nereites* ichnofacies (Narbonne 1984).

Extent and depth of bioturbation

Some researchers have argued that bioturbation in the early to middle Palaeozoic was substantially less effective in altering soft substrates than at later times (Thayer 1983). Specifically, Ausich and Bottjer (1982) argue that during the Silurian maximum burrowing depths were not greater than perhaps about 6 cm. Later this estimate was revised to about 10–15 cm (Text-fig. 11). The deep-burrowing tier among shelly organisms, today represented by numerous siphonate bivalves, irregular echinoids, and some crustaceans, was largely vacant in the early Palaeozoic offshore settings (Ausich and Bottjer 1982, 1985). Nonetheless, several other researchers countered that deep burrows, including *Thalassinoides*-like galleries, already existed in the Cambrian (Sheehan and Schiefelbein 1984; Miller and Byers 1984).

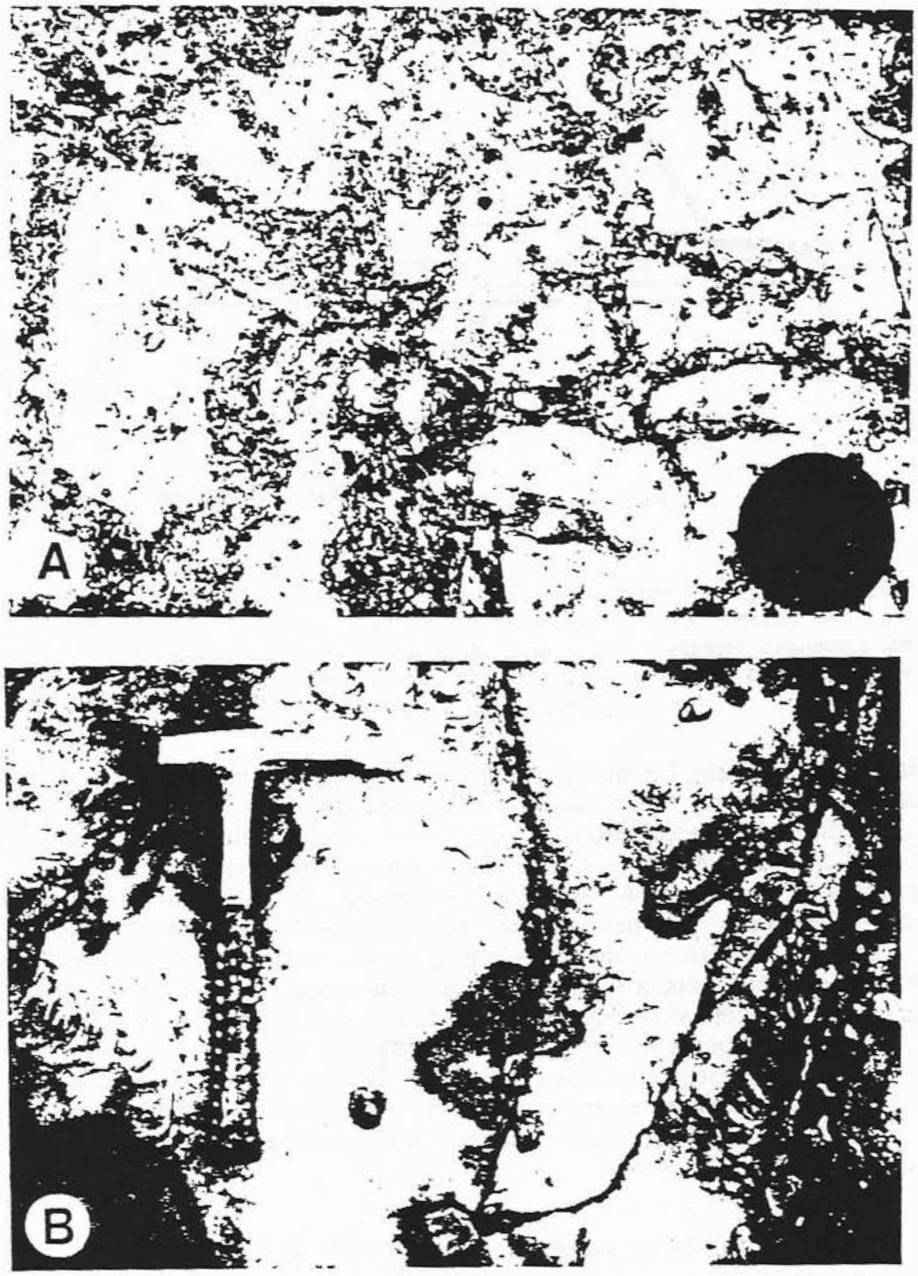


TEXT-FIG. 9. Silurian offshore trace fossil assemblages. *A*. transverse section through *spreite* of *Teichichnus*; note lamellae of pale grey, pelleted carbonate. × 1. *B*. lateral view of sand-filled horizontal tunnels of *Chondrites* in dark grey shale. × 1. *C*. bedding plane view of branching burrow network of *Chondrites* in calcisiltite bed. × 0·5. *D*. polished slab of laminated calcisiltite showing lateral section of *Teichichnus* (lower right), *Planolites*, and possible oblique escape burrows; × 1. *E*. polished drill core of interbedded dark shale and laminated tempestite sandstones showing partial disruption of bedding by bioturbation; note diffuse burrowing (upper right), pellet-filled vertical burrow (upper left), and *Teichichnus*. × 0·5. Figs. *A*, *C*, *D* – Wenlock, lower Rochester Shale, Greece, Monroe Co., NY. *B*, *E* – lower Llandovery, Power Glen Shale, drill core from Niagara Falls, Niagara Co., NY.

However, it appears that both views are partly correct. Indeed, many very nearshore silt and fine sandstone facies possess relatively deep burrows. A notable example of this is the complex vertical spreiten structures of *Daedalus*, an apparent mining trace unique to the early Silurian of the Appalachian basin and the Baltic region (Text-fig. 8*C*). Individual burrows of this ichnogenus may extend nearly a metre into the sediment. Few body fossils are associated with these deeply bioturbated sediments, and indeed, a form of trophic group amensalism may have existed in these cases. Similarly, in some Ordovician and Silurian nearshore carbonates, *Thalassinoides*-like (Text-fig. 10*A*) galleries may extend tens of centimetres into the sediment (Sheehan and Schiefelbein 1984; Narbonne 1984).

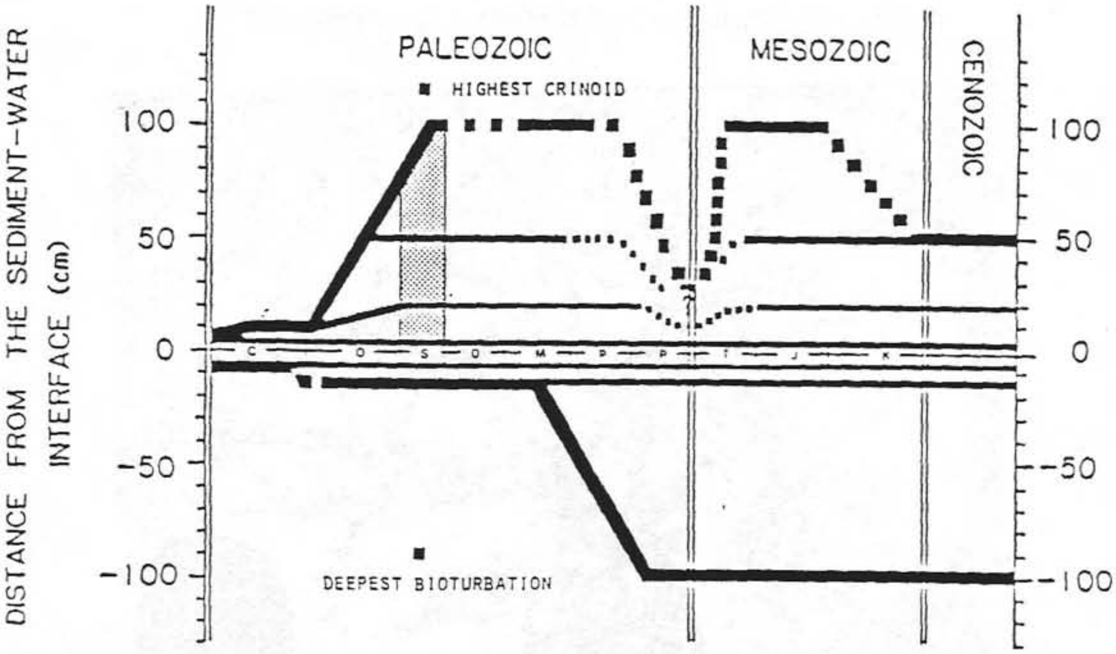
Nonetheless, Silurian offshore facies rarely, if ever, display deep bioturbation (Text-fig. 11). Tunnels of the traces *Chondrites*, *Teichichnus*, and others may extend downward perhaps 10–15 cm through tempestite layers (Text-figs 9*D*, *E*). These are discrete burrows and most offshore Silurian facies do not appear thoroughly homogenized; bioturbation indices around 3–4 are typical in the Silurian (Droser and Bottjer 1986).

Larson and Rhoads (1983) observed a significant increase in bedding thickness of analogous facies from the Middle Ordovician into the Lower Devonian. They attributed this change to increased effectiveness of bioturbation through time. Most Silurian facies more nearly resemble the Ordovician than the Devonian endpoint. Heterolithic facies comprising relatively thin (1–10 cm) storm generated beds alternating with muds are still relatively widespread in the Silurian, and they



TEXT-FIG. 10. Silurian trace fossils. *A*. *Thalassinoides*-like burrow galleries in dolomitic mudstone: Ludlow, Eramosa Formation, Wiarton, Ontario. *B*. *Zoophycos*, a rare Silurian trace fossil, here shown on a bedding plane of argillaceous dolostone: upper Wenlock, Gasport Formation, Clarendon, Orleans Co., NY.

closely resemble Ordovician counterparts. In contrast, analogous facies in the Middle Devonian and later times consist instead of relatively massive, bioturbated, gritty, and sometimes calcareous mudstones with few thin interbeds. A major cause of this change in sedimentary fabric seems to be the rise of producers of the trace fossil *Zoophycos* in shallow, offshore marine habits during the late Silurian (Text-fig. 10*B*). This trace is demonstrably responsible for producing the churned and



TEXT-FIG. 11. Model of tiering in soft substrate suspension-feeding communities through the Phanerozoic. Note presence of low (10 cm), intermediate (50 cm), and high (> 100 cm) level epifaunal suspension feeders, but only shallow infaunal suspension feeders during Silurian (shaded). Points are added to denote the approximate longest stemmed crinoid and deepest (probably infaunal deposit feeding) burrow known from the Silurian. Modified from Bottjer and Ausich (1986).

swirled fabrics typical of many Devonian and later Palaeozoic mudrocks. In contrast, *Zoophycos* appears to have been relatively rare or absent in most shallow shelf environments of Silurian and earlier Palaeozoic times. This factor, alone, may account for the profound differences between some facies of Silurian and later Palaeozoic time. Some Silurian siltstone and mudstone facies are dominated strongly by small shallow-burrowing bivalves and/or trace fossils. Substrate instability and increased turbidity near the sediment/water interface, may have inhibited colonization on the sea floor in these cases by sessile suspension-feeding organisms. Such trophic group amensalism seems to have operated particularly in mid-Palaeozoic lower aerobic to dysaerobic muddy environments, which favoured shallow infaunal deposit feeders, such as nuculoids.

In general, observations appear to support Thayer's (1983) hypothesis that 'biological bulldozing' was relatively minor in the early to middle Palaeozoic. This presumably left most sediment/water interfaces relatively little disturbed except in some offshore muds and nearshore tidal flat settings. In turn, this stability permitted continued colonization of offshore soft substrates by a variety of sessile, epifaunal suspension feeders.

SUBSTRATE–ORGANISM INTERACTIONS

General considerations

Substrates may be subdivided fundamentally into hard and soft (unconsolidated) categories, each of which, in turn, may be further subdivided. Benthic organisms are typically classified as epifaunal or infaunal depending upon their dominant position above or within the sediment; furthermore, different grades of each broader category can be recognized based on distances above, or below the sediment/water interface; thus *shallow* or *deep infauna* (approx. 10 to 100 cm, respectively, below the sediment surface) and *low*, *intermediate*, and *high level suspension feeders* (upper limits about 5, 20, and 100 cm, respectively) following the usage of Ausich and Bottjer 1982; Text-fig. 11). Most Silurian benthic communities possessed organisms at several of these levels forming a stratified or 'tiered' community structure (Ausich and Bottjer 1982, 1985; Bottjer and Ausich 1986). Further subdivisions of benthic 'niches' typically involve a consideration of trophic groups such as suspension feeding (including filter feeding), deposit feeding, predation and herbivory (for terminology see Walker and Bambach 1974; West 1977). Substrate and trophic relationships are commonly combined to recognize broadly defined guilds of organisms. As noted below, the number of types of guilds within benthic communities has varied considerably on different substrates, as well as temporally. During the Silurian Period, organisms displayed a wide array of adaptations to substrates of varying consistency comparable to that of the preceding Ordovician Period, but with some significant additions.

