# Eocene animal trace fossils in 1.7-billion-year-old metaquartzites

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**The Paleoproterozoic (1.7 Ga [billion years ago]) metasedimentary rocks of the Mount Barren Group in southwestern Australia contain burrows indistinguishable from ichnogenera *Thalassinoides*, *Ophiomorpha*, *Teichichnus*, and *Taenidium*, known from firmgrounds and softgrounds. The metamorphic fabric in the host rock is largely retained, and because the most resilient rocks in the sequence, the metaquartzites, are too hard for animal burrowing, the trace fossils have been interpreted as predating the last metamorphic event in the region. Since this event is dated at 1.2 Ga, this would bestow advanced animals an anomalously early age. We have studied the field relationships, petrographic fabric, and geochronology of the rocks and demonstrate that the burrowing took place during an Eocene transgression over a weathered regolith. At this time, the metaquartzites of the inundated surface had been weathered to friable sandstones or loose sands (arenized), allowing for animal burrowing. Subsequent to this event, there was a resilicification of the quartzites, filling the pore space with syntaxial quartz cement forming silcretes. Where the sand grains had not been dislocated during weathering, the metamorphic fabric was seemingly restored, and the rocks again assumed the appearance of hard metaquartzites impenetrable to animal burrowing.**

Paleoproterozoic | Eocene | trace fossils | geochronology | regolith

The report of animal trace fossils in metasedimentary rocks of the 1.7 Ga (billion years ago) Paleoproterozoic Mount Barren Group in Western Australia (1) presents a tantalizing riddle. The sediments are more than a billion years older than the earliest known body fossils of animals (2), but they harbor a diversity of burrows undoubtedly made by animals. The Mount Barren rocks—the Kundip Quartzite and the Kybulup Schist—were metamorphosed at ca. 1.2 Ga, so if the trace fossils were not indigenous to the original sediments (3) it would remain to be explained how animals could later bore through rocks as uncompliant as metaquartzites.

An essential quality of trace fossils is that they reflect the local life environment. Because they comprise sedimentary structures, they cannot have been transported (or are easily recognized as such when they have been) but represent the activities of organisms in the very substrates where they are found. This principle is one of the tenets behind the concept of ichnofacies (refs. 4, 5 and part 4 in ref. 6).

We have investigated the Mount Barren trace fossils in relation to their host rock and performed U–Pb geochronology on detrital, diagenetic, metamorphic, and igneous minerals. The results confirm the Paleoproterozoic age of the Mount Barren Group but show that the traces were formed during the Phanerozoic. We present a model explaining how animals were able to move through the seemingly impenetrable metasedimentary rocks.

## Geological Setting

The Mount Barren Group is a Paleoproterozoic succession of lower greenschist to upper amphibolite facies metasedimentary rocks located in the Proterozoic Albany–Fraser Orogen along the southern margin of the Archean Yilgarn Craton, Western Australia (Fig. 1). The group, which comprises mostly quartzite, phyllite, and schist, with minor conglomerate and dolomite, is interpreted to have been deposited in a shallow marine environment (7). The succession has been divided into the Steere Formation, Kundip Quartzite, and Kybulup Schist (1, 7–9). The Steere Formation overlies Archean rocks of the Yilgarn Craton and consists of a thin conglomerate overlain by pebbly sandstone and dolomitic limestone (7, 8). The overlying Kundip Quartzite comprises a thick succession of thickly bedded, mature quartz arenite, with minor metapelite and metaconglomerate (7, 8, 10). Sedimentary cross-bedding and ripple marks are locally preserved (7). The Kundip Quartzite is intruded by the previously undated Cowerdup Sill, a 300-m-thick layered mafic–ultramafic intrusion that is broadly conformable to stratigraphic layering (1, 7, 10). Above the metaquartzites is the Kybulup Schist, which comprises thinly bedded mudstone and sandstone of variable metamorphic grade. In the northwest, it is dominated by slate and phyllite, whereas in the southeast, it comprises amphibolite facies kyanite-, staurolite-, and garnet-bearing schists (1, 7, 11, 12).

Detrital zircon geochronology of the Mount Barren Group indicates a maximum depositional age of ~1.79 Ga (13). Diagenetic

## Significance

Strained 1.7-billion-year-old metasedimentary rocks in southwestern Australia contain traces of burrowing animals, structures only known from the last half billion years of Earth history. As metamorphic events had made the sediment too hard for burrowing by ~1.2 billion years ago, it has been suggested that the burrows were made during the Paleoproterozoic by early animals with no other fossil record. We found, however, that the quartzite had been deeply weathered by about 50 Mya, allowing burrowing during an Eocene flooding. Subsequent rehardening of the sediment by silica precipitation restored the impenetrable quartzite with its metamorphic fabric. However, the burrows lack that fabric and contain detrital grains that are much younger than the matrix in which they occur.

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The authors declare no competing interest.

