Arthropod ichnofossils from the Ordovician Stairway Sandstone of central Australia

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Strata from the Darriwilian stage of the Middle Ordovician in central Australia yield a number of ichnofossils that are usually considered to have been produced by arthropods, mainly those of *Cruziana*, *Diplichnites*, *Monomorphichnus* and *Rusophycus*. Three new ichnospecies are identified, described and illustrated, along with eight previously described and one indeterminate ichnospecies. The three new ichnospecies are: *Cruziana penicillata*, *Diplichnites arboreus* and *Monomorphichnus sinus*. The arthropod traces occur with other biogenic sedimentary structures in a fine to medium grained sandstone with minor mudstone interbeds of the Stairway Sandstone. The substrate composition and ichnological evidence places the trace-rich unit (upper part of the Stairway Sandstone) in the *Cruziana* ichnofacies.

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ICHNOFOSSILS typically ascribed to trilobites, such as *Cruziana* and *Rusophycus*, among others, are described from the upper unit of the Stairway Sandstone (Wells *et al*. 1970, Ritchie & Gilbert-Tomlinson 1977), Amadeus Basin of central Australia. This unit yields abundant biogenic sedimentary structures with rare fragmented and/or disarticulated trilobite sclerites and some bivalves and fishes (Ritchie & Gilbert-Tomlinson 1977). Though other traces do occur within this unit, only the Palaeozoic arthropod traces are addressed herein, due to this paper being part of a larger project on arthropod traces.

The age of the upper Stairway Sandstone was initially considered to be of 'Upper Llanvirnian to Llandeilian' age by Gilbert-Tomlinson (in Cook 1970, p. 71), that is, equivalent to the upper Middle Ordovician or in the upper portion of the Darriwilian Stage based on the revised global stratigraphic framework (Webby *et al*. 2004). However, Ritchie & Gilbert-Tomlinson (1977, p. 356) subsequently suggested a slightly older 'uppermost Arenigian-lower Llanvirnian' age for the Stairway Sandstone, that is, earlier in the Middle Ordovician (lower-middle Darriwilian). Shergold (1986, p. 11, fig. 1) later recognised that the age within the Stairway Sandstone depended on what part of the tripartite subdivision had been sampled for fossils, and was able to show that the upper part belonged wholly within the 'Llanvirnian', that is equivalent to the middle part of the Darriwilian Stage (Webby *et al*. 2004). But even that age may now need to be revised slightly upwards, for Zhang & Barnes (2003) recognised conodont zones from the apparently conformably overlying Stokes Siltstone, and the lower zone in the sequence is likely to have an early Late Ordovician (early Caradocian) age. That is more or less equivalent to the upper portion of the recently approved Sandbian Stage (Bergström *et al*. 2006).

Ichnofossil 'biological' names should be "based solely upon the morphological characteristics of the structure" (Kelly 1990, p. 424). The "ichnotaxa should be treated as non-biological form names only and their association with named organisms should be a matter of careful discussion, especially when there is no body fossil present. Even if there is a body fossil present, it may not be that of the original constructor" (Kelly 1990, p. 425). This methodology is followed in this paper, for as numerous authors have commented, a behaviour can be identical even when the organisms are different (Bromley & Fürsich 1980, Ekdale *et al*. 1984, Kelly 1990). The categories of behaviour identified from

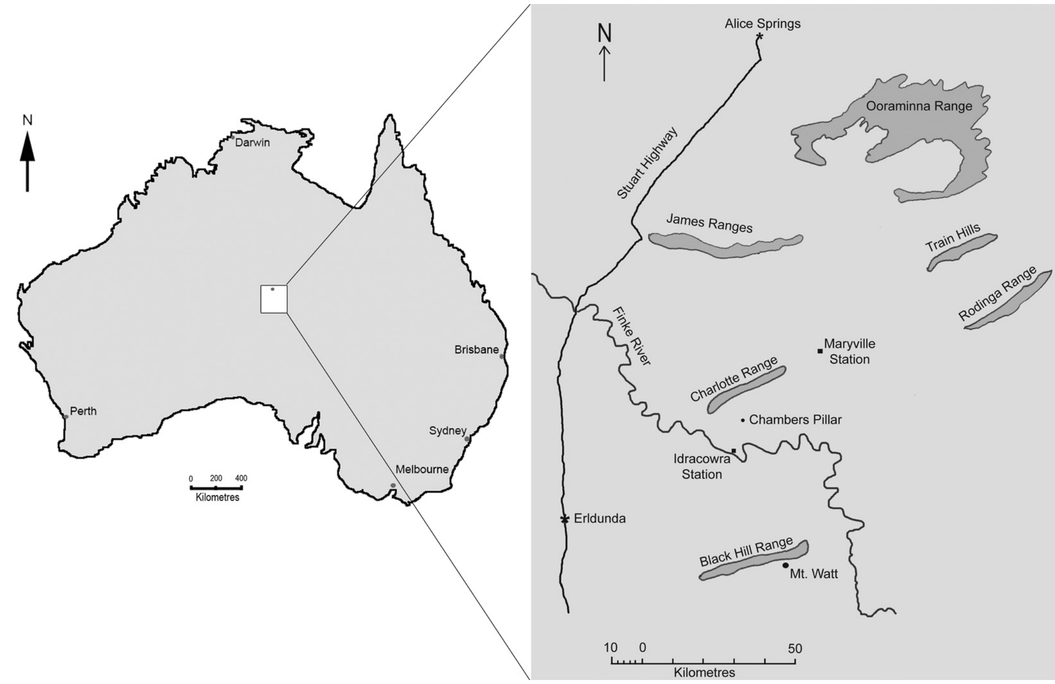


Fig. 1. **A**, generalised map of mainland Australia modified from Google Maps. **B**, locality map indicating positions of Charlotte Range and Mount Watt.

the Stairway Sandstone are digging, scratching and walking, that is repichnia, or crawling and fodichnia or feeding, and/or possibly cubichnia or resting traces within or upon the substrate. Traces in the upper Stairway Sandstone are almost exclusively preserved in exogenic convex hyporelief (Seilacher 1964, Osgood 1970).

GEOLOGICAL BACKGROUND

Geological focus is on sedimentary rocks of approximately 9144 metres (stratigraphic thickness), preserved in an area of 155000 square kilometres within an 800 kilometre long region referred to as the Amadeus Basin (Fig. 1). The basin is situated within central Australia (Wells 1970, p. 1; Cook 1970, p. 71; Shergold 1986, p. 10). The Stairway Sandstone, is the defined focus of the present study, within the Amadeus Basin and is part of the Larapinta Group (Chewings 1935, Prichard & Quinlan 1962, Wells *et al*. 1965, Wells *et al*. 1970) that was originally termed by Chewings (1935) in a table as the 'Stairway Quartzite'. Later, Prichard & Quinlan (1962, p. 21) referred to this lithological unit as the 'Stairway Greywacke'. Finally, Wells *et al*. (1965, p. 26) amended the formation name to the 'Stairway Sandstone'.

The regions of the Amadeus Basin that we focus upon are the Charlotte Range and Mount Watt (Fig. 1). We collected from eight localities on the Charlotte Range and one locality at Mount Watt (Table 1, coordinates with associated illustrated and unillustrated ichnofossils). We also examined and photographed a number of specimens housed in the Australian Museum collections that were collected on an earlier field excursion (in 1987) to the Charlotte Range and Mount Watt by Alex Ritchie, Robert Jones and Brian Chatterton.

As the formation name implies, the clasts of the trace-bearing beds are sand. The sand grains are medium-sized, subrounded to rounded. The sandstones are an orange-buff colour on fresh surfaces and a darker orange-brown on weathered surfaces at the Charlotte Range. Thinner, interbedded mudstones are recessive and not usually visible in surface exposures. The Mount Watt specimens are similar in colour on weathered surfaces, but a slightly lighter buff colour on fresh surfaces, and the sands are of a finer grain size. The variation in colouration and grain size is minor between the Charlotte Range and Mount Watt.

Ritchie & Gilbert-Tomlinson (1977, p. 354) reported that at the Charlotte Range, the Stairway Sandstone disconformably overlies the Jay Creek Limestone of Middle Cambrian age. While the Stairway Sandstone at Mount Watt disconformably caps the Winnall Beds of the late Proterozoic (Ritchie & Gilbert-Tomlinson 1977, p. 354).

Based purely on the lithologies and the ichnotaxa

LOCALITY	GPS COORDINATES		ICHNOTAXON/TAXA
Charlotte Range = CRR	24° 47' 27.2" S	133° 48' 57.6" E	*Cruziana furcifera, C. golfussi, C. penicillata*
Charlotte Range = CR1	24° 44' 04.7" S	133° 56' 43.7" E	*Cruziana barriosi, C.* indet., highly bioturbated specimen
Charlotte Range = CR1F	24° 43' 51.1" S	133° 56' 31.4" E	*Cruziana omanica*
Charlotte Range = CR2	24° 43' 25.1" S	133° 59' 47.4" E	*Cruziana barriosi, C. furcifera, C. penicillata, C.* indet., *Rusophycus ?unilobus*
Charlotte Range = CR3	24° 44' 27.5" S	133° 55' 37.0" E	*Cruziana furcifera, C. omanica*
Charlotte Range = CR4	24° 47' 27.9" S	133° 49' 05.1" E	*Cruziana omanica, Monomorphichnus lineatus,* highly bioturbated *Monomorpichnus* spp., *Rusophycus unilobus*
Charlotte Range = CR5	24° 47' 35.5" S	133° 49' 07.6" E	*Cruziana furcifera, C. omanica, C.* indet.
Charlotte Range = CR6	24° 47' 34.0" S	133° 49' 07.4" E	*Cruziana furcifera, C. omanica, Diplichnites arboreus, Monomorpichnus lineatus,* highly bioturbated *Monomorpichnus* spp.
Charlotte Range = CR7	24° 47' 20.1" S	133° 49' 28.6" E	*Cruziana barriosi, C. furcifera, C. goldfussi, C. omanica, C. indet., Monomorphichnus lineatus, M. multilineatus, M. sinus, M.* spp.
Mount Watt = MW	25° 19' 42.6" S	133° 53' 39.8" E	*Cruziana furcifera, C. penicillata, C.* indet., *Diplichnites arboreus, Monomorphichnus lineatus*
R.d. C1 = A. Ritchie Collection	24° 50' 52" S	133° 41' 29" E	*Diplichnites arboreus*

Table 1. GPS coordinates for the localities collected, with an ichnospecies list of traces collected from these localities, including some traces not mentioned within the paper.

found at these localities, the palaeoenvironment was reconstructed. The strata are interbedded sandstone and mudstone. A marine setting that fits this lithological signature is one that is distal lower shoreface and/or proximal upper offshore, or 'transition' between the lower shoreface and upper offshore (Pemberton *et al*. 2001, fig. 69, p. 89, p. 95) within the region of the fairweather wave base (Walker & Plint 1992, fig. 1, p. 219). Therefore, this would suggest a water depth of approximately 15 metres (Walker & Plint 1992, fig. 1, p. 219), in an epeiric sea (Cook 1970, p. 78). To substantiate this palaeoenvironmental setting, the ichnotaxa dominance and diversity confirms that the setting is that of an archetypal *Cruziana* ichnofacies with dominant deposit feeders and subordinate grazers and foragers (Pemberton *et al*. 2001, fig. 69, p. 89, p. 95, fig. 74, p. 96). The arthropod ichnotaxa collected from the Stairway Sandstone localities are approximately 72% *Cruziana*, 20% *Monomorphichnus*, 5% *Diplichnites* and 3% *Rusophycus* (see Appendix). These traces are indicative of the *Cruziana* ichnofacies.

