

Modern mucociliary creeping trails and the bodyplans of Neoproterozoic trace-makers

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Abstract.—The bulk of Neoproterozoic trace fossils can be interpreted as horizontal creeping trails produced by minute vermiform organisms moving on or just beneath the seafloor or under algal mats. We have investigated the formation of trails by living cnidarians and platyhelminths that creep by cilia on mucus ribbons. These relatively simple metazoans produce trails that are similar in size and morphology to some Neoproterozoic traces, owing to the entrainment of sediment within their mucus trails. Thus a mucociliary locomotory system provides sufficient means to form some types of Neoproterozoic traces. It follows that the body architectures of the Neoproterozoic trace-makers may have been quite simple, though complex bodyplans are, of course, not ruled out. Thus, the use of Neoproterozoic trace fossils to constrain the time of origin of bilaterians or of any crown-group bilaterian taxon remains questionable.

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Accepted: 6 October 1999

Introduction

*“Some trails are happy ones, others are blue
It’s the way you ride the trail that counts. . . .”*

Dale Evans

Neoproterozoic trace fossils form a critical source of information about early metazoans. Although these traces have been studied for decades, the trace-makers have remained unknown. Here we report experiments and observations on trace-making by living metazoans of relatively simple grades, with bodyplans that lack body cavities: diploblastic, radiate cnidarians; and triploblastic, bilaterian, acoelomate platyhelminths. The locomotory systems observed in these forms are mucociliary and do not directly involve the use of body-wall muscles. We describe creeping trails that these simply constructed metazoans are capable of forming, and assess their significance for the interpretation of Neoproterozoic trace fossils.

The earliest undoubted trace fossils date from about 570 Ma (Jensen et al. 1999), and traces are found in numerous sections throughout the remainder of the Neoproterozoic. There are numbers of reports of earlier trace fossils, but when restudied those structures have proven to be misdated or have not been confirmed as traces. Many features that

resemble trace fossils may represent algal remains (Seilacher 1998), including the beadlike traces termed *Neonereites* that are commonly interpreted as fecal pellet strings (Fedonkin 1992; Crimes 1992). Possible traces from India that have been reported to date from 1100 Ma (Seilacher et al. 1998) are evidently much younger and their authenticity as traces has been questioned (Kerr 1999; Rai and Gautam 1999; but see Seilacher et al. 1999). Other possible traces date from about 600 Ma (Brasier and McIlroy 1998), but these too lack confirming features. Throughout the Neoproterozoic, most traces were small horizontal trails (<5 mm in width, chiefly near 1 mm) and have been interpreted as being formed either at the surface of the seafloor or as shallow burrows (see Narbonne and Aitken 1990; Crimes 1992). The earliest trails are relatively featureless but later ones display grooves, ridges, or levees. In some facies, traces (as well as body fossils) occur with fossil microbial mats; the fossil traces may have been formed beneath mats, and may have been preserved because of taphonomic processes associated with the mats (Gehling 1999). Some slight local bioturbation and rare, minute, penetrating burrows have been reported in Neoproterozoic rocks, but biological disturbance to any depth, such as would pro-

