A NEW DECAPOD TRACKWAY FROM THE UPPER CRETACEOUS, JAMES ROSS ISLAND, ANTARCTICA

*by* DUNCAN PIRRIE, RODNEY M. FELDMANN *and* LUIS A. BUATOIS

ABSTRACT. A new trace fossil, *Foersterichnus rossensis* igen. nov. and isp. nov., is described from the Coniacian Hidden Lake Formation, James Ross Island, Antarctica. The trace fossil is a trackway comprising straight, or slightly curving, paired rows of elongate to tear-shaped impressions, parallel or slightly inclined to the long axis of the trackway. *Foersterichnus* is interpreted to be the trackway of a brachyuran decapod crustacean. It occurs in transgressive shallow marine deposits formed above the storm wave base in a shelf setting. Preservation of the trackway may have been linked to a rapid deoxygenation event during drowning that led to cessation of bioturbation allowing preservation of mixed layer trackways.

KEY WORDS: trace fossils, decapods, Cretaceous, Antarctica.

T R A C E fossils attributed to the activities of crustaceans are common in late Mesozoic and younger deposits (e.g. Frey *et al*. 1984, 1987; Curran 1985; Gingras *et al*. 2000; Carmona *et al*. 2002). The most common of these ichnogenera are burrow networks and mazes (e.g. *Ophiomorpha*, *Thalassinoides* and *Spongeliomorpha*) and Y-shaped vertical burrows (*Psilonichnus*). Such burrow systems have a much higher preservation potential than trackways, although the latter may be preferentially preserved as undertracks (cf. Goldring and Seilacher 1971). Numerous trackways have been described and commonly interpreted to have been formed by arthropods, particularly in freshwater settings (e.g. Walter 1983; Pollard 1985; Walker 1985; Buatois *et al*. 1998a). However, few trackway taxa have been attributed to crustaceans (Braddy 2001). In this paper we describe a crustacean trackway from shallow marine deposits of the Coniacian Hidden Lake Formation, James Ross Island, Antarctica, and assign it to the new ichnogenus and ichnospecies *Foersterichnus rossensis*. Additionally, we provide a discussion of its palaeoenvironmental framework within a sequence-stratigraphic setting that may help to understand taphonomic conditions leading to preservation of these trackways.

GEOLOGICAL SETTING

An extensive succession of Cretaceous and Tertiary strata crop out within the James Ross Basin, Antarctica (Hathway 2000) (Text-fig. 1). The Cretaceous strata are subdivided into the predominantly deep marine Gustav Group and the overlying shallow marine Marambio Group (Ineson *et al*. 1986). Trace fossils are common throughout the Gustav Group succession and include *Arenicolites*, *Chondrites*, *Cladichnus*, *Cylindrichnus*, *Didymaulichnus*, *Diplocraterion*, *Fuersichnus*, *Nereites*, *Ophiomorpha*, *Phycosiphon*, *Planolites*, *Palaeophycus*, *Skolithos*, *Teichichnus*, *Teredolites*, *Thalassinoides*, *Tissoa* and *Zoophycos* (Ineson 1987; Buatois and López Angriman 1991, 1992*a, b*; Buatois and Mangano 1992; Buatois 1995). The Hidden Lake Formation is the uppermost unit within the Gustav Group and crops out on northern James Ross Island (Ineson *et al*. 1986). The formation is overlain conformably by the Santa Marta Formation (the lowermost unit of the Marambio Group). Recent Sr isotope dating has placed the Coniacian-Santonian boundary some 150 m above the top of the Hidden Lake Formation which is now considered to be entirely Coniacian in age (McArthur *et al*. 2000). Previous micropalaeontological studies had suggested a Coniacian to earliest Santonian age for the Hidden Lake Formation (Riding *et al*. 1992; Medina *et al*. 1999). The samples described here were collected from a single bed at the gradational
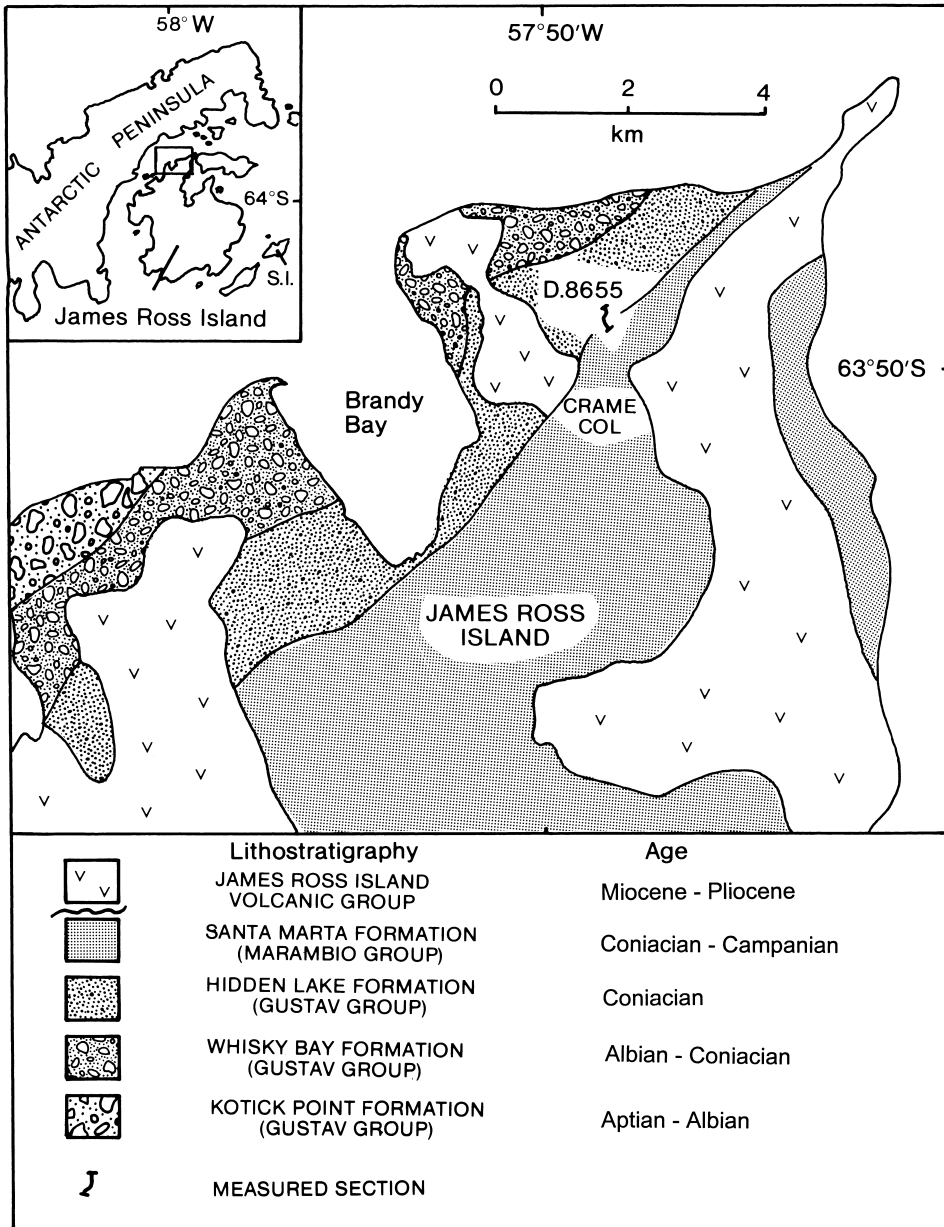
TEXT-FIG. 1. Geological sketch map of northern James Ross Island showing the location of the trace fossil locality (D.8655) (Ineson *et al.* 1986). Inset map shows the location of the study area relative to the northern Antarctic Peninsula. S.I., Seymour Island.

