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Ichnofacies of the Stairway Sandstone fish-fossil beds (Middle Ordovician, Northern Territory, Australia)

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The Stairway Sandstone is a 30–560 m thick succession of Middle Ordovician siliciclastic sedimentary rocks within the Amadeus Basin of central Australia, deposited in the epeiric Larapintine Sea of northern peri-Gondwana. The Stairway Sandstone is significant as one of only two known Gondwanan successions to yield articulated arandaspid (pteraspidomorph agnathan) fish. Herein we use the ichnology of the Stairway Sandstone to reveal insights into the shallow marine habitat of these early vertebrates, and compare it with that of other known pteraspidomorph-bearing localities from across Gondwana. The Stairway Sandstone contains a diverse Ordovician ichnofauna including 22 ichnotaxa of *Arenicolites, Arthrophycus, Asterosoma, Cruziana, Didymaulichnus, Diplichnites, Diplocraterion, ?Gordia, Lockeia, Monocraterion, Monomorphichnus, Phycodes, Planolites, Rusophycus, Skolithos* and *Uchirites*. These ichnofauna provide a well-preserved example of a typical Ordovician epeiric sea assemblage, recording the diverse ethologies of tracemakers in a very shallow marine environment of flashy sediment accumulation and regularly shifting sandy substrates. New conodont data refine the age of the Stairway Sandstone to the early Darriwilian, with ichnostratigraphic implications for the *Cruziana rugosa* group and *Arthrophycus alleghaniensis*.

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THE MIDDLE ORDOVICIAN Stairway Sandstone is part of the Larapinta Group of the Amadeus Basin in the Northern Territory, central Australia (Fig. 1). The Larapinta Group consists of a succession of mostly shallow marine, mixed clastic and carbonate strata, whereas the Stairway Sandstone consists of siliciclastic shallow marine sandstone, mudstone and siltstone, with lesser phosphatic beds and calcareous sandstone (Cook 1970, 1972, Laurie *et al.* 1991). The thickness of the formation is highly variable, ranging from 30 m on the shallower southern margin of the basin to 560 m on the northern margin. It has a tripartite division into a relatively thin (25–60 m) lower sandy unit dominated by cross-bedded quartzites, a poorly exposed fine-grained middle unit of shales, siltstones, fine sandstones and phosphorites, and an upper unit (30–300 m) comprising very fine to medium-grained quartz sandstones, with minor intercalated siltstones. The sandy facies of the lower and upper units have been interpreted as deposits of shallow intertidal–subtidal environments, whereas the middle unit constitutes deeper water deposits (Laurie *et al.* 1991). This study describes the ichnology of the Stairway Sandstone, with a particular focus on the sandy facies, in order to improve understanding of the palaeoecology of early fish habitats. Trace fossils were identified and

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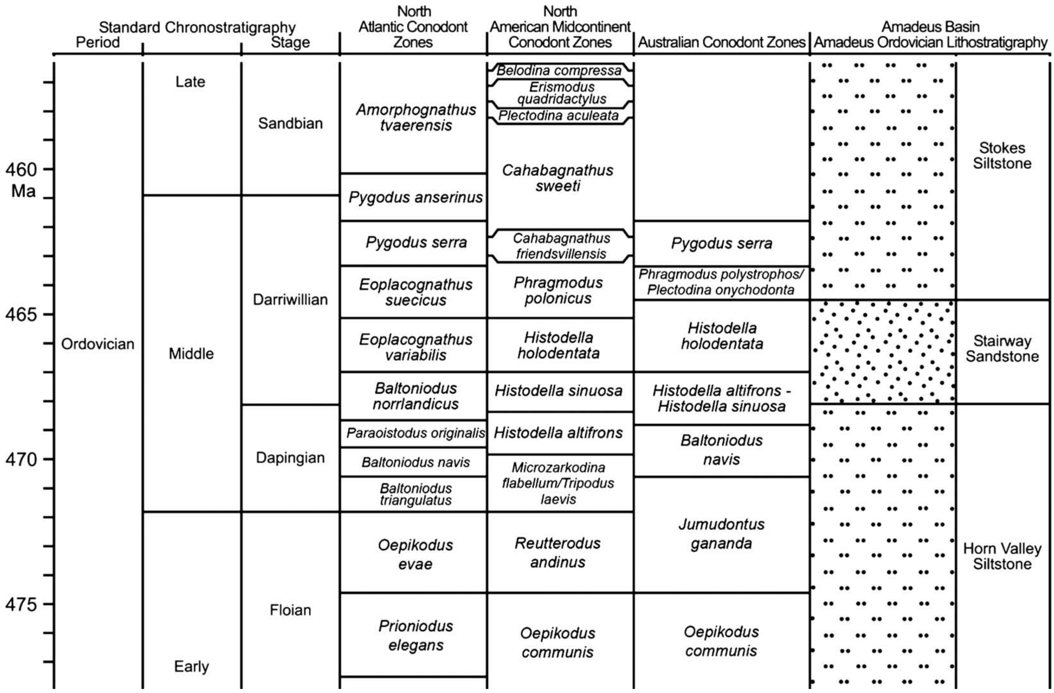


Fig. 1. Stratigraphy of the Ordovician Larapinta Group, Amadeus Basin, Northern Territory, Australia. Alignment of the formation boundaries based on Nicoll *et al.* (1991) and Young (1997).

described during visits to four field localities and from samples held within the collections of Geoscience Australia, Canberra, and at the Australian Museum, Sydney. The localities studied in this research were areas where the sandy facies of the Stairway Sandstone crops out as a cliff-forming unit to the south and west of Alice Springs: namely, Mount Watt (25°19.46′S, 133°53.37′E), Mount Charlotte (24°42.01′S, 134°02.11′E), Dry Creek (24°15.16′S, 131°42.22′E) and Maloney Creek (24°30.09′S, 133°16.31′E: Fig. 2).

