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INFORMATION ON THE FOOT MORPHOLOGY, PEDAL SKIN TEXTURE AND LIMB DYNAMICS OF SAUROPODS: EVIDENCE FROM THE ICHNOLOGICAL RECORD OF THE MIDDLE JURASSIC OF THE CLEVELAND BASIN, YORKSHIRE, UK

MIKE ROMANO[1],
MARTIN A. WHYTE[1]

RESUMEN

Se han encontrado recientemente nuevas pistas saurópodas, en el Grupo Ravenscar del Jurásico Medio de la Cuenca de Cleveland, Yorkshire, Reino Unido. La mayor parte de las huellas afloran dando contramoldes de arenisca. Las rastrilladas se encuentran en rocas de las Formaciones Saltwick, Cloughton y Scalby, de edad Aaleniense-Batoniense. De las huellas bien preservadas se extrae información precisa sobre: a) la forma de las manos y pies saurópodos, el número y la estructura de los dedos con garras de los pies; b) la textura con escamas poligonales de la mano; c) la dinámica de las extremidades del saurópodo durante la locomoción mediante el análisis de los contramoldes en 3D y de las estrias conservadas en las paredes de la huella.

Las huellas de las manos, en general, no son diagnósticas en icnotaxonomía porque sus formas, probablemente debido a estructuras extramorfológicas, son variadas. Solo hay un contramolde que tiene marca de pollex, situado encima de la palma. Las icnitas se han asignado a pies de *Brontopodus* ichnosp. indet. con cinco dedos de los cuales tres (I-III) tienen garras envueltas por la piel en su parte proximal. Solo hay un contramolde de mano que muestra un trozo con marcas de escamas poligonales similares a los encontrados en otros lugares. Esta es la primera icnita del Jurásico Medio con marca de piel. Las estrías de las paredes de las huellas de manos y pies son tanto de la fase T como de la fase K de la dinámica de la marcha.

Se analiza brevemente la asignación de los icnogéneros a icnopoyetas saurópodos y la validez de la correspondencia. Se conocen tres icnotaxones en el Jurásico medio de Yorkshire, Inglaterra, basados en los caracteres de

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los pies saurópodos: *Brontopodus*, ichnosp. indet., *Breviparopus*? ichnosp. indet. y una tercera ichnogen. et ichnosp. indet. Casi no se encuentran rastrilladas ni tampoco pares asociados de manos y pies, debido al tipo de afloramientos en la costa, expuestos al oleaje.

Palabras clave: huellas saurópodas, morfología de la pisada, textura de la piel, dinámica de las extremidades, icnotaxonomía, Jurásico, Yorkshire, Inglaterra.

New specimens of sauropod tracks, preserved mainly as sandstone casts, have recently been found in the Middle Jurassic Ravenscar Group of the Cleveland Basin, Yorkshire, UK. The tracks are of Aalenian-Bathonian age and occur in the Saltwick, Cloughton and Scalby formations. The well-preserved tracks provide accurate information on: a) the shape of the sauropod foot that made both manus and pes tracks, and the number and structure of the pes clawed digits; b) the skin texture of polygonal scales on the manus; and c) the limb dynamics of the sauropod maker during locomotion, based on the 3D dimensions of the sandstone cast and the preserved striations down the sides of the casts.

The manus prints are generally non-diagnostic ichnotaxonomically and show a range of outlines that may in part be due to preservation. Only a single manus cast exhibits the presence of a pollex, sited above the palmar surface. The pes specimens assigned to Brontopodus *ichnosp. indet., had five digits of which three (I-III) were clawed and each proximally enclosed by skin. A single manus print shows a small area of skin impression with polygonal scales and typical of other reported sauropod skin textures. This is the first recorded Middle Jurassic dinosaur skin impression. Striations on the sides of manus and pes casts are identified as representing both the T and K phases of leg dynamics.*

A brief review of selected ichnogenera assigned to a sauropod maker is presented and the validity of these is discussed. Three distinct ichnotaxa from the Middle Jurassic of Yorkshire, England, are recognised, based on pes characteristics, as having been made by sauropods: Brontopodus *ichnosp. indet.,* Breviparopus? *ichnosp. indet. and Ichnogen. et ichnosp. indet., even though associated trackways are generally lacking, and manus-pes couples are relatively rare (both due to the type of coastal exposures).*

Key words: *sauropod tracks, foot morphology, skin texture, limb dynamics, ichnotaxonomy, Jurassic, Yorkshire, UK.*

1. INTRODUCTION

In spite of their often enormous size and correspondingly large skeletal elements, ‘most sauropodomorphs are known from incompletely preserved material, often missing their heads, parts of their tails, and their feet’

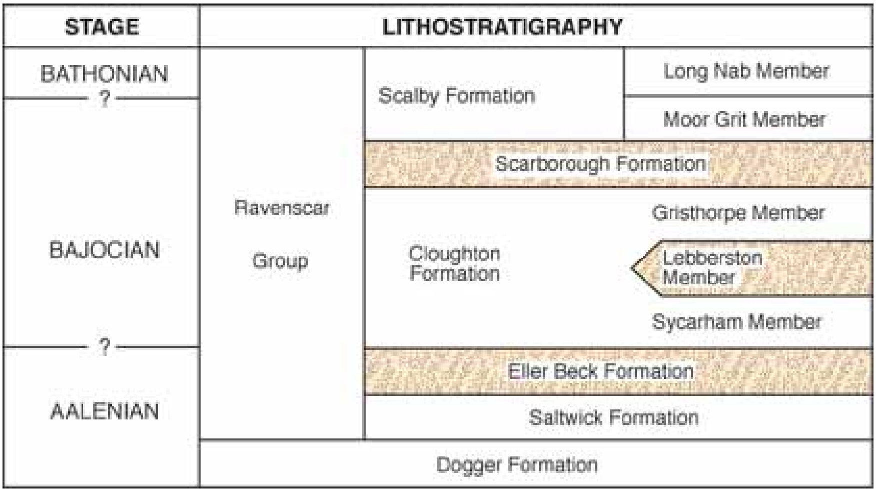

Figure 1. Lithostratigraphy and chronostratigraphy of the Middle Jurassic rocks of the Cleveland Basin, Yorkshire (after Romano & Whyte, 2003). Marine units are stippled. Note that thicknesses of units are not drawn to scale.

(Fastovsky & Weishampel, 1996, p. 247). However, well-preserved sauropod tracks can provide morphological details of foot outline and digit and claw orientation, skin texture and limb dynamics. The present paper investigates all these three aspects of sauropod palaeobiology based on new evidence from tracks of the Ravenscar Group of the Middle Jurassic of the Cleveland Basin, Yorkshire, UK.

Sauropod tracks from the Early Middle Jurassic of Yorkshire were first described just over 10 years ago (Romano *et al.*, 1999). At the time the tracks, which were all from the Saltwick Formation (the lowest unit of the Ravenscar Group, and of Aalenian age, figure 1), were provisionally assigned to the groupings '*Brontopodus*-like' and '*Breviparopus*-like' owing to the lack of convincing manus-pes couples and associated trackways; thus, the absence of Aalenian sauropod tracks reported by Wilson (2005, figure 2, p. 406) is incorrect. Romano *et al.* (1999) essentially concentrated on the description and ichnotaxonomy of the prints, although observations were made on the possible existence of pads on the base of the pes. Since then, sauropod tracks have been found by the present authors in the younger (Bajocian-Bathonian) non-marine units of the Ravenscar Group (figure 1), the Cloughton and Scalby formations (Romano & Whyte, 2003, figure 24; Whyte *et al.*, 2007, figure 11) together with trackways (Romano & Whyte, 2003, figure 26); although the latter are generally not well preserved, nor particularly extensive owing to the nature of the coastal outcrops.

The majority of sauropod prints first described from the Saltwick Formation were identified as 'surface or near-surface prints (Romano *et al.*, 1999, p. 361), and were generally rather shallow prints. The more recently discovered sauropod tracks described here are much deeper and 1) often exhibit details of the claws; 2) may show longitudinal markings down the sides of the track, that record coarseness of skin texture and entry/extraction of the foot in the sediment; and 3) in an isolated case, preserve details of the original surface texture and ornament of the scales of the skin. It is these tracks that form the basis of this paper. These three aspects (morphology, skin texture, limb dynamics) will be described separately, although it is not unusual for more than one of these to be resolvable on a single specimen.

2. PRESERVATION OF PRINTS

Before any conclusions can be drawn on the foot shape of the maker, skin texture or limb dynamics, it is of fundamental importance that the type of track preservation is determined. The terminology used in describing the preservation of vertebrate prints is varied and, at times, confusing with terms such as *true track, transmitted track, ghost track, natural cast, underprint, undertrack and overtrack, tracking surface, convex hyporelief* and *negative epirelief* having been used in different ways by different authors. Some of these terms have been discussed by Romano & Whyte (2003) and are not further considered here, beyond noting that it is necessary to clearly and unambiguously describe the type of preservation.

Most of the tracks described here were found as loose specimens on the foreshore of the Yorkshire coast, between Port Mulgrave in the north and Gristhorpe Bay in the south (Figure 2). In many cases the source horizon could be located in the adjacent cliff section. Most of the tracks are preserved as the infill of prints by sand, made as the animal's foot was first impressed into and then extracted from the substrate; the resulting structure being either passively and/or actively filled with sediment. When the surrounding sediment (usually mudrock) has been removed through erosion, the remaining (sandstone) infill may be referred to as a sandstone cast of a print (Lockley *et al.*, 1992, *fide* Meyer *et al.*, 1995) and, where it can be proven that it occurs on the underside of the casting medium, it may also be identified as a convex hyporelief preservation. The implication of using the term sandstone cast is that in loose specimens the only preserved part of the original tracking surface (that surface on which the animal moved) is the palmar (manus) or plantar (pes) surface of the track.

Tracks that are preserved as transmitted features (*sensu* Romano & Whyte, 2003, figures 13, 14), which are relatively common on the wave-cut platform of the Yorkshire coast, generally do not yield details of foot morphology or limb dynamics, and will never provide evidence of skin texture (Allen, 1997; Gatesy, 2003; Jackson *et al.*, 2009). However, not all surface tracks may necessarily show details of foot morphology, since the water content of the substrate is important in determining the amount of detail that will be preserved in the track (Jackson *et al.*, 2009, 2010). The

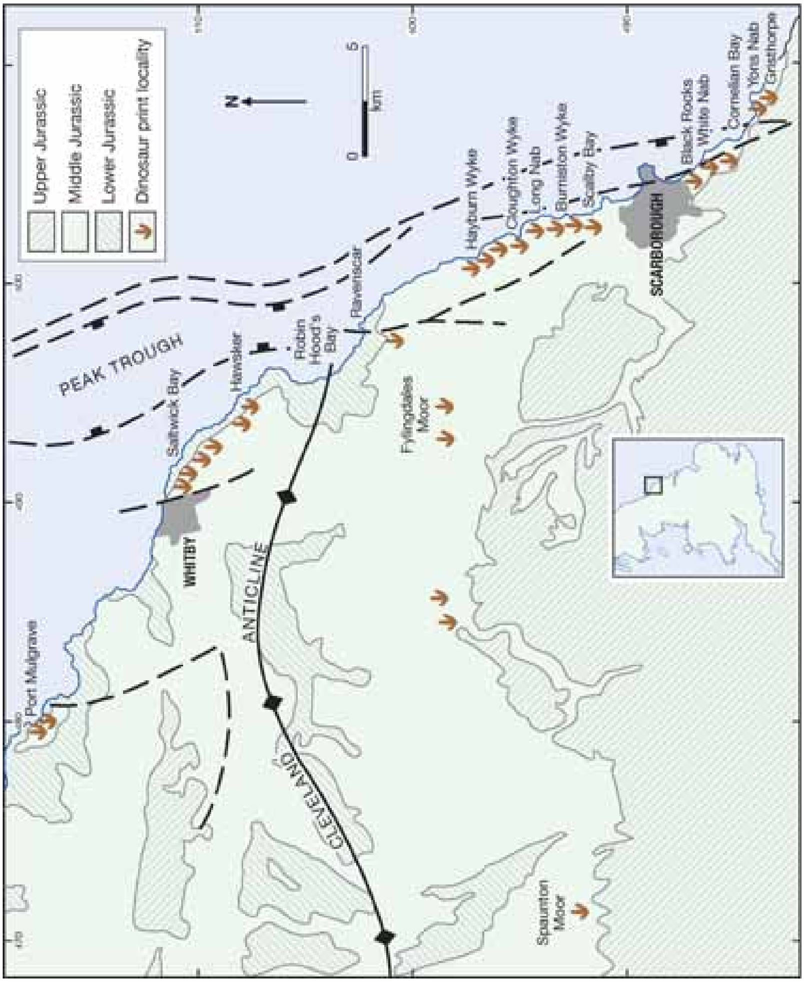

Figure 2. Simplified geological map of part of Yorkshire showing localities mentioned in the text, and the principal sites where dinosaur footprints have been recorded. The inset map shows the location of the area.