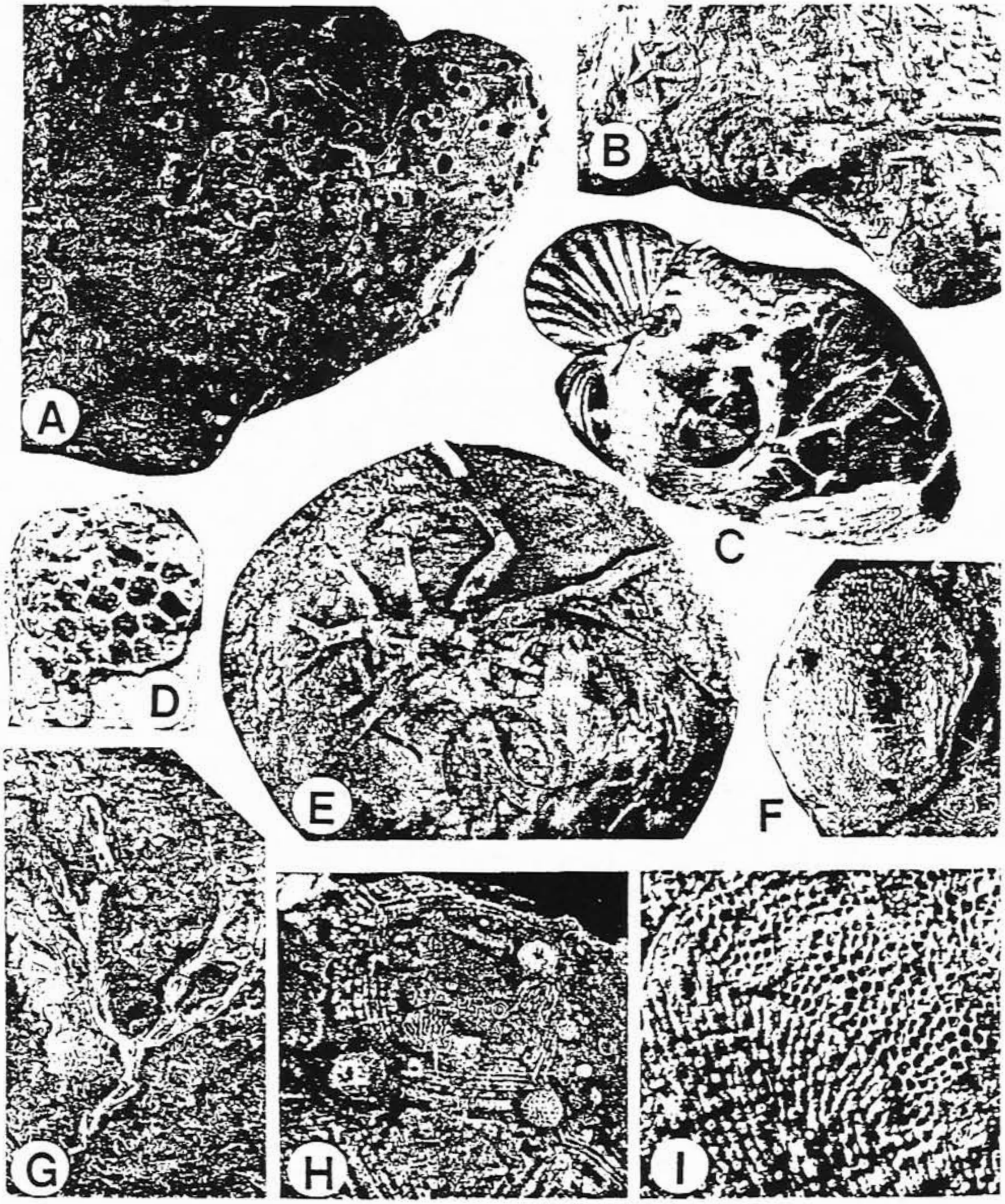
Substrate as a limiting factor

The role of substrate in controlling distribution of early Palaeozoic organisms has been debated widely. However, the answer appears to depend largely on the scale of observations. Distribution of organisms into broadly defined 'communities', as in the definitions of Ziegler *et al.* (1968) appears to have been controlled by a combination of bathymetric and sedimentological factors. The degree of association between fossil assemblages and broadly defined lithofacies is highly variable among taxonomic groups. It has been found commonly that the same Silurian brachiopod associations may occur in both carbonate and siliciclastic facies (Noble 1979); however, bivalves are commonly confined to nearshore siliciclastics but may range into carbonates, whilst many corals, bryozoans, and pelmatozoans are confined largely to calcareous facies. On the other hand, features of substrate, as perceived by settling larvae, are not the same bulk properties such as grain size and texture used by geologists in defining lithofacies. It is clear, in most cases, that the relationship between distribution of the organisms and the broad scale lithofacies pattern is an indirect one, but the environments of most palaeobathymetrically related communities were defined initially using lithofacies and grain size. The chemical composition of sediments (e.g. siliciclastic *versus* carbonate) and even grain size *per se* are probably not the critical determinants of organism–substrate associations. Most sediments are heterogeneous at a finer scale and it is the very localized differences among grains (including organism skeletons) that may be critical in determining settlement behaviour in relation to substrate hardness, texture, and degree of exposure or chemical properties. Organisms may be, therefore, very selective of substrate on a fine scale and yet be distributed in quite contrasting lithofacies on a coarse scale. For example, the rhombiferan cystoid *Caryocrinites* is found both in mudstone deposits and coarse-grained calcarenites. Closer examination, however, reveals that in both cases the cystoid's holdfasts were anchored to particular types of ramose bryozoan, which grew either on soft muddy areas or in protected regions within skeletal banks (Brett 1978*b*, 1985). Hence the cystoid was actually very selective of substrate although at a broader scale this organism occurs in varied distinctive lithofacies.

The effectiveness of a given size of hard substrate object for support and anchorage depends upon environmental energy. For example, small bits of crinoidal or shell debris apparently provided sufficiently stable anchorage for many small crinoids and bryozoans in quiet water areas, but were quite unsuitable in highly turbulent environments. These turbulent settings, though favourable for organism growth in other respects (abundant food, well aerated water, turbulence for suspension feeding), typically display very low-diversity fossil assemblages. The presence of large, immobile hard substrates, such as coral heads or small bioherms, may have been an important factor in permitting distribution of many sessile organisms in high-energy environments. In the vicinity of stabilized bioherms, or even small coral heads, these environments provided habitats for diverse assemblages of attached pelmatozoans, bryozoans, brachiopods, and other organisms.

Hard substrate biotas

Nature of hard substrate habitats. Hard substrates include rock-grounds (e.g. intertidal rocky settings) and submarine carbonate hardgrounds, as well as skeletal substrates. Silurian hard



TEXT-FIG. 12. Silurian hard substrate assemblages. *A*, platter-like hardground cobble intensely bored by *Trypanites*; Llandovery, Neahga Shale, Merritton, Ontario, Canada, × 0·75. *B*, undescribed hemicystitid edrioasteroids encrusting hardground cobble; Ludlow, McKenzie Formation, Castanea, Pennsylvania, × 1; specimen courtesy of G. J. Kloc. *C*, large gastropod shell, *Naticonema niagarense*, serving as 'micro-hardground'; note encrusting *Cornulites* sp. worm tubes and associated brachiopods *Stegerhynchus indianense*, which were probably attached by pedicles to the substrate; the gastropod, in turn, may have been commensal on a crinoid; Wenlock, Waldron Shale, Waldron, Indiana, × 1·5. *D*, *Favosites* cf. *F. parasiticus*; a small substrate biotas comprise diverse tabulate and rugose corals, bryozoans, worm tubes, edrioasteroids, and pelmatozoans with cemented holdfasts (Text-figs 12, 13). Several taxa of Silurian organisms bored or embedded their bodies into hard substrates; these included rare sponges, ctenostome bryozoans, and a variety of soft-bodied organisms that produced distinctive trace fossils (e.g. *Trypanites*) (Text-figs 12*A*–13*A*, *B*). Copper (pers. comm. 1989) reports that some skeletal substrates from the Silurian of Anticosti Island and Gotland are riddled with small borings. However, the diversity of endolithic organisms in the Silurian remained quite low compared with later times. Notably, clionid sponges, duraphagous fish, and boring bivalves were absent and the rates of bioerosion must have been an order of magnitude lower than in analogous marine environments at the present time.

Descriptions of Silurian hardgrounds are under-represented in the literature by comparison with those of the Ordovician or Devonian; however, the relatively few studies that have been made (e.g. Halleck 1969; Cherns 1982) seem to indicate a continuity of trends established in the Middle Ordovician (see for example Palmer 1982; Brett and Brookfield 1984). A carbonate hardground from the Wenlock of Indiana displays encrustation by auloporid corals, some bryozoans, and dendritic holdfasts of the crinoid *Eucalyptocrinites*; however, it is peculiar in lacking borings (see Halleck 1969). Several undescribed examples are known from the Silurian of Gotland, Anticosti, and the Appalachian Basin (Text-fig. 12*B*, *G*). These also appear to have many of the same general taxa of organisms found in Middle Ordovician and Lower Devonian samples, indicating a relatively conservative nature to hardground communities. An example of a rocky intertidal 'community', consisting solely of porostromatolites was described from the Silurian of Gotland (Cherns 1982). Johnson and Baarli (1987) described a latest Ordovician or earliest Silurian rocky shore from Manitoba with boulders encrusted by tabulates.

In contrast, skeletal hard substrates were abundant and thoroughly encrusted during the Silurian (Text-fig. 12): these include corals and stromatoporoids (Kershaw 1984; Nield 1986; Segars and Liddell 1988), brachiopods (Spjeldnaes 1984; Archer and Feldman 1986), and pelmatozoan remains (Liddell and Brett 1982). Some fixosessile fossils now found as loose aggregates in offshore dark, fine-grained sediments may have attached originally to flexible, soft organisms such as benthic algae which decayed subsequently (Sheehan 1977).

Hard substrate adaptations. Benthic organisms display a variety of morphological strategies for life on hard substrates. Sedentary benthic organisms such as corals, bryozoans, brachiopods, bivalves, and pelmatozoans may be classified as either *fixosessile*, attached throughout life to hard substrates, or *liberosessile*, sedentary but free-lying as adults (e.g. see Bassett 1984).

Fixosessile, endolithic and cemented organisms require hard substrates for settling. However, these organisms could occur in areas of mixed shelly and unconsolidated sediments, provided skeletal substrates of sufficient size existed on the sea floor. Most Silurian sessile organisms were attached directly to hard substrates at some stages in their life cycles. In some cases, adults remained permanently attached by cementing the basal portion of their skeleton directly to the substrate (e.g.