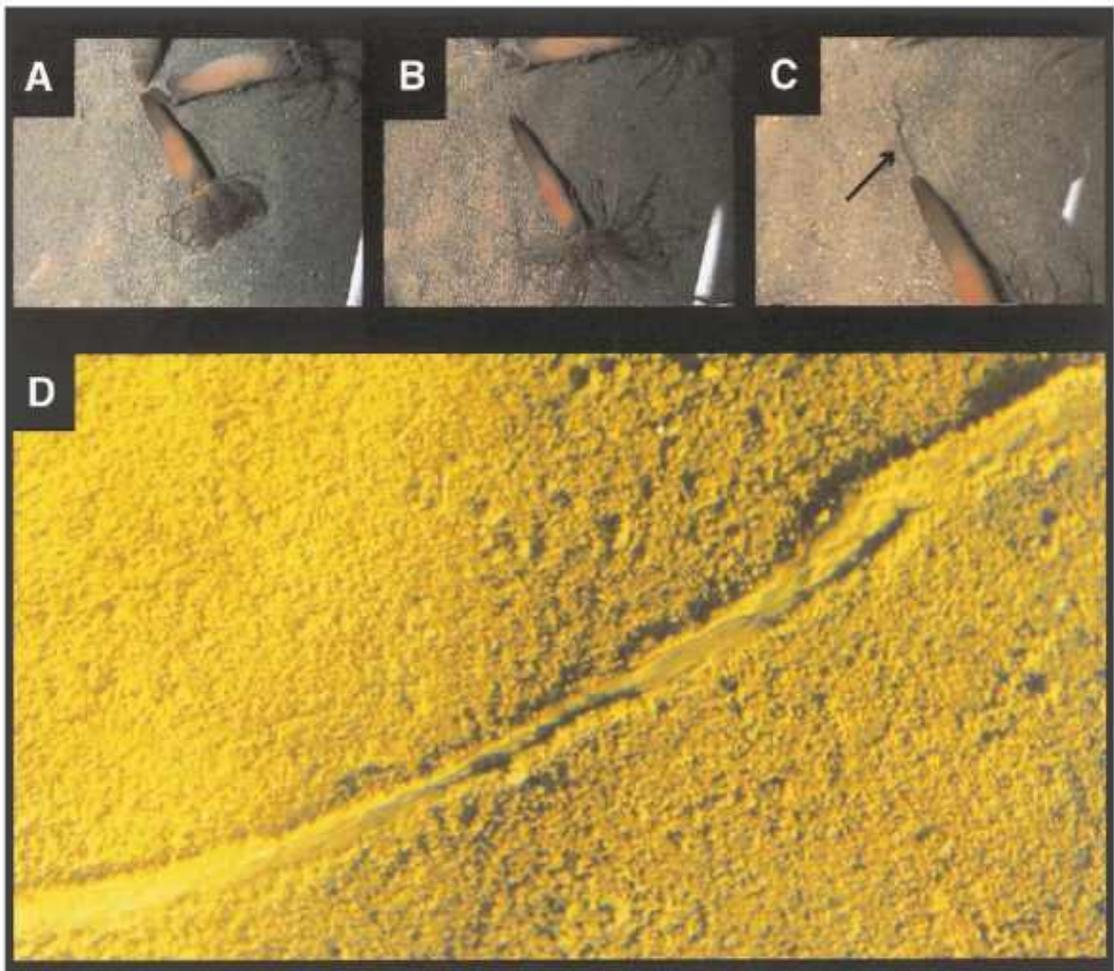


FIGURE 1. Creeping trails of the ceriantharian anemone *Pachycerianthus* sp. in an aquarium. Still frames taken from video. A, Three specimens in proximity. B, A specimen creeps away from neighbors via ciliary gliding. C, Relatively narrow trail (arrow) 2 mm wide left under anteroposterior band of cilia that is involved in locomotion. D, Second type of trail formed by *Pachycerianthus*, about 3 mm wide.

duce important ichnofabrics, has not been observed (Droser et al. 1999; McIlroy and Logan 1999).

During the Lower Cambrian, the width of horizontal trails increased into the centimeter range, 3–5 cm being common, and burrows that penetrated the seafloor became increas-

ingly abundant and widespread (Crimes 1992; McIlroy and Logan 1999). Indeed, the appearance of *Treptichnus pedum*, a penetrating burrow, defines the base of the Cambrian (Landing and Westrop 1998), which dates to about 543 Ma (Grotzinger et al. 1995). During the “Cambrian explosion” (530–520 Ma) there



FIGURE 2. Cross-sectional cartoons of ceriantharian anemone and polyclad flatworm trails. A, First type of ceriantharian trail, which can appear similar to some *Gordia* and *Helminthopsis* traces. B, Second type of ceriantharian trail, similar to *Aulichnites*. C, Polyclad trail, similar to *Aulichnites* and *Sellaulichnus*.