Articulated arandaspids have been recovered from the first two of these localities (Ritchie & Gilbert-Tomlinson 1977), and microremains of arandaspids and other fishes have been recovered from the last (unpublished data). Some confusion exists over the stratigraphy of the sandy facies at Mount Charlotte and Mount Watt, with Ritchie & Gilbert-Tomlinson (1977, p. 351) describing the articulated arandaspid fossils as being 'restricted to a narrow horizon low in the formation,' while Gibb *et al.* (2009, p. 695) considered the same sections as representing 'the upper unit of the Stairway Sandstone'. The additional sections we have studied, at Dry Creek and Maloney Creek, are clearly from the upper part of the Stairway Sandstone but it is important to note here that the similarity in ichnofauna and sedimentology at all of these localities suggests that the sandy facies of the Stairway Sandstone, be they from the lower or the upper units, represent very similar depositional environments. Correlation between the outliers at Mount Charlotte and Mount Watt sections and the rest of the Stairway Sandstone is hampered by the incomplete and comparatively thin sequences that are present, the base of both sections being unconformable and erosion having removed any upper contact. The

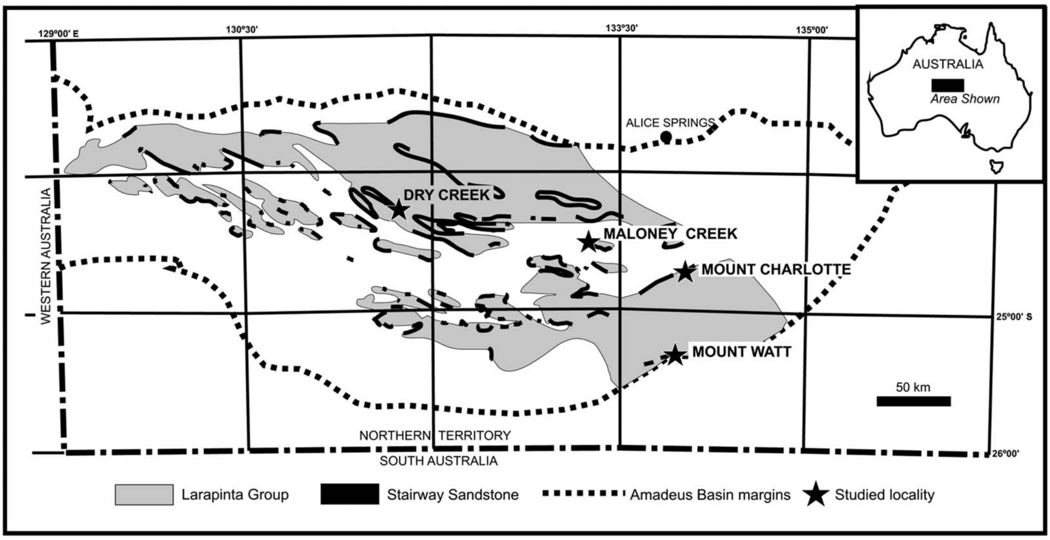


Fig. 2. Map of the Amadeus Basin in the Northern Territory, central Australia, showing outcrop of the Stairway Sandstone and studied localities.

exact stratigraphic location of the trace fossils in the museum collections was not always clear, and they are described herein only where they occurred within sedimentary rocks typical of the sandy facies, as identified in the field.

Sedimentology and palaeontology

The shallow marine sandstones and siltstones of the Stairway Sandstone were deposited during the maximum marine inundation of the peri-Gondwanan epeiric Larapintine Sea, within a semi-arid to arid climate at a latitude of around 15°N (Wells *et al.* 1970, Cook 1972, Nicoll *et al.* 1988, Walley *et al.* 1991). The sandy facies of the succession consists of predominantly white and grey, tabular quartz-rich sandstone and poorly exposed siltstone or mudstone beds (Fig. 3). Sedimentary structures are limited to trough and planar cross-bedding, parallel lamination and sporadic wavy lamination, together with rare desiccation and synaeresis cracks that suggest very shallow water conditions. Soft-sediment deformation features, in the form of contorted laminations and loading structures, are locally common at the base of beds and are likely related to rapid sedimentation (Cook 1972) because the structures do not appear to be restricted to specific stratigraphic horizons, as would be expected if they had a seismogenic origin (Davies *et al.* 2005). As such, the sedimentary facies of the Stairway Sandstone are typical of those found in other lower Palaeozoic shallow epeiric marine successions, typified by tabular sandstone beds formed by inundations of terrigenous sediment from sand-rich coastal areas (Lindsey & Gaylord 1992, Johnson & Baldwin 1996, Davies *et al.* 2007, Davies & Sansom 2009, Long & Yip 2009). The Stairway Sandstone is of particular significance due to the occurrence of the arandaspid pteraspidomorph *Arandaspis prionotolepis*. The first specimens were collected in 1959 from Mount Charlotte, with more material coming from Mount Watt in the 1960s (Fig. 2), including the type specimen described by Ritchie & Gilbert-Tomlinson (1977), who also recorded a second taxon, *Porophoraspis*

