Palaeoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA

Nicholas J. Minter [a],*, Karl Krainer [b], Spencer G. Lucas [c],
Simon J. Braddy [a], Adrian P. Hunt [c]

[a] *Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, UK*
[b] *Institute of Geology and Paleontology, Innsbruck University, Innrain 52, Innsbruck, A-6020, Austria*
[c] *New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, New Mexico 87104, USA*

Abstract

The Early Permian Choza Formation of the Clear Fork Group at Castle Peak in Texas, USA, contains a diverse and remarkably abundant trace fossil assemblage comprising exquisitely preserved arthropod trackways (*Diplichnites gouldi* types A and B, *Diplichnites* isp. A and B, *Lithographus* isp. and cf. *Kouphichnium* isp.), striated trails (*Cruziana problematica*) and isolated resting traces (*Rusophycus carbonarius* and *R. furcosus*), surface or shallow subsurface grazing trails or burrows (*Gordia indianensis*, *Helminthoidichnites tenuis*, *Treptichnus* isp., a nodular trail and unilobate epichnial trails), backfilled deposit-feeding burrows (*Planolites beverleyensis*), meniscate backfilled burrows (*Taenidium barretti*), horizontal branching networks, and tetrapod trackways (*Dromopus palmatus*, *Erpetopus willistoni*, *Varanopus curvidactylus* and cf. *Amphisauropus* isp.). Trace fossils formed in, and around the margins of, a shallow, ephemeral (playa) lake within an alluvial plain, and provide evidence of temporary communities, comprising arthropods, most notably notostracan branchiopod crustaceans, as well as euthycarcinoids, myriapods, insects, and tetrapods, including protorothyridid, captorhinid and araeoscelid reptiles and rare amphibians. Periodic influxes of water into the alluvial plain filled various depressions, creating temporary habitats and flourishes of life and activity.

The trace fossil assemblage is typical of the *Scoyenia* ichnofacies, and is similar to other assemblages from a range of different transitional subaqueous to subaerial settings, indicating that the distribution of trace fossils is not inextricably linked to the depositional setting itself, but rather to the environmental factors that arise. Such diverse trace fossil assemblages probably reflect relatively long-lived ephemeral water bodies, whereas more impoverished examples probably represent shorter-lived ephemeral water bodies. Assemblages such as Castle Peak, with abundant delicate arthropod trackways, probably reflect low energy conditions, conducive to the presence of an abundant vagile epifauna and the preservation of their trackways, whereas assemblages with open vertical burrows tend to lack arthropod trackways and probably reflect higher energy conditions. Trace fossil assemblages dominated by arthropod and tetrapod trackways may represent fleeting preservation windows following sheetfloods on floodplains.

* Corresponding author. Tel.: +44 117 3315181; fax: +44 117 9253385.
  E-mail address: N.J.Minter@bris.ac.uk (N.J. Minter).

1. Introduction

Nonmarine ichnology is in its infancy compared to marine ichnology in terms of our understanding of the distribution of trace fossils across different depositional settings. Three archetypal ichnofacies are widely accepted as being indicative of nonmarine depositional settings: *Scoyenia* (Seilacher, 1964, 1967), *Mermia* (Buatois and Mángano, 1993a, 1995) and *Coprinisphaera* (Genise et al., 2000). The body of literature on nonmarine trace fossil assemblages is increasing (Table 1), and continued, rigorous, rational documentation of trace fossils from a range of depositional settings can only aid the evaluation of these models, and potential recognition of additional ichnofacies.

The Early Permian trace fossils from Castle Peak in Texas were some of the first to be reported from North America (Williston, 1908). Much of the work to date has focussed on the tetrapod trackways (Moodie, 1929, 1930; Sarjeant, 1971; Haubold and Lucas, 2001, 2003). The ichnotaxonomy of tetrapod trackways has been through somewhat of a renaissance lately, with large-scale revisions of ichnotaxa based on the identification of minor preservational or behavioural variations (Haubold et al., 1995; Hunt et al., 1995; Haubold, 1996; McKeever and Haubold, 1996). Haubold and Lucas (2001, 2003) restudied the material from Castle Peak and made additional collections, considering only three tetrapod ichnotaxa to be valid: *Erpetopus willistoni*, *Varanopus curvidactylus* and *Dromopus palmatus*. Invertebrate trace fossils from Castle Peak have only been afforded passing mention to date (Williston, 1908; Moodie, 1929), which is surprising considering their remarkable abundance, diversity, and excellent preservation. This report presents the first systematic documentation and analysis of these invertebrate trace fossils, nearly 100 years after the locality was first discovered. In addition, we discuss the producers of these traces, their palaeoecological significance and the implications of the Castle Peak trace fossil assemblage for ichnofacies models.

2. Geological setting

Castle Peak is a round butte (Fig. 1A) approximately 16 km south of Merkel, Taylor County, Texas (UTM 405821E, 3581675N, zone 14, NAD 27). It is capped by Lower Cretaceous strata, and trace fossils occur in the Early Permian (Artinskian) Choza Formation of the Clear Fork Group, which is exposed along a small arroyo on the northern slope of Castle Peak. The exposed thickness of the Choza Formation measures 20.5 m and comprises intercalated: (a) red mudstone; (b) nodular mudstone; (c) fine-grained siltstone; (d) caliche; (e) sandstone (Figs. 1 and 2). The mineralogical composition of the sediments was determined by X-ray powder diffraction analysis. The trace fossil bearing horizon is a ledge-forming unit in the middle of the exposed section (Fig. 1B).

2.1. Facies descriptions

2.1.1. Red mudstone

The majority of the section comprises massive, locally indistinctly laminated red mudstones, consisting mainly of quartz, muscovite/illite and chlorite (clinochlore). Throughout the section, spherical and irregular patches of green mudstone, partly following cracks, are present (Fig. 1C). Locally, in the lower part of the section, small current ripples with ripple cross lamination are developed and irregular-shaped, light-grey, coarse-crystalline nodules of barian Celestine with diameters of up to 0.15 m are present (Fig. 1D). Small amounts of dolomite are present in the upper part of the section.

2.1.2. Nodular mudstone

The nodular mudstone beds are 0.15–0.5 m thick, red and greenish-grey in colour and contain small carbonaceous nodules. The mudstone contains significant amounts of dolomite in addition to quartz, muscovite/illite and chlorite (clinochlore). This facies only occurs in the lower part of the section.

2.1.3. Fine-grained siltstone

The fine-grained siltstone beds are 0.1–0.6 m thick, with small-scale current ripples and horizontal laminations. Under the microscope, the siltstones are extremely finely laminated. Individual laminae are mostly 0.02–0.2 mm thick. Sample CP 3 (unit 2; Fig. 2A) consists of alternating laminae composed of abundant small angular quartz grains, subordinate micas and dolomitic grains, and laminae composed dominantly of recrystallized reddish-brown dolomite grains and minor amounts of quartz and micas. Laminae of samples CP 10 (unit 14; Fig. 2A) and CP 11 (unit 17, the trace fossil bearing horizon; Figs. 2A and 3A) are composed of recrystallized dolomitic grains, detrital quartz and micas. Grain size is 0.01–0.03 mm. Small asymmetrical current ripples, 4.0 mm high and 30 mm long, with well-developed ripple-crossbedding are present in thin sections of samples of CP 10 and CP 11 (Fig. 3B).

2.1.4. Caliche

The caliche beds are 20–50 mm thick and red in colour. Sample CP 7 (unit 10; Figs. 2A and 3C) is from a caliche horizon composed of mostly spherical to ovoid,

Table 1
Trace fossil distribution across transitional subaqueous to subaerial nonmarine depositional settings

Setting	Period	Location	Trackways		Surface/shallow subsurface trails/burrows				Striated traces		Pits
			Vertebrate	Arthropod	Simple	Pattern	Probing	Branching	Trails	Isolated	
Closed lake margin	Tertiary	Spain	x								
	Tertiary	Namibia	x								
	Tertiary	Spain									
	Jurassic	USA									
	Triassic	Greenland									x
	Triassic	Germany								x	
	Triassic	Germany		x			x		x	x	x
	Permian	Argentina		x					x		
	Permian	USA	x	x	x	x	x		x	x	
Open lake margin	Tertiary	England						x			x
	Tertiary	USA									
	Cretaceous	England	x	x	x						x
	Cretaceous	Korea			x						
	Cretaceous	Korea	x	x	x						
	Triassic	USA									
	Triassic	USA	x		x	x					x
	Triassic	USA		x	x		x				x
	Triassic	USA	x		x	x	x				
	Triassic	Argentina	x		x				x	x	
	Carboniferous	Canada			x	x		x			
	Carboniferous	Canada			x				x	x	
	Devonian	Scotland		x	x				x		
Desiccated overbank	Tertiary	USA									
	Cretaceous	USA									
	Cretaceous	England	x		x						x
	Cretaceous	Korea									
	Cretaceous	USA									
	Cretaceous	Korea	x		x	x					
	Jurassic	USA									
	Triassic	Greenland									
	Triassic	India									
	Triassic	India									
	Triassic	Poland	x			x			x		

Setting	Period	Country									
	Triassic	N. Ireland	x	x	x			x		x	
	Triassic	Argentina	x	x	x			x		x	
	Permian	France	x	x				x			
	Permian	France	x	x	x	x		x			
	Permian	Argentina			x			x			
	Permian	South Africa	x	x	x	x					
	Permian	Spain	x					x			
	Permian	Germany	x								
	Permian	USA	x	x	x			x		x	
	Permian	USA	x	x	x					x	
	Carboniferous	Canada	x	x		x		x		x	x
	Devonian	Norway		x	x			x			
	Devonian	Wales		x	x			x		x	
Inactive fluvial	Tertiary	USA									
	Cretaceous	England	x								
	Cretaceous	USA									
	Cretaceous	Korea									
	Triassic	Germany		x				x		x	
	Triassic	England	x	x		x		x			
	Triassic	India									
	Triassic	India									
	Triassic	Canada			x	x		x		x	
	Triassic	Germany						x			
	Triassic	Argentina	x	x							
	Permo-Triassic	Antarctica			x			x			
	Carboniferous	Ireland									
	Carboniferous	Canada		x				x		x	
	Devonian	Norway									
Overfilled overbank	Tertiary	Switzerland	x		x		x		x		
	Cretaceous	New Zealand			x						
	Triassic	Lesotho			x						
	Triassic	Argentina	x		x						
	Permian	Argentina			x						
	Carboniferous	England			x						x
	Carboniferous	England	x	x	x	x					x
	Carboniferous	Poland		x	x						x
	Carboniferous	Canada	x				x				
	Carboniferous	Argentina			x						
Active fluvial	Triassic	India									
	Triassic	India									
	Permian	Antarctica									
	Carboniferous	Canada			x						

Trace fossil assemblages have been grouped following the depositional setting categories of Buatois and Mángano (2004). Trace fossils are sorted into broad morphological groups (modified after Kim et al., 2005), which are then subdivided into more specific types. Trackways; tetrapod (e.g. *Dromopus*, *Erpetopus* and *Varanopus*), arthropod (e.g. *Diplichnites* and *Lithographus*, note where *Diplopodichnus* has been described along with *Diplichnites* we have regarded it as a minor preservational variant). Surface/shallow subsurface burrows/trails; simple (e.g. *Cochlichnus*, *Helminthopsis*, *Helminthoidichnites*, and other trails such as *Protovirgularia*), pattern (e.g. *Gordia* and *Mermia*), probing (e.g. *Treptichnus*), branching (e.g. branching networks such as *Labyrintichnus*). Striated traces; continuous trails (e.g. *Cruziana*, *Monomorphichnus* and *Stiallia*, note where *Didymaulichnus* has been described along with *Cruziana* we have regarded it as a minor preservational variant), isolated traces (e.g. *Rusophycus* and *Tonganoxichnus*). Pits (e.g. *Lockeia*). Open burrows; vertical (e.g. *Skolithos*), horizontal (e.g. *Palaeophycus*), U-shaped (e.g. *Arenicolites* and *Diplocraterion*), chamber (e.g. *Tambia*), network (e.g. *Ophiomorpha* and *Spongeliomorpha*). Backfilled burrows; massive (e.g. *Planolites*), meniscate (e.g. *Beaconites*, *Scoyenia* and *Taenidium*), branched (e.g. *Chondrites*). Spreiten-like burrows (e.g. *Fuersichnus*). Displacement burrows (e.g. *Tumblagoodichnus*). The number of specific morphological types is given for each assemblage and the number in common with Castle Peak provided in brackets. The number of broad morphological groups has also been given and the number in common with Castle Peak in brackets.

Table 1 (*continued*)

Setting	Open burrows					Backfilled burrows			Spreiten burrows	Displacement burrows	Number of types	Number of groups	Reference
	Vertical	Horizontal	U-shaped	Chamber	Network	Massive	Meniscate	Branched					
Closed lake margin	x						x				3(2)	3(2)	Rodríguez-Aranda and Calvo (1998)
	x		x			x	x	x			6(3)	3(2)	Smith and Mason (1998)
	x				x		x				3(1)	2(1)	Uchman and Álvaro (2000)
	x					x					2(1)	2(1)	Gierlowski-Kordesch (1991)
	x	x				x			x		5(1)	4(1)	Bromley and Asgaard (1972, 1979)
	x						x				3(2)	3(2)	Schlirf et al. (2001)
	x		x					x	x		9(4)	7(4)	Knaust and Hauschke (2004, 2005)
		x	x								4(2)	3(2)	Aceñolaza and Buatois (1993), Zhang et al. (1998)
						x	x				9(-)	4(-)	This study
Open lake margin							x				3(1)	3(2)	Daley (1968)
							x				1(1)	1(1)	Squires and Advocate (1984)
		x	x			x	x				8(5)	5(3)	Goldring and Pollard (1995), Goldring et al. (2005)
	x	x					x	x			5(2)	3(2)	Kim et al. (2002)
	x	x				x	x				7(5)	4(3)	Kim et al. (2005)
	x	x	x		x	x	x				6(2)	2(1)	Gillette et al. (2003)
		x			x	x	x				8(5)	5(3)	Metz, (1989, 1993)
					x	x	x				7(5)	5(3)	Metz (1995)
		x			x	x	x				8(6)	4(3)	Metz (1996)
		x			x		x				7(5)	5(4)	Melchor et al. (2006)
		x				x					5(3)	3(2)	Pickerill (1992)
		x									3(3)	2(2)	Keighley and Pickerill (1997, 1998, 2003)
			x								4(3)	4(3)	Smith (1909); Pollard and Walker (1984), Walker (1985)
Desiccated overbank	x	x					x				3(1)	2(1)	d'Alessandro et al. (1987)
	x						x				2(1)	2(1)	Bracken and Picard (1984)
							x				4(3)	4(3)	Goldring and Pollard (1995), Goldring et al. (2005)
	x		x			x	x				4(2)	2(1)	Kim and Paik (1997)
							x				1(1)	1(1)	Savrda et al. (2000)
	x	x			x	x	x	x			9(5)	4(3)	Kim et al. (2002)
	x	x				x	x		x	x	6(2)	4(1)	Gierlowski-Kordesch (1991)
	x					x	x				3(2)	2(1)	Bromley and Asgaard (1972, 1979)
						x					1(1)	1(1)	Maulik and Chaudhuri (1983)
	x	x					x				3(1)	2(1)	Sarkar and Chaudhuri (1992)
		x	x			x					6(4)	5(4)	Gradziński and Uchman (1994)

	x			x						7(6)	5(4)	Buckman et al. (1997)
	x	x		x		x	x			10(6)	5(4)	Melchor et al. (2006)
						x				4(4)	3(3)	Debriette and Gand (1990)
	x				x	x				8(7)	5(4)	Demathieu et al. (1992)
		x				x				4(3)	4(3)	Aceñolaza and Buatois (1993)
					x	x				6(6)	3(3)	Smith (1993)
	x					x				4(3)	4(3)	Gand et al. (1997)
			x		x					3(2)	3(2)	Eberth et al. (2000)
						x				6(6)	4(4)	Lucas et al. (2005a)
										4(4)	3(3)	Lucas et al. (2005b)
						x				7(6)	5(4)	Keighley and Pickerill (1997, 1998, 2003)
										3(3)	3(3)	Pollard et al. (1982)
Inactive fluvial		x				x			x	7(5)	6(4)	Morrissey and Braddy (2004)
	x					x				2(1)	2(1)	Stanley and Fagerstrom (1974)
					x	x				3(3)	2(2)	Goldring and Pollard (1995), Goldring et al. (2005)
				x						1(0)	1(0)	Savrda et al. (2000)
	x				x					2(1)	2(1)	Kim et al. (2002)
	x	x			x	x				7(4)	4(3)	Bromley and Asgaard (1972, 1979)
				x	x					6(5)	5(4)	Pollard (1981)
					x					1(1)	1(1)	Maulik and Chaudhuri (1983)
	x				x					3(1)	2(1)	Sarkar and Chaudhuri (1992)
	x	x			x	x		x	x	10(6)	6(3)	MacNaughton and Pickerill (1995)
	x									2(1)	2(1)	Schlirf et al. (2001)
	x	x				x				5(3)	3(2)	Melchor et al. (2006)
	x	x								4(2)	3(2)	Miller and Collinson (1994), Miller (2000)
					x					1(1)	1(1)	Graham and Pollard (1982)
	x			x						5(3)	3(2)	Pickerill (1992)
					x					1(1)	1(1)	Pollard et al. (1982)
Overfilled overbank	x				x					6(4)	4(3)	Uchman et al. (2004)
				x						2(1)	2(1)	Fordyce (1980)
										1(1)	1(1)	Turner (1978)
				x		x				4(3)	4(3)	Melchor et al. (2006)
		x		x						3(1)	2(1)	Buatois et al. (1997)
					x				x	4(2)	4(2)	Miller (1986)
										5(4)	3(2)	Pollard and Hardy (1991)
					x	x			x	6(4)	5(3)	Głuszek (1995)
				x	x	x				5(4)	4(3)	Keighley and Pickerill (1997, 1998, 2003)
		x			x					3(2)	3(2)	Buatois and Mángano (2002)
Active fluvial	x									1(0)	1(0)	Maulik and Chaudhuri (1983)
	x								x	2(0)	2(0)	Sarkar and Chaudhuri (1992)
	x									1(0)	1(0)	Fitzgerald and Barrett (1986)
		x								2(1)	2(1)	Keighley and Pickerill (1997, 1998, 2003)

subordinate irregular-shaped, reddish-brown micritic grains (caliche peloids). These grains are mostly 0.3–1.5 mm in diameter, dolomitic in composition, densely packed and partly recrystallized. The pore space is filled with two generations of unstained dolomite cement. Small detrital quartz grains are very rare, as are shrinkage fissures.