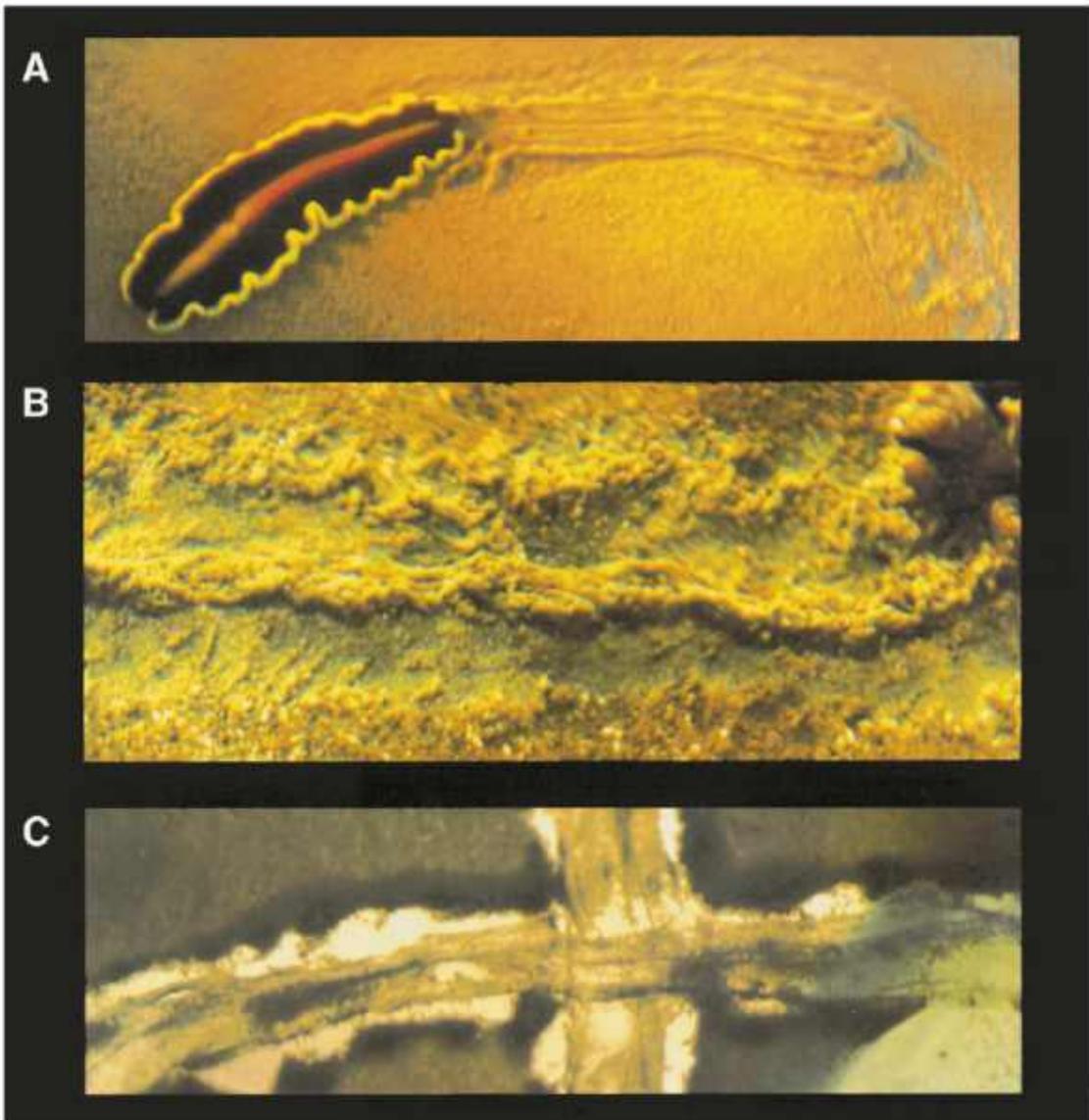


FIGURE 3. Creeping trails of polyclad flatworms. A, Polyclad flatworm *Pseudobiceros paralaticlavus*, leaving trail about 6 mm wide. B, Polyclad flatworm *Paraplanocera* sp. (upper right), leaving trail about 10 mm wide. C, Trail left by *P. paralaticlavus* on glass plate, photographed from below.

was a further increase in the diversity of traces, especially at larger sizes, accompanied by the first appearances of a broad diversity of novel bodyplans. Although the Neoproterozoic traces are likely to have been made at least in part by the ancestors of the explosion taxa, the bodyplans of the Neoproterozoic trace-makers are unknown. The vermiform bodyplans that appeared during the Cambrian explosion, many of which were relatively complex, clearly possessed the biomechanical

capability of making traces similar to those of the Neoproterozoic, but none of them are represented by body fossils during that period.