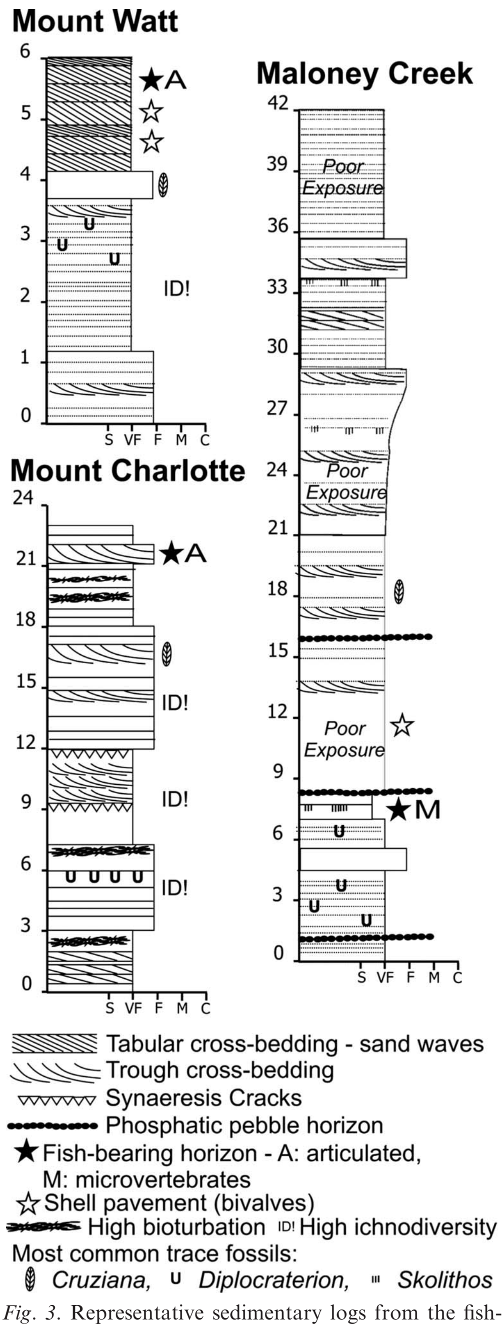


Fig. 3. Representative sedimentary logs from the fish-bearing horizons in the upper Stairway Sandstone at Mount Watt, Mount Charlotte and Maloney Creek. Note that the exact location of the articulated vertebrate specimens from Mount Charlotte is unclear.

crenulata, from Mount Watt. Further collections by Ritchie at Mount Watt have yielded an additional two, as yet undescribed, taxa from the Stairway Sandstone that are also interpreted to be part of the arandaspid clade (Ritchie 1990). Wider studies of the Larapinta Group have yielded microvertebrate remains from the Horn Valley Siltstone, Stokes Siltstone and Carmichael Sandstone (Young 1997), while recent work by the current authors has yielded a diverse microvertebrate assemblage from fine-grained strata within the upper part of the Stairway Sandstone from near Maloney Creek.

A diverse invertebrate body fossil fauna has been described from the full extent of the Stairway Sandstone and, taken as a whole, this is a shallow marine assemblage typical of the Ordovician (Webby *et al.* 2000), including trilobites, brachiopods, rostroconch and pelecypod molluscs, gastropods, cephalopods and monoplacophora (see extensive faunal lists presented by Pojeta & Gilbert-Tomlinson 1977, Shergold 1986). Other fossils present include acritarchs, sponges and conodonts (Ritchie & Gilbert-Tomlinson 1977, Shergold 1986, Nicoll 1991) in addition to the arandaspid fish mentioned above.

It is important to note that, although the whole of the Stairway Sandstone yields a diverse fauna, the beds that have yielded the macroscopic remains of *Arandaspis* (i.e. the sandstones at the top of the Mount Watt section—the type specimen horizon from Mount Charlotte has not been identified within that exposure) that are most likely representative of the habitat of this organism, have a restricted invertebrate fauna. This fauna is dominated by the nuculoid bivalve *Alococoncha crassatelliformis* (Tate 1896), shell accumulations of which commonly drape the foresets of the quartzite beds of the Stairway Sandstone at Mount Watt (Fig. 4), and sparse unidentified orthoconic nautiloids.

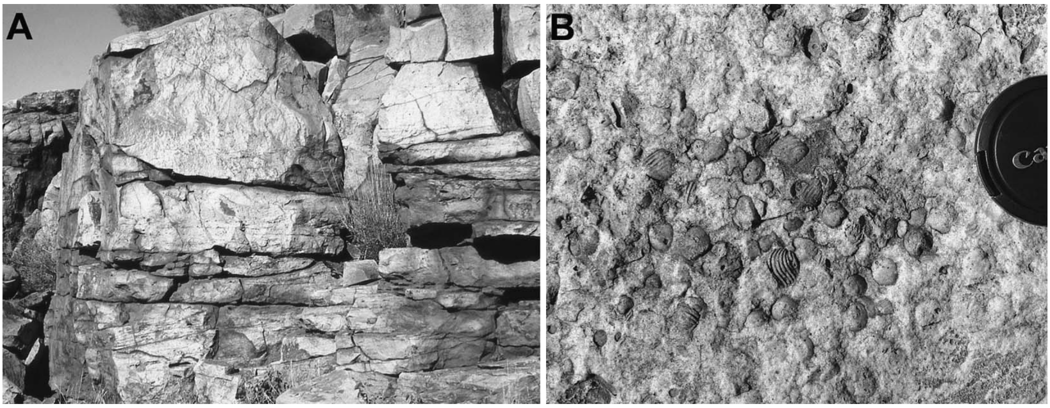


Fig. 4. **A**, Photograph showing the tabular, cross-bedded quartzitic sandstones that comprise the fish-bearing horizon at Mount Watt; **B**, Shell pavement of the bivalved mollusc *Alococoncha crassatellaeformis* (Tate 1896) from the fish-bearing horizon at Mount Watt.

