



A review of footprints from the Wessex Formation (Wealden Group, Lower Cretaceous) at Hanover Point, the Isle of Wight, southern England

JEREMY A. F. LOCKWOOD^{1*}, MARTIN G. LOCKLEY² and STUART POND¹

¹*Ocean and Earth Science, National Oceanography Centre, University of Southampton, Southampton SO14 3ZH, UK*

²*Dinosaur Trackers Research Group, CB 172, University of Colorado at Denver, PO Box 173364, Denver, CO 80217-3364, USA*

Received 6 February 2014; revised 7 May 2014; accepted for publication 7 May 2014

Hanover Point on the Isle of Wight, England, is a Lower Cretaceous (Barremian) site yielding a large number of dinosaur footprints from the Wessex Formation. These footprints, hitherto often referred to as ‘*Iguanodon*’ tracks, have generated interest and speculation since the beginning of the Victorian era. Today, Hanover Point largely yields sandstone casts (convex hyporeliefs) of footprints but also includes some impressions (concave epireliefs), a few of which form short trackways. The majority belongs to large ornithopods, many with foot lengths in excess of 50 cm. Theropods and the occasional thyreophoran track are also represented. The site represents the Wessex Formation within the Wealden Group and can be described ichnologically as a category 3a deposit. Most of the large ornithopod footprints have a distinctive quadripartite morphology and are best assigned to the ichnogenus *Caririchnium* or in some cases *Amblydactylus*. Few are morphologically compatible with *Iguanodontipus* which was described from pre-Wealden deposits and appears to be little represented in the Wealden ichnofaunas. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 707–720.

ADDITIONAL KEYWORDS: *Amblydactylus* – *Caririchnium* – *Iguanodon* – *Iguanodon bernissartensis* – *Iguanodontipus* – *Mantellisaurus atherfieldensis* – Ornithopod.

ABBREVIATIONS: FL, foot length; FW, foot width; IWCMS, Isle of Wight County Museums Service; MIWG, Museum Isle of Wight geology.

INTRODUCTION

The following paper documents more than 150 dinosaur footprints and casts, which became exposed by marine erosion at Hanover Point on the Isle of Wight (Fig. 1) between October 2006 and October 2013. Many are large natural casts of dinosaur footprints, a mode of preservation that almost exclusively produces true tracks preserved as natural casts (convex hyporeliefs). The Wealden facies in this area can be described ichnologically as a category 3a deposit: i.e.

footprints and bones occur in about equal proportions, and the footprints are generally consistent with known skeletal remains (Lockley, 1991; Lockley & Hunt, 1994). The ichnotaxonomic labels applied to these tracks and the importance of consistent terminology for comparative study are also reviewed.

HANOVER POINT STRATIGRAPHY

Hanover Point (Grid Reference SZ 370849–385834) is situated on the south-west coast of the Isle of Wight where it forms part of an extended Site of Special Scientific Interest. The rocks at the Point comprise the oldest units of the Cretaceous Wealden Group on the Island, situated just above the Hauterivian–Barremian boundary (Allen & Wimbledon, 1991).

*Corresponding author. E-mail: jlockwood156@aol.com
The term ‘cast’ is used to denote a natural cast of a footprint (convex hyporelief).

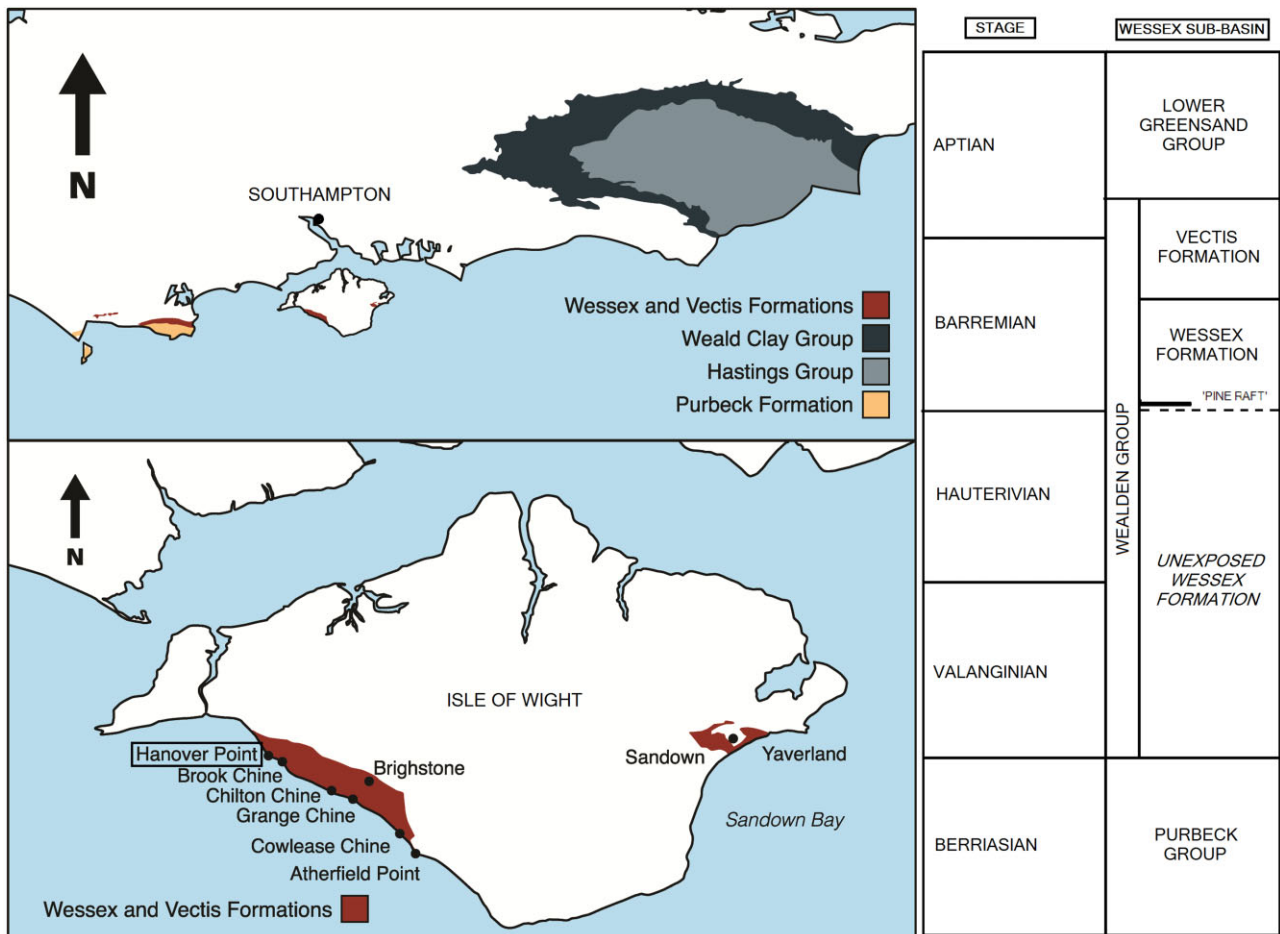


Figure 1. The south coast of England with enlarged view of the Isle of Wight. Generalized stratigraphical log modified from Allen & Wimbledon (1991).

Lack of volcanic ash and fossils that provide reliable indicators for biostratigraphic correlation means that the dating of the deposits is not very precise. However, work on fossil pollens and spores suggests that the exposed Wessex Formation of the Wealden Group on the Isle of Wight is entirely Barremian (Hughes & McDougall, 1990) while carbon-isotope stratigraphy places local plant remains, known as 'the Pine Raft' (Fig. 1) at approximately 125 Myr within Chronozone CM3 (Robinson & Hesselbo, 2004). This is about 10 Myr younger than the Hastings Group on the south coast of England which has its base in the Berriasian, extends up through the Valanginian (Hopson, Wilkinson & Woods, 2010) and forms the other main locality for 'Iguanodon' footprints.

Hanover Point owes its existence to a 0.4–0.75 m thick bed of hard sandstone (Radley, 1994) (Fig. 2A), whose underside forms a natural cast of a heavily dinoturbated area. The sandstone is interpreted as being formed by a crevasse-splay event (Insole &

Hutt, 1994). Overlying the sandstone is a plant debris bed (CL2), providing a major source of plant and vertebrate fossils including crocodylians, turtles, *Iguanodon* and other dinosaur bones.

Underlying the sandstone and visible at low tide is another plant debris bed (CL1), known as the 'pine raft', famously described by Gideon Mantell (1846: 92–93) in his account of the geology of Brook. It is comprised of the trunks of fossilised conifers with visible growth rings, which were originally washed down into the basin and became stranded on a point bar (Sweetman, 2011: 70). The bed also contains the remains of *Tempskya*, pinecones, the teeth and fish scales of *Lepidotus mantelli* (Osborne White, 1921) and much charcoaled plant debris (Robinson & Hesselbo, 2004). It was probably the result of a flash-flood debris flow event (Insole & Hutt, 1994) (Wright, Taylor & Beck, 2000) (Sweetman & Insole, 2010). Allen (1981: 200) suggested a log jam that developed and collapsed during heavy rains after ponding back considerable volumes of water.