2.1.5. Sandstone

The sandstone bed is 20–50 mm thick, medium-grained, poorly sorted and indistinctly laminated. The sandstone bed occurs at the same stratigraphic level as a fine-grained siltstone bed (unit 14; Fig. 2A) within the measured composite section. Sample CP 9 (unit 14; Figs. 2A and 3D) comprises grains mostly 0.2–0.5 mm, but up to 2.0 mm, in diameter. The majority of grains are subrounded, but rounded and subangular grains are also present. The sandstone is composed entirely of sedimentary rock fragments in the form of reworked reddish mudstone and fine-grained siltstone fragments embedded in a reddish-coloured, fine-grained silty matrix, that has the same composition as the sand grains (recrystallized dolomitic mudstone with a few angular quartz grains up to 0.1 mm in diameter). Sand grains are more red coloured than the matrix. A few opaque grains are present, and locally, the sandstone is bleached.

2.2. Trace fossil bearing horizon

The trace fossil bearing horizon (unit 17; Fig. 2A) comprises siltstones interbedded with thin mudstones, and forms a distinct ledge in the middle of the exposed section (Fig. 1B). This horizon is up to 0.25 m thick and thins out laterally, extending over a distance of about 200 m NE–SW and about 50 m NW–SE (Haubold and Lucas, 2003). From a 0.2 m thick succession of the trace fossil bearing horizon we recognize 28 distinctive beds (Fig. 2B), most less than 10 mm thick (although bed 11 is 25–30 mm thick) and commonly separated by thin mudstone partings. The mineralogical composition is similar to the mudstone and siltstone above and below, mainly quartz, muscovite/illite, chlorite and dolomite in varying amounts. Bed 27 contains significantly higher amounts of dolomite than beds 6, 10 and 16. A slight colour change is observed in the middle of the horizon, between beds 14 and 15. The lower part is darker red than the upper part.

A number of sedimentary structures are observed within the trace fossil bearing horizon (Fig. 4). The individual beds either appear massive or are laminated. The most common internal structure is ripple cross lamination. Horizontal lamination is also observed.

Ripples of different size occur: (a) asymmetrical current ripples with wavelengths of 50–120 mm and heights of several millimetres; (b) small symmetrical to asymmetrical ripples with wavelengths of 10–50 mm and heights of 1.0–3.0 mm; and (c) microripples (mini-ripples of Singh and Wunderlich, 1978; Reineck and Singh, 1980) are small straight-crested ripples with wavelengths of about 5.0 mm and heights of less than 1.0 mm. The larger asymmetrical and small asymmetrical ripples show internal unidirectional ripple cross lamination. The larger current ripples of bed 11 are crescentic to linguoid in shape.

Desiccation mudcracks of varying scales occur in many beds throughout the trace fossil bearing horizon (Fig. 4A), and small-scale lenticular shrinkage cracks are present locally. Chevron marks are rare, other than on the upper bedding surface of bed 12 and the lower bedding surface of bed 11, and are associated with other small-scale tool marks (Fig. 4B). Raindrop imprints, 3.0–5.0 mm in diameter (Fig. 4C), parting lineations, small-scale load structures, ?gas bubble structures and very small halite pseudomorphs, up to 1.0 mm in size, are also present (Fig. 4D).

2.3. Interpretation

The Choza Formation was deposited on the eastern shelf of the marine Midland Basin as fluvial and lacustrine red beds interbedded with thin dolomites of marine origin (Presley and McGillis, 1982). The red mudstones formed by settling from ephemeral muddy sheetfloods on a flat, wide, distal alluvial plain (element FF, floodplain fines of Miall, 1996). Channels are poorly defined or absent. Periodically, coarser, mostly silty material was transported, resulting in the formation of small current ripples (lower flow regime) in very shallow, broad channels. Thin siltstone layers with horizontal lamination represent sheetflood deposits probably resulting from plane-bed flow. The presence of nodular mudstone horizons, containing small caliche nodules overlain by thin caliche beds composed of caliche peloids, indicates that the alluvial plain dried out over longer periods, causing the formation of pedogenic horizons. The caliche peloids are similar to pellets described from calcretes of southwestern USA by Hay and Wiggins (1980). The lack of detrital material and the presence of unbroken caliche peloids indicate that they formed *in situ*. Caliche peloids may represent small concretions that grew by accretion or may have formed by cementation of pellet-shaped grains of porous micrite (Hay and Wiggins, 1980). According to Flügel (2004), such peloids may also represent calcified faecal pellets
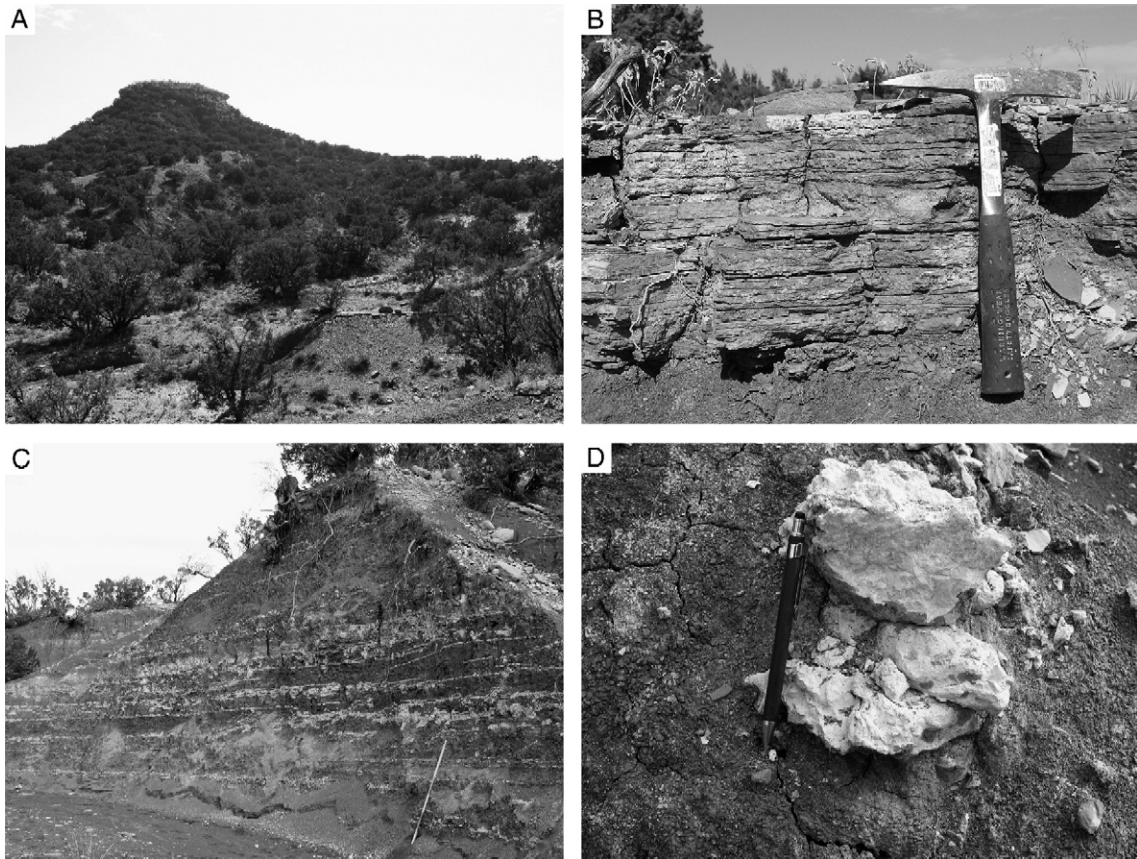
Fig. 1. Castle Peak, Taylor County, Texas, USA. (A) Castle Peak, a round butte comprising the Early Permian (Artinskian) Choza Formation of the Clear Fork Group, capped by Cretaceous strata. (B) Ledge-forming trace fossil bearing horizon, note the thicker bed 11 with large current ripples in the middle of the unit. (C) Base of the exposed section with massive, locally indistinctly laminated red sheetflood mudstones, with irregular patches of green mudstone. (D) Celestine nodules at the base of the exposed section.

of small soil-dwelling arthropods. Celestine nodules are indicative of an evaporitic environment. Under these semiarid-to-arid climatic conditions, sediment may also have been transported and deposited by wind (aeolian dust/silt). The thin sandstone bed composed entirely of reworked intraclasts most likely represents a sandy sheetflood deposit that formed by reworking of previously deposited mudstone/fine siltstone.

The trace fossil bearing horizon represents deposits of a small ephemeral (playa) lake that formed in a shallow depression on the alluvial plain. Each thin bed of the trace fossil bearing horizon represents one single event of sedimentation. Sediment was periodically transported into the lake by ephemeral, shallow, broad streams producing thin layers with current ripples. Some coarser material may have been transported into the lake by the wind (aeolian sediment). The wet phases (when the lake was filled with a standing body of water) were quite short, and small ripples may have formed as wave ripples, in shallow water depths of less than 1 m, and

current ripples, probably resulting from wind-driven currents. Microripples formed in the very shallow shore zone by slow-moving waves in water depths of a few centimetres (see Reineck and Singh, 1980). Larger ripples are probably the result of fluvial input of silty sediment into the pond. The thin mudstone intervals represent lake suspension deposits. The presence of chevron marks indicates that currents (wind induced?) periodically drove tools over the soft sediment surface. The occurrence of many small halite pseudomorphs indicates rapid crystal growth through high evaporation and increasing the salinity of the water. Mudcracks and raindrop imprints demonstrate that the pond periodically dried out. Raindrop imprints are poorly developed when there is heavy rain, and their preservation potential is much higher when there is only occasional and slight rain. The lake was ephemeral for most of its history, and the trace fossil bearing horizon was probably deposited within a relatively short time span of less than 1000 years.
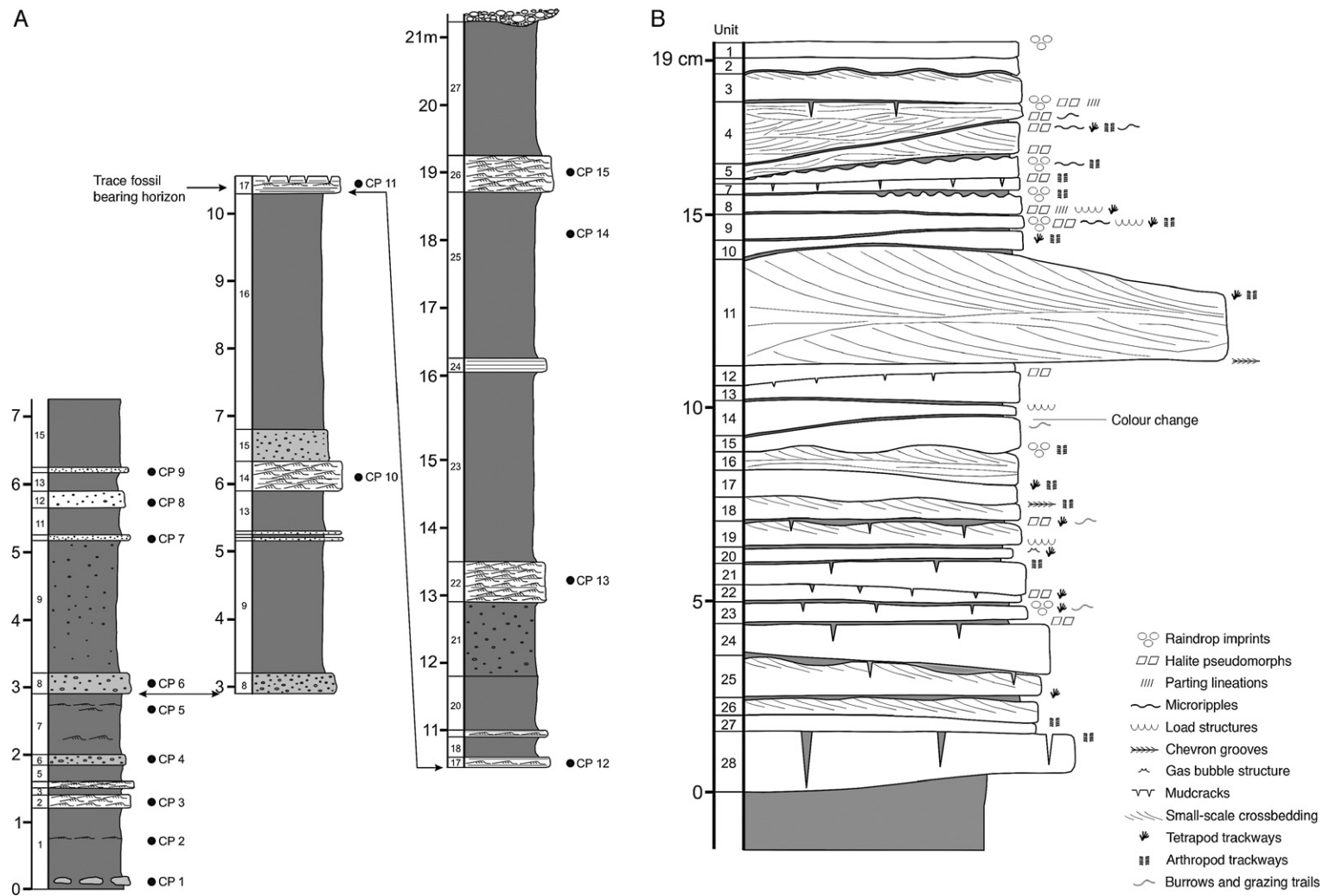
Fig. 2. Castle Peak sections. (A) Stratigraphy of the Early Permian (Artinskian) Choza Formation of the Clear Fork Group. (B) Detail of the 0.2 m thick section of the trace fossil bearing horizon.

3. Trace fossils

3.1. Cruziana problematica (Schindewolf, 1928) (Fig. 5)

3.1.1. Description

Straight to slightly curved bilobate trails. External width ranges from 0.6–9.4 mm, and follows a bimodal distribution with modal classes at 1.0–2.0 mm and 5.0–6.0 mm (Fig. 6A). The lobes range from 0.3–4.3 mm in width and are separated by up to 1.5 mm. The lobes preserve closely spaced striations, transverse to the midline of the trail (Fig. 5A). Some trails consist of just two parallel rows of striations, and have a greater medial separation than the examples with lobes (Fig. 5B). The striations are not always present for part or all of the length of some trails (Fig. 5C–D).