Methods

We observed modern trails at the R. B. Gump Research Station of the University of California, Berkeley, on Moorea, French Polynesia. Sediment was collected from the marine lagoon, screened to remove particles larger than 1 mm, and used as substrate on the floor

of an aquarium, to a depth of several cms. A variety of animals was collected from shallow subtidal habitats (<20 m) using SCUBA and placed on the aquarium substrate. Locomotion was observed and traces recorded on still photographs and videotape. We studied the ceriantharian anemone *Pachycerianthus* sp., a burrowing tube-dweller, by removing specimens from their tubes and placing them on the substrate. They did not creep spontaneously unless in close proximity to other anemones, in which case they moved away from their nearest neighbors. We also studied polyclad flatworms of the genera *Pseudobiceros*, *Acanthozoon*, and *Paraplanocera*. These polyclads are normally found on firm substrates, but in the aquarium they crept spontaneously and freely over the unconsolidated sediment. To observe creeping activity better, we placed some polyclads on glass panes thinly covered by water and sediment and photographed them from below; the traces produced on the panes were similar to those on thick substrates. We also studied a variety of other animals, but here we focus on the polyclads and anemones as representing morphological grades and mucociliary locomotory systems that may have been common during the Neoproterozoic.

Results

Creeping Traces Made by Ceriantharian Cnidarians.—Although ceriantharian movements involving muscular activity have been studied previously (Ross and Horridge 1957; Arai 1972), this is apparently the first description of mucociliary creeping in ceriantharian anemones. These anemones live within burrows which they form, and they use their rich supply of mucus glands in constructing their burrows. Ceriantharian living tubes are composed of sediment bound by the mucus and abundant discharged cnidocysts (Mariscal et al. 1977). When placed on the sedimentary substrate, most individuals began to burrow unless they were in close proximity to one another, and then they often crept apart (Fig. 1A–C). When the anemones are creeping, the mucus secretions are restricted to the antero-posterior band that is in contact with the substrate, producing a ribbon of mucus on the

sediment. The anemones glide in an oral direction on this ribbon by ciliary activity. To our surprise, the anemones produced clear trails of more than one type. The trails ranged from 2 to 3 mm in width, forming only under the narrow band of anemone body wall in contact with the mucus-coated substrate, and significantly narrower than the body widths of the anemones, which ranged from 1 to 3 cm.

We observed two principal trail types that involved binding of the substrate by mucus. One type is a single trail of mucus-bound sediment (Fig. 1C) that closely resembles the Neoproterozoic trace fossils *Gordia* and *Helminthopsis* (Fig. 2A). A second type of anemone trail has levees along the trail margins (Fig. 1D). This trail resembles the Neoproterozoic trace *Aulichnites* in cross-section (Fig. 2B). In most cases, the anemone trails were linear and fairly regular over distances of 10–30 cm, distance being limited in the experiments by the size of the trays. Upon reaching the side of a tray, the anemones commenced burrowing.

Creeping Traces Made by Platyhelminths.—Although polyclads do not form sediment-bound dwelling structures, their mucociliary locomotory systems nevertheless can produce characteristic trails, evidently through the aggregating and binding properties of the mucus. In the polyclads that we studied in Moorea, locomotory mucus is produced by paired mucus glands that form a bilobed mucus pad. The two thicker mucus strings, each of which entrains sedimentary particles, create paired ridges of sediment, which maintain a rather constant distance and characterize their trails (Fig. 3). The cilia that drive the flatworms forward beat against their mucus ribbon but not directly against the substrate. Nevertheless, topographic relief is created on the substrate, greatest beneath the thickened portion of the mucus pad. On either side of the ridges, hollows formed where the particles had been moved into the ridges. In the largest flatworms, the ventrolateral body margins sometimes impinge on the substrate and displace sediment at the trail margins, as has been previously noted for terrestrial flatworms (Crozier 1918; Clark 1964), but that process did not make a significant contribution to the trails that we observed. In a preliminary study at



FIGURE 4. *Aulichnites* sp., about 3 mm wide, from the Neoproterozoic Ust Pinega Formation, Winter Coast of the White Sea, Russia; specimen in Paleontological Institute, Moscow.

the University of California, Berkeley, polyclad flatworms collected locally were observed in sediment-covered trays under seawater. They crept readily but did not produce thick mucus ribbons, and their gliding progress did not disturb the substrate so as to produce any relief.

