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Application of vertebrate trace fossils to palaeoenvironmental analysis

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ABSTRACT

This is a review of the main uses of vertebrate trace fossils, ichnofabrics and ichnofacies in the palaeoenvironmental analysis of sedimentary sequences. The article accounts for the significant developments produced in the last three decades, including the application of the ichnofacies concept to vertebrate trace fossils. Recognition of footprints in cross-sectional view and their distinction from inorganic structures and burrow fills, is first discussed. The response of different substrates, showing contrasting water content and imprinted by different animals or devices, is compared in terms of the morphology of the resultant footprint. Trackways with sand crescents are typical of aeolian cross-strata and are absent in associated flat-lying to low-angle deposits. Thick packages of highly bioturbated sandy dune and interdune sediments have been interpreted as reflecting periods of increased rainfall. Neoichnological observations in modern lake basins suggest that distinct zones can be recognized in the margins of fossil ponds and lakes, including onshore, shoreline and shallow subaqueous zones. Abundant flamingo-like footprints and flamingo nest mounds are good indicators of alkaline and/or saline lake waters. Hippopotamus trails are found closely associated with modern and fossil freshwater wetlands. Dinosaur and pterosaur swim traces from lacustrine and fluvial deposits can be used to estimate water depth. Turtle, crocodile, amphibian, hippopotamus and fish swim traces allow one to infer a subaqueous substrate. Certain modern intertidal fish feeding traces are oriented with the predominant tidal current and can be used as palaeocurrent indicators. The preferential orientation of tetrapod trackways in lacustrine and fluvial deposits is analyzed. Vertebrate trace fossils can help to infer discharge variability in fluvial channels. The descriptions of vertebrate ichnofabrics are commonly limited to heavily bioturbated beds due to trampling by vertebrates, and to a few examples of ichnofabrics with discrete trace fossils. The nature and implications of the recognized vertebrate ichnofacies are still being debated and have a limited utility in palaeoenvironmental analysis. The distinction of a potential vertebrate burrow ichnofacies in carbonate-bearing palaeosols is proposed to represent well-drained soils, developed under arid or semiarid climate.

1. Introduction

Vertebrate trace fossils have been used as sources of information for palaeontological, palaeoecological and palaeoenvironmental analyses. One of the primary interests of vertebrate palaeontologists is the identification of the producer of tetrapod footprints and its contribution to palaeocommunity reconstruction (in conjunction with the bone record), evolutionary studies and potential biostratigraphic implications (e.g., Haubold, 1971, 1984; Lockley, 1991; Lockley and Hunt, 1995; Lockley and Meyer, 2000). Considerable effort has been devoted to the biomechanical and behavioural interpretation of tetrapod trackways using information from biology, laboratory and computational experiments and neoichnological observations on living animals (e.g., McKee, 1947; Padian and Olsen, 1989; Allen, 1997; Gatesy, 2001; Milàn, 2006; Jackson et al., 2010). A less explored source of information is the use of vertebrate trace fossils as an aid to palaeoenvironmental analysis (e.g., Lockley, 1986; Loope, 1986; Brand and Tang, 1991; Meyer, 1999; Whyte and Romano, 2001; Moratalla and Hernán, 2010; Scott et al., 2012b), description and interpretation of vertebrate ichnofabrics (Tobin, 2004; Melchor et al., 2012c), and the potential distinction of vertebrate ichnofacies (Lockley and Conrad, 1989; Lockley et al., 1994; Hunt and Lucas, 2007).

Lockley (1986) reviewed the use of dinosaur footprints on palaeobiology and palaeoenvironmental analysis. Since the publication of that review, a significant number of contributions emphasizing the use of vertebrate trace fossils in palaeoenvironmental analysis have been published, and also the ichnofacies concept has been applied to vertebrate trace fossils. This contribution builds upon Lockley (1986) and aims to compile and discuss the potential use of various vertebrate trace fossil types, of fish and tetrapod origin, to palaeoenvironmental analysis. The types of vertebrate trace fossils covered in this contribution are: footprints, trails (continuous traces on a bedding plane), burrows, nests, and coprolites. The environmental distribution of

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vertebrate bioerosion trace fossils in bones (like biting and gnawing traces) is poorly known (e.g., Mikuláš et al., 2006), so this type of trace fossils is not considered.

Vertebrate ichnofossils are studied by researchers with different backgrounds and interests. Many studies describe and interpret in detail the trace fossils under a broad stratigraphic and palaeonvironmental setting, whereas other studies add significant information by including details of the hosting sedimentary facies. The latter studies allow obtaining the maximum palaeoenvironmental information from the vertebrate trace fossils. This procedure can link a particular vertebrate trace fossil to specific environmental parameters.

The applications discussed in this review include: a) identification of tetrapod footprints in cross-sectional views; b) assessment of relative moisture content of different substrates as inferred from the morphology of footprints; c) sand crescents of footprints as indicators of aeolian dune cross-strata; d) identification of pluvial episodes in aeolian dune successions; e) zonation of tetrapod trace fossils in lacustrine margins; f) potential use of flamingo-like footprints in the recognition of alkaline, saline lake facies; g) hippopotamus traces as characteristic of wetlands in arid settings; h) use of vertebrate swim trace fossils to infer water depth, subaqueous substrates and palaeocurrents; i) fish feeding traces as prospective palaeocurrent indicators; j) orientation of tetrapod trackways in comparison with associated primary sedimentary structures; k) the significance of some vertebrate trace fossils for distinguishing perennial from intermittent discharge in fluvial channels; l) significance of vertebrate ichnofabrics; and m) assessment of the utility of vertebrate ichnofacies for palaeoenvironmental analysis.