With regard to the preservation of the traces, Seilacher (1994, p.752) noted that one must have a "sharp interface between a sand veneer and an underlying mud layer. The erosional bases of thin stormsands provided such a tabula rasa". The traces of the upper Stairway Sandstone are near flawless in their preservation of behavioural activities of organisms digging, scratching and walking upon and within a sand layer that overlies a finer muddy substrate. It was previously thought the organisms were attempting to find shelter, though Seilacher (2007, p. 34) later stated the organisms "dug primarily for feeding, not to hide". Thus, after deposition of a mantling sand sheet upon a 'muddy' substrate, the trace may indicate that an organism was attempting to gain access to the possible food/microbial nutrients within the mud. Sand was later deposited to account for the thicker quartzitic sandstone layers in the Stairway Sandstone, though the ease with which the traces were found and/or extracted implies that a recessive layer normally existed under the quartz-rich sandstone bed of all preserved traces. Therefore, the organisms were moving the sandy layer to get to the mud layer in an attempt to find food. Since they disturbed a mud layer with an overlying sand layer, the sand immediately infilled the excavations within the mud thus preserving the trace (Seilacher 1982, p. 346; Goldring 1985). Fine mudstone/shale inclusions are sometimes found clinging to the surfaces of trace-bearing sandstone beds. Also some sandstone beds contain shale rip-up clasts, attesting to the original presence of mud layers that were eroded during storm events.

Ritchie & Gilbert-Tomlinson (1977) and Ritchie (1985) described a variety of organisms from the uppermost Stairway Sandstone including: the fish *Arandaspis prionotolepis* and bivalves, along with the aforementioned *Cruziana*, which they identified as *Cruziana* cf. *furcifera* from the Mount Watt locality.

SYSTEMATIC PALAEONTOLOGY

The specimens we collected were all assigned catalogue numbers (from F133006-133027, F133861-F133958, F135853-F135856 and F58984, and are listed in Appendix 1), and they are housed in the Australian Museum, Sydney. The ichnogenera and ichnospecies are based purely upon their morphological features. The ichnospecies is based upon the definition of an ichnotaxon: "A taxon based on the fossilised work of an organism including fossilised trails, tracks or burrows (trace fossils) made by an animal" (Ride *et al*. 1999, p.118). We however prefer the simpler definition for an ichnotaxon of Bertling *et al*. (2006, p. 238) which states: "a taxon based on a trace fossil, including fossilised trails, tracks or burrows". No mention of the organism that may have produced the lebensspuren (Trewin 1994, p. 812) is made other than in the discussion, in accordance with Osgood's suggestion "to base the names strictly on morphology" (Osgood 1970, p. 303). Specific morphological terminology follows Trewin (1994).

Cruziana d'Orbigny, 1842

Type ichnospecies. *Cruziana rugosa* d'Orbigny, 1842. Subsequent designation of ichnospecies by Miller (1889).

Diagnosis. An elongate, bilobate furrow that can vary in depth with respect to the bedding plane, may be straight and/or gently curved (not tightly or sharply) within or upon the bedding surface, and may be composed of repetitive sets (or series) of imprints (ridges) along its length (though in most cases these ridges cannot be differentiated into distinctive set patterns); ridges in central part of furrow usually aligned in a herringbone shape and more or less continuous along length of furrow; also, sometimes, outside herringbone-aligned ridges, the trace may exhibit pair of narrow, comparatively smooth outer zones with or without fine brush-like impressions, and additionally there may be presence of lateral ridges.

Remarks. Häntzschel (1975, p. W55) emphasised that *Rusophycus* is not at all equivalent to *Cruziana*. *Cruziana* consists of "elongate bandlike furrows covered by herringbone-shaped ridges" (Häntzschel 1975, p. W55) and not "short bilobate bucklelike forms, resembling [the] shape of coffee beans" (Häntzschel 1975, p. W101) as observed with *Rusophycus*. This is contrary to Seilacher's (1990, p. 651) statement that: "They are united under the ichnogeneric name *Cruziana* d'Orbigny, whether made in a stationary (coffee bean-shaped 'rusophyciform' expression) or in a bulldozing manner (band-shaped 'cruzianaeform' expression)." Consequently, the two forms are clearly distinguishable from their distinctive morphological character traits so the ichnogenera *Cruziana* and *Rusophycus* should not be synonymised but recognised as distinct and separate. This follows Fillion & Pickerill (1990, p. 24), who stated: "Although Seilacher (1970, p. 455) united both long furrows and short excavations (=*Rusophycus*) under *Cruziana* because similar scratch marks made it possible to 'attribute burrows of very different outline to the same animals', most subsequent authors considered, as we do, their morphologies to differ significantly and preferred to retain the two distinctive ichnogenera because knowledge of the tracemaker is not taxonomically significant in ichnology."

Cruziana barriosi Baldwin, 1977 (Fig. 2A – B)

1977 *Cruziana barriosi*; Baldwin, p. 17-19, pl. 1C.
1990 *Cruziana barriosi*; Fillion & Pickerill, p. 25, pl. 2, fig. 6.

Material and locality. F133880 (CR2) and F133884 (CR7) from the Charlotte Range.

Diagnosis. See Baldwin (1977, p. 17).

Description. Refer to Baldwin (1977, p. 17).

Remarks. Due to the ridges running parallel to the midline of the trace, with little divergence, many other *Cruziana* ichnospecies are easily eliminated from consideration in the specimens assigned to this taxon. The width of the Stairway Sandstone specimens are narrower (maximum width of 13.1 to 34.5 mm) than that of specimens collected by Baldwin (1977, p. 17), and Fillion & Pickerill (1990, p. 24). The morphological characteristics of the trace are, however, similar: little divergence from the midline, no lateral ridges and a possibility of a median groove are observed (though due to weathering it is difficult to ascertain if the adjacent trace is the left exopodite trace in F133884). The number of ridges is greater than those stated by Fillion & Pickerill (1990, p. 24) of up to sets of six, while Baldwin (1977, p. 24) stated that they occur "with at least 5 ridges per set". The specimens from Australia depict, possibly up to 11 (F133880: weathering has eliminated the definition of the ridges) and 12 ridges (F133884).

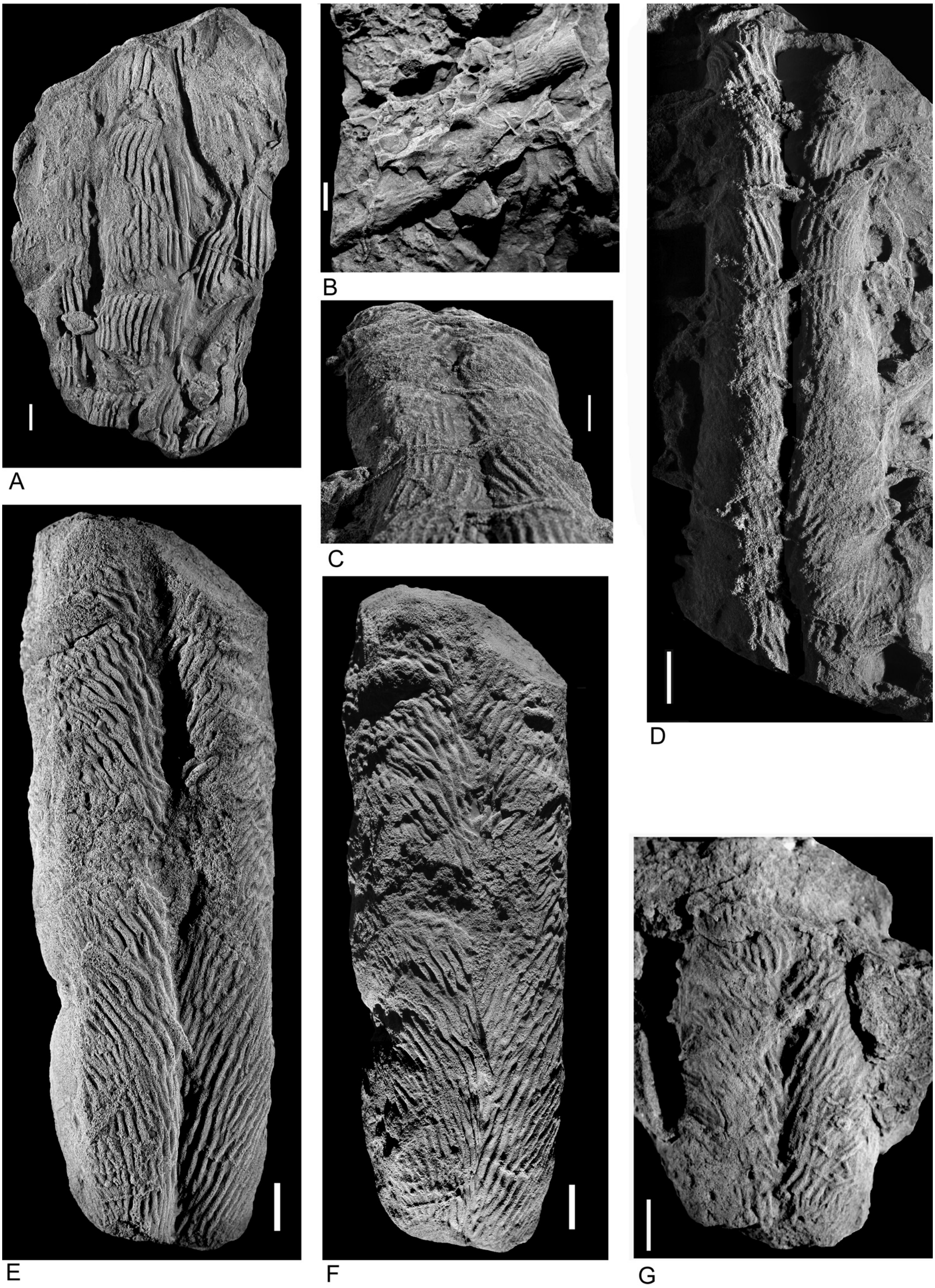


Fig. 2. Specimens are all convex hyporelief. **A-B**, *Cruziana barriosi* Baldwin, 1977 from the Charlotte Range. **A**, F133884 from CR2. **B**, F133880 from CR7. **C-G**, *Cruziana furcifera* d'Orbigny, 1842. **C-D**, F133871 from CRR from the Charlotte Range. **C**, anterioventral oblique view. **D**, ventral view. **E-F**, F133938 from CR7 from the Charlotte Range. **G**, F135852 from Mount Watt. Scale bar = 1 cm.