3.1.2. Remarks

The nomenclature of bilobate trace fossils, in particular the use of Isopodichnus and Cruziana–

Rusophycus, is debated (Bromley and Asgaard, 1972; Trewin, 1976; Bromley and Asgaard, 1979; Pollard, 1985; Keighley and Pickerill, 1996). The type material of Isopodichnus problematicus includes a range of intergrading morphologies and behavioural patterns; ribbon grazing traces, short bilobate resting traces, and 'coffee-bean' resting traces (Schindewolf, 1928; Pollard, 1985). Various authors have subsequently advocated the retention of Isopodichnus (e.g. Trewin, 1976; Pollard, 1985), or its synonymy with Cruziana and Rusophycus (e.g. Bromley and Asgaard, 1972, 1979; Keighley and Pickerill, 1996). A range of criteria have been proposed to differentiate Isopodichnus from Cruziana–Rusophycus, including morphology, its occurrence in non-marine facies, and presumed non-trilobite producer (Pollard, 1985). In terms of ichnotaxonomy, the primary ichnotaxobase used to diagnose and differentiate ichnotaxa should be morphology (Bromley, 1990; Bertling et al., 2006). Trace fossils are rarely preserved together with body fossils of their producer,
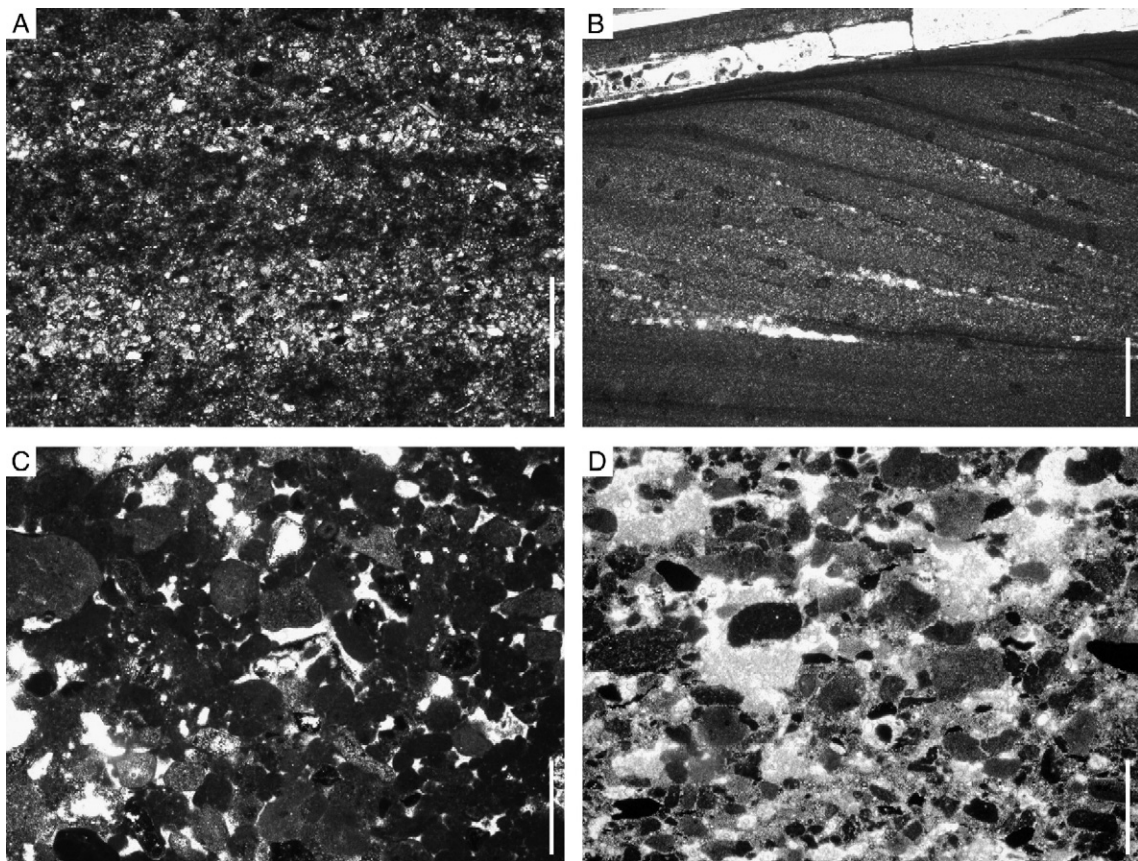
Fig. 3. Thin sections taken from the Choza Formation (identifications relate to the units identified in Fig. 2A). (A) CP 11, mudstone laminae composed of recrystallized dolomitic grains, detrital quartz, and micas. (B) small asymmetrical current ripples in CP 11. (C) CP 7, caliche horizon composed caliche peloids. (D) CP 9, poorly sorted, indistinctly laminated, medium grained sandstone. Scale bars 0.5 mm in A and 1 mm in B–D.
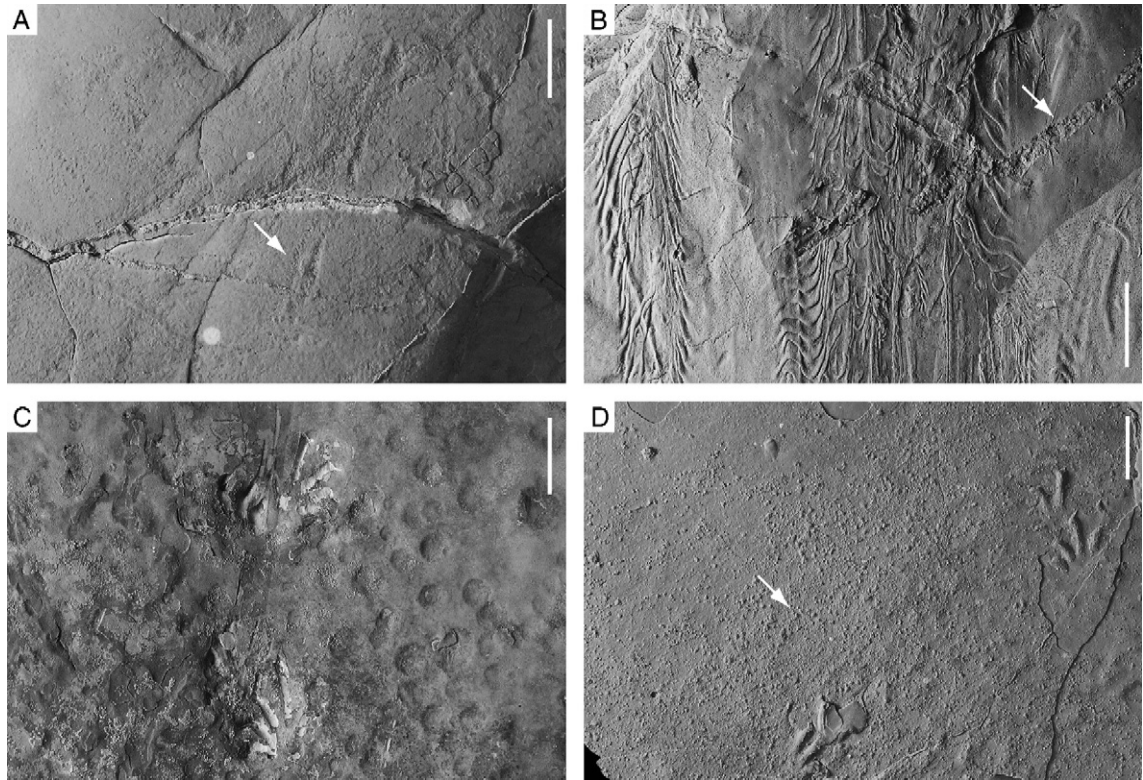
Fig. 4. Sedimentary structures of the trace fossil bearing horizon. (A) Desiccation mudcracks crosscutting *Cruziana problematica*, NMMNH P-46695 (arrow). (B) Chevron grooves preserved in hyporelief and crosscut by *Taenidium barretti* (arrow). (C) Raindrop imprints overprinted by *Erpetopus willistoni*. (D) Numerous small halite pseudomorphs (arrow) overprinted by *E. willistoni*. Scale bars 10 mm.

so any inferences about producers are interpretations, albeit informed, and are therefore subject to change. Facies associations should also be rejected as an ichnotaxobase, because any palaeoenvironmental inferences based on the presence of those ichnotaxa would result in circular reasoning. A range of morphological criteria have been proposed to distinguish *Isopodichnus* from *Cruziana–Rusophycus*, including size (Seilacher, 1970; Hakes, 1976; Trewin, 1976), the nature of terminations (Trewin, 1976), and scratch mark patterns (Birkenmajer and Bruton, 1971; Trewin, 1976); however, none of these are reliable, and they require well-preserved material. Material referred to *Isopodichnus* does tend to be narrower than *Cruziana–Rusophycus* (Seilacher, 1970; Hakes, 1976; Trewin, 1976), although size is not an ideal ichnotaxobase, especially at the ichnogeneric level. If size is to be used as an ichnotaxobase, it should preferably be used when distinct size classes can be identified, ideally separated by an order of magnitude.

We follow Bromley and Asgaard (1972, 1979) and Keighley and Pickerill (1996) and regard *Isopodichnus* as synonymous with *Cruziana–Rusophycus*, even though this splits established ichnospecies of *Isopodichnus*

across *Cruziana* and *Rusophycus* (Pollard, 1985). Intergrading material can be used to justify synonymy between ichnotaxa; however, this should only be applied to intergradation between minor behavioural or preservational variations. The intergradation between long ribbon and short bilobate or 'coffee-bean' traces represents major behavioural variation (i.e. separate ethological categories) between grazing and resting behaviour respectively, so they should not be synonymized. Keighley and Pickerill (1996) proposed a length:width ratio of 2:1 to distinguish between *Cruziana* and *Rusophycus*. Following this recommendation, ribbon traces of *I. problematicus* are referred to *C. problematica* and short bilobate and 'coffee-bean' traces would be referred to *R. problematicus*, although *R. carbonarius* may be available for such forms (see below); a situation not so far removed from the suggestion of Pollard (1985) to supplement *Isopodichnus* as being 'rusophyciform' or 'cruzianiform.'

The material from Castle Peak conforms to *C. problematica* in possessing closely spaced transverse striations (Keighley and Pickerill, 1996). Reported external widths of *C. problematica* range from 1.0–11.0 mm
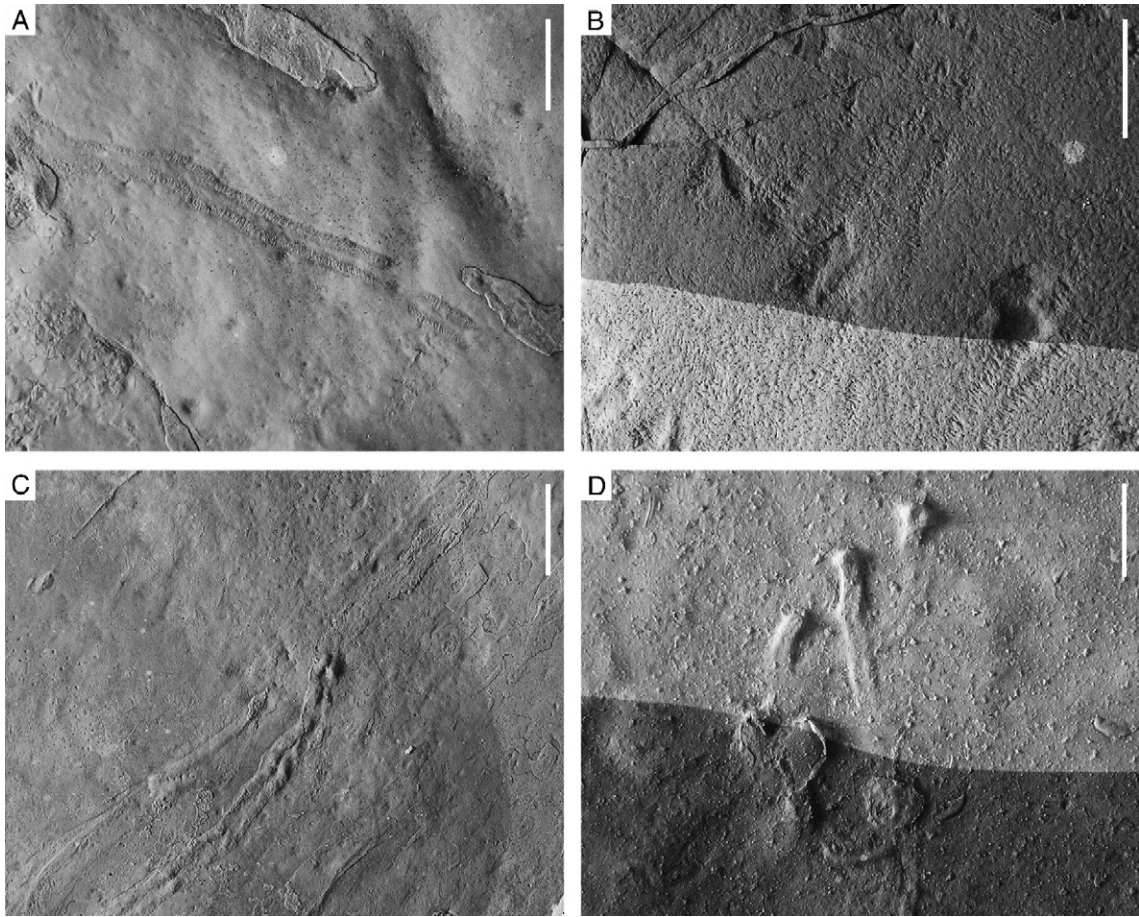
Fig. 5. *Cruziana problematica*. (A) NMMNH P-46706. (B) NMMNH P-46710, note the presence of 'appendage marks' and lack of well-defined grooves. (C) NMMNH P-46916, note the poorly developed striations similar to *Didymaulichnus*, and periodic deeper sections corresponding to *Rusophycus carbonarius*. (D) NMMNH P-46732, note the lack of striations, and expanded terminations similar to *R. stromnessi*. Scale bars 5 mm in A and D, and 10 mm in B–C.

(Bromley and Asgaard, 1979; Fillion and Pickerill, 1990; Schlirf et al., 2001). Some of the material from Castle Peak consists of two parallel rows of striations (Fig. 5B), similar to the 'appendage mark' traces of Trewin (1976). Keighley and Pickerill (1996) considered these forms to be *Diplichnites sensu lato*, but we regard them as minor preservational or behavioural variations of *C. problematica* because the imprints are too closely spaced to be tracks as opposed to striations. In some examples, the striations are poorly developed or lacking (Fig. 5C–D), which is a condition of *Didymaulichnus* (Young, 1972). However, where there are large samples of *Cruziana* and *Rusophycus* it is perhaps most parsimonious to regard them as minor preservational or behavioural variants and include them within these ichnogenera (Trewin, 1976; Bromley and Asgaard, 1979). Some specimens of *C. problematica* intergrade with *R. furcosus* (Fig. 12D) and *R. carbonarius* (Figs. 5C and 12B), whereas some

terminations are expanded and similar to *R. stromnessi sensu* Keighley and Pickerill (1996) (Fig. 5D).

