Pterosaur tracks from the Purbeck Limestone Formation of Dorset, England

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WRIGHT, J. L., UNWIN, D. M., LOCKLEY, M. G. & RAINFORTH, E. 1997. Pterosaur tracks from the Purbeck Limestone Formation of Dorset, England. *Proceedings of the Geologists' Association*, **108**, 39–48. *Purbeckopus pentadactylus*, an unusual vertebrate track, is found in the Intermarine Member of the Purbeck Limestone Formation (Lower Cretaceous) of southern England. Only three slabs of biosparrudite containing the trace fossil have been found. These rocks were deposited on intertidal to supratidal flats.

Purbeckopus is a quadrupedal vertebrate trace comprising a tetradactyl elongate subtriangular plantigrade pes and an elongate tridactyl manus. It is very similar to the ichnogenus *Pteraichnus* (Stokes) and it seems likely that both tracks were made by the same type of animal.

Re-examination of *Purbeckopus* led us to the conclusion that it is probably pterosaurian in origin. This conclusion is based on two main features of the tracks. Firstly, the pes tracks show indications of elongate penultimate phalanges, a pterosaur characteristic. Secondly, the trackway has an unusual configuration wherein the impression of the manus lies well outside that of the pes. Only an animal with forelimbs longer than hind limbs would be likely to make such a track.

The pterosaur that produced *Purbeckopus* is calculated to have had a wingspan of approximately 6 m. The identification of *Purbeckopus* as a pterosaur track indicates that large pterosaurs must have existed somewhat earlier than previously thought.

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1. INTRODUCTION

The Purbeck Limestone Formation of Dorset has yielded one of the richest mid-Mesozoic terrestrial faunas in the world (Benton & Spencer, 1994; Howse and Milner, 1995). It also contains one of the most diverse dinosaur footprint assemblages in Britain, due largely to the number of quarries for building stone that formerly operated in this area. Dinosaur footprints have been known from the Purbeck for over a hundred years (Beckles, 1854; Mansell-Pleydell, 1888, 1896).

Purbeckopus pentadactylus (Delair, 1963) was discovered in 1960 in Dorset, southern England (Delair, 1960), and occurs in rocks of the Intermarine Member of the Purbeck Limestone Formation (Early Cretaceous).

The holotype was described by Delair (1963), and figured under the name *Purbeckopus pentadactylus*. The holotype had been acquired *c.* 1936 by W. J. Haysom and cemented into a path in his garden. Delair (1963) noted that at the time the specimen was procured by Mr Haysom, another slab bearing two pentadactyl impressions was in existence, although later lost (Delair, 1963). Delair thought it probable that both slabs came from the same place. He states that locals remembered that other pentadactyl footprints 'of identical character' were found at the same time in Chinchen's Quarry [SY 9919 7872; Fig. 1], but not preserved (Delair, 1963). There is some uncertainty about the exact source of these slabs (Ensom, 1995; Cat. No. 12); they may have come from underground workings in the same area [SY 9919 7872].

In 1983 Haysom presented his slab to the Dorset County Museum (DORCM G. 6664) which gave Ensom (1984, fig. 2.1–2.4) an opportunity to examine the specimen under more favourable lighting conditions. Ensom (1984) noted that the specimen had survived remarkably well, considering it had spent the last 50 years exposed to the elements, but he disputed Delair's conclusion that the prints had five toes – identifying only four.

In 1986, Ensom reported the rediscovery of the lost *Purbeckopus* slab (DORCM 9481), in the garden path of Mr A. Kirk of Cocknowle at Church Knowle. In addition, another slab containing one imprint identified as *Purbeckopus* (DORCM 9482) was found as the headstone of a dog's grave (Ensom, 1986, fig. 3). The lithology and faunal elements of these two slabs are almost identical, and it is likely that they all came from the same locality (Ensom, 1986). It is likely that the three impression-bearing slabs all come from the 'pink' bed (Fig. 2) (Delair, 1963; Clements, 1993) of the 'roach' stone (DB 125) and are probably all from Chinchen's Quarry. However, this bed number refers to the Durlston Bay type section and is only a suggested equivalent for this inland location.