Figure 3. Sandstone cast of a sauropod print *in situ*, showing connection to the overlying sandstone bed. Long Nab Member, Scalby Formation, Burniston Bay. Scale bar 10 cm long.

large sauropod tracks with marginal rims figured by Romano & Whyte (2003, figure 10) from the Scalby Formation in Cornelian Bay may well be true surface tracks (although marginal rims also continue at depth; see Allen 1997; Jackson *et al*., 2009), yet details of foot shape and digit outlines are difficult to make out. Thus the new prints described here are particularly valuable in determining details of foot structure, skin texture and movement because the mode of preservation (mainly as sandstone casts) yields generally accurate and explicit details.

Approximately 15 years ago, Meyer *et al*. (1995, p. 58) stated that only three examples were known of sauropod tracks preserved as casts. One of these, originally reported as a sauropod manus from the Morrison Formation of Utah, USA (Lockley *et al*., 1992), is now considered to be a pes (*fide* Lockley & Hunt, 1995). The second example was from a trackway of the new ichnotaxon *Deltapodus brodricki* (Whyte & Romano, 1993, 1995) from the Middle Jurassic Saltwick Formation of Yorkshire, UK. This ichnotaxon is now regarded as having been made by a stegosaurid (Whyte & Romano, 2001).

The third example was from the Lost Springs site in Utah (Meyer *et al*., 1995). Although Meyer *et al*. (1995) mentioned two additional, but poorly preserved casts from the Morrison Formation at Dinosaur Ridge, Colorado; and (in a note added in proof) further material from the Morrison Formation at the Purgatoire River site, also in Colorado, (shown as a plaster cast in Lockley, Farlow & Meyer, 1995, figure 4), relatively few examples of sauropod sandstone casts had been reported at that time. Since then, examples have been described from the non-marine formations of the Middle Jurassic Ravenscar Group of Yorkshire, UK (Whyte *et al*., 2010), parts of the Upper Jurassic Lastres Formation of Asturias, N, Spain (García Ramos *et al*., 2004, 2006), the Upper Jurassic Lourinhã Formation of Portugal (Mateus & Milàn, 2010; Mateus *et al*., 2011), and the Late Jurassic-Early Cretaceous Villar del Arzobispo Formation, Galve (Teruel) in Spain (Castanera *et al*., 2010). All these more recently described examples occur in alternating sandstone/mudrock sequences of coastal plain or deltaic environments where fluvial activity dominates. In these environments, the footprint frequently was made in the soft (high water content) muds or silts and the resulting mould was infilled (either immediately or later) with sand. Thus sandstone casts frequently appear like pillars of sandstone as downward projections below a sandstone bed (figure 3). When the infilling sediment has completely bypassed the cast and left no immediate cover, an isolated cast is left (figure 4). Sauropod sandstone casts have also been described from the younger Late Cretaceous Nemegt Formation in the Gobi of Mongolia (Currie *et al*., 2003).

3. FOOT MORPHOLOGY

Fully articulated sauropod manus and pes (Gallup 1989) skeletons and articulated legs (González Riga *et al*., 2009) are rare, However, even with such skeletal records of sauropod feet the reconstruction and disposition of the elements are open to subtly different interpretations, and do not necessarily give any indication of the presence of padding. Thus well-preserved tracks are an important contribution to understanding the form of sauropod feet.

Tracks that have been attributed to a sauropod maker are frequently only indistinct round to oval depressions (Farlow, 1992, p. 100) with little indications of digit impressions (for example see; Lockley *et al*., 1986, figure 7; Thulborn, 1990, figure 6.15b,c,d; Thulborn *et al*., 1995; Pittman & Lockley, 1995). Indeed the only reasons for assigning them to sauropod makers have usually been on account of their large size (up to and even greater than 1m across), or their arrangement in the associated quadrupedal trackways, where small and large tracks have been interpreted as manus and pes prints respectively. Such tracks are commonly preserved as ghost (Pittman & Lockley, 1995) or transmitted (Thulborn, 1990; Romano & Whyte, 2003) tracks, and occasionally were primarily interpreted as having been made by ornithopods (e.g. see discussion of ‘iguanodont’ tracks described from the Guadalupe River site, Texas, by Pittman, 1989, that were subsequently reinterpreted as ‘sauropod’ tracks by Pittman & Lockley, 1995; Lockley *et al.*, 1995). Other vague tracks were

Figure 4. Cast of a sauropod (manus) print *in situ*, surrounded by mudrock. Long Nab Member, Scalby Formation, Cornelian Bay. Scale bar 10 cm long. Specimen same as in Figure 7A.

afforded a theropod origin before being reinterpreted as having been made by a sauropod (for instance the tracks from La Griega Beach, Asturias, Spain, reinterpreted by Lires *et al.* [2001]; Lockley *et al.* [2007]).

However, footprints are known of undoubted sauropod origin in which the outline of the tracks are more perfectly preserved, thus replicating the shape of the foot that made them and the individual digit imprints (Farlow *et al.*, 1989; Meyer *et al.*, 1995; Milàn *et al.*, 2005; Milàn & Bromley, 2005; Castanera *et al.*, 2010). A number of tracks, both of the pes and manus, exhibiting such informative morphological preservation have been previously recorded from the Middle Jurassic rocks of the Cleveland Basin (Romano *et al.*, 1999, 2007; Romano & Whyte, 2003); and those, with the new examples preserved as sandstone or sideritic casts, are considered here. The possible sauropod makers of the tracks will be discussed at a later date.

3.1. Sauropod manus tracks

The outline of tracks made by the sauropod manus are variously described as a crescent (Ishigaki & Matsumoto, 2009a, p. 443), "double crescent" (Farlow *et al.*, 1989, p. 377), "U"-shaped (Upchurch, 1995, p. 163), semilunate (Milàn *et al.*, 2005, p. 49), semi-circular (Lockley *et al.*, 1995, p. 140), horseshoe (Ishigaki, 1989, p. 84), half-moon (Ishigaki & Matsumoto, 2009b, p. 3) or "kidney-shaped" (Castanera *et al.*, 2011). A posterior indentation and lack of distinct digit impressions are also frequently referred to. The presence of a pollex (Digit I) impression has been noted by a number of authors (Lockley *et al.*, 1986; Santos *et al.*, 1995; Upchurch, 1995; Milàn *et al.*, 2005; Castanera *et al.*, 2010).

The newly discovered sauropod manus prints preserved as casts from Yorkshire suggest two additional foot types (figure 5) to the single manus described by Romano *et al.* (1999, figure 3C). The three types now recognised from the Middle Jurassic of the Cleveland Basin are characterised by those with:

1) a crescentic outline with a Width:Length Ratio (*W*:*L*) of between 1:1.5-1:1.8 (figure 5A, B, D).
2) a semi-circular outline with a *W*:*L* of 1:1.2 (figure 5C).
3) a semi-circular outline with a *W*:*L* of *c*. 1:1.5, and with one or two deep indentations on the curved (anterior) margin, and two along the nearly straight posterior margin (Romano *et al.*, 1999, figure 3C and figure 23I).

No clear digit impressions occur around the anterior margin of types 1) or 2), although irregular shallow indentations around the anterior margin of one of the examples from Cornelian Bay (figure 5A) may suggest their presence. However, it is important to note that of the three examples shown, the one from Scalby (figure 5C) represents the upper surface of the sandstone cast, at an unknown distance above the palmar surface. The outline of the

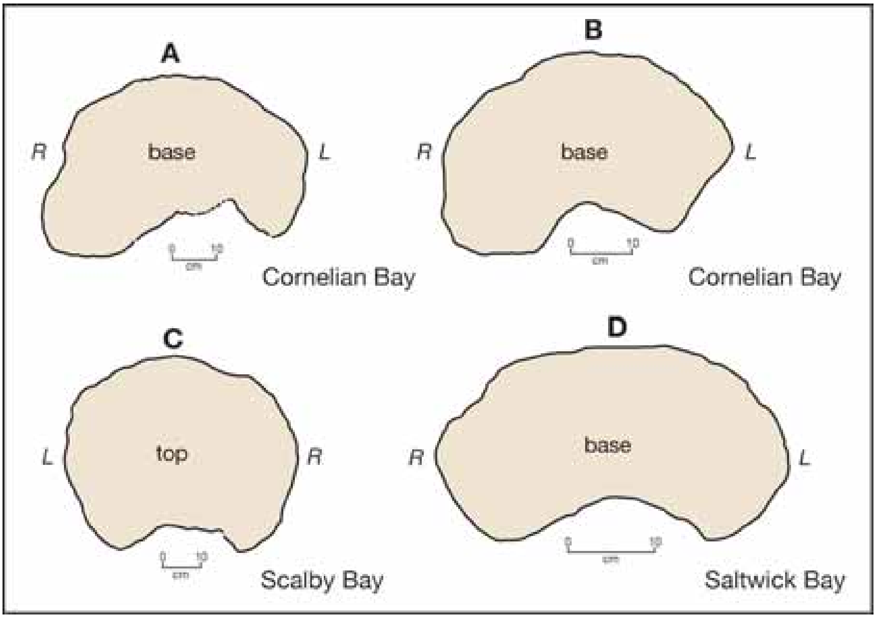

Figure 5. Outlines of four sauropod manus casts (A-D) with locations indicated (see Figure 2). Specimens A, B and C from the Long Nab Member, Scalby Formation; D from the Saltwick Formation. Note that all except C are outlines of the palmar surface viewed from below. Specimen B is housed in Rotunda Museum, Scarborough – Cat. No. SCARB:2011.146 (see also Figures 7, 8).

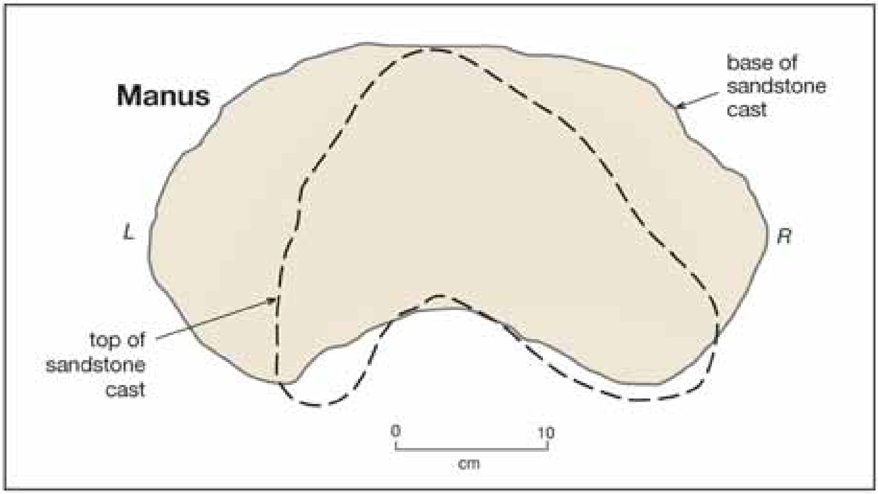

Figure 6. Outlines viewed from above of top and base (palmar) of sauropod manus cast. Specimen the same as that in Fig 5D.

manus print may vary considerably in a single cast depending on whether the outline was observed from the lower (palmar) or upper surface (figure 6) (see also the section on limb dynamics, Section 4 below). This may be further complicated since the upper surface may not represent the top of the cast (see Milàn *et al*., 2005, figure 2 where the authors describe a 'horizontal section through the cast'). It is probable that the base of the sandstone cast replicates the outline of the manus most accurately since the upper (and top in particular) of the original mould may have been altered by either parasagittal movement of the limb during locomotion (see Section 4), or by partial collapse of the walls before being cast in sand.

Although the two examples of the manus prints from Cornelian Bay (figure 5) Yorkshire, have slightly more angular posterolateral outlines on one side, no clear indication of a pollex (with or without a claw impression) is present; unlike the manus prints figured by Santos *et al*. (1995, figure 6), Castanera *et al.* (2010, figure 2A) and Milàn *et al*. (2005, figure 2b). While the absence of distinct digit impressions is common in previously documented sauropod manus prints, the apparent absence of a pollex imprint warrants further comments. Depending on where the pollex was situated on the manus would determine whether it left an impression in the footprint. In shallow surface tracks, unless the pollex extended posteromedially at the level of the palmar surface, no impression of Digit I would be left. Yet, as Upchurch (1995, p. 170) pointed out, in some trackways the evidence suggests that the claw was not always carried above the substrate surface. In the example from Teruel, Spain (Castanera *et al*., 2010) it is not clear at what level the section through the sandstone cast of the manus was preserved, thus it is uncertain whether the pollex extended outwards at palmar level or higher up the limb.