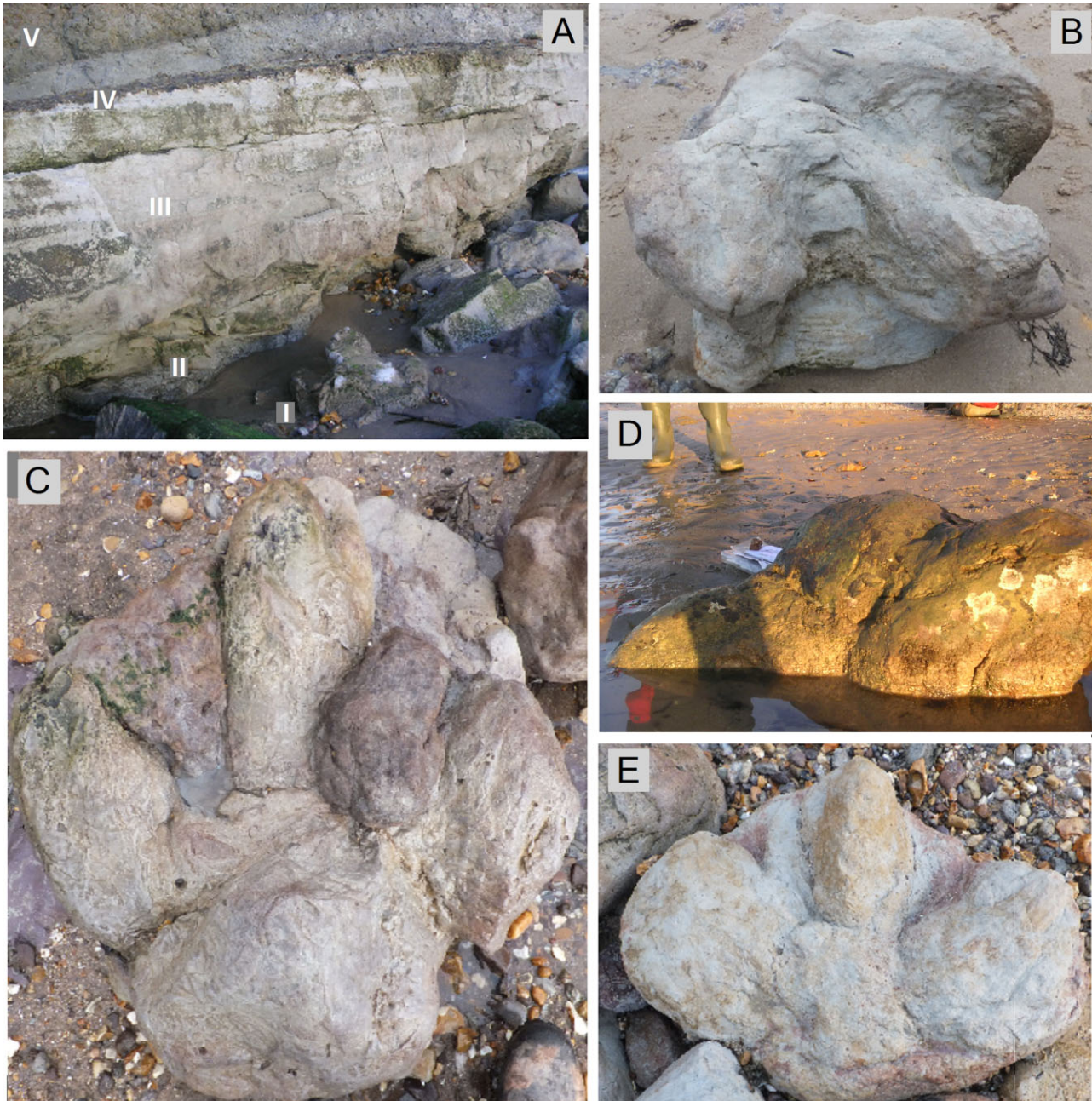


Figure 2. A, Hanover Point beds (I, natural cast of ornithopod footprint; II, dinoturbated underside; III, crevasse-splay sandstone; IV, plant debris bed, a frequent source of bones; V, Wealden Mudstone). B, natural cast of ornithopod footprint (FL = 68 cm). C, natural cast of ornithopod footprint (FL = 63 cm). D, lateral view of ornithopod natural cast showing metatarsal impression. E, natural cast of ornithopod footprint (FL = 57 cm).

The sandstone and plant debris beds are interbedded between varicoloured mudstones which dominate the succession. Footprints occur at several different levels (Radley & Allen, 2012) often presenting a dense mixture of sizes and alignments (Fig. 13), indicating an area overrun by dinosaurs, at least seasonally. Ornithopod body fossils found

in the Hanover Point area are predominantly from *Mantellisaurus atherfieldensis* although *Iguanodon bernissartensis* (Norman, 2013) and *Valdosaurus canaliculatus* are also represented.

The palaeoenvironment has been interpreted as a sequence of alluvial meander plains which overran the Wessex Sub-basin (Allen, 1998), together with

seasonally ephemeral lakes and ponds (Martill & Naish, 2001a). The climate was variable 'Mediterranean' and the differentiated soils show swelling and shrinkage features typical of modern warm semi-arid areas (Allen, 1998: 208). The uneven ring structure in the locally found fossil conifer *Pseudofrenelopsis paraceramosa* also indicates a probable annual change from hot-drier to cool-wetter weather of a Mediterranean type rather than monsoonal (Francis, 1987).

Higher ground to the north had forested areas of fir trees, with cycads and tree ferns also present. Forest fires and floods were common, washing plant debris into the basin. High-sinuosity rivers in the basin provided for a rich riparian ecosystem (Sweetman, 2011) and an excellent environment for the preservation of bioturbation.

HISTORICAL ASSOCIATIONS

Traditionally, the footprints and casts at Hanover Point have been linked to *Iguanodon*. This attribution dates back to the time of Beckles (1862: 445) who first described and figured dinosaur foot casts in the Brook Bay area. Beckles (1851: 117) was also the first to publish on the 'Supposed casts of footprints in the Wealden' and makes mention in this paper of the discovery by Dr. Mantell of a specimen on the Isle of Wight. He figured a cast in 1854 (Fig. 3) which was discovered on the south coast of East Sussex, west of

Hastings, by which time he had collected several specimens the largest possessing a FL of 53 cm. The link with dinosaurs was made by Owen in 1853 after Beckles showed him an almost complete hind limb of a juvenile *Iguanodon* from the Isle of Wight. During 1862 three further papers were presented to the Geological Society of London linking such footprints/casts with *Iguanodon* (Delair, 1989).

Gideon Mantell also wrote about his discoveries on the Isle of Wight although the exact horizon is not documented. His description is certainly reminiscent in size, shape and colour of the Hanover Point casts – 'This specimen is a solid tripartite mass of fawn-coloured sandstone; the middle process is 15 inches, and the lateral projections are 12 inches in length; the processes are laterally compressed and rounded at the extremities, and united to a common base . . . As the origin of these singular concretions is very problematical, every specimen should be preserved; and if several occur in the same bed, their relative position should be ascertained' (Mantell, 1854: 238).