In addition to the above specimens a poorly preserved ?tetradactyl print of similar size is held in Oxford University Museum (OUM.J 21 791). It has been referred to *Purbeckopus pentadactylus* and is preserved in the Pink

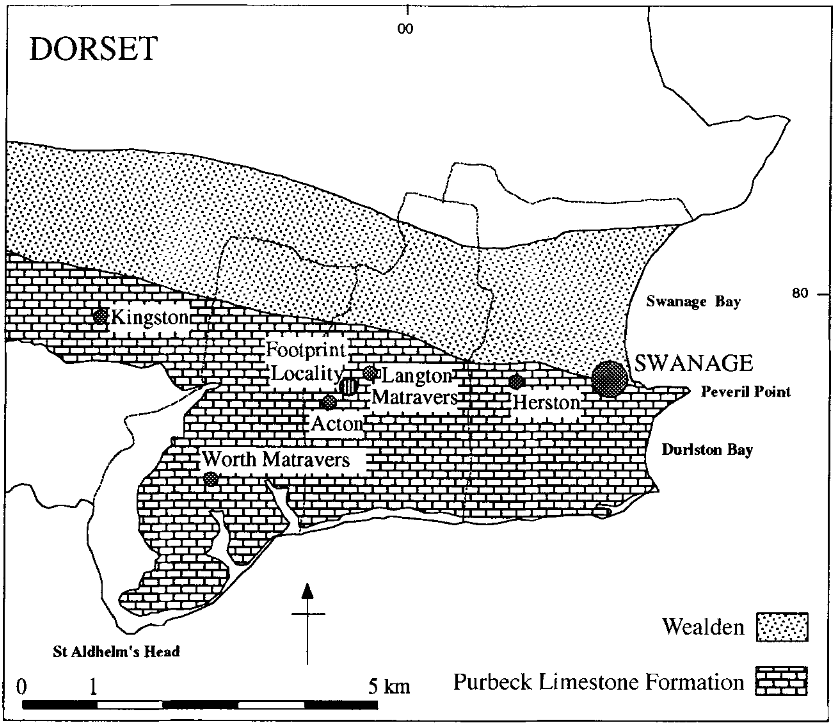


Fig. 1. Simplified geology of the Isle of Purbeck, Dorset showing the locality from which the pterosaur footprints came. After Ensom, (1995).

Bed of the Roach Stone (Cat. No. 96, Ensom, 1995). As it comes from the same horizon and is indistinct it adds little to this discussion.

Delair (1963) suggested that the footprints were made by an animal that walked like a crocodile or a lizard, which is at least compatible with the body fossils found in the Purbeck Limestone Formation (Benton & Spencer, 1994). Ensom (1984, 1986) did not attempt to attribute these imprints to any particular tetrapod. Most other workers who referred to these specimens attributed them either to crocodiles (MacFayden, 1970; Delair & Lander, 1973; Prince & Lockley, 1989), or an unknown track-maker (Walkden & Oppé, 1969; Haubold, 1971; Ensom, 1984), although Sarjeant (1974) thought that they could be the manus impressions of *Iguanodon*. Prince & Lockley (1989) noted that *Purbeckopus pentadactylus* resembles *Pteraichnus saltwashensis*.

2. SEDIMENTOLOGY, STRATIGRAPHY AND PALAEOENVIRONMENTS

The Purbeck Limestone Formation spans the Jurassic–Cretaceous boundary, but the position of the System boundary in the sequence remains very uncertain. The boundary was previously thought to be at the base of the 'Cinder Bed' (DB 120) (Casey, 1963), but the palaeontological evidence for this has been challenged by Wimbledon & Hunt (1983) who suggested that the Cinder Beds of the Wessex and Weald Basins are not the same age. Allen & Wimbledon (1991) have suggested that the Jurassic–Cretaceous boundary is much lower in the sequence and just above the Portland Limestone Formation. Charophyte evidence, however, supports the view that the Wessex and Weald Basins are roughly coeval and this method places the System boundary near the base of the Cypris Freestones Member (Feist, Lake & Wood, 1995). Either way, the *Purbeckopus* prints are earliest Cretaceous in age.