Due to the morphological similarities of being 'parallel' to the midline striations, the striation count has little significance to the trace itself. Rather than create a number of similar species, with characteristics based on exact counts of striations, we include these Australian specimens in *C. barriosi*.

Seilacher (1962, fig. 2, 1990, p. 652, fig. 32.2, 2007, p. 37, pl. 12) illustrated endopodal claw impressions and figured a possible *Illaenus* endopod with 12 'claws' on the limb, therefore presenting a possible trace maker of the specimen (F133884) found in Australia. Seilacher (2007, p. 37) suggested that *Cruziana rugosa* may have been produced by a species of *Illaenus*. Baldwin (1977, p. 17) stated for his *C. barriosi* that: "At a number of points the appendage impressions are interrupted and a surface morphology similar to that of *C. rugosa* is produced." This pattern is not observed by us, though it does correlate well with Seilacher's (2007, p. 37) findings of *Illaenus* and *C. rugosa*. Thus possibly it demonstrates the adoption of two different behaviours, by *Illaenus*, with the ichnospecies of *C. rugosa* and *C. barriosi*, as Baldwin (1977, p. 17) proposed.

The feeding traces of primitive Ordovician fishes have not been described, although it is often assumed that some, if not most, primitive fishes were bottom feeders (Long, 1995). It is conceivable that *Arandaspis* or one of the other primitive fishes that occurred in the Stairway Sandstone could have produced a trace that includes a series of parallel scratches. The mouth parts of these animals are not well known (Ritchie and Gilbert-Tomlinson, 1977). Herein, we only suggest that these animals could possibly have made such traces, but believe that it is more probable that they were made by an arthropod (fish specimens are certainly as common as, or more common than trilobites in this unit).

Cruziana furcifera d'Orbigny, 1842 (Fig. 2C-G)

1842 *Cruziana furcifera*; d'Orbigny, p. 21, pl. 1, figs 2-3.
1970 *Cruziana furcifera*; Seilacher, p. 464.
1977 *Cruziana* cf. *furcifera*; Ritchie & Gilbert-Tomlinson, p. 354.
1990 *Cruziana furcifera*; Fillion & Pickerill, p. 25, pl. 2, fig. 11 (see also for further synonymy).
2007 *Cruziana furcifera*; Egenhoff *et al*., p. 291-292, figs 3d-e, 4a-b.
?2007 *Cruziana furcifera*; Seilacher p. 194.

Material and locality. F133938 (CR7) and F133871 (CRR) from the Charlotte Range and F135852 (MW) from Mount Watt.

Diagnosis. The most comprehensive diagnosis was provided by Fillion & Pickerill (1990, p. 25), and they stated: "scratch marks are regular, some criss-crossing in a faint rhombic pattern, acute angled, and typically associated in sets; they may swing towards parallelism with the median line in a median posterior direction."

Description. Refer to Fillion & Pickerill (1990, p. 25).

Remarks. The key feature is the parallelism of the scratch mark sets along the median line at the posterior of the trace. The Stairway Sandstone specimens (F133938, F133871 & F135852) lack lateral ridges, therefore discriminating them from the ichnospecies *Cruziana goldfussi*. The associated bundle sets are not well defined in the Stairway Sandstone traces, therefore they can not be assigned to *C. rugosa*.

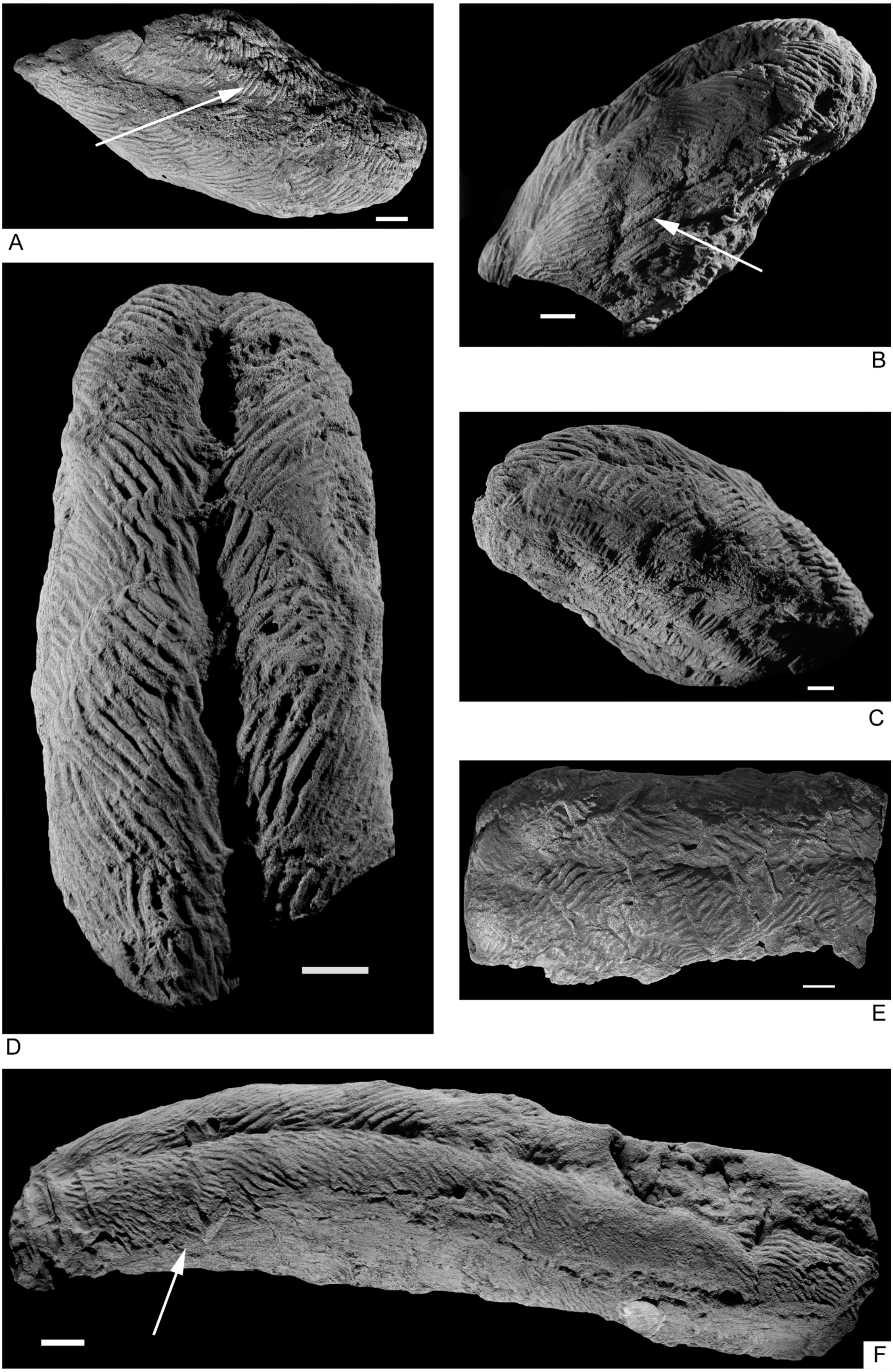
Ritchie & Gilbert-Tomlinson (1977, p. 354) also identified *Cruziana* cf. *furcifera* from the Mount Watt locality (fig. 5A, B). The images of Ritchie & Gilbert-Tomlinson (1977) indicate that the traces are *C. furcifera*. We also found and identified this ichnospecies at the same locality and bedding plane as a fish plate of *Arandaspis prionotolepis* Ritchie & Gilbert-Tomlinson 1977 (p. 367).

Seilacher (1970, P. 462-464) classified *Cruziana furcifera* within the '*Rugosa* Group' and he commented that the group was cosmopolitan and occurred in abundance. *Cruziana furcifera* also occurred in abundance, in the upper Stairway Sandstone of the Middle Ordovician, but members of the '*Rugosa* Group' mainly occur in Early Ordovician of other Gondwana regions (Seilacher 2007, p. 191, pl. 66).

Cruziana goldfussi (Rouault, 1850) (Fig. 3A-F)

1970 *Cruziana rugosa* Seilacher p. 450, fig. 2a.
1990 *Cruziana goldfussi* Fillion & Pickerill p. 26, pl. 3, fig. 1 (see for further synonymy).

Fig. 3. *Cruziana goldfussi* (Rouault, 1850). Specimens are all convex hyporelief. **A-D**, F133937 from CR7. **A**, lateral view, arrow depicts scratch marks up the trace. **B**, oblique lateral view and arrow pointing to lateral ridge marking. **C**, opposite oblique lateral view of B. **D**, view of ventral surface of hyporelief. **E**, ventral surface of F133887 from CRR. **F**, ventrolateral view of F133936 from CR7. All from the Charlotte Range. Scale bar = 1 cm.


A
B
C
D
E
F

2007 *Cruziana goldfussi* Egenhoff *et al*., p. 292-294, figs 4c-e, 5a-b .
2007 *Cruziana goldfussi* Seilacher p. 194, pl. 68.

Material and locality. F133887 (CRR), F133936 and F133937 (CR7) from the Charlotte Range.

Diagnosis. After Fillion & Pickerill (1990, p. 26).

Description. The dimension ranges of the specimens are: maximum trace length = 113.6-180.5 mm; maximum trace width = 45.6-59.6 mm; maximum ridge width = 1.8 mm; and distance between ridges = 0.5-1.3 mm.

Remarks. Crimes & Marcos (1976, p. 352-353) and Fillion & Pickerill (1990, p. 26) presented the most comprehensive descriptions and Seilacher's (2007, pl. 11) sketch based on a specimen from the Lower Ordovician of France provided the depth and morphology this ichnospecies should display.

Two slightly different 'forms' of *Cruziana goldfussi* have been recognised among the Stairway Sandstone samples. F133937 (Fig. 3A – D) is similar to the schematic representation figured by Seilacher (1970, p. 450, fig. 2a) as *C. rugosa*, though this was later amended to *C. goldfussi*. This Stairway form is a relatively deep trace, dug for some behavioural need, with a maximum recorded depth of 61.6 mm. The organism appeared to have dug into the substrate at a slight angle and upon reaching the 'bottom', extended its legs for maximum digging. The oddity of this trace (Fig. 3A – D) is that the upper portion of the trace is slightly narrower than the lower part of the trace (measured from mid-length of the trace the 'bottom' has maximum width of 54.4 mm, and the 'top', a maximum width of 39.8 mm). One possible explanation is that the organism implemented maximum leg extension at the base of the trace and in retreat from the burrow, withdrew its legs and possibly flexed the body towards the midline and then pushed up with its legs. The trace has scratch marks laterally that were probably produced as the organism retracted itself from beneath the substrate. There are also lateral ridge markings, and posteriorly the trace has scratch markings that are more or less parallel to the median line/furrow. There are also 'cephalon' markings at the anteriormost end of the 'burrow'. The 'burrow' is angled into the substrate at approximately 30-35° to the horizontal (bedding plane).