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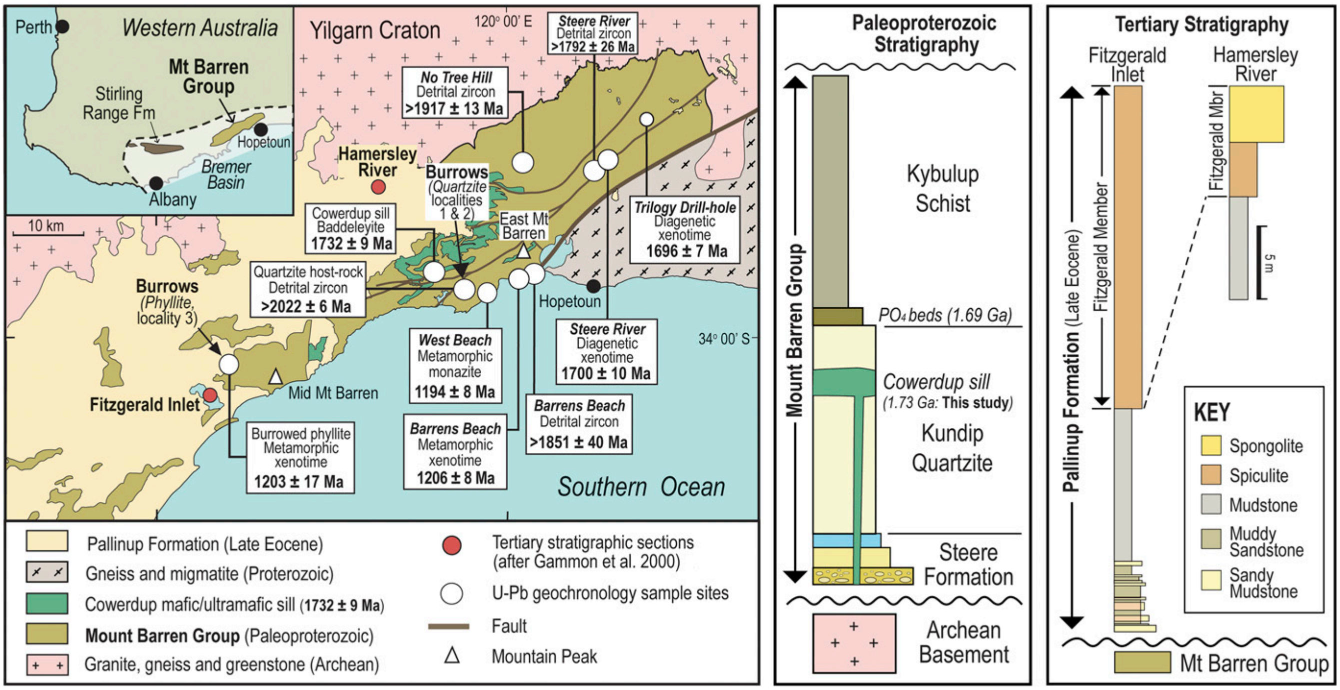

**Fig. 1.** Map of the Mount Barren Group showing location of three fossil localities and U–Pb geochronology of major units. Paleoproterozoic and Tertiary stratigraphy. Coordinates: Locality 1 [locality R2 of Thom (1)], S 33°56.4, E 119°56.4; Locality 2, S 33°56.1, E 119°57.7; and Locality 3, S 34°03.5, E 119°37.1.

xenotime in phosphatic horizons at the base of the Kybulup Schist yielded a U–Pb age of 1.69 Ga (14), interpreted to represent a close approximation of the depositional age. In the Mesoproterozoic, the succession experienced greenschist to upper amphibolite facies metamorphism and deformation, with the development of foliated kyanite-, staurolite-, and garnet-bearing schists (1, 7) indicating peak metamorphic conditions of ∼8 kbar and ∼650 °C (10). Monazite and xenotime aligned with the dominant foliation yielded U–Pb ages between 1.22 and 1.19 Ga (11, 12), corresponding with the timing of regional metamorphism during the second stage of the Albany–Fraser Orogeny (1.21 to 1.14 Ga). The fabrics are axial planar foliations associated with isoclinal folds that are attributed to N–S compression, consistent with the overall trend of structures in this part of the orogen.

Sometime between the late Mesozoic and early Tertiary, deeply weathered regolith and planar surfaces (etchplains) developed over the Archean and Proterozoic rocks in southwestern Australia (15). The general slope of the old land surface is less than a degree (∼0.4°) toward SSE in the Hopetoun area (16). Subsidence in the Paleocene was followed by shoreface erosion of regolith horizons and deposition of the shallow marine Plantagenet Group below a paleo-escarpment north of the Mount Barren Group and along inland paleovalleys (15, 16). The Plantagenet Group, consisting of the Werrilup Formation and Pallinup Formation, represents deposition during the last two marine transgressions (Middle and Late Eocene) into the onshore Bremer Basin (15). The most extensive unit in the Mount Barren area is the Pallinup Formation, where it comprises basal quartz sandstones overlain by mudstones rich in spiculite and an uppermost unit of spiculite and spongolite. At the Fitzgerald Inlet and Hamersley River sections (Fig. 1), the Pallinup Formation contains spiculitic mudstones with abundant *Thalassinoides* and strongly silicified horizons (15). Uplift during the Oligocene (16) helped to preserve the Pallinup Formation from burial.

Overlying the Kundip Quartzite in places is a breccia-ferricrete with angular to semirounded clasts of quartzite (*SI Appendix*, Fig. S1) of centimeter to meter size.

## Materials and Methods

Samples of fossil-bearing Mount Barren quartzite and phyllite, slate, dolerite (Cowerdup sill), and Tertiary ferricrete were collected in 2002 and 2003 from Hamersley Inlet, Mid Mount Barren, West Beach, and Barrens Beach and complemented with material collected in previous studies (Fig. 1) (1, 10).

The samples were investigated by optical and scanning electron microscopy (SEM), combined with backscattered electron (BSE) imaging, energy-dispersive X-ray spectrometry (EDS) and cathodoluminescence (CL). Baddeleyite, xenotime, monazite, and zircon grains were analyzed using a sensitive high-resolution ion microprobe; procedures and data are provided in *SI Appendix*. The weighted mean $^{207}Pb/^{206}Pb$ ages quoted in the text have 95% confidence limits.