Theoretically, only in deep casts can it be shown where the pollex was situated if it was carried above the palmar surface, since the indentation left by that digit in the sediment would leave a record along the side of the cast. In only one of the manus casts from the Cleveland Basin, that from Cornelian Bay (figure 5B), is there a suggestion of a pollex on the manus. In this specimen (figure 7A) a vertical sideritic ridge is present on the posterolateral part of the crescent-shaped print. The ridge extends for approximately 15 cm up the side of the cast, and starts 15 cm above the palmar base. This ridge is suggested to have been made by a protruding pollex, either during entry into, and/or withdrawal from, the sediment. If this suggestion is correct, then the cast is of a right manus (see restoration in figure 7B).

Since none of the other sauropod prints from the Cleveland Basin preserved as deep sandstone casts exhibit evidence of a Digit I impression, we conclude that the other Middle Jurassic sauropods who inhabited this region did not have a visible and/or protruding pollex. However it is clearly possible that other manus prints, such as the Scalby Bay example (figure 5C), may not show an impression of a pollex owing to the level of present day erosion through the cast. As it is unclear at what level in the sandstone cast

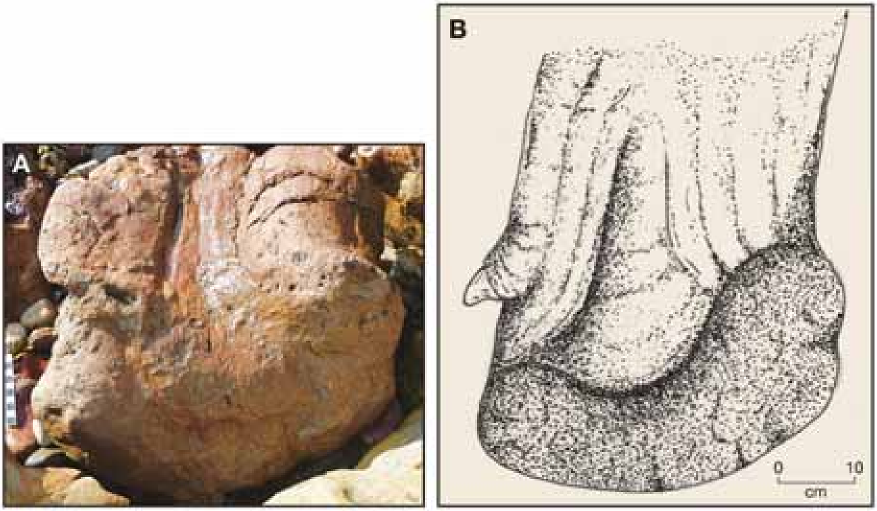

Figure 7A. Sauropod manus sideritic cast from the Long Nab Member, Scalby Formation, Cornelian Bay, showing posterolateral ridge down part of the length of the cast. See text for explanation. Scale bar 10 cm long. Specimen housed in Rotunda Museum, Scarborough – Cat. No. SCARB:2011.146. B. – Restoration of manus cast shown in Figure 7A.

the pollex protrusions identified by Castanera *et al.* (2010) and Milàn *et al.* (2005) were preserved, the height of the pollex above the palmar surface cannot be determined from their photographs, although the latter authors reconstruct the manus with the distal end of the pollex in contact with the substrate (Milàn *et al.*, 2005, figure 4b). In all of the manus prints previously illustrated, we are not aware of any that have shown a clawed pollex with its partially enclosing skin on the proximal part (see below for the pes). Although the pollex of some sauropods bears a prominent claw (Dalla Vecchia *et al.*, 2000, figure 33A; 2005, figure 18.4A) the imprint of the distal end of the enclosing skin appears to be rarely (if ever) preserved.

The lack of distinct digit imprints (apart from that of the pollex in some tracks) indicates a digitigrade manus with metacarpals arranged vertically (Wilson, 2005, p. 415 and figure 4B). The arrangement of the metacarpals would be reflected in the tightness of the arc in the print. In the manus prints from Yorkshire (figure 5) both open arcs and tighter arcs appear to be represented. The ichnotaxonomic implications of this are dealt with in Section 5. Although distinct pads have not been recognised on the palmar surface of the prints, there are faint suggestions of posterolateral digital pads (*sensu* Platt & Hasiotis, 2006, figure 5B) on the specimen from Cornelian Bay (figure 7). Finally, the base of the sauropod manus probably expanded slightly during the weight-bearing phase (W phase of Thulborn & Wade, 1989). This is indicated by the wider (c. 10%) and longer outline of the cast of the palmar surface in the specimen from Cornelian Bay (figure 8), although

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Figure 8. Cast of sauropod manus from the Long Nab Member, Scalby Formation, Cornelian Bay (see also Figure 7), showing expansion of cast at the base. Specimen housed in Rotunda Museum, Scarborough – Cat. No. SCARB:2011.146. Scale bar (on top of cast) 10 cm long.

the possibility of slight contraction of the vertical sides of the manus cast following withdrawal of the foot cannot be discounted. González Riga (2011, figure 4) also noted the possible increase in foot, and consequently print, length during the weight-bearing phase with an 'elastic plantar pad' on the pes. On this basis, González Riga (2011) estimated that the print length may vary by as much as 5%.

3.2. Sauropod pes tracks

The tracks made by the sauropod pes are, like those of the manus, commonly recognized on the basis of their shape; but also on their size. The outlines of sauropod pes prints are less easy to classify, but are usually described in terms of Length:Width Ratio (often being longer than wide), characteristics of digit shape and +/- claw impressions, and orientation of the long axis with reference to the trackway midline. The size of prints, especially when preserved as transmitted features, can be a very tenuous method of identification; however, prints up to 120 cm across (Thulborn *et*

Figure 9. Top view of a large sauropod pes track preserved as a sandstone cast from the Saltwick Formation, a few metres above the Dogger Formation (see Figure 1), Saltwick Bay, Whitby. Length of track is 48 cm.

al., 1995, p. 89) are almost certainly of sauropod makers particularly when they form part of a quadrupedal trackway.

Two, possibly three, distinct sauropod pes track types representing two or three different ichnotaxa were first described by the authors (Romano *et al*., 1999). These were all shallow prints and contrast in preservation with the sandstone casts of pes tracks described or referred to here. Since the latter were found either on isolated blocks not *in situ*, or as single prints in the cliff face that could not be related to a trackway, their diagnostic characteristics relate only to pes outline and digit characteristics.

A large pes track preserved as a sandstone cast was found loose in Saltwick Bay (figure 9). Its source horizon could be identified high up in the adjacent cliff face as a prominent sandstone bed near the base of the Saltwick Formation, just a few metres above the Dogger Formation (figure 1). It is similar to Ichnospecies A (Romano *et al*., 1999, figure 3A) which was referred to as a '*Brontopodus*-like' track. The shape of the present track is broadly oval in outline, 48 cm long and 35 cm wide (Length:Width Ratio of 1.4:1), with a slightly more pointed posterior margin with the maximum width occurring approximately one-third the length from the anterior margin. The digit impressions in this track are well-preserved and when viewed laterally (figure

Figure 10. Anterolateral view of a large sauropod pes track preserved as a sandstone cast from the Saltwick Formation, a few metres above the Dogger Formation (see Figure 1), Saltwick Bay, Whitby. Same specimen as in Figure 9. Scale bar 10 cm long.

10) five digit impressions can be recognised as steeply dipping lobes down the anterior and anterolateral sides of the cast. In this specimen it is possible to identify three clawed digits (Digits I-III) by the presence of slightly protruding digit imprints with sediment-filled embayments on their posterior sides (compared with simple rounded bumps associated with the imprints of Digits IV and V).

Further morphological details of the pes digits can be determined in a specimen from Cornelian Bay, discovered over 10 years ago and now covered by a landslip of glacial Boulder Clay. The Cornelian Bay specimen (figure 11) was first figured by Romano & Whyte (2003, figure 7) and later by Whyte *et al.* (2010, figure 12b(i)). In this specimen, digit imprints I-III are curved outwards and backwards and terminate with a gently curved claw impression. Approximately halfway along each of these digit imprints there is a shallow furrow. Proximal to this furrow the digit imprint has a slightly greater diameter and is interpreted as representing the enclosing skin on the ungual. Digits IV and V in the Cornelian Bay specimen are represented by rounded bulges on the margin of the track and were presumably not clawed. Another pes sandstone cast is illustrated from the Saltwick Formation at Hayburn Wyke (figure 12). This specimen exhibits vertically elongate digit imprints made during movement of the limb through the sediment, of which at least three also show evidence of a single median furrow extending down their length that marks the junction between the skin-contained and exposed

Figure 11. Sandstone cast of a sauropod pes showing imprints of clawed digits. Specimen is from Cornelian Bay; Long Nab Member of the Scalby Formation. Scale bar 10 cm long.

parts of the claw. However, the Hayburn Wyke specimen is unusual in that it appears to preserve the imprints of possibly four clawed digits. No phalangeal pads have been identified on the Yorkshire prints available to the authors.

Czerkas (1995, p. 177) observed that the "size and shape of the claw was not too different from the bone itself", even though presumably the claw had a nail-like sheath. Indeed, Gallup (1989, p. 72) asserted that the preserved claws of *Pleurocoelus* sp. indet. were probably covered with a large, horny sheath, making them appear 'even larger' in life

The well-marked digit imprints and pes outlines of these specimens enables a restoration to be made of the makers foot (figure 13). The presence of three clawed digits on the pes is characteristic of Neosauropoda (Farlow, 1992; Wilson, 2005; Wright, 2005) and contrasts with the four claws present on, for example, the Early Cretaceous form *Pleurocoelus* (Gallup, 1989). In the present reconstruction the curved clawed pes digits are shown to lie sub-parallel to the margin of the pes, and with the ends directed posteriorly. This is assumed to have been their position when the animal was in (?) normal locomotion. However, Gallup (1989, figure 3) illustrated a restored pes of

Figure 12. Sandstone cast of a sauropod pes from the Saltwick Formation at Hayburn Wyke (see Figure 2) showing four vertically elongate digit impressions and evidence of a single median groove extending down their length that marks the junction between the skin-contained and exposed parts of the claw. Scale bar 10 cm long.

Pleurocoelus sp. indet. in which the clawed digits (four in his example) were elevated (levated) and directed more laterally, and with the terminations pointing downwards. It is not known whether the Yorkshire Middle Jurassic sauropods were capable of such digit movement.

4. SAUROPOD SKIN

When Richard Owen worked with the sculpture Benjamin Waterhouse-Hawkins to produce life-size reconstructions of dinosaurs for the Crystal Palace Exhibition in London in the middle of the 19th Century, they portrayed the skin of these animals as either scaly or smooth. In fact the patterns of scales they envisaged bear a surprising similarity to those now known for individuals from a number of dinosaur families. By the late 19th to mid 20th Century the public image of dinosaurs was strongly influenced by the drawings of Charles Knight (1874-1953) and Neave Parker (1910-1961), who represented their admittedly more lifelike reconstructions, with a leathery-looking elephantine-like skin. In more modern reconstructions, feathers are

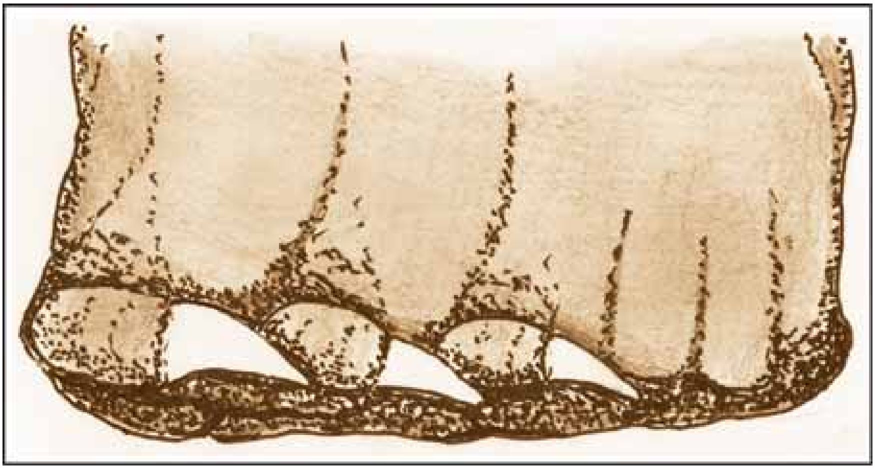

Figure 13. Restoration of sauropod pes based on specimens illustrated in Figures 9 and 11.

a frequent addition to the dinosaur integument. Thus, the skin texture and ornament of dinosaurs has always stimulated much controversy.

