



Bilaterian Burrows and Grazing Behavior at >585 Million Years Ago

Ernesto Pecoits *et al.*
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10-event record at Pallett Creek near Wrightwood yielded a COV estimate of 0.60 (28). On the Jordan Valley Fault section of the Dead Sea Transform system, Ferry *et al.* (9) described clustered behavior from a 14,000-year, 12-event record in which recurrence intervals ranged from 280 to 1160 years. Marco *et al.* (7) estimated COVs for earthquake recurrence in the Dead Sea Graben ranging from 1 (random) to 1.75 (clustered).

In light of the periodicity exhibited by the Alpine Fault, we can identify characteristics that may be good indicators of quasi-periodic recurrence on other faults. In a global context, the Alpine Fault is a prime example of a transform plate boundary fault that has a simple structure (long, straight trace with few large step-overs), large total offset (~480 km), and a high slip rate (23 ± 2 mm/year at Hokuri Creek) (13, 29). However, perhaps the most important feature in this context is the lack of other major structures nearby for much of the length of the fault. In the southwestern South Island, one third of relative plate motion (13, 14) is taken up on structures other than the Alpine Fault, but these have little effect on regulating the timing of Alpine Fault earthquakes. Structures that accommodate residual motion in this part of the plate boundary have low slip rates and are distributed broadly across the margin (14, 15). The slightly less periodic (higher COV) San Andreas fault is known to be influenced by major faults nearby (30), and the aperiodic Dead Sea Transform is a more complicated system and slower slipping (9) than either the San Andreas or the Alpine Fault. Other faults that have similar characteristics to the Alpine Fault are sections of the North Anatolian in Turkey and the Denali Fault in Alaska.

Existing examples of long earthquake records suggest a continuum of recurrence behavior with more periodic recurrence on fast-moving, simple and smooth at seismogenic depth, isolated structures at one end of the spectrum (such as this Alpine Fault example) and aperiodic recurrence on low slip-rate, complex, rough, and networked structures at the other end. Thus, in the absence of long paleoseismic records, fault characteristics such as total slip, slip rate, geometric complexity, and possible interaction with other nearby major faults can enable the choice of appropriate statistical models for use in earthquake forecasting and hazard analysis. Regular earthquake recurrence can be considered an end-member of fault behavior. Our study highlights that the regularly repeating earthquake cycle is a realistic foundation on which to base earthquake forecasting and seismic hazard efforts, especially where a fault is acting in isolation to accommodate a high proportion of plate motion.

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Supplementary Materials

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Materials and Methods
Figs. S1 and S2
Table S1
References (33–36)
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Bilaterian Burrows and Grazing Behavior at >585 Million Years Ago

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Based on molecular clocks and biomarker studies, it is possible that bilaterian life emerged early in the Ediacaran, but at present, no fossils or trace fossils from this time have been reported. Here we report the discovery of the oldest bilaterian burrows in shallow-water glaciomarine sediments from the Tacuarí Formation, Uruguay. Uranium-lead dating of zircons in cross-cutting granite dykes constrains the age of these burrows to be at least 585 million years old. Their features indicate infaunal grazing activity by early eumetazoans. Active backfill within the burrow, an ability to wander upward and downward to exploit shallowly situated sedimentary laminae, and sinuous meandering suggest advanced behavioral adaptations. These findings unite the paleontological and molecular data pertaining to the evolution of bilaterians, and link bilaterian origins to the environmental changes that took place during the Neoproterozoic glaciations.

Animals with bilateral symmetry, segmentation, and musculature probably emerged in the Neoproterozoic and were a major

part of the subsequent Cambrian “explosion,” but it has proven difficult to date the appearance of the first bilaterians. Recent molecular clock analyses

give dates ranging from 1153 to 1443 million years ago (Ma) (1) to 580 to 635 Ma (2, 3) for the emergence of stem-group bilaterians, yet no definite bilaterian fossils have been found within this broad time interval. Putative microscopic bilaterian fossils from the Doushantou Formation in China (4) are probably about 580 million years (My) old (5), but their attribution to bilaterians remains controversial (6, 7). Similarly, putative trace fossils ranging in age between 565 My and 2.1 billion years have been described, but only those younger than about 555 My satisfy the strict criteria for bilaterian burrows (8–11). The oldest widely accepted evidence for bilaterians comes from fossil burrows and probable body fossils such as *Kimberella* in shallow-water deposits from Russia that are approximately 555 My old (12, 13).