boundary between the Hidden Lake and Santa Marta formations, north of Crame Col, on northern James Ross Island (location D.8655, Text-fig. 1).

The Hidden Lake Formation represents deposition in a fan-delta to shelf setting (Macdonald *et al.* 1988; Pirrie *et al.* 1991; Buatois and López Angriman 1992*c*; Buatois 1993). Sedimentation was directly controlled by concurrent arc volcanism within the Antarctic Peninsula magmatic arc to the west, and

reflects an episode of tectonically controlled basin shallowing (Pirrie *et al.* 1991). The formation has yielded a sparse marine macrofauna (Ineson *et al.* 1986) along with an abundant and diverse palynofloral (Medina *et al.* 1999) and megafloral assemblage (Buatois 1993; J. E. Francis, pers. comm. 2001). Buatois and López Angriman (1992*b*) recorded the presence of various ichnofossils in the Hidden Lake Formation, including *Asterosoma*?, *Didymaulichnus*, *Ophiomorpha*, *Palaeophycus*, *Planolites*, *Skolithos*, *Teredolites*, *Thalassinoides* and *Tissoa*. Subsequently, Buatois (1995) described a new ichnospecies of *Fuersichnus* from this unit. The transition from the Hidden Lake Formation to the overlying Santa Marta Formation is marked by a fining- and thinning-upward sequence and a corresponding increase in macrofaunal diversity and abundance. Thirty metres above the trace fossil locality described herein the Santa Marta Formation is highly fossiliferous, yielding abundant ammonites (e.g. nostoceratids, *Pachydiscus*), belemnites (e.g. *Dimitobelus*), bivalves (e.g. *Pinna*, *Nucula*), serpulids, crinoids, and corals (Thomson 1984; Scasso *et al.* 1991) along with decapod crustaceans (Feldmann *et al.* 1993). This change in fauna and facies reflects the upward transition from high energy fan delta/tidal shelf environments to a deeper marine, lower energy, sub-storm wave base depositional system in response to a decrease in concurrent arc volcanism (Pirrie 1989; Pirrie *et al.* 1991; Scasso *et al.* 1991)

The ichnogenus recorded in this paper occurs within a preferentially indurated sandstone bed that weathers to form a resistant bench within otherwise recessive slopes. The sandstone bed is ripple-cross laminated. Ripple heights are 2–3 cm with wavelengths of up to 15 cm (average 10 cm). Laminae are defined by concentrations of comminuted plant debris, with larger wood fragments up to 5 cm long on the upper bed surface. *Foersterichnus rossensis* is associated with *Ophiomorpha nodosa* and *Thalassinoides suevicus*. Palaeocurrent measurements suggest sediment transport towards the east (Text-fig. 2), away from the inferred palaeoshore line. The lower bed surface is highly irregular as a result of both bioturbation and loading. This bed was deposited from traction and suspension fallout below the normal wave base, but above the storm wave base. The upper bed surface contains both epichnial (*F. rossensis*) and endichnial (*O. nodosa* and *T. suevicus*) traces (Text-fig. 3). The epichnial trackways are commonly sharp and well-preserved, although discontinuous, whilst the endichnial burrows are distinct. The epichnial trackways migrate across the ripple bedforms. The trace fossil horizon is overlain by a mudstone-dominated succession mostly deposited by suspension sedimentation in a mid to outer shelf setting below the storm wave base (Pirrie 1991), reflecting a deepening trend at the transition with the Santa Marta Formation.

SYSTEMATIC PALAEONTOLOGY

Descriptive terminology follows that proposed by Trewin (1994). All specimens are housed in the collections of the British Antarctic Survey, Cambridge, UK.

Ichnogenus FOERSTERICHNUS igen. nov.

#### *Foersterichnus rossensis* isp. nov.

Text-figures 4–5

Derivation of names. *Foersterichnus*, in honour of the late Dr Reinhard Förster, who contributed to the collection of these trace fossils, and was an expert on fossil decapods; *rossensis*, after the type locality on James Ross Island, Antarctica.