4.1. Texture of sauropod skin

Although there are only relatively few occurrences where actual skin of dinosaurs has been preserved, examples of skin texture pattern, whether of the skin or from impressions made in the sediment, are now known for ornithopods (Lockley, 1989; Currie *et al.*, 1991; Manning *et al.*, 2009; Herrero & Farke, 2010), theropods (Gatesy, 2001; Currie *et al.*, 2003; Medrano *et al.*, 2005-2006) and stegosaurids (Xing *et al.*, 2008; Christiansen & Tschopp, 2010; García Ramos *et al.*, 2006 (see below); Mateus *et al.*, 2011). Examples of skin texture from unidentified dinosaurs have also been recorded by Paik *et al.* (2010). However, records of sauropod skin textures are rarer (Lockley *et al.*, 1992, *fide* Lockley & Hunt, 1995; Czerkas, 1995; Garcia-Ramos *et al.*, 2002, 2004, 2006; Currie *et al.*, 2003; Mateus & Milàn, 2010; Yang et al., 2003, *fide* Kim *et al.*, 2010), and to date less than fifteen have been described (Table 1). Of these, only two are of actual skin, the rest being impressions made in the sediment.

Apart from the dermal spines recorded by Czerkas (1992, 1995) from Howe Quarry, Wyoming, USA –the so-called 'spiky skin' of diplodocids (Fastovsky & Weishampel, 1996, p. 244)–, all photographs and drawings of sauropod skin textures show skin patterns that are usually described as having been made by non-overlapping hexagonal (Hooley, 1917, p. 149) or polygonal (Platt & Hasiotis, 2006, p. 256) scales. An exception is the skin texture of an embryonic sauropod first described by Chiappe *et al.* (1998) (see Section 3.2 below).

Manus or pes skin impressions may leave a faithful replica in the fossil tracks of sauropods, and very recently, a single sandstone cast of a sauropod manus track (F00961; University of Sheffield collections) has been found from the Saltwick Formation, in Saltwick Bay east of Whitby, Yorkshire that shows a small area of skin impression (figure 14A, B). The specimen was found loose on the foreshore, but its source horizon could be located high up in the adjacent cliff as being at the base of a sandstone unit less than 1.0 m above the top of the Dogger Formation (figure 1). This is the first figured specimen of sauropod skin impression from the Middle Jurassic Ravenscar Group of Yorkshire, and is in fact the first recorded Middle Jurassic dinosaur skin impression**.** The area of skin impression is approximately 6 cm by 6 cm and is located at the rear of the print, just above the palmar surface. Although over 40 scales are present, only 8 could be confidently used to determine their shapes. Of these, 4 are pentagonal, 3 hexagonal and 1 heptagonal; the largest scale is 12 mm diameter. The scales are between 1-2 mm apart from neighbouring scales and the depth of scale impression (see Kim *et al.*, 2010) varies from very shallow to 2 mm. Note that in this specimen both imprints of scales and striations are preserved. It would be expected that on the sides of the cast, where the scales imprint is preserved, the withdrawing of the foot from the mould would have streaked-out and destroyed the imprint of the skin texture. The fact that it is preserved supports the suggestion above (Section 2.1) that the base of the sauropod manus probably expanded slightly during the weight-bearing phase (W phase of Thulborn & Wade, 1989) (see also Section 4 on limb dynamics below).

While trying to compare the type and pattern of scales of the skin texture of the Whitby specimen with other published material, it became apparent that there existed a range of sauropod skin textures that had been recorded from different parts of the animal’s body and from different ages. To ascertain whether any recognisable pattern was characteristic of either of these two variables, a review of the literature on sauropod skin textures was undertaken. For each recorded example of skin texture the following features were documented: whether the example was actual skin or an impression, its position on the body, the number of scales, area and maximum size of scales, shapes of scales (tetragonal to octagonal), locality, lithostratigraphy and age (Table 1). The presence of any overall regular pattern was also recorded. Although it was attempted in the review to also follow the recent suggestions of Kim *et al.* (2010, table 2) in their proposed categories and descriptive terms of dinosaur skin impressions, not all of their categories could be adopted. For example, ‘Depth of scale impression’ and ‘Deformation of sediments’ could not be determined from the published descriptions in every case. Thirteen examples were taken from the literature, in addition to the recently found specimen from Yorkshire (but excluding the embryonic example recorded by Chiappe *et al.*, 1998 and Coria & Chiappe, 2007; see below), and the following observations were made:

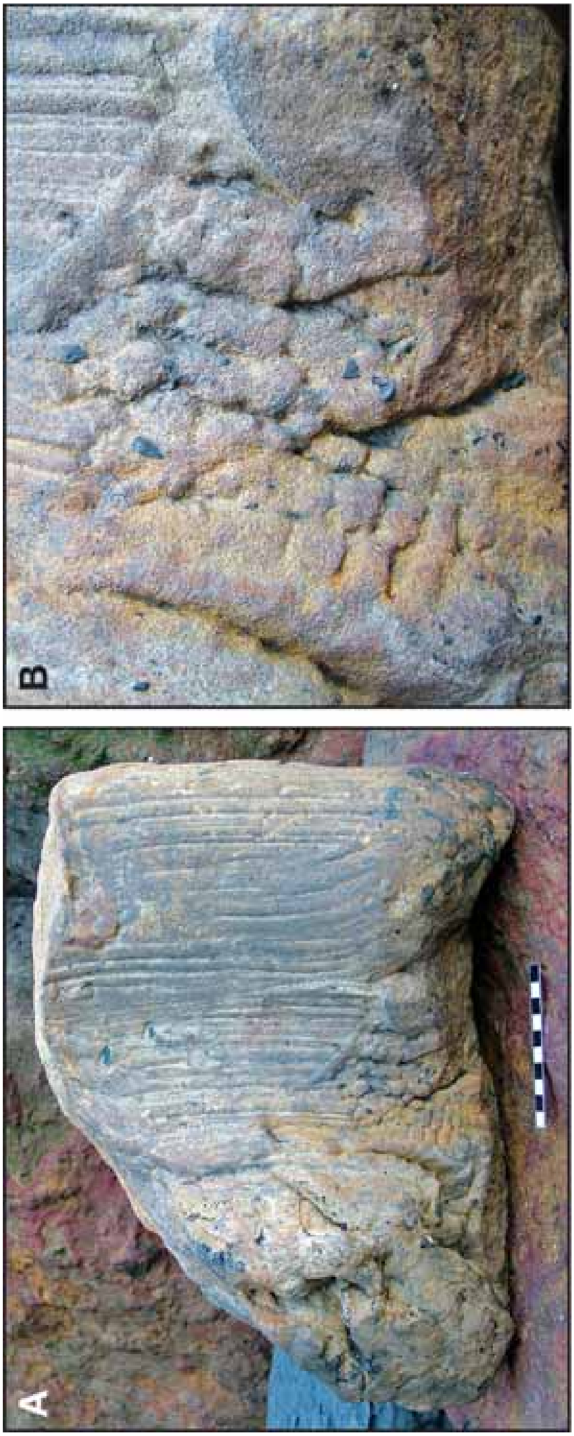

Figure 14. Sandstone cast of a sauropod manus track (F00961; University of Sheffield) from the Saltwick Formation, Saltwick Bay east of Whitby (see Figure 2). A – general view from the rear showing striations and small area of skin impression. Scale bar 10 cm long. B – detail of area showing skin impression. The source horizon was located high up in the adjacent cliff as being at the base of a sandstone unit less than 1.0 m above the top of the Dogger Formation (Figure 1).

- **Actual skin or skin impression**: All but two of the examples studied were of skin impression. The only examples of fossilised skin were those reported by Czerkas (1995, figures 1B, 1C).
- **Position on the body**: This could be identified in 12 out of the 14 cases to varying degrees of accuracy (Table 1). Examples are known from the cervical vertebrae and humerus regions of the body; but the majority are from the distal parts of the limbs. Of the latter, four were definitely identified as coming from the manus or palmar surface, while the remainder were from the pes (or unidentified 'foot') (Table 1).
- **Area of skin under consideration**: The areas of skin investigated in this study varied from 5-165 sq. cm., and only those scales with a recognisable number of surrounding scales were measured. Thus some authors quoted areas in excess of those listed in Table 1; in fact Czerkas (1995, p. 176) recorded skin impression of 1875 sq. cm. (25 x 75 cm.) from Howe Quarry, Wyoming, USA (Morrison Formation, Late Jurassic). Since it was not possible to use a constant area to compare skin textures from different specimens, no statistical implications may be drawn regarding size and/or shape of scales.
- **Number and size of scales recorded in analysis**: The number of scales (not necessarily correlated with area) listed in Table 1 varied from 3 to 61. The maximum scale size (longest diameter) in each sample varied from 4 to 40 mm. These numbers may not exactly equate with those quoted in the source reference, but in most cases were calculated by the present authors from the photographs or drawings in these references (see Table 1 for details). In the specimen figured by García Ramos *et al.* (2006, p. 126, lower figure) from the Upper Jurassic of north Spain, a large scale appears to be more than 50 mm across; this specimen is not included in table 1 or figure 15) as insufficient scales could be recorded.
- **Shapes of scales and most common scale shape**: The maximum range of scale shape for all examples was from tetragonal to octagonal. This was found in only one specimen (Czerkas, 1995, figure 1C), although tetragonal to heptagonal scales were found in two examples. The most common range was pentagonal to heptagonal; and the most frequently occurring scale shape was hexagonal (Table 1, and figure 15). Czerkas (1995, p. 177) stated that no 'additional ornamentation, such as diamond shaped clusters like that on some hadrosaurs are discernible'; but Mateus & Milàn (2010, figure 6C) figured a skin impression from the side of a manus which they described as a pattern of 'triangular overlapping scales'. In fact, from their figure, the scales appear to be more rhomboid in shape, and are unlike any other recorded scale shape of sauropod origin.

TABLE 1.

Database of records of sauropod skin ornament where original texture may be determined. Number of specimen refers to those in Figure 15. Specimens 12-14 have not been used in Figure 15. Specimen 7 was subsequently attributed to a stegosaurian (Lockley *et al.*, 2008, figure 10). NK indicates 'not known'.

Sample	Taxon/ Ichnotaxon	Skin (S) or Impression (I)	Site on body	Number of scales used	Area of scales used (sq. cm)	Largest (longest) scale (mm)	Most common scale shape	Location	Lithostratigraphy	Age	Source(s) of reference(s)
1	*Morosaurus becklesii*	I	humerus	61	106	36	hexagonal	Hastings, UK	Wealden Beds	Early Cretaceous	Hooley, 1917; pl. X, Fig. 2 Czerkas, 1995; Figure 1A
2	*Barosaurus*	S	cervical vertebra	27	62	26	pentagonal/ hexagonal	Dinosaur Nat. Mon., USA	Carmel Formation	Late-Middle Jurassic	Czerkas, 1995; Figure 1B
3	sauropod	S	NK	43	117	30	pentagonal	Howe Quarry, Shell, Wyoming, USA	Morrison Formation	Late Jurassic	Czerkas, 1995; Figure 1C
4	sauropod	I	side of manus	9	9	12	hexagonal	Bighorn Basin, Wyoming, USA	Morrison Formation	Late Jurassic	Platt & Hasiotis, 2006; Figure 7C
5	sauropod (F00961)	I	base of manus	8	5	12	pentagonal	Saltwick Bay, Whitby, UK	Saltwick Formation	Middle Jurassic	present paper
6	?sauropod	I	NK	23	27	10	hexagonal	Tazones Lighthouse, Asturias, Spain	Lastres Formation	Late Jurassic	Garcia-Ramos *et al.*, 2006; p. 127 (upper Figure)
7	sauropod or stegosaurian	I	manus	21	9	7	hexagonal	Villaviciosa, Asturias, Spain	Lastres Formation	Late Jurassic	Garcia-Ramos *et al.*, 2006; p. 127 (lower Figure)
8	sauropod	I	?plantar surface	17	*c.* 2	4	hexagonal	Bullfrog, Utah, USA	Morrison Formation	Late Jurassic	Lockley & Hunt, 1995; Figure 4.44
9	sauropod	I	plantar or palmar surface	5	84	4	hexagonal	Lourinhã, Portugal	Lourinhã Formation	Late Jurassic	Mateus & Milàn, 2010; Figure 6B
10	sauropod	I	plantar surface	3	165	40	hexagonal	Lourinhã, Portugal	Lourinhã Formation	Late Jurassic	Mateus & Milàn, 2010; Figure 4A
11	sauropod	I	pes (digit I)	6	16	16	hexagonal	Nemegt, Gobi, Mongolia	Nemegt Formation	Late Cretaceous	Currie *et al.* 2003; Figure 6
12	sauropod	I	'foot'	16	78	'30'	hexagonal	Deogmyeongri, Korea	Jindong Formation	Early Cretaceous	Kim *et al.*, 2010, Figure 2A
13	sauropod	I	'foot'	-	-	'25'	pentagonal/ hexagonal	Gainri, Korea	Haman Formation	Early Cretaceous	Kim *et al.*, 2010, Figure 2B
14	sauropod	I	'foot'	-	-	'27'	pentagonal/ hexagonal	Sinsu, Korea	Haman Formation	Early Cretaceous	Kim *et al.*, 2010, Figure 2C