All geographical coordinates in this paper were measured in the field with a Garmin GPS 12 using the global WGS84 datum.

## Results

**Morphology and Field Relations.** Trace fossils occur in isolated exposures (localities 1 and 2 in Fig. 1) of the Kundip Quartzites at the northern edge of an extensive deposit of Tertiary sediments (1). The most common trace fossils consist of ferruginous burrows, straight or slightly curved (Fig. 2 *A*–*I*). They form conspicuous networks with Y-shaped (Fig. 2*C*, arrow, and Fig. 2*D*) and T-shaped (Fig. 2 *G* and *H*) branches, as well as false branching due to superposition of differently oriented burrows. These network galleries mainly occur on present-day horizontal or subhorizontal surfaces of the quartzite, and they are combined with vertical or subvertical shafts expressed as filled holes (Fig. 2 *A*–*D* and *I*). Short bulb-like protrusions from burrows also occur (Fig. 2 *E* and *F*). The fill in most of these burrows is a homogenous quartz sandstone cemented by ferruginous matter; there is no evidence of a burrow wall, such as differences in structure or composition from fill and matrix (Fig. 2*H*).

The diameter of the horizontal burrows is fairly stable, varying between 5 and 10 mm. The vertical shafts may, however, be up to 20 mm in width. Occasionally, the horizontal network includes finer branches a few millimeters in width (e.g., Fig. 2*B*, arrow). In general, there is no change of width at branching points.

