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The Cambrian Substrate Revolution

David J. Bottjer, Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089-0740, dbottjer@usc.edu
James W. Hagadorn, Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, CA 91125, hagadorn@caltech.edu
Stephen Q. Dornbos, Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089-0740, sdornbos@usc.edu

ABSTRACT

The broad marine ecological settings prevalent during the late Neoproterozoic–early Phanerozoic (600–500 Ma) interval of early metazoan body plan origination strongly impacted the subsequent evolution and development of benthic metazoans. Recent work demonstrates that late Neoproterozoic seafloor sediment had well-developed microbial mats and poorly developed, vertically oriented bioturbation, thus producing fairly stable, relatively low water content substrates and a sharp water-sediment interface. Later in the Cambrian, seafloors with microbial mats became increasingly scarce in shallow-marine environments, largely due to the evolution of burrowing organisms with an increasing vertically oriented component to their bioturbation. The evolutionary and ecological effects of these substrate changes on benthic metazoans, referred to as the Cambrian substrate revolution, are presented here for two major animal phyla, the Echinodermata and the Mollusca.

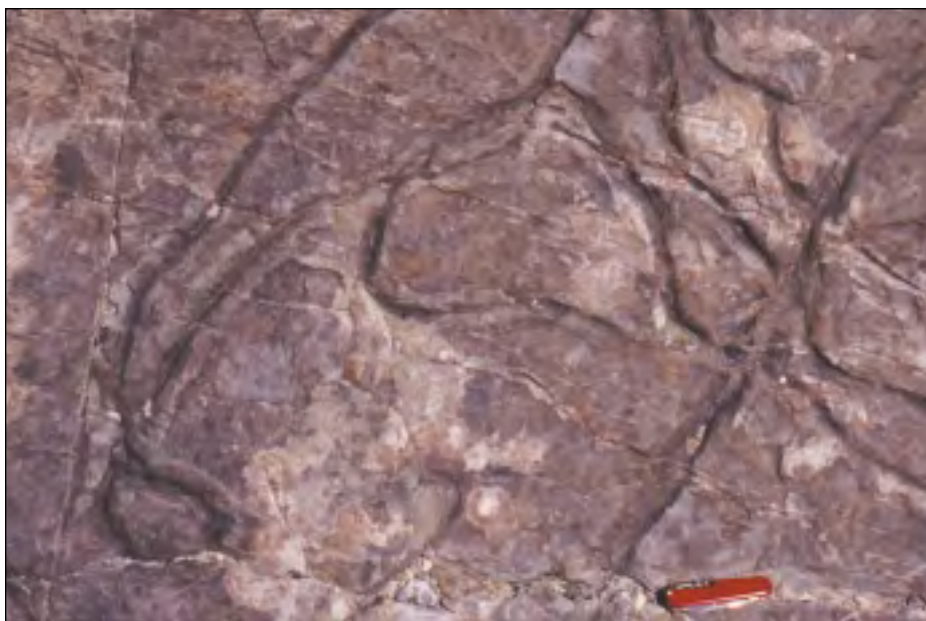


Figure 1. Looping and meandering trace fossil *Taphrhelminthopsis*, made by a large Early Cambrian bioturbator, on a bedding plane from Lower Cambrian Poleta Formation, White-Inyo Mountains, California. Such traces, consisting of a central trough between lateral ridges, occur in sandstones deposited in shallow-marine environments. Evidence indicating original presence of microbial mats is found in associated strata, and morphological features of these traces suggest they were produced on seafloor by active ingestion, or perhaps grazing, of underlying sediments (Hagadorn et al., 2000).

INTRODUCTION

Late Neoproterozoic and early Phanerozoic body and trace fossils commonly exhibit strange morphological adaptations and paleoenvironmental distributions (e.g., Fig. 1). At this time, the basic body plans of large metazoans were first evolving, and much research has been expended toward understanding the evolutionary relationships of these ancient animals. Of particular importance is that while this evolutionary play of metazoan body plan evolution was taking place, the ecological stage was shifting. Two changes in the biological dimensions of the marine ecological stage were especially important. First was the advent and development of predation, which, together with additional biological and geochemical factors, fostered the evolution of mineralized skeletons (e.g., Vermeij, 1989; Bengtson, 1994).