The early Purbeck climate was seasonal and semi-arid (West, 1975; Francis, 1983). Later it became sub-humid and warm temperate and the middle Purbeck strata, in which these impressions were found, were deposited in predominantly brackish water (Arkell, 1947; Allen & Keith, 1965). Strata of the Purbeck Limestone Formation were deposited in a large very shallow lagoon which partly dried out from time to time. The salinity in this lagoon was initially very high; later it fluctuated from marine to freshwater (Sellwood & Wilson, 1991).

A high proportion of the footprints found in the Purbeck Limestone Formation occur in the Intermarine Member (DB 112–145). These beds contain fossils such as *Myrene*, *Liostrea* and *Protocardia* which thrived in brackish water conditions; the absence of cephalopods, brachiopods and

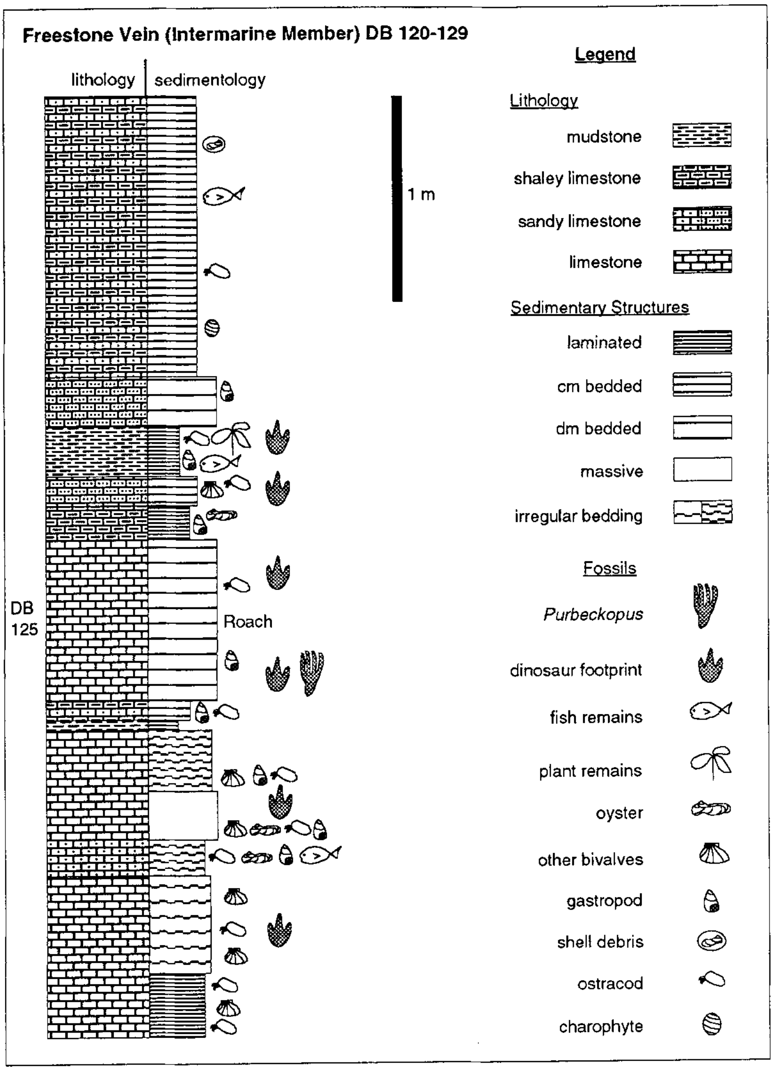


Fig. 2. Simplified stratigraphic section of the Intermarine Member at Durlston Bay indicating footprint horizons. After Clements (1993), El-Shahat & West (1983) and Ensom (1995).

corals in these beds also supports the conclusion that there was dilution of seawater by freshwater (Delair & Lander, 1973). Thus it is likely that all the footprints and trackways discovered in the Intermarine Member were made by animals moving across intertidal to supratidal flats. The presence, in this member, of turtle and crocodile remains, now often found in similar conditions, supports this general conclusion (Delair & Lander, 1973).

The *Purbeckopus* tracks all appear to come from the 'pink' bed (Fig. 2) of the 'roach' stone (DB 124 c) in the Intermarine Member (Middle Purbeck). The Intermarine Member comprises well-bedded, sometimes massive, generally light-coloured, biosparrudites, biomicrudites, clays and shales. This member yields brackish water faunas including fish and turtle remains.

