Limulid Trackways in the Late Palaeozoic Ecca Sediments and their Palaeoenvironmental Significance

It is widely believed that the Ecca sediments in the Great Karroo basin accumulated under brackish to marine conditions, but unambiguous faunal evidence has proved elusive. The situation was reviewed recently by McLachlan.[1] He concluded that there was little support for a normal marine environment and that the available palaeontology suggested no connection with the ocean and its invertebrate faunas. Marine invertebrates are notoriously scarce in the Ecca: in spite of the extensive outcrop, they have been reported from only one locality.[2,3] There are three specimens on record from the abandoned Aletta iron ore mine in the Middle Ecca of northern Natal.

In the absence of body fossils, it has been necessary to resort to trace fossils,[4] but, as Seilacher[5] has pointed out, these can be misleading because the biological activities controlling trace morphology are largely independent of salinity. This is especially true where, as is usually the case, the traces cannot be referred to the creature responsible.[6,7] One of the rare exceptions is the limulid trackway (Fig. 1).[8,10]

Modern limulids (commonly known as king- or horseshoe-crabs) are marine animals.[11,12,34] The presence of their fossilised trackways therefore has some palaeoenvironmental significance.

In 1965 Toerien[13] recorded limulid trackways (Fig. 2) from the uppermost Ecca sediments. This and two other localities are included in the present study. All three are stratigraphically above the the White Band.

Three limulid trackway localities in the Ecca

(a) Gradley (29° 49′ 12″ S, 25° 02′ 54″ E.):

The locality visited by Toerien[13] is about 25 km WSW of Fauresmith in the southwestern Orange Free State. The outcrops are on the farm Cradley, close to its eastern boundary, in the Berg River bed.

Less than half a metre of pale fine-grained flagstones are exposed. They are finely laminated and often oscillation-rippled marked. Dolerite directly underlies the flagstones. The horizon is about 100 m below the first prominent sandstone denoting the start of the Beaufort series, but this interval includes dolorite intrusion of unknown thickness.

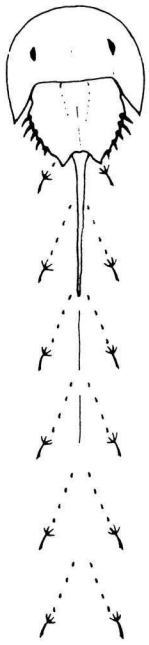

Fig. 1 Sketch of *Limulus* and its trackway (after Caster[9]).

Fig. 2 Limulid trackway with simple and digitate tracks from the Ecca sediments in the Orange Free State (Gr. 1, x 0.5).

(b) Vendutiekop (29° 43′ 54″ S, 25° 37′ 24″ E):

The second locality, on the farm Vendutiekop 120, is about 45 km east of Toerien's locality. It is a small quarry in the bed of a tributary of the Kromellenboogspruit, northwest of the homestead and cultivated lands.

About 2 m of light grey fine-grained sandstones are being quarried. Beaufort series type sandstone outcrops in the vicinity less than 30 m stratigraphically above the flagstones, but it could not be established whether similar sandstone occurs below as well. The 1:1 000 000 geological map (1970) indicates that the site falls within the Beaufort. However, the map was based on reconnaisance mapping,[14] and, in view of the interfingering of the two characteristic lithologies (Ecca shale/Beaufort sandstone), the boundary must be regarded as somewhat arbitrarily defined at present.[15] The trackways at Vendutiekop are preserved in a lithology typical of the Upper Ecca in the vicinity.

(c) Goeie Hoop (28° 20′ S, 17° °[′ E):

The third locality is in South West Africa, on the farm Goeie Hoop about 50 km north of Viool's Drift on the Orange River.

The diagnostic digitate tracks (Fig. 3) occur at the top of the White Band, 3 cm above palaeoniscoid fish fossils in a similar lithology.

Material

(i) South African Museum specimen K1124 (1 trackway) illustrated by Toerien.[13]

(ii) Bernard Price Institute for Palaeontological Research specimens selected in the field:

Gr./K.E.	1–26	(12 trackways from Gradley)
Vd./K.E.	1–16	(12 trackways from Vendutiekop)
G.H./K.WB.	1–7	(a few distinctive digitate tracks, no clear trackways; from Goeie Hoop).