3.2. Diplichnites gouldi (Bradshaw, 1981) (Figs. 7 and 8)

3.2.1. Description

Two separate morphotypes of *Diplichnites gouldi* are identified from Castle Peak. Type A comprises two parallel track rows with low angle, V-forming series of six to eleven tracks (Fig. 7). It is sometimes difficult to determine the number of tracks per series due to the low angle and overlap between series and the number of tracks per series varies within trackways, with sometimes as few as five tracks. In some examples, the low angle series and high degree of overlap between series result in tracks from different series overprinting to form composite V-shaped tracks (Fig. 7C). The external widths of the trackways are normally distributed, with a
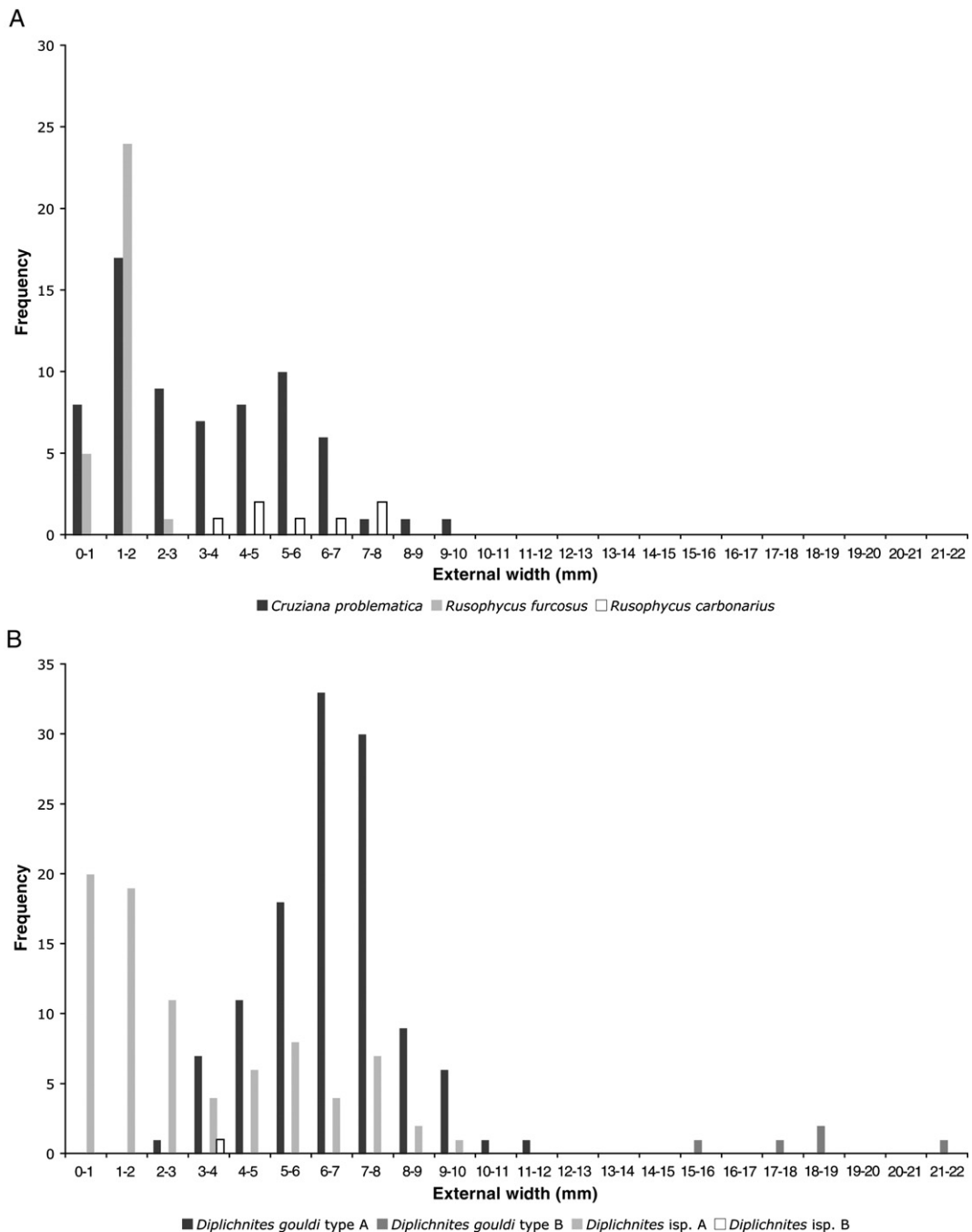
Fig. 6. External widths of striated trails and isolated traces, and arthropod trackways. (A) Striated trails *Cruziana problematica* and isolated traces *Rusophycus carbonarius* and *R. furcosus*. (B) Arthropod trackways *Diplichnites gouldi* types A–B and *Diplichnites* isp. A–B.

range of 2.7–11.0 mm and modal class of 6.0–8.0 mm (Fig. 6B). Tracks are mostly linear, and are elongated transversely or highly obliquely to the midline of the trackway, but may also be curved, ovate, or rounded. The majority of trackways lack medial impressions (Fig. 7A–C), although they are present in some

(Fig. 7D–E) and intermittent in others. Two linear impressions are present in some specimens (Fig. 7F), and tend to be situated just inside the track row on either side, or both may be displaced to one side.

Type B comprises two parallel track rows with V-forming series of eight tracks at a low angle to the
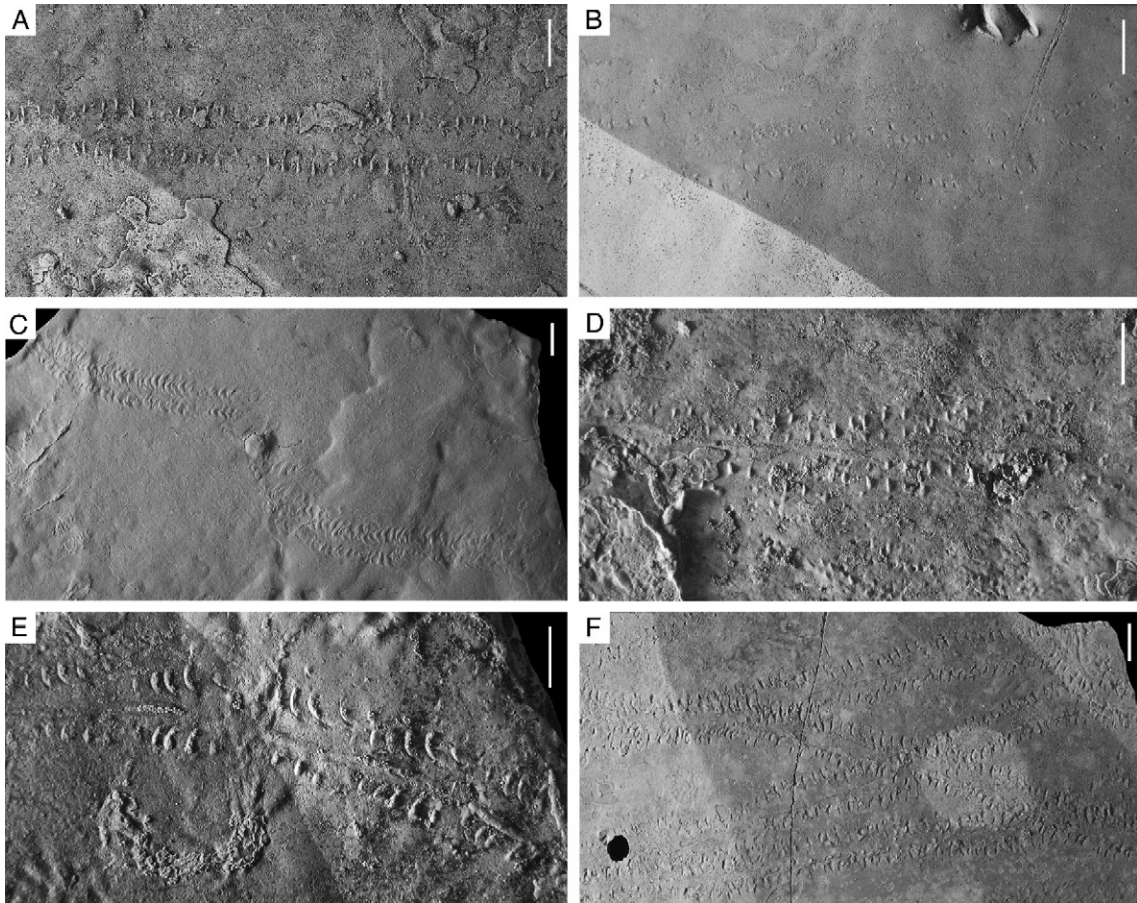
Fig. 7. *Diplichnites gouldi* type A. (A) NMMNH P-46934, with series of ten tracks. (B) NMMNH P-46921, with series of eight tracks. (C) NMMNH P-46931, note the very low angle series of tracks with a high degree of overlap and composite V-forming tracks. (D) NMMNH P-45747a, with series of 11 tracks and a continuous medial impression. (E) NMMNH P-45750, with series of six tracks and a continuous medial impression. (F) NMMNH P-46794, with series of six tracks, and P-46800, with series of seven tracks and two intermittent medial impressions. Scale bars 5 mm.

midline of the trackway (Fig. 8). Tracks are ovate, rounded, or curved to comma-shaped. All specimens lack medial impressions. The external width ranges from 15.9–21.9 mm (Fig. 6B). Tracks are generally transverse to the midline of the trackway, although they are oblique in one example, with the tracks on both sides of the trackway having the same orientation (Fig. 8A). The overlap between series ranges from two to four tracks.

3.2.2. Remarks

The classification of *Diplichnites* has a protracted history, and a comprehensive review of the relationships between *Diplichnites* and similar ichnotaxa is long overdue, but beyond the scope of this manuscript. The situation has not been aided by the relatively inadequate original description and illustration, compounded by the fact that the holotype cannot be located. *Diplichnites* was first described as comprising two parallel rows of closely

spaced, transversely elongated tracks (Dawson, 1862). *Diplichnites* has also been used, following Seilacher (1955), for trackways with various numbers of tracks arranged into V-forming series (Osgood and Drennen, 1975; Fillion and Pickerill, 1990; Trewin and McNamara, 1995; Smith et al., 2003). The relationships between *Diplichnites* and *Acripes*, *Asaphoidichnus*, *Lineatichnus*, *Merostomichnites*, *Multipodichnus*, *Pentapodichnus*, *Petalichnus*, *Protichnites*, *Tasmanadia*, *Trachomatichnus* and *Umfolozia* need to be resolved before even attempting to untangle the web of ichnospecies. The Castle Peak trackways are similar to material described as *D. gouldi* by Trewin and McNamara (1995) and Smith et al. (2003), and therefore, to aid future revisions, we refer this material to *D. gouldi*.

Diplichnites gouldi types A and B both comprise recognisable series of V-forming tracks, but there is a clear size distinction (Fig. 6B). Some specimens of type
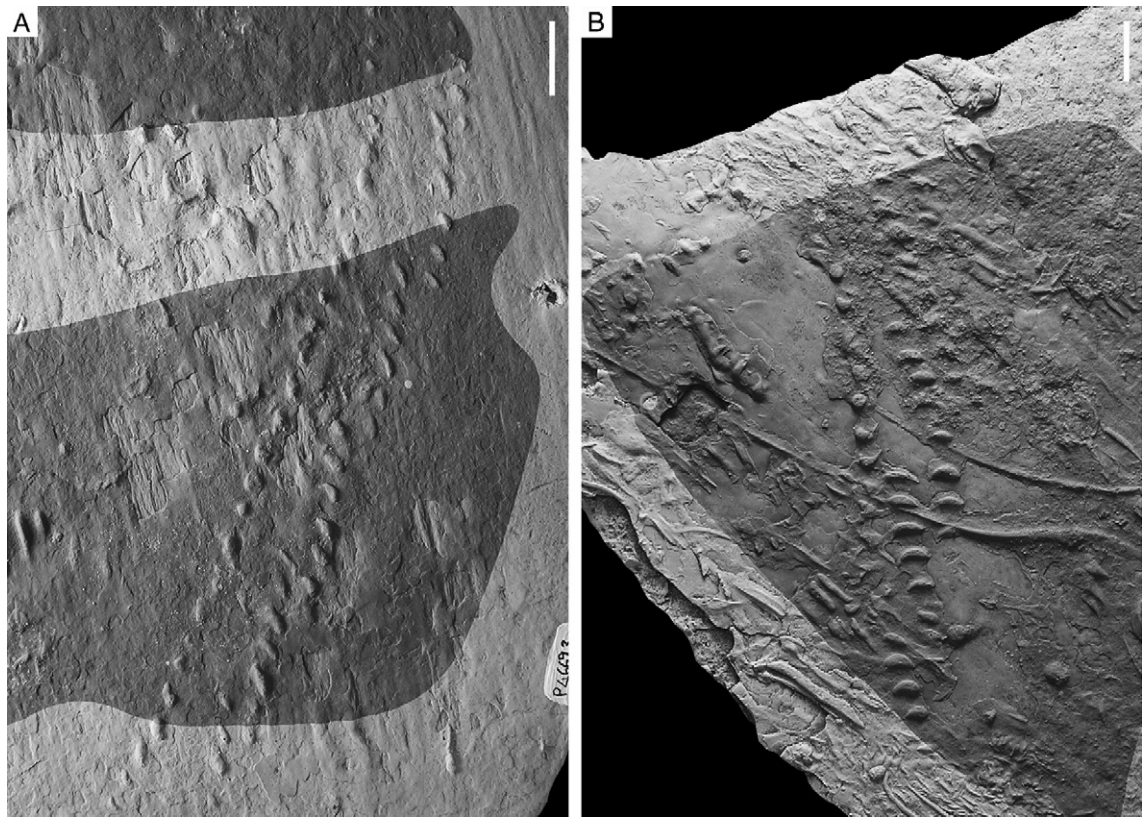
Fig. 8. *Diplichnites gouldi* type B. (A) NMMNH P-46693. (B) NMMNH P-46913. Note the asymmetrical form of the trackways and that the tracks on both sides of the trackway in (A) have the same orientation. Scale bars 10 mm.

A possess medial impressions, whilst *Diplichnites* is considered to lack a medial impression, and such material is generally referred to *Protichnites*. Gevers et al. (1971) describe *D. gouldi* as lacking a medial impression, although Bradshaw (1981) observed medial impressions in material from the same locality. Material from Castle Peak demonstrates a range of forms, from those lacking medial impressions, through intermittent, to those with continuous medial impressions. Such a feature could easily be regarded as a minor preservational or behavioural variation and therefore not an ideal ichnotaxobase, particularly at the ichnogeneric level. A similar situation has been documented in *Paleohelcura* (Gilmore, 1926; Brady, 1961).

3.3. Diplichnites isp. A (Fig. 9A–E)

3.3.1. Description

Trackways with two parallel track rows, but lacking any identifiable V-forming series of tracks. The external width of trackways ranges from 0.4–9.2 mm, but the distribution is skewed with the majority in the range 0.0–2.0 mm (Fig. 6B). The vast majority of tracks are

linear, but some are curved, ovate, rounded or comma-shaped. Tracks are orientated transversely to highly obliquely to the midline of the trackway. A continuous medial impression is present in some examples (Fig. 9D).

3.3.2. Remarks

These trackways are differentiated by the lack of identifiable V-forming series of tracks. In rare examples, the tracks merge into paired furrows similar to *Diplopodichnus biformis* (Fig. 9E).

3.4. Diplichnites isp. B (Fig. 9F)

3.4.1. Description

One specimen with two parallel track rows with three to five tracks across the width of the track row. There are no identifiable V-forming series of tracks and no medial impression. Tracks are closely spaced, small, and rounded. The external width of the trackway is 3.1 mm.

3.4.2. Remarks

This trackways differs from all of the other *Diplichnites*-like trackways from Castle Peak, in that it comprises
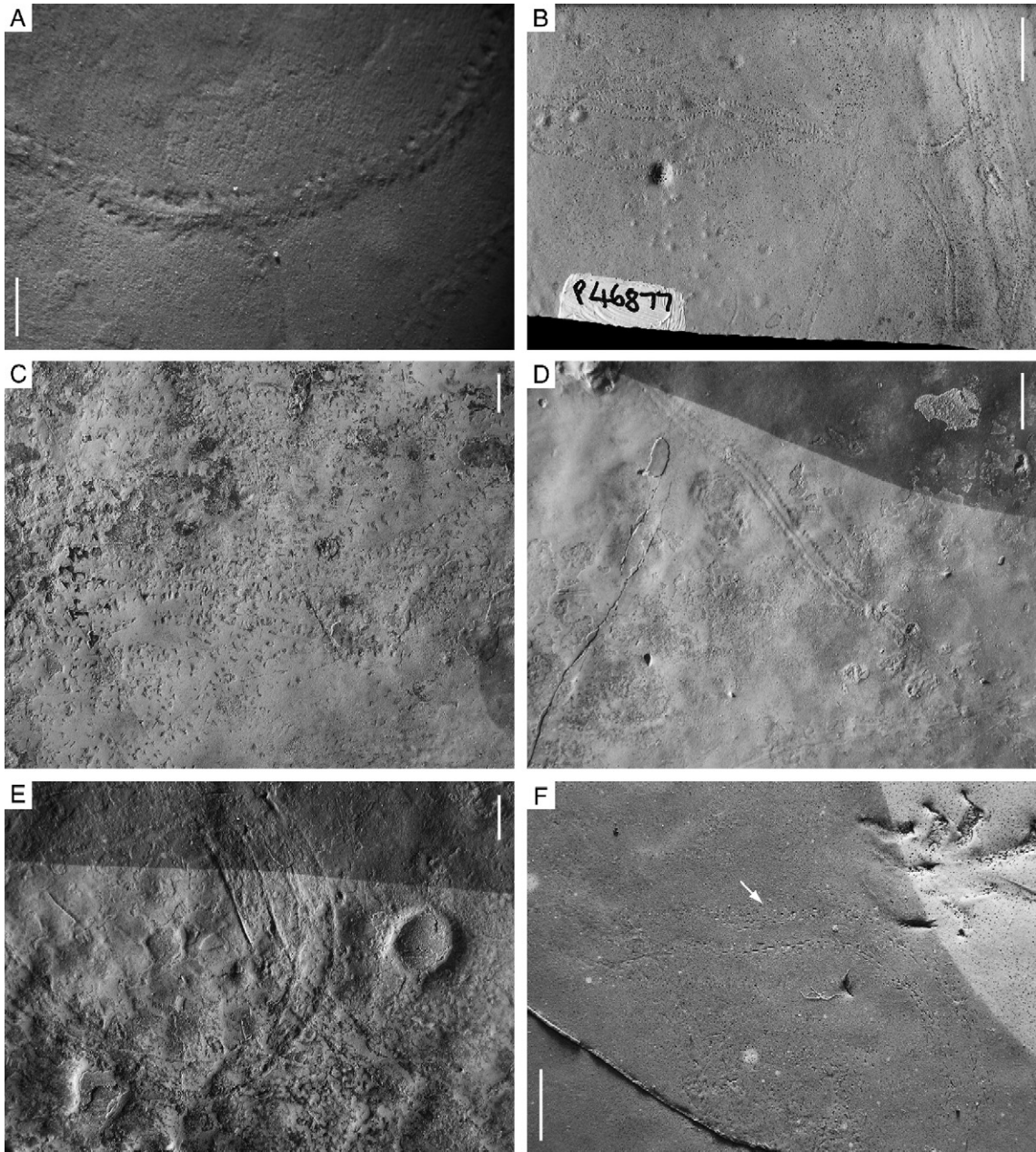
Fig. 9. (A–E) *Diplichnites* isp. A. (A) NMMNH P-47753. (B) NMMNH P-46877. (C) NMMNH P-32409, with multiple trackways on a single surface. (D) NMMNH P-32408, with a continuous medial impression. (E) NMMNH P-32401, note the intergradation from paired furrows with tracks to paired furrows similar to *Diplopodichnus biformis*, and a ?gas bubble structure. (F) *Diplichnites* isp. B, NMMNH P-46848 (arrow). Scale bars 1 mm in A and 5 mm in B–F.

multiple tracks across the width of the track row for the length of the row, and there are no identifiable series. Various forms of *Diplichnites* have been described as having multiple tracks across the track row (Briggs et al., 1979; Bradshaw, 1981; Briggs et al., 1984; Trewin and McNamara, 1995).