Material. Four specimens preserved in four slabs: holotype, D.8655.38; paratypes D.8655.26, D.8655.39, D.8655.70.

Type locality. All material is from the Coniacian Hidden Lake Formation, northern James Ross Island, Antarctica (geological station D.8655; Text-fig. 1).

Generic diagnosis. As for ichnospecies.
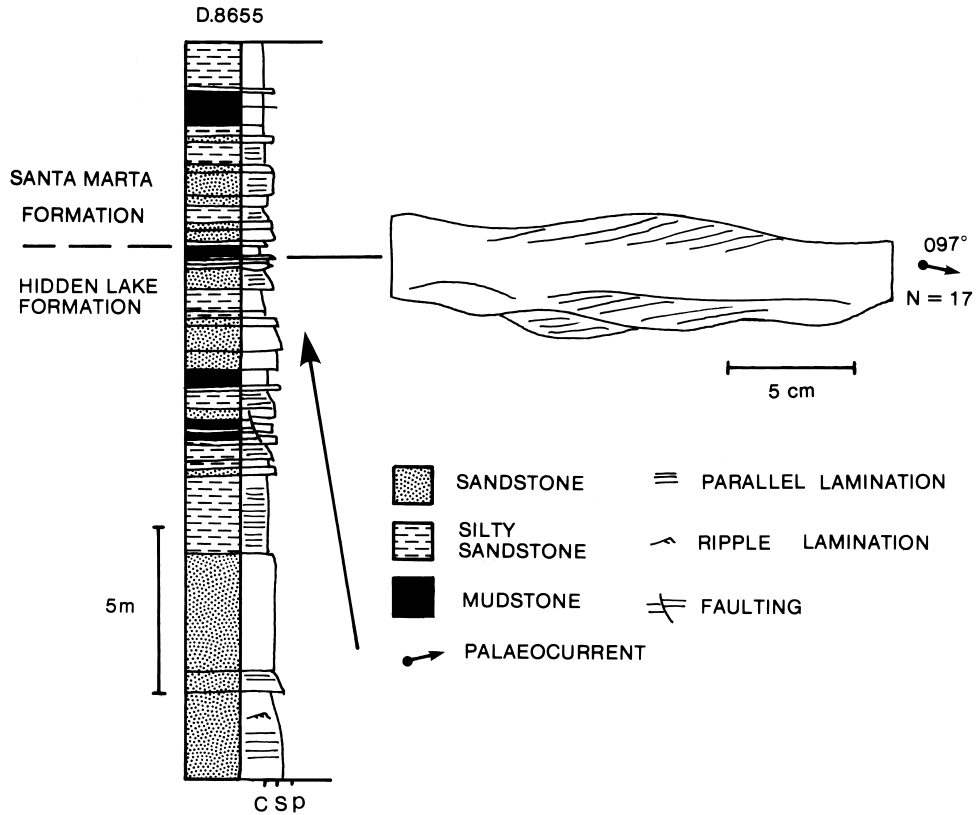
TEXT-FIG. 2. Sedimentary log through the top of the Hidden Lake Formation and the base of the Santa Marta Formation (Station D.8655); trace fossil horizon enlarged. Arrow indicates fining-upward trend; C, clay; S, very coarse sandstone; P, pebble conglomerate.

Diagnosis of ichnospecies. Straight or slightly curving, paired rows of elongate to tear-shaped impressions; parallel or slightly inclined to long axis of trace; track rows compound and organised in series of three or four imprints.

Description. Trackways consist of a repetition of a series of typically three or four tear-shaped, elongate or, more rarely, ellipsoidal imprints 2–4 mm wide and 5–9 mm long (Text-fig. 6). Trackway external width is 3–3·8 cm, while internal width is 1·8–2·3 cm. The imprints are shallow, narrow, closely spaced at one end of a series, and deeper, broader, more widely spaced at the other (Text-fig. 5, left). The imprints are oriented parallel or oblique to the trace mid line. The expression of the traces varies from distinct (Text-fig. 4, left) through blurred (Text-fig. 4, right) to obscure (Text-fig. 5, right). Track rows are compound and organised in series of three or four imprints. Superposition of imprints upon one another produced complex impressions (Text-fig. 5, left). Trackway symmetry is highly variable from bilateral symmetry to remarkable asymmetry. The traces are generally straight but may turn forming gentle curves (Text-fig. 4, right). Medial impressions were not observed. There is no relationship between the topography of the bedform and the location of the trackway.

Remarks. Traces composed of a series of prod marks, similar to those described above, have frequently been ascribed to the walking activity of decapod crustaceans in modern marine environments (Kitchell *et al.* 1978; Frey *et al.* 1987). However, fossil counterparts are remarkably rare. Trackways confidently ascribed to decapod crustaceans (though as yet undescribed) have been recorded from the Jurassic Solnhofen Lithographic Limestone, where the lobster *Mecochirus longimanatus* occurs at the end of its

TEXT-FIG. 3. Field photograph showing *Thalassinoides suevicus* radiating from a central cross-over point (above and to the right of the scale bar). Scale bar represents 15 cm.

trackway (Glaessner 1969; Viohl 1990; Barthel *et al.* 1990). As in *Foersterichnus*, the Solnhofen trackway has elongate impressions oriented parallel with or slightly inclined to the axis and organised in series of three or four imprints. The main difference is the presence of a pair of vague internal continuous marks produced by dragging subchelae in the *Mecochirus* trackway. However, internal marks have low preservation potential due to the 'undertrack fallout effect' (Goldring and Seilacher 1971) and are not good ichnotaxobases. Accordingly, the *Mecochirus* trackway may well be included under *Foersterichnus*.