Ichnofauna of the Stairway Sandstone

The sandstone-dominated facies of the Stairway Sandstone provide a relatively rare record of an Ordovician epeiric shallow marine trace fossil assemblage. Some of the arthropod traces of the sandy facies of the Stairway Sandstone have recently been described in detail by Gibb *et al.* (2009), who described five ichnospecies of *Cruziana*, one of *Diplichnites*, three of *Monomorphichnus* and one of *Rusophycus* (Table 1). Readers are referred to Gibb *et al.* (2009) for detailed descriptions and figures of these traces; 13 other ichnotaxa are identified and described in this study.

In total, 22 ichnospecies from 16 ichnogenera have been recorded, and these represent a mixture of different trophic styles, including the traces of deposit-, suspension- and filter-feeding benthic organisms, together with those of both mobile and passive carnivores (Table 1, Fig. 5). Descriptions of the additional trace fossils identified in this study are presented below.

Arenicolites carbonarius

Specimens of *Arenicolites carbonarius* (Fig. 5A) are relatively abundant within the Stairway Sandstone, although they are less common than the other vertical burrows (*Diplocraterion*, *Monocraterion*, *Skolithos*). The traces are commonly preserved in full relief, but may also be identified in plan view as fills of paired burrow apertures. *Arenicolites carbonarius* is represented in the Stairway Sandstone as a simple, sand-filled, U-shaped burrow with no evidence of spreiten between the two vertical limbs of the burrow. The diagnosis to ichnospecific level is determined by the presence of slightly funnel-shaped burrow apertures, wider (3–5 mm diameter) than the vertical shafts (1–3 mm diameter) of the burrow. *Arenicolites carbonarius* is interpreted to record suspension- or filter-feeding activity of an annelid worm or small crustacean (Pemberton *et al.* 2001).

Arthrophycus alleghaniensis

Specimens of *Arthrophycus alleghaniensis* (Fig. 5J) have been recovered from the Stairway Sandstone as discrete individual traces. The traces are preserved as sole casts in convex hyporelief on the base of fine-grained sandstone beds, and consist of fanned bundles of up to six arthrophycid burrows (up to 90 mm long, each up to

Ichnotaxon	Interpretation	Abundance	Selected references
Arenicolites carbonarius	Suspension- or filter-feeding activity of an annelid worm or small crustacean	Common	Pemberton *et al.* (2001)
Arthrophycus alleghaniensis	Burrows of arthrophycid worms or small arthropods	Common	Rindsberg & Martin (2003), Seilacher (2007)
Asterosoma isp.	Deposit-feeding structure of vermiform organism	Very common	Pemberton *et al.* (2001), Seilacher (2007)
Cruziana barriosi	Arthropod scratched furrow	Rare	Gibb *et al.* (2009)
C. furcifera	Arthropod scratched furrow	Very common	Gibb *et al.* (2009)
C. goldfussi	Arthropod scratched furrow	Rare	Gibb *et al.* (2009)
C. omanica	Arthropod scratched furrow	Very common	Gibb *et al.* (2009)
C. penicillata	Arthropod scratched furrow	Very common	Gibb *et al.* (2009)
Didymaulichnus lyelli	Locomotion of a bilaterally symmetrical infaunal tracemaker	Rare	Fillion & Pickerill (1990)
Diplichnites arboreus	Arthropod scratch marks	Common	Gibb *et al.* (2009)
Diplocraterion yoyo	Burrow of suspension-feeding organism in aggrading sediment	Very common	Goldring (1962), Bromley (1996)
?*Gordia* isp.	Looping trails of arthropod or vermiform organism	Common	Fillion & Pickerill (1990)
Lockeia isp.	Protractional action of the foot of a pelecypod bivalve	Rare	Seilacher & Seilacher (1994)
Monocraterion isp.	Passively filled vertical burrows of suspension-feeding organisms	Very common	Jensen (1997), Buck & Goldring (2003)
Monomorphichnus lineatus	Arthropod scratch marks	Common	Gibb *et al.* (2009)
M. multilineatus	Arthropod scratch marks	Common	Gibb *et al.* (2009)
M. sinus	Arthropod scratch marks	Common	Gibb *et al.* (2009)
Phycodes circinatum	Retrusive spreite of backfill lamellae from arthrophycid tracemaker	Very rare	Seilacher (2007)

(*continued*)

Table 1. (*Continued*)

Ichnotaxon	Interpretation	Abundance	Selected references
Planolites isp.	Sediment processing by (polychaete?) deposit-feeder	Common	Pemberton *et al.* (2001)
Rusophycus unilobus	Arthropod resting trace	Rare	Gibb *et al.* (2009)
Skolithos linearis	Suspension- or filter-feeding vermiform burrow	Common	Vossler & Pemberton (1988)
Uchirites isp.	Bivalve locomotion	Very rare	Mángano *et al.* (1998), Seilacher (2007)