Here we report bilaterian burrows from shallow-water Ediacaran sediments in the Tacuarí Formation in east-central Uruguay. We found abundant trace fossils at six different localities, three of which are within 5 m of the intrusive contact (detailed geological data are presented in figs. S1 to S9). The Tacuarí Formation comprises basal diamictites, varved sandstones, and minor pelites that grade upward into fine-grained rhythmites containing abundant outsized clasts. The clasts, interpreted as dropstones within the diamictites, are faceted and striated and provide evidence for the glacial origin of the varve-containing strata. Trace fossils occur within the uppermost fine-grained rhythmites that mark the waning stages of glaciation (Fig. 1).

To provide accurate age constraints for the deposition of these sediments, we obtained laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS) ($n = 10$ spot analyses) and sensitive high-resolution ion microprobe (SHRIMP) ($n = 20$ spot analyses) U-Pb zircon ages from an intrusive granite that cross-cuts and deforms the Tacuarí Formation (14). These combined dates constrain the minimum depositional age for the fossil-bearing unit to 585 ± 3 Ma (see Fig. 1 and tables S1 and S2). A maximum depositional age for the Tacuarí Formation is 600 ± 9 Ma, based on the youngest detrital zircon age cluster recorded in the fossil-bearing unit (tables S2 and S3). This age reinforces the Neoproterozoic age previously assigned to the Tacuarí Formation, which was based on structural and stratigraphic relationships with more-precisely dated units (15). The cross-cutting rocks comprise leucocratic, undeformed granite that is discordant to the locally foliated sedimentary strata of the Tacuarí Formation (figs. S2 to S5). The granite shows a well-developed chill margin, whereas the sedimentary strata at the contact are sintered

and show evidence of extensive silicification and hematitization (figs. S3 to S8). Additional evidence of the intrusive nature of the granite comes from the presence of country rock xenoliths (both rafts and stoped blocks) along the margin and in the roof zone of the intrusion (fig. S9).

The trace fossils are preserved in fine detail on laminae tops and soles in association with siltstone laminae. Two modes of preservation are observed (Fig. 2 and fig. S10). The most common comprises downward-protruding (concave hyporelief) bilobate grooves, locally containing a beaded backfill (inset in Fig. 2A and Fig. 2G). The beaded backfill consists of very small, ovate sediment piles, the long axes of which are oriented transverse to the burrow length. The second type of burrow preservation entails irregular burrows that generally are upward-protruding (convex epirelief) from the plane of preservation: These structures locally show collapse features on their tops (Fig. 2B). Both types of burrows are 2 to 3 mm in width, and some of the collected specimens pass laterally from one form to the other along the length of the burrow. The bilobate grooves commonly possess raised lateral ridges adjacent to the burrow margins. Rarely, small

circular indentations are preserved near the edges of bilobate furrows (insets in Fig. 2, D and H). The dents are approximately 0.5 mm in diameter and are serially emplaced along the trail. Plan-view morphology ranges from straight (Fig. 2B) to curvilinear (Fig. 2, A and E) to low-amplitude sinusoidal (Fig. 2, B and C). Abrupt adjustments in curve radius accompanied by small lateral movements are observed (Fig. 2, E and F). Three of the specimens show the burrow abruptly leaving the plane of preservation and reappearing 4 to 10 mm away (Fig. 2E and fig. S10). We also observed several instances of one burrow crossing another, with no evidence of avoidance (Fig. 2A). In three examples, a later burrow intersects a preexisting burrow, turns, and follows the earlier structure, then resumes its initial trajectory (Fig. 2F).

The two modes of trace-fossil preservation suggest that these burrows were emplaced within the sediment (i.e., intrastratally). Well-preserved bilateral furrows represent the bottom of the burrow. The irregularly defined examples represent the top of the burrow. Given the shallow intrastratal occurrence of this trace fossil, it is likely that the animal grazed on organic material within the sedimentary laminae. Rare but clear depar-