Probable crustacean trackways include *Merostomichnites* Packard, most likely the product of phyllopods, and the ichnogenera *Umfolozia* Savage (together with related ichnotaxa, such as *Maculichna* Anderson and *Tasmanadia* Chapman), interpreted as made by syncarid or peracarid crustaceans (Savage 1971; Anderson 1981; Braddy 2001). *Foersterichnus* clearly differs from these trackways attributed to crustaceans by the organisation of its track series. While *Foersterichnus* has three to four tracks per series (Text-fig. 6), *Merostomichnites* has nine tracks per series and *Umfolozia* five (Anderson 1981; Braddy 2001). The crustacean affinity of *Siskemia* is still uncertain (Walker 1985). Notably, these trackways are common in freshwater environments, rather than in open marine settings (e.g. Aceñolaza and Buatois 1993). No trackways produced by brachyuran crustaceans have been formally defined from the fossil record.

Other arthropod trackways, such as *Diplichnites*, *Dimorphichnus* and *Petalichnus*, superficially resemble *Foersterichnus*. The ichnogenus *Diplichnites* was proposed by Dawson (1873) for trackways reported from Carboniferous deposits of Nova Scotia, which were believed to be produced by crustaceans, annelids, or myriapods. Subsequently, Seilacher (1955) applied this name to trilobite trackways from the Cambrian of Pakistan. The organisation of imprints in series of three or four and the asymmetry of *Foersterichnus* clearly distinguishes this ichnotaxon from *Diplichnites*. A 'crabwalking' locomotion is expressed by the trilobite trackway *Dimorphichnus*, orginally described by Seilacher (1955). However, *Dimorphichnus* is characterized by two types of imprints, sigmoidal, recording raking movements and blunt, supporting imprints (Seilacher 1955; Osgood 1970). Track organization in *Foersterichnus* is
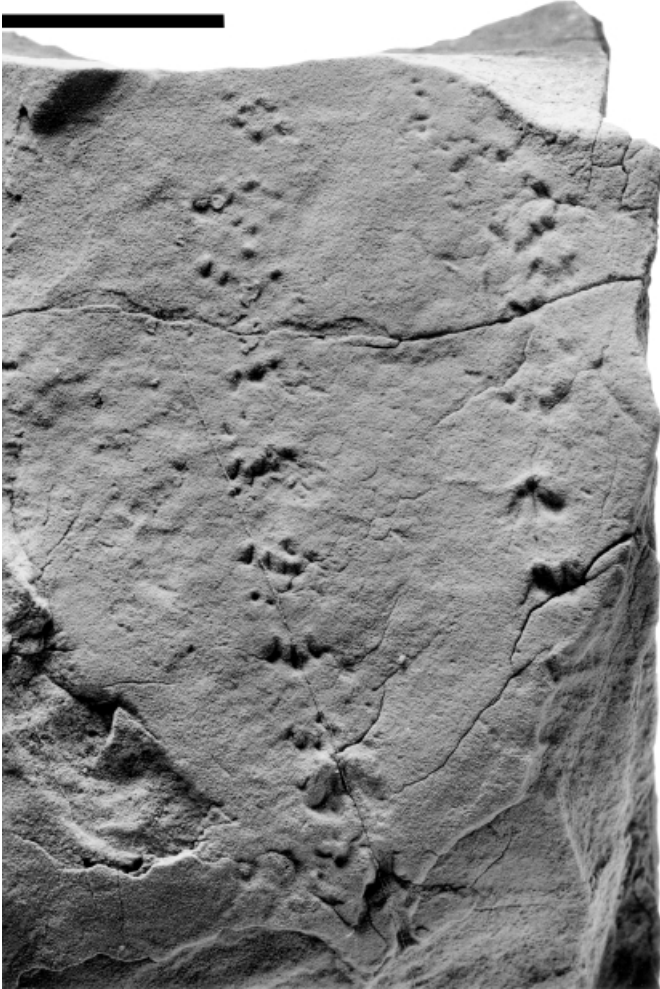
TEXT-FIG. 4. Photograph showing epichnial surface trackway *Foersterichus rossensis* igen. nov., isp. nov., James Ross Island, Antarctica; specimen number D.8655.38; scale bar represents 2 cm.

remarkably different. The ichnogenus *Petalichnus* Miller also resembles *Foersterichnus* in having impressions grouped in series of three to four (Briggs and Rolfe 1983; Braddy and Anderson 1996; Buatois *et al.* 1998*b*). However, track series in *Petalichnus* are oriented at a high angle with respect to the trace axis. Additionally, a median continuous mark is commonly preserved in *Petalichnus*, with the exception of the ichnospecies *P. pottsae* (Braddy and Anderson 1996). Finally, there is general agreement that *Petalichnus* was produced by chelicerates (Braddy 2001).