The second change in the biological dimensions of the ecological stage occurred in seafloor sediments, which act as the substrate on and in which benthic organisms live. This change was caused by increasing disturbance of sediments by bioturbation (e.g., Droser, 1987; Droser and Bottjer, 1989) (Fig. 2). Through analogy with the development of agriculture and its resulting effects upon soils, Seilacher and Pflüger (1994) have termed this

change the agronomic revolution. Late Neoproterozoic seafloors were typically characterized by well-developed microbial mats (e.g., Gehling, 1986, 1996, 1999; Schieber, 1986; Hagadorn and Bottjer, 1997, 1999) and poor development of sediment mixing by vertically oriented burrowing (e.g., Droser et al., 1999; McIlroy and Logan, 1999) (Fig. 2). Sediment layers on the seafloor thus had relatively low water content and were characterized by a sharp water-sediment interface. Work on carbonates (e.g., Awramik, 1991) and more recently on siliciclastics (e.g., Hagadorn and Bottjer, 1997, 1999) has shown that in the Cambrian shallow marine environments characterized by seafloors covered with microbial mats became increasingly scarce, largely due to increasing vertically oriented bioturbation (Fig. 2). This change to a more Phanerozoic-style seafloor resulted in relatively greater water content of seafloor sediment and a blurry water-sediment interface, which led to the first appearance of a mixed layer. Mixed layers constitute the soupy upper few centimeters of the substrate that are homogenized by bioturbation and are characteristic of later Phanerozoic fine-grained substrates (e.g., Ekdale

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In Memoriam

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Cambrian Substrate *continued from p. 1* ing extinction, adaptation, and environmental restriction.

et al., 1984). With near elimination of microbial mats in shallow-marine environments, microbial or mat-related food sources in sediment changed from being well layered to having a more homogeneously diffuse distribution in the sediment layers on the seafloor. Thus, this agronomic revolution led to the soft-sediment substrates we commonly see in shallow carbonate and siliciclastic marine environments today (Fig. 2). We term the effects this transition had on benthic organisms the Cambrian substrate revolution (Bottjer and Hagadorn, 1999). The Cambrian substrate revolution involved both evolutionary and ecological changes occurring at different time scales, includ-

EVOLUTIONARY AND ECOLOGICAL IMPACTS

Paleobiologists have long been interested in the morphological features evolved by organisms that live on soft sediment seafloors (e.g., Thayer, 1975). Until recently such adaptations could only be adequately assessed for later Phanerozoic benthic organisms, due to an incomplete understanding of late Neoproterozoic and Cambrian paleobiology and paleoenvironments. New data from the Neoproterozoic-Phanerozoic transition have allowed paleobiologists to begin to address the adaptive morphology of these early animals. Environments of the Neoprotero-



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Service at GSA: Programs for Students

Last month in "Dialogue," Jack May, Julie Williams May, and I discussed a few of the benefits GSA offers to students, especially those programs available at our Section Meetings. Last month's article was the first in our series on our third value—service. This month, I want to highlight several other GSA programs we offer to students.

Mentoring

Jack touched on one of the mentoring programs we offer that is made possible through the generosity of Roy Shlemon. With Roy's gift, GSA is able to arrange for applied geoscientists to meet with students at Section Meetings. For some students, this may be their first glimpse into the working life of an applied geoscientist. Roy envisioned a program that would facilitate bridging the gap between the applied and academic geology communities—with a special emphasis on providing information about potential career paths to students.

The John F. Mann Mentor Program in Applied Hydrogeology also works to provide guidance for students and help them prepare for careers. This one-on-one mentoring program brings geoscientists together with undergraduate and graduate students and faculty to foster relationships between the professional community and local colleges and universities, and to generate enthusiasm for career opportunities in applied hydrogeology.

Internships

GSA coordinates two intern programs with our partners, the National Park Service (NPS) and the Department of Agriculture U.S. Forest Service (USFS). Since 1996, GSA has placed 31 interns in national parks across the United States. These advanced undergraduate students spend a summer as geological interpreters or in resource management in the parks. Given the success of our NPS partnership and this intern program, GSA partnered with the USFS to place four undergraduates with Forest Service geologist mentors in the Pacific Southwest Region this summer. This Forest Service program is called *Geology in the Forests*.

Looking Ahead

In an upcoming issue of *GSA Today*, you'll read about GeoCorps America, a new program that will allow our sister societies to participate as partners in placing interns on public lands. Plans also include expanding the types of participants to allow career and retired professionals an opportunity to participate. This program's goal is to

place 500 interns each year on America's public lands.