3.5. Gordia indianensis (Miller, 1889) (Fig. 10A)

3.5.1. Description

Unbranched overcrossing hypichnial ridge, 0.5–1.0 mm wide, with curved segments 8.0–39.0 mm in length. Segments are joined by sharp-angled
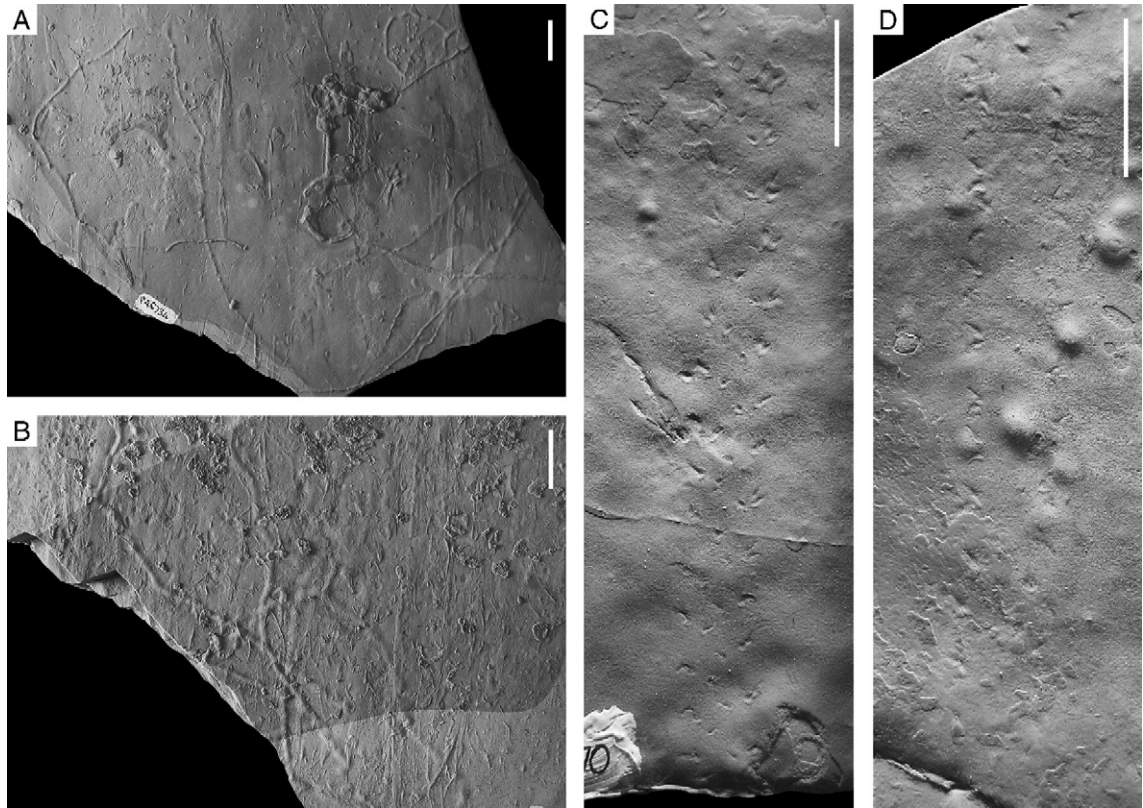
Fig. 10. (A) *Gordia indianensis*, NMMNH P-46734. (B) *Helminthoidichnites tenuis*, NMMNH P-46849. (C–D) *Lithographus* isp. (C) NMMNH P-37470, with series of three tracks. (D) NMMNH P-32481, with series of two tracks. Scale bars 10 mm.

turns in places, although smoother turns are also present.

3.5.2. Remarks

Gordia is a thin surface trail or shallow subsurface burrow characterized by overcrossing and looping. The presence of overcrossing distinguishes it from *Helminthoidichnites* and *Helminthopsis* (e.g. Buatois et al., 1998). *Mermia* has a similar form, but more intense looping (Walker, 1985). Buatois et al. (1998) placed *Haplotichnus indianensis* in *Gordia* as a distinct ichnospecies, regarding these traces as representing essentially the same behaviour, and the differences more meaningful at the ichnospecific level. The segmented form and angular turns in this material are most similar to *G. indianensis*, whereas the other ichnospecies have smooth turns (e.g. Buatois et al., 1998).

3.6. Helminthoidichnites tenuis *Fitch, 1850 (Fig. 10B)*

3.6.1. Description

Unbranched horizontal hypichnial ridges, 0.9–1.3 mm wide, following straight to slightly curved courses.

Overlapping occurs between, but not within individual traces.

3.6.2. Remarks

Helminthoidichnites is a simple, unbranched horizontal surface trail or shallow subsurface burrow that can be straight to slightly curved and may follow a circular course, whereas *Helminthopsis* is meandering. Individual traces do not overcross, unlike in *Gordia* and *Mermia*, although overcrossing between traces is common (e.g. Buatois et al., 1998). Only one ichnospecies, *H. tenuis*, is known.

3.7. Lithographus isp. *(Fig. 10C–D)*

3.7.1. Description

Trackways comprising series of two to three linear tracks with different orientations. External widths range from 5.5–6.9 mm. Some trackways comprise series of three tracks, the inner of which is orientated obliquely backwards, whereas the middle and outer tracks are both orientated obliquely forwards from the midline of the trackway (Fig. 10C). Other specimens

comprise series of only two tracks, one of which is orientated obliquely forwards and the other obliquely backwards (Fig. 10D).

3.7.2. Remarks

Lithographus and *Hexapodichnus* both comprise series of three linear tracks with different orientations, the relative positions of which were used to differentiate between them (Hitchcock, 1858), whereas *Permichnium* comprises series of two linear tracks that are V-forming (Guthörl, 1934; Walter, 1983). However, material from the Lower Permian Saar-Nahe Basin in Germany demonstrates that some of these morphologies can occur within individual trackways (Minter et al., in press). Thus, some ichnospecies of *Hexapodichnus* are regarded as minor behavioural variants of *Lithographus*, and *Permichnium* is regarded as a minor preservational variant of *Lithographus*. A full review of the validity of the ichnogenera *Lithographus*, *Hexapodichnus*, and *Permichnium*, and their ichnospecies is currently underway; herein these specimens are referred to *Lithographus* isp.

3.8. Planolites beverleyensis (Billings, 1862) (Fig. 11)

3.8.1. Description

Unlined straight to slightly curved cylindrical trace fossils with a texturally different infill from the host sediment. They are predominantly horizontal, following bedding planes, or slightly undulatory, with some vertical and oblique examples. Observed widths, although not necessarily diameters, range from 2.0–5.9 mm. The infill appears to be pelleted in nature (Fig. 11B), and not arranged into discrete packets or menisci.

3.8.2. Remarks

The distinction between *Planolites* and *Palaeophycus* has been discussed extensively (Pemberton and Frey, 1982; Fillion and Pickerill, 1990; Keighley and Pickerill, 1995, 1997). Pemberton and Frey (1982) identified *Planolites* as an unlined burrow, the infill of which differs from the host sediment, differentiating it from *Palaeophycus*, which is lined and has an identical infill to the host sediment; although Keighley and Pickerill (1995) considered the primary distinction to be the presence or absence of a lining because *Palaeophycus* may have a different infilling to the host sediment and equally, *Planolites* may have a similar infill. The backfill of *Planolites* is not meniscate, which distinguishes it from *Taenidium*. The material from Castle Peak is referred to *P. beverleyensis* because it has a smooth wall and lacks the sinuosity of *P. montanus*, although it is smaller than *P. beverleyensis* (*sensu* Pemberton and Frey, 1982).

3.9. Rusophycus carbonarius (Dawson, 1864) (Fig. 12A–B)

3.9.1. Description

Short bilobate traces, 3.7–7.9 mm wide (Fig. 6A). The lobes are expanded at one end with lobe widths up to 3.4 mm, and taper towards the other end. The lobes are generally separated by a medial ridge or groove up to 1.4 mm wide, although the lobes are connected in some examples (Fig. 12A). The lobes preserve fine transverse striations, although they are not present in all examples.

3.9.2. Remarks

Most authors consider '*I.*' *eutendorfensis* to have transverse to oblique striations (Bromley and Asgaard,
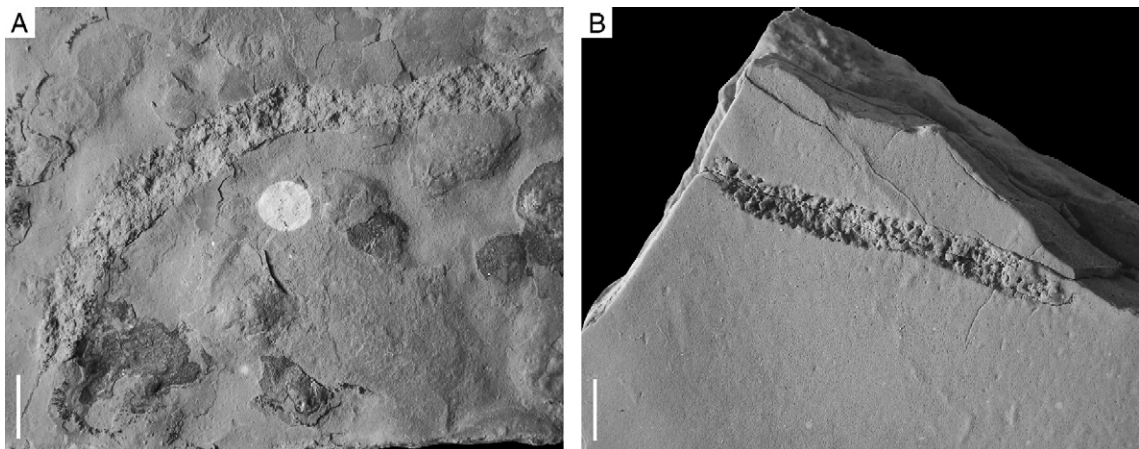

Fig. 11. *Planolites beverleyensis*. (A) NMMNH P-46681. (B) NMMNH P-46702. Scale bars 5 mm.

1979; Fillion and Pickerill, 1990), but Schlirf et al. (2001) point out that this is incorrect, and Linck's (1942) original description identifies the most important morphological feature as the mostly smooth lobes, which bear longitudinal furrows. The transverse striations of the material from Castle Peak therefore distinguish it from *R. eutendorfensis* (Schlirf et al., 2001), and it lacks the expanded, smooth, lily-like ends of *R. stromnessi* (Trewin, 1976; Keighley and Pickerill, 1996). *R. minutus* has a characteristic triangular-shape (Debriette and Gand, 1990), and

R. furcosus is 'arrow-shaped' (Gand, 1994). *R. didymus* is invalid (Bromley and Asgaard, 1979; Keighley and Pickerill, 1996). There appears to be no morphological difference between *R. carbonarius* and what could be reassigned from '*I.*' *problematicus* to *R. problematicus*, both possessing fine, transverse to oblique striations. Examples of *Rusophycus* from Castle Peak intergrade with *C. problematica* (Figs. 5C and 12B), but *R. carbonarius* has priority for such forms (Keighley and Pickerill, 1996) so we refer them to this ichnospecies.
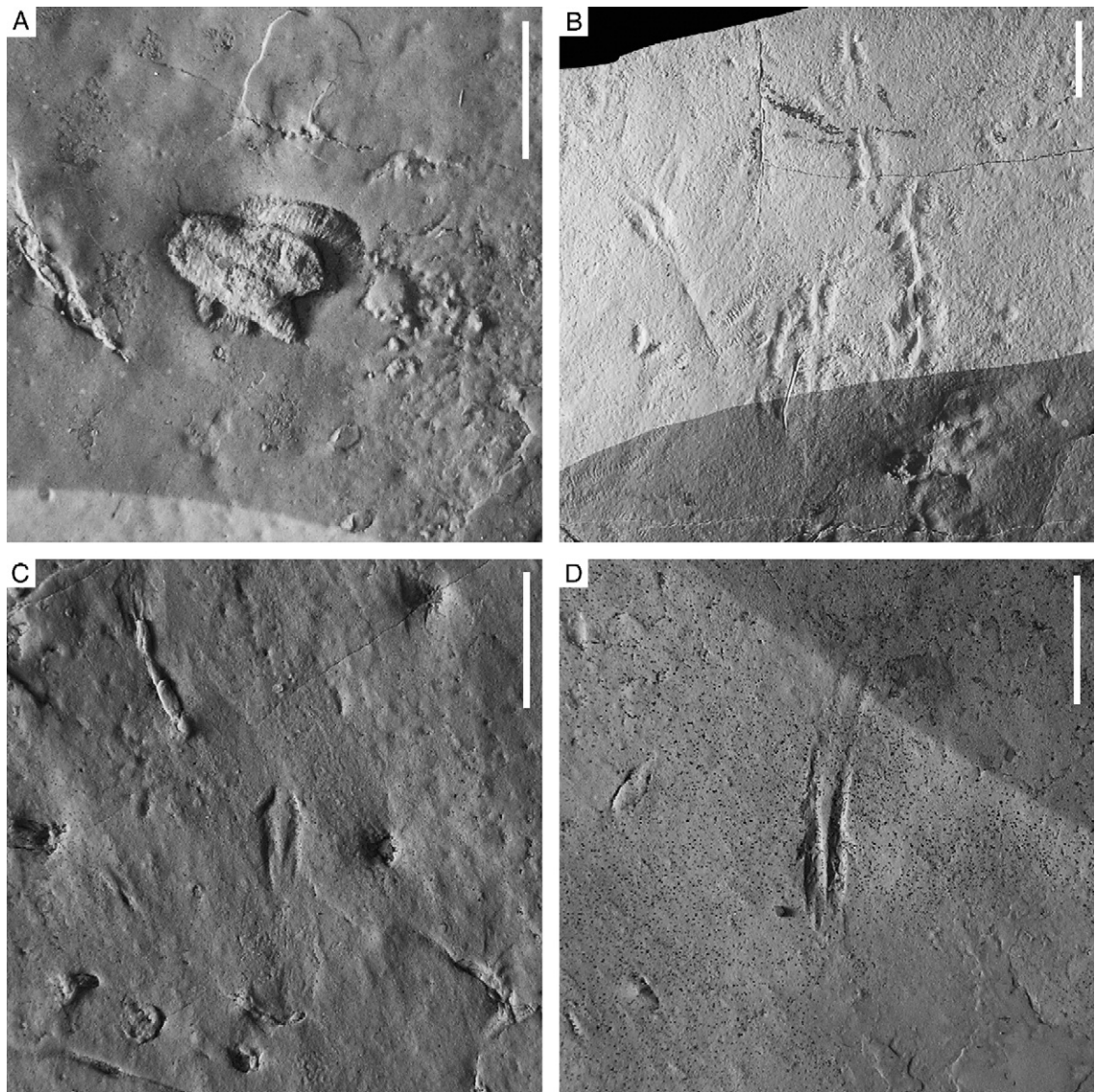
Fig. 12. (A–B) *Rusophycus carbonarius*. (A) NMMNH P-46886. (B) NMMNH P-46725, intergrading with *Cruziana problematica*. (C–D) *Rusophycus furcosus*. (C) NMMNH P-47758, note the pair of parallel, bifurcated imprints. (D) NMMNH P-47766, note intergrading with paired furrows of *C. problematica*. Scale bars 5 mm in A, C–D and 10 mm in B.

3.10. Rusophycus furcosus (Gand, 1994) (Fig. 12C–D)

3.10.1. Description

Small, 'arrow-shaped' traces, 1.7–4.3 mm long and 0.7–2.5 mm wide (Fig. 6A), comprising a pair of deflected imprints forming a V-shape at the one end and a pair of parallel imprints, 0.6–2.5 mm wide, at the other end, some of which are bifurcated (Fig. 12C).