The lithology of the slabs is very similar. They are all biomicrosparrudites, 40–60 mm thick, and crossed by calcite-filled joints (Ensom, 1986). *Neomiodon* is the predominant bivalve and there is scattered oyster debris (Ensom, 1986). The gastropod *Hydrobia* is often abundant with rarer *Viviparus* and *Ptychostylus* ?spp (Ensom, 1986). The ostracod *Cypridea fasciculata* and a possible charophyte stem are also present along with scattered fish remains (Ensom, 1986).

El-Shahat & West (1983) classified beds of this lithological type as 'uncompacted biosparrudites'. They

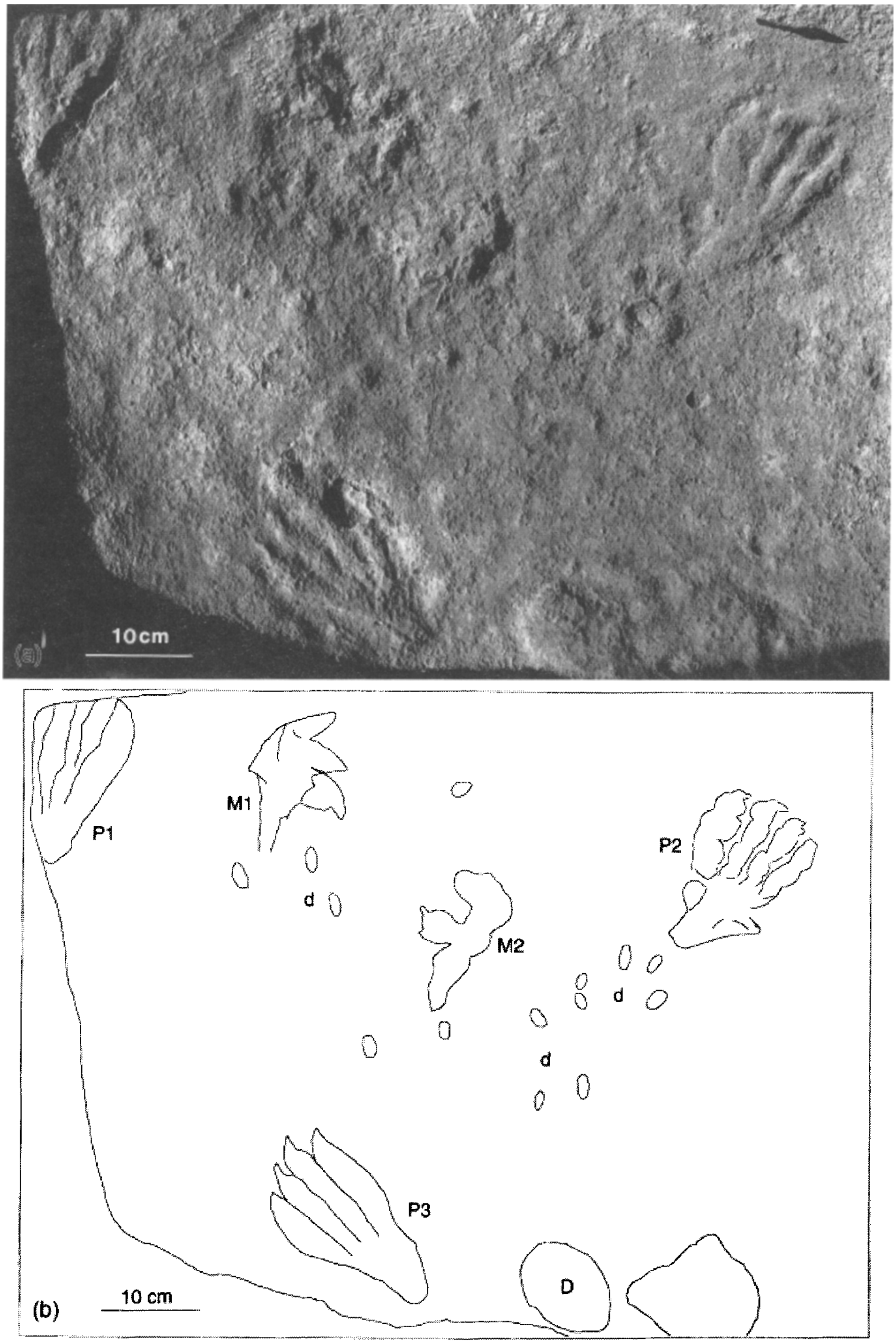


Fig. 3. (**a**). DORCM G6664. (**b**) Sketch of DORCM G6664, showing the three pes prints, P1 (right pes), P2 (left), P3 (left). Pes impression P1 is associated with manus impression M1 (right); pes impression P2 (left) is associated with manus impression M2. Also shown is a large oval depression, D, which may be a poorly preserved manus print, and possible beak marks, d.