Service to students is one of the tenets of GSA. These two programs—mentoring and internships—are prime examples of how GSA helps students gain experience in geoscience careers and transition from the classroom. Neither program would be possible without partnerships, either with a donor or with the NPS and USFS. Partnering creates the link between the GSA, students, and hands-on geoscience experiences. Our ability to create effective partnerships stems directly from the generosity of donors to the GSA Foundation, such as the late John Mann, his wife Carol Mann, and our friend Roy Shlemon, all of whom believed in investing in the next generation of geoscientists.

Each of us can look back over our careers and see who or what helped us at each of the transition points—from undergraduate to graduate school, from school to career, and from research to applied geoscience. GSA programs provide an opportunity to learn about career choices and experience the life of a working geologist. GSA offers members and students an opportunity to make transitions as our careers evolve. ■



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zoic-Phanerozoic transition were different from those today, requiring the use of nonuniformitarian approaches to analyze the paleobiology and paleoecology of animals living at this time (e.g., Bottjer, 1998). For example, Seilacher (e.g., 1999) has postulated that lifestyles of organisms that lived on late Neoproterozoic sediments characterized by microbial mats, or matgrounds, would include: (1) mat encrusters, which were permanently attached to the mat; (2) mat scratchers, which grazed the surface of the mat without destroying it; (3) mat stickers, which were suspension feeders that were partially embedded in the mat, and comprise a subset of adaptations resulting in organisms broadly termed sediment stickers; and (4) undermat miners, which burrowed under-

neath the mat and fed on decomposing mat material.

The presence of metazoan fossils perhaps as old as 570 Ma (e.g., Fig. 1 in Martin et al., 2000), and molecular data indicating a possibly earlier origin of metazoans (e.g., Wray et al., 1996), suggests that there was an early stage of evolution for most benthic metazoan groups before they evolved mineralized skeletons (e.g., Fortey et al., 1996, 1997). This early stage of evolution for benthic organisms was within the environmental context of a Neoproterozoic-style minimally bioturbated seafloor covered with microbial mats. Thus, how did this late Neoproterozoic-Phanerozoic transition to more Phanerozoic-style seafloor conditions affect the evolution, dispersal, and paleoenvironmental distribution of metazoans,

which were adapted to these Neoproterozoic seafloor sediments? Were there animals and perhaps entire communities that were adapted to these seafloor conditions, in the manner proposed by Seilacher (1999)?

We cannot yet fully answer these questions. However, mounting evidence suggests that many evolutionary and ecological changes, which took place during this time interval, were due to the transition in substrate style from the late Neoproterozoic marine environments and lifestyles described by Seilacher (e.g., 1999), to the bioturbated sedimentary environments and morphological adaptations documented for later Phanerozoic benthic organisms (e.g., Thayer, 1975).