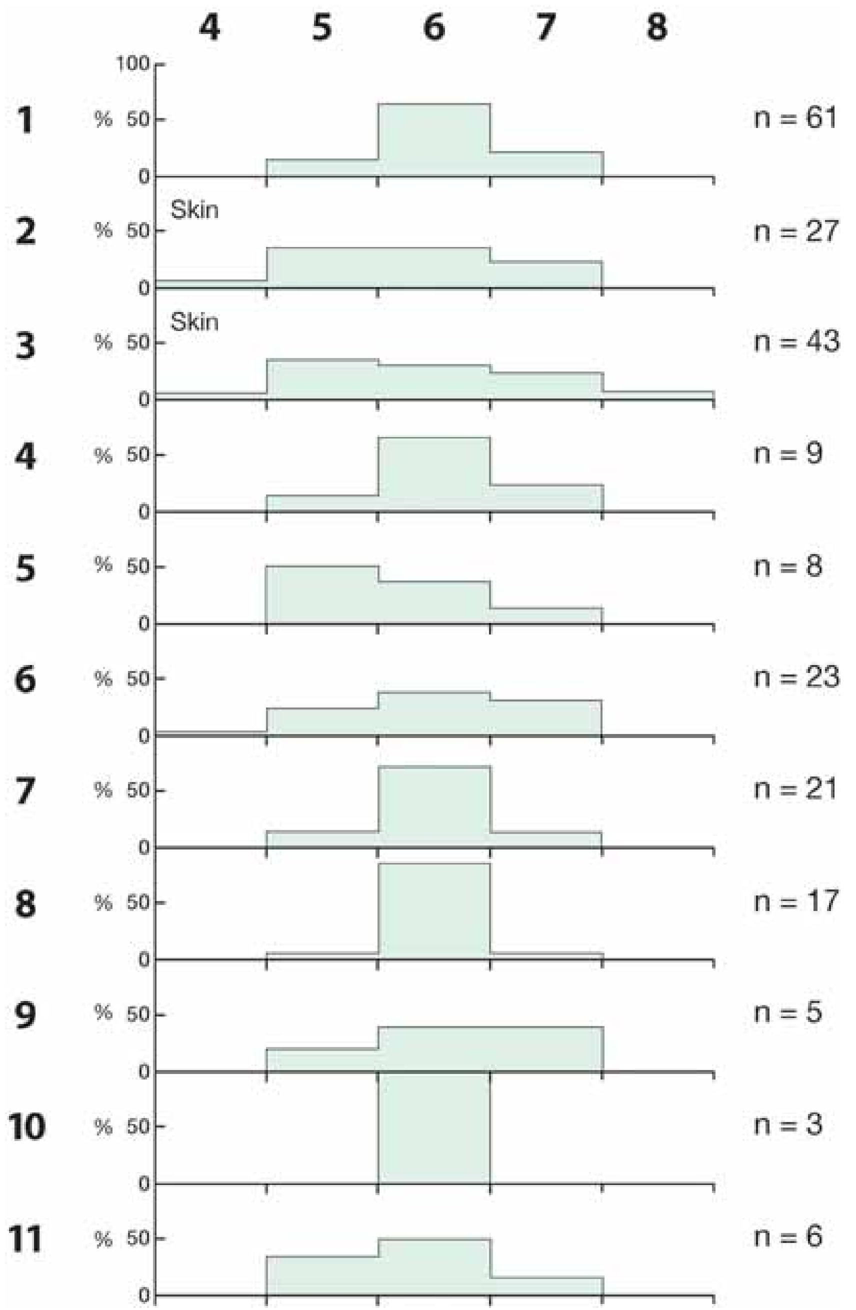

Figure 15. Graphs of scale shape (horizontal axis) in selected sauropod skin textures. Number of specimens (left vertical axis) refers to those in Table 1. 'n' indicates number of specimens used to construct each graph. Note: examples numbered 2 and 3 are of actual skin. Specimen 5 is the present example from Saltwick Bay (Figure 14).

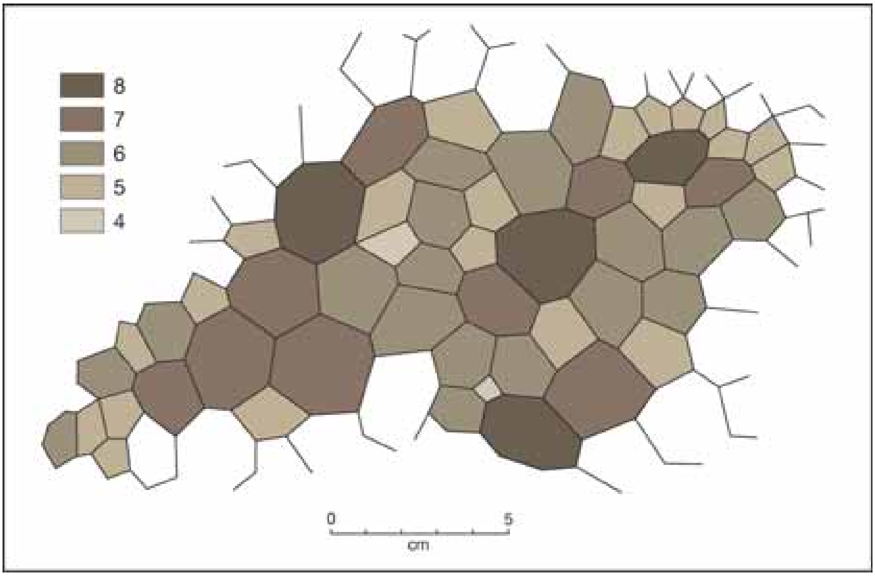

Figure 16. Scale pattern of sauropod skin showing variable shapes (4-8 sided) with occasionally prominent 'rosettes'. Example taken from Czerkas, 1995, figure 1C; Upper Jurassic Morrison Formation of Howe Quarry, Wyoming, USA.

– **Regular pattern**: When scale size is fairly uniform over a limited area, scale arrangement is comparatively regular. However in some examples, where scale size is more irregular, occasionally prominent 'rosettes' are present (figure 16) but without any obvious regular distribution or pattern. Although Czerkas (1995, p. 177) noted that the scales tended to be moderate in size (2-3 cm), non-overlapping and in 'rosette pattern', the present authors have only noticed rosettes rarely, and without any apparent relationship to position on the body or age of the material.
– **Age of specimen**: The specimens range in age from Middle Jurassic to Late Cretaceous. Although no significant differences may be recognised between the oldest and youngest specimens in terms of any of the parameters used, it is noticeable that the oldest Whitby, Yorkshire specimen (Middle Jurassic)) and the Howe Quarry, Wyoming, USA (Late Jurassic) specimen are the only ones in which the most common scale shape is pentagonal, not hexagonal. However, the size of the sample for the Whitby specimen (8 scales used) is inadequate to definitely confirm this apparent similarity.

Since the data base is very sparse, no firm conclusions concerning types and patterns of scales, size with respect to position of the skin on the animal or age may be drawn. Neither does the scant data allow the recognition of any possible correlation between scale shape, size or pattern and the sauropod family or clade. However, future records may resolve some, or all, of these unknowns.

The impression of the skin texture on the Saltwick sauropod manus was made during the weight-bearing (W) phase (Thulborn & Wade, 1989) during locomotion, and so may represent the pattern of a deformed (?stretched) skin (see Section 5). Platt & Hasiotis (2006, p. 256) made a similar point when describing the skin impression on a manus track from the Upper Jurassic of Wyoming as being a result of pad deformation during the mid-stance phase of locomotion, and thus does not represent a perfect replica of the actual skin texture (Gatesy, 2001). However, the amount of deformation is probably insignificant in the overall pattern and size of the scales.

4.2. Texture of embryonic sauropod skin

The above review does not include the beautifully preserved embryonic (probably titanosaur) sauropod skin casts described by Chiappe *et al.* (1998) and Coria & Chiappe (2007) from the Late Cretaceous of Auca Mahuevo in the Patagonian province of Neuquén, Argentina. These embryonic specimens exhibit areas of skin with 1) a (triple) row (*c*. 2 mm wide) of large subrectangular and seemingly overlapping scales crosses an area of smaller (< 0.3 mm) overlapping scales, and 2) a general skin pattern of non-overlapping scales (c. 0.3 mm in diameter) with occasional rosette structures of up to 10 small scales surrounding a large one (Chiappe *et al.*, 1998, figure 3). While, as Chiappe *et al.* (1998) noted, the non-overlapping scales and rosettes pattern compares well with the that of other non-avian dinosaurs, we are not aware of any adult sauropod (or dinosaur) skin texture where the pattern is similar to the row of overlapping scales present in the embryonic form. Chiappe *et al.* (1998, p. 259) suggested that the row (stripe) of larger plates probably ran along the back of the embryo.

4.3. Skin texture deduced from striations

Although striations associated with sauropod tracks are relatively common (Milàn *et al.*, 2005; García Ramos *et al.*, 2006; Mateus & Milàn, 2010), they do not record the shape or arrangements of the scales. However, they do give an indication of the size of the scales, and occasionally it is possible to make out a transition from an area of scale impressions to the associated striations as the foot was extracted from the sediment (or conversely from striations to skin pattern texture as the foot entered the sediment). In the example in García Ramos *et al.* (2004, p. 34), and refigured in García Ramos *et al.* (2006, p. 127, lower figure) (see table 1, specimen number 7 and figure 15) the scales merge into the corresponding striations (although Lockley *et al.*, 2008 and recent communication from Laura Piñuela, Museo del Jurásico de Asturias, Spain, indicates that this specimen may be better referred to *Deltapodus*, an ichnite afforded a stegosaur origin [Whyte & Romano, 2001]). In the example of a manus sandstone cast from the Saltwick Formation of

Figure 17. Frontal view of the surface of a sandstone sauropod manus cast showing widely spaced striations. Scale bar 10 cm long. Specimen, locality and horizon same as that in Figure 14.

Whitby, the striations are generally the same distance apart (*c*. 10 mm) as the maximum diameter of the scales (Table 1). However, on the frontal surface of the cast (figure 17) some striations (grooves) are up to 20 mm apart, up to twice the width of the scale impressions preserved on the posterior side of the cast. There are three possible explanations: 1) the scales that made these widely-spaced striations were also of this size (up to 20 mm); 2) the front of the manus bore rounded and relatively smooth 'hooves' that did not leave any corresponding grooving in the sediment, or 3) if the preservation is not sufficiently good to record the finer striations.

In an example of a pes sandstone cast from the Saltwick Formation, near Whitby (figure 10) the distal end of the clawed digit imprints (I-III) do not bear the finely spaced grooves (striations) present over much of the sides of the cast. This is interpreted as the part of the digit that exposed the claw and thus did not bear sufficient texture (ornament) to leave a mark in the sediment.

4.4. Fine details of skin texture

Hooley (1917), Czerkas (1995) and Paik *et al*. (2010) commented on the detailed 'papilliform' texture of the scales. No fine texture was present on the skin impression of the Whitby specimen, but whether this was because of preservation, scale type or position on the animal is not possible to deduce.

5. SAUROPOD LIMB DYNAMICS

The limb dynamics envisaged for sauropods has often been compared to that of extant proboscideans (Christiansen 1997). Tracks that record foot entry and withdrawal within the substrate may provide unequivocal evidence of limb movement and locomotor dynamics (Gatesy *et al*., 1999; Manning, 2004; Milàn *et al*., 2005; Whyte & Romano, 2008; Jackson *et al*., 2009). Tracks that have formed by deep penetration of the foot into sediment which has a high moisture content may result in a sequence of structures that record angle of limb entry, movement while the foot is in contact with the ground, and angle of foot extraction (Gatesy *et al*., 1999; Gatesy, 2001; Avanzini *et al*., 2011). The recently discovered sandstone casts of sauropod tracks in the Ravenscar Group allow us to go some way in attempting to resolve some of these questions.