concluded that rocks of this type were deposited in a supratidal environment and were subject to early lithification. During deposition such sediments were subject to a high degree of subaerial exposure and often preserve fossil vertebrate footprints.

3. DESCRIPTION

Only three slabs bearing this ichnogenus are known. The original (and largest) slab (DORCM G 6664) is sub-rectangular in shape and measures 1.0 × 0.8 m in size. It bears three pes prints, two of which are associated with manus prints, and a possible third manus print (Fig. 3a, b). The second slab (DORCM G 9481) is more elongate with major dimensions of 1.09 m and 0.44 m. It shows two, possibly three, pes prints, one of which is associated with a manus print (Fig. 3c). The third slab (DORCM G 9482) is triangular in shape, is 0.6 m at the base and 0.73 m high and bears a solitary pes print. No consecutive footprints are preserved on these three slabs, so neither the stride length nor the pace length can be determined. Neither can the gleno-acetabular length be determined nor the width of the trackway.

The prints are shallow, with a maximum depth of 5 mm. The length of the pes varies from 187 to 225 mm, and the width from 98 to 123 mm; the ratio of length to width is approximately 2:1. The pes is triangular in shape with a narrow heel and four digits of sub-equal length (Fig. 4a, b), although the two middle digits are slightly longer than the two outer digits. The impressions of the toes, especially the outer toe (digit IV), curve inwards towards the axis of the trackway, and the impressions of the claws curve in the same direction. The digits are quite wide with little interdigital space. Although the prints are shallow they still retain morphological details and the outlines of many of the phalangeal pads are visible.

In contrast to the pes prints, which are very consistent in shape, the manus prints are less well-preserved and this may account for their variable morphology (Fig. 5a–d). The manus prints are of similar length to the pes prints or slightly shorter. They are about half the width of the pes prints. They show three digits, one pointing antero-laterally, one pointing laterally and the third pointing postero-laterally or posteriorly. In one case (Fig. 5b, c) there is, in addition, a faint impression extending posteriorly which may be the imprint of the fourth digit.

The manus prints always lie outside and level with, or posterior to the pes prints (Fig. 3a, b; 5a). In one case (DORCM G 9481), the manus print lies immediately lateral to the pes print (Fig. 3c; 5a), but in most cases (DORCM G 6664) the manus print is 0.1 to 0.14 m outside the pes print (Fig. 3a, b). The preservation of the manus and pes impressions on these slabs indicates that both sorts of impressions were made at the same time. The manus and pes impressions are of a similar size and the consistent arrangement of manus–pes pairs indicates that these are real associations.

In addition to the manus and pes prints preserved on these three slabs there are also several small, round to oval shaped depressions on the track-bearing surfaces of the slabs. These are between 10 and 25 mm in diameter and occur in clusters.

Other features on the slabs consist of a few elongate, shallow depressions and a roughly circular indentation referred to by Ensom (1984) as a 'heel-like impression'. This is very similar in size and general shape to one of the manus prints (Fig. 5b, c) and it may be a very poorly preserved manus impression. The elongate shallow depressions are of the same order of size, or slightly smaller, as the manus prints and may also be very poorly preserved manus impressions.

At the top of DORCM G 9481 there are two faint impressions. One of these is a pes print and the other may be a pes or a manus print.