Many Neoproterozoic trace fossils contain longitudinal ridges and/or flanking grooves. The polyclad trails from *Moorea* most closely resemble *Aulichnites* (Fig. 4) and *Sellaulichnus* in cross-section (Fig. 2C). The *Moorea* trails are also somewhat reminiscent of the trace fossils *Bilinichnus* and *Didymaulichnus*, reported from the Neoproterozoic. However, those traces record paired furrows or grooves, rather than ridges and levees, and thus differ from the polyclad trails in cross-section. The Californian flatworms did not displace sediment.

Other Creeping Trails.—Some animals with more complex bodyplans also produce copious mucus during locomotion so as to leave three-dimensional ribbons in their creeping trails. Mucus strands produced by the Moo-

rean nudibranch *Tambja morosa* and by the Californian nemertine *Amphiporus bimaculatus* harden into three-dimensional ribbons, which become rigid enough to maintain their shape even when picked up from the trails. Although such ribbons may soon be destroyed by microorganisms or perhaps by chemical interactions, their taphonomic signal could be preserved if sedimentation occurred during or shortly after their formation. Three-dimensional ichnostructures produced by reasonably thick mucus ribbons might be confused with the traces of horizontal burrows.

Discussion

Mucociliary Transport Systems and Locomotion.—The use of mucociliary systems is widespread throughout the Metazoa, except within Ecdysozoa, which molt and do not have motile ectodermal cilia. Mucociliary systems are involved in feeding tracts, in cleansing pulmonary or other epithelial surfaces, and in the locomotion of small-bodied creeping forms. A two-layer model for mucociliary transport has

been postulated (see Sleight et al. 1988; Beninger et al. 1997). The system has been carefully studied using bivalve ctenidia, for which the two-layer model is indeed confirmed (Beninger et al. 1997). In short, the inner mucus layer is watery, permitting cilia to beat freely. The outer mucus layer, however, is stiff, and the tips of the beating cilia impinge upon its lower surface and propel it along the ciliary tract. Particles trapped in the stiff outer mucus layer are transported therein. The two-layer model has not been confirmed for creeping locomotion though it has been suggested to be general in metazoan mucociliary systems (Beninger et al. 1997). We infer that in creeping locomotion, stiff mucus is secreted as a locomotory ribbon, adhering to the substrate; the watery layer lies over the stiff layer and against the locomotory organ—commonly a ventral epithelium or a pedal sole—and cilia beating therein impinge on the stiff layer and propel the organism along the substrate. Although direct muscular activity is not involved in mucociliary creeping, there is clearly sufficient energy available within the system to transport the body mass of the organisms. The detailed mechanics that produce the relief observed in the substrate sediments deserve careful study.

Body Plans of the Trace-Makers.— The finding that metazoans of relatively simple grades of construction can produce creeping trails similar to trace fossils found in Neoproterozoic rocks complicates the evaluation of those fossils. Usually such trace-making has been assumed to involve the use of body-wall muscles, perhaps antagonized by a fluid skeleton, to displace the sedimentary particles and produce the cross-sectional relief observed in some of the trace fossils. Therefore the Neoproterozoic traces are widely believed to have been produced by triploblastic organisms—bilaterians (for example, see Crimes 1992; Fedonkin and Runnegar 1992; Brasier and McLroy 1998). A typical suggestion is that, since the traces displayed relief, the trace-makers were not flat-bodied but were probably at the paracoelomate grade (like “roundish flatworms” [Valentine 1994]). However, the finding that creeping organisms are able to produce copious mucus ribbons that can create

three-dimensional trails introduces a new element into trace fossil interpretation.