Cambrian Substrate *continued on p. 4*

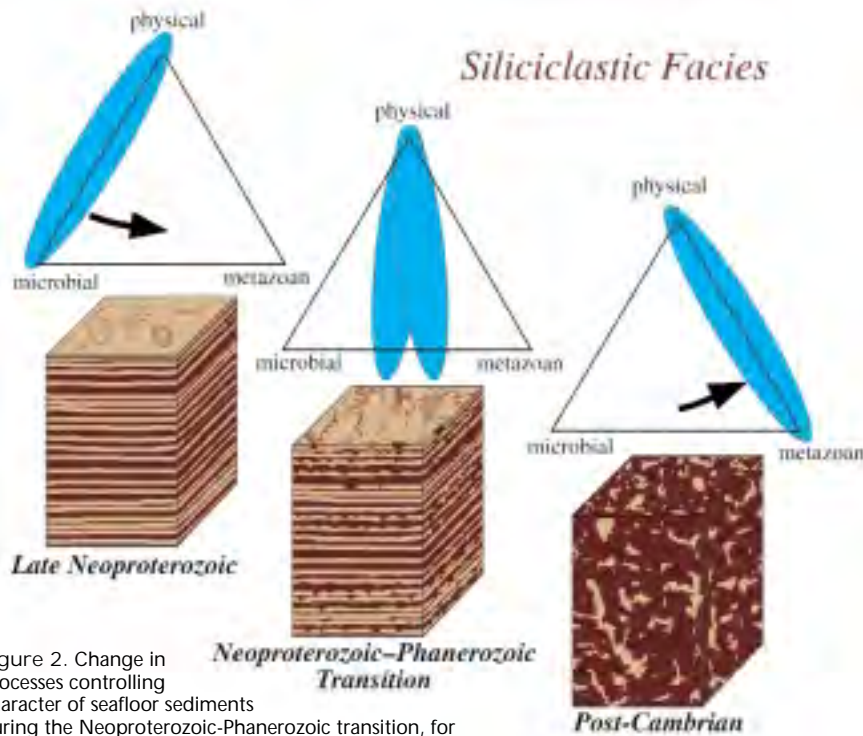


Figure 2. Change in processes controlling character of seafloor sediments during the Neoproterozoic-Phanerozoic transition, for siliciclastic neritic (below normal wave base to shelf edge) environments. These processes, indicated on the triangular diagrams, are physical (causing primary deposition of sediments), microbial (also producing primary structures), and subsequent bioturbation by metazoans. Changes in triangular diagram blue fields show change in relative dominance of these processes through this transition. Schematic seafloor cores indicate characteristic physical and biogenic sedimentary structures during this transition, from laminated and thin bedded (left), to partially bioturbated (center), to completely bioturbated (right). Derived from data in Droser (1987), Hagadorn and Bottjer (1997, 1999), Droser et al. (1999), and McIlroy and Logan (1999).

Early suspension-feeding echinoderms and grazing polyplacophoran and monoplacophoran mollusks (and their likely soft-bodied ancestors) provide two examples of the effects of this change in substrate character.

SESSILE SUSPENSION-FEEDING ECHINODERMS

Evolution of Cambrian suspension-feeding echinoderms that had an immobile, or sessile, lifestyle provides strong evidence for the short-term impact of the Cambrian substrate revolution. For example, the unusual Early Cambrian helicoplacoid echinoderms were well adapted for survival on Neoproterozoic-style substrates. These small (1–5 cm) suspension-feeding echinoderms (Fig. 3) lived as sediment stickers on a substrate that underwent only low-to-moderate levels of horizontally directed bioturbation and did not have a mixed layer (Dornbos and Bottjer, 2000a). Helicoplacoids lacked typical Phanerozoic soft-substrate adaptations, such as the ability to attach to available hard substrates or presence of a root-like holdfast. Significant increase in depth and intensity of bioturbation in shallow-water muds and sands through the Cambrian (e.g., Droser, 1987) destroyed the stable substrates that these small echinoderms required and likely led to their extinction (Dornbos and Bottjer, 2000a) (Fig. 3).

In contrast, both edrioasteroids and eocrinoids, the other groups of undisputed Cambrian sessile suspension-feeding echinoderms, were able to adapt to the change in substrates created by increased bioturbation. The earliest edrioasteroids lived unattached on the seafloor during the Early and Middle Cambrian, but by the Late Cambrian edrioasteroids lived attached to available hard substrates (e.g., Sprinkle and Guensburg, 1995) (Fig. 3). Similarly, several Early and Middle Cambrian eocrinoids were stemless and lived unattached on the seafloor (Ubaghs, 1967; Sprinkle, 1992) (Fig. 3). By the Late Cambrian, however, eocrinoids had evolved stems and also lived attached to available hard substrates (Fig. 3). Thus, by attaching to hard substrates or by developing stems, each of these Cambrian echinoderm groups avoided the detrimental effects of increased substrate instability caused by increasing bioturbation (Fig. 3), and they survived into the post-Cambrian Paleozoic. The remaining undisputed Cambrian echinoderms were all mobile deposit- or suspension-feeders (e.g., Sprinkle, 1992). Their mobility likely exacerbated the substrate changes occurring during this time, and, because they could adjust their position relative to the sediment-water interface, they would have been relatively