The other form (F133936: Fig. 3F) of the trace of *Cruziana goldfussi* is that of the 'standard' horizontal trace, whereas F133887 (Fig. 3E) seems to be an intermediate between both F133937 and F133936, with a slight angle (approximately 20°) to the trace at the anterior end. Both specimens (F133887: Fig. 3E & F133936: Fig. 3F) have a defined median line with little to no cross-over of scratch marks, with the scratches appearing as sets and approaching parallel at the posterior end of the trace (Seilacher 1970, p. 464, 1991, p. 1572). Seilacher's (1970, p. 462, 1991, p.1572) *C. goldfussi* was classified by him in the '*Rugosa* Group' and the other ichnospecies within this group are all from the Ordovician.

Due to the lateral ridges on all of the specimens, and other morphological characteristics already mentioned, they are assigned to *Cruziana goldfussi*. The specimens do not demonstrate outer lobe markings, therefore eliminating them from *C. semiplicata*, and they have lateral ridge markings, thus are not *C. furcifera*.

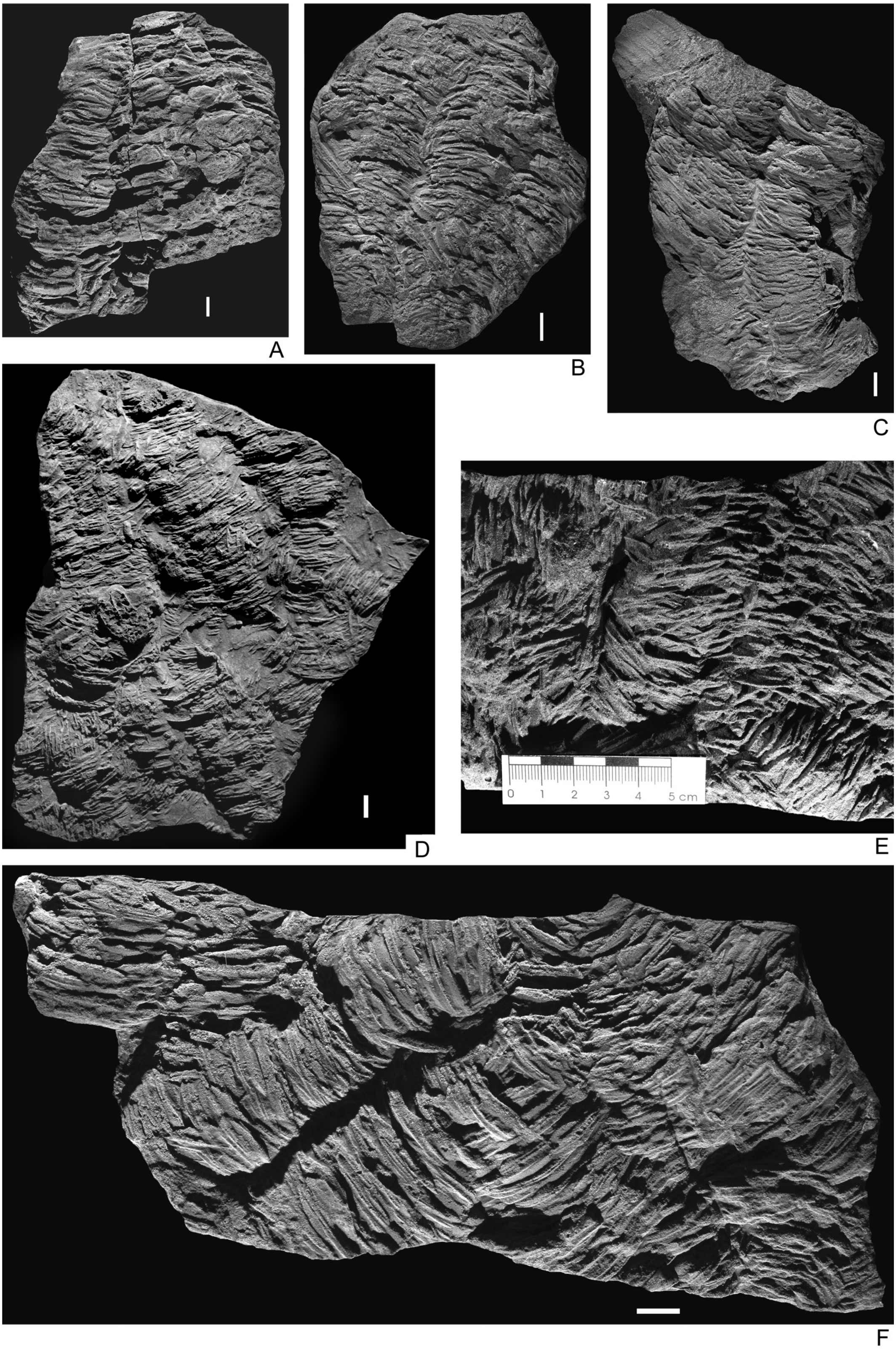
Cruziana omanica Seilacher, 1970 (Fig. 4A-F)

1970 *Cruziana omanica*; Seilacher, p. 466, fig. 9a,b.
1983 *Cruziana warrisi*; Webby, p. 63-65, fig. 2B.
1983 *Rusophycus latus*; Webby, p. 69-72, figs. 2A, 4A, 4C-D, 5A, 5C, 6.
1991 *Cruziana* cf. *omanica*; Seilacher, p. 1570, pl. 1, fig. a.
2004 *Monomorphichnus podolicus*; Uchman *et al*., p. 75, fig. 5.
2007 *Cruziana lata* (Webby, 1983); Seilacher, p. 192.
2008 *Cruziana lata* (Webby, 1983); Seilacher, p. 36.

Material and locality. F133007, F133886, F133877, F133883, F133893 and F133895 (CR7) from the Charlotte Range.

Diagnosis. Shallow bilobate structure with equally shallow median furrow. Median furrow has scratch marks diverging into furrow, occasionally crossing to opposite side. Scratch marks that are

Fig. 4. *Cruziana omanica* Seilacher, 1970. Specimens are all convex hyporelief. **A**, F133893 (CR7). **B**, F133886 (CR7). **C**, F133895 with fragment of possible external mould of trilobite pygidium (CR7). **D**, F133007 (CR7). **E**, portion of sample of F133877(CR7). **F**, F133883 (CR7). All from the Charlotte Range. Scale bar = 1 cm.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long, blunt and tricuspidate, with median scratch that is stronger and more raised than lateral ones. Right and left markings are almost 180° to each other. Can be straight, curved, and/or partial ridge bundles.

Description. Large bilobate traces, that range mainly between about 7-12 cm in width and up to over 20 cm in length. Form extensive irregular to straight burrows preserved in convex hyporelief. Lateral lobes are fairly flat, with most of relief near middle and sides of traces. Lateral lobes are clearly separated by irregular median furrow. Considerable irregularity to median furrow is caused by crossing of subparallel trifid scratch marks from both sides. Coarse scratch marks are markedly transverse to general axis of trace, only curving slightly backward near middle and sides of trace. Scratches show minor degree of bundling of 3-4 scratches in some traces. Surfaces with this ichnospecies are often intensely bioturbated, and adjacent traces interfere with another so sides are often quite irregular (Fig. 4F).

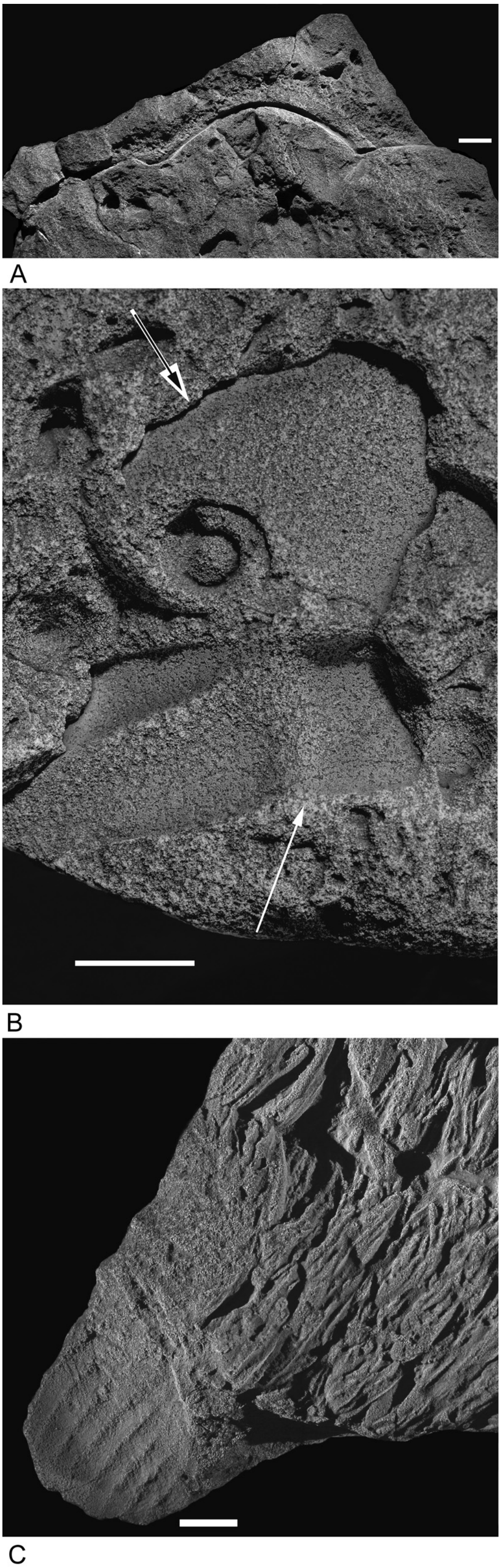
Remarks. *Cruziana* cf. *omanica* was figured by Seilacher (1991) from the Pacoota Sandstone near Alice Springs. He considered the trace to have an Upper Cambrian age. This Pacoota trace is identical to the traces found in the Stairway Sandstone (Fig. 4). Seilacher (2008, p. 36) stated "a form that is closely related or even identical is found in the lowermost Ordovician of Oman" even though he had previously stated that *C. omanica* is a Cambrian, more specifically an Upper Cambrian (1991, p. 1569, fig. 3) trace. This brings into question the use of this species as a biostratigraphic marker in the ichnostratigraphic concept of Seilacher for Gondwana, given that the Pacoota Sandstone specimen was first thought to be Upper Cambrian (Seilacher 1990, p. 660, fig. 32.5, 1991, fig. 3, 2007, p. 192, pl. 67), though later Seilacher stated it to be lowermost Ordovician (2008, p.36), and Lindsay & Korsch (1991, p.21) have also stated that the Ordovician sedimentary rocks of the Amadeus Basin include both the Pacoota and Stairway sandstones. *Cruziana omanica* may have a range from the Upper Cambrian (if this interpretation of age is the correct, or Lower Ordovician, if incorrect) and the younger age must range upwards into the Middle Ordovician. The range of *Cruziana omanica* may even be extended upwards if the synonomy of *Monomorphichnus podolicus* Uchman *et al*. (2004, p. 76) from the Lower Devonian is accepted. *Monomorphichnus podolicus* appears identical to *C. omanica* in most respects, but it is narrower than Seilacher's types (1970, p. 466), and size may not be a good reason for rejecting the synonymy.