Systematic description

Phylum: Arthropoda
Subphylum: Arachnida
Class: Xiphosura
Type species: Ichnogenus *KOUPHICHNIUM* Nopsca 1923
Ichnites lithographicus Oppel 1862

Diagnosis: In each of the two track rows of the trackway there is classically one digitate track to a finite number of simpler tracks. The digitate tracks characteristically consist of a bunch of "fingers" at one end of a long "heel". The simpler tracks are slender, acuminate, straight or slightly curved, and each may be V-shaped. They are arranged in opposing oblique lines, with up to five tracks in a line. There is a straight median line and there may be lateral drag lines beyond the outer limits of the tracks (individual footprints). The full complement of markings is not necessarily present in any one preserved trackway: the complement depends on the degree of "undertrack fallout".[16]

Comparison: The disposition of the various components of the trackway is distinctive, and the digitate tracks are unique. However, the digitate form does simulate vertebrate tracks (see below). If there are complete or nearly complete *Kouphichnium* trackways in a collection this confusion usually can be avoided because there are too many tracks in one cycle reasonably to have been left by a tetrapod.

In those trackways where the digitate track is missing there is further potential for misidentification, e.g. *Paleohelcura* Gilmore 1926,[17–19] like *Kouphichnium*, has as one of its variations a trackway in which the tracks on each side are arranged in oblique lines of three, opposing one another on either side of a median line. In this case it is necessary to examine the accompanying variations to determine which ichnogenus it is that is present.

Discussion

(a) *Kouphichnium* trackways formerly were attributed to vertebrates.[20–23] Now it is recognised that the fossil trackways correspond well with those left by the modern king crab *Limulus polyphemus*.[8–10,24] The digitate tracks are left by the last pair of legs, the pushers, and the simple tracks by three, four or five pairs of more anterior legs, the pincers (*see* Fig. 4).

(b) No species synonymy is attempted here because it has not been possible to obtain some of the original descriptions, and neither has any but the South African Permian material been examined by this author. In the light of recent findings by Goldring and Seilacher,[16] many of the existing species names are likely to be synonymous, necessitating a general review of the ichnogenus.

(c) Recent king crabs inhabit turbulent shallow marine environments from which they may at times come up on to the beaches.[11] Their fossil record (both body and trace) is mainly from non-marine deposits. Superficially, this suggests a phylogenetic change in habitat through time. Goldring and Seilacher[16] comprehensively reviewed the situation and concluded that:

"The main habitats of limulids have always been in a shallow sea; but the fossilization potential for both carcasses and tracks, was so much lower in the true biotope than marginal and partly nonmarine environments that the fossil representation of the limulids is now stronger in these than in their main biotopes . . ."

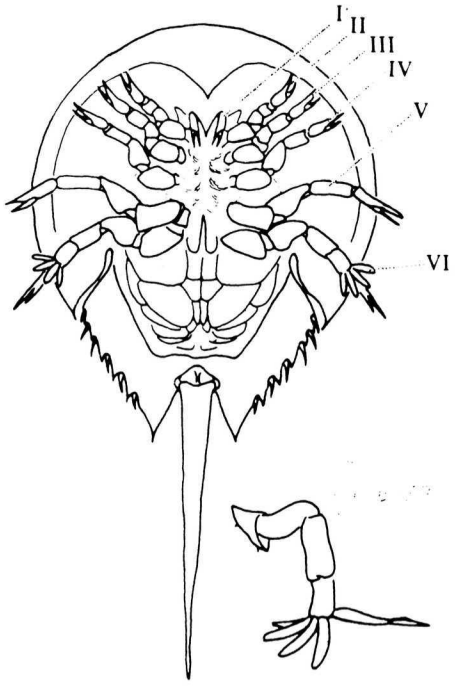

Fig. 3 Ventral view of *Limulus polyphemus* showing its five pairs of pincers (I–V) and one pair of pushers (VI). On the right/bottom one of the pushers, which are responsible for the digitate tracks, is shown in lateral view. (After Caster[8]).