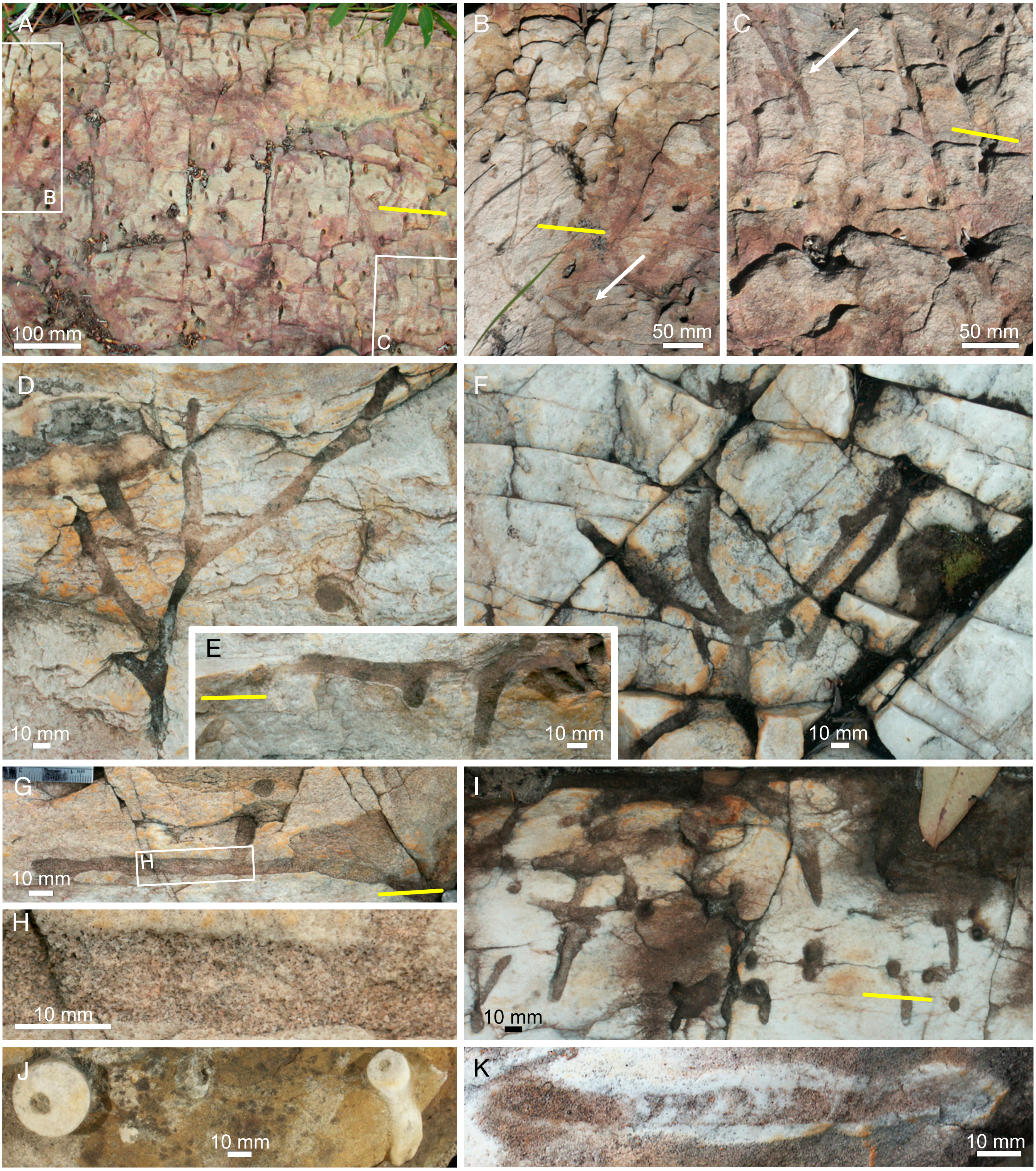

**Fig. 2.** Field images (except for *J*) of trace fossils in Kundip Quartzite. Yellow lines indicate approximate direction of remnant bedding or foliation. (*A*–*C*) *Thalassinoides* isp. (ichnospecies), top surface of rock with subhorizontal branching galleries and vertical shafts; overview (*A*) and details (*B* and *C*). White arrow in *B* points to region with millimeter-wide branches; white arrow in *C* points to Y-branch. S 33°56.107, E 119°57.782. (*D*) *Thalassinoides* isp., subhorizontal burrow with repeated Y-branching. S 33°56.444, E 119°56.365. (*E*) *Thalassinoides* isp., subhorizontal branch aligned with remnant bedding or foliation in quartzite. S 33°56.444, E 119°56.365. (*F*) *Thalassinoides* isp., complex subhorizontal branching system. S 33°56.066, E 119°57.702. (*G* and *H*) *Thalassinoides* isp., T-branching. Enlargement in *H* shows homogenous ferruginous sandstone infill and absence of burrow wall. S 33°56.008, E 119°57.743. (*I*) *Thalassinoides* isp., top surface of rock with subhorizontal branching galleries and tendency toward alignment with remnant bedding or foliation in quartzite. S 33°56.082, E 119°57.714. (*J*) Burrows with light halo. UWA180711. (*K*) Meniscate burrow with irregular light halo. S 33°56.037, E 119°57.699; UWA180705.

There is an occasional tendency of alignment of burrows along what appears to be planar lithological inhomogeneities resulting from either relict bedding or the predominant foliation, which is generally striking NE–SW and nearly perpendicular to the present horizontal plane (dip ~80° to SE). This can be seen in sections (*SI Appendix*, Fig. S2) but is also suggested in outcrop where specimens send out perpendicular lateral branches (Fig. 2 *E* and *I*, *Left*) or where vertical shafts are aligned in a row (Fig. 2*I*, round holes to the right).

The branching galleries conform to the morphology of the ichnogenus *Thalassinoides*, domichnial burrow systems usually attributed to decapod crustaceans burrowing in firmgrounds or softgrounds (17–20).

In addition to the *Thalassinoides* galleries, the Kundip Quartzite contains rare 6- to 16-mm-wide burrows with pellets embedded within the burrow lining (Fig. 3 *A*–*E*), suggesting a behavior like that represented by ichnogenus *Ophiomorpha*, in which the burrow walls in loose sediment are reinforced by embedded pellets (21). The pellets are mostly weathered out from the rock, leaving irregularly shaped cavities. The inner surface of the wall is smooth, whereas the outer surface is knobbly (Fig. 3*A*), a condition characteristic of mature *Ophiomorpha* in sandy sediments (21). As with the *Thalassinoides*, the *Ophiomorpha* fill is a homogenous sandstone, indicating passive infill after the tube has been abandoned.

There are a few burrows with structures suggesting a meniscate, active fill (Fig. 2*K* and *SI Appendix*, Fig. S3). Where observable in more than one plane of section, they can be seen to represent retrusive spreiten of the ichnogenus *Teichichnus* (*SI Appendix*, Fig. S3 *A*–*C*) (22) as well as backfilled cylindrical burrows (*SI Appendix*, Fig. S3*F*; possibly also the specimens in Fig. 2*K* and *SI Appendix*, Fig. S3 *D* and *E*). Because of the rarity and poor preservation of the backfilled burrows, no inferences are made about their preferred orientation and ichnotaxonomy.

Burrows are occasionally surrounded by a regular zone of white quartzite, resulting in weathering-resistant white cylinders with a central or subcentral core of darker quartzite (Fig. 2*J* and *SI Appendix*, Fig. S4). Such a zone may also form more irregular envelopes of whitish material around a burrow (Fig. 2*J*).

Trace fossils in good preservation (Fig. 4) also occur in phyllites of the Kybulup Schist found as ex situ debris west of the quartzite exposures (locality 3 in Fig. 1). They comprise burrows forming more-or-less dense networks along or across the direction of cleavage. Burrows are 0.5 to 5 mm wide, sometimes extending for centimeters without change of diameter (Fig. 4*A*) but commonly expanding or contracting (Fig. 4 *B*–*D*). Meniscate backfill is common, particularly in the wider specimens (Fig. 4 *C*–*E*); these traces are referable to the ichnogenus *Taenidium*, a widespread trace fossil in both marine and terrestrial deposits (23–27). Although the rock is strongly cleaved, there is no evidence of compression of the traces; burrows at different orientations to the rock cleavage maintain a roughly circular cross-section (Fig. 4*H*).

**Petrography.** Fig. 5 shows a cross-section through a burrow in metaquartzite. The quartz grains in the host rock are elongated, indicating the direction of extension during metamorphism. The burrow fill, however, shows no such oriented elongation, neither in the quartz grains nor in the cross-sectional morphology of the burrow. This difference between matrix and burrow fill is confirmed by the crystallography of the quartz grains. There is a distinct alignment of the crystallographic axes in the host rock, whereas the axis directions in the burrow fill appear to be random [Fig. 5*A*, see also figure 30 of Thom (1)]. A further difference between host rock and burrow fill regards porosity, which is very