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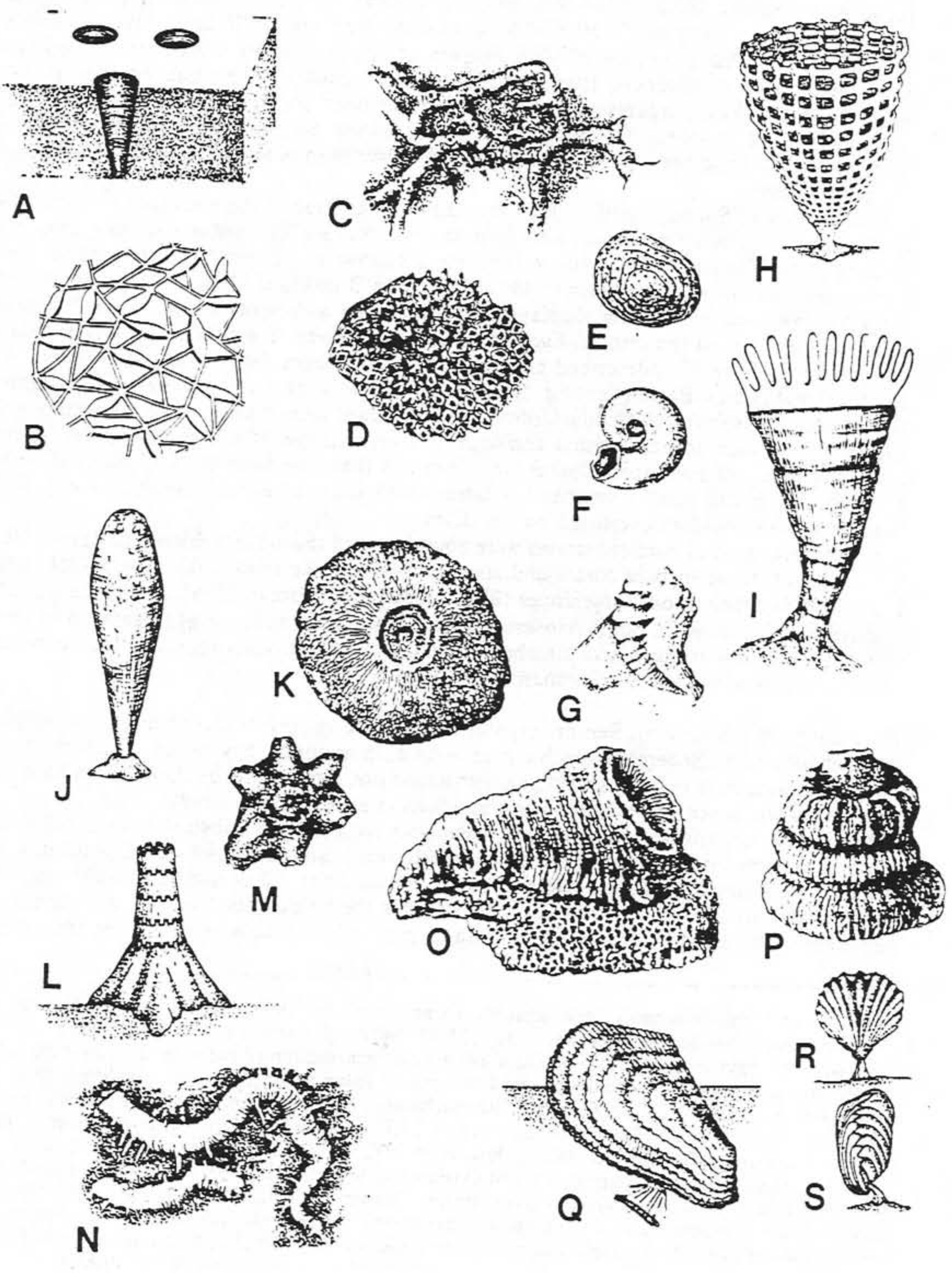
tabulate coral that commonly grew attached to pelmatozoans; here encrusting a crinoid cup; Wenlock, Waldron Shale, Newsom, Tennessee, ×3; UMMP 64090. *E*, dendritic holdfast of *Eucalyptocrinites* sp., encrusting the base of a calyx also of *Eucalyptocrinites*; cementation of radicular cirri over the column facet shows that the substrate crinoid was dead at time of colonization; Wenlock, Waldron Shale, Newsom, Tennessee; ×2; UMMP 64080. *F*, inarticulate brachiopod, *Petrocrania* sp., encrusting skeletal hard substrate; Wenlock, Waldron Shale, Newsom, Tennessee, ×2. *G*, vine-like auloporid coral encrusting a hardground surface; Llandovery, Reynales Limestone, Rochester, NY, ×0·5. *H*, encrusting 'microcommunity' on crinoid calyx substrate; note small trepostome and cystoporate bryozoan colonies; crinoid holdfast (upper right), *Spirorbis*, and possible foraminifer (lower centre); Wenlock, Waldron Shale, Newsom, Tennessee, ×2; UMMP 64081. *I*, intersection of two encrusting bryozoans; *Sagenella* sp. (lower left) has partly overgrown an unidentified trepostome; Wenlock, Much Wenlock Limestone near Dudley, England, ×7; photo from Taylor (1984); UMMP = University of Michigan Museum of Paleontology collections.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certain corals, many bryozoans, inarticulate brachiopods, cornulitid and spirorbid worm tubes, edrioasteroids and some deploporitan cystoids; Text-figs 12, 13*C–G*). Other organisms (e.g. pelmatozoans and ptilodictyid bryozoans) possessed specialized attachment discs (holdfasts) (Franzén 1977; Nestor 1984; Text-fig. 13*H–M*) or non-preservable pedicles or byssal threads (e.g. some articulate brachiopods and bivalves) (Text-fig. 13*Q–S*).

A number of Silurian brachiopods, particularly orthids and rhynchonellids, apparently maintained a functional pedicle into adulthood, and were thus fixed permanently to hard substrates (Text-figs 12*C*, 13*R*, *S*). Vogel (pers. comm. 1989) has recently discovered *Podichnus*, traces of brachiopod pedicle attachment sites, on shells from the Silurian of Gotland. These are the oldest pedicle attachment traces known to date. Apparently most pedically attached brachiopods made no such marks. Certain strophomenids evidently attached by numerous byssus-like fibrils that penetrated the umbonal region through many tiny openings.

Fixosessile attachment by true byssus was characteristic of the majority of Silurian bivalves (Text-fig. 13*Q*). Kříž (1984) documents the expansion of byssate bivalves through the later Silurian and shows a well defined trend from endobyssate infaunal, through endobyssate semi-infaunal to epibyssate modes of life in several lineages of suspension-feeding bivalves. An adaptive radiation of small, epibyssate bivalves, especially the Cardiolidae and Lunulicardiidae, in the Wenlock to Přídolí of the Bohemian area, appears to be associated with the development of pavements of empty nautiloid shells on the sea floor ('cephalopod limestones') that provided hard substrates for byssal attachments (Text-figs 4*E*, 17). Paedomorphic reduction in size and retention of the byssus into adulthood, are considered to have been the key evolutionary pathways for this mode of life.

Pelmatozoans had differing needs for attachment. In addition to simple support on unconsolidated substrates, many stalked echinoderms required an anchorage against lateral movement by currents. They developed a variety of fixosessile holdfast structures, including small cemented discs, runner-like stem endings ('creeping roots'), distally coiled stems, and root-like or dendritic holdfasts (Franzén 1977; Brett 1981; Text-figs 12*E*, *H*; 13*L–N*, *P*; 18*L*). In such cases, the distribution of adult pelmatozoans may have been controlled closely by the distribution of appropriate larval settlement substrates, as the echinoderms became attached permanently at an early stage.

Many crinoids utilized a portion of the distal column as a recumbent or creeping holdfast. Attachments were commonly supplemented by cemented finger-like pseudocirri (Text-fig. 13*N*). Similarly, certain rugose corals developed talon-like outgrowths of the epitheca to aid in attachment on patches of skeletal debris (Text-fig. 13*O*). In some cases, mutual cementation to conspecific solitary corals led to the development of pseudocolonies (Neumann 1988).

Environmental partitioning and organism interactions. Segars and Liddell (1988) report 38 species of encrusting bryozoans, corals, stromatoporoids, worm tubes, and pelmatozoans on the top and

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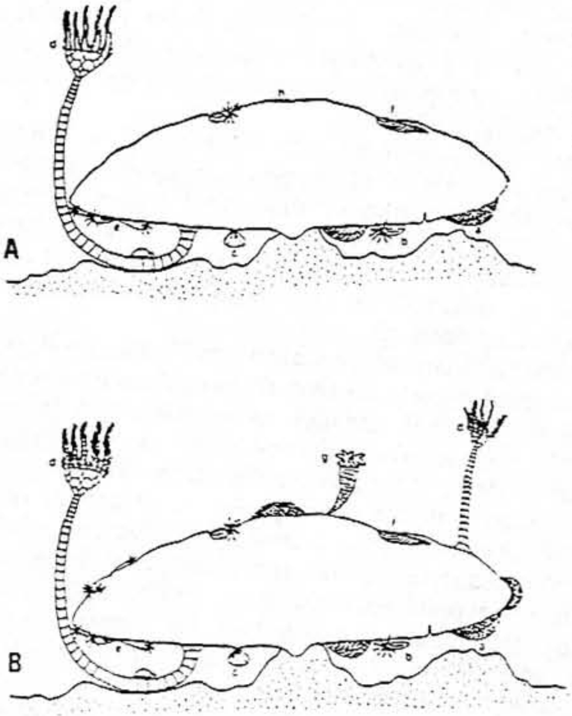
TEXT-FIG. 13. Hard substrate adaptations among Silurian organisms: reconstructions approximately ×1, unless otherwise indicated. *A*, *B*, endolithic adaptation. *A*, *Trypanites* boreholes in hardground, ×2. *B*, ctenostome bryozoan etchings, ×10. *C–G*, cemented skeletons. *C*, vine-like tubuliporate bryozoan *Corynotrypa*, ×5. *D*, discoidal ceramoporid bryozoan, *Ceramopora*, ×5. *E*, cemented inarticulate craniid brachiopod. *F*, *Spirorbis*, spiral worm tube, ×4. *G*, *Cornulites*. *H*, *I*, cemented, non-articulated holdfast. *H*, *Fenestella*, funnel-shaped fenestrate bryozoan cemented by conical holdfast. *I*, small rugose coral with base of corallum cemented to a shell. *J–M*, articulated holdfast discs. *J*, *K*, lateral view of ptilodictyid bryozoan and closeup (enlarged ×4) of cemented fibrous holdfast. *L*, *M*, lateral view and close up (enlarged ×2) of digitate holdfast disc of a crinoid. *N*, *O*, runner-like encrustation: *N*, creeping roots of stolons of crinoids; note small pseudocirral outgrowths cemented to substrate; *O*, analogous runner-like mode of growth in rugose coral. *P*, coiled attachment, distal column of crinoid coiled around another crinoid stem, ×2. *Q*, byssal attachment: endobyssate bivalve *Rhombopteria*. *R*, *S*, pedicle attachment; dorsal and lateral views of rhynchonellid brachiopod *Stegerhynchus*. Figs *B*, *H*, *J* modified from Brood (1984); *K*, *N* redrawn from Franzén (1977); *I*, *O* modified from Neumann (1988).



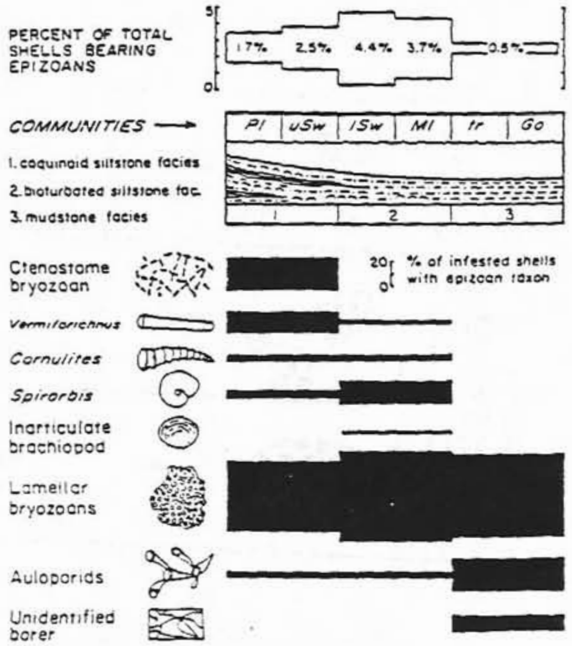
TEXT-FIG. 14. Ecological zonation of hard substrate encrusting organisms on an undercut stromatoporoid from the Silurian of Gotland. *A*, inhabitants before death of stromatoporoid. *B*, inhabitants after death of stromatoporoid. Organisms shown include: (*a*) encrusting bryozoan; (*b*) *Spirorbis* worm tube; (*c*) rhynchonellid brachiopods; (*d*) crinoid; (*e*) auloporid tabulate; (*f*) cornulitid worm tube; (*g*) rugose coral; (*h*) living cells of stromatoporoid. From Segars and Liddell (1988); reprinted by permission of SEPM.

bottom surfaces of large stromatoporoid heads from the Wenlock of Gotland (Text-fig. 14). As with Middle Ordovician hardground and cavity biotas (Brett and Liddell 1978), Silurian communities display some polarization into exposed upper surface and cryptic (cavity or undersurface) subcommunities and some horizontal zonation from inner to outer edges of the stromatoporoid heads (see also Kershaw 1984). Spjeldnaes (1975) also described associations of shade-loving bryozoans from cavities within Gotland reefs.

Encrusting epibionts on brachiopods display preferential distribution patterns that provide important insights into the behaviour of their hosts (Spjeldnaes 1984). Moreover, similar skeletal substrates in different facies evidently supported distinctive suites of encrusters: for example ctenostome bryozoans appear most characteristic of nearshore areas, whilst auloporid corals are typical of shelly substrates from the shallow subtidal into deeper water areas (Watkins 1981; Text-fig. 15); very similar patterns of epibiont distribution persisted into the Devonian (Brett and Bordeaux 1988, work in progress).

Silurian encrusting communities also yield some of the earliest evidence for competition for substrate. Certain bryozoans that encrusted brachiopod shell and crinoid calyx substrates displayed dominance networks in terms of overgrowth of one another (Liddell and Brett 1982; Taylor 1984; Text-fig. 12*H*, *J*). Overgrowth ability was related to zoarial morphology; thin sheet-like and vine-like bryozoans appear to be relatively early colonizers with poor competitive overgrowth abilities, while ceramoporid and fistuliporoid bryozoans with thickened, continuously growing outer edges to the colonies commonly overarch and encrust other bryozoan species (Taylor 1984; Text-fig. 16).

Silurian epibiontic encrusters displayed varying degrees of host–substrate selection. For example, preferences of cornulitid and spirorbid worm tubes and bryozoans for certain species of brachiopods may reflect selection for distinctive surface textures and microtopographies (Hurst 1974; Spjeldnaes 1984). Preferential orientation and distribution patterns (e.g. absence of overgrowth of apertures or commissures of host shells) prove that many epibionts attached to living



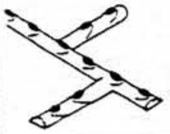
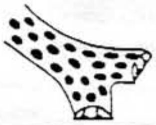
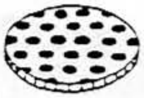
TEXT-FIG. 15. Environmental zonation of epizoans in the type Ludlow Series. The histograms above the reconstructed gradient show epizoan-bearing shells as a percentage of observed shells. Abbreviations for communities, with total number of shells examined for epizoans in parentheses, are Pl–*Protochonetes ludloviensis* Association (1095); uSw–upper phase of *Sphaerirhynchia wilsoni* Association (203); lSw–lower phase of *S. wilsoni* Association (293); Ml–*Mesopholidostrophia laevigata* Association (672); tr–transition association (24); Go–*Glassia obovata* Association (874). Histograms below the reconstructed gradient use a different scale than those above; they consider only infested shells, and are based on 36 epizoan occurrences in facies 1, 69 epizoan occurrences in facies 2, and 8 epizoan occurrences in facies 3. From Watkins (1981); reprinted by permission of the author and the Paleontological Society.