Implications of these observations

Modern limulids are tolerant of wide ranges of salinity,[25] so the environment need not necessarily have been normal marine, but it was at least brackish. This corroborates McLachlan's[1] evidence. Nonetheless, even if the trackway horizons themselves were non-marine, the presence of limulids does suggest that the Great Karroo basin was lined with open ocean during Ecca times, and then it would appear that the marine connection persisted almost to the dawn of Beaufort times when terrestrial tetrapods flourished in the Karroo.

McLachlan and Anderson showed[26,27] that a marine incursion into the basin followed the withdrawl of the Dwyka glaciers, leaving widespread marine invertebrate fossils. This marine fauna has been found well below the White Band at the contact between the Dwyka and Ecca in the southern/western portion of the Great Karroo basin. In the northern/eastern portion of the basin, the White Band is not developed.[15] In that portion all the post-glacial deposits below the Beaufort and including the Coal Measures are termed Ecca. The dearth of obvious fossils common to both portions is largely responsible for the uncertainty about the correlation between the two. The Middle Ecca Coal Measures of the Great Karroo basin traditionally,[15,28,29] but not universally,[30–32] are

Fig. 4 Characteristic limulid digitate track at the top of the White Band in South West Africa (G. H. 3, x 1).

regarded as being younger than the White Band. A mineral deposit identified as "glauconite" associated with the coals has been quoted in support of marine conditions in the northeast.[33] This prompted the suggestion that the coals in the northeast might have been the time equivalent of the marine horizon at the top of the glacial succession in the southwest.[26] The indication by the limulid trackways of marine conditions extending *above* the White Band in the southern/western portion of the Great Karroo basin diminishes the consequence of that argument. However, it must be added that the Ecca limulids could have been part of a relic fauna surviving in a closed basin after an earlier brief marine incursion.