Based upon the morphology and size of *Foersterichnus* the most likely trace-making organism is a brachyuran decapod crustacean. Although brachyurans have not been described from the Hidden Lake Formation, body fossils do occur in the overlying Santa Marta Formation (Feldmann *et al.* 1993). Although it would be extremely difficult to relate these traces to any specific brachyuran, it is possible to estimate the size of the animal. Assuming the interpretation of the traces to be correct, the animal would have been moving forward and the width of the carapace would, therefore, be equal to, or somewhat less than, the width of the trace. Known brachyuran decapods from the Santa Marta Formation include *Plagiophthalmous collinsi* (Feldmann *et al.* 1993) which has a carapace width of 1·2 cm, *Torynomma* (*Torynomma*) *australis* (Feldmann *et al.* 1993), with a carapace width of 2·5 cm, and two species of
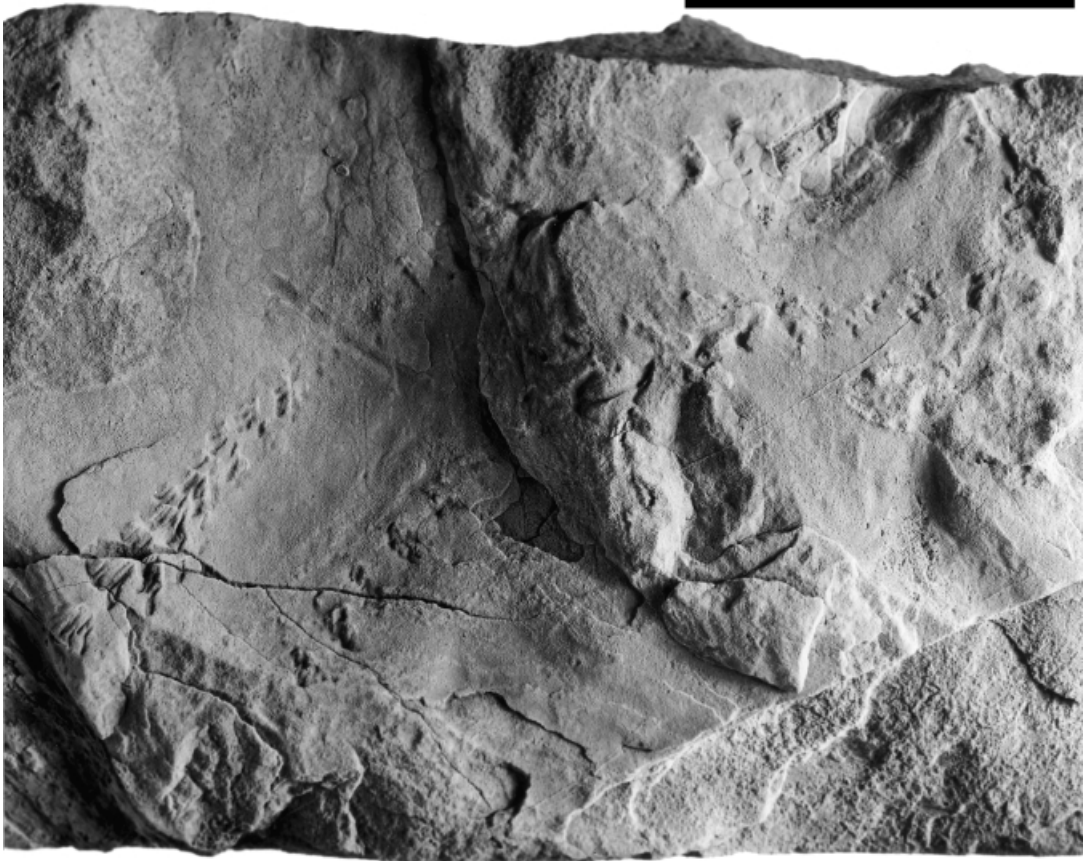
TEXT-FIG. 5. Epichnial surface trackway *Foersterichnus rossensis* igen. nov., isp. nov., James Ross Island, Antarctica; specimen number D.8655.70; scale bar represents 5 cm.

Necrocarcinus, with carapace widths from 1·9 to 2·5 cm. It is possible that any of these taxa could have been the tracemaker. The macrurous decapods from the Santa Marta Formation are much larger and have sufficiently long legs that the spacing of the traces would be quite different from those described here.

The variation in expression of *Foersterichnus rossensis* may be related to changes in the activity of the organisms producing the trackways and to the timespan the traces were exposed on the seafloor prior to burial. The patterns shown in three instances (Text-fig. 4, right and left; Text-fig. 5, right) are interpreted to represent a striding pattern in which the organism was moving in a direction from the bottom of the figure to the top. The variation in expression of the trackways may reflect differences in the viscosity of the sediment (Knox and Miller 1985), the time of exposure prior to burial, or a change from forward walking to 'crabwalking'. Because the trackways all occur on the same bedding plane and are all preserved in the same lithology, the latter interpretation would seem to be more likely. The more complex trackway may be interpreted as several patterns of prod traces superimposed upon one another.

PALAEOENVIRONMENTAL INTERPRETATION

Buatois and López Angriman (1992*b*) noted that the fan delta deposits of the Hidden Lake Formation includes elements of both the *Skolithos* and *Cruziana* ichnofacies. Dwelling traces of suspension feeders and predators, such as *Skolithos*, *Palaeophycus* and *Thalassinoides*, are dominant in delta front
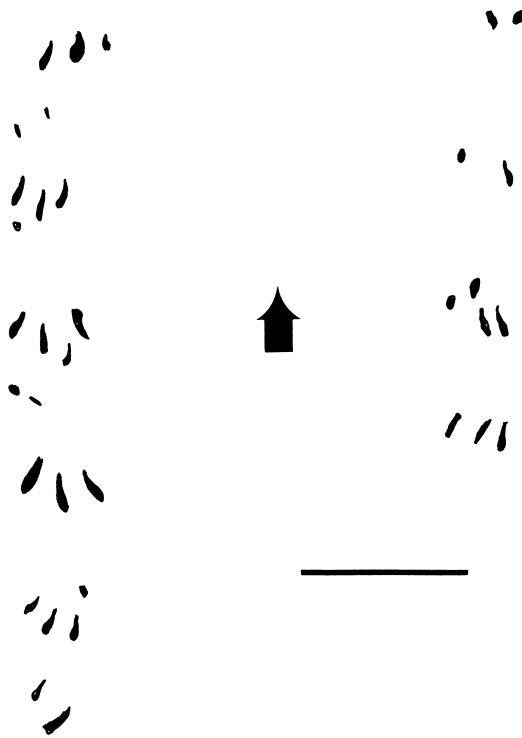
TEXT-FIG. 6. Interpretative drawing of *Foersterichnus rossen-sis* indicating the marks made by the organism in walking in the direction indicated by the arrow. The left side of the trace shows at least five clusters of impressions of three or four marks and the right side of the trace shows four clusters of impressions; scale bar represents 1 cm.