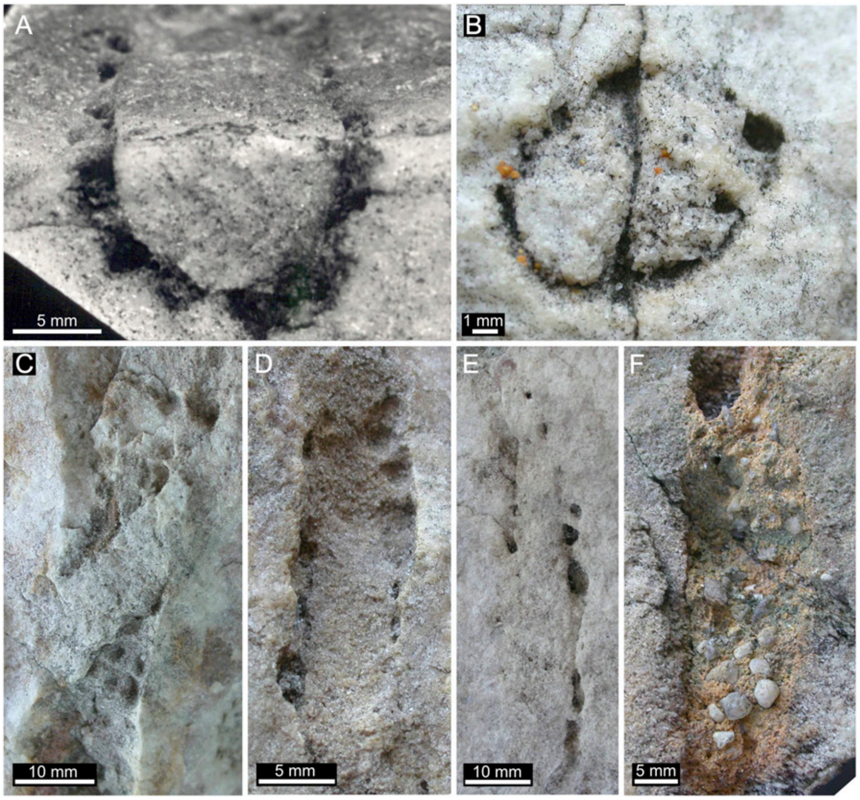

**Fig. 3.** (*A*–*E*) *Ophiomorpha* in Kundip Quartzite, with pelletal linings in the burrow walls. Pellets mostly weathered out, leaving voids. Note smooth inner and knobbly outer wall surface in *A*. (*F*) Unidentified burrow with granular infill. Specimens collected from loose material at Locality 1 (Fig. 1) but subsequently lost.

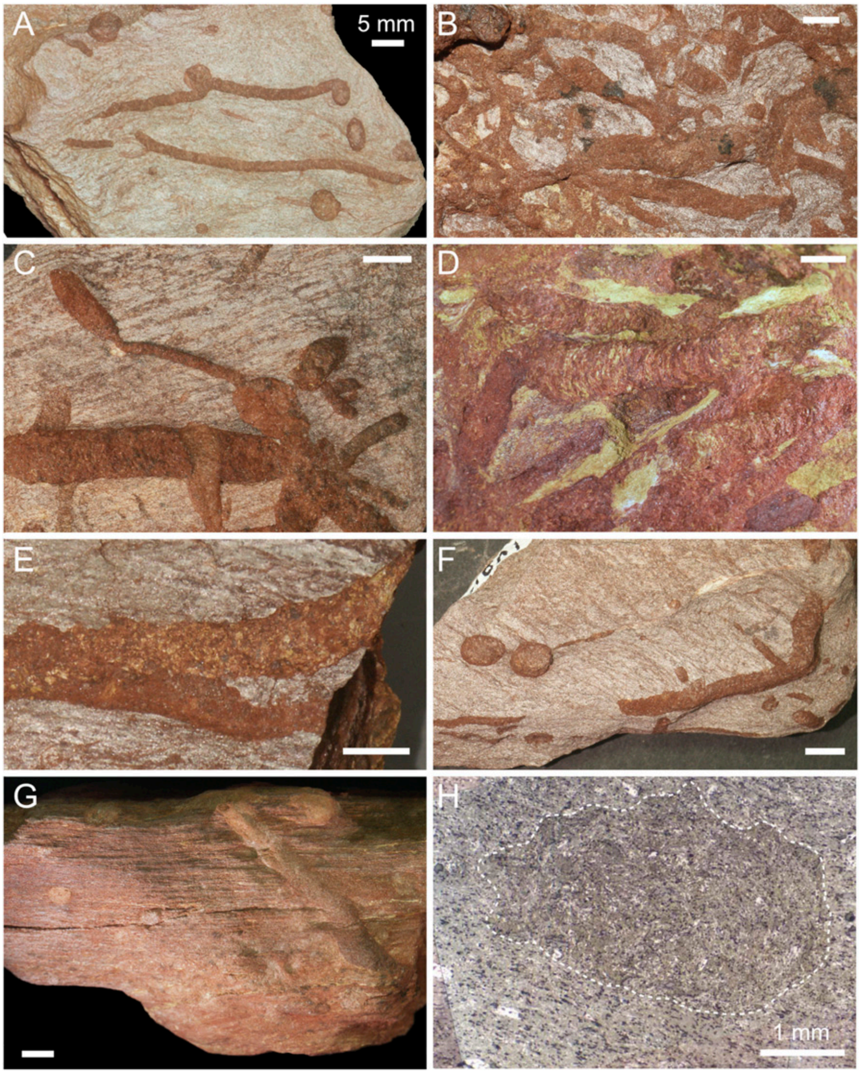

**Fig. 4.** Kybulup Schist phyllite with trace fossils. Material consists of loose slabs not in situ, collected at Locality 3 (Fig. 1). Traces mainly aligned along parting planes of phyllite, at narrowly oblique angles to metamorphic cleavage. (*A*) Cylindrical traces with globular protrusion and possible vertical shafts; UWA180696. (*B*) Complex bioturbation fabric; UWA131809. (*C*) *Taenidium* (broad burrow with meniscate fill) cut by narrower burrows of different color. Narrow cylindrical burrow (*Top*) ending in an expanded termination following a constriction; UWA131812. (*D*) Heavily bioturbated fabric mostly consisting of *Taenidium*; UWA131818. (*E*) False branching in *Taenidium*-like juxtaposed burrows; UWA131803. (*F*) Cylindrical burrow with abutting narrower burrow; possible vertical shafts; UWA131801. (*G*) Burrow traversing the phyllite parting planes and cleavage; UWA131843. (*H*) Section through burrow (outlined) showing obliterated cleavage fabric in burrow fill; UWA180739. (All scale bars, 5 mm, except *H*, 1 mm.)

limited in the host rock (Fig. 5 *C*, *E*, and *G*) but considerable in the fill (Fig. 5 *B*, *D*, and *F*).

