The known complexity of the Mn oxides derives from the small crystal size—in some cases samples are x-ray amorphous—and the potential for chemical solid solution and structural intergrowths. The present study has demonstrated that intergrowths are common between the hollandite and romanechite structures. Furthermore, HRTEM has been used to show that even wider tunnels can occur as coherent intergrowths. In light of these observations, it is not surprising that the mineralogy of the Mn oxides is complex and has been confusing. It may be expected that HRTEM will be a powerful technique for studying and helping to unravel the structural and chemical complexities of the Mn oxides.

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1. Psilomelane has also been used as a mineral name, but the Commission of New Mineral Names voted on 25 August 1969 to make romanechite the name for the specific mineral and psilomelane the general term (M. Fleischer, personal communication). 2. The exact formulas for both hollandite and romanechite are a matter of dispute in the literature. Two suggested formulas are: for hollandite, $(\text{Ba,K, Pb})(\text{Mn,F e})_{10}(\text{OH, O})_{20}$(7); for romanechite, $(\text{Ba, H})_{10}\text{Mn}_{6}O_{19}$(12).


15. We thank J. M. Cowley, I. Mackinnon, and D. Veblen for valuable discussions; J. Hunt for microprobe work; and J. Wheatley for assistance in the electron microscope laboratory in the Center for Solid State Science at Arizona State University. We thank D. J. Fischer for recommending and the Rocky Mountain Mineralogical Society for awarding S.T. a scholarship. The research was supported in part by grant EAR 77-00128 from the National Science Foundation Earth Sciences Division.

2 August 1978; revised 2 October 1978

Biological Bulldozers and the Evolution of Marine Benthic Communities

Abstract. During the Phanerozoic, the diversity of immobile suspension feeders living on the surface of soft substrata (ISOSS) declined significantly. Immobile taxa on hard surfaces and mobile taxa diversified. Extinction rates of ISOSS were significantly greater than in other benthos. These changes in the structure of benthic communities are attributed to increased biological disturbance of the sediment (bioturbation) by diversifying deposit feeders.

Most marine fossils are preserved in fine-grained, originally soft sediments. In the Paleozoic these habitats were dominated by immobile suspension feeders (1, 2), articulate brachiopods, dendroid graptolites, tabulate and rugose corals, bryozoa, cystoids, blastoids, and Archecysta (the only known extinct phylum). Physically equivalent environments are now occupied primarily by deposit feeders (3, 4), for example, probranch bivalves, irregular echinoids, and certain crustaceans, holothurians, and annelids. I suggest that newly evolved deposit feeders and other sediment-disrupting taxa displaced the immobile suspension feeders on soft substrata (ISOSS).

Deposit feeders “mine” organic particles from mud or sand (5, 6), whereas suspension feeders filter food particles from the water column. In Recent marine communities, deposit feeders may exclude suspension feeders by bioturbation (7, 8). This includes suspending sediment or feces that foul biological filters, fluidizing mud substrata (9), accidental ingestion (10), as well as bulldozing: overturning or burial of ISOSS. The effects of bulldozing will be greatest when the deposit feeders are much larger than the ISOSS; juvenile ISOSS will be especially susceptible (3, 6). If the ISOSS cannot complete their life cycles before the sediment is disturbed, they are unlikely to persist. Scavengers and predators may also act as bulldozers (3, 11, 12).

Modern bulldozers—holothurians, irregular echinoids (13), malacostracan
crustacea—diversified after the Silurian (Table 1). They rework sediment an order of magnitude faster than do living taxa that were present in the early Paleozoic (annelids, protobranch bivalves) (14-16). Among the latter, ophiuroids have blind guts (17) and are virtually seasonal (18), while scaphopods are selective carnivores (19) and, by analogy with ecologically similar polychaetes (20), produce minimal bioturbation. Tri-lobites had small mouths, suggesting selective ingestion of small volumes. Their tracks indicate surface feeding (21) and minimal disturbance of sediment (6, 22). The feeding of Limulids, a modern tri-lobile analog, reinforces this inference (12, 22).

Thus rates of bioturbation probably increased several orders of magnitude since the Silurian, and the record of trace fossils supports this conclusion. Other factors being equal, the rate of bioturbation is proportional to the cross-sectional area of the burrower (12, 24). Through- out the Phanerozoic, the width (diameter) of trace fossils from shell sediments increased, and systematic foraging became more efficient (25). Most important, bioturbation seems to have increased with time (26). Although the critical rate of bioturbation cannot be determined without knowing deposition rate, this uncertainty can be diminished by comparing sediments which accumulated in the same kind of environment. My observations of Devonian and Cre- taceous deltaic deposits are consistent with the trend.