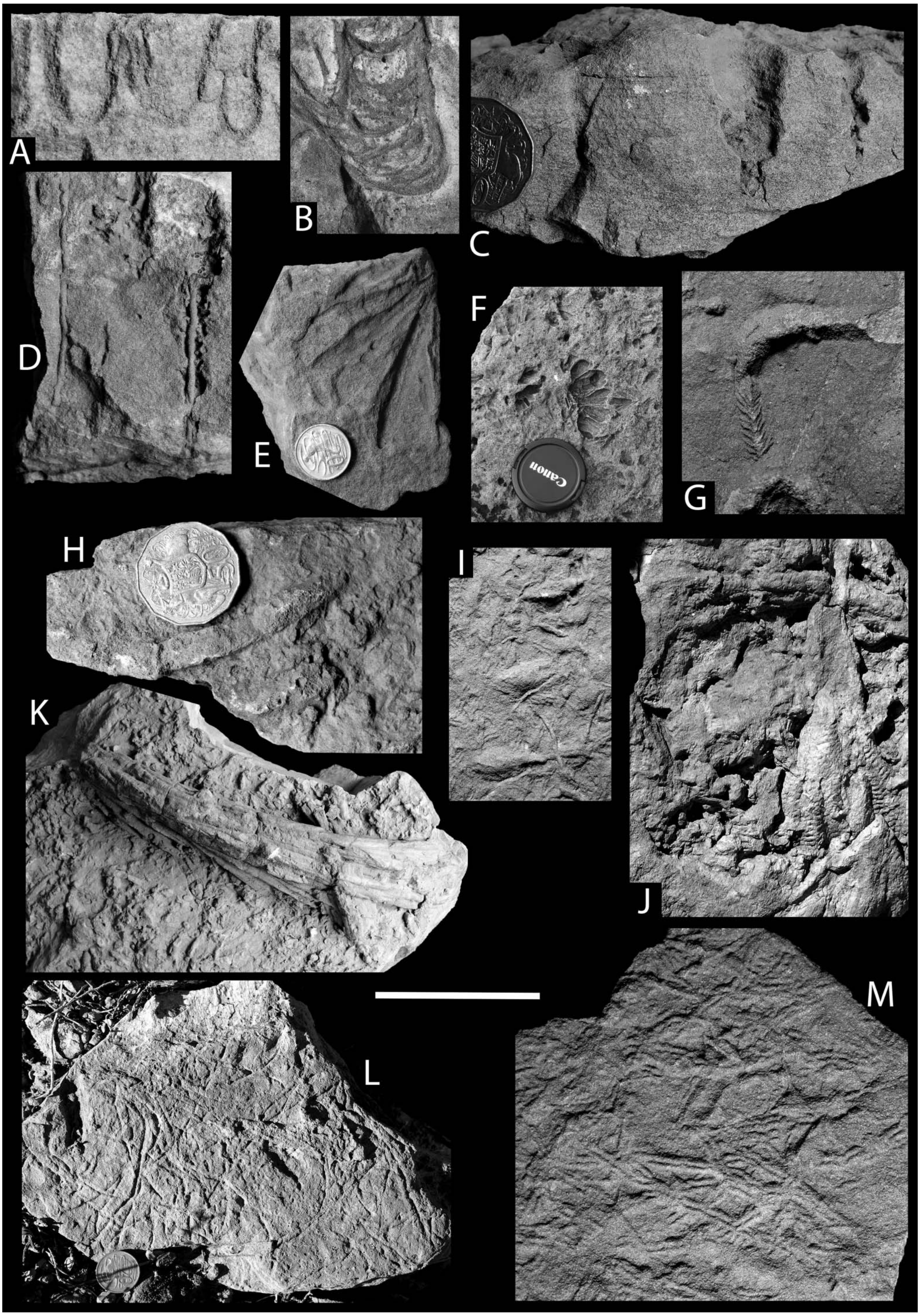
Table 1. Full list of ichnotaxa, potential tracemaker activities and their abundance in the sandy facies of the Stairway Sandstone.

12 mm wide) that are typified by their longitudinal arrangement of pronounced transverse ridges. Potential tracemakers include worms or small arthropods (Rindsberg & Martin 2003, Seilacher 2007).

Asterosoma isp.
Asterosoma burrows (Fig. 5E, F) are extremely common within the Stairway Sandstone and individual lobes of the traces range in length from 10 to 65 mm. The traces at the larger end of this spectrum tend to be found discretely (Fig. 5E), but the smaller traces commonly cover the surface of extensively exposed bedding planes (Fig. 5D) and occur as an elite trace fossil (*sensu* Bromley 1996). The traces consist of between three and seven bulbous fusiform arms, radially or semi-radially arranged, which taper inwards to a common centre. The arms are preserved as concave epirelief, usually with no burrow fill remaining, and the number of arms tends to be greater on the smaller, more abundant traces (3–7) than the larger discrete traces (<4). Along the centre of the arms, or in cross-sectional form towards the centre of the trace fossil, the traces of small (<2 mm) cylindrical burrows containing different sediment fill than the host rock are evident in some cases. *Asterosoma* within the Stairway Sandstone are locally known as 'dingo paws' in light of the fact that they rarely have the sediment fill of their bulbous arms preserved and the tendency to preserve only asymmetric arrangements of the arms. *Asterosoma* is interpreted to have been formed by a deposit-feeding vermiform organism (Pemberton *et al.* 2001, Seilacher 2007).

Didymaulichnus lyelli
Slabs covered in *Didymaulichnus lyelli* (Fig. 5M) exhibit preservation as convex hyporelief on the base of very fine and fine-grained sandstone beds, and consist of simple unornamented bilobate traces with a shallow median furrow (2–4 mm wide, up to 60 mm long, <2 mm relief). *Didymaulichnus lyelli* is locally very abundant, and the traces commonly cross one another. The traces are repichnia, recording the activity of an infaunal bilaterally symmetrical tracemaker, although the exact type of organism responsible is unclear since several potential producers exist (Fillion & Pickerill 1990).

Diplocraterion yoyo
Diplocraterion yoyo (Fig. 5B) is extremely abundant in the Stairway Sandstone,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representing the most common vertical burrow in the succession. The traces are identifiable in full relief, and consist of U-shaped burrows (up to 70 mm wide, 50–70 mm deep; individual shafts are 3–6 mm wide) with prominent spreite. The traces can be diagnosed to ichnospecific level due to the presence of both protrusive (above the horizontal component of the U-shaped shaft) and retrusive (below the horizontal component) spreiten between the two vertical components of the burrow. As such, the traces are equilibrichnia structures, whereby the endobenthic tracemaker organism constantly shifted the vertical position of its burrow to compensate the aggradation or degradation of the seafloor (Goldring 1962, Bromley 1996). Some of the burrows exhibit apparent overprinting of burrows, with the overprinted structure having a wider separation between burrow apertures, wider shafts (5–6 mm), and sharing only one limb of the earlier structure. This possibly indicates different growth stages of the tracemaker organism (Bromley 1996). The trace was made by a suspension-feeding organism such as a polychaete, echiuroid or crustacean (Pemberton *et al.* 2001).