3.10.2. Remarks

The morphology and size of these traces are consistent with '*Isopodichnus*' *furcosus* (Gand, 1994). Some specimens of *R. furcosus* are found in association, at the terminations, or along the length of *Cruziana problematica* (Fig. 12D).

3.11. Taenidium barretti (Bradshaw, 1981) (Fig. 13A–C)

3.11.1. Description

Smooth-walled, unlined, cylindrical trace fossils with meniscate backfill. Observed widths, although not necessarily diameters, range from 1.4–6.3 mm. They are predominantly horizontal, following bedding planes, although many are undulose, and individual examples can be traced in and out of the bedding plane. Oblique and vertical sections are also present. Menisci are short, arcuate, and densely packed. In some examples, the lateral margins of menisci merge to form apparent linings (Fig. 13B). They are unbranched, although there are some cases of false branching due to overcrossing or reworking (Fig. 13C).

3.11.2. Remarks

The nomenclature of meniscate backfilled burrows is somewhat confused, and a consensus is yet to be reached (d'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994; Goldring and Pollard, 1995; Keighley and Pickerill, 1997; Retallack, 2001; Morrissey and Braddy, 2004). The main point of contention is between *Beaconites* and *Taenidium*, with the problem arising from the nature of their margins. We follow Keighley and Pickerill (1994) in regarding *Taenidium* as unlined and *Beaconites* as lined, and that *B. barretti* should be reassigned as *T. barretti* because it only has an apparent lining formed by lateral merging of menisci. Bradshaw (1981) originally erected *T. barretti* for large meniscate backfilled burrows, however smaller burrows have also been referred to this ichnospecies (Keighley and Pickerill, 1994). The ichnospecies of *Taenidium* have been revised by Keighley and Pickerill (1994) and Uchman (1999). The material from Castle Peak has

short, arcuate, and closely spaced menisci, characteristic of *T. barretti*.

Vertical burrow sections are also present from Castle Peak, typically in association with horizontal and undulatory sections of *T. barretti* (Fig. 13A, C). The vertical sections are often observed in plan view due to the platy nature of the lithology, but rare longitudinal sections through them demonstrate menisci and no obvious linings. The lithology throughout the trace fossil bearing horizon is uniformly fine-grained, whereas the infilling of the vertical burrow sections is texturally distinct and similar to that of the horizontal sections of *T. barretti*. This suggests that they were actively backfilled rather than passively, and that they are vertical sections of *T. barretti* as opposed to *Skolithos*.

3.12. Treptichnus isp. (Fig. 13D)

3.12.1. Description

Continuous zig-zag-shaped hypichnial ridge. Only one specimen has been recovered, and is 1.0 mm wide, with segments of varying lengths, ranging from 2.5–6.5 mm. No projections or pits are present at the junctures between segments, and there are no longitudinal striations.

3.12.2. Remarks

The ichnotaxonomy of *Treptichnus* and its relationship to *Plangtichnus* has been discussed extensively, and Buatois and Mángano (1993b) synonymized *Plangtichnus* with *Treptichnus*, a view that is largely accepted (although see Archer et al., 1995). The zig-zag-shape of the material from Castle Peak is characteristic of *Treptichnus*; however, the limited material, and lack of details preclude ichnospecific assignment.

3.13. Tetrapod trackways (Figs. 14 and 15)

3.13.1. Remarks

The vertebrate trackways from Castle Peak have been described and reviewed in detail (Williston, 1908; Moodie, 1929, 1930; Sarjeant, 1971; Haubold and Lucas, 2001, 2003). Three ichnospecies are currently recognised: *Dromopus palmatus* (Fig. 14A–B), *Erpetopus willistoni* (Fig. 14C–D) and *Varanopus curvidactylus* (Fig. 15A). *D. palmatus* is generally larger than *E. willistoni* and *V. curvidactylus*. There is some overlap in the general dimensions between *E. willistoni* and *V. curvidactylus*, but *E. willistoni* has a relatively short digit imprint V, similar in length to digit imprint I, whereas digit imprint V is longer in *Varanopus*, being
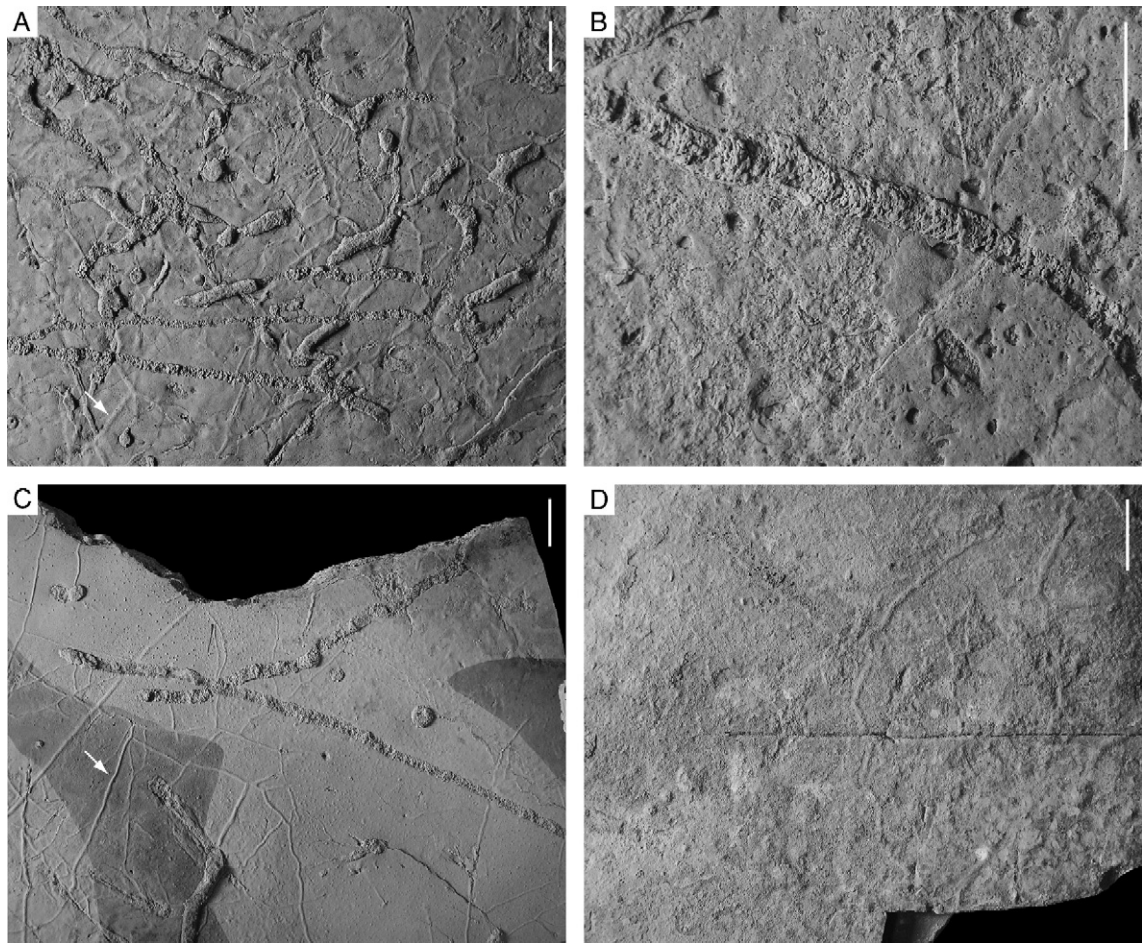
Fig. 13. (A–C) *Taenidium barretti*. (A) Horizontal and undulatory sections of *T. barretti*, NMMNH P-32439, and horizontal branching networks (arrow). (B) NMMNH P-46900, note the lateral merging of menisci to form an apparent lining. (C) Horizontal and vertical sections of *T. barretti*, NMMNH P-47745, and horizontal branching networks (arrow). (D) *Treptichnus* isp., NMMNH P-46667. Scale bars 10 mm.

similar in length to digit imprints II or III. *V. curvidactylus* has robust digit imprints whereas they are relatively slender in *D. palmatus* and *E. willistoni*. The digit imprints of *V. curvidactylus* are also separated by a similar angle whereas digit imprint V is strongly divergent from digit imprint IV in *D. palmatus* and *E. willistoni*. The claw imprints are bifurcated or elongated in some examples (Fig. 14C–D). Soft tissue anatomy also appears to be present in some examples of *D. palmatus* (Fig. 14B).

A further specimen is quite distinct, with broad, plantigrade tracks in which width is similar to length and the manus and pes are pentadactyl (Fig. 15B). These tracks are similar to *Amphisauropus*; although, given that there are only two relatively poorly preserved tracks, this specimen is identified as cf. *Amphisauropus* isp.

3.14. Other trace fossils (Figs. 13A, C, and 16)

3.14.1. Remarks

A couple of other types of trace fossils are present from Castle Peak, but are not dealt with formally herein, either because they do not easily conform to existing ichnotaxa or because they are only represented by one or two specimens. In particular, a number of slabs preserve unusual horizontal branching networks that tend to be preserved in positive epirelief and follow bedding planes (Fig. 13A, C), suggesting that they are subsurface interface traces. There is overprinting between specimens, and within individual specimens there are main branches, typically 1.0–2.0 mm wide, off which come narrower branches, often at 90°. These traces are similar to *Vagorichnus* and *Labyrintichnus*, but they are more regular than *Vagorichnus* (Buatois et al., 1995) and lack
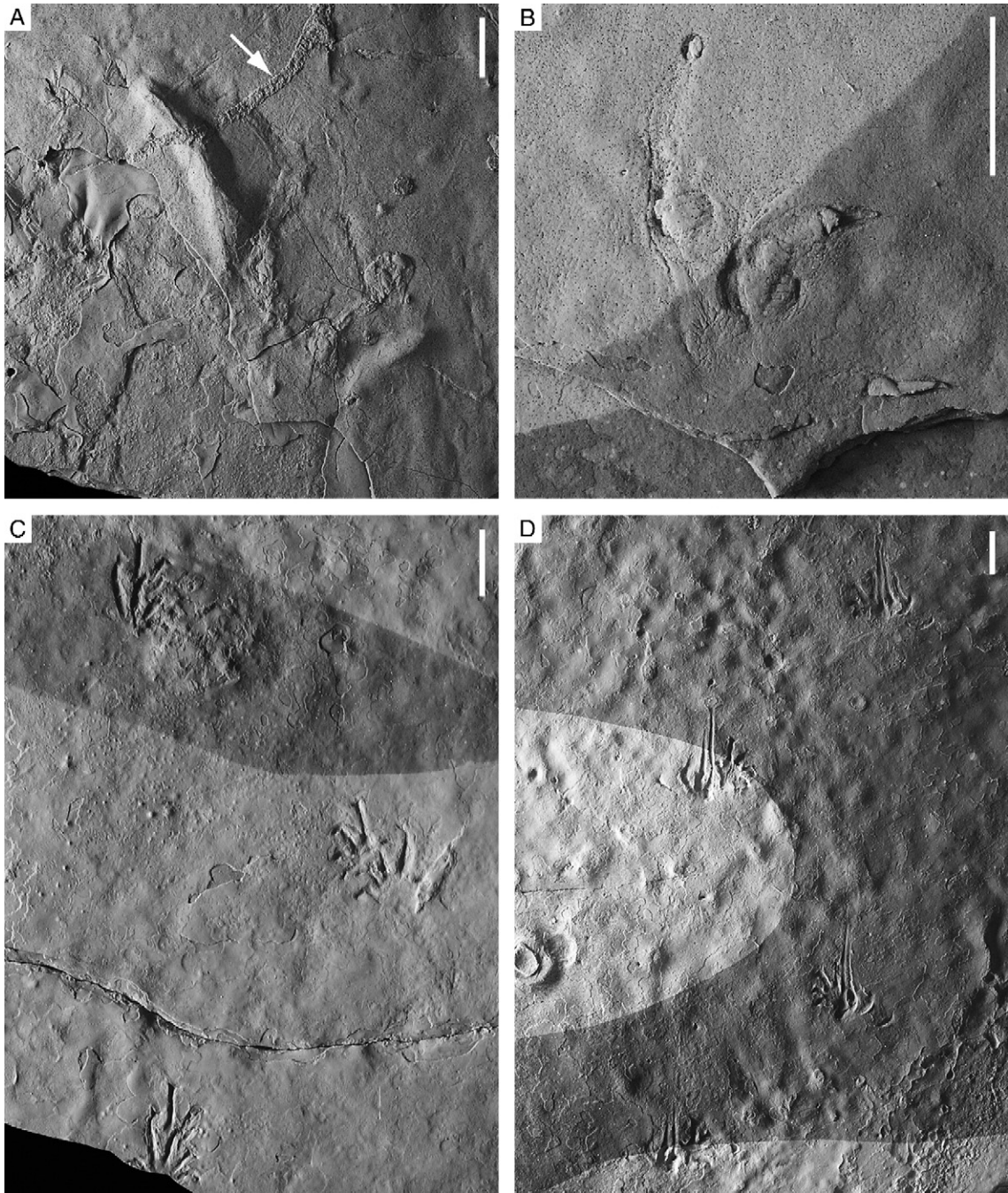
Fig. 14. (A–B) *Dromopus palmatus*. (A) *D. palmatus*, NMMNH P-46986, large didactyl track, cross-cut by *T. barretti*, NMMNH P-46985 (arrow). (B) NMMNH P46873, tridactyl track with some outline of soft-tissue anatomy. (C–D) *Erpetopus willistoni*. (C) NMMNH P-32410, note the bifurcated tips of digit imprints. (D) NMMNH P-32400, note the digit drag marks and ?gas bubble structures. Scale bars 10 mm.

the lining of *Labyrintichnus* (Uchman and Álvaro, 2000). Similar structures have been reported from the Early Permian of New Mexico (Lucas et al., 2005a,b). A partial arthropod trackway with an outer trifid track (Fig. 16A) is identified as cf. *Kouphichnium* isp. One

trace fossil consists of a string of nodular bodies with up to four nodular bodies across the width of the string and a depressed medial region (Fig. 16B). This trace fossil is superficially similar to *Walpia*, although *Walpia* is a cylindrical trace fossil with a nodular lining
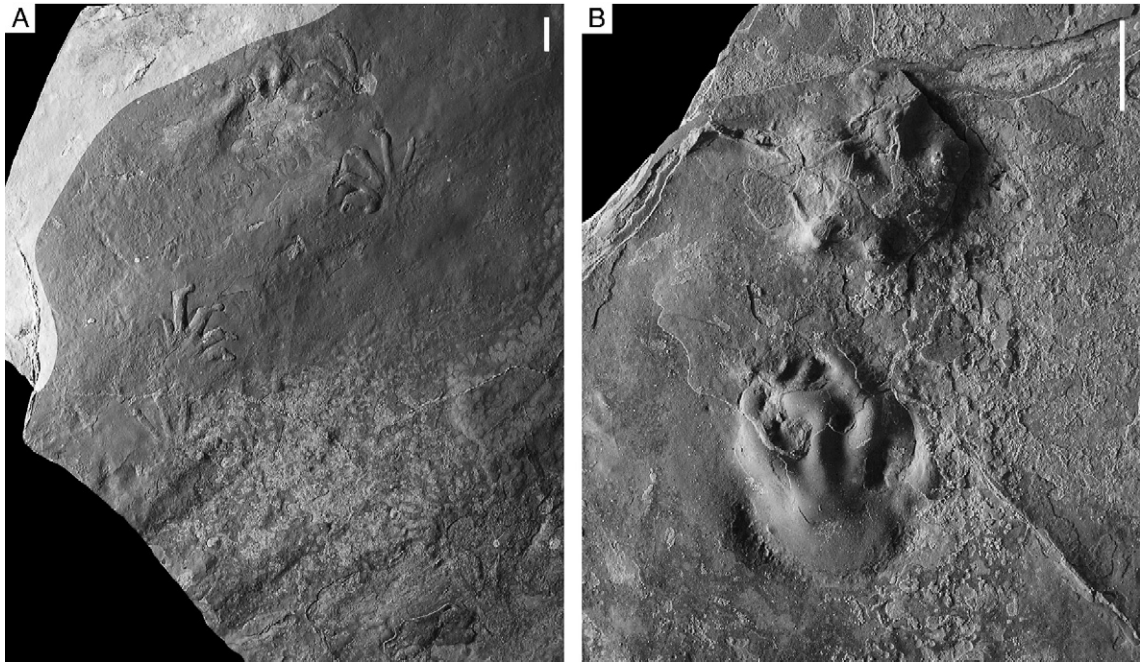
Fig. 15. (A) _Varanopus curvidactylus_, NMMNH P-32391. (B) cf. _Amphisauropus_ isp., NMMNH P-37460. Scale bars 10 mm.

(White, 1929), and a cross-sectional cut through this specimen demonstrates that it is a trail, with some resemblance to _Nereites_ or _Neonereites_. Finally, a couple of unilobate epichnial trails are also present (Fig. 16C–D). These trails have levees, some of which are rucked, and are similar to _Protovirgularia_ in some respects.