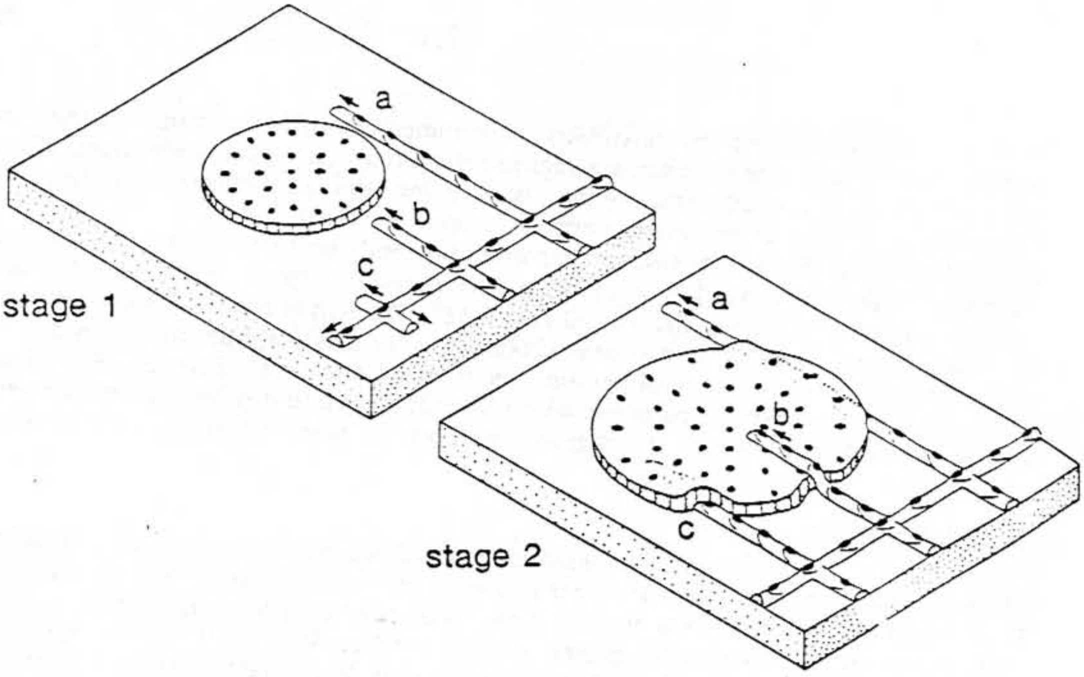
hosts and further suggest the possibility of commensal and/or parasitic interactions. Many cornulitid worm tubes, for example, are aligned preferentially along the commissures of brachiopod shells, apparently to take advantage of the host's feeding or exhalant currents (Copper, pers. comm., notes that in atrypid brachiopods, cornulitids are commonly aligned in relation to the host's exhalant currents). Bryozoans such as *Reptaria* apparently encrusted living nautiloid hosts: their preferential aperture-forward orientation of the zooecia suggests distinctive alignment with a unidirectionally moving, live host (Baird *et al.* 1989). Silurian crinoids yield evidence for some of the oldest known parasitic interactions. Unknown ectoparasitic organisms embedded themselves into the mesodermal skeletons of certain species of host crinoids (Franzén 1974; Brett 1978*a*). Evidently these host/parasite pairs coevolved for spans of up to one hundred million years during the later Palaeozoic. However, the interactions appear to have originated in the Silurian.

Soft substrate biotas

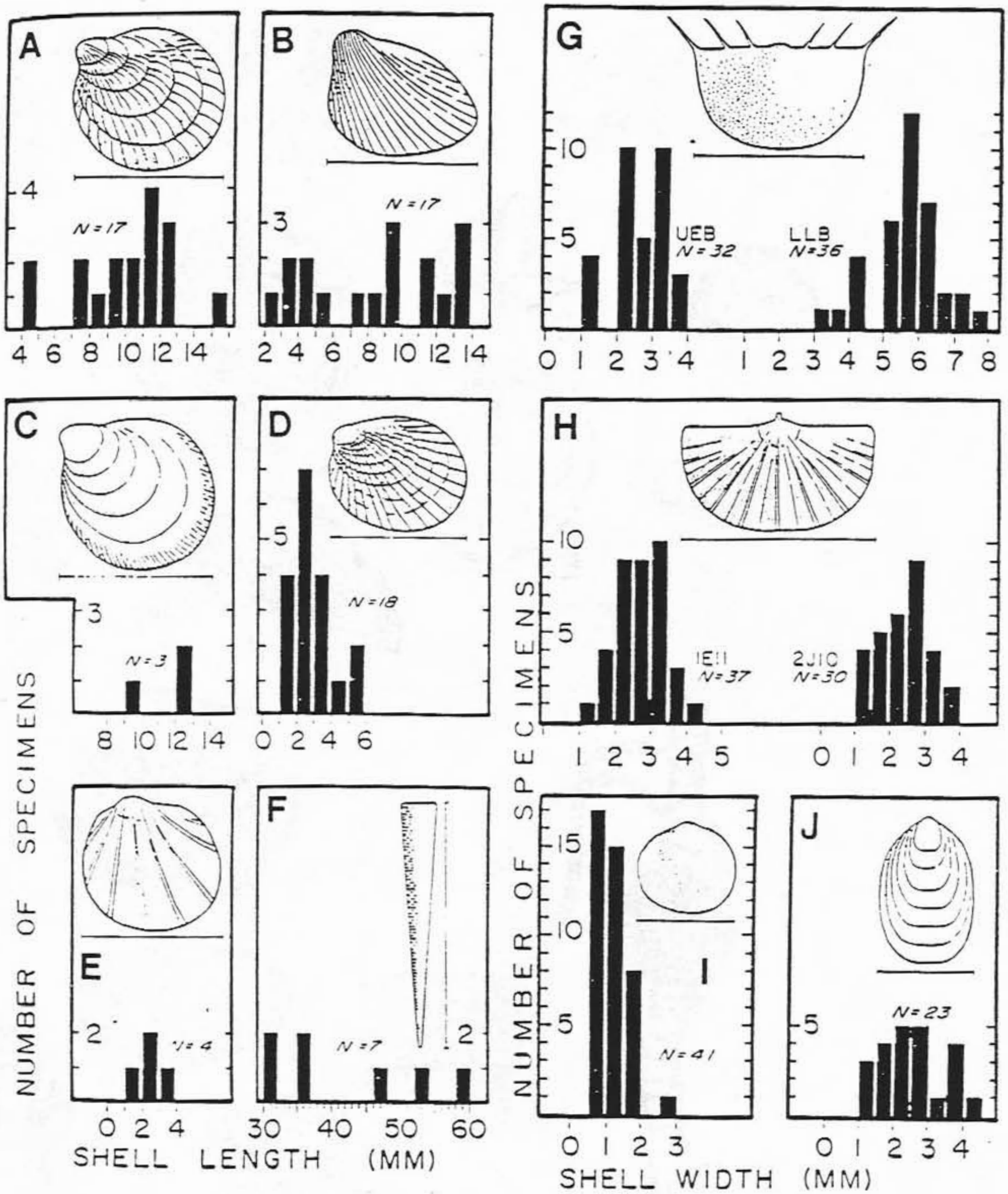
Nature of soft substrate habitats. Unconsolidated or soft sediment substrates comprise a broad range of different habitats each with particular problems for benthic infaunal and epifaunal organisms. These range from firmgrounds to very soft, water-rich 'soupgrounds'. Grain size also differs considerably, from coarse-grained gravels or sands to muds. Sand substrates are often unstable and provide some of the poorest settling areas for organisms. In contrast, many silty or muddy bottom areas possess a diversity of sessile and vagrant organisms. Soft thixotropic muds are particularly favoured by vagrant epifaunal or burrowing infaunal organisms whose activities may inhibit settlement by sessile epifauna. Instability of substrate and high turbidity associated with bioturbated, soft mud bottoms may have been particularly stressful for juveniles of epifaunal organisms. Richards and Bambach (1975) plotted survivorship curves for Silurian (as well as Ordovician and Pennsylvanian) brachiopods. They observed higher juvenile mortality patterns for populations associated with mudstones than those from firmer substrates.

Conversely, where sediments were anoxic to the surface, infauna may have been excluded, and an exaerobic zone fauna (Savrda and Bottjer 1987), totally dominated by low oxygen-adapted

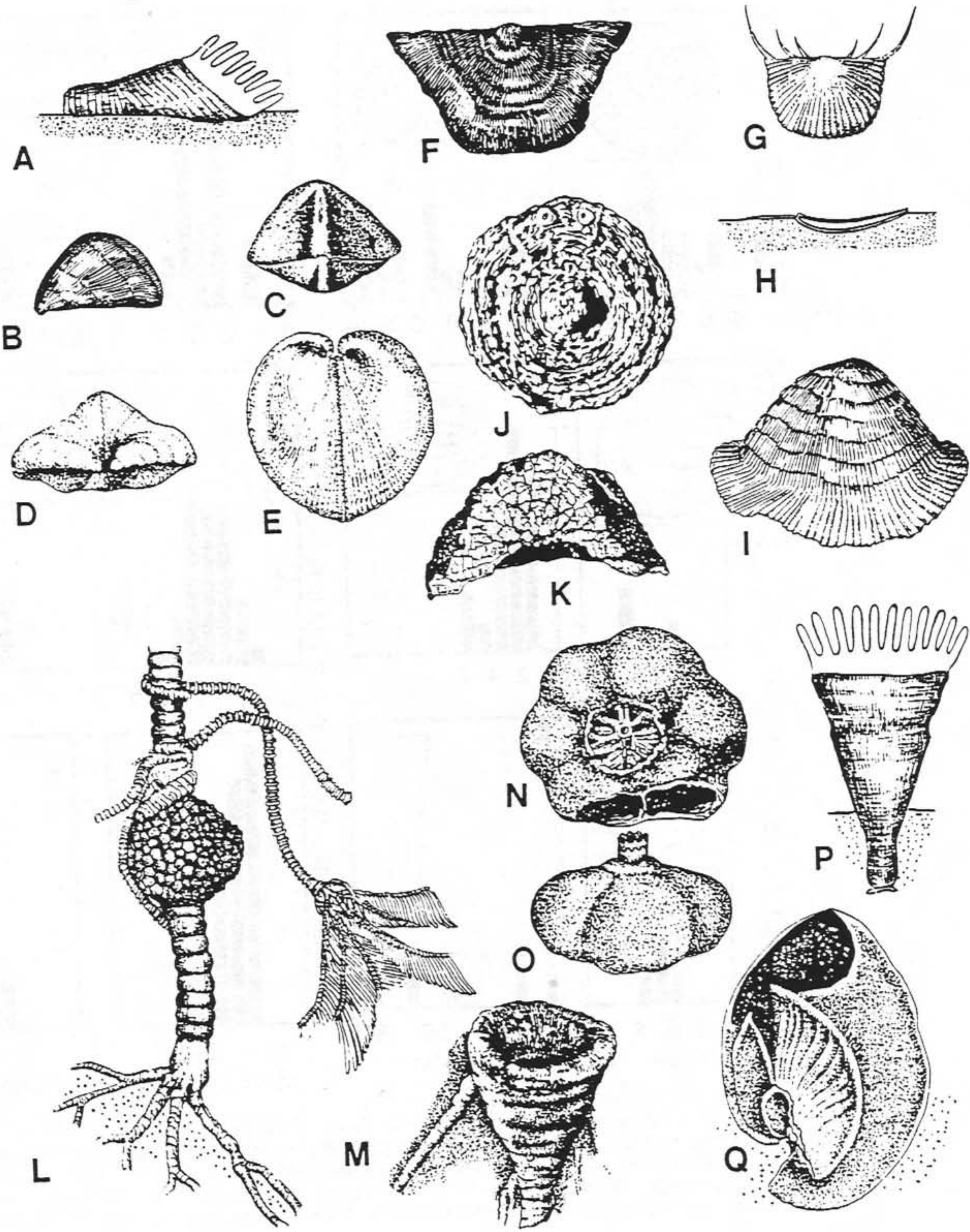
		Order Cyclostomata	Order Trepostomata	Order Cystoporata
Increasing fugitive commitment ↑ Increasing confrontational commitment ↓	 runner	common e.g. *Corynotrypa*	unknown	unknown
	 ribbon	rare e.g. *"Proboscina"*	uncommon	unknown
	 sheet	common e.g. *Sagenella*	common e.g. *Asperopora*	common e.g. *Ceramopora*



TEXT-FIG. 16. Colony shapes and competitive overgrowth in Silurian bryozoans. *A*, taxonomic distribution of three main colony types (runners, ribbons, sheets) in three orders of Silurian encrusting bryozoans. *B*, diagram of encounters between sheet-like bryozoan with holoperipheral growing edge; and three branches of a runner-like bryozoan. Note that in lateral encounters sheet bryozoan readily overgrows runners, but in growing edge-to-growing edge encounters the runner may overgrow the sheet (*b*) or vice versa (*c*). Modified from Taylor (1984).