These natural casts and footprints have been known since Victorian times as '*Iguanodon* Footprints' and their association with skeletal remains of *Iguanodon* make this attribution highly likely although unproven. Although frequently mentioned in the literature, more specific reference to the tracks may be found in Sarjeant (1974: 351-3), Martill & Naish (2001b: 310-318), Delair (1983: 609-615) and

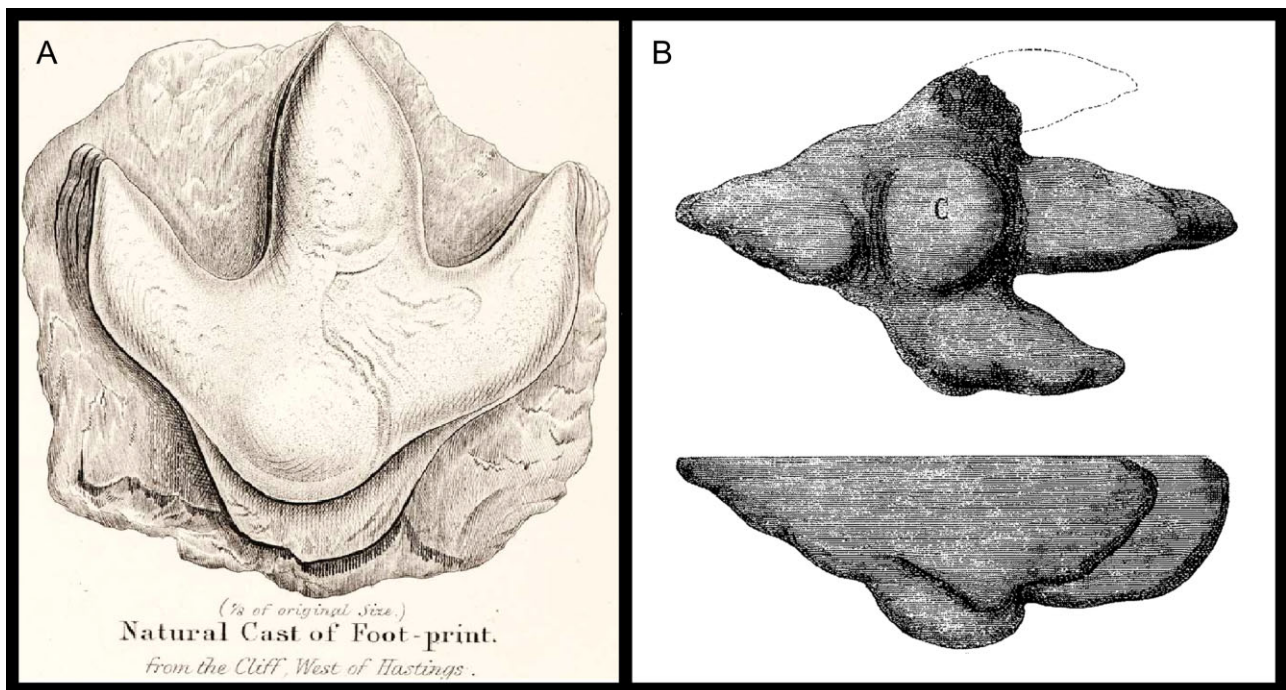


Figure 3. A, natural cast from the Hastings area, East Sussex, after Beckles (1854). B, natural cast of an *Iguanodon* footprint, Hanover Point area, after Beckles (1862). Track morphologies resemble ichnogenus *Caririchnium*.

Radley (1997: 107-13). Dinosaur Isle (MIWG) also have photographic records, co-ordinates and measurements of 95 Wessex Formation foot casts from a survey undertaken by Dr Martin Munt in 2005/6. An exposure of the mudflats in 1982 revealed a large number of prints which were mapped by Stephen Hutt (MIWG) and are reproduced herein (Fig. 13).

METHODS OF DOCUMENTATION

The main purpose of this study was to survey the dinosaur foot casts and prints found at Hanover Point. Due to shifting beach debris and sand, the degree of exposure is very variable.

Each cast/print was photographed from directly overhead with the picture including a scale and reference number. Photographs from other angles were taken as appropriate and field sketches were made. Measurements were made of the foot length (FL) and foot width (FW) in situ. Drawings were made using a combination of photographs and field sketches to facilitate interpretation (Sarjeant, 1989). Two possible thyreophoran natural casts found in 2009 by Stephen Hutt (MIWG) have also been included.

RESULTS

Records were compiled for 150 footprints:

- 138 *Ornithopod* (92%) 122 casts and 16 prints. 28 were complete enough to allow measurements of FL and FW; 56 yielded only FL measurements (Figs 2, 4–11).
- 10 *Theropod* (7%) five casts and five prints. (Figs 6, 9A, D, E)
- 2 *Thyreophoran* (1%) two casts (collected by Stephen Hutt (MIWG) in 2009 Fig. 8A, B).

Many casts were too distorted by dinoturbation or damage (from falling, the sea or sadly by collector's hammers), to allow meaningful interpretation and have not been included in the above numbers.

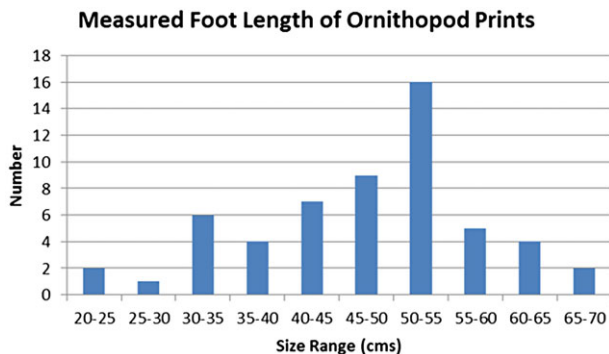


Figure 4. Measured FL of ornithopod specimens ($n = 56$).

Although the National Trust discourage the removal of casts, it may be that smaller examples have been collected illicitly. This would cause a sample bias towards larger examples. (The foreshore is Crown Property and the casts are classified as boulders, requiring application to DEFRA/Natural England before removal. The cliff is National Trust land and their permission is required for access and removal of casts. Unauthorised removal may be considered as theft.)

As variation of footprint morphology is multifactorial, it is not possible to infer that each shape represents a different individual. This means that inferred censuses based on tracks needs to be interpreted with caution. Nevertheless, a database based on well preserved (non-distorted) tracks probably serves as a proxy census of individuals and foot size variation.

The ornithopod casts/prints have FLs varying from 14–68 cm (mean = 50.2 cm), with a modal size class of 50–55cm (Fig. 4). Overall, foot length was only slightly larger than foot width with a mean value for FL/FW of 1.037. Theropods had a significantly longer digit III compared with the lateral digits. However, bigger ornithopod and theropod tracks tend not to show discrete digital pads and differentiation can be difficult.

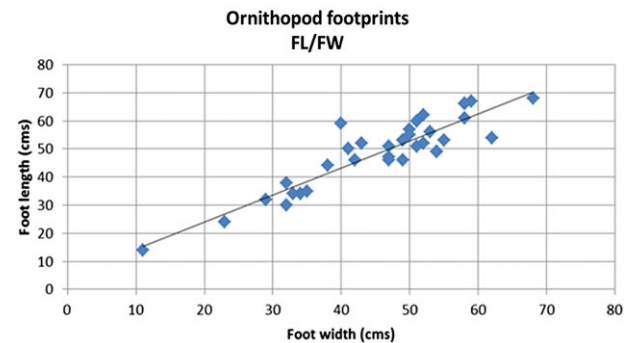


Figure 5. Ornithopod casts FL/FW.

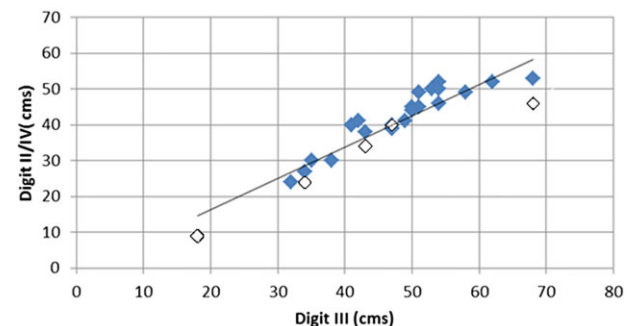


Figure 6. Digit III length vs. longest of digits II and IV measured from heel. Filled diamond, ornithopod; empty diamond, theropod.