The sauropod sandstone casts found in the formations of the Ravenscar Group are generally characterised by well-marked striations down the length of the cast. Previous authors have used such striations in sauropods to suggest limb movement, and Milàn *et al*. (2005) proposed an essentially vertical leg (manus) movement, both entry into and withdrawal from the sediment, on account of the vertical striations on a sandstone cast that was more or less vertical and with a constant diameter. This example was referred to by Falkingham *et al*. (2011) when simulating sauropod manus-only trackways. However, the interpretation of Milàn *et al*. (2005) for the specimen from the Upper Jurassic of Portugal would appear to present some problems regarding limb dynamics. A sauropod leg penetrating at least 32 cm of sediment during locomotion (the length of the sandstone cast described by Milàn *et al*. [2005]) would be expected to leave a cast where the upper (proximal) surface was longer (parasagitally) than the lower (distal) surface (figure 18). If the two surfaces were the same size (length and width, and assuming there was no subsequent closure of the mould following retraction of the foot) then it is difficult to envisage any locomotion taking place. Indeed, even if the animal was stationary while inserting and retracting its limb from the sediment, differences in shape and area of the lower and upper ends of the cast would be expected due to articulation (bending) at the joints of the limb. In the examples from the Ravenscar Group, sets of striations occur at varying angles to each other, presumably representing both foot entry and withdrawal during locomotion, and the upper and lower surfaces of the sandstone cast often exhibit major differences in shape and area.

A cast of a pes from Saltwick Bay (figure 19) is 52.5 cm deep and *c*. 50 cm wide at the (plantar) base. At the top of the cast the print is 35 cm wide, a narrowing of *c*. 33%. The relatively even narrowing of the cast from the base upwards suggests that the smaller top of the cast may be due to a slight

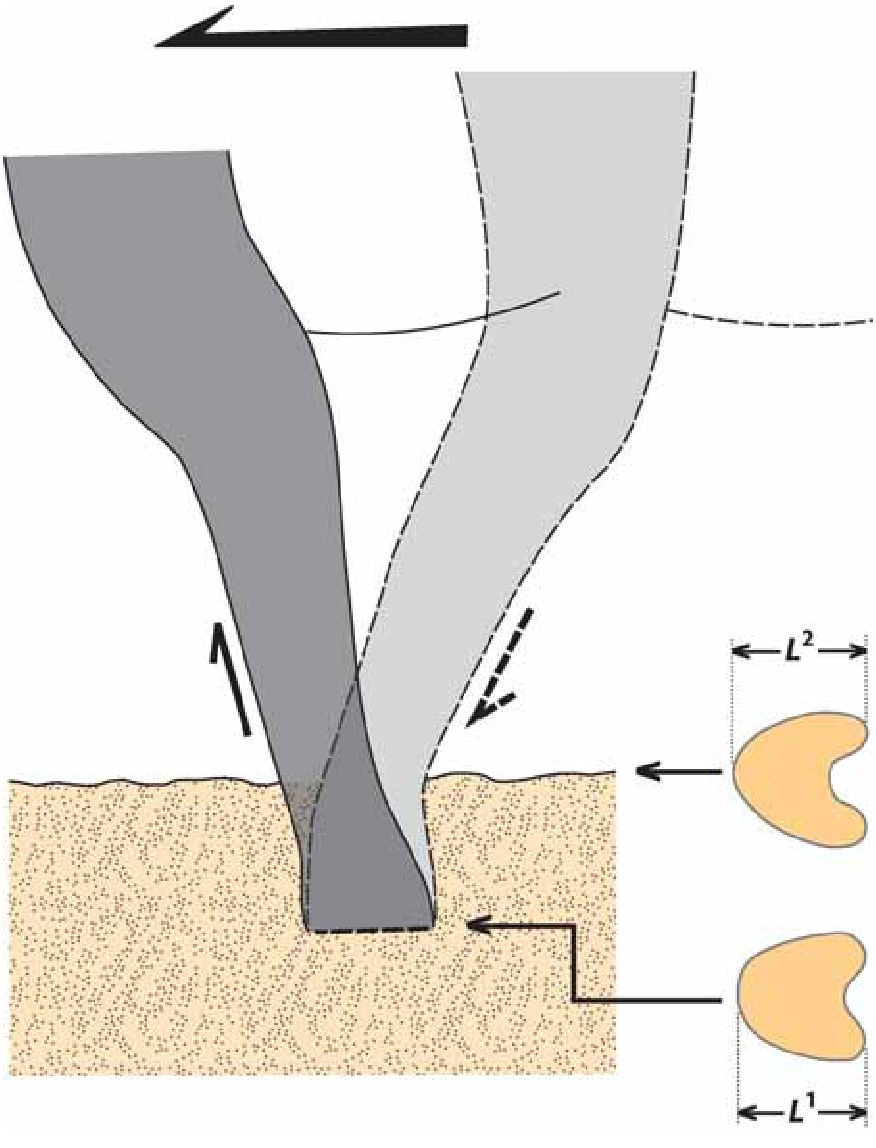

Figure 18. Schematic diagram showing differences in length of the foot cast at the lower (L^1) and upper surfaces (L^2) when the animal is moving. Direction of movement from right to left.

Figure 19. A sandstone cast of a sauropod pes from Saltwick Bay showing marked reduction in width at the top compared with that at the plantar surface. Specimen from the Saltwick Formation, Saltwick Bay, Whitby (Figure 2). Scale bar 10 cm long.

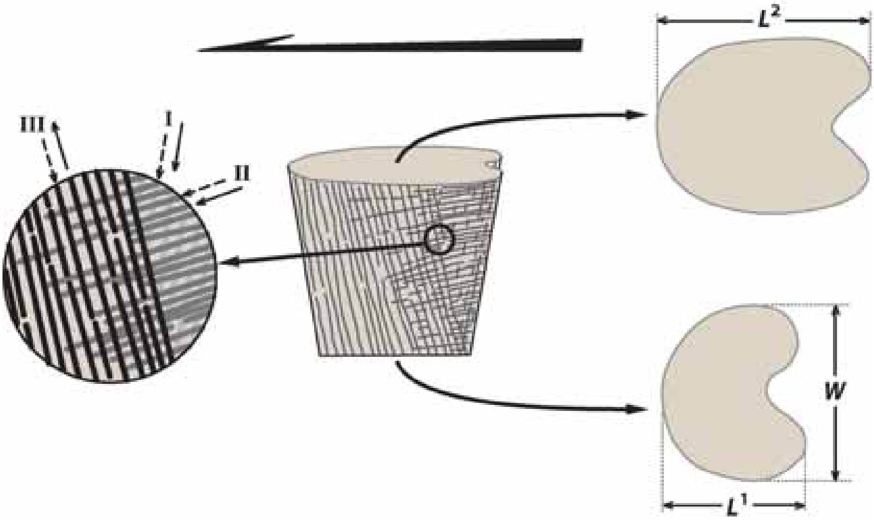

Figure 20. Diagrammatic representation of three sets of striations (I, II, III) on the sides of a (sandstone) manus cast that might be expected to have resulted from the three phases (T, W, K) during locomotion. Direction of locomotion from right to left.

collapsing in of the print walls prior to infilling with sand. Thus, in this case, the different dimensions of the top and bottom of the cast are probably due solely to preservation. Another specimen from Saltwick Bay, the manus example described above that exhibits skin texture (figure 14), also shows markedly different outlines of the palmar and proximal surfaces of the sandstone cast (figure 6). This too may have resulted from partial collapse of the mould walls prior to infilling and/or movement of the limb during locomotion (the T, W and K phases of Thulborn & Wade, 1989). While it is not always possible to determine why the sandstone cast has different shapes and dimensions at the base and top, based purely on measurements of the cast, striations on the sides of the cast may provide the clues. Thus, if the relative time relationships of the striations can be determined, the angles of slope of the striations should indicate the angles at which the foot entered and left the sediment, and their cross-cutting relationships would indicate the step cycle. This may be illustrated diagrammatically (figure 20) by three sets of striations that represent foot entry (T phase), forward movement while foot is in contact with the sediment (W phase) and foot withdrawal (K phase) (Thulborn & Wade, 1989). It must be emphasised however, that if subsequent foot movement completely obliterated the earlier set(s) of striations, the time relationships of the different sets could not be established. Although we have not observed three sets of cross-cutting striations on any specimen, two sets are not uncommon. We illustrate here two such examples of sandstone casts of sauropod prints, a manus and a pes, from which data on step cycles may be determined.

– **Manus:** It is not possible to determine whether the manus print is of a left or right foot. The manus cast is 28 cm deep and shows two sequences of striations at back of the cast (figure 14) with apparent cross-cutting relationships; presumably representing entry and withdrawal of the foot in the sediment. The two sets are both approximately vertical and parallel for most of their length, but are at a slight angle with cross-cutting relationships towards the base. The evidence for priority is equivocal; since a case may be made for either set being made first (i.e. during foot entry); but the set which may be the later, those that appear to cut across the others, bend outwards slightly towards the base of the cast. This may be explained in terms of limb dynamics as a slight inward and forward movement of the foot as it was withdrawn from the mould.

– **Pes:** The sandstone cast of the right pes is 20 cm deep, and also shows two sets of striations with apparent cross-cutting relationships. The striated digit impressions slope forwards at an angle of c. 72^{o} to the horizontal (taken as the plantar surface). However, posterior to the impression of Digit V there are two striated surfaces that exhibit divergent relationships (figure 21). The lower surface bears striations which parallel those on the digit impressions; while the upper surface slopes inwards, also at a steep angle to the plantar surface. Although the striated surfaces are well-preserved, the sequence of movements constituting the step cycle are open to alternative interpretations. Adding to the uncertainty is that it is not possible to determine whether the plantar surface of the track was indeed horizontal or if it was at an angle to the bedding (see below). However, in view of the fact that the lower set slopes upwards and forwards, it is most likely that this set represents foot withdrawal (K phase) from the sediment, made when the animal was in normal locomotion. This interpretation would still be valid if the plantar surface was an angle to the horizontal.

In most of the sandstone casts described here, and for others observed in the field, two additional features commonly occur. The first is that the pes digit impression lobes bearing striations down the sides of the cast are frequently at an angle to the base of the plantar surface, rather than at right angles (figure 11). The second feature is that when the casts are seen *in situ*, the plantar base of the pes is often at an angle to the bedding (figures 11, 22). The former would be expected for an animal in locomotion, since parasagittal motion of the limb would result in the leg reaching forwards at an angle to make contact with the substrate (T phase) and then pulling forwards and upwards (K phase) as locomotion continued. The second feature observed, particularly in deep pes prints, is that the base of the print frequently slopes towards the direction of locomotion. This may be explained by normal progression in a compressible substrate; whereby rotation of the foot occurs prior and during the kickoff (K) phase. This feature is well shown in the example of a pes sandstone cast *in situ* from the lower part of the

Figure 21. Lateral view of sandstone cast of right sauropod pes showing two sets of striations with apparent cross-cutting relationships. Scale bar 10 cm long. Specimen, locality and horizon as in Figure 9.

Figure 22. Field photograph of a sandstone cast of a sauropod pes *in situ*. Specimen is from either Prism I (Moor Grit Member) or Prism III (see Eschard *et al*., 1991) of the Scalby Formation, on Long Nab at the northern end of Burniston Bay. Scale bar is 10 cm long.

Scalby Formation (Moor Grit Member or Prism III of the basal Long Nab Member) on the southern side of Long Nab Point, Burniston Bay (figure 22). In this specimen the rear of the sandstone cast is approximately at right angles to bedding; indicating that the foot descended vertically on to the sediment surface (T phase). During the weight-bearing phase (W) the front of the foot rotated downwards resulting in the plantar surface making an angle of approximately 15º to the bedding. Finally, the forward motion of the body during the kickoff phase (K) meant the leg was withdrawn from the sediment at an angle of 65º-70º to the surface of the sediment. This feature has also been observed by Lüthje *et al.* (2006, figure 6) when describing prints of a fossil pantodont of Palaeocene age.

6. ICHNOTAXONOMY

6.1. Review of selected ichnogenera assigned to sauropodomorph makers

Up until about 10 years ago there were only three generally agreed valid ichnotaxa attributed to sauropod makers (Lockley *et al.*, 1995) in which the diagnoses included details of the pes: *Brontopodus* (ichnotype *B. birdi*; see Farlow *et al.*, 1989) from the Lower Cretaceous Glen Rose Limestone, Paluxy River, Texas; *Breviparopus* (ichnotype *B. taghbaloutensis*; see Dutuit & Ouazzou, 1980; Ishigaki, 1989; Ishigaki & Matsumoto, 2009a,b) from the Upper Jurassic Iouaridène Formation, High Atlas Mountains of Morocco; and *Parabrontopodus* (ichnotype *P. mcintoshi*; see Lockley *et al.* 1995) from the Upper Jurassic Morrison Formation, Colorado. Lockley *et al.* (1995, p. 138) listed a number of ichnogenera that they regarded as *nomina dubia* or *nomina nuda*. Their list included *Iguanodonichnus frenkii* (Casamiquela *in* Casmiquela & Fasola, 1969) from the Late Jurassic Baños del Flaco Formation, Chile, on the basis of it lacking a "diagnostic trackway morphology", as well as having an inappropriate name. However, recently Moreno & Benton (2005) redescribed *Iguanodonichnus frenkii* [spelt as *frenki* by these authors], based also on new data collected in the field. These authors noted the similarity of *I. frenkii* tracks to those of *Parabrontopodus*, with the exception of the Digit I impression being parallel to the long axis of the pes in the former. Also Moreno & Benton (2005) stated that the absence of prominent claw impressions in Digits II to IV of *Iguanodonichnus frenkii* distinguished it from *Parabrontopodus mcintoshi* [spelt as *macintoshi* by Moreno & Benton, 2005] (Lockley *et al.*, 1995), and the *Brontopodus* tracks from eastern Utah and Portugal (Meyer *et al.*, 1995).