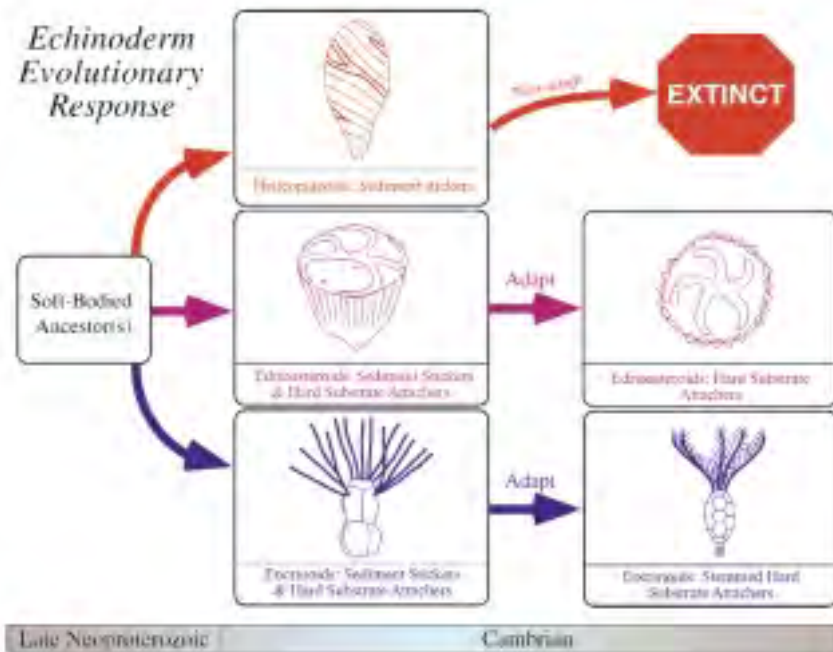


Figure 3. Evolutionary response of Cambrian sessile suspension-feeding echinoderms as part of the Cambrian substrate revolution. Arrows do not represent a direct evolutionary relationship between specific echinoderms shown, but imply a general evolutionary trend through the Cambrian within each of the groups examined, with these echinoderms serving as individual examples. Helicoplacoid drawing is modified from Paul and Smith (1984); specimen is 3 cm in height. For edrioasteroids, *Camptostroma* (left) is modified from Paul and Smith (1984); specimen is 5 cm in height. Edrioasteroid on right is a schematic of a typical attaching edrioasteroid, modified from Paul and Smith (1984); size is 5 cm in width. For eocrinoids, *Lichenoides* (left) is modified from Ubaghs (1967); specimen is approximately 2.5 cm in height. Eocrinoid on right is *Tatonkacystis*, modified from Sumrall et al. (1997); specimen is approximately 5 cm in height. Geological time not to scale and boxes do not represent the precise age range of the echinoderms they contain.

immune to the effects of this change in substrate character.

EARLY GRAZING MOLLUSKS

Similarly, how did mobile organisms that grazed the sediment surface (a life habit likely typical of early mollusks) respond to this change in substrate character? If organisms crawled on top of the sediment surface in late Neoproterozoic marine environments and scratched or scraped microbial mats for food, disappearance of mats from these settings might have restricted them to marine hard substrate environments where mats still flourished, such as those typical of the nearshore (e.g., rocks or reefs), where scratching or scraping microbial layers and biofilms off hard substrates was still a viable strategy. In addition, if organisms depended upon the relatively sharp water-sediment interface that the combination of mats and minimal vertical bioturbation produced in marine soft sediments, then, in response to this widespread change in substrate character, they also could have become restricted to soft substrate environments where these conditions still prevailed. The most likely environments in which to find such conditions are in the deep sea, where: (1) mats built by chemoautotrophic and heterotrophic microbes occur (e.g., Hagadorn and Bottjer, 1999; Simonson and Carney, 1999; and references within); and (2) biogenic reworking, although highly variable, may be several orders of magnitude less than on the shelf (e.g., Thayer, 1983; Gage and Tyler, 1991).

The evolutionary relationships of the mollusks are still controversial (e.g., Runnegar, 1996). Aplacophorans, polyplacophorans, and monoplacophorans are the most primitive mollusks living today (e.g., Salvini-Plawen and Steiner, 1996). Aplacophorans are generally thought to be the most primitive, because of their worm-like body form and spiculate skeleton, but they have no fossil record (Pojeta et al., 1987). Polyplacophorans, or chitons, have a broad muscular foot covered by eight dorsal shell plates (Fig. 4), and living representatives graze surficial microbial mats and biofilms (Pojeta et al., 1987). The oldest known polyplacophorans lived in the Late Cambrian and grazed on shallow-water stromatolites (Runnegar et al., 1979) (Fig. 4). Living monoplacophorans have a broad foot and are also surface grazers, but unlike chitons they have a single continuous dorsal shell (Fig. 4). Fossil monoplacophorans have a broader variety of shell morphologies than living genera, (e.g., Pojeta et al., 1987), and this complexity is reflected in the variety of interpretations that exist concerning monoplacophoran evolutionary relationships (e.g., Pojeta et al., 1987; Salvini-Plawen and Steiner, 1996; Runnegar, 1996). The oldest known monoplacophorans are