The specimens from the Stairway Sandstone are identified as *Cruziana omanica* based on the diagnosis provided by Seilacher (1970, p. 466) and his illustration (p. 465, fig. 9a, b) of "long, blunt tricuspidate endopodal markings, in which the median scratch is stronger than the lateral ones". The width of the trace also corresponds with Seilacher's (1970, p. 466) definition of the trace of up to 8-9 cm, though the range should be slightly expanded to be that of 7-12 centimetres to account for both the smaller and larger sized traces found in Australia. In terms of Seilacher's (1970, p. 465) taxonomic classification of groups within *Cruziana*, the Australian trace of *C. omanica* belongs to the '*Petraea* Group' given the number of claw markings (between three and five).

Cruziana kufraensis Seilacher *et al*. (2002) from the Early Silurian Tanezzuft Formation of SE Libya is similar in having near 180° between right and left limb markings, but the authors of that ichnospecies indicated that these markings were made by legs that "had probably no more than two claws" (p. 262). Consequently *C. omanica*, is defined as having trifid scratch marks, hence the scratches based on claw morphology discriminates between these two ichnospecies.

Webby (1983, p. 63-65) erected the ichnospecies *Cruziana warrisi*. Since ichnofossils are based purely on morphology, we believe that *C. warrisi* and *C. omanica* are synonyms. In several works, Seilacher (1970, p. 466, 1991, p. 1571-1572, 2007, p. 183, pl. 67, 2008, p.36) referred to *C. omanica* occurring in both Oman and Australia. It is not possible to differentiate a trace fossil into a distinct ichnospecies based upon geographical position. Scotese's (2001, p. 13) Middle Ordovician reconstruction of Gondwana has it encompassed by a large continental shelf, thus allowing for intracommunication along this eastern Paleo-Tethys Ocean shelf. A possible trilobite group, of the appropriate size range, found in the Stairway Sandstone that could make traces of this size is the Asaphida. Asaphids had planktonic larvae; the asaphoid protaspis (Fortey & Chatterton 1988, p. 178). The pelagic asaphoid protaspid could have dispersed these animals widely, including along the shallow shelf, thus allowing Oman and Australia to have similar ichnofossils; in this case, *C. omanica*. The adults were also large and active enough that, given time, they could also have dispersed widely. Ritchie & Gilbert-Tomlinson (1977, p. 353) found an endemic asaphid taxon in the uppermost Stairway Sandstone: '*Asaphus*' *thorntoni* Etheridge, 1892 (=*Basilicus*? *thorntoni* [Etheridge, 1892]).

The geographical argument can also be used for *Monomorpichnus podolicus* that was erected



by Uchman *et al*. (2004, p. 75-77). Though the trace is found in Devonian strata in Ukraine, the morphological character states synonomise it with *Cruziana omanica*. Uchman *et al*. (2004, p. 75-77, fig. 5) recognised the trace as intermediate between *Monomorphichnus* and *Cruziana*, though from their figure and description, the ichnospecies is definitely *Cruziana*, more specifically, *C. omanica*. The characteristics that synonomise the ichnospecies: parallel to subparallel striations, bundle of 4-6 striations (placing it within Seilacher's (1970) '*Petraea* Group', though Seilacher had stated "3 to about 5", it is the 'about' that allows interpretation to account for 6 striations/bundle), "striae…whose axis is straight to slightly curved and perpendicular to the bundle" (Uchman *et al*. 2004, p. 77), and bilobate ridges. The trace also conforms to the adjusted size range mentioned above.

Rusophycus latus Webby 1983 is synonomised within *Cruziana omanica* for a number of clear morphological reasons. The diagnosis of the ichnospecies stated that the trace could consist of straight, sinuous, and/or partial bundles. A number of Stairway Sandstone specimens (fig. 4d-f), and Webby's (1983, fig. 2a, 4c) specimens, consist of bundles of ridges in a highly bioturbated sandstone. Due to the high degree of bioturbation, the 'typical' cruzianaeform morphology is overprinted a number of different times. When the bundle is a single representation, as seen by Webby (1983, fig. 6), it is still cruzianaeform though the organism dug deeper into the substrate at that point. Webby (1983, p. 71) stated that the ridges are bifid or trifid, therefore not being excluded from a taxon with a diagnosis of tricuspidate ridges. If the ridges were not so tightly overlapped, one would possibly observe that they are trifid. The size ratios cited by Webby (1983, p. 71), also fit within the ratios obtained from the Stairway Sandstone specimens. We consider that *R. latus* represents short segments of *C. omanica*, some perhaps the result of slightly deeper digging while making a longer trail.

The organism that created this particular

Fig. 5. Disarticulated and fragmented trilobite sclerites. **A**, impression of thoracic segment (F133950) from the Charlotte Range (CR3). **B**, external mould of axial region and portion of pleural region of thoracic segment, pleural furrow, anterior and posterior band have similar morphology to *Lycophron howchini* (Etheridge, 1894), indicated by the white arrow; black on white arrow is pointing at the typical gastropod found in the region (F133949 – CR3). **C**, external mould of left pleural region of fragmented pygidium, similar morphology to asaphid pygidia (F133895 – CR7). Scale bar = 1 cm.

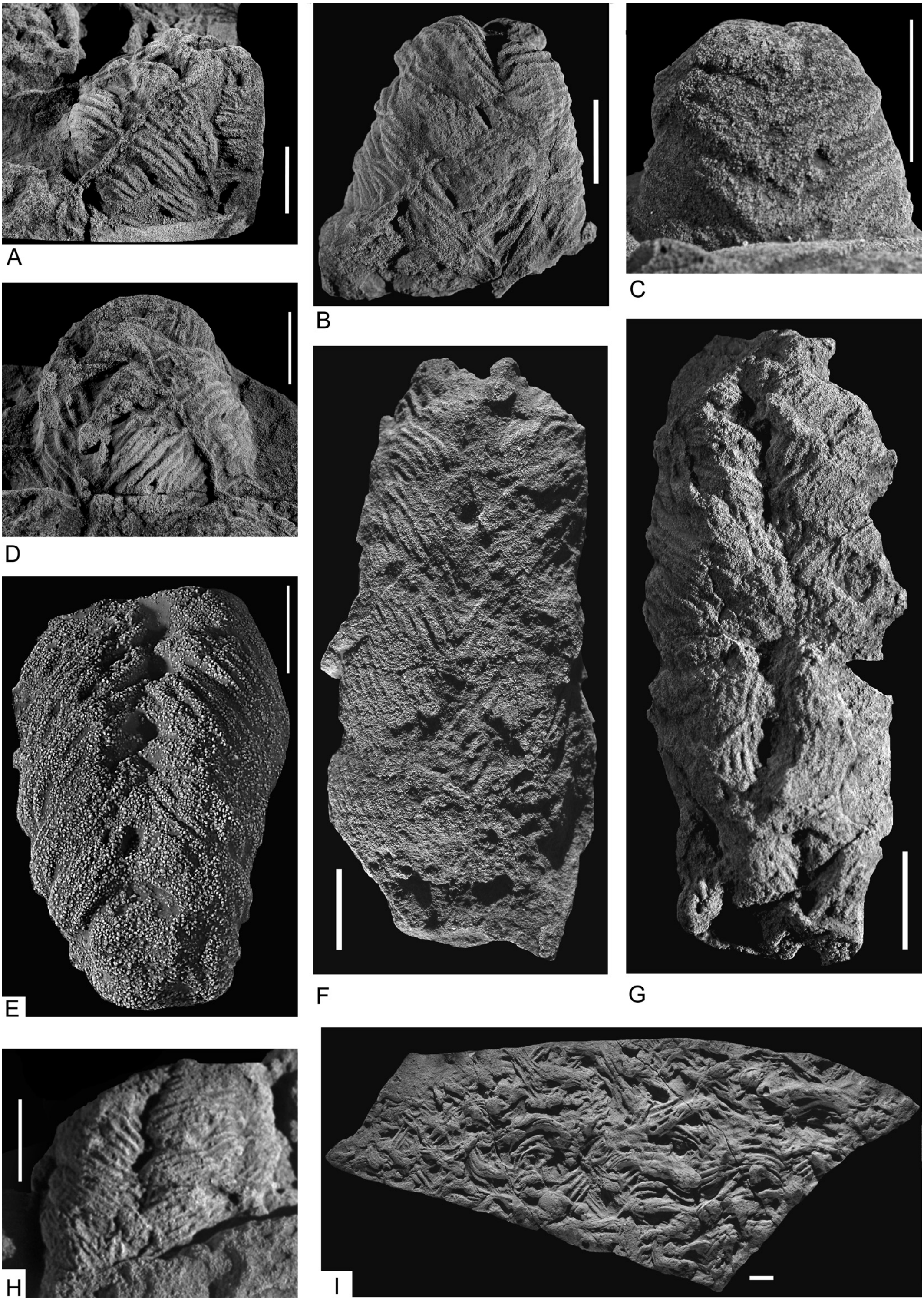


Fig. 6. **A-H**, *Cruziana penicillata* isp. nov. All convex hyporelief. **A-B**, paratype (F133018) from the Charlotte Range. **A**, lateral view. **B**, ventral view of convex hyporelief. **C**, paratype: anterior portion of trace (F133871) from the Charlotte Range. **D**, paratype: F135855 from Mount Watt. **E**, holotype: F133868 from the Charlotte Range. **F**, paratype: F135853 from Mount Watt. **G**, paratype: F135856 from Mount Watt. **H**, paratype: F133021 from Mount Watt. **I**, *Monomorphichnites* spp. F133890 (CR7) from the Charlotte Range. Scale bar = 1 cm.

trace may have been a trilobite, since trilobites are almost always interpreted as having made *Cruziana* and *Rusophycus*. Few trilobites have been found in the Stairway Sandstone (only a few disarticulated sclerites have been found) due to the clastic nature of the unit and the fact that the upper unit was likely subjected to storm reworking and to comparatively high energy regimes. The Horn Valley Siltstone is an Ordovician trilobite-bearing sedimentary unit that occurs below the Stairway Sandstone in some parts of the Amadeus Basin. The Horn Valley Siltstone outcrops neither at the Charlotte Range nor at Mount Watt. At the Charlotte Range, the Stairway Sandstone disconformably overlies the Jay Creek Limestone of Middle Cambrian age (Ritchie & Gilbert-Tomlinson 1977, p. 354). While at Mount Watt, the Stairway Sandstone overlies the Winnall Beds of late Proterozoic age (Ritchie & Gilbert-Tomlinson 1977, p. 354). The trilobite fauna of the Horn Valley Siltstone can still be considered for possible candidates for the traces in the Stairway Sandstone, at least at the family level. The most likely suspects are trilobite members of the Order Asaphida Salter, 1864, based on a few sclerites and fragments that have been found in close proximity to biogenic sedimentary structures within the Stairway Sandstone of the Charlotte Range (Fig. 5) and that occur in abundance in other Ordovician clastic units within Australia. Another reason to consider asaphids as the trace makers is their size. Laurie (2006, p. 303-305, pl. 13) described and figured *Lycophron howchini* (Etheridge 1894) which has a thorax of comparable width to the large *Cruziana omanica*. Some of the asaphid sclerites in the upper Stairway Sandstone are large enough for the animals that secreted them to have made *C. omanica* (Fig. 5).