TEXT-FIG. 17. Diminutive fossil assemblage from shales of the type Ludlow series. Histograms show sizes obtained from numerous samples. These were interpreted as pelagic or epipelagic fossils by Watkins and Berry (1977). *A–E*, bivalves; *G–J*, brachiopods. *A*. *Cardiola interrupta*. *B*. *Dualina striata*. *C*. *Slava fibrosa*. *D*. *Butovicella migrans*. *E*. '*Buchiola*' sp. *F*. '*Orthoceras*' sp. (lengths of complete shells shown). *G*. *Shagamella ludloviensis*. *H*. *Aegiria gravi*. *I*. discoidal inarticulate. *J*. *Lingula lata*. Modified from Watkins and Berry (1977).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epifauna, could exist on the seafloor. Silurian exaerobic faunas are poorly known but may be represented by assemblages of small, thin-shelled brachiopods such as *Lingula*, *Craniops*, *Protochonetes*, and *Skenidioides*, ostracodes, and small byssally attached bivalves such as *Cardiola* (Watkins and Berry 1977; Sheehan 1977; Watkins 1978; Text-fig. 17). Watkins and Berry (1977) argued that this type of assemblage from Silurian dark shales in Wales represents epiplanktic organisms attached to floating seaweeds. However, other authors have argued for a benthic mode of life for most of these supposedly epiplanktic organisms (Sheehan 1977; Bassett 1984). The small sizes of these organisms may represent an adaptation to low levels of oxygen or food (Text-fig. 17).

Sea bottoms with mixed mud and pebbles or skeletal debris may support diverse epifaunal suspension-feeding associations. At a fine scale many of these organisms were actually adapted to hard substrates, but others lived directly on unconsolidated substrates.

Soft substrate adaptations in Silurian organisms. Silurian liberosessile organisms were mainly ambitopic; i.e. requiring at least small grains of hard substrate for initial settlement, but later becoming free-lying or reclining on soft substrate. Maintenance of support on the surface of soft sediment, especially thixotropic muds, poses a problem for which there are various morphological solutions (Thayer 1975). These include the development of relatively large surface areas which act as 'snowshoes', 'skis', or 'stilts' (Thayer 1975). Alternatively, other organisms have a mud-sticking strategy with a submerged ballast to support the vital feeding portions of the organism above the sediment/water interface ('iceberg strategy'; e.g. *Gypidula*, *Pentamerus*). Both morphological strategies are evident among Silurian organisms derived from soft mud substrate communities (Text-fig. 18).

The snowshoe strategy is well illustrated by numerous reclining brachiopods such as the concavo-convex to flattened or disc-shaped strophomenids, which probably rested with the convex valve lowermost. Certain genera, such as *Leptaena* (text-fig. 18*F*) and *Amphistrophia*, became quasi-infaunal with the shell partially sunken into the substrate and a pronounced trail that raised the commissure above the sediment/water interface (Bassett 1984; see Spjeldnaes 1984 for a dissenting opinion). The evolution, during the Silurian, of hinge spines in the first chonetaceans (Text-figs 17, 18*G*, *H*) and extension of cardinal angles into alae in many strophomenids and some spiriferids represent adaptations for increasing bearing surface area in a ski-like fashion. Similarly, production of broad, thin frills in some atrypids suggests an adaptation for resting on soft muds (Text-fig. 18*I*).

In an analogous way, the large, triangular interarea in *Cyrtia* also provided a broad support base (Text-fig. 18*B*, *C*). Similar adaptations for reclining on soft substrates were evolved independently in Silurian bivalves (Kříž 1984). *Dualina* was markedly inequivalved, with a deeply convex valve

TEXT-FIG. 18. Soft substrate adaptations in Silurian organisms. All reconstructions approximately × 1, except as otherwise indicated. *A*, reclining liberosessile organism: rugose coral *Holophragma* lying on side of corallum. *B*, *C*, *Cyrtia*: lateral and posterior views of brachiopod with broad bearing area provided by large triangular interarea. *D*, *E*, bivalve *Slavinka*, dorsal and lateral view showing broad escutcheon which rested on substrate. *F*, brachiopod *Leptaena* with flattened rugate pedicle valve and geniculate margin adapted for quasi-infaunal mode of life. *G*, *H*, dorsal and lateral cross section views of *Protochonetes*: very thin flattened shells and hinge spines provided 'snowshoe' support on soft muds. × 3. *I*, *Atrypa* sp.: lateral oblique view showing broad frill that provided increased surface area. × 1·5. *J*, *K*, tabulate *Favosites* sp., basal and cross-sectional views showing domical colony with flat to slightly concave basal surface with concentrically wrinkled coenosteum for support. × 1·5. *L*, camerate crinoid, *Eucalyptocrinites*, possessed a dendritic holdfast that rooted in soft mud; the epizoic tabulate coral *Favosites parasiticus* and small crinoids (*Dimerocrinites*) attached by distal coils, utilized the larger crinoid's column as a substrate. × 2. *M*, rugose coral *Ketophyllum* possessed long prop-like rhizoids for anchorage in soft substrates with skeletal ossicles. *N*–*Q*, iceberg strategies. *N*, *O*, bulbous holdfast of the crinoid *Scyphocrinites* may have served as a float for support of large column and crown. *P*, conical rugose corals were partly sunken in soft muds *Q*, brachiopod *Kirkidium* had thickened umbonal regions that weighted the lower (posterior) of the shell. × 0·5. Figs *A*, *M*, *P* modified from Neuman (1988), *B*, *H*, *I* modified from Bassett (1984), and *J*, *K* modified from Gibson and Broadhead (1989). Drawings by K. White.

TEXT-FIG. 19. Liberosessile organisms. *A*, *Palaeocyclus rotuloides*; a solitary, discoidal and free-living rugose coral; upper Llandovery, Willowvale Shale, Chadwicks, Utica Co., NY; × 1·5. *B*, basal surface of *Chaetetes lycoperdon* showing wrinkled growth lines; Reynales Limestone, western New York, approx. × 1. Lithograph from Hall (1852, pl. 16).

(either the left or the right) lowermost and a flattened upper valve, whilst *Slavinka*, like living *Corculum*, possessed a broad, flattened, triangular escutcheon on which it rested in a manner very similar to the mode of orientation in *Cyrtia* (Text-fig. 18*D*, *E*).

The broad, flattened basal epitheca of many dome-shaped colonies of small corals, stromatoporoids, chaetetids and bryozoans represents another snowshoe strategy (Text-figs 18*J*, *K*; 19). These forms may be common in otherwise sparsely fossiliferous mudstones. For example, Gibson and Broadhead (1989) note that small, flat-based colonies of *Favosites* were adapted to brief colonization (one breeding cycle) of mud substrates between pulses of sediment influx; such forms are common in many Silurian shales. Calceolid rugose corals, such as *Holophragma*, developed a recumbent mode of life resting on a flattened side of the corallum (Text-fig. 18*A*). Other corals produced smoothly curved corallites typically oriented with the alar plane in the plane of bilateral symmetry on the convex side; these corals rested on the substrate with the curved, convex surface lowermost, an adaptation reminiscent of concavo-convex brachiopod shells (Neumann 1988).

Certain Silurian organisms produced a ramifying network of attachment structures for rooting or silt-like support on soft substrates. Bassett (1984) notes that most Silurian brachiopods probably possessed a single, unbranched pedicle (plenipedunculate). However, he also speculates that certain small discinacean brachiopods with open pedicle foramina may have possessed many-branched pedicles that were rooted directly on soft substrates, as in the case of some recent brachiopods, a condition termed rhizopedunculate. Dendritic holdfasts of cortical material were present in some dendroid graptolites (Bates and Kirk 1984). Likewise, many pelmatozoans 'outgrew' their initial hard attachment substrates and developed secondary features for support on surrounding soft muds. For example, *Eucalyptocrinites* and *Caryocrinites* developed composite holdfasts with primary discs cemented on small objects, typically bryozoans, but with root-like pseudocirri ramifying into the surrounding soft substrate (Text-fig. 18*L*). A few ketophyllid and cystiphyllid rugose corals produced tube-like rhizoids somewhat analogous to dendritic holdfasts in crinoids. The rhizoids emanated from different points on the skeleton and anchored to small skeletal grains in the surrounding soft substrate (Text-fig. 18*M*). Similarly, some Silurian brachiopods (e.g. *Eospinatrypa*) possessed a 'stilt strategy', with elongate spines that raised the shell above the substrate.

The mud-sticking or iceberg strategy was less common among Silurian organisms, but nonetheless, abundant in certain taxa. For example, numerous solitary rugose corals, and a few tabulates, evolved rapidly growing, conical (Text-fig. 18*P*) skeletons which evidently served as a ballast to support the feeding polyps above soft muds (Gibson and Broadhead 1989). Such mud-sticking corals initially attached to very small skeletal grains but later apparently sank into soft substrate under their own weight. In some cases, later toppling of tall corallites and regrowth to vertical orientations led to highly contorted or scolecoid corallites. The analogous adaptation in brachiopods involved the thickened umbonal deposits (Text-fig. 18*Q*), which provided a ballast that served to keep the shell in an upright position above loose substrates. Clustered *in situ* articulated pentamerid and stricklandiid brachiopods are consistently oriented with the weighted umbonal areas downward and lying above areas of shell debris that probably provided initial attachment substrates. Where the brachiopods are very densely packed, they may have been cosupportive.

A few Silurian pelmatozoans also display iceberg strategies in their holdfasts. For example, the large bulbous roots of *Scyphocrinites* (Text-fig. 18*N*, *O*) could have been flotation devices (Haude 1968) but are more reasonably interpreted as free-resting anchors (Thayer 1975). A much larger group of pelmatozoans had 'transferred ballast' attachment strategies, utilizing other objects such as bryozoans or shells to provide a ballast and a tether against lateral movement.

Finally, in rare instances, otherwise sessile organisms may have acted as weakly mobile life forms. For example, Neumann (1988) speculates that certain small discoidal corals (e.g. *Palaeocyclus*; Text-fig. 19*A*) may have been capable of some autolocomotion using their tentacles to move slowly on the substrate. The encrustation of live, or secondarily occupied shells of gastropods or hyoliths may have led to a mobile 'towed' mode of existence. This is known for rare Silurian bryozoans and small favositid corals; the habit became more stereotyped in the Devonian tabulate *Pleurodictyum* (Brett and Cottrell 1982).

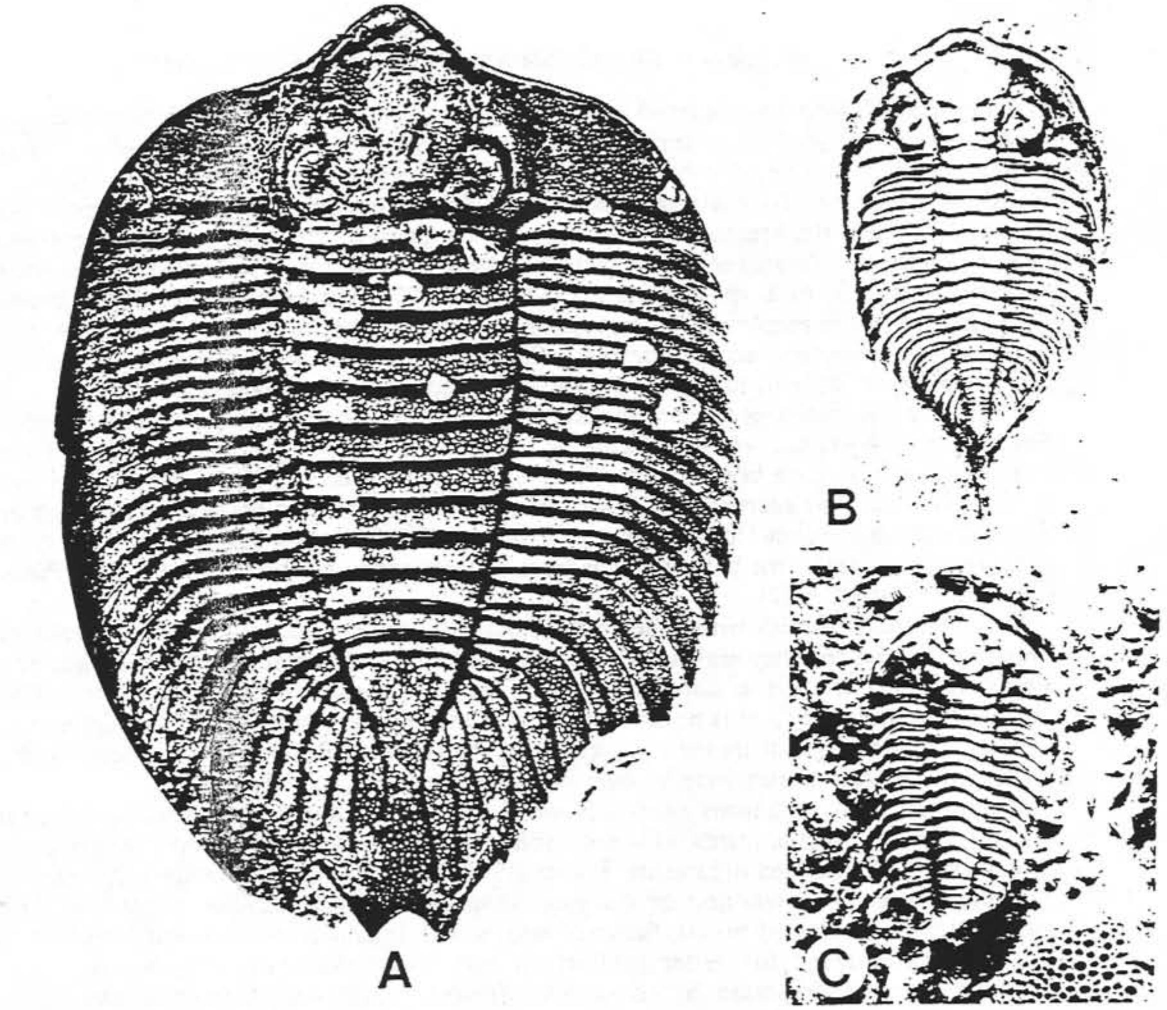
Many Silurian crinoids with coiled distal holdfasts, and especially those with cirral appendages, were liberosessile and they may have bordered on mobility. Crinoids with flexible whorled cirri were almost certainly capable of adjusting their position on unstable shifting substrates (Watkins and Hurst 1977; Brett 1981). It is notable that this mode of attachment, which first appears in the late Ordovician, increased in frequency greatly during the later Palaeozoic in concert with apparent destabilization of soft substrate by burrowers (Brett 1986).