Sections through burrows with a whitish halo (cf. Fig. 2 *J* and *K*) show a somewhat different picture (*SI Appendix*, Fig. S4): quartz grains in the burrow core, halo, and host rock have crystallographically and morphologically random orientations, the only difference between the phases being a higher porosity in burrow core and halo than in the host rock.

The quartz grains have a homogenous appearance under the petrographic microscope and SEM-BSE, indicating uniform crystals of quartz. Where the quartz grains are in contact, the boundaries between them have an irregular-stylolitic appearance in both burrow fill and host rock (e.g., Fig. 5 *B*–*E* and *SI Appendix*, Figs. S4 *C*–*E* and S5 *A* and *C*). However, SEM-CL images of the same grains show several generations of quartz, with the core overgrown by a secondary layer or layers that form most of the contacts between grains (Fig. 5 *F* and *G* and *SI Appendix*, Figs. S4 *F*–*H* and S5 *B* and *D*). These outer portions may be homogenous (as in *SI Appendix*, Fig. S4 *F*–*H*) or comprise a palisade-like layer (Fig. 5 *F*, *Upper Left* and *SI Appendix*, Fig. S5 *B* and *D*).

Backfilled burrows in the schist (Fig. 4*H*) have a similar relationship to their host rock as those in the quartzites: the sericite crystals in the host rock are strongly aligned, but the burrows cut the metamorphic fabric without deflecting it, and there is no visible compression of the burrows.

**Geochronology.** In situ secondary-ion mass spectrometry U–Pb analysis of baddeleyite from the metamorphosed Cowerdup mafic sill, which intrudes Kundip Quartzite a few kilometers north of the fossil locality 1, yielded a weighted mean $^{207}$Pb/$^{206}$Pb date of 1,732 ± 8 Ma ($n$ = 10; mean squared weighted deviation [MSWD] = 1.3) (Fig. 6 and *SI Appendix*). This date approximates the age of intrusion and provides a minimum age for the intruded rocks. Uranium–lead geochronology of authigenic xenotime in quartzite from Steere River, which is in the same structural domain as fossil localities 1 and 2, yielded an oldest population of ~1.7 Ga (1,691 ± 18 Ma; MSWD = 1.4; $n$ = 6) (Fig. 6), providing a

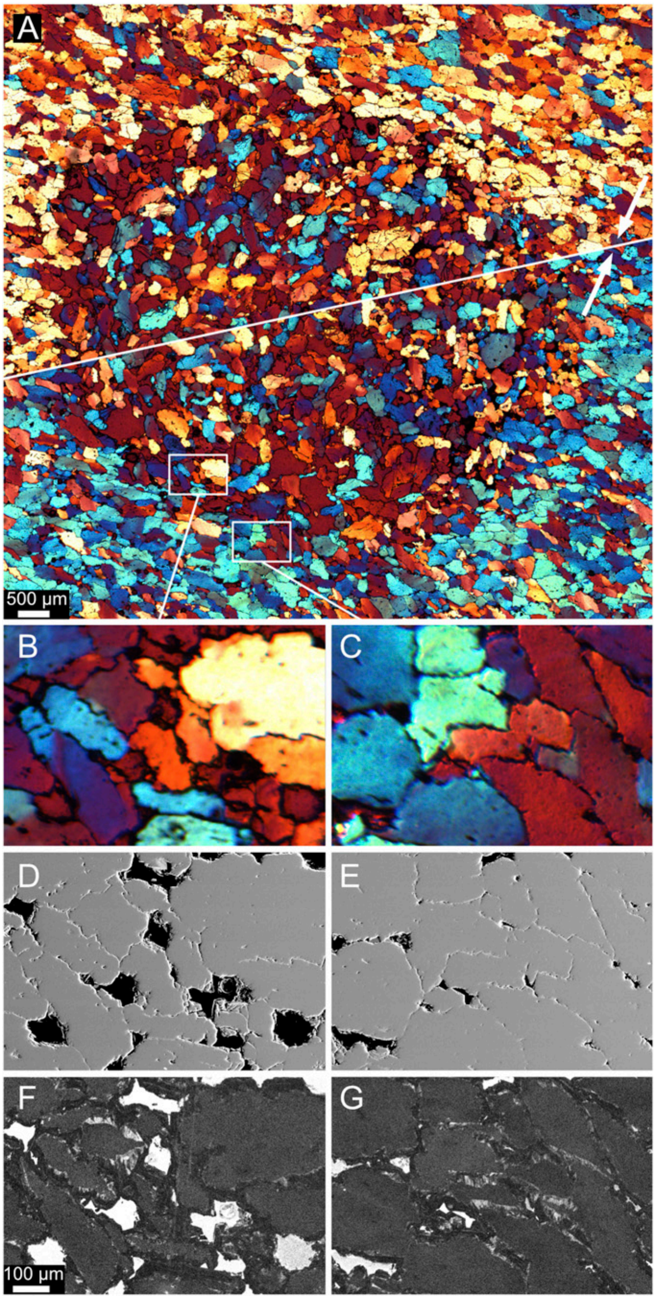

**Fig. 5.** Thin section through cylindrical burrow in Kundip Quartzite retaining metamorphic fabric; UWA180740. (*A*) Petrographic microscopy, crossed nicols, lambda plate. Target rotated 90° between the views separated by oblique line. White arrows in *A* are perpendicular to cleavage. (*B* and *C*) Details of *A*. (*D*–*G*) SEM-BSE (*D* and *E*) and CL (*F* and *G*) images of regions in *B* and *C*. Porosity seen as black in *D* and *E* and white in *F* and *G*.