Gordia isp.

Irregularly looping or winding, thin (<4 mm) trails and burrows that irregularly cross one another are common and are tentatively assigned to the ichnogenus *Gordia* (Fig. 5L). The traces are usually preserved in concave epirelief, but isolated examples in convex hyporelief are also known, and individual specimens may reach a preserved length of up to 160 mm. The potential tracemaker is unclear as *Gordia* is a facies-crossing trace fossil, but it may have been an arthropod or vermiform organism (Fillion & Pickerill 1990).

Lockeia isp.

Isolated specimens of *Lockeia* (Fig. 5I) are known from the underside of fine-grained sandstone slabs in the Stairway Sandstone. *Lockeia* comprises an almond-shaped undertrace, averaging 25 mm in length and 12 mm width, preserved in convex hyporelief. The traces are interpreted to represent the protractional action of the foot of a pelecypod bivalve (Seilacher & Seilacher 1994).

Monocraterion isp.

Several specimens of *Monocraterion* (Fig. 5C) are known from discrete horizons within the Stairway Sandstone. The traces are cylindrical or sub-cylindrical vertical or inclined burrows that are diagnosed by the presence of a funnel-shaped aperture at the top of the burrow. The funnel tops may reach up to 40 mm in diameter and burrows can been traced up to 80 mm in length. The funnel-shaped tops of the burrows are interpreted to represent sediment collapse at the

Fig. 5. Trace fossils of the upper Stairway Sandstone. **A**, *Arenicolites carbonarius*, specimen number 39514, stored at Geoscience Australia (GA), Canberra; **B**, *Diplocraterion yoyo*, specimen number 39528 (GA); **C**, *Monocraterion* isp., specimen number 39519 (GA); **D**, *Skolithos linearis*, specimen number 39526 (GA); **E**, *Asterosoma* isp., large discrete trace, specimen number 39515 (GA); **F**, *Asterosoma* isp., small traces covering bedding plane, uncollected specimens, Dry Creek; **G**, *Uchirites*, specimen number 39527 (GA); **H**, *Planolites* isp., specimen number 39523 (GA); **I**, *Lockeia* isp., specimen number 39518 (GA); **J**, *Arthrophycus alleghaniensis*, uncollected specimen, Mount Watt; **K**, *Phycodes* isp., specimen number 39522 (GA); **L**, ?*Gordia* isp., uncollected specimen, Mount Charlotte; **M**, *Didymaulichnus lyelli*, specimen number 39517 (GA). Scale bar = 50 mm in A, 70 mm in B, 40 mm in D, G, M, 60 mm in I, 75 mm in J and 85 mm in M, 50 cent coin in C and H is 31.5 mm in diameter, 20 cent coin in E and L is 28.5 mm in diameter, and the lens cap in F is 52 mm in diameter.

burrow aperture (e.g. Buck & Goldring 2003), and the traces are interpreted as the passively filled vertical burrows of suspension-feeding organisms (Jensen 1997).

Phycodes isp.
A very large example of *Phycodes* (Fig. 5K) with a preserved length of 200 mm, a maximum width of 50 mm, and a relief of 40 mm is preserved in convex hyporelief from the base of a very fine grained sandstone bed in the Stairway Sandstone. The trace consists of a bundle of smoothly curved apparent burrows (each *ca* 4 mm wide), with a gentle U-shaped form, and which is narrower (38 mm) at one end. The apparent burrows are actually the retrusive spreite of backfill lamellae, and the tracemaker is thus interpreted as similar to that which produced *Arthrophycus alleghaniensis* (Seilacher 2007).

Planolites isp.
Several samples of the ichnogenus *Planolites* (Fig. 5H) have been recovered from the Stairway Sandstone. The traces are preserved in convex hyporelief as straight, unlined, unbranched burrows (up to 10 mm wide, 60 mm length) with a structureless infill that is compositionally different from the sedimentary matrix of the host rock. Unlike many of the other horizontal burrows in the Stairway Sandstone, they generally occur as discrete, isolated examples, and record sediment processing by deposit-feeding infauna, such as polychaetes (Pemberton *et al.* 2001).

Skolithos linearis
Vertical burrows of the ichnospecies *Skolithos linearis* (Fig. 5D) are relatively common within the Stairway Sandstone, but less so than *Diplocraterion* or *Monocraterion*. The traces consist of a single cylindrical or sub-cylindrical vertical or inclined shaft between 4 and 8 mm in diameter and at least 20 mm in length. *Skolithos* is interpreted as having a suspension- or filter-feeding vermiform tracemaker (e.g. Vossler & Pemberton 1988).

Uchirites isp.
Several specimens of *Uchirites* (Fig. 5G) recovered from the Stairway Sandstone consist of sharply curved ridges (in convex hyporelief) with a transverse V-shaped ornamentation crossing each flank of the ridge. They resemble deeply impressed *Protovirgularia*. The traces are typically *ca* 4 mm wide, 60 mm long and 6 mm in relief. Mángano *et al.* (1998) and Seilacher (2007) inferred a potential bivalve tracemaker for *Uchirites*.