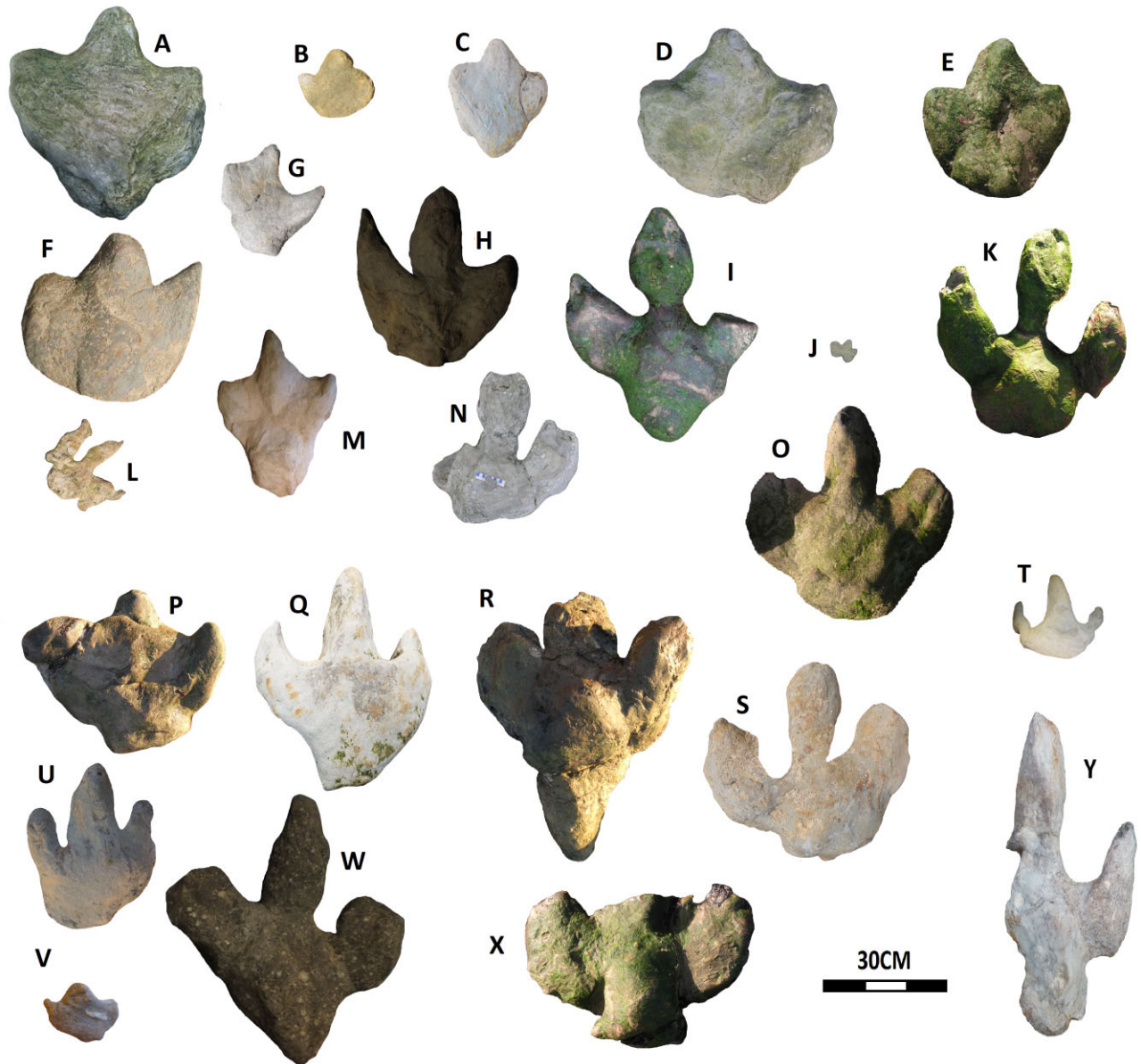


Figure 7. A selection of natural casts of footprints from Hanover Point. (To facilitate recognition of the foot shape the background rock has been erased from the images, leaving only the actual footprint markings.)

In most track assemblages, including those from Hanover Point, smaller ornithomimid casts are less common. This may be the result of a preservational and erosion-induced bias, although smaller prints are sometimes seen in the foreshore mudstones and are commoner in other localities, implying that historical collecting may be a factor. Alternatively, it could be that smaller animals were less common (Matsukawa, Lockley & Hunt, 1999) due to such factors as rapid growth rates, different habitat preferences among different age groups or adults migrating to feeding areas without their young.

Ratios allow hip height (h) to be estimated from the FL. Alexander (1976: 129) suggested $h = 4FL$ while Thulborn (1989: 42) using osteometric data gave $h = 5.9FL$ for ornithomimids with $FL > 25$ cm. However, using measurements taken from the Bernissart specimens (Norman, 1980, 1986) and reconstructions by Paul (2008: 194), h/FL approximates to 4.5. Given the high likelihood of the prints being made by Iguanodonts the latter is probably the most valid. This would give a hip height of 2.25 m for a FL of 50 cm and for the largest prints with $FL = 68$ cm a hip height of 3.06 m. Paul's (2008: 194) reconstructions show that a

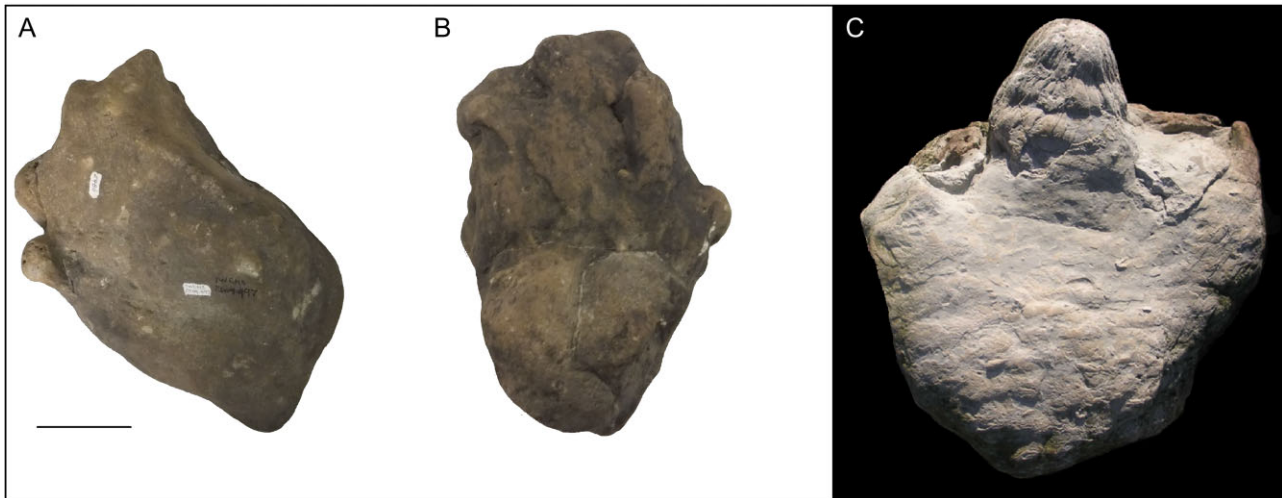


Figure 8. A, natural cast of presumed thyreophoran pes IWCMS.2009.497. B, natural cast of presumed thyreophoran pes IWCMS.2009.399. C, ornithopod footprint showing rippled underside. Scale bar = 10 cm.

hip height of 2.3 m for *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* specimens equates to a femur length of approximately 1.0 m. This makes the modal FL group (50–55 cm) at Hanover Point compatible with the largest Bernissart specimens.

Figure 7 shows a wide range of tridactyl track morphotypes, preserved as natural casts. Casts shown in Figure 7A–E lack deep hypicies separating the digits traces, and therefore contrast sharply with most of the remaining examples (Fig. 7F–Y). Several however on close inspection do show faint markings that are consistent with the outlines of the more quadripartite prints.

The majority of the aforementioned ornithopod casts (Fig. 7) conforms quite closely to *Caririchnium* morphology (Fig. 12C), especially those (e.g., Figs 2C, and 7I,K,N,O,R,W,X) that have a well defined quadripartite morphology (Lockley *et al.*, 2014). These prints have a FW almost equal to the FL, a digit III slightly longer than the lateral digits and sometimes a slight indentation at the heel. Most have ‘fleshy’ oval digital pads (e.g. Fig. 7I, K) typical of *Caririchnium*. The lateral digits are usually slightly unequal in size and shape with one sometimes more blunt or rounded than another (*vide infra*). Although it is well established that *Caririchnium* and *Amblydactylus* represent ornithopods that presumably had relatively blunt unguis (Lockley *et al.*, 2014), individual digit traces are often quite pointed, while others have broad unguis traces (Woodhams & Hines, 1989). This suggests we do not adequately understand how the dynamics of footprint registration may affect footprint shape. Figure 7 F,G,H all demonstrate such slightly curved pointed lateral digit traces. Some tracks (Figs 2E, 7D) are very transverse:

i.e. much wider than long, and in this regard they resemble *Amblydactylus* (Currie & Sarjeant, 1979). However, such forms appear to be in a minority in the sample described here, and in some cases (e.g. Fig. 7D) their apparent width may in part be due to post-exhumation erosion.

The Hanover Point sandstone is generally described as having ‘both small and large scale cross-bedding with some fluid escape structures and desiccation cracks’ (Insole, Daley & Gale, 1998: 92). Several ornithopod casts appear to have somewhat irregular ripple marks on their under surfaces. Ripples were reported by Currie (1983: 66) in *Amblydactylus* tracks from the Peace River Canyon in Canada and considered to be the result of the prints being especially shallow and made under water. In Figure 8C one can see from the damaged tip of digit III that in this case the cast is actually made up of many thin layers and that the linear surface markings represent a cross section of an internal sedimentary structure caused by current cross-stratification.