4. Trace fossil producers

4.1. Striated trails and isolated traces

Branchiopod crustaceans, particularly notostracans, are the most likely producers of _Cruziana_ and _Rusophycus_ from Castle Peak. However, anostracan and lipostracan branchiopods cannot be ruled out entirely. Branchiopods are a very successful group of primitive crustaceans that have an almost global distribution, inhabiting various nonmarine environments including ephemeral pools. Notostracans include the extant genera _Triops_ and _Lepidurus_, and body fossils are known from the Permian of Oklahoma (Ruedemann, 1922). Notostracans lead a generally benthic mode of life, crawling along the bottom of ponds and burrowing into the substrate, but they can also swim (Schram, 1986). They feed upon detritus by digging with the endopodites of their anterior limbs (Cannon, 1933; Fox, 1949; Fryer, 1988). Fox (1949) observed that young _Triops_ produce

a characteristic trail with a ridge down the middle, and Bromley and Asgaard (1972) found that _Lepidurus_ ploughed through the substrate while searching for food, producing trails very similar to _Cruziana_. _Lepidurus_ was also found to produce isolated traces similar to _Rusophycus_ (Bromley and Asgaard, 1972). The morphology of _R. furcosus_ is very similar to that of notostracans (Gand, 1994).

Fryer (1966, 1983) observed that anostracans belonging to the genus _Branchinecta_ fed by scraping the substrate using the distal spines of the endopodites of their limbs, and _B. mackini_ has been observed to remain almost stationary above the substrate while scraping and then swimming off (Fryer, 1966). Lipostracans are extinct, but comparative functional morphology suggests that they too fed by scraping the substrate with their limbs (Fryer, 1985), although they are small, 3 mm long, so could have only produced the smallest traces. Anostracans and lipostracans scrape the substrate rather than ploughing through it (Fryer, 1966, 1983, 1985), so they are more likely to produce scratch traces rather than furrows. It is interesting that there is no overlap between the ranges of external widths of _R. carbonarius_ and _R. furcosus_, but their combined distribution mirrors that of _Cruziana problematica_ (Fig. 6A). This may therefore represent two different branchiopods, or ontogenetic changes in a single branchiopod, producing different resting traces, but similar foraging traces.
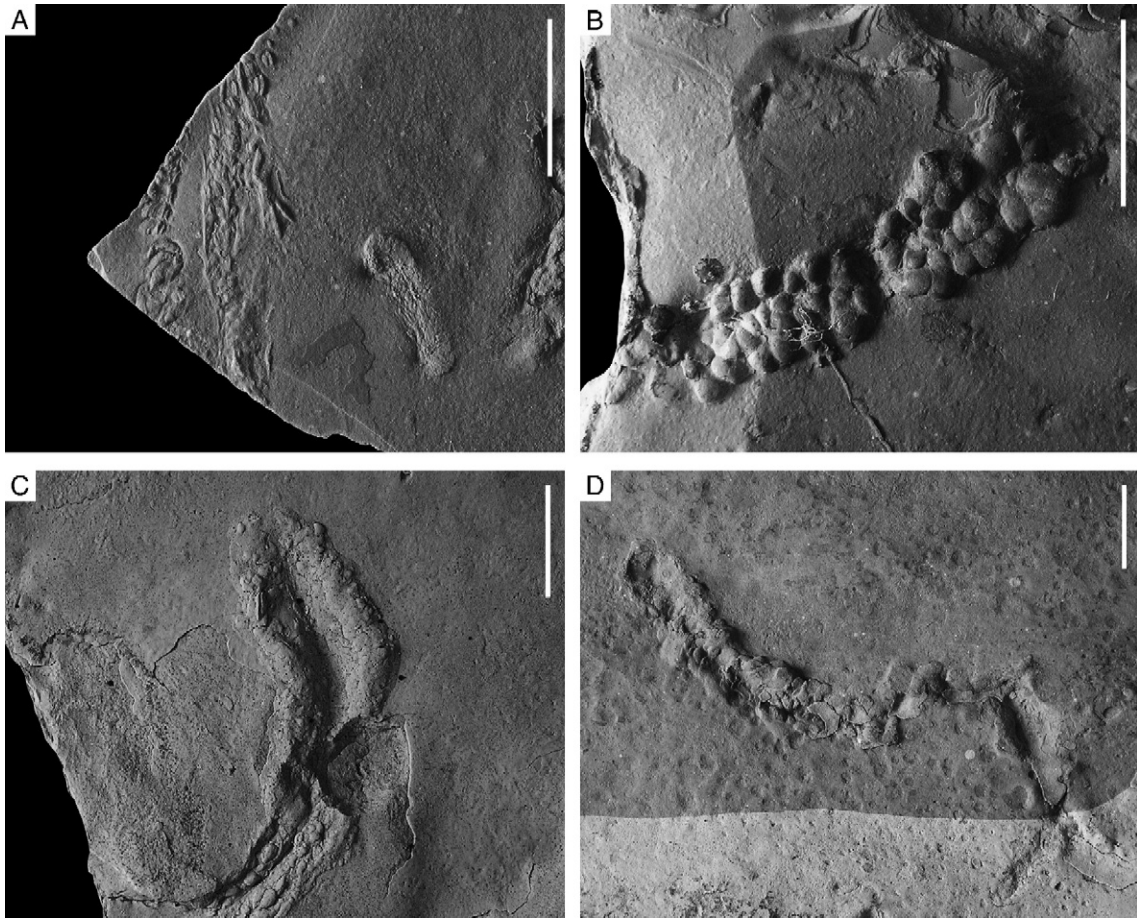
Fig. 16. Other trace fossils. (A) cf. *Kouphichnium* isp., NMMNH P-46721. (B) Nodular trail, NMMNH P-46910. (C–D) Unilobate epichnial trails. (C) NMMNH P-47788. (D) NMMNH P-46859. Scale bars 10 mm.

4.2. Arthropod trackways

The producers of *Diplichnites* were most likely crustaceans, myriapods, and euthycarcinoids. Among crustaceans, branchiopods, syncarids, and peracarids are the most likely candidates. Within the Branchiopoda, anostracans, while potential producers of *Cruziana* and *Rusophycus*, are unlikely to have produced *Diplichnites* because their limbs are adapted for filter feeding rather than walking and they predominantly live in the water column (Cannon, 1933; Fryer, 1966, 1983). Notostracans lead a more benthic mode of life. Trusheim (1931, fig. 2) illustrated experimental trackways produced by *Triops* walking subaqueously on mud, which consisted of two parallel track rows with linear, comma, or curved tracks orientated transversely to the midline of the trackway, very similar to *Diplichnites* isp. A. Notostracans possess 11 thoracic segments, each of which bears a single pair of large, well-developed limbs, the first of which is modified, and subsequent limbs decrease in length (McLaughlin, 1980; Schram, 1986). Notostracans are therefore likely candidates for trackways with series of up to ten tracks. The V-forming series of tracks in *D. gouldi* types A and B reflect variation in limb length.

We note that the distribution of external widths of *Diplichnites* isp. A is skewed with the majority of trackways being small, while that of *D. gouldi* type A follows a normal distribution, and are larger on average. It is possible that this represents ontogeny, with the differences in limb length becoming more pronounced with size and age. Notostracans can reach up to 0.1 m in length, so they would have been large enough to produce *D. gouldi* type B. The experimental trackways illustrated by Trusheim (1931) also had two parallel medial impressions, which represented the marks left by the paired rami of the telson, so specimens of *D. gouldi* type A with paired medial impressions (Fig. 7F) can be

attributed to notostracans with some confidence. Specimens lacking medial impressions could also have been produced by notostracans, but those with single, central medial impressions were probably produced by a different animal.

Palaeocaridacean and anaspidacean syncarids, as well as mysidacean and isopod peracarids are also potential producers of *Diplichnites*. They inhabit a range of environments, including nonmarine, and their fossil records extend back to the Permian in the case of anaspidaceans and terrestrial and freshwater isopods, whereas the mysidaceans extend back to the Carboniferous (Schram, 1986). Palaeocaridaceans are extinct, ranging from the Lower Carboniferous to Permian (Schram and Schram, 1974; Schram, 1981, 1986). They all possess eight thoracic limbs, the first of which are modified into maxillipedes or have a sensory function (Manton, 1930; Schram, 1986), and so are potential producers of *Diplichnites* isp. A, and examples of *D. gouldi* type A with series of up to seven tracks. The telsons and uropods of these four groups are fan-like in arrangement, so they are unlikely producers of examples with sharp, single medial impressions. Experimental trackways produced by woodlice (*Oniscus asellus*) are similar to *Diplichnites* isp. B (Davis, 2006).

Myriapods are the most commonly invoked producers of *Diplichnites* (Gevers et al., 1971; Briggs et al., 1979; Bradshaw, 1981; Briggs et al., 1984; Trewin and McNamara, 1995; Smith et al., 2003), and are potential producers of *Diplichnites* isp. A and B, although they typically possess more limbs than the number suggested by *D. gouldi* types A and B, and lack a telson. Euthycarcinoids are an enigmatic group of extinct arthropods that range from the Cambrian (Vaccari et al., 2004) to the Triassic (Edgecombe and Morgan, 1999), and have been recovered from marine to freshwater settings, including ephemeral pools (Anderson and Trewin, 2003). They are also interpreted as the producers of the earliest terrestrial trackways (MacNaughton et al., 2002). Euthycarcinoids all possess a tail spine and comprise two distinct groups, the sottyxerxids, and the euthycarcinids (Wilson and Almond, 2001). Sottyxerxids have 28 or 31 limbs (Schram and Rolfe, 1982), whereas euthycarcinids possess 10 or 11 limbs (Schram and Rolfe, 1982; Schneider, 1983; McNamara and Trewin, 1993; Anderson and Trewin, 2003; Vaccari et al., 2004). Euthycarcinids are therefore likely candidates for *Diplichnites*, especially *D. gouldi* type A with series of 10 or 11 tracks and a medial impression (Fig. 7D), and sottyxerxids could have produced *Diplichnites* isp. A or B.

Lithographus, with series of three linear tracks with differing orientations and alternate symmetry, is indicative of an insect, in particular pterygote insects that possess plantigrade distal tarsi as opposed to apterygote insects which have pointed distal tarsi (Sharov, 1958). Experimental trackways similar to *Lithographus* have been produced with yellow and dark mealworm beetles (*Tenebrio molitor* and *T. obscurus*), and discoid cockroaches (*Blaberus discoidalis*) (Davis, 2006). The trifid outer track of cf. *Kouphichnium* isp. suggests that it was made by a xiphosuran.

4.3. Surface and shallow subsurface trails and burrows

Gordia, *Helminthoidichnites*, and *Treptichnus* are all interpreted as surface or shallow subsurface grazing trails or burrows, and in nonmarine settings, are attributed to arthropods, particularly insect larvae, and vermiform animals (e.g. Buatois et al., 1998). Structures similar to *Gordia* have been observed to be produced by various insect larvae in ephemeral puddles (Metz, 1987), and chironomid and tipulid insect larvae produce *Treptichnus*-like traces under laboratory conditions (Uchman, 2005). The unilobate epichnial trails could have been produced by an arthropod, but more likely a gastropod or vermiform animal, because an arthropod would be expected to produce a bilobate trail. The unusual horizontal branching networks were probably not produced by animals because they have a main branch off which come narrower branches, which is suggestive of root traces or fungal hyphae. A range of invertebrates could have produced the nodular trail and the individual nodular bodies probably represent excremental pellets of a deposit feeder.

4.4. Burrows

A variety of animals have been proposed as the originators of *Taenidium*, including polychaetes (Gevers et al., 1971), amphibians or reptiles (Ridgway, 1974), and arthropods (Bradshaw, 1981; Keighley and Pickerill, 1997; Morrissey and Braddy, 2004). The distribution of burrow widths from Castle Peak also falls within that of the external widths of the arthropod trackways and trails, supporting an arthropod producer. The presence of menisci and lack of lining in *T. barretti* indicate that it was actively backfilled, with each meniscus representing a period of activity. *T. barretti* from Castle Peak probably represent burrowing in search of moisture to aestivate during dry periods, and a range of extant arthropods, including insects and millipedes, are known to exhibit such behaviour (Stanley and Fagerstrom, 1974; Dangerfield and Chipfunde, 1995). *Planolites* is generally interpreted as the burrow of deposit-feeding animals,

including annelids, and the burrow fill is faecal (Pemberton and Frey, 1982). The material from Castle Peak is similar in size to *Taenidium*, so they were probably produced by the same animals.

4.5. Tetrapod trackways

Erpetopus is the dominant tetrapod trackway from Castle Peak, *Dromopus* is fairly common, and *Varanopus* is rare. Williston (1908) originally interpreted the trackways as those of a salamander-like animal, and Moodie (1929) later attributed them to reptiles and amphibians. The deflected distal ends of the digit imprints represent claw imprints, which indicates that they were produced by reptiles (amniotes). *Erpetopus* and *Varanopus* were probably produced by small Permian reptiles such as protorothyridids or captorhinids (Haubold and Lucas, 2003), and body fossils of captorhinids are known from the Choza Formation (Olson, 1958; Murry and Johnson, 1987). The bifurcated tips of digit imprints are probably a preservational artefact due to the entrance and exit of the foot from the substrate and a flexible claw. *Dromopus* is widely attributed to a lacertoid reptile, most likely an araeoscelid, which are known from contemporaneous deposits (Haubold and Lucas, 2003). The proportions of the foot skeletons of *Petrolacosaurus* and *Araeoscelis* agree with those of *Dromopus* tracks. The specimen identified as cf. *Amphisauropus* isp. was probably made by an amphibian.

5. Trace fossil taphonomy

Trace fossils from Castle Peak are preserved throughout the trace fossil bearing horizon, but are most common in beds 1–11. Trace fossils are incredibly abundant, literally present on every surface, and multiple ichnotaxa are often found in association. Trackways exhibit a range of preservational states. The majority of arthropod and vertebrate trackways are sharply defined. Some arthropod trackways are less than a millimetre in external width, but have clearly preserved tracks (Fig. 9A). These trackways must have formed in a stabilised stiffground substrate
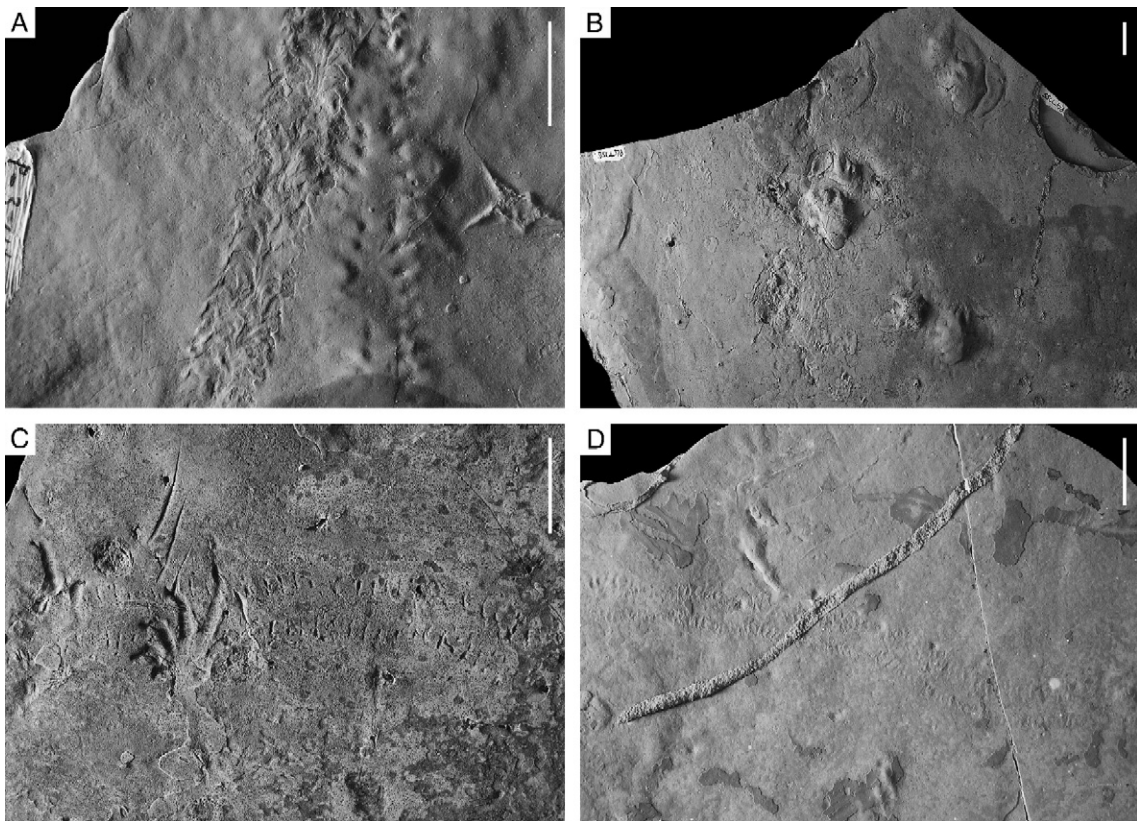

Fig. 17. Trace fossil taphonomy. (A) NMMNH P-37469, poorly defined *Diplichnites gouldi* type A overprinted by a more sharply defined *Diplichnites* isp. A. (B) NMMNH P-47755, poorly defined *Erpetopus willistoni*. (C) NMMNH P-46983 and P-46984, sharply defined *D. gouldi* type A overprinted by *E. willistoni*. (D) NMMNH P-46965 and P-46966, *Diplichnites* isp. A crosscut by *Taenidium barretti*. Scale bars 10 mm.