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[1] McLachlan, I. R. (1973). Problematic microfossils from the lower Karroo beds in South Africa. *Palaeont. afr.*, 15, 1–21.
[2] Rilett, M. H. P. (1963). A fossil cephalopod from the Middle Ecca beds in the Klip River Coalfield near Dundee, Natal. *Trans R. Soc. S. Afr.*, 37, 73–74.
[3] Teichert, C. and Rilett, M. H. P. (1974). Revision of Permian Ecca series cephalopods, Natal, South Africa. *Palaeont. Contr. Univ. Kans.*, Pap. 68, 1–9
[4] Teichert, C. (1970). Marine Fossil Invertebrate Faunas of the Gondwana region. *Proc. Pap. 2nd I.U.G.S. Gondwana Symposium, South Africa*, 125–138.
[5] Seilacher, A. (1963). Lebenspuren und Salinitätsfacies. *Fortscht. Geol. Rheinld. u. Westf.*, 10, 81–94.
[6] Seilacher, A. (1953). Studien zur Palichnologie. *Neues Jb. Geol. Paläont. Abh.*, 92, 421–452.
[7] Seilacher, A. (1964). Biogenic sedimentary structures. In *Approaches to Paleoecology*, eds. Imbrie, J. & Newell, N. D. Wiley, New York. Pp. 296–316.
[8] Caster, K. E. (1938). A restudy of the tracks of *Paramphibius*. *J. Paleont.*, 12, 3–60.
[9] Caster, K. E. (1939). Were *Micrichnus scotti* Abel and *Artiodactylus sinclairi* Abel of the Newark serie (Triassic) made by vertebrates or limulids? *Am. J. Sci.*, 237, 786–797.
[10] Malz, H. (1964). *Kouphichnium walchi* die Geschichte einer Fährte und ihres Tieres. *Natur Mus., Frankf.*, 94, 81–97.
[11] Shuster, C. N. (1957). Xiphosura (with especial reference to *Limulus polyphemus*). *Geol. Soc. Am. Mem.* 67, Vol I, pp. 1171–1174.
[12] Barthel, K. W. (1974). *Limulus:* a living Fossil. *Naturwissenschaften*, 61, 428–433.
[13] Toerien, M. J. (1965). Fossielspore in die Fauresmith distrik. *S. Afr. J. Sci.*, 61, 289–290.
[14] Ryan, P. J. (1967). *Stratigraphic and paleocurrent analysis of the Ecca series and lowermost Beaufort beds in the Karroo basin of South Africa.* PhD Thesis, University of the Witwatersrand.
[15] Haughton, S. H. (1969). *Geological History of Southern Africa.* Geological Society of South Africa, Johannesburg.
[16] Goldring, R. & Seilacher, A. (1971). Limulid undertracks and their sedimentological implications. *Neues Jb. Geol. Paläont. Abh.*, 137, 422–442.
[17] Gilmore, C. W. (1926). Fossil footprints from Grand Canyon: first contribution. *Smithson, misc. Collns*, 77 (9), 41 pp.
[18] Brady, L. F. (1947). Invertebrate tracks from the Coconino sandstone in northern Arizona. *J. Paleont.*, 21, 466–472.
[19] Brady, L. F. (1961). A new species of *Palaeohelcura* Gilmore from the Permian of northern Arizona. *J. Paleont.*, 35, 201–202.
[20] Nopsca, F. B. (1923). Die Familien der Reptilien. *Fortschr. Geol. Paläont.*, H.2, 210 pp.
[21] Jaekel, O. (1929). Die spur eiens neuen Urvogels (*Protornis bavarica*) und deren Bedeutung fur die Urgeschichte der Vogel. *Paläont. Z.*, 11, 201–238.
[22] Abel, O. (1935). *Vorzeitliche Lebensspuren.* Jena, 644 pp.
[23] Willard, B. (1935). Chemung tracks and trails from Pennsylvania. *J. Paleont.*, 9, 43–56.
[24] Häntzchel, W. (1962). Trace fossils and Problematica. In *Treatise on Invertebrate Paleontology*, ed. Moore, R. C., Geological Society of America and Kansas University. Pp. W177–245.
[25] Shuster, C. N. (1960). Xiphosura. In *Encylopedia of Science and Technology*, 14, 563–567. McGraw-Hill, New York.
[26] McLachlan, I. R. & Anderson, A. M. (1973). A review of the evidence for marine conditions in southern Africa during Dwyka times. *Palaeont. afr.*, 15, 37–64.
[27] McLachlan, I. R. & Anderson, A. M. The marine incursion into southern Africa during Dwyka times. *Proc. Pap. 3rd I. U. G. S. Gondwana Symposium, Canberra, 1973.* (In press).
[28] Du Toit, A. L. (1954). *The Geology of South Africa.* Oliver & Boyd, Edinburgh.
[29] Anderson, A. M. (1974). *Arthropod trackways and other trace fossils from the Early Permian lower Karroo beds of South Africa.* PhD thesis, University of the Witwatersrand.
[30] Plumstead, E. P. (1962). Fossil Floras of Antarctica. *Trans-Antarctic Expedition 1955–1958 Scientific Report No. 9*, pp. 1–154. Trans-Antarctic Expedition Committee, 22 Gayfree St., London SWI.
[31] Van Eeden, O. R. (1973). The correlation of the subdivisions of the Karroo System. *Trans. geol. Soc. S. Afr.*, 76, 201–206.
[32] Anderson, J. M. (1973). The biostratigraphy of the Permian and Triassic Part 2 (Charts 23–35): A preliminary review of the distribution of Permian and Triassic strata in time and space. *Palaeont. afr.* 16, 59–83.
[33] Hart, G. F. (1964). Where was the Lower Karroo sea? *Scientific S. Afr.*, 1, 289–290.
[34] Stephens, W. M. (1964). The incredible horseshoe crab. *Sea Front*, 10, 130–138.

BOOK REVIEWS

Bushman Languages

The Compleat Guide to the Koon. By A. Traill. Pp. 50. (African Studies Institute Communication No. 1, University of the Witwatersrand, Johannesburg; 1974.)

In this research report on linguistic fieldwork undertaken in Botswana and South West Africa Traill states his aims namely to provide a complete account of a single !xõ dialect, and to present a dialectal survey of the whole !xõ area. When it is finished this research project should enhance our insight into the relationship between Bushman and Hottentot languages of Southern Africa. Throughout the report it is apparent that immediate large scale linguistic research is imperative before the remaining speakers of unrecorded or unsatisfactorily recorded dialects die out.

The interesting photographs, which did not appear in the 1973 edition of this report, are a welcome addition; especially so in the case of !gurice, his son Malxas and grandson Abraham.

Traill has already, at this early stage of