Some casts (e.g., Fig. 7L,T) may represent theropods, having thinner digits and a stronger mesaxony (Lockley, 2009). Figure 7Y has a markedly thin digit III and is 68cm long. If theropodan this would equate to those of the largest Tetanurae. It is sometimes difficult to distinguish between theropod and ornithopod prints in Lower- to mid-Cretaceous assemblages. Likewise, there may be a bias towards categorising prints as theropodan (Romilio & Salisbury, 2011; Castanera *et al.*, 2013). These difficulties are accentuated by the lack of trackways which normally help distinguish theropod and ornithopod ichnotaxa. Trackways are recorded on the Isle of Wight. Figure 9G, for example, shows a three ornithopod

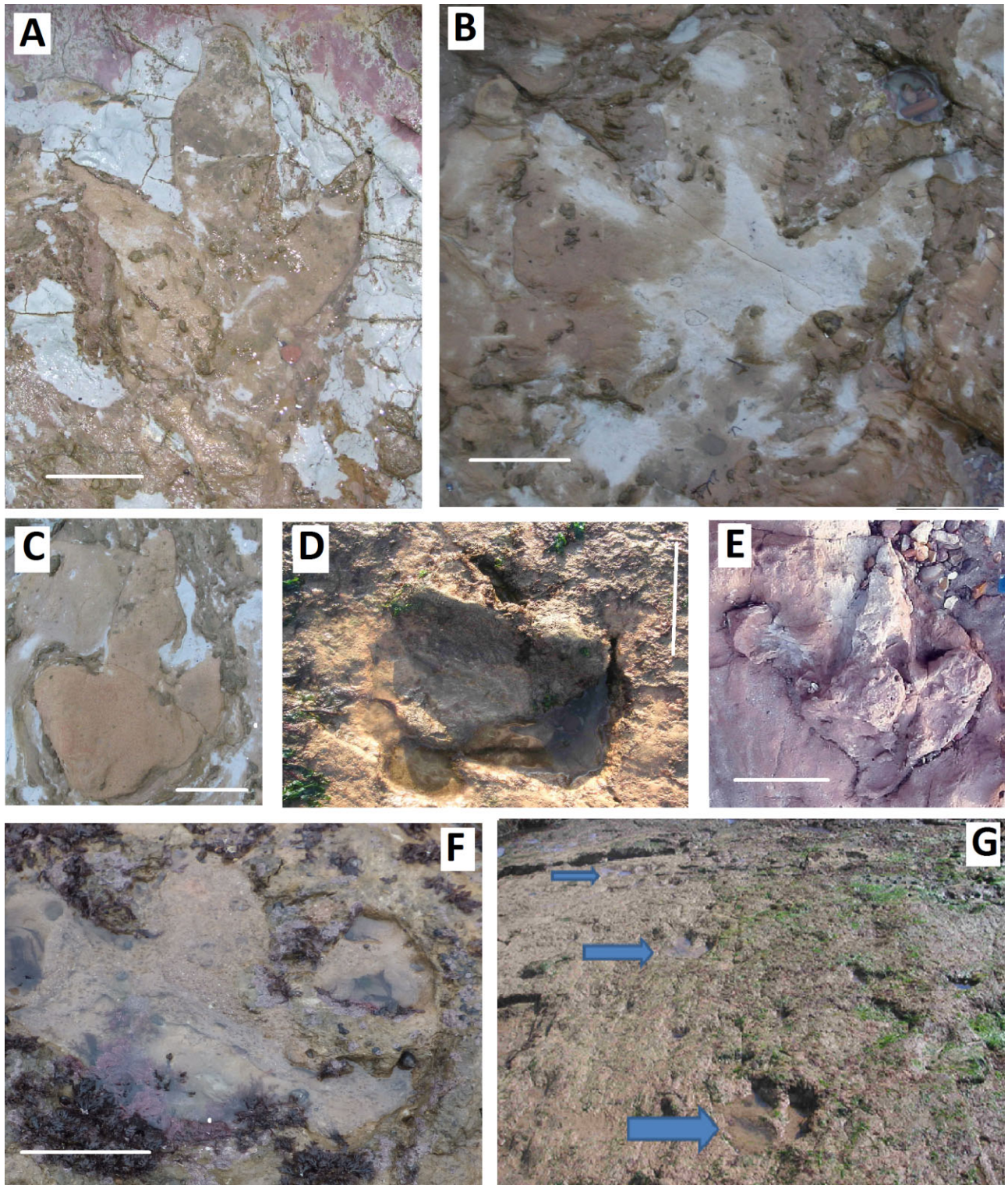


Figure 9. Footprints at Hanover Point. Scale bar = 10 cm. A, theropod. B, ornithopod. C, Theropod print (one of a pair with a stride of 183 cm). D, theropod print with what appear to be claw marks. E, theropod print (photo Bill Webb). F, ornithopod print. G, three sequential ornithopod prints on a wave cut platform off Hanover Point.

prints with a relatively long step and pronounced digitigrade stance (Pond *et al.*, 2014) while Figure 10 shows stronger heel impressions and shorter strides.

Tracks shown in Figure 7L and T, show signs of segmentation in the lateral digits, which are rare in large Cretaceous ornithopod tracks. Such features therefore strengthen the case that these may be theropod tracks. Figure 9A, D, E show tridactyl tracks with rather more typical theropod characteristics such as pointed digit (claw) traces and prominent digit III (9A), separate digital pads (9E). Figure 9D appears to show segmentation and large claw marks.

Figure 11 is an image generated using 3D data recorded using photogrammetry of a natural cast showing what we infer to be a manus and pes set. This is clear evidence of an animal using a

quadrupedal gait and is suggestive of a species like *I. bernissartensis*. A few other specimens also show some indication of an associated manus (Fig. 2C). However, due to their small size and relatively simple, rounded to semi-circular morphology, casts of manus prints are difficult to identify with confidence, especially when found isolated.

Figure 13 has been redrawn from a map constructed by Stephen Hutt (MIWG) in 1982. A large area of the foreshore had been stripped of sand and beach debris to reveal the underlying mudstones. One bed contained infilled footprints and over a hundred were recorded. These footprints have subsequently eroded. The footprints were drawn approximately to scale so we can judge that FL ranged up to about 80 cm with the majority being about 50 cm and few less than 30 cm. This equates well with FL size range for the casts and suggests that small footed animals were genuinely less common. Allen (1998: 200) proposed that the pattern of a large size range coupled with a lack of alignment may represent a 'favourite, perhaps shrinking, watering place'.

DISCUSSION

The ichnotaxonomy of large Cretaceous ornithopod tracks is in a state of flux and is reviewed elsewhere in this volume (Lockley *et al.*, 2014). Lockley, Nadon & Currie (2004: 238), recognized three large ornithopod ichnogenera, *Iguanodontipus*; *Amblydactylus* and *Caririchnium*, based on Lower Cretaceous type specimens and erected *Hadrosauropodus* for the Upper Cretaceous. More recently however Lucas *et al.*, (2011: 358) have considered *Iguanodontipus* a

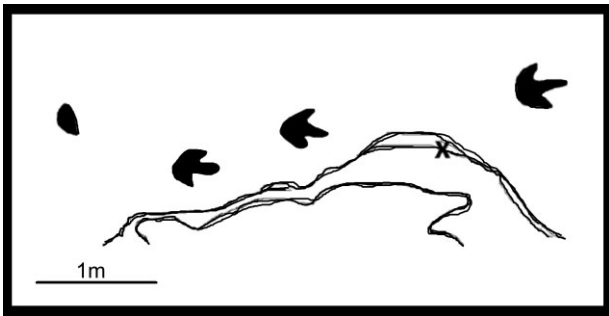


Figure 10. Ornithopod trackway 200 m west of Hanover Point. Mudstone bed eroded at position X. FL approx. 40 cm; FW approx. 32 cm; stride 220 cm. Relative stride assuming hip height = $4 \times \text{FL} = 1.11$ indicates a slow walk.

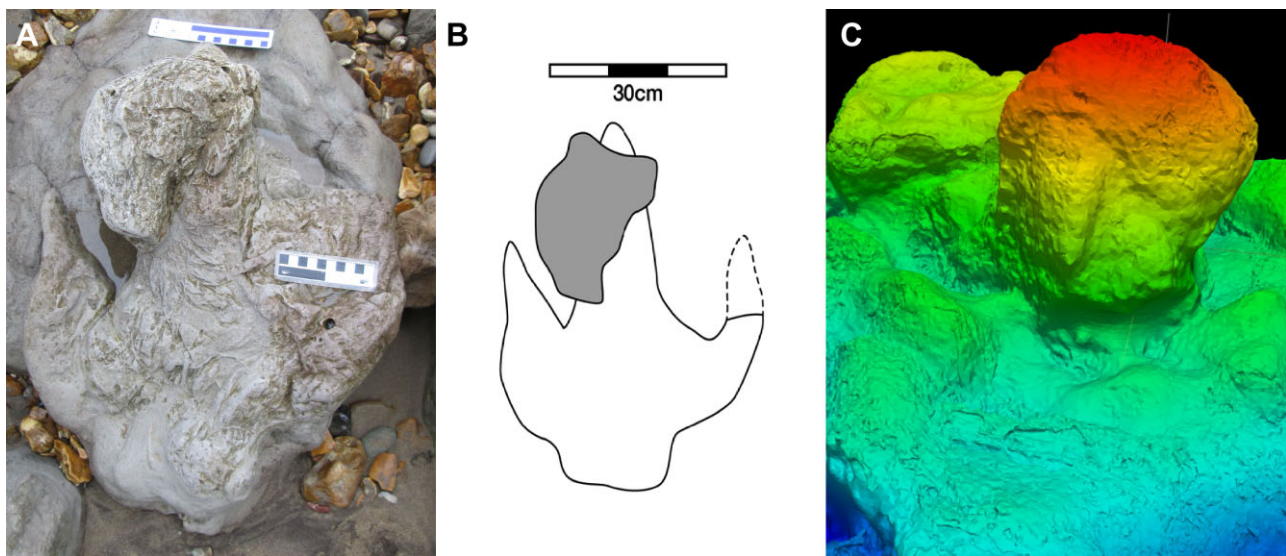


Figure 11. Photogrammetry image of ornithopod print showing natural casts of pes and manus (A). B, drawing of print complex. C, false colour image of manus, perhaps showing pollex impression. Photographs and image by Stuart Pond.