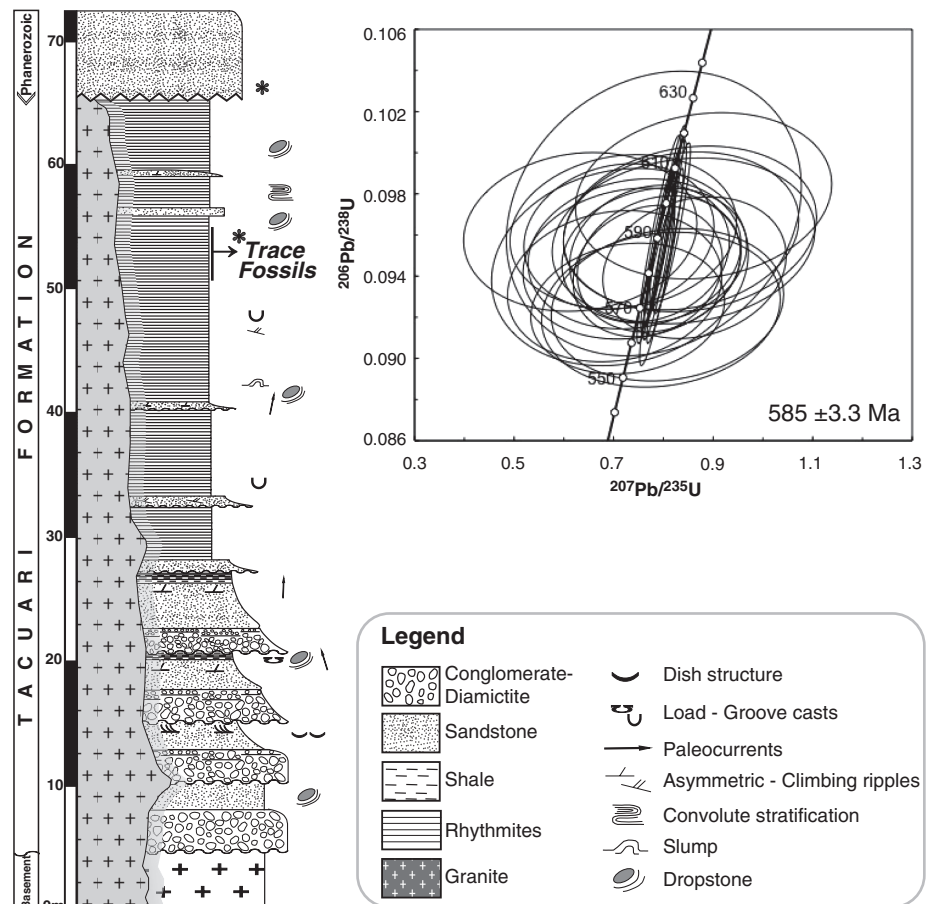


Fig. 1. Detailed stratigraphic section of the Tacuarí Formation with labeled trace-fossil horizon. Asterisks on the section indicate detrital zircon sampling sites (fig. S1). The U-Pb concordia diagram displays the LA-MC-ICPMS (narrow ellipses) and SHRIMP analyses of zircon grains from the granite intruding into the trace fossil-bearing strata.

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tures of some burrows from the plane of grazing may represent movement of the tracemaker to the sediment/water or sediment/biomat interface, or shifting to other shallow laminae in the search of food. The reappearance of the burrow nearby and in the same plane suggests the former, because these examples show the animal's subsequent return to the food source. Curvilinear to low-amplitude sinusoidal trails suggest that the tracemakers were engaged in rudimentary spatial optimization of patchy food resources or used a search pattern that improved the likelihood of intersecting optimal food resources. The lack of mutual burrow avoidance suggests that phob-

taxis had not yet evolved. The specimens that show later burrows becoming coincident with pre-existing burrows may imply primitive chemotaxis or may reflect the greater ease of burrowing through previously burrowed sediment.

The presence of raised lateral ridges and the preservation of a beaded backfill show that the animals moved by peristaltically pushing against the sediment. The spacing of the backfilled beads reveals forward movement of less than 0.5 mm (per peristaltic push); serial indentations along the burrow margin have a similar spacing. The indentations further show that the tracemaker had prehensile "feet" of sorts and could extend those

parts into the sediment to assist motility. Abrupt changes in the meander radius with abrupt lateral jogs further suggest that the animal, although possibly elongate, did not exceed 1 cm in length. The bilateral furrow reflects the bilateral symmetry of the tracemaker, and when coupled with the mode of locomotion, strongly points to an early bilaterian tracemaker.

A variety of inorganic sedimentary processes can superficially mimic the shape of simple burrows (11, 16), but none of these seem applicable to the Uruguay trace fossils: All of the specimens exhibit remarkably consistent width and morphology. There is no evidence of alignment such as might be produced by depositional currents, nor are there abrupt changes in orientation, diameter, or relief along the length of the structures that might reflect tool markings or shrinkage cracks. The bilobate lower surface of the structures is typical of many modern and Phanerozoic bilaterian burrows, especially but not exclusively molluscan and annelid burrows, and would be difficult to produce consistently in numerous specimens by any known inorganic sedimentary process. Poorly preserved algal filaments or tubular animals can also mimic simple trace fossils (16, 17), but there are no carbonaceous or calcareous films, and angular (i.e., broken) edges that might mark a body fossil are not observed (Fig. 2E).