minimum age for the fossil-bearing quartzite host rock. Quartz-mica schist and garnet-chloritoid quartzite along strike length from fossil locality 1 contain elongate xenotime and monazite aligned within the metamorphic fabric that grew at ∼1.2 Ga (28), corresponding with U–Pb ages for peak metamorphism in schist from West Beach and Barrens Beach (11, 12).

Detrital zircon grains in the trace-fossil hosting Kundip Quartzite yielded a youngest population of 2,022 ± 6 Ma ($n = 56$; MSWD = 1.5) (Figs. 1 and 6; reference *SI Appendix*). Most of the detrital zircon grains separated from the burrow fill display similar age distribution patterns to the host rock, except for ferruginous sandstone filling burrows, which yielded ages as young as 530 Ma (Fig. 6 and *SI Appendix*, Fig. S2). The age distribution from the ferruginous burrow fill closely matches that of detrital zircon from the nearby Tertiary ferricrete (*SI Appendix*, Fig. S1), suggesting that the burrows were filled by Tertiary sediment.

Samples of the burrowed phyllite from northwest of Mid Mount Barren contain xenotime that yielded age peaks at ∼1.7 Ga and ∼1.2 Ga, which is interpreted to reflect diagenetic and metamorphic growth, respectively (28), confirming its Paleoproterozoic depositional age.

## Discussion

The burrow systems in the Kundip Quartzites are undoubtedly trace fossils made by animals, most likely arthropods. Thom (1) concluded that the burrows were made by Proterozoic animals, but the ≥1.7 Ga age of the Mount Barren metasedimentary rocks (Fig. 6) is more than a billion years older than any accepted animal fossils (2). The ≤530 Ma age of the burrow fills and adjacent ferricrete (Fig. 6) rather indicates that the Paleoproterozoic metasedimentary rocks were inundated and burrowed during a Phanerozoic event, and the mature quartz sand of the fills is consistent with a marine event. An analogous case would be the invasion of Cretaceous *Thalassinoides* trace makers into weathered and weakly lithified Triassic sandstones and Paleozoic metavolcanites in Czechia (29, 30). A likely candidate for the event involving the Mount Barren rocks is the widespread Eocene transgression (31, 32) that produced a sedimentary succession overlying a deeply weathered regolith (15). In the Paleocene and Eocene, the climate in Western Australia was moist, temperate to tropical (33), thus conducive to deep chemical weathering.

Yet, the host rocks often preserve their older metamorphic fabric (Fig. 5*A*), which cannot be younger than 1.2 Ga, the time of the last episode of regional metamorphism (Fig. 6). Runnegar (3) suggested that the apparent metamorphic fabric of the host rock was somehow derived from an inherited grain shape. If the trace fossils are of Eocene age, we need to explain how the animals could burrow through a substrate that preserves even today the hardness and metamorphic fabric of a Paleoproterozoic metaquartzite.

Whereas animal borings in carbonate rocks are common (34, 35), trace fossils in noncarbonate rocky substrates, harder and less susceptible to chemical attacks, are limited to a low diversity of domicilial borings in igneous rocks, schists, slates, and siltstones (35–41). Bioeroders of such rocks mainly use mechanical means, attacking weaknesses due to crystal heterogeneities (36). As for borings in even harder substrates, comparable to the Kundip metaquartzites, such a record is almost nonexistent. A report from a Cambrian–Ordovician transgressive setting describes shallow depressions in quartzites and vein quartz that may have been caused by animals aided by microendoliths (42), but these simple borings do not come near the Kundip-hosted trace fossils in complexity and penetration.

The Kundip traces correspond to burrows rather than borings, more similar to the complex galleries of *Thalassinoides* type common in the *Glossifungites* ichnofacies of Phanerozoic firmgrounds than to the simpler domiciles of the hardground *Trypanites* ichnofacies (4, 34, 43–45). Furthermore, the backfills, spreiten, and occasional pelletal linings of the tubes suggest that at least some of the burrows were made in a shifting substrate of loose sand.