Cruziana penicillata isp. nov. (Fig. 6A - H)

Material and locality. Holotype: F133868 (almost complete biogenic sedimentary structure, minus most posterior end); paratypes: F133018 (partial trace of posterior portion), and F133871 (only anterior portion of trace is visible, co-occurring with *Cruziana furcifera*, among other ichnofossils) (all occurring at CRR) from Charlotte Range; F135853, F135855 and F135856 all isolated specimens from Mount Watt.

Etymology. Latin *penicilla*, brush, alluding to individual scratch mark sets that are similar to a brush mark.

Diagnosis. Ridges (scratch marks) occurring in distinct bundles that repeat and overlap previous bundlelike-sets, creating step-like appearance. Trace either angled ~30° from horizontal bedding plane or horizontal.

Description. Ridges (or scratch marks) are clearly defined. Single, well-defined ridges (or scratch marks). Approximately five to seven ridges per bundle set. Ridges form bundles as overlapping sets that appear like a sequence of descending steps, when viewed as an entire specimen rather than as a convex hyporelief. Angle of trace relative to bedding plane varies from ~30° inclination to horizontal. No lateral ridges. Faint cephalon markings may occur anteriorly. Ridges criss-cross median furrow. Median furrow is not clearly defined. Striations occur at approximately 45°-50° angle to median furrow (anterior to posterior). Dimensional ranges of specimens (even if incomplete or partially enclosed within the rock): maximum trace length = 14.5-52.0 mm; maximum trace width = 17.6-31.3 mm; maximum trace depth = 10.4-38.1 mm; maximum ridge width = 1.0-1.9 mm; maximum width between ridges = 0.3-1.0 mm and angle of trace from horizontal = 20° – 35°.

Remarks. This species occurs in only one locality within the Charlotte Range, with some other traces in situ and from Mount Watt. It represents an ethology that was unusual and was made by an organism that may have been restricted geographically or ecologically. The trace bears a slight similarity to *C. rugosa*, though the scratch marks of *C. rugosa* are more 'feather-like' in appearance, having a posterior edge, and the angle of the scratch marks of *C. rugosa* is much greater relative to the median furrow (anterior to posterior). Also, *C. rugosa* differs in having a more clearly defined median furrow.

The claw markings per leg are difficult to differentiate either due to the coarseness of the grain size of the sand relative to the size of the ridges, and/or dependent on some degree of post-production erosion. The holotype usually has at least five claw markings per bundle, and this seems to be consistent, though in places a slight variation of up to seven striations per bundle is observed.

Cruziana penicillata falls within Seilacher's (1970, p. 462-464, 1991, p. 1572) "*Rugosa* Group" due to the fact that it exhibits multiple and sharp scratches represented by up to 12 subequal claw-marks (Seilacher 1970, p. 462). It also occurs only in the form of a short cruzianaeform ribbon or deeper 'bath tub' furrow, rather than a stationary rusophyciform burrow (Seilacher 1991, p. 1572).

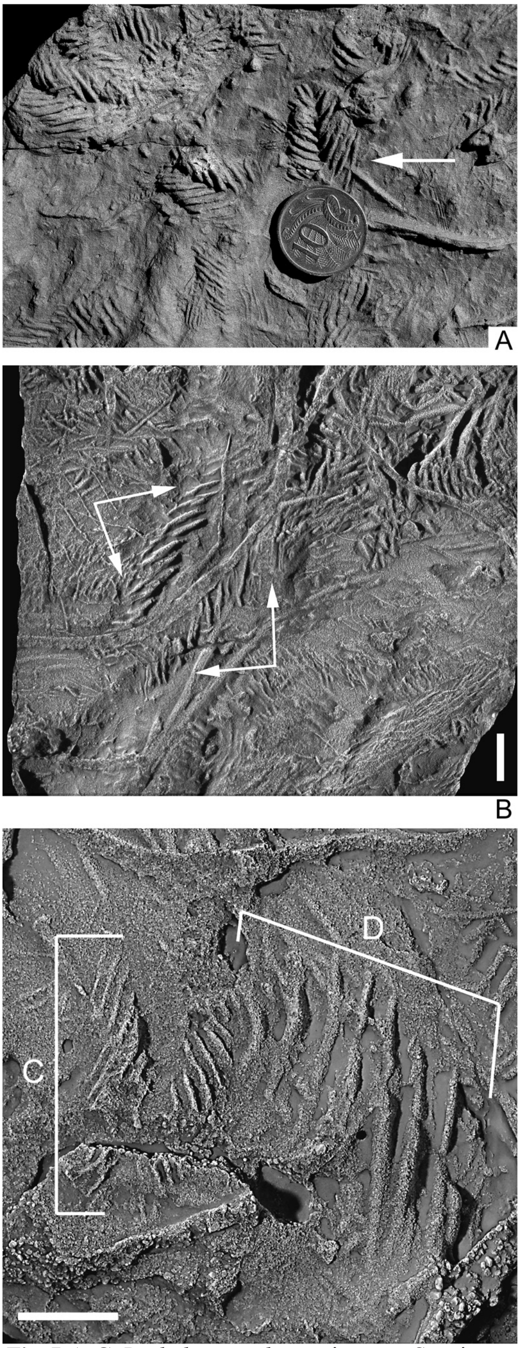


Fig. 7. **A-C**, *Diplichnites arboreus* isp. nov. Specimens are all convex hyporelief. **A**, holotype indicated by white arrow (F58984) from the Charlotte Range (R.d. C1) (coin for scale is 23.6 mm diameter). **B**, paratype underprint, highlighted by white arrows (F133014) from Mount Watt. **C**, paratype (F133022) from Mount Watt. **D**, *Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboyleya, 1977 (F133022) from Mount Watt. Scale bar = 1 cm.

Diplichnites Dawson, 1873

Type ichnospecies. *Diplichnites aenigma* Dawson, 1873 by monotypy.

Remarks. Häntzschel (1975) provided a comprehensive account of the ichnogenus.

Diplichnites arboreus isp. nov. (Fig. 7A – C)

1983 *Diplichnites* sp. A; Webby p. 68, fig 3C.

Material and locality. Holotype: F58984 from the Charlotte Range (collected by A. Ritchie: recorded as R.d. C1); paratype: F133014 and F133022 from Mount Watt.

Etymology. Latin for tree: Trace resembling a stick drawing of a conifer, lacking a stem/trunk.

Diagnosis. Single, regular, almost straight scratch marks. Posterior to anterior tapering of markings. Paired rows of scratch marks to right and left form V-angle near 90°. No lateral ridge impression.

Description. Single scratch markings, though one or two scratches show forking to produce bifid markings. Regularly spaced scratch marks, straight or with slight curvature. Posterior scratches are longer, whereas scratch marks along longitudinal median 'furrow' taper to anterior, where right and left scratch marks meet almost at a point. Longitudinal median furrow can be narrow and deep anteriorly, only slightly widening posteriorly (Holotype: F58984) or distinctly wider and shallow (F133014 and F133022) towards posterior end. Holotype dimensions: maximum width = 20.6 mm; maximum length = 28.9 mm; ridge width = 1.2-2.2 mm; and ridge spacing = 0.5-1.6 mm.

Remarks. *Diplichnites arboreus* isp. n. is not equivalent to *Rusophycus crimesi* Fillion & Pickerill, 1990 (p. 54) owing to the scratch marks not being strictly bifid. One or two scratch marks do give the appearance of bifid marking, though the majority of the scratches are either vertically or slightly inclined single markings. These taxa share some morphological traits, but are different enough to keep them as separate ichnospecies: the longitudinal median furrow in *R. crimesi* does not taper to the extent observed in *D. arboreus* and the scratch marks in that taxon are bifid. As Fillion & Pickerill (1990, p. 54) stated for their *R. crimesi*, it can be a rusophycid-like equivalent of a *Cruziana* ichnospecies, or an undertrace of a *Cruziana* or *Rusophycus* ichnospecies. Crimes (1970a, pl. 5d, 1970b, pl. 9d, e) illustrated two different forms of *Diplichnites*, but both were only identified at the generic level. Both of these examples, from the Cambrian of Wales, have some resemblance to *D. arboreus* from the Stairway Sandstone, but the width at the anterior of the trace is far too wide and never appears to come to a point. Crimes (1970a, b), illustrated *Diplichnites* with irregular spacing between the endopodal markings, and the angle between the right and left striations is greater than 90°.

Monomorphichnus Crimes, 1970b

Type ichnospecies. *Monomorphichnus bilinearis* Crimes, 1970b.

Remarks. See diagnosis provided by Crimes 1970b (p. 57) and discussion by Fillion & Pickerill (1990, p. 40-41).

Monomorphichnus lineatus Crimes, Legg, Marcos & Arboleya, 1977 (Figs 7D, 8A-C)

Material and locality. F133896 and F133931 (CR7) from the Charlotte Range and F133022 from Mount Watt.

Diagnosis. Refer to diagnosis by Crimes *et al*. (1977, p. 103), and Fillion & Pickerill (1990, p. 42).

Description. See Fillion & Pickerill (1990, p. 42).

Remarks. The description provided by Crimes *et al*. (1977, p. 103) presented the possibility of the trace being 'straight to slightly sigmoidal'. Traces collected from the Charlotte Range display a straight morphology.

There is some variation among two traces of this species illustrated herein, though each was made by a single set of leg scratches. They do not occur as bifid scratches, as seen in *Monomorphichnus bilinearis* Crimes, 1970b, nor are they similar to *M. multilineatus* Alpert, 1976 (p. 234), which, as stated by Crimes *et al*. (1977, p. 103) exhibits central ridges that are "deeper than the outer ridges".

The variation between the two specimens presented as *Monomorphichnus lineatus* is just a representation of the same morphological characteristics, presented by either different organisms or organisms of varying sizes. The largest of the two specimens (F133896: Fig. 8A) is very large: trace length = 68.5 mm, trace width = 48.0 mm, maximum ridge width = 3.1 mm, minimum ridge width = 1.4 mm, maximum width between ridges = 11.0 mm, and minimum width between ridges = 6.1 mm. Crimes *et al*. (1977, p. 104) presented *M. lineatus* var. *giganticus* but based upon their description of the trace, it is composed of 10 ridges, and this is not the ridge count in any of the Stairway Sandstone specimens found. Up to seven ridges occur within the Stairway ichnospecies sample of *M. lineatus*.