There are several possible explanations for the continued diversification of bulldozers. (i) Deposit feeders exploit a seasonally stable food source (27, 28). (ii) This resource probably increased through geologic time. Land plants now dominate global primary productivity (29) and contribute detritus that is an important food for marine deposit feeders (30). The diversification of both land plants and holothurians in the Devonian may be coupled. (iii) Many deposit feed- ers occupied a relatively stable environment within the sediment (31). None of the infaunal deposit feeding taxa in Table 1 have become extinct. (iv) Diversification of predators in the Mesozoic placed a premium on escape by “infaunal-ization” (2, 32). (v) Predators (such as brachiopods and naticids) “followed” prey into the sediment.

There has been a major reorganization of marine benthic communities over the span of the Phanerozoic (Fig. 1). All ben- thic groups show a statistically significant (P < .05) reduction in ISOSS since the Devonian and a corresponding increase in mobile taxa. Hard substrata are not bulldozed, and the occupants of this adaptive zone increased significantly. My conservative definition of ISOSS consigned many probable ISOSS to an intermediate adaptive zone (immobile on or soft substrata), which also experienced significant decline. When analysis is restricted to soft substrata, both brachiopods and bivalves as well as other benthos show a significant (P < .001) decline of ISOSS.

Articulate brachiopods are the dom- inant preserved macrobenthos of most marine communities in the Paleozoic, but during the late Paleozoic and early Mesozoic their abundance and diversity declined to present minor levels. All articulates were immobile suspension feeders (33) and many were ISOSS. The obvious early success of ISOSS brachio-

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**Table 1. First appearances of bioturbation agents (bulldozers). Only trilobites are extinct. Chrono- stratigraphic data from (49). Malacostracan crustacea italicized.**

<table>
<thead>
<tr>
<th>Age</th>
<th>Deposit feeders</th>
<th>Nondeposit feeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tertiary (T)</td>
<td>Hippidea</td>
<td>Amphipoda</td>
</tr>
<tr>
<td>Cretaceous (K)</td>
<td>Tellinacean bivalves</td>
<td>Brachyura</td>
</tr>
<tr>
<td>Jurassic (J)</td>
<td>Irregular urchins</td>
<td>Burrowing suspension feeding bivalves</td>
</tr>
<tr>
<td>Permian (P)</td>
<td>Myisacea</td>
<td>Brachyura</td>
</tr>
<tr>
<td>Carboniferous (C)</td>
<td>Holothuroi (50)</td>
<td></td>
</tr>
<tr>
<td>Devonian (D)</td>
<td>Protobranch bivalves (51)</td>
<td></td>
</tr>
<tr>
<td>Silurian (S)</td>
<td>Ophiuroi</td>
<td>Scaphopods</td>
</tr>
<tr>
<td>Ordovician (O)</td>
<td>Protobranch bivalves (51)</td>
<td></td>
</tr>
<tr>
<td>Cambrian (E)</td>
<td>Agnath fish (52)</td>
<td></td>
</tr>
<tr>
<td>Precambrian</td>
<td>Trilobites</td>
<td>Annelids</td>
</tr>
</tbody>
</table>

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**Fig. 1. Percentage of taxa in major adaptive zones as a function of geologic time. Brachiopods and bivalve mollusks are analyzed in detail because preserved, hard parts are reliable indicators of life habit. (A) Brachiopod genera. Free-lying, ISOSS; I, intermediate; F.B., free-burrowing; Cement, and Pedunculate, animals attached to hard substrata. Chronostratigraphic data from (53). Life habits after (53, 54). (B) Genera of sus- pension feeding bivalves (55). Chronostratigraphic data from (53). Life habits after (53, 55). Endobyssate, byssally attached and partially buried in sediment. (C) Higher taxa (usually families) of well-skeletonized marine invertebrates (brachiopods and bivalves excluded). Chronostratigraphic data from (49). Twofold labels record hardness of substrate and mobility of organisms. Slashes represent intermediates: “hard/soft” inhabited soft bottoms but some attached to hard surfaces (such as dead shells). Often these objects were too small to stabilize the adults, which thus became functional ISOSS (for example, corals, bryozoa). “Soft (hard)” was predominantly soft.**

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2 FEBRUARY 1979
pods posed an enigma that was compounded by the suggestion (34) that brachiopods are exceptionally tolerant of turbidity. If so, why do they no longer inhabit mud? Increased “bulldozing” may be responsible.