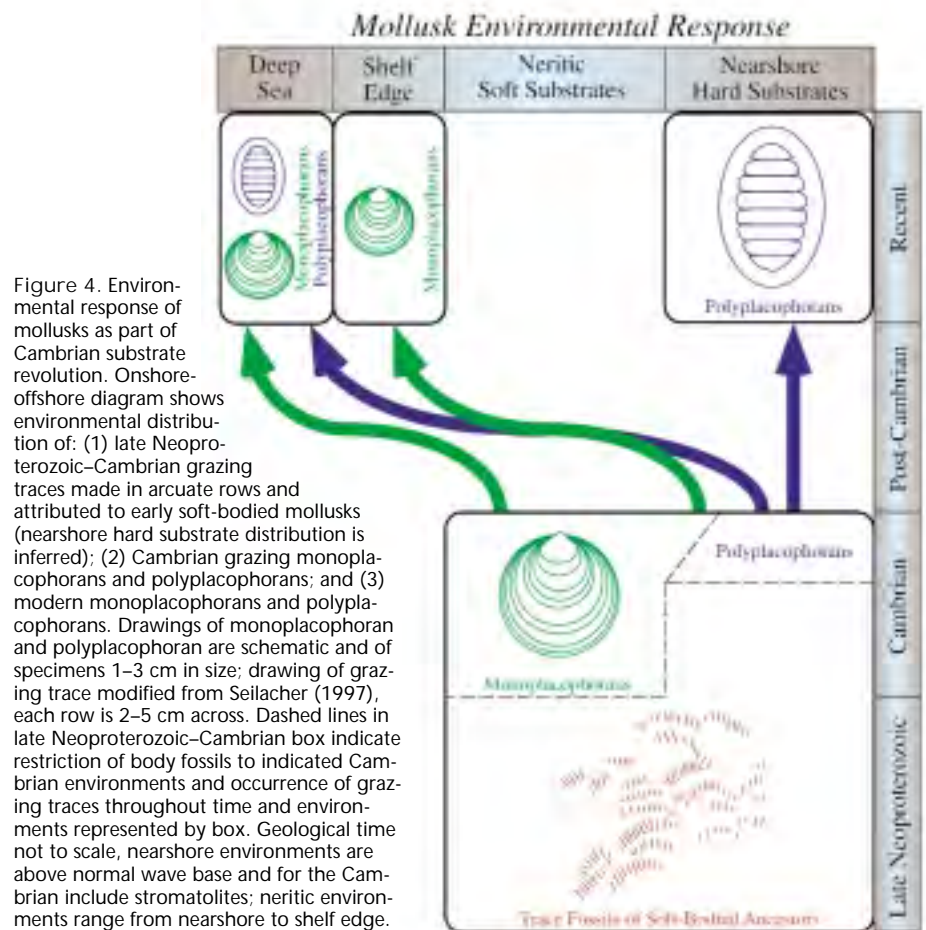
Early Cambrian, and include substrate grazers (e.g., Pojeta et al., 1987) (Fig. 4). The post-Cambrian fossil record of both polyplacophorans and monoplacophorans is poor, and little is known about how and where they lived (e.g., Pojeta et al., 1987; Squires and Goedart, 1995; Cherns, 1998).

However, the modern occurrence of chitons and monoplacophorans exhibits the type of environmental distribution that one would predict as a long-range consequence of the Cambrian substrate revolution. Modern polyplacophorans typically occur in rocky coastline environments but some live in the deep sea (Pojeta et al., 1987; Squires and Goedart, 1995) (Fig. 4). Living monoplacophorans occur in the deep sea on soft substrates, although one genus lives on hard substrates at the shelf edge (Pojeta et al., 1987) (Fig. 4). Thus, although little currently is known about the ecology of soft-bodied late Neoproterozoic and Cambrian ancestors of polyplacophorans and monoplacophorans, they may have lived on soft as well as hard substrates in shallow marine environments and grazed microbial mats that covered the seafloor, a lifestyle that today is typically restricted to hard substrates and the deep sea.