Any given organism may leave a variety of different traces, depending upon the substrate type and the purpose of the trace-making activity—different stimuli produce different behaviors. The makers of Neoproterozoic trace fossils that have internal furrows or grooves (e.g., *Bilinichnus* and *Didymaulichnus*) are difficult to interpret. During the Phanerozoic, nonstriated traces are sometimes continuous with bilobate trails that contain striations (*Diplichnites* and *Cruziana*), which are interpreted as having been made by arthropod limbs (Keighley and Pickerill 1996). Changes from smooth to striated traces may indicate variation in sediment type or locomotory mode (Anderson 1981). Although smooth traces were presumably made by arthropods in cases where they are associated with striated traces, smooth traces cannot be interpreted as having been formed by a limbed arthropod when not associated with striated traces. The nonstriated Neoproterozoic *Bilinichnus* and *Didymaulichnus* pre-date the earliest arthropod body fossils as well as their characteristic striated traces, and for that matter pre-date the first appearance of durable skeletons in any taxa that might serve to produce such traces. The production of bilobed grooved traces by peristaltic locomotion seems unlikely. Thus, the possibility remains that smooth bilobed Neoproterozoic traces involved mucociliary activities, perhaps in conjunction with other locomotory techniques.

We conclude that some of the patterns of cross-sectional relief that have been recorded in Neoproterozoic traces could reflect mucociliary locomotion. Organisms with somewhat different patterns of mucus secretion or transport, varying perhaps in number and placement of mucus glands or of mucociliary tracts, might produce distinctively different trails based on the mucus pattern rather than on some feature of body-wall musculature or associated morphology. We have not observed pulses of mucus production during locomotion, but if they occurred they could produce longitudinally differentiated structures along a trace (mucus pulses do occur on bivalve ctenidia [Beninger et al. 1997]). For example, pe-

riodic thickening of mucus strands could create a series of oval pelletlike sedimentary aggregates. It is now not difficult to imagine organisms, somewhat vermiform diploblasts or triploblasts, flat or not, and entirely lacking body spaces, that could be responsible for some of the Neoproterozoic traces, particularly the earlier ones.

Living Clades as Proterozoic Trace-Makers.—The ancestral branching order of the more basal living metazoan phyla, as indicated by small-subunit ribosomal RNA sequence comparisons, begins with Porifera and continues with Ctenophora and then Cnidaria and Placozoa, either or both of which are sisters to Bilateria (Collins 1998; Kim et al. 1999). None of the pre-bilaterian clades have body cavities, and early stem bilaterians probably lacked them also. The only living bilaterian taxon that may have branched earlier than the last common protostome-deuterostome ancestor is Acoela (see Haszprunar 1996; Ruiz-Trillo et al. 1999), also lacking body cavities and traditionally assigned to Platyhelminthes. There are no published observations of acoel trails.

Mucus production, widespread among marine invertebrates, contributes to ciliary creeping of small individuals in a number of phyla other than Cnidaria and Platyhelminthes, probably including Ctenophora, and certainly including Gastrotricha, Nemertinea, Mollusca, and Annelida (Fransen 1980; Brusca and Brusca 1990; Emson and Whitfield 1991; personal observations). The complexity of metazoan bodyplans that was attained during the Neoproterozoic is in dispute (for review see Valentine et al. 1999). Some workers hold that relatively advanced forms, such as arthropods, must have appeared significantly before the Cambrian (Fortey et al. 1996), while others suggest that they may not have evolved until Early Cambrian time. Regardless of whether limbs were present in some Neoproterozoic forms, they seem not to have been involved in making the horizontal trails that dominate the ichnofauna of that time. Molecular-clock dates have consistently suggested that the divergences between lineages leading to crown bilaterians occurred before the record of trace fossils even begins (Wray et al. 1996; Ayala et al. 1998; Bromham et al. 1998; Wang et al.

1999; Lynch 1999). However, these molecular-clock dates have ranged widely; for example, clock dates that can be associated with the founding of the protostome and deuterostome clades have ranged from about 1500 to 630 Ma. Furthermore, the bodyplans of crown-group taxa may be derived long after the divergences of their clade founders. Clearly, molecular-clock dates are not very helpful as yet. At any rate, there is no conclusive evidence that crown-group bilaterians were involved in Neoproterozoic trace formation.