(*sensu* Wetzel and Uchman, 1998), either subaqueously or while the substrate was still moist after exposure, and the fine-grained nature of the lithology accounts for the preservation of these delicate structures. Some of the trace fossils are cross-cut by mudcracks, indicating that they formed before desiccation (Fig. 4A). Digit drags are present with some vertebrate trackways (Fig. 14D), suggesting a stiff, but cohesive substrate. More rarely, arthropod and vertebrate trackways are poorly defined, with relatively diffuse tracks (Fig. 17A–B), suggesting that they formed on a softground substrate. In some examples, relatively poorly defined arthropod trackways are overprinted by more clearly defined arthropod trackways (Fig. 17A), indicating a change from softground to stiffground with increasing stabilisation of the substrate.

Multiple, sharply defined, cross cutting arthropod trackways are often found on a single surface (Fig. 9B–C), representing omission surfaces and a prolonged period of trackway formation. Vertebrate and clearly defined arthropod trackways are frequently found in association, and when observed, the vertebrate trackways always overprint the arthropod trackways (Fig. 17C), indicating that the arthropod trackways formed first. Vertebrate trackways also overprint raindrop imprints (Fig. 4C) and halite pseudomorphs (Fig. 4D), indicating that they formed subaerially.

Backfilled burrows are found throughout the trace fossil bearing horizon, and are well preserved, with sharply defined margins, indicating that they formed in stabilised stiffgrounds after subaerial exposure. The majority are horizontal, or undulating relative to bedding, and also cross cut tool-marked surfaces and arthropod and vertebrate trackways (Figs. 4B, 14A, and 17D). Vertical and oblique sections are also present, indicating that they formed after burial of several trace fossil bearing layers. Chevron grooves and other tool marks are abundant on the top of bed 12/base of bed 11. Large *D. gouldi* type B are commonly preserved on such surfaces, and overprint the tool marks (Fig. 8). The trackways are generally asymmetrical, suggesting that they formed subaqueously and their course was offset by the current responsible for the tool marks, or, alternatively, the animal may have been moving on a slope.

6. Palaeoecological reconstruction

The Castle Peak trace fossil assemblage provides evidence of a diverse community of arthropods (branchiopod crustaceans, insects, myriapods and euthycarcinoids) and tetrapods (reptiles and rare amphibians) inhabiting a playa lake and its margins (Fig. 18). The
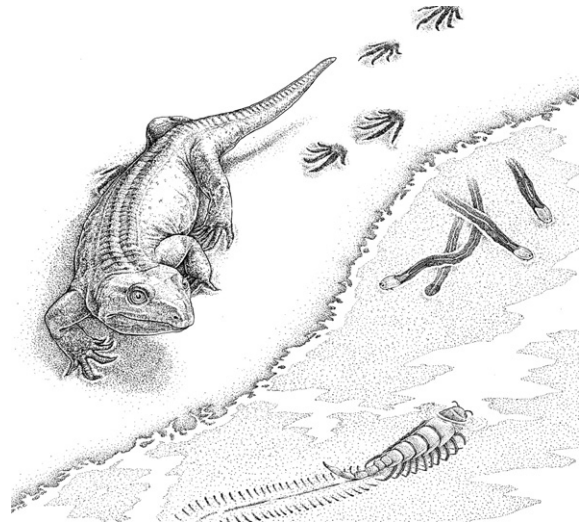

Fig. 18. Palaeoecological reconstruction of Castle Peak. Captorhinimorph reptile producing *Varanopus curvidactylus*, notostracan branchiopod crustaceans producing *Cruziana problematica* and a euthycarcinoid producing *Diplichnites* isp. A. Drawing by Matt Celeskey.

community structure is comparable to that of modern ephemeral water bodies (e.g. Hancock and Timms, 2002; Graham, 2002; Anderson and Smith, 2004). Extant branchiopod crustaceans, including notostracans and anostracans, are adapted to live in temporary water bodies in arid environments. Notostracans and anostracans have r-selected life history strategies with short life spans, rapid growth, and early reproduction (Hamer and Appleton, 1991). The species persist in such settings through remarkably hardy resting eggs, or cysts, which can survive in dry mud for tens of years (Dexter, 1973), and the cysts of *Triops* are still viable after temperatures of up to 80° (Carlisle, 1968). To take advantage of the formation of temporary habitats, the cysts hatch within a few days after hydration and incomplete hydration enhances hatching following subsequent complete hydration (Su and Mulla, 2002).

The morphologies of the majority of arthropod trackways, trails and resting traces at Castle Peak are similar to those produced by modern notostracans, and the palaeoenvironmental setting is consistent with that of extant notostracans. Each individual bed of the trace fossil bearing horizon is interpreted as a single sedimentation event, and the abundance of arthropod trackways on such bedding planes suggests periods of high activity, presumably as a result of hatching of cysts *en masse* following hydration and fresh input of sediment. The presence of the euthycarcinoid *Heterocrania* in restricted ephemeral pool deposits from the Early Devonian Windyfield cherts of Scotland led Anderson

and Trewin (2003) to speculate that they may have possessed a resting cyst similar to that of branchiopods.

The dominance of surface traces and lack of open burrows indicate a predominantly vagile epifaunal community. Reptiles and amphibians were probably drawn to ephemeral water bodies within the arid alluvial plain to prey upon arthropods around the margins. The *Taenidium barretti* burrows are interpreted as being produced by arthropods seeking moisture to aestivate during dry periods when the water body contracted. Notostracans are not known to burrow to survive dry periods, their r-selected life history strategies preclude this, but millipedes are known to burrow to avoid desiccation (Dangerfield and Chipfunde, 1995), and some insects produce meniscate backfilled burrows as shelters (Stanley and Fagerstrom, 1974). Meniscate backfilled burrows from the Lower Old Red Sandstone of Wales have also been interpreted as being produced by myriapods to avoid desiccation (Morrissey and Braddy, 2004).

7. Ichnofacies

Three archetypal ichnofacies are widely accepted as being indicative of nonmarine depositional settings: *Scoyenia* (Seilacher, 1964, 1967), *Mermia* (Buatois and Mángano, 1993a, 1995), and *Coprinisphaera* (Genise et al., 2000). The *Scoyenia* ichnofacies, as originally defined (Seilacher, 1967, fig. 2), was rather vague, referring to 'nonmarine sands and shales, often red beds, with a distinctive association of trace fossils.' Seilacher's (1964, 1967) other ichnofacies, *Nereites*, *Zoophycos*, *Cruziana* and *Skolithos* were each based on recurrent associations of trace fossils with no implicit controls on their distribution, but were found to be indicative of particular depositional settings. The introduction of the *Scoyenia* ichnofacies was therefore at odds with this, leading to circular reasoning for any palaeoenvironmental inferences. The original definition of the *Mermia* ichnofacies also implied a palaeoenvironmental constraint 'to include nonmarine, fully aquatic trace fossil suites' (Buatois and Mángano, 1995, p. 151), although their summary table (Buatois and Mángano, 1995, p. 155) clearly separated the characteristic trace fossils of these assemblages from the palaeoenvironmental implications. The definitions of the *Scoyenia* and *Mermia* ichnofacies have been subsequently emended (e.g. Frey et al., 1984; Buatois and Mángano, 1993a, 1995; Keighley and Pickerill, 2003). Keighley and Pickerill (2003) emended these ichnofacies to be based purely on morphological grounds, although Melchor et al. (2006) criticized the exclusion of particular ichnotaxa from one ichnofacies that were thought to be typical, but not exclusive, of another. The *Scoyenia* ichnofacies is generally considered to be indicative of transitional subaqueous to subaerial substrates, typical of floodplains, ephemeral lakes, ponds, wet interdunes and transitional alluvial-lake zones; whilst the *Mermia* ichnofacies is indicative of unconsolidated, fine-grained, permanent subaqueous substrates that are well oxygenated, with episodic sedimentation, and typical of deep and shallow lakes (Buatois and Mángano, 1993a, 1995). The *Coprinisphaera* ichnofacies is characterized by insect nests and is indicative of palaeosols (Genise et al., 2000).

The distribution of trace fossil assemblages across transitional subaqueous to subaerial settings demonstrates some general trends (Table 1). The trace fossil assemblages in Table 1 have been grouped by their inferred depositional settings (following the categories of Buatois and Mángano, 2004) to identify whether there are any recurrent associations that could be indicative of particular depositional settings. Trace fossil assemblages from active fluvial channels are depauperate, often comprising only open vertical burrows such as *Skolithos* and displacement burrows (Table 1). These trace fossil assemblages are comparable with the *Skolithos* ichnofacies, which is characteristic of high-energy shifting sand substrates (Buatois and Mángano, 2004). Some trace fossil assemblages characteristic of the *Mermia* ichnofacies have also been found within floodplain settings (Table 1). Buatois and Mángano (2002, 2004) considered these examples to reflect the subaqueous production of these traces in floodplain settings and referred to them as overfilled overbank assemblages, whereas trace fossils typical of the *Scoyenia* ichnofacies reflect production in transitional subaqueous to subaerial substrates. In common with fully subaqueous lacustrine trace fossil assemblages, they are dominated by surface or shallow subsurface grazing trails or burrows, with some open dwelling burrows and backfilled deposit-feeding burrows. Striated trails and isolated traces such as *Cruziana* and *Rusophycus* are absent, as are meniscate backfilled burrows. Vertebrate and arthropod trackways are occasionally present and probably formed around the margins of the floodplain water bodies. The impoverished nature of these trace fossil assemblages compared to those typical of the *Mermia* ichnofacies has been interpreted as a result of the short-lived nature of these water bodies (Buatois and Mángano, 2002, 2004).

The trace fossil assemblages of closed and open lake margins, abandoned or inactive fluvial channels and desiccated overbank settings are all rather similar (Table 1) and can be broadly referred to the *Scoyenia* ichnofacies. The Castle Peak trace fossil assemblage is dominated by arthropod and tetrapod trackways, together

with meniscate backfilled burrows, striated trails and isolated traces, and minor surface or shallow subsurface burrows or trails. It is typical of the *Scoyenia* ichnofacies, although some of the elements of this and other assemblages, such as the surface or shallow subsurface burrows or trails, are more typical of the *Mermia* ichnofacies. Keighley and Pickerill (2003) and Kim et al. (2005) argued that such assemblages represented composites of the *Scoyenia* and *Mermia* ichnofacies, although Melchor et al. (2006) argued that the *Scoyenia* ichnofacies is composite by definition, but that pre-desiccation and desiccation suites can be identified.

The majority of trace fossil assemblages from transitional subaqueous to subaerial settings are dominated by backfilled and open burrows, and only a minority, including Castle Peak, have a substantial number of arthropod trackways. Some trace fossil assemblages are more similar to those from different depositional settings when compared to others from the same setting (Table 1). This reflects the fact that trace fossil distribution is not incipiently linked to particular depositional settings, but rather to a variety of environmental factors, particularly the availability of water (Gierlowski-Kordesch, 1991; Buatois and Mángano, 2002), which in turn influences the animals present that can produce traces. An ephemeral pool formed on a floodplain after overbank flooding, or by channel migration in a braided fluvial system, is still an ephemeral pool. In terms of transitional subaqueous to subaerial settings, the likely controlling factors on the occurrences of trace fossils are the longevity and stability of the water body and levels and availability of resources. The differences between these trace fossil assemblages may therefore represent real differences in the communities that inhabited them. Diverse trace fossil assemblages with seven or more trace fossil types that fall into four or more broad morphological groups such as those of Castle Peak and the Permian of France (Demathieu et al., 1992) probably represent relatively long-lived ephemeral water bodies, with time for a diverse community to become established. Assemblages that are generally more impoverished, with fewer than four trace fossil types that fall into fewer than three broad morphological groups, probably represent more ephemeral water bodies (Table 1). The trace fossil assemblage described from Permian floodplain deposits from the Fra Cristobal Mountains in New Mexico (Lucas et al., 2005a) is superficially similar to that of Castle Peak; however, this takes no account of the relative abundances of the different types of trace fossils. The trace fossil assemblages from the Fra Cristobal Mountains and nearby Caballo Mountains (Lucas et al., 2005b) are

dominated by tetrapod trackways with fairly common arthropod trackways and only very rare examples of other types of trace fossil. Contrary to the majority of trace fossil assemblages listed in Table 1, these two assemblages formed in sheetflood deposits, as opposed to ephemeral water bodies, and the dominance of trackways probably represents a brief preservation window when substrate conditions enabled the trackways of animals inhabiting the floodplain to be recorded.

Taphonomic factors may also play a role in the distribution and occurrence of trace fossils (Bromley and Asgaard, 1991). The Castle Peak trace fossil assemblage is preserved in very fine-grained clastics in a transitional subaqueous to subaerial setting that was ideal for the preservation of delicate arthropod trackways. Other similar settings without such arthropod trackways may reflect coarser grain sizes or higher energy depositional settings that precluded the preservation of numerous delicate trackways. This may also be reflected by the presence of open vertical burrows such as *Skolithos*, frequently coinciding with the absence of arthropod trackways (Table 1). *Skolithos* burrows are interpreted as domiciles of suspension feeders or shelters of predators, and are produced under moderate to high-energy conditions (e.g. Seilacher, 1964), which precludes the presence of an abundant vagile epifauna, and the preservation of delicate arthropod trackways. Future documentation of trace fossils from floodplains and ephemeral water bodies will help to validate these inferences.

8. Summary

The Early Permian Choza Formation of the Clear Fork Group at Castle Peak, Texas, USA contains a relatively diverse trace fossil assemblage that formed in, and around the margins of, an ephemeral (playa) lake situated within a semi-arid to arid alluvial plain. The trace fossil assemblage comprises the invertebrate traces *Cruziana problematica*, *Diplichnites gouldi* types A and B, *Diplichnites* isp. A and B, *Gordia indianensis*, *Helminthoidichnites tenuis*, *Lithographus* isp., *Planolites beverleyensis*, *Rusophycus carbonarius*, *R. furcosus*, *Taenidium barretti*, *Treptichnus* isp., cf. *Kouphichnium* isp, a nodular trail, unilobate epichnial trails and horizontal branching networks, as well the tetrapod trackways *Dromopus palmatus*, *Erpetopus willistoni*, *Varanopus curvidactylus* and cf. *Amphisauropus* isp. The trace fossils from Castle Peak provide evidence of a diverse community, consisting of arthropods, most notably notostracan branchiopod crustaceans, myriapods, euthycarcinoids, and insects, as well as protorothyridid, captorhinid and araeoscelid

reptiles, and amphibians. Reptiles and amphibians probably inhabited the alluvial plain and were drawn to the area in search of food. Myriapods may have survived dry periods by producing *Taenidium barretti* burrows to avoid desiccation. Extant notostracans are adapted to inhabit ephemeral water bodies in arid environments with cysts resistant to desiccation and short life spans, and euthycarcinoids may have had similar life-history strategies. Influx of water into the alluvial plain, through broad ephemeral channels or sheetfloods, filled shallow depressions, creating temporary habitats and resulting in flourishes of life and activity.

The Castle Peak trace fossil assemblage is broadly typical of the *Scoyenia* ichnofacies; however, there is some heterogeneity between assemblages assignable to the *Scoyenia* ichnofacies. The distribution of trace fossils across transitional subaqueous to subaerial settings is not inextricably linked to specific depositional settings, but rather to a variety of environmental factors, and taphonomic factors may also play a role. Trace fossil assemblages similar to that of Castle Peak occur across a range of depositional settings, including desiccated overbank and abandoned or inactive fluvial channels. Such diverse trace fossil assemblages probably reflect the relatively long-lived nature of some ephemeral water bodies. Those with abundant delicate arthropod trackways probably reflect low energy conditions, whereas those with open vertical burrows tend to lack arthropod trackways and probably reflect higher energy conditions. Impoverished examples of the *Scoyenia* ichnofacies may reflect shorter-lived water bodies, whereas trace fossil assemblages dominated by arthropod and vertebrate trackways may represent fleeting preservation windows following sheetfloods on floodplains. Continued documentation of such assemblages will help to evaluate the validity or potential division of the *Scoyenia* ichnofacies.

Acknowledgements

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