The smaller of the two samples of *Monomorphichnus lineatus* (F133931, Fig. 8B) has the following sizes: trace length = 71.5 mm (though could be longer due to the trace being at the edge of the rock); trace width = 10.2 mm; maximum ridge width = 1.5 mm; minimum ridge width = 0.6 mm; maximum width between ridges = 2.0 mm; and minimum width between ridges = 0.2 mm. As illustrated in Figure 8B and C, F133931 displays two types of *Monomorphichnus*, and the sketched Figure 8C demonstrates that these are two separate, partly superimposed ichnospecies: *M. lineatus* and *M. sinus* isp. nov. (see below).

Monomorphichnus multilineatus Alpert, 1976 (Fig. 8D)

Material and locality. F133943 (CR7) from the Charlotte Range.

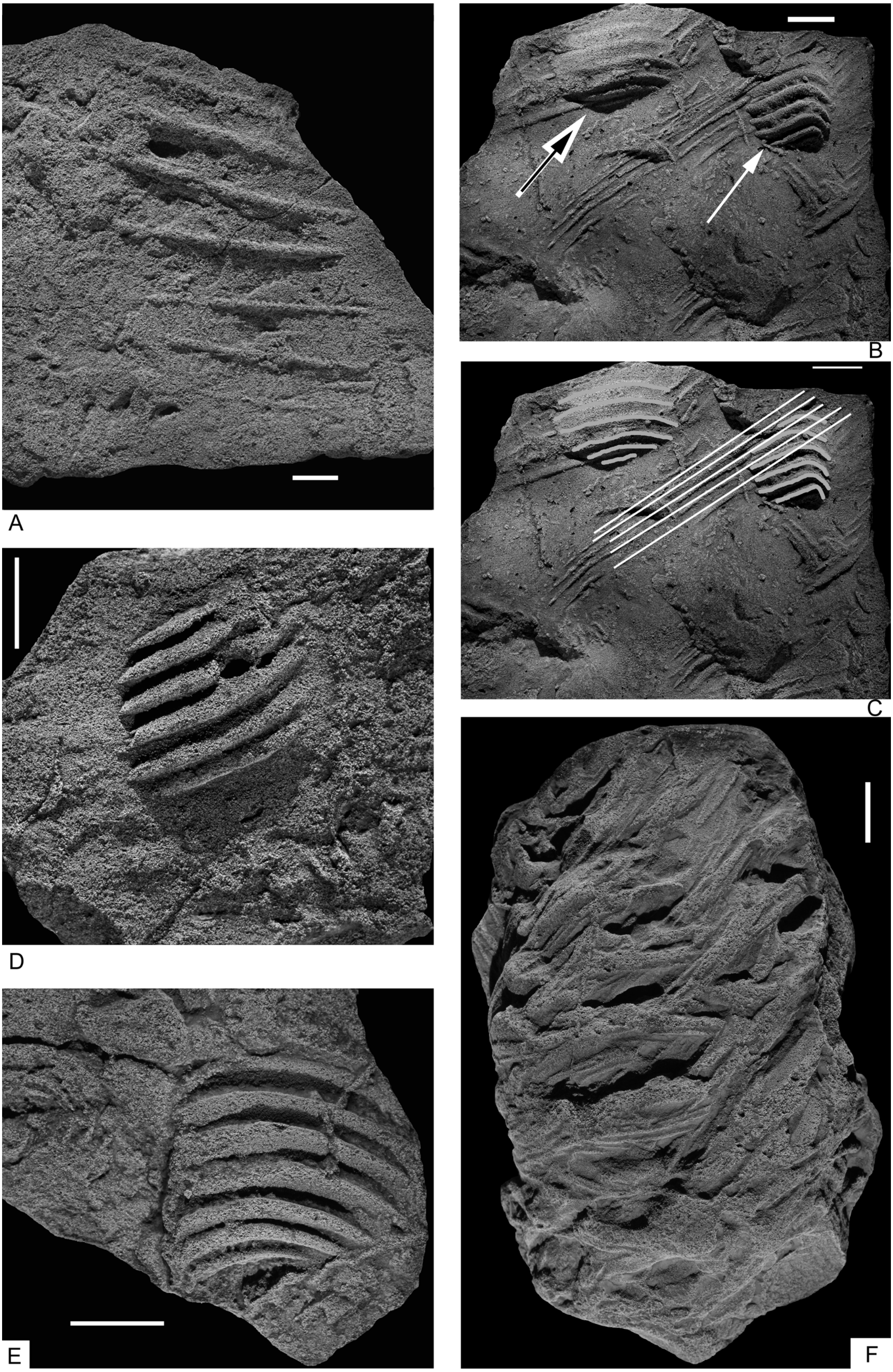
Diagnosis. See Fillion & Pickerill (1990, p. 42).

Description. Refer to Alpert (1976, p. 234) and Fillion & Pickerill (1990, p. 42).

Remarks. The six parallel striations with the central ridges being slightly higher than the two lateral ridges fits the diagnosis of Alpert (1976, p. 234). The length of the trace is also in accordance with Alpert (1976), but the width is much greater in the Stairway specimen (F133943): width and length are almost equivalent, at approximately 16.5 mm. This specimen also resembles GSC 78158 from Fillion & Pickerill (1990, pl. 10, fig. 4), though they had one more striation in their specimen. It differs from *Monomorphichnus lineatus* in the following morphological character states: displays higher central ridges to the lateral ridges, whereas *M. lineatus* has an almost even depth to the ridges, and the lack of a continuous line, more like a digging than a drag-type structure.

Monomorphichnus sinus isp. nov. (Fig. 8B, C, E)

Material and locality. Holotype: F133931 (top right of Fig 8B-C) from the Charlotte Range (CR7); paratypes F133931 (top left of Fig 8B-C) from the Charlotte Range (CR7), and F133919


A
B
C
D
E
F

from the Charlotte Range (CR4).

Etymology. Latin *sinus*; curve.

Diagnosis. Six or seven parallel ridges, with slight to prominent curvature at midpoint.

Description. Bundles of six or seven curved ridges. Ridges angled at approximately 35°-45° from horizontal plane (when observed in convex hyporelief). Angled ridges: innermost ridge, of curve, is typically more shallow and ridges become higher/deeper and wider to fourth ridge and then taper to be more shallow. Curve can be slight to abruptly angled at midpoint. Blunt and/or pointed proximal/distal tips of ridges. Numerical dimensions of the traces are: trace length = 10.2-25.0 mm; trace width = 16.3-21.4 mm; maximum ridge width = 1.8-3.2 mm; minimum ridge width = 0.6-1.3 mm; maximum width between ridges = 1.5-1.7 mm; and minimum width between ridges = 0.6-0.7mm.

Remarks. *Monomorphichnus sinus* isp. nov. is distinct from other ichnospecies of *Monomorphichnus* due to the curvature of the ridges. *Monomorphichnus sinus* is definitely classified within the *Monomorphichnus* ichnogenus, due to the fact that it exhibits claw-like markings from a single side of the organism and no counterpart impressions of the opposite limb(s). Other ichnospecies appear to have a linear 'straightness' or are only slightly sinuous, which is typically defined as a slight flexion or extension as the appendage was dragging along the substrate, for example: *M. bilinearis* and *M. lineatus*. None appear to have the prominent curve seen in this ichnospecies. It has one character state that could link it closely with *M. multilineatus* for the innermost (lateral) ridge of the curve is less defined, as seen in *M. multilineatus*, but the 'other' lateral ridges are well defined, unlike *M. multilineatus*.

Monomorphichnus spp. (Fig. 6I)

Material and locality. F133890 (CR7) from the Charlotte Range.

Remarks. The abundance of scratch marks covering this one rock creates difficulties in differentiating individual ichnospecies, other than *Monomorphichnus sinus*. The number of curved ridges and reworking creates issues as to which ridge may belong to the other ridge. There is a very high probability that *M. lineatus* and *M. multilineatus* are represented here, though due to the extreme reworking, they cannot be further differentiated herein.

Rusophycus Hall, 1852

Type ichnospecies. *Rusophycus bilobatus* Hall, 1852.

Diagnosis. Refer to Fillion &Pickerill (1990, p. 52).

Remarks. As mentioned previously, Seilacher (1970, p. 454, 1990, p.651) synonymised *Cruziana* and *Rusophycus*, thus creating problems within the classification of traces with cruzianae- and rusphyciform expressions. We follow Fillion & Pickerill (1990, p. 24) and Bertling *et al*. (2006, p. 281) in recognising these ichnotaxa as being distinct and useful in the classification of traces.

Rusophycus unilobus (Seilacher, 1970) (Fig. 8F)

1970 *Cruziana uniloba*; Seilacher, p. 473, fig. 7.26.

Material and locality. F133920, one complete specimen (CR4) from the Charlotte Range.

Diagnosis. Refer to Seilacher (1970, p. 473).

Description. Evidence of bilobate structure that lacks median furrow. Extensive scratch marks eliminate any possible median furrow, criss-crossing and creating interfingered braided structure. Angle of left and right scratch marks approximately 140°, being slightly offset. Length is longer than width of trace.

Remarks. Seilacher (1970, p. 473) originally named this trace *Cruziana uniloba*, though in the diagnosis he recognised it as a resting trace. Due to its form and since it is an accepted hypothesis

Fig. 8. All convex hyporelief. **A**, *Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya, 1977 (F133896) from CR7 of the Charlotte Range. **B**, *Monomorphichnus sinus* isp. nov. (white, and black-on-white arrows) and *Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya, 1977 (F133931) from CR7 in the Charlotte Range. **C**, Same as B: *Monomorphicnus lineatus* depicted as white straight lines and *Monomorphichnus sinus* traced by curved grey lines. **D**, *Monomorphichnus multilineatus* Alpert, 1976 (F133943) from CR7 in the Charlotte Range. **E**, *Monomorphichnus sinus* isp. nov. (F133919) from CR4 in the Charlotte Range. **F**, *Rusophycus unilobus* (Seilacher, 1970) (F133920) from CR4 in the Charlotte Range. Scale bar = 1 cm.

that *Rusophycus* represents 'resting traces', this ichnospecies is assigned to *Rusophycus*. Seilacher (1970, p. 473, fig. 7.26) illustrated and diagnosed *R. unilobus* as lacking a median furrow due to the right and left striations interfingering across the midline. The width of the Stairway trace (F133920) is 54.9 mm, which is a little more than twice the width quoted by Seilacher (1970, p. 473) of 20-25 mm, but his trace was from the Lower Devonian, while ours is Middle Ordovician in age. This size difference between Ordovician and Devonian specimens of this taxon calls into consideration the *Cruziana* biostratigraphy that Seilacher has promoted in several works (Seilacher 1970, 1990, 1991, 1994, 2007 and Seilacher *et al*. 2002). It demonstrates that different organisms of different ages can produce morphologically similar traces, even though they may vary in size. Seilacher (1970, p. 471) also referred to *R. unilobus* as a member of the '*Pudica* Group', he observed that "this group needs to be revised before it can possibly be used stratigraphically." *Rusophycus unilobus* is very distinctive, with no other ichnospecies previously identified in the literature that even closely resembles it.