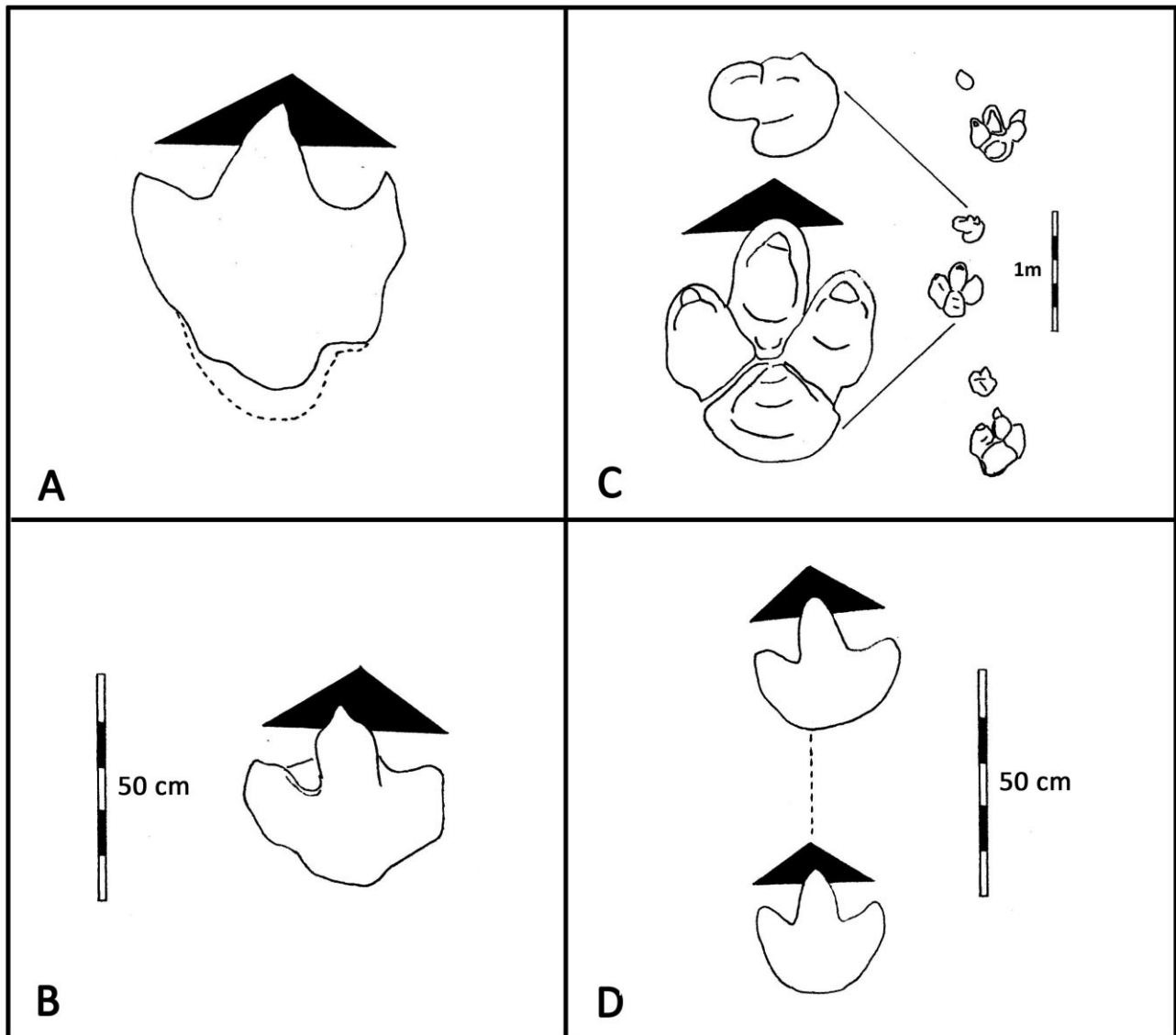


Figure 12. Holotypes of large ornithopod tracks from the Lower Cretaceous discussed in text. A, *Amblydactylus gethingi*. B, *Amblydactylus kortmeyeri* (after Currie & Sarjeant, 1979). C, *Caririchnium magnificentum* after Leonardi (1984). D, *Iguanodontipus burreyi* (after Sarjeant *et al.*, 1998). Modified after Lockley *et al.* (2014).

junior synonym of *Amblydactylus* and *Hadrosauro-podus* a junior synonym of *Caririchnium*. For consistency we adhere to the arguments put forth elsewhere in this volume (Lockley *et al.*, 2014) which retain the four disputed ichnogenera but discuss in some detail the similarities and differences.

Iguanodontipus burreyi AND THE HANOVER POINT CASTS

Ichnogenus *Iguanodontipus* was erected by Sarjeant, Delair & Lockley (1998) in order to resolve the long standing problems of designating all possible

iguanodontid tracks as ‘*Iguanodon* tracks’, an informal practice not permitted by formal International Commission on Zoological Nomenclature rules of ichnotaxonomy (Ride *et al.*, 1985). They based their ichnogenus and new ichnospecies, *Iguanodontipus burreyi*, on natural casts from the Purbeck Group at Paine’s Quarry, Herston in Dorset (Sarjeant *et al.*, 1998). It can be argued that the more typical iguanodontid tracks of the type reported by Beckles (1854), Dollo (1906) and subsequent workers originated from the Wealden Group, and are different from those from the Purbeck Group. Moreover, the Purbeck Group is considerably older than most of the Wealden