Behavioral evidence, in the form of trace fossils, provides additional insight

into the life habits of early metazoans that lived on these soft substrates. For example, Upper Cambrian bedding surfaces from Oman contain large scratch marks that are morphologically identical to traces made by the grazing of modern gastropods upon hard substrates. Because these grazing traces are associated with ovate traces most likely produced by a soft-footed organism, they suggest that early mollusks were grazing on soft seafloor sediments (Seilacher, 1977, 1995). Gehling (1996) has also documented grazing traces, together with flattened ovoid body impressions, in Vendian strata of Australia, suggesting association with a soft-footed mollusk. Similar traces occur in Lower Cambrian strata in Yunnan Province, China (Dornbos and Bottjer, 2000b) and Vendian strata of the White Sea area, Russia (Martin et al., 2000). All of these scratch-style traces are associated with diagnostic sedimentary structures indicative of the presence of microbial mats, and all except the White Sea traces are from medium- to coarse-grained arenites. Considered together, these occurrences suggest that early in their evolutionary history, mollusks in nearshore to shelf-edge environments grazed upon sands, which

Cambrian Substrate *continued on p. 6*



GSA Welcomes the Geological Society of South Africa as an Associated Society

At its May 2000 meeting, the GSA Council voted to accord Associated Society status to the Geological Society of South Africa (GSSA).

The GSSA was founded in 1895 after the discovery of gold on the Witwatersrand in 1886 concentrated the South African geological, mining, and financial fraternity in the infant Johannesburg. South African geologic features such as the world-renowned Witwatersrand, the Barberton Mountain Land, the Bushveld Complex, and the fossil-rich Karoo led B.B. Brock to coin the moniker "Land of Geological Superlatives" for this outstanding landscape.

A constitution based upon that of the Geological Society of London was adopted with the following objectives: to promote the study of the earth sciences; to do everything conducive to the advancement of the earth sciences and the earth science professions; to promote the interests of the earth sciences and the earth science professions; and to uphold high professional and ethical standards amongst its members.

GSSA has approximately 1,500 members in 13 geographic branches and five disciplinary divisions. GSSA has sponsored many Geocongress meetings over the years and has published a number of Congress abstract volumes representing documentation of otherwise largely unpublished data.

Affiliation as an Associated Society with GSA will solidify the societies' ties and ensure an increased awareness of the contributions the respective societies and science are making and can make in the future.

Additional information is available from the GSSA Web site at www.gssa.org.za.

Cambrian Substrate *continued from p. 5*

behaved in a semilithified manner due to the presence of microbial mats (Fig. 4).

ADDITIONAL IMPLICATIONS

Because adaptations to these mat-covered and more coherent Neoproterozoic-style soft substrates required different morphologies and behaviors than souper Phanerozoic-style soft substrates, the Cambrian explosion is also characterized by a unique variety of bedding-parallel trace fossils. For example, large meandering trace fossils such as *Plagiogmus* and *Taphrhelminthopsis* (Fig. 1) were common in Early Cambrian shallow-marine environments, yet were likely made by soft-bodied metazoans for which we have no body fossil record (McIlroy and Heys, 1997; Hagadorn et al., 2000). Similarly, several other meandering trace fossils as well as those exhibiting a network pattern, including *Helminthoida* and *Paleodictyon*, also occur in Cambrian strata deposited in shallow-marine environments (Crimes and Fedonkin, 1994). A number of these Cambrian trace fossil genera, as well as ichnogenera with similar morphologies, are found only in deep-sea strata after the Cambrian, and thus are united by a similar paleoenvironmental history of onshore-offshore retreat (Bottjer et al., 1988; Crimes and Fedonkin, 1994;

Hagadorn et al., 2000). This pattern of post-Cambrian restriction to the deep sea by bedding-parallel trace fossils is mirrored by the record of microbial structures produced in siliciclastic sediments (Hagadorn and Bottjer, 1999). Thus, as for grazing mollusks, the environmental restriction shown by trace fossils is likely also an effect of the Cambrian substrate revolution, caused by the broad increase in vertically directed bioturbation and consequent decrease in development of microbial mats, in shallow-marine environments.

Further analysis of the Cambrian substrate revolution may contribute to a better understanding of broader evolutionary phenomena. The Cambrian is characterized by a wide variety of metazoans, reflected in both body and trace fossils, many of which have morphologies that appear strange to the modern eye (e.g., Gould, 1989). Perhaps the co-occurrence during the Cambrian of benthic metazoans adapted more to Neoproterozoic-style soft substrates, with those more adapted to Phanerozoic-style substrates, contributed significantly to the high morphological disparity exhibited by animals of the Cambrian explosion.

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