Vagile epifaunal organisms obviously were capable of adjusting to unstable substrates more readily than were sessile forms. However, some of the same principles apply in this case as in the case of the fixed, attached organisms. Siveter (1984) notes that many Silurian epibenthic ostracodes possessed flattened venters and/or marginal flanges to enhance stability. Many Silurian trilobites such as lichids, possessed broad, flattened bodies with lateral extensions and frills (Text-fig. 20*A*) that may have served for better support on soft, soupy substrates (Thomas and Lane 1974). Similarly, harpids possessed broad cephalic fringes, whilst odontopleurids and raphiophorids display long, horizontally oriented spines (Clarkson 1969). The presence of anterior and posterior arches in many of these trilobites raised the median ventral surface above the substrate and permitted respiratory-feeding currents to flow through beneath the animals' bodies. These morphological adaptations may indicate a relatively sedentary, non-burrowing mode of life, as is suggested further by the rare occurrence of epibionts attached to the dorsal exoskeletons of large (gerontic) individuals (Text-fig. 20*A*).

Trilobites with narrower, relatively smooth-sided exoskeletons and particularly those with protruding eyes, such as calymenids, dalmanitids, and proetids, may have been adaptive for a more active, furrowing mode of life, in which the trilobites ploughed through soft substrate just below the sediment/water interface (Text-fig. 20*B*, *C*). For these organisms an abundance of skeletal debris may have been a hindrance in burrowing, and it is notable that many of these, particularly dalmanitids, are most typical of sparsely fossiliferous mudstones wherein *Cruziana* of approximately appropriate dimensions corroborate a furrowing mode of life (Tetreault 1987).

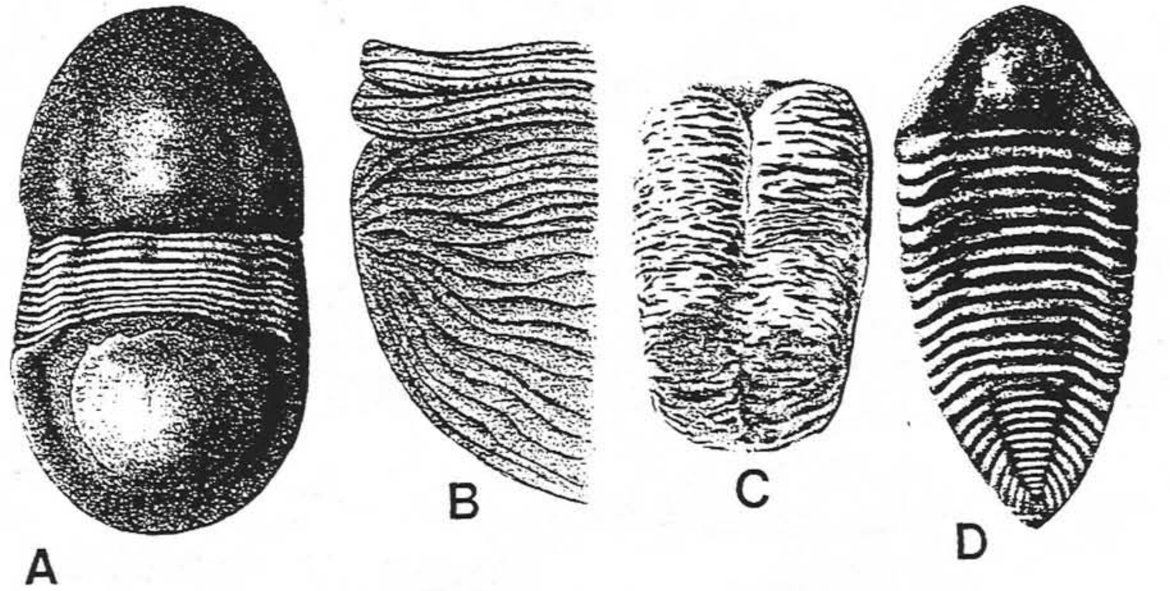
Among gastropods, a number of observations suggest a close relationship between substrate preferences and shell form (Linsley 1977, 1978; Peel 1984). High-spired loxonemataceans are believed to have been actively ploughing or burrowing mesogastropods, well adapted to soft substrates and relatively high levels of turbidity. In contrast, trochiform and turbiniform archaeogastropods appear to be correlated with firmer, sandy substrates. Loosely coiled snails such as *Loxoplocus* were apparently sedentary ciliary feeders and are characteristic of carbonate, often reefy, substrates.

Silurian infaunal burrowing organisms possess differing suites of morphological characteristics; in particular a relatively smooth, streamlined skeleton would appear to be advantageous for



TEXT-FIG. 20. Soft substrate adapted epifaunal trilobites. *A*. *Arctinurus boltoni* possessed a very broad flattened exoskeleton with extended pleural and pygidial lappets: note rhynchonellid and atrypid brachiopods attached to the dorsal exoskeleton; Wenlock. Rochester Shale. Niagara Co., NY. USNM 449453. × 0·75. *B. Dalmanites limulurus* had protruding eyes and a relatively streamlined body; it may have ploughed through the sediment just below the surface: Wenlock. Rochester Shale. Niagara Co., NY. USNM 45467. × 1. *C. Calymene* sp., cf. *C. blumenbachi*: a widespread Silurian trilobite that apparently dwelled in shell-rich muds: Wenlock. Much Wenlock limestone. Dudley, England. × 1. USNM = US National Museum.

movement within soft substrata. These organisms were represented by varied bivalves, lingulid brachiopods, ostracodes and a few trilobites. Smoother, elongate ostracodes with an oval cross section were probably burrowers or swimmers (Siveter 1984). Relatively abundant nuculoid bivalves, analogous to modern nuculoids, were probably very active, shallow-burrowing deposit feeders, highly tolerant of oxygen deficiency (Rhoads 1974; Levinton and Bambach 1975). These organisms were well adapted to soft, fluid substrates and, indeed, they may have contributed to this condition. Their presence may have inhibited settlement by suspension feeders as well as siphonate deposit feeders. Distinct communities dominated by either siphonate or non-siphonate deposit feeders occur in some Silurian mudstones (Levinton and Bambach 1975). Free-burrowing

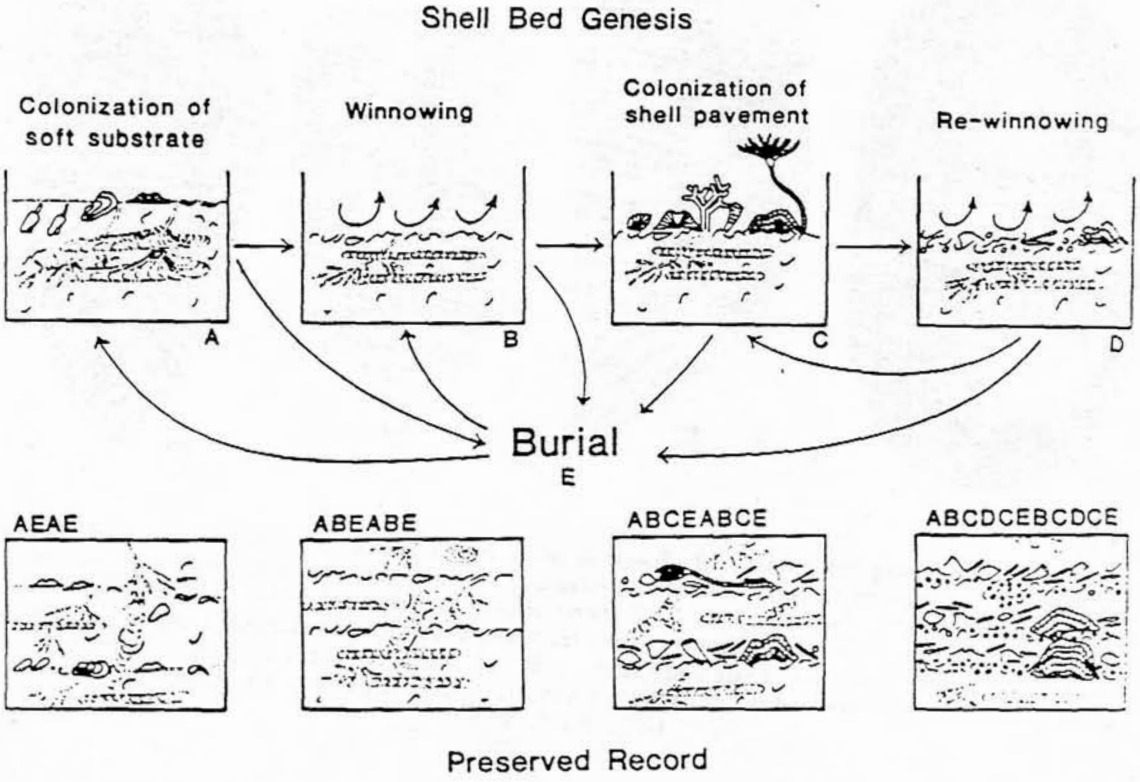


TEXT-FIG. 21. Burrowing trilobites. *A, B. Bumastus ioxus* Hall possessed smooth, rounded cephalon and pygidium; terrace lines (*B*) on dorsal surface may have aided in excavation and anchorage in semi-permanent resting burrows; approx. ×2 and ×5. *D. Trimerus delphinocephalus* exhibits a rounded, shovel-shaped cephalon, presumably adapted for burrowing; the large trilobite is commonly associated with the resting trace *Rusophycus bilobum* (*C*) of similar size and shape. *A, B,* and *D* based on specimens from Rochester Shale, Lockport, NY; Fig. *C* from correlative Herkimer Sandstone, New Hartford, NY. Lithographs from Hall (1852, pls. 9, 66, 68).

suspension feeders are also known among Silurian bivalves and this guild apparently diversified during the later part of the Silurian. These organisms were generally very shallow burrowers as well, probably restricted to the upper 5 to 10 cm of substrate at most. The first relatively deep-burrowing, mucous tube (pseudosiphonate) lucinid bivalves also appeared in the Silurian (Stanley 1982).

Smooth, streamlined shapes of some trilobites also suggest a partly infaunal mode of life. For example, the triangular, shovel-shaped cephalon of *Trimerus* suggests an ability for burrowing and furrowing within soft substrates as do associated large *Rusophycus* (Text-fig. 21*C, D*). Small dorsal terrace ridges with steep faces (scarps) directed posteriorly may have aided in unidirectional, cephalon-forward burrowing by increasing frictional surface areas, as in ratchet sculpture (Schmalfuss 1981). The rounded pygidium and cephalon of some illaenid trilobites suggests a more sedentary burrowed mode of life (Text-fig. 21*A*). As noted in the Ordovician genus *Nileus*, the pygidium and thorax were probably inserted into a semi-permanent burrow, inclined with the sediment, while the cephalon was carried subhorizontally for filter feeding or possibly ambushing small prey. The presence of well-defined dorsal cuticular terraces in these trilobites may have aided in burrowing in firm muds (Text-fig. 21*B*), whilst ventral terraces on the doublures may have been used to compact the sediment walls of the filter-feeding burrow chamber (Schmalfuss 1981).

In addition to the molluscs and trilobites, a host of soft-bodied organisms inhabited unconsolidated substrates. In many Silurian facies, vagrant organisms are known primarily from trace fossils.