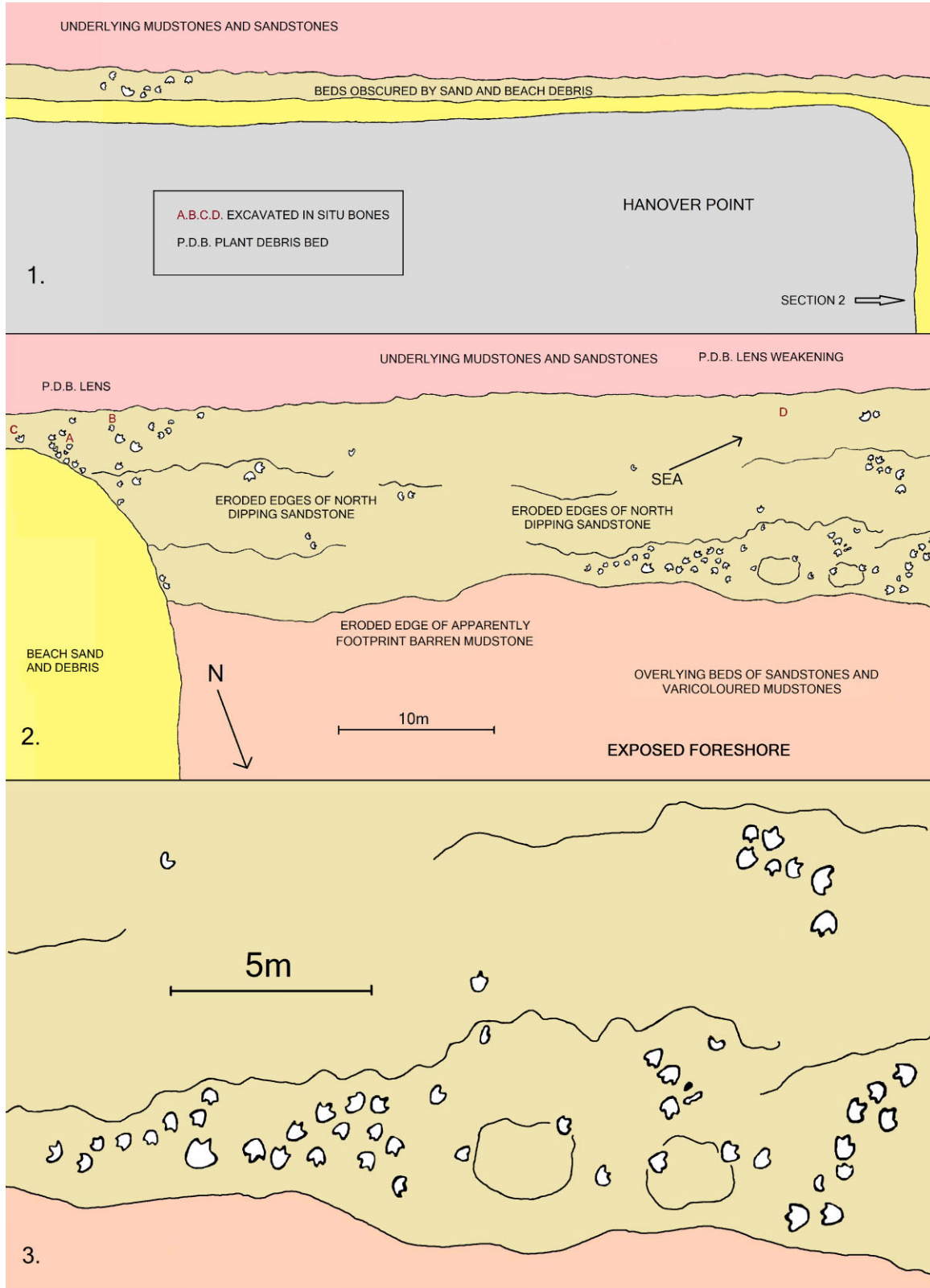


Figure 13. Map of Hanover Point in 1982 showing numerous infilled footprints on the exposed mudstones. Section 1 is continued in section 2. Section 3 shows an enlargement of the area of high footprint density in 2. Footprints are drawn to scale. Reproduced from a map constructed by Stephen Hutt (MIWG).

Group and is dated close to the Jurassic–Cretaceous (Tithonian–Berriasian) boundary, making its basal units about 15 Myr older than the track-bearing beds from the Isle of Wight's Wessex exposure.

Had Sarjeant *et al.* (1998) chosen a Wealden specimen as the basis for their new ichnotaxon (*Iguanodontipus*), they would have been faced with the possibility of recognizing that the typical *Iguanodon*-like Wealden tracks of the type described by Beckles (1854) (cf. Fig. 3 herein) with pronounced hypicies and quadripartite morphology, would have been better accommodated in an existing ichnogenus such as *Caririchnium* or *Amblydactylus*. The relatively small size of the Purbeck holotype of *Iguanodontipus* (FL = 24.1 cm) also brings it into the range of smaller Wealden ornithopods such as *Valdosaurus canaliculatus*. We conclude that *Iguanodontipus* from the Purbeck is not typically recognized in the Wealden Group and so is not the appropriate ichnogenus to accommodate most Wealden ornithopod track casts. There is also the danger that since the generalized label '*Iguanodon* tracks' has been discarded the label *Iguanodontipus* will be applied indiscriminately to all purported '*Iguanodon* tracks'. This is contrary to proper ichnotaxonomic procedure which requires that names be applied based on diagnostic morphological characteristics, not inferences about the track maker's identity.

The collection of casts from Hanover Point does show a few examples of tracks that resemble *Iguanodontipus* but these are in a minority compared with the abundant tracks we assign to *Caririchnium*. Moreover, because tracks conforming to the generally smaller *Iguanodontipus* morphotype are inherently simpler with less well defined or differentiated morphologies i.e. less prominent digits and less well defined digital and heel pads, it is possible that some of the more non-descript casts, with poorly differentiated outlines resemble this ichnogenus. However, the original *Iguanodontipus* diagnosis argues against the use of this name for most tracks from Hanover Point.

Caririchnium AND *Amblydactylus* IN THE WEALDEN

Many of the Hanover Point casts as well as others from the Wealden Group conform quite closely to the morphological diagnoses of two other ornithopod ichnogenera: *Caririchnium* and *Amblydactylus*.

Ichnogenus *Amblydactylus* was originally named for ornithopod prints from the Lower Cretaceous (Aptian–Albian) of Canada (Sternberg, 1932), and is the first named of all the ornithopod tracks discussed here. Sternberg (1932: 72) pointed out that *Amblydactylus* bore some resemblance to the footprints of 'the Wealden of Europe commonly attributed

to *Iguanodon*'. In a general sense we agree with this observation. Sternberg considered the digital pads to be more prominent in *Amblydactylus* and noted that the length:width ratio was much lower in *Amblydactylus*. This sounds as if he was comparing them with specimens such as the Beckles' 1854 drawing.

Non-holotype *Amblydactylus* trackways are associated, in some cases (*not* the types), with hoof like prints which indicate a quadrupedal gait. Unfortunately the original *Amblydactylus gethingi* holotype shows little detail of the pes digits, and has no associated manus. Moreover, the holotype of a second ichnospecies, *Amblydactylus kortmeyeri* (Currie & Sarjeant, 1979) also from Lower Cretaceous (Aptian–Albian) of Canada is also based on limited material without manus prints.

Caririchnium was originally described based on the trackway (named *C. magnificum*) of a quadruped from Brazil (Leonardi, 1984), and later two additional *Caririchnium* ichnospecies (*C. leonardii* and *C. lotus*) were named from Colorado and China respectively. Unlike *Amblydactylus* they were all based on trackways of quadrupeds.

Currie (1995) has suggested that *Caririchnium* may be a junior synonym of *Amblydactylus*, but this conclusion is debatable given the differences between the type material on which the two ichnogenera are based (Lockley *et al.*, 2014). In Currie's description the manus in the non-holotype examples of *Amblydactylus* is also different from the manus in *Caririchnium*. This is another reason to continue to regard the two ichnogenera as separate. Nevertheless, it is possible that these different forms could represent different ends of a morphological continuum. However, this conclusion is speculative and inherently acknowledges 'some' morphological differences.

We therefore suggest that many of the larger ornithopod prints at Hanover Point closely resemble ichnogenus *Caririchnium*, while recognizing that *Amblydactylus* is also an ichnogenus with notable morphological similarities. Determinants of variation in footprints in a large assemblage are likely to be many and various and may include sexual dimorphism; allometric growth during ontogeny; normal intraspecific variation; convergence of foot type in different species with similar lifestyles; differing degrees of digitigrade stance, together with more prosaic factors such as substrate variation, and taphonomic modification of the original tracks by weathering, trampling or other factors.

Lucas, (2007) and Lockley, Lucas & Matsukawa M. Harris, (2012) have noted that large ornithopod tracks dominate many Lower Cretaceous assemblages in Europe, North America and Asia. Ornithopods were also the dominant trackmakers at Hanover

Point and in this sense it is typical of others reported from the Lower Cretaceous around the world. However, the ichnoassemblages at this site and many others in the Wessex Sub-basin (Pond *et al.*, 2014), reveal a unique variety of ornithopod track morphologies and ichnogenera. These mark the area as being of international importance and deserving of further detailed research.

ACKNOWLEDGEMENTS

We thank Gareth Dyke for inviting our participation in the Jehol-Wealden International Conference and his encouragement during the process of manuscript preparations. We thank Dinosaur Isle (Museum of the Isle of Wight, Geology) for access to their collections. We also thank Trevor Price for sharing his knowledge on the Island's geology, Bill Webb for providing detailed photographs, The National Trust for their help and Steve Hutt for his many years of encouragement and for allowing us to use and reproduce his extensive map of Hanover Point tracks. We particularly acknowledge the detailed help and valuable assistance given by our anonymous reviewers.