Although *Brontopodus birdi* is a well-defined ichnospecies, based on manus, pes and trackway morphology, the ichnotaxonomic basis for *Breviparopus taghbaloutensis* is much less robust. Based on the present authors' observations in the field, in association with Dr. Felix Pérez-Lorente, the pes digit impressions of type material of *Breviparopus taghbaloutensis* were probably incorrectly identified in the original and subsequent descriptions

(Dutuit & Ouazzou, 1980, figure 1; Ishigaki, 1989; Ishigaki & Matsumoto, 2009b). *Parabrontopodus* is again less well-defined than *Brontopodus* owing to the poorly defined outlines of the manus and pes prints of the ichnotype, but is apparently characterized by having the 'long axis [of the pes] rotated outward' and 'no space between trackway midline and inside margin of pes tracks' (Lockley *et al.*, 1995, p. 140); i.e a narrow-gauge trackway. With regards the orientation of the pes tracks, in one of the trackway examples of *Parabrontopodus* shown in Lockley *et al.* (1995, figure 3, left hand side) the pes tracks are only slightly rotated outward, and certainly not as much as in the other example in the same figure or as in the type trackway of *Brontopodus* (Farlow *et al.*, 1989). In terms of Trackway Ratio (Romano *et al.*, 2007) the type material of *Brontopodus birdi* has a pes Trackway Patio (TR) of 36%, while that of *Parabrontopodus* is c. 52% (Romano *et al.*, 2007, table 1). The redescription of *Iguanodonichnus frenkii* by Moreno & Benton (2005) included details of the trackway (the absence of which was the basis for the rejection of this ichnotaxon by Lockley *et al.* [1995]), but the lack of manus print description in their diagnosis and poorly preserved pes prints suggest that the proposal by Lockley *et al.* (1995) to regard this ichnotaxon as a *nomen dubium* should be followed.

Since the revision by Lockley *et al.* (1995), both Lockley & Meyer (2000) and Avanzini *et al.* (2003) have further updated and added to the data; and Porchetti & Nicosia (2007) have re-examined other Late Triassic-Early Jurassic large tetrapod trackways of the African collection of P. Ellenberger. Avanzini *et al.* (2003) described a new sauropodomorph ichnotaxa, *Lavinipes cheminii*, from the Lower Jurassic of the Italian Alps, and suggested that it 'would seem to be a synonym of *Pseudotetrasauropus* (cfr. *P. jaquesi*) or *Otozoum*-like track' in terms of pes morphology, but more *Brontopodus*-like with respect to the manus (Avanzini *et al.*, 2003, p. 189). Porchetti & Nicosia (2007) validated just two of Ellenberger's ichnogenera (*Tetrasauropus* and *Pseudotetrasauropus*) as having being made by sauropodomorphs, and considered *Pentasauropus* was made by a theropod, but *Paratetrasauropus* and *Sauropodopus* were of non-dinosaurian origin.

Lockley *et al.* (2007) re-examined the type material of *Gigantosauropus asturiensis* from the Upper Jurassic Tereñes Formation of Asturias, north Spain (Lires *et al.*, 2001). Lockley *et al.* (2007) confirmed the sauropod maker of the trackway, but regarded the ichnotaxon as a *nomen dubium* (as previously suggested in Lockley *et al.*, 1995) which should only be applied to the original material and not used to 'formally describe other poorly preserved specimens'.

More recently González Riga & Calvo (2009) described *Titanopodus* ichnogen nov. from the Late Cretaceous of Argentina. Although the ichnotaxon is unique for sauropods with its particularly wide-gauge trackway (Pes Trackway Ratio [*PTR*] quoted as 26-31 by these authors, but calculated by us from their figure 4D as even higher [22.2-24.1] - see Romano *et al.* (2007)

for calculation of *PTR*), the strongly outward-rotated pes tracks are generally rather poorly preserved and lack any digit imprints.

Diedrich (2010) redescribed *Elephantopoides barkhausenensis* (Kaever & Lapparent, 1974) as a sauropod trackway from the Upper Jurassic (Kimmeridgian) of Barkhausen, Germany; an ichnotaxon that Lockley, Farlow & Meyer (1995, p. 139) had earlier regarded as an invalid name. Later, after visiting the Barkhausen site, Lockley & Meyer (2000, p. 159, figures 7.8, 7.9) still regarded the original description as inadequate (and the name inappropriate), but pointed out that the trackways trended in an opposite direction to that proposed originally by Kaever & Lapparent (1974). Although Diedrich (2010) expanded and corrected the original description of Kaever & Lapparent (1974) the material is rather poorly preserved and perhaps justifies the use of inverted commas by Lockley & Meyer (2000, figure 7.8) when referring to the ichnotaxon.

The ichnotaxa assigned to sauropod makers was further reviewed by Castanera *et al.* (2011). These authors assigned trackways from the Villar del Arzobispo Formation (Jurassic–Cretaceous transition) of the Iberian Range to *Sauropodichnus giganteus,* an ichnotaxon regarded by Lockley *et al.* (1995) as non-diagnostic as the pes prints of the “type trackway” were circular and without digit impressions. Another figured example of this ichnotaxon (Calvo & Mazzetta, 2004; *fide* Castanera *et al.*, 2011, figure 9,I) again shows no indication of pes digit imprints, so the presence of *Sauropodichnus giganteus* in the Villar del Arzobispo Formation is based mainly on trackway configuration and the shape of the manus; although Castanera *et al.* (2011) point out that the pes of this ichnospecies is characterised by a large Digit I imprint and ‘narrow heel’.

6.2. Ichnotaxonomy of sauropod tracks from the Cleveland Basin of Yorkshire

In the first description of Yorkshire Middle Jurassic tracks assigned to sauropod makers (Romano *et al.*, 1999), the classification of the prints was attempted at ichnogeneric level. Subsequently the authors preferred to use the term morphotypes when referring to prints which were, at that time, rather sparse and lacked any associated trackway (Romano & Whyte, 2003). Although at some horizons sauropod prints are very common, the limited lateral extent of exposures makes resolution of trackways difficult and as yet only one poorly-preserved trackway has been described (Romano & Whyte, 2003, figure 26). Despite this, the newly discovered well-preserved sandstone casts of manus and pes tracks have allowed a more confident taxonomic approach and, where possible, the tracks again have been assigned to ichnotaxa.

In attempting to assign the Yorkshire sauropod prints to named (or new) ichnotaxa the classification used by Avanzini *et al.* (2003, figure 9) is adopted, whereby sauropodomorph ichnotaxa are subdivided into four groups on the basis of pes track morphology; *Tetrasauropus*-like, *Otozoum*-like, *Breviparopus*-like, *Brontopodus*-like. The first two groups are represented by ichnotaxa of Late Triassic-Early Jurassic age, the latter two groups range from the Early Triassic-Early Cretaceous. The *Tetrasauropus*-like and *Otozoum*-like pes (and manus) prints show a number of features which distinguish them from any of the Yorkshire prints; in particular the inward rotation of the pes digit imprints. These two groups are not further discussed here. The other two groups (*Breviparopus*-like and *Brontopodus*-like) are characterised by pes tracks with outwardly directed digit or claw imprints (Avanzini *et al.*, 2003, p. 189). No general consensus has been proposed for the recognition of groups using manus morphology, but Dalla Vecchia (1999) and Dalla Vecchia *et al.* (2000) proposed three subgroups within what Avanzini *et al.* referred to as the *Brontopodus*-like group. These subgroups were based on the 'three basic sauropodan forefoot configurations' (Dalla Vecchia *et al.*, 2000, p. 267, figure 33) and characterise manus prints with: 1) a well-developed Digit I claw impression, 2) an intermediate development of a Digit I claw impression, and 3) an absence of Digit I claw impression, and with rounded digit imprints.

However, in view of the scarcity of manus-pes couples and trackways, the following ichnotaxonomy for the Cleveland Basin prints is based essentially on pes track configuration. The manus tracks are considered separately, except for those assigned to *Breviparopus*? ichnosp. indet. We consider that well-preserved manus and pes prints that reflect foot morphology are the most important factors in determining ichnotaxonomic names, since trackway characteristics such as gauge (Trackway Ratio) and distance between manus and pes prints may vary along a single trackway (Romano *et al.*, 2007; Ishigaki & Matsumoto, 2009b respectively) and are more behaviour-dependent.

6.2.1. ***Brontopodus* ichnosp. indet** (Figure 23A, B)

Ichnospecies A: *Brontopodus*-like print (Romano *et al.*, 1999, figure 3A, E).

Sauropod: Romano & Whyte, 2003, figure 7.

Morphotype Ai: Romano & Whyte, 2003, figure 20.

Sauropod: Romano *et al.*, 2007, figure 11.

Sauropod: Whyte *et al.*, 2010, figure 12bi.

Description: Very large (up to 1 m long) sub-oval pes prints; length 1.3 times the width. Widest part of pes print at midlength. Five digit imprints along anterior and anterolateral border. Digit imprints I-III with backwardly curved terminal claws and reducing in size posteriorly; digit imprints IV and V represented by subdued, clawless protuberances. Indication of pads on plantar surface, but with no recognisable pattern.

The pes prints originally assigned to '*Brontopodus*-like' by Romano *et al.* (1999, figure 3A, E), are here definitely assigned to this ichnogenus and are

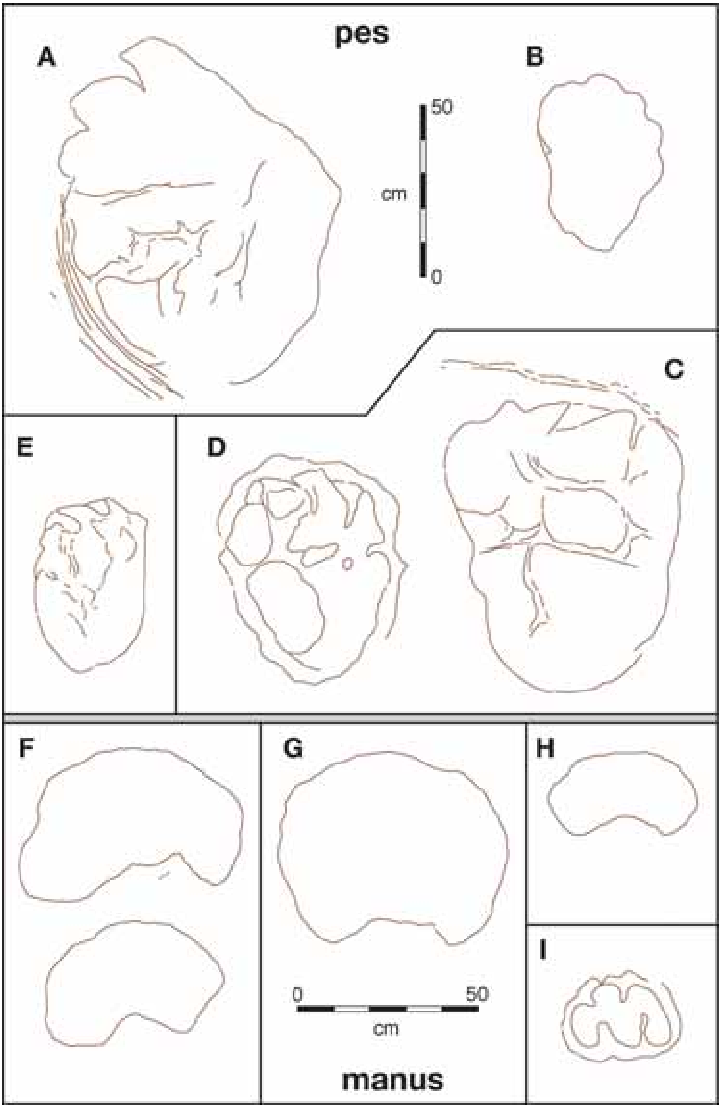

Figure 23. Summary diagram of representatives of all known distinct sauropod pes and manus outlines presently known from the Middle Jurassic of the Cleveland Basin, Yorkshire

Pes tracks (A-E): A, B - *Brontopodus* ichnosp. indet., both specimens from the Saltwick Formation, Whitby; C, D - *Breviparopus*? ichnosp. indet., both specimens from the Saltwick Formation, C from Whitby, D from Hawsker. E - Ichnogen. et ichnosp. indet. from the Saltwick Formation, Whitby.