and distributary channel deposits. Assemblages from interdistributary bay and abandoned channel deposits include both dwelling traces of suspension feeders and predators (*Palaeophycus*) and feeding traces of deposit feeders (*Planolites*). Overall, the fan delta ichnofauna had a low diversity and is dominated by simple traces of opportunistic organisms, recording stressful conditions, most likely high sedimentation rates or turbidity. However, the uppermost interval of the Hidden Lake Formation contains a more diverse ichnofauna that includes *Didymaulichnus*, *Ophiomorpha*, *Palaeophycus*, *Planolites*, *Skolithos*, *Thalassinoides* and *Tissoa*, reflecting the transgressive event that led to the drowning and abandonment of the fan delta system, and the subsequent establishment of a marine shelf setting (Buatois and López Angriman 1992*b*). Additionally, the increase in ichnodiversity parallels an increase in macrofossil diversity.

Buatois (1995) documented firmground surfaces indicated by the *Glossifungites* ichnofacies in the upper part of the Hidden Lake Formation. The assemblage includes *Fuersichnus striatus*, sharp-walled *Thalassinoides* and striated *Diplocraterion* (Buatois 1995). In siliciclastic settings the *Glossifungites* ichnofacies records erosional exhumation of compacted and dewatered sediments that usually takes place during changes in sea level, indicative therefore of allostratigraphic surfaces (Pemberton and Frey 1985; MacEachern *et al*. 1992; Pemberton and MacEachern 1995; MacEachern and Burton 2000). In the case of the Hidden Lake Formation, the *Glossifungites* surfaces characterise ravinement surfaces of erosion that are associated with the abandonment of the fan delta system during widespread transgression (Buatois *et al*. 2002). The trace fossil horizon described here occurs a few metres above the firmground *Glossifungites* surfaces, at the transition from the Hidden Lake Formation to the overlying Santa Marta Formation. This has previously been interpreted to represent the transition from the underlying fan delta into a mid to outer shelf setting in response to a decrease in proximal arc volcanism and a reduction in the amount of syndepositional tectonism along the basin margin (Pirrie 1989; Pirrie *et al*. 1991; Buatois 1993). It is possible that the trace fossil horizon described here represents an omission surface related to widespread flooding during a change in basin tectonics. Fine-grained deposits overlying the trace fossil horizon were

deposited in an offshore mid to outer shelf setting. The associated ichnofauna (*Planolites*, *Thalassinoides* and *Ophiomorpha*) most likely records bioturbation in a soft substrate, whereas *Foersterichnus* was most likely emplaced on the firm sediment substrate that resulted from a pause in sedimentation concomitant with the major drowning event. Unfortunately, no cross-cutting relationships between *Foersterichnus* and the associated trace fossils were observed which would have provided unequivocal evidence for the sequence of events.

Preservation potential of surface to near-surface trackways formed in the mixed layer is low. Very shallow structures are usually subject to erosion and affected by subsequent bioturbation due to the activity of infaunal organisms in deeper tiers that tend to obliterate less penetrative traces (Bromley 1996). Progressive infaunalization through the Phanerozoic exerts a major control on secular changes in taphonomic conditions. While shallow biogenic structures are common in Proterozoic and early Palaeozoic shallow marine clastic successions, they became increasingly rare in younger strata (Thayer 1983; Droser and Bottjer 1993). Savrda and Ozalas (1993) noted that the potential for preservation of shallow traces is enhanced when environmental conditions deviate from the steady state. Preservation of decapod trackways in Cretaceous open marine deposits may be explained by invoking stress factors that may have isolated the mixed layer from subsequent bioturbation. In the present case, rapid deoxygenation associated with a drowning event probably led to cessation of bioturbation. Deoxygenation events of previously oxygenated sea floors usually freeze burrowing profiles allowing preservation of mixed layer bioturbation (Savrda and Ozalas 1993).

REFERENCES

ACEÑOLAZA, F. G. and BUATOIS, L. A. 1993. Nonmarine perigondwanic trace fossils from the Upper Paleozoic of Argentina. *Ichnos*, **2**, 183–201.

ANDERSON, A. 1981. The *Umfolozia* arthropod trackways in the Permian Dwyka and Ecca Series of South Africa. *Journal of Paleontology*, **55**, 84–108.

BARTHEL, K. W., SWINBURNE, N. H. M. and CONWAY MORRIS, S. 1990. *Solnhofen. A study in Mesozoic palaeontology*. Cambridge University Press, Cambridge, 245 pp.

BRADDY, S. J. 2001. Trackways – Arthropod locomotion. 389–693. *In* BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaeobiology II*. Blackwell Science, Oxford, 600 pp.

—— and ANDERSON, L. I. 1996. An Upper Carboniferous eurypterid trackway from Mostyn, Wales. *Proceedings of the Geologists' Association*, **107**, 51–56.

BRIGGS, D. E. G. and ROLFE, W. D. I. 1983. A giant arthropod trackway from the Lower Mississippian of Pennsylvania. *Journal of Paleontology*, **57**, 377–390.

BROMLEY, R. G. 1996. *Trace fossils. Biology, taphonomy and applications*. Chapman and Hall, London, 361 pp.

BUATOIS, L. A. 1993. Depósitos de fan-delta y plataforma en la Formación Hidden Lake, Cretácico de la isla James Ross, Antártida. *Segundas Jornadas de Comunicaciones sobre Investigaciones Antárticas 1991*. Conicet, Buenos Aires, 215–218.

—— 1995. A new ichnospecies of *Fuersichnus* from the Cretaceous of Antarctica and its palaeoecological and stratigraphic implications. *Ichnos*, **3**, 259–263.

—— and LÓPEZ ANGRIMAN, A. O. 1991. Icnologia de la Formación Whisky Bay (Cretácico, Isla James Ross, Antartida): implicancias paleoecologicas y paleoambientales. *Ameghiniana*, **28**, 75–88.