TEXT-FIG. 22. Schematic flow chart showing interpreted sequence of events responsible for generating the variety of preserved shell bed types. Different possible scenarios can be traced by following arrows through different pathways, as illustrated in the lower four boxes. From Miller *et al.* (1988).

TAPHONOMIC FEEDBACK AND SUCCESSION IN SILURIAN COMMUNITIES

Shell beds and level-bottom succession

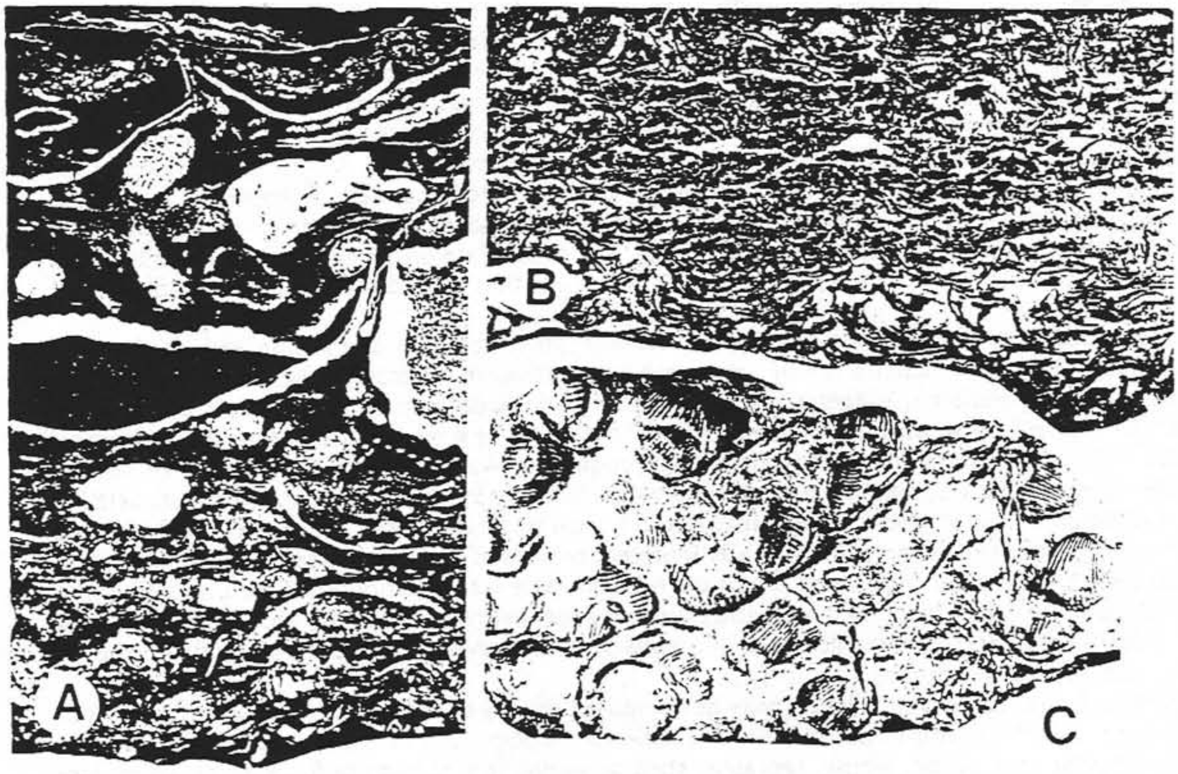
Shelly debris provided local hard substrates on soft, muddy bottom areas, and, in turn, enabled a diversity of hard-substrate-adapted organisms to colonize these environments. Short-term (tens to hundreds of years) directional changes of mud bottom communities, typically termed 'succession' (Walker and Alberstadt 1975) were mediated by physical disturbance of the substrate, taphonomic feedback, true (autogenic) succession, or combinations of these effects. Major storms probably played a critical role in modifying substrates and inducing community change in shallow-water areas. The resultant modifications can be classified into two contrasting effects. In areas directly affected by storm waves, fine-grained sediments would be winnowed away, leaving behind concentrations or pavements of hard shells that could be colonized by epifaunal communities; conversely, deeper-water areas, below storm wave base, would receive blankets of fine-grained sediments winnowed from upslope areas which would abruptly smother epifaunal communities (Miller *et al.* 1988; Text-fig. 22). Mud blankets were colonized subsequently by low-diversity associations of soft substrate-adapted infaunal and quasi-infaunal organisms such as burrowing and epibyssate bivalves and strophomenid brachiopods. Random alternations of winnowing and blanketing led to complex, local, patchy fossil beds of contrasting types (soft and hard substrate specialists) within certain intermediate water depth biofacies (Johnson 1989).

Rate of background sedimentation, ambient environmental gradients, and synsedimentary lithification all played significant roles in faunal succession on Silurian sea floors. In environments receiving regular heavy inputs of siliciclastic sediments, there was rarely sufficient time between depositional events for complex shelly communities to develop. Such areas favoured the development of low-diversity, soft substrate-adapted associations; e.g. quasi-infaunal brachiopods, such as chonetids, infaunal bivalves, and numerous soft-bodied burrowers. Good examples of this type of facies include thick siliciclastic sequences such as those exposed in the Silurian shales of Arisaig, Nova Scotia (Levinton and Bambach 1975). In these shallow-water areas, storm winnowing and aggregation of shells produced only scattered, thin shell pavements. In general, pavements are thin and discontinuous due to the scarcity of available shell material. Commonly these shell aggregations occur at the bases of graded storm silt, and sand layers and, therefore, were not exposed to subsequent colonization by epifuana. The tops of the silty and sandy tempestites were commonly colonized by soft bodied burrowing organisms that left a distinct post-event ichnofacies (Text-fig. 9).

Lower net rates of deposition yielded sequences of shell-rich beds alternating with shell-sparse sediments. The high concentration of shells within coquinites in contrast to the scarcity of shells in the surrounding sediment suggests that such accumulations cannot represent simple ablation lag deposits, derived by winnowing of 'background' sediments (e.g. see Parsons *et al.* 1988). In most cases, the concentration of skeletal material in coquinites would require the removal of several metres of mudstone, if these shell layers were produced simply by winnowing. Furthermore, detailed microstratigraphical studies indicate that some horizons of coquinoid limestone can be traced laterally for tens of kilometres. They clearly represent periods of low net sediment accumulation that interrupted background conditions. The occurrence of early diagenetic phosphates, glauconite, and haematite in certain of these shell beds also points to a low net rate of accumulation. The occurrence of thicker shell beds (1–10 cm thick) within otherwise shell-starved units signals a significant change from background conditions.

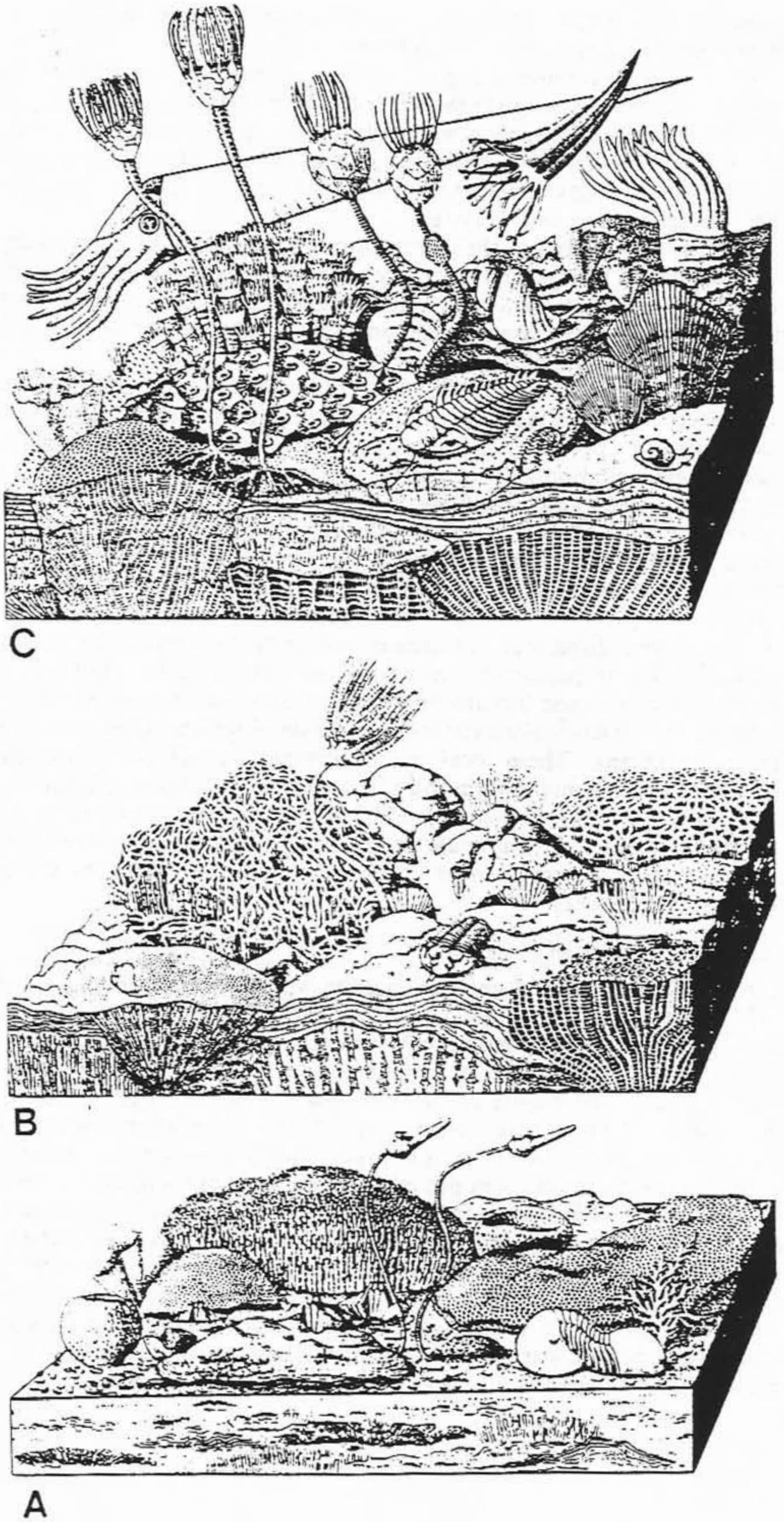
However, the fact that such layers may be composed mainly or entirely of soft substrate-adapted forms (e.g. coquinites composed of quasi-infaunal brachiopods, such as *Eoplectodonta*; Text-fig. 23), indicates that they cannot simply represent shell accumulation on the sea floor in the absence of sedimentation. The latter is unlikely to occur, in any case, because of the rapid rate of shell dissolution and disintegration on most sea floor environments (see Davies *et al.* 1989). Furthermore, some coquinite lenses contain intercalated mud layers. The 'Jeram model' of event condensation (see Seilacher 1985) provides a reasonable solution to the paradox. Highly concentrated coquinas do not simply represent shell buildup on the sea floor, nor single-event storm winnowing. Rather, they are condensations of multiple (perhaps hundreds of) events of mud deposition, and colonization by benthic organisms, followed by winnowing and shell concentration during storms. Winnowed pavements were, in turn, colonized by hard substrate encrusters before being reburied. It is probable that shells were covered in sediment except for very brief intervals of time following exhumation. The lenticular, graded, and sharply based nature of many coquinites presumably records the 'fingerprint' of the last major storm that reworked and winnowed the entire deposit. Therefore, these beds truly represent remains of dozens or hundreds of generations of organisms, which were buried temporarily and then reworked. Such event condensation probably only developed during periods of low net sedimentation. It may have been initiated by the development of hard shelly pavements on discontinuity surfaces. Provided that the rate of blanketing of the original sediments was low, the pavement itself formed a base level or reference horizon onto which additional material was juxtaposed by later storm winnowing events.

The upper surfaces of shell-rich beds commonly show intact and *in situ* preservation of epifaunal organisms (e.g. attached crinoids or brachiopods in life positions; Text-figs 22, 23*C*), which were blanketed by, and may extend upward into, the overlying sediment. This implies that the long-term development of shell beds was finally terminated by major pulses of fine-grained sediments that were sufficiently thick to smother the upper surfaces and prevent their later exhumation. This implies further than many sequences composed of alternating shell beds and mudstones present a bimodal representation of geological time. The shell layers probably represent a majority of the time of the



TEXT-FIG. 23. Complex, multiple-event shell beds. *A*, polished slab of complex brachiopod, bryozoan, and pelmatozoan-rich shell bed; note lag of pelmatozoan, multiple reworked ossicles and shell fragments in base of bed and complete articulated (but compressed) mud- and spar-filled brachiopods in upper portion of bed; Wenlock, Rochester Shale, Niagara Gorge, Niagara Co., NY, ×4. *B*, shell bed of brachiopod-rich grainstone (biosparite) composed of packed shells of *Eoplectodonta transversalis*; note nested stacking shells; also note sharp basal surface. This is a winnowed tempestite bed but the constituent brachiopods were adapted as semi-infaunal mud-substrate fauna; they may have been concentrated by numerous alternating episodes of winnowing and mud deposition; upper Llandovery, Williamson Shale, Walcott, Wayne Co., NY, ×1·25. *C*, upper surface of complex shell bed showing numerous articulated and probably *in situ* specimens of the brachiopods *Homoeospira* sp. covered with silty mudstone; these represent the last generation of organisms that inhabited the shell pavement and were smothered by a mud layer; Ludlow, McKenzie Formation, Keyser, West Virginia, ×0·9.