4. ICHNOTAXONOMY

Purbeckopus shows a remarkable similarity to *Pteraichnus* from North America and Europe (Stokes, 1957; Lockley, Logue, Moratella, Hunt, Schultz & Robinson, 1995; Mazin, Hantzpergue, Lafaurie & Vignaud, 1995). Although *Purbeckopus* is much larger than any of the specimens of

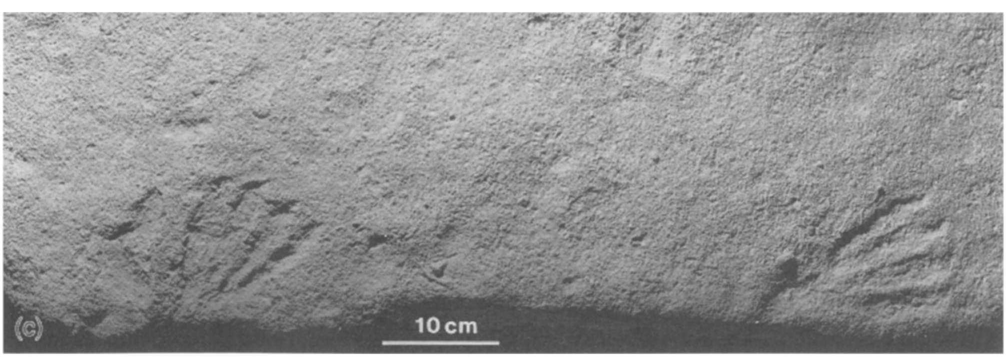


Fig. 3. (c) DORCM G9481 showing a manus–pes pair (left) and a solitary pes impression (right).

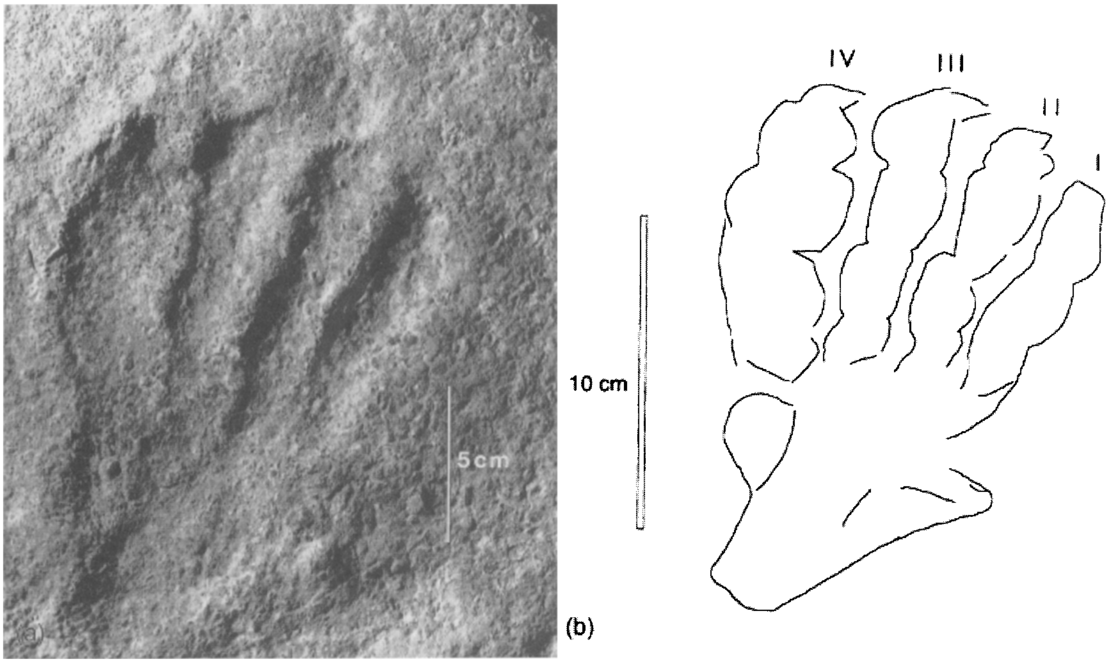
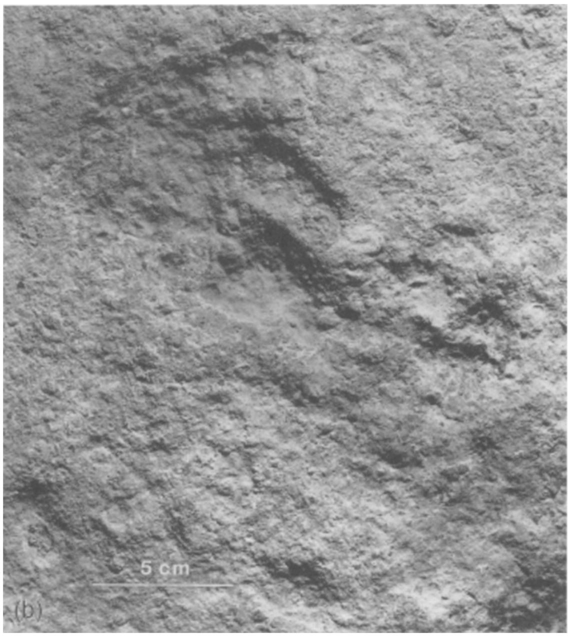