Proterozoic Taxa as Proterozoic Trace-Makers.—Few Neoproterozoic body fossils are candidates for producing the Neoproterozoic trace fossils, even though they are sometimes found in association. The earliest animal remains that might represent trace-makers are embryos from the Doushantuo Formation, southern China, preserved in phosphorite (Xiao et al. 1998). These unusual fossils are not closely constrained in age but are probably between 550 and 590 million years old. They were interpreted as possible bilaterian embryos, and subsequently they have been claimed to demonstrate the presence of bilaterians at that time (Balavoine and Adoutte 1998; Bromham et al. 1998; Seilacher et al. 1998; Thomas 1998). The embryos do not display micromere cycles and cannot be assigned either to radialian or spiralian cleavage types. The embryos are rather large and may belong to direct-developing forms, as suggested by Xiao et al. (1998). While indirect developers commonly have cleavages characteristic of major bilaterian clades, direct developers are notorious for having idiosyncratic cleavages, associated with large yolk contents, that are restricted to a single clade. While a bilaterian relationship for these embryos is certainly not excluded, neither is it demonstrated. Possible affinities of the embryos include sponges (possible sponge remains have also been reported from the Doushantuo Formation [Li et al. 1998]), vendobionts (Buss and Seilacher 1994), and other pre-bilaterians (Valentine et al. 1999). If the embryos do represent bilaterians, they could be stem-group forms.

Several Proterozoic body fossil taxa, such as vendomiids, sprigginids, and *Parvoancorina* (see Glaessner 1984 and Fedonkin 1992) are

differentiated antero-posteriorly and have segmentlike body subdivisions. The locomotory techniques they used, if any, are unknown. The adults of these forms are too large to have been responsible for the Neoproterozoic traces unless some quite unique locomotory system was involved. *Kimberella*, a putative bilaterian body fossil (Fedonkin and Waggoner 1997), appears to be a creeping form, reconstructed with a sluglike creeping foot, but again the adults are far too large to produce the contemporary traces. Possibly only juveniles of these forms had mucus trails of the sort that produce traces with relief, but it seems far more likely that other animals that have not been found as body fossils are responsible for the fossil trails.

Conclusions

The ability of mucus secretions to enable locomotory mechanisms that produce creeping traces with cross-sectional relief suggests that restudy of many of the horizontal Neoproterozoic traces may be profitable. Many Neoproterozoic traces are no more complex than those that can be produced by flatworms and anemones. The organisms we have studied do not necessarily have the same bodyplans as the Neoproterozoic trace-makers, but if many of those early forms used mucociliary creeping systems, as seems quite likely at the small sizes suggested by the traces, they could have formed trails by the same mechanisms as the living flatworms and creeping cnidarians that we observed.

Clearly, body cavities were not required of Neoproterozoic trace-makers, which could conceivably have been diploblastic. Nevertheless it seems most likely to us that the Neoproterozoic traces were made by organisms with a range of body types that arose during an early bilaterian radiation and included both the acoelomate and psedocoelomate grades, and perhaps by diploblastic forms as well. It also seems reasonable that many Neoproterozoic traces were left by organisms that moved via peristaltic (or pedal) waves or by introverts. The position of the last common protostome-deuterostome ancestor within the stratigraphic succession that preceded the Cambrian explosion becomes even more un-

certain than it already has been; hope of locating this important branch point from trace fossil evidence seems dim. We are continuing studies of trace-making by a variety of creeping invertebrates on a variety of substrate conditions to extend these findings.

Acknowledgments

We thank S. and P. Strand, K. Flanagan, K. Kober, and J. Johnson for assistance in collecting specimens at the R. B. Gump Research Station, Moorea. Dr. M. A. Fedonkin, Paleontological Institute, Moscow, discussed Vendian traces and kindly furnished photographs. Soren Jensen and Tim Littlewood provided thoughtful reviews of the manuscript, with significant improvements in the treatment of trace fossils resulting from Soren's comments; remaining errors and misinterpretations are ours alone. A. G. C. was supported by grants from the graduate student grant-in-aid program, Paleontological Society, and the College of Natural Resources, University of California, Berkeley. Research supported by National Science Foundation grants EAR-9304694 and EAR-9184845 to J. W. V. and J. H. L. Contribution No. 1709, Museum of Paleontology, University of California, Berkeley.

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