TEXT-FIG. 24. Succession of palaeocommunities during the development of a typical Wenlock bioherm from the Great Lakes region of North America. *A*, pioneer community (early quiet-water stage of Lowenstam 1957): note *Astylospongia* (lower left); tabulate corals, *Favosites* and fasciculate *Syringopora* (upper left); ramose bryozoan (right); brachiopods *Rhynchotreta* (centre) and *Atrypa*; inadunate crinoids (*Pisocrinus*); and trilobite *Bumastus*. *B*, intermediate community (semi-rough water stage); diverse tabulate corals include *Syringopora* (lower left), *Favosites* (lower right), *Halysites* (upper right and left); at lower centre colonial rugosian *Synaptophyllum*, is encrusted by a stromatoporoid; also note rugose coral *Enterolasma*, ramose bryozoan *Trematopora* (centre), gastropod *Cyclonema*, trilobite *Calymene*, and inadunate crinoid *Gissocrinus*. *C*, 'climax' community (rough-water stage); note predominance of *Favosites* (lower face) overgrown by stromatoporoids; also *Heliolites* (beneath trilobite), colonial fasciculate rugosan (*Synaptophyllum*), and cerioid rugose coral *Arachnophyllum* (both upper left), fenestellid bryozoan, brachiopod *Kirkidium*, trilobite *Cheirurus*, camerate crinoid *Eucalyptocrinites* anchored by dendritic holdfasts, rhombiferan *Caryocrinites* (one with *Favosites parasiticus* on the column), gastropods *Hormotoma* (right centre) *Phragmolites* and *Naticomena*; orthocerid nautiloid and conulariid shown in the water column. Drawings by T. Chase; reprinted by permission of the artist.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entire deposit, whilst intervening mudstone layers may only record single events of sediment deposition (Parsons *et al.* 1988; Johnson 1989).

Not surprisingly, bundles of shell beds may occur non-randomly in many stratigraphical intervals and may alternate with much thicker intervals of sediment containing fewer and much thinner shell beds. In many instances, the condensed shell horizons are associated with episodes of rapid sea level rise, during which general sediment starvation occurred due to nearshore sediment entrapment. Probably the best development of shell-rich layers is as transgressive lags immediately overlying the tops of shallowing upward cycles.

Obviously, the types of shell beds developed during a particular interval of sediment starvation and winnowing will depend upon the ambient environment. Hence, complex, high-diversity shell beds were typical of well-oxygenated shallow shelf and platform settings, whereas dysaerobic environments in the Silurian yielded only thin accumulations of nautiloids, small bivalves, and other hardy epibenthic faunas (Text-fig. 17).

A final consideration of shell-bed formation is that early diagenetic cements may develop within pore spaces, provided that the sediment/water interface remains stable. Commonly, firmgrounds or hardgrounds may form on the tops of simple or complexly amalgamated storm layers. Silty tops of these layers commonly were intensely burrowed by a post-event community of soft-bodied organisms. In such cases, the firm- or hardground may inherit an irregular topography derived from the erosion of old burrow galleries. Later erosion may also rip up and rework hardground fragments or platters (Text-fig. 12*A*). Such hard sea floor areas provided sites for colonization by hard substrate biotas. Walker and Diehl (1986) argue that patchy synsedimentary sedimentation was common in many Palaeozoic shell-rich sediments. Such early lithification may have been less common in later geological time, either due to increased substrate disturbance by burrowers or changes in seawater chemistry. Where patches of sea floor were cemented, for example, in areas around shells or in regions which escaped bioturbation, local firm substrate communities could develop. Archer and Feldman (1986) have called attention to the development of microbioherms in the Silurian Waldron Shale in Indiana. These local patch communities of bryozoans and brachiopods commonly developed around small 'hardgrounds' composed of skeletal objects such as crinoid calices or large brachiopods on otherwise soft, muddy sea floors. The mosaic of hard shells and possibly patches of cemented sea floor surrounded by soft substrates provided a heterogeneous substrate for colonization by a large number of different guilds of organisms and increased diversity of many seafloor communities.

Succession in Silurian bioherms

Larger Silurian bioherms apparently underwent several stages of autogenic succession (Lowenstam 1957; Crowley 1973; Walker and Alberstadt 1975; Brett 1985; Copper 1988) (Text-fig. 24). The initial or pioneering community commonly developed on substrates of stabilized pelmatozoan skeletal debris. This pioneer community consisted primarily of thickets of ramose bryozoans, a few small tabulate and rugose corals, and low diversity clusters of pelmatozoans, which commonly attached to the bryozoans. Lowenstam (1957) referred to this as the 'quiet water stage' of the reef development. In the diversification stages (climax community of Copper 1988), the mound built up upon the stabilized platform provided by initial thickets of organisms and their baffled sediments. At this point, binders, especially porostomatolitic algae, became very common, as did heads of corals, stromatoporoids, and relatively diverse pelmatozoan associations. Finally, in the domination or rough-water stage of the bioherm, the biotic diversity tended to fall off markedly as massive and encrusting stromatoporoids became the dominant members of the reef community. Many of the more diverse corals, bryozoans, and pelmatozoans disappeared. It is not entirely clear if this latter stage was a normal part of autogenic succession or whether it was an allogenic response to stress brought on by lowering of sea level.

SUMMARY DISCUSSION

Sedimentary controls on Silurian organisms

Silurian benthic organisms and sediments formed a complex interactive system as they do throughout the Phanerozoic. The inter-related factors of sedimentation rates, turbidity, and substrate types undoubtedly provided major controls on the distribution of Silurian benthic organisms, along with bathymetrically related factors (see Brett *et al.* submitted). Epifaunal suspension-feeding organisms were undoubtedly sensitive to high rates of sedimentation and turbidity. This factor may account for the paucity of bryozoans and pelmatozoans in thick siliciclastic sequences where both turbidity and sedimentation rates were relatively high. Conversely, many detritivores, including some bivalves, trilobites, and doubtless many soft-bodied 'worms' favoured areas of high detrital input, particularly of muds that contain abundant intercalated and absorbed organic material. Brachiopods appear to have been less sensitive to sedimentation controls than many other organisms, and are therefore distributed more uniformly among Silurian carbonate and siliciclastic facies; in this instance, bathymetric factors including oxygenation and turbulence, probably played the most significant role in distributional ecology (see Boucot, this volume).

Soft mud and fine-grained sand substrates favoured infaunal burrowing taxa, particularly bivalves and semi-infaunal brachiopods, such as lingulids and strophomenids, as well as many vagrant burrowers and detritus feeders, such as trilobites. Many of these organisms developed morphological adaptations for support and/or movement on soft muddy substrates including: 1, a broad bearing surface (e.g. concavo-convex brachiopods); 2, subsurface ballasts or floats (e.g. many rugose corals); 3, ramifying networks of rooting structures (many crinoid rootlets); and 4, streamlined shapes for movement through loose substrate. On the other hand, most epifaunal organisms required hard, or at least firm, substrates for initial settlement and, frequently, for later attachment. Small sedimentary particles such as coarse sand grains or skeletal ossicles provided sufficient anchorage for certain organisms, particularly in low energy environments. Other epifauna required large hard surface areas provided by hardgrounds, larger shells or corals for firm anchorage, particularly in more turbulent settings. Strategies used by these organisms included: 1, cementation of the entire shell; 2, development of rigid or articulated holdfasts; or 3, frequently a permanent or semi-movable attachment by flexible appendages such as pedicles, byssus, or cirri. At a fine scale, many Silurian organisms display a high degree of selectivity for substrates: features such as grain surface textures, degree of exposure to light and wave action, and chemical properties of substrates evidently played a role in inducing settlement of larvae in epifaunal organisms as has been demonstrated in many studies of modern marine invertebrates.

In turn, Silurian benthic organisms modified sea floor sedimentary environments. The incorporation of clay particles into faecal pellets of suspension feeders may have aided in accumulation of mud (biodeposition) and further pelletization of sediment by infauna altered the properties of mud from those of pure clay to silt or even fine sand-sized particles. This increase in grain size also made the sediment more fluid and more easily resuspendable by minor currents (see Rhoads 1974). Hence, heavily bioturbated muds were both unstable and often associated with increased turbidity. These factors discouraged settlement by epifaunal benthic species in many instances (trophic group amensalism; Rhoads 1974). On the other hand, during times of low sedimentation, the buildup of skeletal debris on Silurian sea floors probably inhibited burrowers and allowed additional epifaunal organisms to colonize as a result of taphonomic feedback. Hard skeletal objects provided plentiful colonization sites for the numerous cemented and encrusting organisms. Winnowing and aggradation of shell bearing sediments by storm currents produced variably complex shell pavements as well as thicker shell beds that were self-perpetuating due to taphonomic feedback effects. Such complex shell beds commonly mark out intervals of net sediment starvation as in transgressive parts of cycles.

The most common sediment producers in the Silurian varied from onshore to offshore. Pelmatozoan echinoderms, bryozoans, corals and stromatoporoids were abundant in midshelf, particularly carbonate shoals settings, whilst brachiopods and/or bivalves dominated in siliciclastic-rich settings. Trilobites, ostracodes, and tentaculitids form thin limestones in various other settings. Early cementation of carbonate grains led to the formation of firm- and hardgrounds and consequent hard substrate organism colonization. Blanketing of shelly or hard-bottom sea floors by sediment greatly altered conditions and enabled colonization by an entirely different suite of soft-bodied and shelled, burrowing and scavenging organisms. In some shallow carbonate environments of the Silurian, buildups of organisms produced an array of new microenvironments which enabled additional organisms to colonize the sea floor. For example, thickets of crinoids or bryozoans provided substrates for other organisms, probably increased water turbulence, and had the effect of baffling and trapping sediment. Bioherms and reefs obviously formed complex arrays of microenvironments, such as low-energy reef pockets and stabilized firm surfaces, which were available for colonization by a wide variety of epifaunal organisms. In the buildup of bioherms a complex succession of changes was brought on by the organisms themselves. Corals and stromotoporoids secreted framework developing skeletons, whereas numerous other organisms including algae, bryozoans, crinoids, and others helped baffle and bind sediment in the formation of mounds. Thus a regular suite of successional stages is commonly observed in certain Silurian reefs, ranging from early pioneering thickets of bryozoans and crinoids to later domination phases characterized by tabulate corals and stromatoporoids.

Were Silurian organism interactions different in significant ways from those of modern marine environments? The answer at this point seems to be a qualified yes. The escalation of organism interaction through time (Vermeij 1987) has led to an intensification of many processes that were weakly developed in the Silurian. Free living (liberosessile) organisms—so common on Silurian soft sea floors—are largely absent today. The evolutionary rise of predatory fish, arthropods, gastropods, and others, as well as the destabilization of substrate by deeper burrowing organisms, have relegated these free-lying forms to minor protected refugia environments. The destruction of hard substrates by bioeroding organisms (particularly clionid sponges, fishes, echinoids, and algae) is almost certainly an order of magnitude greater in modern carbonate shelf environments than it was in the Silurian. Although some shells display abundant borings, the degree of riddling of substrates observed in most modern reefal settings is much greater than in the Silurian.

Bioturbation depth in nearshore Silurian environments was probably fairly similar to that observed in comparable modern environments. This is surprising in view of the fact that the quantity of detritus derived from terrestrial environments was probably considerably lower in the Silurian than it is at the present time. Nonetheless, large burrows extending upward to nearly a metre into the sediment are not uncommon in the tidal flat to shallow shelf muds. However, in more offshore environments the degree of homogenization of sediment by organisms was substantially lower in the Silurian than even in the later Palaeozoic. This appears, in large measure, to be due to the scarcity of deep homogenizing burrowers, particularly those that produced the trace *Zoophycos*. Perhaps as a result, many adaptations for stabilization in shifting loose substrate that appear in abundance in later time are less well developed in the Silurian. For example, crinoids with adjustable cirri were only beginning to evolve during the Silurian Period and still constituted a small fraction of the overall pelmatozoan fauna (see Brett 1986).

Competition for substrate seems to have been substantially lower in the Silurian than it is at the present time. Although complex dominance networks have been documented among Silurian bryozoans, the main strategy of early Palaeozoic organisms appears to have been simple avoidance (see Gibson and Broadhead 1989). However, some degree of vertical stratification or tiering (see Bottjer and Ausich 1986) was apparent in Silurian benthic communities; the tiers ranged from a few centimetres into the sediment to low, intermediate and high-level suspension feeders up to one metre above the sediment/water interface. Similar stratification is apparent at later times, although the depth of infaunal tiers greatly increased in later Palaeozoic and Mesozoic times.

Thus, while the present provides a key to understanding of some Silurian organism interactions, we must look to the empirical record of Silurian fossils for better insight into the actual interrelationships between organisms and sediment at this time. Many more field-based studies are needed to develop a sound data base for producing models of distributional ecology of Silurian organisms framed in terms of organism/sediment interactions.

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CARLTON E. BRETT

Department of Geological Sciences
University of Rochester
Rochester, New York 14627
USA