2. Identification of footprints preserved in cross-section

The recognition of footprints in exposures at high angle to bedding may help to identify subaerially-exposed, or relatively shallow subaqueous intervals, that may be overlooked during sedimentological analysis of sedimentary successions. Footprints in cross section have been recognized in a number of environmental settings including wind-ripple strata of sand flats, interdune and toesets of aeolian dunes (Loope, 1986; Lea, 1996), damp interdunes (Melchor et al., this volume), ephemeral fluvial deposits (Loope, 1986; Smith et al., 1993), floodplain deposits of anastomosed (Nadon, 2001; Difley and Ekdale, 2002) or meandering (Currie et al., 2003) rivers, wetlands (Ashley and Liutkus, 2002; Melchor et al., 2006), and sinkhole deposits (Laury, 1980).

The terminology used by different authors to describe surface footprints and the footprint features observed in cross-section is far from uniform. Allen (1997) proposed a set of terms that are mostly followed here with minor modifications from Jackson et al. (2010) (Fig. 1). The sediment surface directly in contact with the foot is the true track or surface footprint. True tracks may be preserved at nearly the same level that the sediment surface or be limited by sloping track walls, at a depth below the tracking surface. The empty, nearly cylindrical space limited by the track walls is the shaft (also named axis by Fornós et al. 2002), which is recognized in deeply seated footprints produced in cohesive substrates. The track wall may be smooth

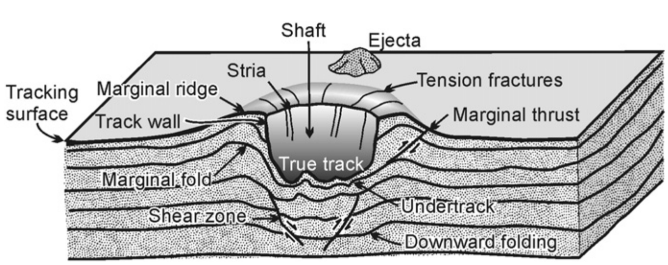

Fig. 1. Block diagram illustrating the morphological features of footprints in cross-section and on bedding plane. Modified from Allen (1997).

or contain striae, which are produced during foot withdrawal. If some sediment adheres to the foot, it may result in a mound projected outside the shaft on the tracking surface, at the anterior part of the footprint. The footprint may exhibit a continuous or discontinuous raised rim, the marginal ridge or marginal upfold, that corresponds with underlying marginal folds and may be limited by a marginal thrust (Fig. 1). Packages of sediment bounded by microfaults that appear in the posterior end of footprints have been termed "pressure pads" (Fornós et al., 2002). Pressure pads are produced when a deeply penetrating limb pivots and creates a backward force to propel the animal forward (Fornós et al., 2002; fig. 21). In practice, pressure pads may be considered a particular type of marginal ridge, and are difficult to distinguish from sand crescents, which are semi-circular mounds of sediment that point downslope in trackways produced on inclined surfaces. Depending upon substrate cohesion, the marginal ridge may be cut by radial tension fractures. In layered sediment, impressions of the foot will be formed in the layers subjacent to the true foot. These impressions have been termed undertracks (Lockley, 1991), undertraces (Allen, 1997) or transmitted (foot)prints (Thulborn, 1990; Romano and Whyte, 2003). Romano and Whyte (2003) used underprint for a case when the rock splits on a surface below the tracking surface, intersecting part of the footprint.

Footprints in cross-section can be distinguished from inorganic deformation structures like convolute bedding, load casts, cryoturbation and ice-wedge thaw structures by a number of criteria (Loope, 1986; Lea, 1996). 1) Footprints tend to be laterally discontinuous in a bed, instead of the laterally repetitive forms of like convolute bedding and load casts. 2) Footprint size distribution displays limited variability and is consistent with potential producers. 3) Footprints display a shaft that may be infilled by texturally different sediment, whereas load structures lack a shaft and are texturally similar to overlying sediments. 4) Downward deformation structures in tightly-packed wind-ripple strata are likely footprints. Wind-ripple strata are not prone to deformation by inorganic processes (such as liquefaction) as are loosely packed grain flow and avalanche strata. Some additional features that apply especially to sauropod footprints include (Difley and Ekdale, 2002; Platt and Hasiotis, 2006): 5) absence of upward mud injection features that are typical of load casts; and 6) the track wall (or the corresponding cast) exhibits grooves and striations as result of digit or claw and skin dragging during withdrawal of foot.

Features for the distinction of footprints from vertebrate burrow fills has been discussed by Lea (1996). Vertebrate burrow fills share with cross-sectional views of footprints the truncation of host strata and may contain a structurally distinct fill. Vertebrate burrow fills usually form inclined cylinders that extend by a distance several times its diameter, whereas footprint shafts are nearly vertical structures that are much shorter than burrow fills. Footprints also lack enlargements and bifurcations that may appear in vertebrate burrow fills. In addition, the host rock adjacent to and underlying a burrow fill commonly is not deformed, although burrow collapse may produce some deformation in the fill of a burrow (Lea, 1996).

3. Relative moisture content of trampled substrates

The surface or cross-sectional features of footprints can help to infer the moisture content of the substrate at the time of their production. The formation of tetrapod footprints is a poorly known subject due to a complex interplay of variables (e.g., Padian and Olsen, 1984; Falkingham, 2014), even if in the last decades there have been a number of studies aiming to ascertain, both qualitatively and quantitatively, different aspects of footprint formation and preservation. The problem has been approached intuitively (Laporte and Behrensmeyer, 1980; Scrivner and Bottjer, 1986; Sarjeant and Leonardi, 1987; Avanzini et al., 2012), through experimental work with live animals (McKee, 1947; Brand, 1979; Brand and Tang, 1991; Brand, 1996; Gatesy et al.,