The homogenous crystallographic fabric indicating a metaquartzitic host rock for the trace fossils (Fig. 5 *A*–*C*) is, however, modified by the CL evidence of growth zones around each grain, even where the metamorphic crystal alignment is retained (Fig. 5 *F* and *G*). This suggests that the original metaquartzite was partly dissolved along grain boundaries before the advent of the trace-fossil makers and that the rock was subsequently resilicified, producing syntaxial layers of quartz cement filling up most of the pore space resulting in a silcrete retaining an older

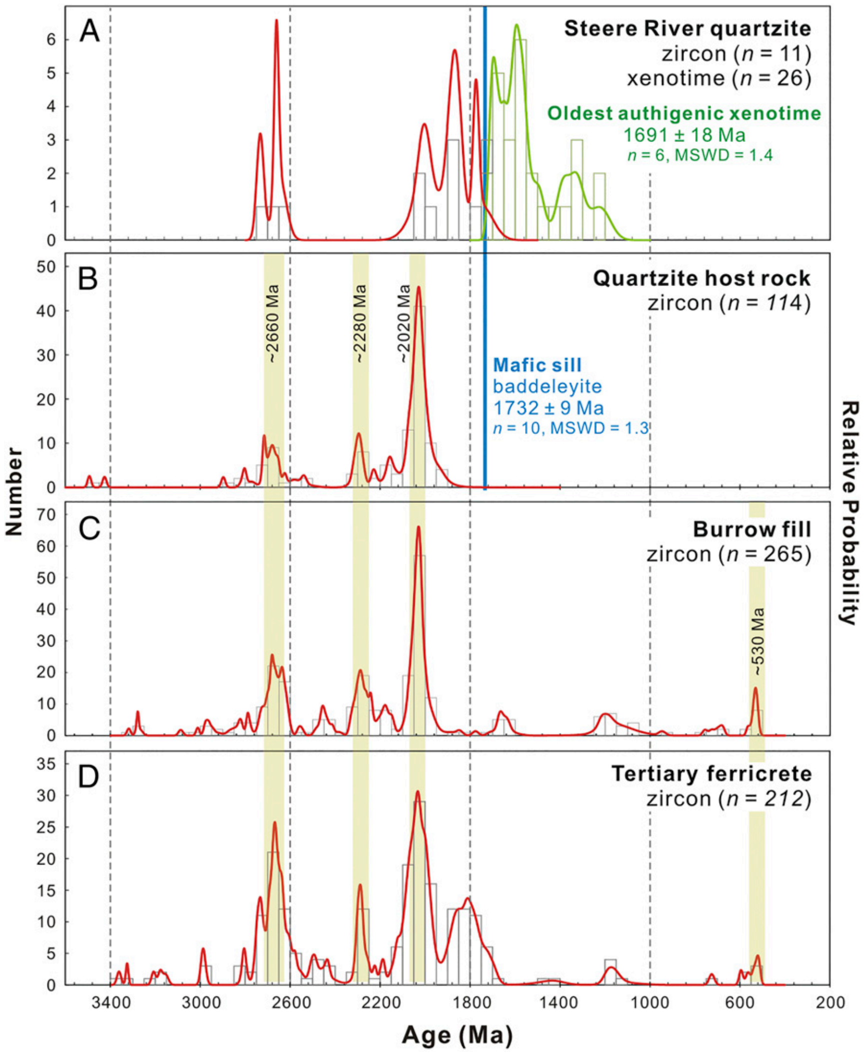

**Fig. 6.** Probability density plots and histograms (50 million years bin width) of U–Pb ages of detrital zircon (red curves in *A*–*D*) and authigenic xenotime (green curve in *A*). Baddeleyite age of the mafic sill intruding the quartzite is also shown (blue band in *A* and *B*). Weighted mean ages for the oldest authigenic xenotime in *A* and baddeleyite in *B* are at 95% confidence limits.

metamorphic fabric. This sequence of events would at the time of burrowing have presented the animals with a substrate of a more-or-less friable sandstone. Instances where the metamorphic fabric has not been preserved (*SI Appendix*, Fig. S4) would represent places where the substrate consisted of loose sand. The rare cases of seeming alignment of burrows with Proterozoic bedding or foliation directions (Fig. 2 *E* and *I*) may be due to differential weathering along layers with different porosity. Solutional weathering of siliceous rocks, such as metaquartzites, into sandstones and of sandstones into sand, "arenization," is frequent in tropical and subtropical regions with high annual rainfall but can be found also in arid and cold regions (46). A well-studied example is the Roraima quartzite caves of southern Venezuela (47, 48), where evidence also indicates subsequent resilicification in the resulting pore spaces (49). Exposures of quartzites with silcrete structures in the Mount Barren Group (*SI Appendix*, Fig. S6) confirm that such processes were active in the region (cf. ref. 50). The silcretization of the regolith was likely facilitated by the presence of burrows that acted as conduits for fluids, permitting deeper penetration into the subsurface.

The Kybulup phyllites would have been even more susceptible to weathering during the time preceding the Eocene transgression and would likely have presented to the animal burrowers a firm mudground that preserved the metamorphic cleavage where it was not directly penetrated. A part analog would be the ~1 Ga sediments of the Zambian Copperbelt, which contains structures originally interpreted as the world's oldest trace fossils (51). These were subsequently shown to be considerably younger than the sediments and interpreted as made by modern termites burrowing through the weathered rock for groundwater (52). The Kybulup Schist traces, in contrast, are now lithified and form part of rocks resilient enough to be broken up as slabs. They are thus fossil and may belong to the same inundation event as the nearby quartzite burrows, the difference in trace-fossil composition between the localities being attributable to which part of the folded Paleoproterozoic sequence was exposed in the local area. Alternatively, it is possible that the Kybulup trace fossils represent a terrestrial event of burrowing not directly related to the marine transgression.

In conclusion, we propose that the Mount Barren trace fossils were formed during an Eocene marine transgression over arenized Paleoproterozoic metaquartzites that presented a substrate ranging from friable sandstone to loose sands and over weathered schists that would have had the consistency of muddy firmgrounds. After this event, the rocks were again hardened by resilicification. Syntaxial cement around the quartz grains then produced the paradoxical impression of animal burrows in substrates too resilient for burrowing.

**Data Availability.** All study data are included in the article and/or *SI Appendix*.

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