Ichnofacies and palaeoenvironment

The ichnodiversity of the Stairway Sandstone indicates that its environment of deposition was able to support an ecosystem incorporating a wide variety of ethological strategies. The traces of both suspension- or filter-feeding activity (*Arenicolites, Diplocraterion, Monocraterion, Skolithos*) and deposit-feeding activity (*Arthrophycus, Asterosoma, Didymaulichnus, Gordia, Phycodes, Planolites, Uchirites*) are present, as are the repichnia and cubichnia of arthropod (*Cruziana, Diplichnites, Monomorphichnus, Rusophycus*) and bivalve (*Lockeia*) tracemakers (Table 1). The sandy facies of the Stairway Sandstone thus contains roughly equal proportions of trace fossils belonging to two shallow marine ichnofacies—archetypal *Skolithos* and *Cruziana* ichnofacies—in many cases within the same bed. Such mixed *Skolithos*-*Cruziana* ichnofacies typically occur in areas where there are fluctuating depositional conditions, such that nutrients are held both in suspension and deposited on the substrate. Such environments include tidal or brackish water environments (Benyon & Pemberton 1992, Pemberton & Wightman 1992, Stanley & Feldmann 1998, Buatois *et al.* 2005), environments where there is a periodic change in depositional regime resulting from an influx of terrigenous sediment and freshwater (Davies *et al.* 2007), or sub-wave base regions where there are localized reduced energy conditions (Howard & Frey 1973, Mángano *et al.* 1996, Olóriz & Rodríguez-Tovar 2000).

In the case of the Stairway Sandstone, terrigenous sediment would have been supplied to the shallow marine realm by minimally vegetated fluvial systems that were prone to flashy discharge and rapid sediment supply during seasonal extreme precipitation events (e.g. Hiscott *et al.* 1984, Lindsey & Gaylord 1992, MacNaughton *et al.* 1997, Davies *et al.* 2007, 2011, Davies & Gibling 2010). Comparable lower Palaeozoic environments have been reported to contain a mixed *Skolithos*-*Cruziana* ichnofacies (Buatois & Mángano 2003, Baldwin *et al.* 2004, Buatois *et al.* 2005) as the fluctuating depositional conditions associated with them enabled nutrients to be both deposited and held in suspension.

Similar Ordovician environments are also known to be typified by the presence of numerous shell pavements (Aceñolaza *et al.* 2003), which develop as nearshore benthic communities are killed and buried by the influx of particulate sediment (and, potentially, freshwater) during periods of flooding. Such a scenario may explain the development of the *Alococoncha* shell pavements recorded at the Mount Watt section of the Stairway Sandstone, in which the *Arandaspis* fossils are present.

Age of the trace fossils

Previous biostratigraphic dating of the Stairway Sandstone, which relied on endemic pelecypod and rostroconch molluscs, the pteraspidomorph fish, and a small sample of poorly preserved conodonts, yielded slightly discrepant potential ages ranging from the Floian (Arenig) to ?Dapingian (Llanvirn) depending upon correlation with the revised Ordovician chronostratigraphic scheme; these alternative views are understandable given the previous absence of biostratigraphically diagnostic taxa (Pojeta & Gilbert-Tomlinson 1977, Pojeta *et al.* 1977, Ritchie & Gilbert-Tomlinson 1977, Webby 1981, Shergold 1986, Nicoll 1991, Young 1997). However, the recovery of new conodont samples, in the form of *Lenodus* sp. cf. *L. variabilis* from shale samples in the middle part of the Stairway Sandstone (SS06-10H) at Maloney Creek (Fig. 3), suggest an early Darriwilian age for that part of the unit as true *Lenodus variabilis* and *L. antivariabilis* have very restricted ranges from the upper part of the *Baltoniodus norrlandicus* Zone and into the *Lenodus variabilis* and *Yangtzeplacognathus crassus* zones (Löfgren & Zhang 2003).

This new biostratigraphic age helps shed light on the merits of certain Stairway Sandstone trace fossils as stratigraphic markers. Some of the ichnospecies recorded from the Stairway Sandstone (*Arthrophycus alleghaniensis*, *Cruziana furcifera*, *C. omanica*, *Rusophycus unilobus*) have previously been argued to have narrow stratigraphic significance, but the ages that these are supposed to denote are not concordant (Shimer & Shrock 1944, Seilacher 1970, 1992, 2000, 2007). Gibb *et al.* (2009) have already suggested that the Stairway Sandstone samples of *Cruziana omanica* and *Rusophycus unilobus* indicate clear limitations to the stratigraphic potential of those trace fossils, but the merits of *Arthrophycus alleghaniensis* and *Cruziana furcifera* require further appraisal.

Seilacher (1970, 1992, 2007) ascribed the *Cruziana rugosa* group (of which he designated *C. furcifera* a member) a 'Lower Ordovician' stratigraphic range. Seilacher's (1970, 1992, 2007) subdivision of the Ordovician did not include a Middle Ordovician interval and instead extended from the base of the system to the top of the 'Arenig'. Using the new global Ordovician series (see Cocks *et al*. 2010), the *C. rugosa* group thus has a stratigraphic range extending from the Tremadocian to the lower Darriwilian. The Stairway Sandstone samples of *C. furcifera* thus occur at the very top end of this range [though it should be noted that some Gondwanan successions may contain *C. rugosa* group traces into the Upper Ordovician (Egenhoff *et al*. 2007)].