Fig. 4. (**a**) Close-up of pes (P2) from DORCM G6664, showing the phalangeal pads which indicate that an elongate penultimate phalanx was present. (**b**) Interpretative diagram of pes (P2).

Pteraichnus, the morphology of the pes tracks of *Purbeckopus* and *Pteraichnus* is very similar. The digits of *Purbeckopus* are much thicker than those of *Pteraichnus*, but both sets of tracks show the same elongate triangular shape of the pes, inward curve of the toes and four digits of sub-equal length. In addition, there appear to be elongate penultimate phalanges in digits two and three of some prints (Fig. 4a, b)

Fig. 5. (**a**) Manus–pes pair (left) from DORCM G9481.



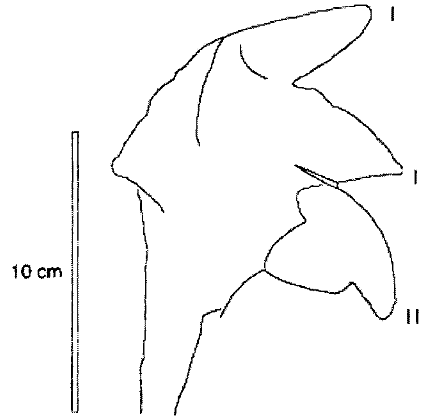


Fig. 5. (**b**) Manus (M1) from DORCM G6664. (**c**) Interpretative diagram of manus (M1) from DORCM G6664.

Purbeckopus is also very similar to tracks from France, recently described by Mazin *et al.* (1995) as 'morphologically similar to the ichnotaxon *Pteraichnus saltwashensis*'. A manus print of *Purbeckopus* (Fig. 5d) bears a strong resemblance to one of the French impressions

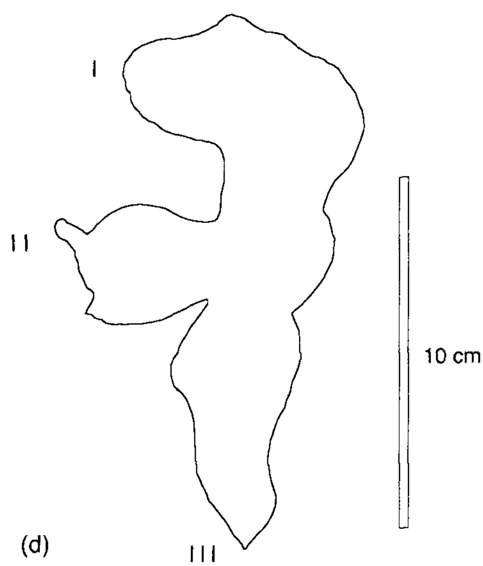


Fig. 5. (**d**) Sketch of manus (M2) from DORCM G 6664.

(Mazin *et al.*, 1995, fig. 3a). Another of the *Purbeckopus* manus prints (Fig. 5b, c) appears very similar to those figured by Stokes (1978, fig. 2). The manus of *Purbeckopus* has a much more variable morphology than the pes, as in *Pteraichnus* (Lockley *et al.*, 1995) , possibly reflecting the dynamics of print formation.

The differences in pes and manus morphology indicate that *Purbeckopus* is a separate ichnogenus from *Pteraichnus*. However, similarities between the two ichnogenera suggest that they were produced by a similar trackmaker.

Purbeckopus pentadactylus Delair, 1963

Holotype

DORCM G. 6664

Illustrations

Delair, 1963, figs 1–3 & 6; Ensom, 1984, plate 2.1–2.5; Ensom, 1986, plate 3a, b.