The Uruguay structures exhibit abundant evidence for sediment displacement and processing in the formation of these structures. These include lateral ridges of displaced sediment flanking a bilobate furrow at the base, the meniscate fill of the structures, and the collapse features that followed the abandonment of partly open structures; the latter very strongly suggest that they represent the burrows of muscular organisms. Some prokaryotes and protists are capable of moving on sediment and can leave traces of their activity (18), but are too small and lack evidence for the strong musculature used in the construction of eumetazoan burrows. Although large protists have been shown to make traces similar to some surficial bilaterian traces (19), such animals are incapable of producing some of the features we observe in the Tacuarí tracks, including infaunal movements, meniscate backfill, and the small, regularly spaced indentations observed locally on either side of the medial furrow. Among the simple Eumetazoa, flatworms and anemones can produce lateral ridges of displaced sediment as they move across a surface using mucociliary creeping (20), but no modern Platyhelminthes or Cnidaria are known to construct horizontal burrows that are either infaunal or backfilled. The combination of features seen in the Uruguay trace fossils makes it difficult to regard them as representing the activity of anything below the biological grade of the Eumetazoa, and in modern seas, these fossils are consistent only with those produced by bilaterian eumetazoans.

Although the internal structure of the Uruguay burrows is very similar to that of Phanerozoic and modern bilaterian burrows, their behavior