—— —— 1992*a*. The ichnology of a submarine braided channel complex: the Whisky Bay Formation, Cretaceous of James Ross Island, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **94**, 119–140.

—— —— 1992*b*. Trazas fósiles y sistemas deposicionales, Grupo Gustav, Cretácico de la isla James Ross, Antártida. 239–262. *In* RINALDI, C. A. (ed.). *Geología de la isla James Ross. Buenos Aires*. Publicación del Instituto Antártico Argentino, Buenos Aires, 389 pp.

—— —— 1992c. Evolución de sistemas deposicionales en el Cretácico del Grupo Gustav, Isla James Ross, Antártida. 263–297. In RINALDI, C. A. (ed.). Geología de la isla James Ross. Buenos Aires. Publicación del Instituto Antártico Argentino, Buenos Aires, 389 pp.

—— and MANGANO, M. G. 1992. La oxigenacion como factor de control en la distribucion de asociaciones de trazas fosiles, Formacion Kotick Point, Cretacico de Antartida). Ameghiniana, 29, 69–84.

—— —— and ACEÑOLAZA, F. G. 2002. Trazas fósiles: Señales de comportamiento en el registro estratigráfico. Museo Paleontológico Egidio Feruglio, Publicación 2, Trelew, 382 pp.

—— —— MAPLES, C. G. and LANIER, W. P. 1998a. Ichnology of an Upper Carboniferous fluvio-estuarine paleovalley: the Tonganoxie Sandstone, Buildex Quarry, eastern Kansas. Journal of Paleontology, 71, 152–180.

—— —— —— —— 1998b. Taxonomic reassessment of the ichnogenus Beaconichnus and additional examples from the Carboniferous of Kansas, U.S.A. Ichnos, 5, 287–302.

CARMONA, N. B., BUATOIS, L. A. and MÁNGANO, M. G. 2002. The trace fossil record of the decapod crustacean radiations. First International Palaeontological Congress, Abstracts, Sydney, 29–30.

CURRAN, H. A. 1985. The trace fossil assemblage of a Cretaceous nearshore environment: Englishtown Formation of Delaware, USA. In CURRAN, H. A. (ed.). Biogenic structures: their use in interpreting depositional environments. 261–276. Society of Economic Paleontologists and Mineralogists, Special Publication, 35, 347 pp.

DAWSON, J. W. 1873. Impressions and footprints of aquatic animals and imitative markings on Carboniferous rocks. American Journal of Science and Arts, 5, 16–24.

DROSER, M. L. and BOTTJER, D. J. 1993. Trends and patterns of Phanerozoic ichnofabrics. Annual Reviews of Earth and Planetary Sciences, 21, 205–225.

FELDMANN, R. M., TSHUDY, D. M. and THOMSON, M. R. A. 1993. Late Cretaceous and Paleocene decapod crustaceans from James Ross Basin, Antarctic Peninsula. The Paleontological Society, Memoir, 28, 41 pp.

FREY, R. W., CURRAN, H. A. and PEMBERTON, S. G. 1984. Tracemaking activities of crabs and their environmental significance: the ichnogenus Psilonichnus. Journal of Paleontology, 58, 333–350.

—— HOWARD J. D. and HONG, J. 1987. Prevalent lebensspurren on a modern macrotidal flat, Inchon, Korea: ethological and environmental significance. Palaios, 2, 571–593.

GINGRAS, M. K., HUBBARD, S. M., PEMBERTON, S. G. and SAUNDERS, T. 2000. The significance of Pleistocene Psilonichnus at Willapa Bay, Washington. Palaios, 15, 142–151.

GLAESSNER, M. F. 1969. Decapoda. R400–533. In MOORE, R. C. (ed.). Treatise on invertebrate paleontology, Part R, Arthropoda 4 (2). Geological Society of America, Boulder, and University of Kansas Press, Lawrence, R399–651.

GOLDRING, R. and SEILACHER, A. 1971. Limulid undertracks and their sedimentological implications. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 137, 422–442.

HATHWAY, B. 2000. Continental rift to back-arc basin: Jurassic–Cretaceous stratigraphical and structural evolution of the Larsen Basin, Antarctic Peninsula. Journal of the Geological Society, London, 157, 417–432.

INESON, J. R. 1987. Trace fossils from a submarine fan-slope apron complex in the Cretaceous of James Ross Island, Antarctica. British Antarctic Survey, Bulletin, 74, 1–16.

—— CRAME, J. A. and THOMSON, M. R. A. 1986 Lithostratigraphy of the Cretaceous strata of west James Ross Island, Antarctica. Cretaceous Research, 7, 141–159.

KITCHELL, J. A., KITCHELL, J. F., JOHNSON, G. L. and HUNKINS, K. L. 1978. Abyssal traces and megafauna: comparison of productivity, diversity and density in the Arctic and Antarctic. Paleobiology, 4, 171–180.

KNOX, L. W. and MILLER, M. F. 1985. Environmental control of trace fossil morphology. In CURRAN, H. A. (ed.). Biogenic structures: their use in interpreting depositional environments. 167–176. Society of Economic Paleontologists and Mineralogists, Special Publication, 35, 347 pp.

MACDONALD, D. I. M., BARKER, P. F., GARRETT, S. W., INESON, J. R., PIRRIE, D., STOREY, B. C., WHITHAM, A. G., KINGHORN, R. R. F. and MARSHALL, J. E. A. 1988. A preliminary assessment of the hydrocarbon potential of the Larsen Basin, Antarctica. Marine and Petroleum Geology, 5, 34–53.

MACEACHERN, J. A. and BURTON, J. A. 2000. Firmground Zoophycos in the Lower Cretaceous Viking Formation, Alberta: a distal expression of the Glossifungites ichnofacies. Palaios, 15, 387–398.