Manus tracks (F-I): F – Ichnogen. ichnosp. indet. A, both specimens from the Long Nab Member, Scalby Formation, Cornelian Bay; G - Ichnogen. et ichnosp. indet. B, from the Long Nab Member, Scalby Formation, Scalby Bay; H - Ichnogen. et ichnosp. indet. C, from the Saltwick Formation, Whitby; I - *Breviparopus*? ichnosp. indet., from the Saltwick Formation, Hawsker.

grouped with other recently discovered pes specimens described here (figure 23). Since no manus has been found closely associated with these prints in a trackway, they cannot be assigned to a named (or new) ichnospecies. However it is important to note that the pes digit imprint outlines of the Yorkshire specimens differ slightly from those of the Lower Cretaceous type ichnospecies *B. birdi* (Farlow *et al.*, 1989, figure 42.9) where the terminal claw markings are much more slender, apparently more separated, and have vertically downward projecting claw impressions (observations by MR on cast of ichnotype of *Brontopodus* track on display in the American Museum of Natural History, New York). It is possible though (or perhaps probable) that the claw imprints of *B. birdi* in the type trackway (Farlow *et al.*, 1989) have been modified by subsequent closure following retraction of the foot. The present identification of the Aalenian Yorkshire specimens (Romano *et al.* 1999) as *Brontopodus* predates the specimens at the Galinha site at Fátima, Portugal, which were reported as the oldest occurrence (Bajocian-Bathonian) of the ichnogenus (Santos *et al.*, 1995, p. 10). However, it is worth noting that the assigning of the Fátima tracks by Santos *et al.* (1995) to *Brontopodus* was based mainly on the wide gauge nature of the Portuguese trackways, since the individual pes tracks are not well preserved and the manus:pes ratio is significantly different from *Brontopodus* tracks from the Late Jurassic Purgatoire site in Colorado (Santos *et al.*, 1995, p. 7). It is also now known that trackway gauge may vary along trackway length and may be highly dependent on preservation as well as a particular gait (see discussion in Romano *et al.* [2007]). Our earlier provisional inclusion of this type of print in the ichnotaxon *Brontopodus* (Romano *et al.*, 2007) was also followed by Avanzini *et al.* (2003).

The well-preserved sandstone cast of a pes, first figured by Romano & Whyte (2003, figure 7) and subsequently by Romano *et al.* (2007, figure 11) and Whyte *et al.* (2010, figure 12bi), is here referred to this ichnotaxon. This specimen, from the Long Nab Member of the Scalby Formation, Cornelian Bay (figure 11) is at the time of writing buried under a slide of boulder clay. The pes print (figure 13) from the Saltwick Formation at Hayburn Wyke is provisionally included in this ichnotaxon, although it is recognised that up to four clawed pes digit imprints appear to be present.

An impression of the plantar surface of the pes is known from a number of specimens from the Cleveland Basin preserved as surface prints. Although a few of these appear to show areas which have been provisionally identified as pads (Romano *et al.*, 1999, p. 364) the shapes of these areas have not been consistently recognised on other prints of the same ichnospecies, and therefore cannot be definitely assigned to pads on the sole of the foot instead of sediment disturbance and subsequent suction during foot emplacement and retraction.

6.2.2. ***Breviparopus*? ichnosp. indet** (Figure 23C, D, I)

Ichnospecies B: *Breviparopus*-like print (Romano *et al.*, 1999, figure 3B, C).

Morphotype Aii: Romano & Whyte, 2003, figure 20.

Morphotype Aiii: Romano & Whyte, 2003, figure 20.

Sauropod: Whyte *et al.*, 2007, figure 7, Aii, Aiii.

Description: Large (up to 0.8 m long) bell-shaped pes prints; length 1.2-1.3 times the width. Widest part of pes print towards anterior margin. Five digit imprints along anterior border. At least two of the digit imprints are curved and show evidence of a terminal claw. Indication of distinct pads on plantar surface, but with no recognisable pattern. Associated manus prints with one of the pes prints (Romano *et al.*, 1999, figure 3C; Romano & Whyte, 2003, figure 20, Aiii) are 1.4 – 1.6 as wide as long, broadly semi-circular in outline, with one or two indentations on the anterior margin and up to two along the posterior margin.

This is the only ichnotaxa for which manus and pes tracks are (fairly confidently) known. The manus and pes tracks figured in Romano *et al.*, 1999 (figure 3C), and refigured here (figure 23D and I) were found associated on the same block of sandstone, even though the prints did not constitute a 'couple' (i.e. they did not form part of an identifiable trackway). One other print (Morphotype Aii; Romano & Whyte, 2003, figure 20; and refigured here in figure 23), without associated manus prints, is believed to belong to this ichnotaxon (as was tentatively suggested by Romano & Whyte, 2003, p. 211). The bell-shaped outline of the pes is reminiscent of the pes outline of *Breviparopus* and, although the associated manus prints do not agree closely with those of *Breviparopus*, they are provisionally included in this ichnogenus until further specimens are available. Avanzini *et al.* (2003, figure 9) also included one of these prints (Morphotype Aii, figure 23C; but figured in reverse by Avanzini in order to conform to a 'left print') within his *Breviparopus*-like group.

6.2.3. Ichnogen. et ichnosp. indet (Figure 23E)

?Ichnospecies B: *Breviparopus*-like print (Romano *et al.*, 1999, figure 3D).

Morphotype Aiv: Romano & Whyte, 2003, figure 20.

Sauropod: Whyte *et al.*, 2007, figure 7, Aiv.

Description: Large (up to 0.5 m long) 'U-shaped' pes print; length 1.3 times the width. Print more or less parallel-sided for most of the length, with a rounded posterior margin and nearly straight anterior margin. At least four posteriorly curved and probably clawed digit imprints along the anterior and anterolateral border; reducing in size posteriorly. No clear pad impressions on plantar surface.

This pes track, provisionally identified as '?Ichnospecies B' (Romano *et al.*, 1999, figure 3D) shows features in common with *Breviparopus*? ichnosp. indet in the shape and arrangement of digit imprints, but the outline of the track is more or less parallel-sided and thus quite distinct from either *Breviparopus* or *Brontopodus*. This specimen may represent a possible third sauropod ichnospecies from the Cleveland Basin. No manus tracks were found associated with this track.

6.2.4. Manus tracks (figure 23)

None of the Yorkshire manus tracks is sufficiently morphologically diagnostic to allow a positive identification to any described sauropod manus, even though both open arcs and tighter arcs appear to be represented (see Section 2.1). It is noteworthy that none of the outlines of all the known manus tracks from the Cleveland Basin of Yorkshire exhibits the 'somewhat U-shaped' manus outline of *Brontopodus birdi* (Farlow *et al.*, 1989, p. 391), nor its lateral indentations (Farlow *et al.*, 1989, figure 42.6A; Wilson, 2005, figure 4). Only one type figure 7 has a preserved pollex imprint, but since this was only visible on the side of the cast and not at the palmar level, it is not possible to say whether some or any of the other differently preserved manus prints had similar features.

Thus the manus prints have been classified according to shape, primarily on arc tightness (see Section 2.1), and provisionally four different ichnospecies are proposed. The manus of Ichnogen. et ichnosp. A figure 23F is relatively tighter than that of Ichnogen. et ichnosp. C figure 23H; while Ichnogen. et ichnosp. B figure 23G is distinctive in being almost circular in outline. The manus assigned to *Breviparopus*? ichnosp. indet. figure 23I is the most distinctive with their semicircular outline and characteristic indentations around the anterior and posterior margins.

6.2.5. Stratigraphic ranges of sauropod tracks in the Ravenscar Group of the Clevelan Basin, Yorkshire (figure 24)

Sauropod tracks are now known from all the non-marine units of the Middle Jurassic Ravenscar Group of the Cleveland Basin; although frequently the occurrences are only represented by fragmentary and unidentifiable specimens. (Romano & Whyte, 2003, figure 24; Whyte *et al.*, 2007, figure 11). The current known ranges of the named and distinctive unnamed pes and manus sauropod tracks (Sections 5.2.1-4 above) are shown in figure 24. The pes tracks assigned to *Brontopodus* ichnosp. indet. have been recorded throughout the Ravenscar Group, while *Breviparopus*? ichnosp. indet. and the pes Ichnogen. et ichnosp. indet. are only known from the Saltwick Formation.

Of the four different types of manus tracks illustrated here (figure 23), two were found in the Saltwick Formation, from which *Brontopodus* ichnosp. indet., *Breviparopus*? ichnosp. indet. and the pes Ichnogen. et ichnosp. indet. are all recorded; and two were from the younger Scalby Formation from which only *Brontopodus* ichnosp. indet. is at present known. It is anticipated that further discoveries will result in manus and pes prints being linked to each other, and details of their stratigraphic ranges will be refined. Until then, ranges have been inferred where only two records of the same ichnotaxon are known.

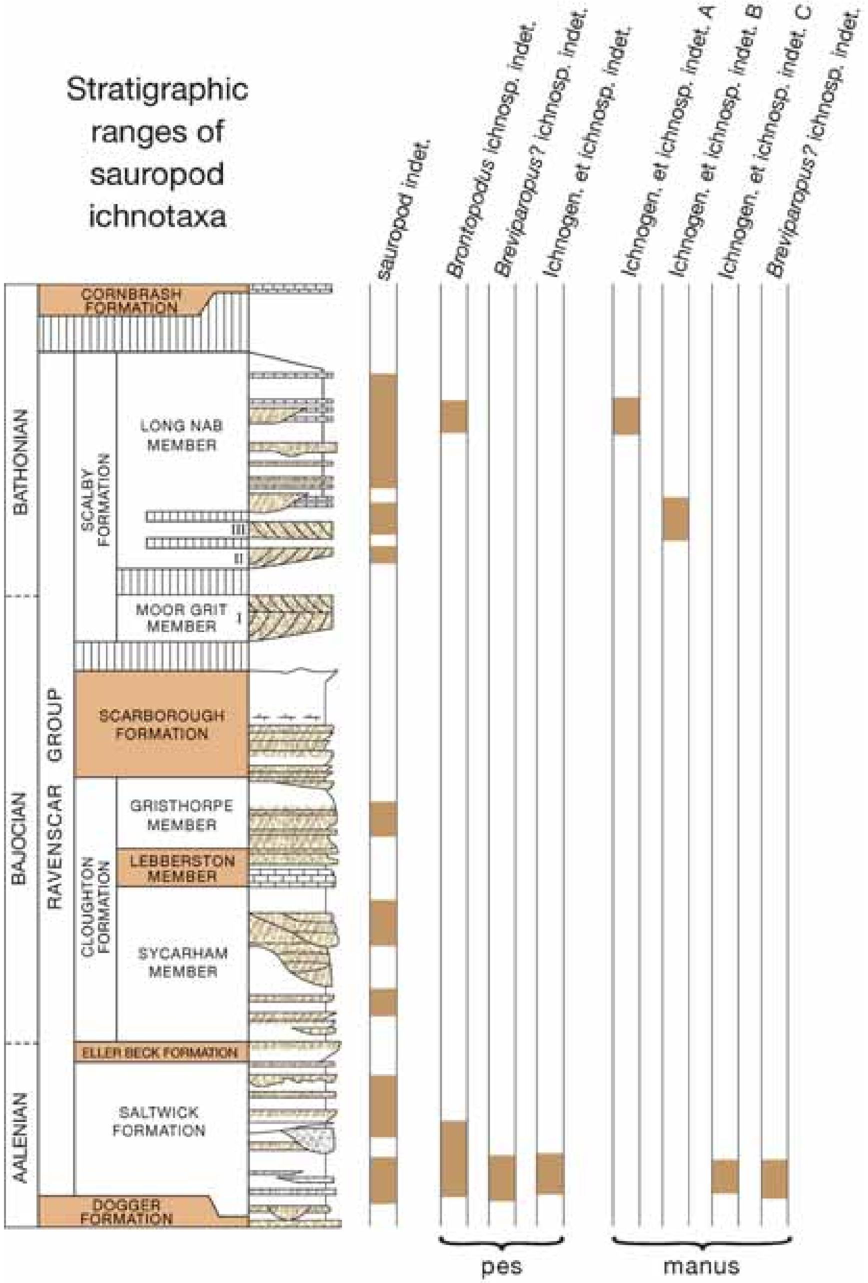

Figure 24. Range chart showing the distribution of manus and pes sauropod tracks assigned to a sauropod maker, from the Middle Jurassic Ravenscar Group of the Cleveland Basin, Yorkshire. Marine units are shaded, and the vertical lines indicate the principal hiatuses. Three sedimentary prisms at the base of the Scalby Formation are labelled I, II, III (diagram from Whyte *et al*., 2007).

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