Stanley (35, 36) has described important evolutionary changes among the brachiopods: a Mesozoic diversification of burrowing suspension feeders and a Paleozoic transition from partial burial and byssal attachment (ISOSS) to byssal attachment on hard substrata. Stanley attributed both radiations to the selective pressure of physically unstable sediments. But why did these changes occur relatively late in geologic time? In the early Paleozoic, bioturbation had not yet placed a premium on mobility or forced the ISOSS onto hard substrata.

The extinction at the end of the Permian was “one of the most striking events in the history of life”; a “crisis in earth history” (37), and the diversification of bulldozers probably contributed to it. In the brachiopods, bivalves, and other benthos (Fig. 1), the ISOSS suffered significantly ($P < 2$) greater extinction rates than non-ISOSS. For inhabitants of soft sediments only, $P$ is $<0.01$. Of course, bulldozing cannot explain the Permian extinction of pelagic taxa.

Living descendants of ISOSS occupy four types of-refugia. (i) Articulate brachiopods are confined to hard substrates. Semi-infaunal byssate bivalves are abundant only in sediment which has been physically or biologically stabilized (2). Unlike Paleozoic corals, Recent scleractinians are more abundant and diverse on reefs as compared to soft bottoms. Perhaps their reef-forming ability (Triassic-Recent) was selected by the concurrent diversification of bulldozers. (ii) Mobile taxa such as gastropods, malacostraca, and regular echinoids were little affected by the Permo-Triassic “crisis.” Originally immobile taxa have evolved mobility since the Paleozoic: comatulid crinoids (38), some ahermatypic corals (39), and lunulitiform bryozoa (40). Significantly, the most persistent “living fossils,” Lingula, Limulus, and Monoplocophora, are mobile. (iii) The stalked crinoids typical of Paleozoic shelf seas are now concentrated in the deep sea (38) where bioturbation is extremely slow (41). Stromatolites survive where physical stress excludes burrowers and herbivores (42). (iv) Two bivalves, Pinna and Placuna persist as ISOSS on unstabilized sediment (43) and apparently grow rapidly to a “refuge-size.”

Early deposit feeders (such as polychaetes and protobranchs) probably selected food particles from organic-rich sediments. After that adaptive zone had filled, a major resource remained unexploited: sediment with a low concentration of organic matter. Deposit feeders could not tap this food source until they evolved the capacity to process large volumes of sediment rapidly. This adaptive threshold delayed the development of holothurians, urchins, and thalassinds.

The diversification of these deposit feeders also may have been linked to the relatively late enrichment of marine sediments by land plants (29, 30). Infaunal suspension feeders did not diversify until bioturbation intensified. I attribute this to the energetics of infauna as compared to epifaunal suspension feeders (ISOSS). Infaunal suspension feeders construct and maintain a conduit through which they pump large volumes of water. Furthermore, most are mobile. In contrast, ISOSS could deploy extensive passive filtration nets directly in the water column (for example, crinoids).

The Phanerozoic proliferation of bulldozers has other implications. The intensification of this relatively predictable disturbance (44) may have aided the increase in global diversity (taxon richness) of marine invertebrates (26). Regeneration (turnover rate) of nutrients from the sediment of the continental shelves was probably increased (15, 29, 30, 45), perhaps contributing to the Mesozoic diversification of phytoplankton (coccoliths, diatoms, dinoflagellates) and, via trophic linkage, zooplankton (radiolaria, foraminifera). Because of increased bioturbation, the temporal resolution of the stratigraphic record has probably decreased during the Phanerozoic. Biological mixing of strata obscures or obliterates the details of geologic history.

Bioturbation cannot be a panacea for extinction problems in general because there are as many possible extinction hypotheses as there are factors controlling the distributions of organisms. Complementary hypotheses invoke marine regression, plate tectonics, trophic resource regime (46), and increased predation (2, 32). However, modern predators appeared too late to contribute to the Permo-Triassic “crisis” and its long prelude (47). Nor does predation explain the differential success of infaunal epifauna on hard versus soft substrata.