—— RAYCHAUDHURI, I. and PEMBERTON, S. G. 1992. Stratigraphic applications of the Glossifungites ichnofacies: delineating discontinuities in the rock record. 169–198. In PEMBERTON, S. G. (ed.). Applications of ichnology to petroleum exploration – a core workshop. Society of Economic Paleontologists and Mineralogists, Core Workshop, 17, 429 pp.

MCARTHUR, J. M., CRAME, J. A. and THIRLWALL, M. F. 2000. Definition of Late Cretaceous stage boundaries in Antarctica using strontium isotope stratigraphy. Journal of Geology, 108, 623–640.

MEDINA, F., BARREDA, V. and PALAMARCZUK, S. 1999. Palinología de la Formación Hidden Lake (Coniaciano–Santoniano), isla James Ross, Antártida. Revista Expañola de Micropaleontología, 31, 53–72.

OSGOOD, R. G. 1970. Trace fossils of the Cincinnati area. *Palaeontographica Americana*, **6**, 277–444.

PEMBERTON, S. G. and FREY, R. W. 1985. The *Glossifungites* ichnofacies: modern examples from the Georgia coast, U.S.A. 227–259. *In* CURRAN, H. A. (ed.). *Biogenic structures: their use in interpreting depositional environments.* Society of Economic Paleontologists and Mineralogists, Special Publication, **35**, 347 pp.

—— and MACEACHERN, J. A. 1995. The sequence stratigraphic significance of trace fossils: examples from the Cretaceous foreland basin of Alberta, Canada. 429–475. *In* VAN WAGONER, J. C. and BERTRAM, G. (eds). *Sequence stratigraphy of foreland basin deposits – outcrop and subsurface examples from the Cretaceous of North America.* American Association of Petroleum Geologists, Memoir, **64**, 500 pp.

PIRRIE, D. 1989. Shallow marine sedimentation within an active margin basin, James Ross Island, Antarctica. *Sedimentary Geology*, **63**, 61–82.

—— WHITHAM, A. G. and INESON, J. R. 1991. The role of tectonics and eustasy in the evolution of a marginal basin: Cretaceous – Tertiary, Larsen Basin, Antarctica. 293–305. *In* MACDONALD, D. I. M. (ed.). *Sea level changes at active plate margins: processes and products.* International Association of Sedimentologists, Special Publication, **12**, 518 pp.

POLLARD, J. E. 1985. *Isopodichnus*, related arthropod trace fossils and notostracans from Triassic fluvial sediments. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 273–285.

RIDING, J. B., KEATING, J. M., SNAPE, M. G., NEWHAM, S. and PIRRIE, D. 1992. Preliminary Jurassic and Cretaceous dinoflagellate cyst stratigraphy of the James Ross Island area, Antarctic Peninsula. *Newsletters on Stratigraphy*, **26**, 19–39.

SAVAGE, N. M. 1971. A varvite ichnocoenosis from the Dwyka Series in Natal. *Lethaia*, **4**, 217–233.

SAVRDA, C. E. and OZALAS, K. 1993. Preservation of mixed-layer ichnofabrics in oxygenation-event beds. *Palaios*, **8**, 609–613.

SCASSO, R. A., OLIVERO, E. B. and BUATOIS, L. A. 1991. Lithofacies, biofacies and ichnoassemblage evolution of a shallow submarine volcaniclastic fan-shelf depositional system (Upper Cretaceous, James Ross Island, Antarctica). *Journal of South American Earth Sciences*, **4**, 239–260.

SEILACHER, A. 1955. Spuren und Lebensweise der Trilobiten; Spuren und Fazies im Unterkambrium. 86–143. *In* SCHINDEWOLF, O. H. and SEILACHER, A. (eds). *Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan).* Akademie der Wissenschaften und der Literatur zu Mainz, Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen, **10**, 190 pp.

THAYER, C. W. 1983. Sediment-mediated biological disturbance and the evolution of marine benthos. 479–625. *In* TEVESZ, M. J. S. and MCCALL, P. L. (eds). *Biotic interactions in Recent and fossil benthic communities.* Plenus Press, New York, 837 pp.

THOMSON, M. R. A. 1984. Cretaceous ammonite biostratigraphy of western James Ross Island, Antarctica. 308–314. *In* de C. PERRILLIAT, M. (ed.). *Memoria, 111 Congreso Latinoamericano de Paleontología, Mexico, 1984.* Universidad Nacional Autonoma de Mexico, Instituto de Geológia, Mexico City.

TREWIN, N. H. 1994. A draft system for the identification and description of arthropod trackways. *Palaeontology*, **37**, 811–823.

VIOHL, G. 1990. Solnhofen lithographic limestones. 285–289. *In* BRIGGS, D. E. G. and CROWTHER, P. R. (eds). *Palaeobiology, a synthesis.* Blackwell Scientific Publications, Oxford, 583 pp.

WALKER, E. F. 1985. Arthropod ichnofauna of the Old Red Sandstone at Danure and Montrose, Scotland. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 287–297.

WALTER, H. 1983. Zur Taxonomie, Ökologie und Biostratigraphie der Ichnia limnisch-terrestrischer Arthropoden des mittleleuropaischen Jungpalaeozoikums. *Freiberger Forschungsheft C*, **382**, 146–193.

DUNCAN PIRRIE

Camborne School of Mines
University of Exeter
Redruth, Cornwall TR15 3SE, UK
e-mail dpirrie@csm.ex.ac.uk

RODNEY M. FELDMANN

Department of Geology
Kent State University
Kent, Ohio 44242, USA
e-mail rfeldman@kent.edu

LUIS A. BUATOIS

Conicet, Instituto Superior de Correlación Geológica
Casilla de Correo 1
4000 San Miguel de Tucumán
Tucumán, Argentina
e-mail ichnolog@infovia.com.ar