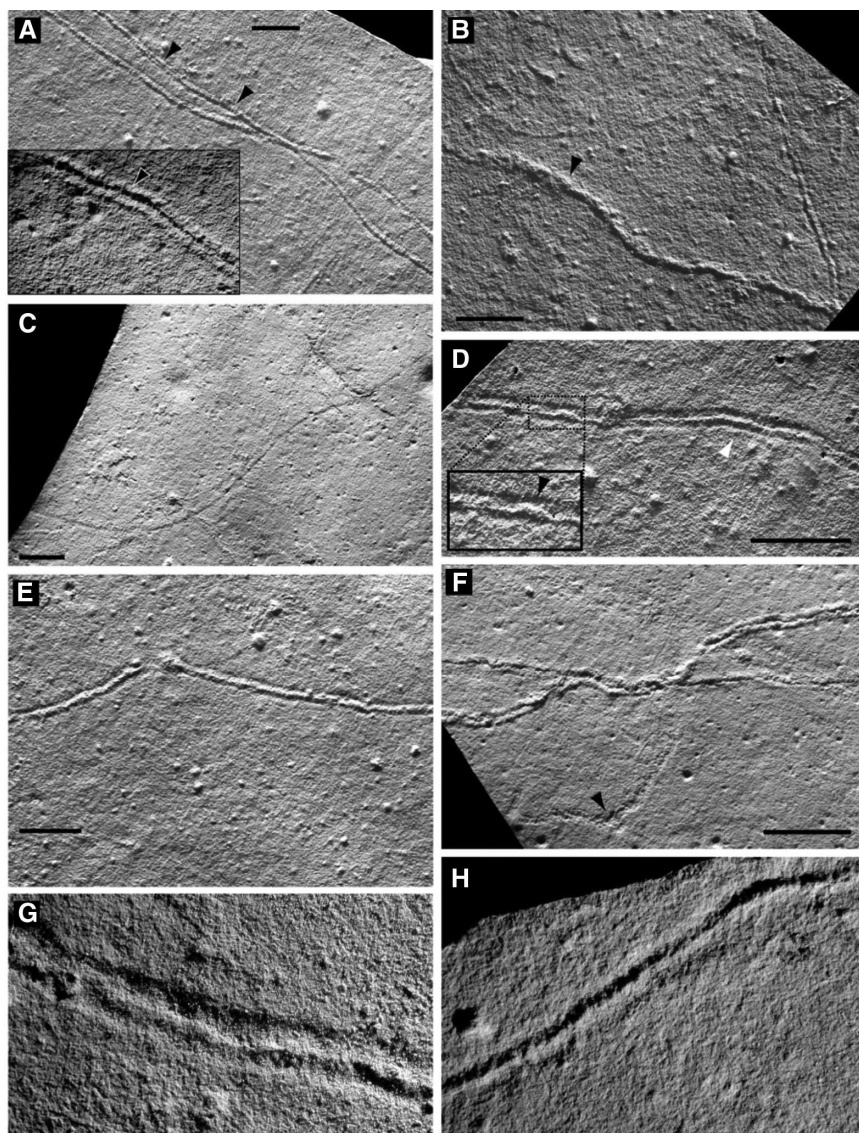


Fig. 2. Photographs of the Tacuarí trace fossils. (A) Typical bilobate furrow with beaded backfill/meniscate visible (black arrows). (B) Irregular trace fossil showing the collapsed top part of the burrow. (C) Sinuous trail illustrating the typical amplitude and wavelength. (D) Well-developed bilobate furrow with circular indentations (black arrow, inset) and raised burrow margins (white arrow). (E) Bilobate furrow showing departure from and return to the plane of preservation. (F) Later burrow intersecting and following a preexisting burrow. (G) Close-up of bedding plane (top view), clearly showing the bilobate furrow that is preserved in many of the burrows. (H) Close-up of the Ediacaran burrow-maker's trail, showing serial indentations along the furrow margin. Scale bars, 1 cm.

is considerably less complex, even in comparison with later Ediacaran burrows from northwest Canada (21) and Australia (22). Conspicuously absent are parallel meanders and three-dimensional avoidance that appeared later in the Ediacaran (21). Nevertheless, sinusoidal grazing probably marks the advent of more sophisticated grazing behaviors and is in itself evidence of early burrowing adaptation.

These findings extend the fossil record of bilaterian eumetazoans at least 30 million years backward to the early Ediacaran, a time consistent with the youngest ages for the appearance of bilaterians predicted by molecular clock analyses (2, 3). The molecular clock dates for the Eumetazoa-sponge divergence have also been corroborated by the recently reported body fossil evidence of sponges from the Trezona Formation (Australia), immediately below the Marinoan-aged Elatina Formation (635.2 Ma), and lipid biomarkers suggestive of Demosponges in strata below the Hadash Formation (Marinoan) cap carbonate in Oman (23, 24). Therefore, it appears as though a maximum interval of 50 My exists between the earliest definitive evidence of sponges and the bilaterians found in the Tacuarí Formation, which implies that early animal evolution took place on a geologically rapid time scale once environmental conditions proved favorable for higher forms of life to colonize the ocean realm. Presently, the occurrence of deep-sea bilaterian burrows at ~550 Ma (25) and the occurrence of deep-water Vendian fauna have led some researchers to suggest that bilaterians have a deep-sea origin (26–29). Based on the Tacuarí trace fossils, the possibility is reopened that bilaterians evolved in shallow-water settings (30), perhaps reflecting greater food availability in this environment and because their mobility and burrowing habit required higher oxygen levels than those of the sessile Ediacarans.

Finally, these early Ediacaran burrows demonstrate very early grazing activity by eumetazoans. The grazing behavior is facilitated by a low-amplitude sinusoidal search pattern and the ability to leave one sedimentary lamination for another. Evidence of active backfilling of the burrow is important, as well as the ability to pass sediment around or through the body and compact it in the animal's wake, which was a crucial advancement for infaunal life-styles. These behavioral characteristics, though primitive, are clearly derived from earlier animal ancestors.

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Supplementary Materials

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References (31–46)

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Early Pottery at 20,000 Years Ago in Xianrendong Cave, China

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The invention of pottery introduced fundamental shifts in human subsistence practices and sociosymbiotic behaviors. Here, we describe the dating of the early pottery from Xianrendong Cave, Jiangxi Province, China, and the micromorphology of the stratigraphic contexts of the pottery sherds and radiocarbon samples. The radiocarbon ages of the archaeological contexts of the earliest sherds are 20,000 to 19,000 calendar years before the present, 2000 to 3000 years older than other pottery found in East Asia and elsewhere. The occupations in the cave demonstrate that pottery was produced by mobile foragers who hunted and gathered during the Late Glacial Maximum. These vessels may have served as cooking devices. The early date shows that pottery was first made and used 10 millennia or more before the emergence of agriculture.

Pottery making—the manufacture of fired, ceramic container forms—differs considerably from the baked clay figurines or

small objects known from the Upper Paleolithic period (1) in its technological demands and in its significance both in subsistence activities, in-

cluding food storage, processing, and cooking, and in social interactions (2). Pottery was until recently thought to have been developed during the so-called “Neolithic Revolution” and first made by settled, farming populations with domesticated plants and animals and ground stone tools, but recent discoveries have found earlier examples, from Late Pleistocene mobile or semimobile hunter-gatherer contexts in China, Japan, and the Russian Far East (2). One notable find, dating to ~18 to 17 thousand calendar years before the present (cal ky B.P.), is at Yuchanyan

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