Unlike many extinction hypotheses, biological bulldozing offers testable corollaries. (i) Diversity and abundance of deposit feeders and other sediment re-workers increased; (ii) ISOSS decreased; (iii) ISOSS had greater extinction rates than non-ISOSS; (iv) among the infaunal epifauna, diversity increased on hard substrata but decreased on soft; (v) rate of bioturbation increased with time; (vi) local extinctions of a given taxon were not synchronous (37); and (vii) relict ISOSS (such as endobystate bivalves and stalked crinoids) occur in relatively non-bioturbated sediment.

Stochastic explanations have been offered for evolutionary patterns (48), but why be defeatist when there are credible deterministic alternatives? I have recorded some major evolutionary patterns and have suggested a specific cause: disturbance by deposit feeders and other bulldozers. This hypothesis is particularly appealing because it integrates a wide variety of data.

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18. J. D. Woodley, J. Exp. Mar. Biol. Ecol. 18, 29 (1975). Although some are carnivores or suspension feeders, most are deposit feeders (17).


Rabbit neutrophil membranes. We report on indirect evidence derived from studies of the neutrophil membranes that cause these effects are of interest for an understanding of neutrophil function.

We took advantage of these fluorescein characteristics of chlorotetracycline. The synthetic chemotactic factor fMet-Leu-Phe was obtained as previously described (5). Its competitive antagonist Boc-Phe-Leu-Phe-Leu-Phe (4) was provided by R. J. Freer, Medical College of Virginia, Richmond. Partially purified C5a, the low-molecular-weight chemotactic fragment of the fifth component of complement, was generated by trypsin treatment of C5 as described by Cochrane and Müller-Eberhard (6). These preparations of C5a exhibited maximal biological activity (lysosomal enzyme release) at a dilution of 1 to 1000.

Immediately after the addition of either fMet-Leu-Phe or C5a, a rapid decrease in the fluorescence of chlorotetracycline-loaded neutrophils was observed (Fig. 1). Comparison of Fig. 1, A and B, shows that essentially similar results were obtained whether or not extracellular calcium was present at the time of stimulation. This indicates that the fluorescence signal reflects one of the initial molecular events that follows the binding of the chemotactic factor to its receptor rather than the net influx of calcium that occurs when chemotactic factors are added in the presence, but not in the absence, of extracellular calcium. The dependence of the fluorescence changes on the concentration of the chemotactic factors is illustrated in Fig. 1B. Fluorescence of 100 μM chlorotetracycline (Sigma Chemical Co., St. Louis, Mo.) in Hanks balanced salt solution containing 10 mM Heps [4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid] (pH 7.3), 1.7 mM Ca++, and no Mg++, to which glucose and bovine serum albumin were added at 1 mg/ml each. The desired number of cells were then washed once, resuspended in Hanks balanced salt solution without Mg++ and bovine serum albumin and with or without 0.5 mM Ca++, and transferred to a Perkin-Elmer MFP 2A fluorescence spectrophotometer equipped with a temperature control cuvette holder and stirrer. All the experiments were performed at 37°C with a cell density of 2.5 × 10⁶ cells per milliliter. The viability of the cells, as measured by lactate dehydrogenase release, and their functional responsiveness, as indicated by their ability to release lysosomal enzymes in the presence of cytchalasin B and fMet-Leu-Phe (4), were not found to be affected by these experimental manipulations. Excitation and emission wave-lengths were 390 and 520 nm, respectively. The excitation and emission slits were adjusted to maximize the signal-to-noise ratio. These experimental conditions are essentially the same as those described by other workers who used chlorotetracycline as a calcium probe (3). The synthetic chemotactic factor fMet-Leu-Phe was obtained as previously described (5). Its competitive antagonist Boc-Phe-Leu-Phe-Leu-Phe (4) was provided by R. J. Freer, Medical College of Virginia, Richmond. Partially purified C5a, the low-molecular-weight chemotactic fragment of the fifth component of complement, was generated by trypsin treatment of C5 as described by Cochrane and Müller-Eberhard (6). These preparations of C5a exhibited maximal biological activity (lysosomal enzyme release) at a dilution of 1 to 1000. Immediately after the addition of either fMet-Leu-Phe or C5a, a rapid decrease in the fluorescence of chlorotetracycline-loaded neutrophils was observed (Fig. 1). 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