This particular specimen has a maximum length = 96.1 mm; maximum width = 54.9 mm; ridge width range = 1.3-4.7 mm and a maximum depth = 30.4 mm. The legs appear to be trifid, with the median claw, in some cases, being slightly higher than the two lateral claws, though in most cases they appear to be equal in size and shape. There are no lateral ridge marks, and the organism appears to have reworked the substrate in a vertically downwards direction.

CONCLUSIONS

The uppermost part of the Stairway Sandstone from the Middle Ordovician (Darriwilian) of central Australia contains exquisite 'arthropod' traces. On some bedding surfaces, the bioturbation is so intense that individual ichnospecies cannot be identified. Eleven ichnospecies are identified. Arthropod traces are not the only biogenic sedimentary structures found in this unit, for a number of other traces such as *Chondrites*, *Planolites* and other nondescript ichnofossils, probably produced by worm-like animals, were found and but are not described herein. From the ichnofossils, the lithology occurring at these localities, and the palaeotectonic setting, we assign the upper Stairway Sandstone to the *Cruziana* ichnofacies, formed under an epeiric sea on a continental shelf. Identification of the organisms that created the traces described is still open for debate. Rare large asaphid and other trilobite exoskeletal sclerites occur in the same strata, as do primitive fishes. The trilobite sclerites are of a suitable size for the animals that secreted them to have made some of the larger traces. However, sclerites are so rare, the traces are so common, and our knowledge of the sclerotised and unsclerotised members of the Arthropoda that may have co-existed with them in the Australian Middle Ordovician seas so incomplete, that we are unwilling to argue that trilobites must have been the only, or even primary, excavators of these traces. We even consider whether primitive bottom feeding fishes could have made one of the traces that we describe. One of the major problems faced by ichnologists who study Palaeozoic 'arthropod' traces, like those described in this work, is that many of the units that contain abundant traces contain few or no body fossils, and the units that contain abundant trilobites or other arthropods often contain few if any traces. Examples where trace makers and traces occur together, such as those of Osgood (1970) and possibly Fortey & Seilacher (1997), are the exception rather than the rule.

ACKNOWLEDGEMENTS

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APPENDIX: SPECIMEN DEATILS

Number	**Location**	**Identification**
F133018	CRR	Paratype: *Cruziana penicillata* isp. nov.
F133865	CRR	*Cruziana goldfussi* (Rouault 1850)
F133866	CRR	Paratype: *Cruziana penicillata* isp. nov.
F133868	CRR	Holotype: *Cruziana penicillata* isp. nov.
F133869	CRR	*Cruziana goldfussi* (Rouault 1850)
F133870	CRR	*Cruziana furcifera* d'Orbigny 1842
F133871	CRR	*Cruziana furcifera* d'Orbigny 1842 & Paratype: *Cruziana penicillata* isp. nov.
F133887	CRR	*Cruziana goldfussi* (Rouault 1850)
F133008	CR1	*Cruziana* indet. (erosion)
F133878	CR1	*Cruziana barriosi* Baldwin 1977
F133894	CR1	highly bioturbated
F133881	CR1F	*Cruziana omanica* Seilacher 1970

Number	**Location**	**Identification**
F133864	CR2	*Rusophycus* ?*unilobus* (Seilacher 1970
F133867	CR2	*Cruziana* indet. (fragment)
F133872	CR2	highly bioturbated
F133873	CR2	*Cruziana* indet. (erosion)
F133874	CR2	*Cruziana furcifera* d'Orbigny 1842
F133875	CR2	*Cruziana* indet. (erosion)
F133876	CR2	*Cruziana penicillata* isp. nov.
F133880	CR2	*Cruziana barriosi* Baldwin 1977
F133882	CR2	*Cruziana barriosi*? Baldwin 1977 or *Cruziana furcifera*? D'Orbigny 1842
F133947	CR3	*Cruziana furcifera* d'Orbigny 1842
F133948	CR3	possible fragment of thoracic segment
F133949	CR3	thoracic fragment, molluscs
F133950	CR3	thoracic segment, molluscs
F133951	CR3	*Cruziana omanica* Seilacher 1970
F133953, F133952	CR3	partial *Cruziana omanica* Seilacher 1970
F133954	CR3	ammonoid
F133955	CR3	molluscan fragments
F133956	CR3	impression of pygidium
F133957	CR3	pygidium
F133010	CR4	*Cruziana omanica* Seilacher 1970
F133011	CR4	*Cruziana omanica* Seilacher 1970
F133913	CR4	highly bioturbated *Monomorphichnus* spp.
F133914	CR4	*Cruziana omanica* Seilacher 1970
F133915	CR4	*Cruziana omanica* Seilacher 1970
F133916	CR4	*Cruziana omanica* Seilacher 1970
F133917	CR4	*Cruziana omanica* Seilacher 1970
F133918	CR4	half of *Cruziana omanica* (one lobe) Seilacher 1970
F133919	CR4	Paratype: *Monomorphichnus sinus* isp. nov.
F133920	CR4	*Rusophycus unilobus* (Seilacher 1970)
F133921	CR4	highly bioturbated *Monomorphichnus* spp.
F133922	CR4	*Cruziana omanica* Seilacher 1970
F133923	CR4	*Cruziana omanica* Seilacher 1970
F133924	CR4	*Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya 1977
F133958	CR4	*Cruziana omanica* Seilacher 1970
F133903	CR5	*Cruziana omanica* Seilacher 1970
F133904	CR5	highly weathered *Cruziana omanica* Seilacher 1970
F133905	CR5	*Cruziana omanica* Seilacher 1970
F133907	CR5	*Cruziana omanica* Seilacher 1970
F133909	CR5	*Cruziana omanica* Seilacher 1970
F133910	CR5	*Cruziana furcifera* d'Orbigny 1842
F133911	CR5	*Cruziana* indet.
F133023	CR6	highly bioturbated *Monomorphichnus* spp.
F133024	CR6	highly bioturbated *Monomorphichnus* spp.
F133025	CR6	*Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya 1977
F133026	CR6	*Diplichnites arboreus* isp. nov. & *Monomorphichnus* spp.
F133027	CR6	highly bioturbated *Monomorphichnus* spp.
F133861	CR6	highly bioturbated *Monomorphichnus* spp.
F133862, F133863	CR6	*Diplichnites arboreus*? & *Monomorphichnus* spp.
F133902	CR6	*Cruziana furcifera*? d'Orbigny 1842
F133906	CR6	*Cruziana omanica* Seilacher 1970
F133908	CR6	*Cruziana furcifera* d'Orbigny 1842
F133912	CR6	*Cruziana omanica* Seilacher 1970
F133006	CR7	*Cruziana omanica* Seilacher 1970
F133007	CR7	*Cruziana omanica* Seilacher 1970
F133009	CR7	*Cruziana omanica* Seilacher 1970
F133877	CR7	*Cruziana omanica* Seilacher 1970
F133879	CR7	*Cruziana omanica* Seilacher 1970
F133883	CR7	*Cruziana omanica* Seilacher 1970
F133884	CR7	*Cruziana barriosi* Baldwin 1977
F133885	CR7	*Monomorphichnus sinus* isp. nov. & *Monomorphichnus* indet.

Number	**Location**	**Identification**
F133886	CR7	*Cruziana omanica* Seilacher 1970
F133888	CR7	*Cruziana omanica* Seilacher 1970
F133889	CR7	*Cruziana omanica* Seilacher 1970
F133890	CR7	*Monomorphichnus sinus* isp. nov. & *Monomorphichnus* indet.
F133891	CR7	*Cruziana omanica* Seilacher 1970
F133892	CR7	*Cruziana omanica* Seilacher 1970
F133893	CR7	*Cruziana omanica* Seilacher 1970
F133895	CR7	*Cruziana omanica* Seilacher with pygidial impression
F133896	CR7	*Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya 1977
F133897	CR7	*Cruziana omanica* Seilacher 1970
F133898	CR7	*Cruziana omanica* Seilacher 1970
F133899	CR7	*Monomorphichnus sinus* isp. nov. & *Monomorphichnus* indet.
F133900	CR7	*Cruziana omanica* Seilacher 1970
F133901	CR7	*Cruziana omanica* Seilacher 1970
F133925	CR7	*Monomorphichnus lineatus*? Crimes, Legg, Marcos & Arboleya 1977
F133926	CR7	*Monomorphichnus sinus* isp. nov.
F133927	CR7	*Cruziana omanica* Seilacher 1970
F133929	CR7	*Cruziana omanica* Seilacher 1970
F133930	CR7	smooth *Rusophycus* indet.
F133931	CR7	*Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya 1977 & Holotype and Paratype: *Monomorphichnus sinus* isp. nov.
F133932	CR7	*Cruziana omanica* Seilacher 1970 (one lobe)
F133933	CR7	*Cruziana omanica* Seilacher 1970
F133934	CR7	Trilobite impression???
F133935	CR7	*Cruziana omanica* Seilacher 1970
F133936	CR7	*Cruziana goldfussi* (Rouault, 1850)
F133937	CR7	*Cruziana goldfussi* (Rouault, 1850)
F133938	CR7	*Cruziana furcifera* d'Orbigny 1842
F133939	CR7	*Cruziana omanica* Seilacher 1970
F133940, F133928	CR7	*Monomorphichnus sinus* isp. nov. & *Monomorphichnus* indet.
F133941	CR7	*Monomorphichnus sinus* isp. nov.
F133942	CR7	*Cruziana furcifera* d'Orbigny 1842
F133943	CR7	*Monomorphichnus multilineatus* Alpert 1976
F133944	CR7	smooth *Rusophycus* indet.
F133945	CR7	*Cruziana* indet.
F133946	CR7	*Cruziana omanica* Seilacher 1970
F133012	MW	*Cruziana penicillata* isp. nov. & *Cruziana* indet. & *Arandaspis* Ritchie & Gilbert-Tomlinson 1977 impression
F133013	MW	*Cruziana furcifera* d'Orbigny 1842
F133014	MW	Paratype: *Diplichnites arboreus* isp. nov. & *Chondrites* or *Planolites*
F133015	MW	*Cruziana penicillata* isp. nov.
F133016	MW	*Cruziana furcifera* d'Orbigny 1842
F133017	MW	Bivalves from upper unit
F133019	MW	*Cruziana penicillata*? isp. nov.
F133020	MW	*Cruziana penicillata* isp. nov. & *Diplichnites arboreus*? isp. nov.
F133021	MW	*Cruziana penicillata* isp. nov. & *Cruziana furcifera*? D'Orbigny 1842
F133022	MW	Paratype: *Diplichnites arboreus* isp. nov. & *Monomorphichnus lineatus* Crimes, Legg, Marcos & Arboleya 1977
F135852	MW	*Cruziana penicillata* isp. nov.
F135853	MW	Paratype: *Cruziana penicillata* isp. nov.
F135854	MW	*Cruziana penicillata*? isp. nov.
F135855	MW	Paratype: *Cruziana penicillata* isp. nov.
F135856	MW	Paratype: *Cruziana penicillata* isp. nov.
F58984	R.d. C1	Holotype: *Diplichnites arboreus* isp. nov.