Arthrophycus alleghaniensis has also been suggested to have potential stratigraphic significance (Shimer & Shrock 1944, Seilacher 2000, 2007). *Arthrophycus alleghaniensis* has been recorded in the Stairway Sandstone at both Mount Charlotte and Mount Watt, the two localities from which the articulated pteraspidomorph fossils are known, and occurs in strata both above and below those containing *Cruziana furcifera*. However, previous studies have suggested that *A. alleghaniensis* is a marker trace fossil for the early Silurian (e.g. Shimer & Shrock 1944, Seilacher 2000, 2007): an age, which for the Stairway Sandstone examples, can not be supported by either biostratigraphy or the co-occurrence with *Cruziana rugosa* group traces. Indeed, other Lower and Middle Ordovician Gondwanan successions are known to contain *A. alleghaniensis* (e.g. Selley 1970, Del Valle 1987, Romano 1991, Kumpulainen *et al*. 2006) and, together with this study, these support the assertion of Rindsberg & Martin (2003) that, in Gondwana, *A. alleghaniensis* can not reliably be used as a Lower Silurian marker and that its stratigraphic range extends back into the Ordovician.

Comparison with other pteraspidomorph-bearing localities

The Stairway Sandstone is one of several similar clastic shallow marine ichnofossil-dominated Ordovician successions from both Gondwana and Laurentia that host pteraspidomorph fossils (Davies & Sansom 2009). These include the Anzaldo Formation (?Sandbian) of Bolivia (Gagnier *et al*. 1986, 1996, Davies *et al*. 2007), the Amdeh Formation (Dapingian/Darriwilian) of Oman (Sansom *et al*. 2009), the Sepulturas Formation (Darriwilian) of Argentina (Albanesi & Astini 2002, Sansom *et al*. 2005), the Harding Sandstone (Sandbian) of Colorado, USA (Walcott 1892, Denison 1967, Lehtola 1983, Elliott 1987, Sansom *et al*. 1997) and the South Piney Member of the Winnipeg Formation (Sandbian) of Wyoming, USA (Darton 1906, Sansom & Smith 2005). Of these, the Stairway Sandstone is best compared with the Anzaldo Formation and Harding Sandstone, these being the only formations from which articulated pteraspidomorph fossils have been recovered; the other successions contain fragmentary and microremains that have the potential for transportation away from their original habitat (e.g. Irmis & Elliott 2006).

The Anzaldo Formation in particular shares several common characteristics with the Stairway Sandstone (Davies *et al*. 2007). The articulated pteraspidomorph fossils are found in close association with shell beds (although they are composed of lingulids, rather than bivalved molluscs), within rapidly accumulated obrution deposits that developed in the nearshore realm during storms and flooding. However, although the Anzaldo Formation does contain a mixed *Skolithos*-*Cruziana* ichnofacies, the articulated fish fossils occur within horizons containing a very reduced *Skolithos* ichnofacies, bounded to the top and bottom by strata from a more typical *Skolithos* ichnofacies. In contrast, within the Stairway Sandstone, the articulated fish occur within a 2 metre-thick sandstone unit that contains only isolated specimens of *Cruziana furcifera*, yet is immediately underlain by strata containing a diverse mixed *Skolithos*-*Cruziana* ichnofacies. The restricted *Skolithos* ichnofacies in the Anzaldo Formation is a result of opportunistic suspension-feeding organisms that colonized the fresh substrate formed by the obrution deposits in which the fish were interred (Davies *et al*. 2007). No evidence for such opportunism is evident in the Stairway Sandstone, but the very low ichnodiversity in the fish horizon (compared with the more diverse assemblages elsewhere in the succession) does indicate that the host sediments may have been deposited very rapidly. As such, both the Stairway Sandstone and Anzaldo Formation contain articulated fish fossils preserved within very rapidly deposited accumulations of terrigenous sediment, as indicated by depauperate examples of the prevalent shallow marine ichnofacies.

The Stairway Sandstone also bears similarities to the Harding Sandstone of Colorado, from which articulated specimens of pteraspidomorphs have been recovered in association with lingulids and bivalved molluscs. The Harding Sandstone, although situated in Laurentia rather than Gondwana, records deposition in another very shallow marine setting, within a mixed *Skolithos*-*Cruziana* ichnofacies, prone to freshwater influxes (Spjeldnæs 1979, Allulee & Holland 2005).

The similarities between the environments of deposition of the Stairway Sandstone, Anzaldo Formation and Harding Sandstone support previous hypotheses that early pteraspidomorph fish occupied a very narrow palaeoecological niche during the Ordovician (Blieck 1985, Davies *et al*. 2007, Davies & Sansom 2009), within very shallow epeiric seas that were prone to influxes of terrigenous sediment and freshwater. The identification of sedimentological, ichnological and palaeontological signatures of these environments, such as evidence of rapid deposition, depauperate representations of a *Skolithos* or mixed *Skolithos*-*Cruziana* ichnofacies and bivalve or lingulid shell pavements, may thus be used as a prospecting tool to search for further Ordovician vertebrate-bearing localities.

Conclusions

(1) The sandy facies of the Stairway Sandstone record sedimentation within the nearshore and shallowest part of an Ordovician epeiric sea, where terrigenous sediment supply was highly variable. Fluctuations in sediment and nutrient supply conditions supported the preservation of the mixed *Skolithos*-*Cruziana* ichnofacies that typifies the succession.

(2) The sandy facies of the Stairway Sandstone bear a diverse ichnofauna consisting of 22 ichnospecies, which represent a range of trophic strategies. Some of these ichnospecies have previously been suggested to have stratigraphic relevance. Conodonts recovered from the Stairway Sandstone date the formation as early Darriwilian providing further evidence that *Arthrophycus alleghaniensis* is not diagnostic of an early Silurian age in Gondwanan successions.

(3) The Stairway Sandstone is one of only three known Ordovician sequences that yields articulated pteraspidomorph fossils, and bears distinct ichnological, sedimentological and palaeontological similarities to the other two localities from which articulated fish have been recovered (Anzaldo Formation and Harding Sandstone). These similarities reflect a common habitat, supporting previous hypotheses of a narrow, very shallow marine palaeoecological range for Ordovician pteraspidomorphs.

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