REFERENCES

- Alexander RMcN. 1976.** Estimates of the speeds of dinosaurs. *Nature London* **261**: 129–130.
- Allen P. 1981.** Pursuit of Wealden models. *Journal of the Geological Society, London* **138**: 375–405.
- Allen P. 1998.** Purbeck-Wealden (Early Cretaceous) climates. *Proceedings of the Geologist's Association* **109**: 197–236.
- Allen P, Wimbledon WA. 1991.** Correlation of NW Purbeck-Wealden (non-marine Lower Cretaceous) as seen from the English type areas. *Cretaceous Research* **12**: 511–526.
- Beckles SH. 1851.** On supposed casts of footprints in the Wealden. *Quarterly Journal of the Geological Society* **7**: 117.
- Beckles SH. 1854.** On the ornithoidichnites of the Wealden. *Quarterly Journal of the Geological Society* **10**: 456–464. Plate XIX.
- Beckles SH. 1862.** On some natural casts of footprints from the Wealden of the Isle of Wight and Swanage. *Quarterly Journal of the Geological Society of London* **18**: 443–447.
- Castanera D, Pascual C, Razzolini NL, Vila B, Barco JL, Canudo JI. 2013.** Discriminating between medium-sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). *PLoS ONE* **8**: E81830.
- Currie PJ. 1983.** Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Palaeontologica Polonica* **28**: 63–73.
- Currie PJ. 1995.** Ornithopod trackways from the Lower Cretaceous of Canada. In: Sarjeant WAS, ed. *Vertebrate fossils and the evolution of scientific concepts*. Amsterdam: Gordon and Breach Publishers, 431–443.
- Currie PJ, Sarjeant WAS. 1979.** Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Palaeogeography Palaeoclimatology Palaeoecology* **28**: 103–115.
- Delair JB. 1983.** Cretaceous dinosaur footprints from the Isle of Wight: a brief history. *Proceedings of the Isle of Wight Natural History and Archaeological Society* **VII**: 600–615. Part VIII.
- Delair JB. 1989.** A history of dinosaur footprint discoveries in the British Wealden. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 19–25.
- Dollo L. 1906.** Les Allures des Iguanodons. *Bulletin of Science France and Belgium* **40**: 1–12.
- Francis JE. 1987.** The palaeoclimatic significance of growth rings in the Late Jurassic/Early Cretaceous fossil wood from southern England. In: Ward RGW, ed. *Applications of tree ring studies. Current research in dendrochronology and related subjects*. BAR International Series 333. Charlottesville, VA: University of Virginia, 21–36.
- Hopson PM, Wilkinson IP, Woods MA. 2010.** A stratigraphical framework for the Lower Cretaceous of England. Research report RR/08/03 British Geological Survey. Keyworth.
- Hughes NF, McDougall AD. 1990.** New Wealden Correlation in the Wessex Basin. *Proceedings of the Geologist's Association* **101**: 85–90.
- Insole A, Daley B, Gale A. 1998.** *The Isle of Wight. Geologists' Association guide, No. 60*. London: The Geologists' Association.
- Insole AN, Hutt SP. 1994.** The palaeoecology of the dinosaurs of the Wessex Formation (Wealden Group, Early Cretaceous) Isle of Wight, Southern England. *Zoological Journal of the Linnean Society* **112**: 197–215.
- Leonardi G. 1984.** Le impronte fossili de dinosauri. In: Bonaparte JF, Colbert EH, Currie PJ, eds. *Sulle orme die dinosauri*. Erizzo: Editrice Venicev, 165–186.
- Lockley MG. 1991.** *Tracking dinosaurs: a new look at an ancient world*. Cambridge: Cambridge University Press.
- Lockley MG. 2009.** New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. *Geological Quarterly* **53**: 415–432.
- Lockley MG, Hunt AP. 1994.** A review of vertebrate ichnofaunas of the Western Interior United States: evidence and implications. In: Caputo MV, Peterson JA, Franczyk KJ, eds. *Mesozoic systems of the Rocky Mountain Region, United States*. Denver, CO: RMS-SEPM (Rocky Mountain Section, Society for Sedimentary Geology), 95–108.
- Lockley MG, Lucas SG, Matsukawa M, Harris JD. 2012.** Cretaceous tetrapod footprint biostratigraphy, biochronology and ichnofacies. *Journal of Stratigraphy* **36**: 503–550.
- Lockley MG, Nadon GC, Currie PJ. 2004.** A diverse dinosaur-bird-footprint assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: implications for ichnotaxonomy. *Ichnos* **11**: 229–249.

- Lockley MG, Xing L, Lockwood JAF, Pond S. 2014.** A review of large Cretaceous ornithopod tracks with special reference to their ichnotaxonomy. *Biological Journal of the Linnean Society* **113**: 721–736.
- Lucas SG. 2007.** Tetrapod footprint biostratigraphy and biochronology. *Ichnos* **14**: 5–38.
- Lucas SG, Sullivan RM, Jasinski SE, Ford TL. 2011.** Hadrosaur footprints from the upper Cretaceous Fruitland Formation, San Juan Basin, New Mexico, and the ichnotaxonomy of large ornithopod footprints. In: Sullivan RM, Lucas SG, Spielmann JA, eds. *Fossil record 3*. Albuquerque: New Mexico Museum of Natural History and Science, Bulletin 53, 357–362.
- Mantell GA. 1846.** Notes on the Wealden Strata of the Isle of Wight, with an account of the bones of Iguanodons and other reptiles, discovered at Brook Point and Sandown Bay. *Quarterly Journal of the Geological Society of London* **2**: 91–96.
- Mantell GA. 1854.** *Geological excursions around the Isle of Wight, and along the adjacent coast of Dorsetshire: illustrative of the most interesting geological phenomena and organic remains*, 3rd edn. London: Bohn.
- Martill DM, Naish D. 2001a.** *Dinosaurs of the Isle of Wight*. London: The Palaeontological Association, 40.
- Martill DM, Naish D. 2001b.** *Dinosaurs of the Isle of Wight*. London: The Palaeontological Association, 310–318.
- Matsukawa M, Lockley MG, Hunt AP. 1999.** Three age groups of ornithopods inferred from footprints in the mid Cretaceous Dakota Group, eastern Colorado, North America. *Palaeogeography Palaeoclimatology Palaeogeography* **147**: 39–51.
- Norman DB. 1980.** On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). *Memoires de l'Institut Royal des Sciences Naturelles de Belgique* **178**: 7–103.
- Norman DB. 1986.** On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin Institut Royal des Sciences Naturelles de Belgique, Science de la Terre* **56**: 281–372.
- Norman DB. 2013.** On the taxonomy and diversity of Wealden Iguanodontian dinosaurs (Ornithischia: Ornithopoda). *Revue de Paleobiologie* **32**: 385–404.
- Osborne White HJ. 1921.** *A short account of the geology of the Isle of Wight*. London: HMSO.
- Paul GS. 2008.** A revised taxonomy of the iguanodont dinosaur genera and species. *Cretaceous Research* **29**: 192–216.
- Pond S, Lockley MG, Lockwood JAF, Breithaupt B, Matthews N. 2014.** Tracking dinosaurs on the Isle of Wight: a review of tracks, sites, and current research. *Biological Journal of the Linnean Society* **113**: 737–757.
- Radley J. 1997.** Geological report 1993–1994. *Proceedings of the Isle of Wight Natural History and Archaeological Society* **13**: 107–114.
- Radley JD. 1994.** Field meeting 24–5 April 1993: the Lower Cretaceous of the Isle of Wight. *Proceedings of the Geologist's Association* **105**: 145–152.
- Radley JD, Allen P. 2012.** The Wealden (non-marine Lower Cretaceous) of the Wessex Sub-basin, southern England. *Proceedings of the Geologist's Association* **123**: 319–373.
- Ride WDL, Sabrosky CW, Bernardi G, Melville RV. 1985.** *International code of zoological nomenclature*, 3rd edn. London: International Trust for Zoological Nomenclature and British Museum (Natural History), 338.
- Robinson SA, Hesselbo SP. 2004.** Fossil-wood carbon-isotope stratigraphy of the non-marine Wealden Group (Lower Cretaceous, southern England). *Journal of the Geological Society, London* **161**: 133–145.
- Romilio A, Salisbury SW. 2011.** A reassessment of large theropod tracks from the mid-Cretaceous (late Albia – Cenomanian) Winton formation of Lark Quarry, Central Western Queensland, Australia. A case of mistaken identity. *Cretaceous Research*. **32**: 135–142.
- Sarjeant WAS. 1989.** ‘Ten paleoichnological commandments’: a standardized procedure for the description of fossil vertebrate footprints. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. New York: Cambridge University Press, 369.
- Sarjeant WAS, Delair J, Lockley MG. 1998.** The Footprints of Iguanodon: a history and taxonomic study. *Ichnos* **6**: 183–202.
- Sarjeant WAS. 1974.** A history and bibliography of the study of fossil vertebrate footprints in the British Isles. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **16**: 265–378.
- Sternberg CM. 1932.** Dinosaur Tracks from the Peace River British Columbia, National Museum of Canada. *Ann. Report* **1930**: 59–85.
- Sweetman SC. 2011.** The Wealden of the Isle of Wight. In: Batten DJ, ed. *English Wealden fossils*. London: Palaeontological Association, 69–71.
- Sweetman SC, Insole AN. 2010.** The plant debris beds of the early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, southern England: their genesis and palaeontological significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* **292**: 409–424.
- Thulborn RA. 1989.** The gaits of dinosaurs. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. New York: Cambridge University Press, 39.
- Woodhams KE, Hines JS. 1989.** A history of dinosaur footprint discoveries in the British Wealden. In: Gillette DD, Lockley MG, eds. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press, 301–306.
- Wright VP, Taylor KG, Beck VH. 2000.** The paleohydrology of Lower Cretaceous seasonal wetlands, Isle of Wight, Southern England. *Journal of Sedimentology Research* **70**: 619–632.