Emended diagnosis:

Tracks of a quadrupedal animal with elongate (approximately twice as long as wide), subtriangular, symmetrical, functionally tetradactyl, plantigrade pes impressions; elongate, asymmetrical tridactyl manus impressions may also be present. The digits of the pes are sub-equal in length and curved slightly inwards, the curvature being most pronounced in the outermost toe (digit IV). Digits II and III of the pes are slightly longer than the outer digits I and IV. Manus impressions, if present, lie outside the pes impressions.

5. THE TRACK-MAKER

Delair (1963, p. 94) tentatively suggested that *Purbeckopus* was produced by 'a reptile that walked rather like a crocodile or a lizard'. Delair only referred to two impressions on DORCM G 6664, both made by the pes. He also described the footprints as five-toed – an observation which has not withstood closer scrutiny (Ensom, 1984, 1986). In addition, the spatial relationships of the two observed footprints in fig. 1 of Delair (1963) are incorrect (Ensom, 1984). Stokes attributed *Pteraichnus* to a pterosaur based on 'the apparent reduction of digits in both manus and pes' (Stokes, 1957 p. 953).

If we compare the morphology of the pes prints of *Purbeckopus* to the skeletal structure of the pes of a pterosaur and of a crocodile (Fig. 6) it is easily seen that the shape of the impressions bears a much closer resemblance to the pterosaur foot. For instance, the sub-equal length of the pes digits corresponds more closely to the shape of the foot of a pterodactyloid pterosaur than to the foot of a crocodile, where digits I and IV are considerably shorter than digits II and III. In addition, on some of the pes prints (Fig. 4a, b) there are indications of an elongate penultimate phalanx. This is a diagnostic feature of pterosaurs (Unwin, 1987a; 1989). It is difficult to distinguish in the *Purbeckopus* prints, but can be seen very clearly in some

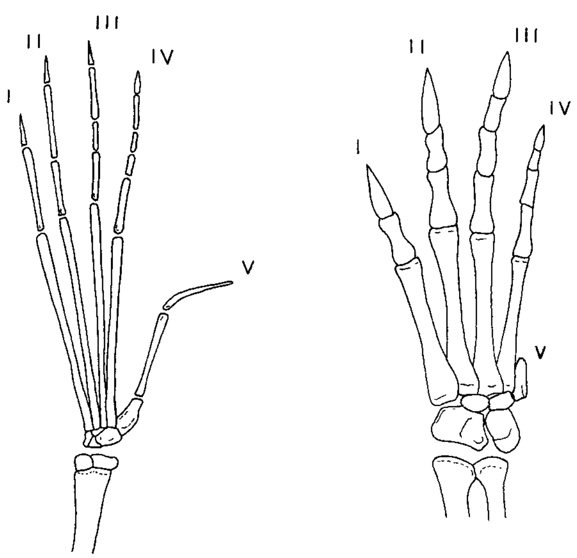


Fig. 6. Comparison of crocodile and pterosaur skeletal structure. Right pes of crocodile (right) and pterosaur (*Rhamphorynchus*) (left).

Pteraichnus-like tracks from the Jurassic of France (Mazin *et al.*, 1995).

The manus tracks of *Purbeckopus* are not as well preserved as the pes prints and the morphological detail that can be gleaned from them is very limited. Nonetheless, they do not resemble a crocodilian pes; they appear to have three or four digits rather than five, and compare well with the manus prints of other *Pteraichnus*-like tracks which are now considered pterosaurian (Lockley *et al.*, 1995; Mazin *et al.*, 1995, Unwin, 1997).

The relationship of the manus and pes tracks to each other is also very distinctive. The manus tracks of *Purbeckopus* (Fig. 3, 5) tend to lie well outside the pes tracks. This is an unusual configuration for most quadrupedal animals; in the trackways of most terrestrial tetrapods the forelimb prints lie in the same, or similar, line as the hind limb prints. The arrangement of the prints in *Purbeckopus* corresponds closely to the pterosaur trackway generated by a 'predictive method for vertebrate ichnite identification' wherein the manus prints lie well outside the pes prints (Unwin, 1989). Similarly, in the tracks from France (Mazin *et al.*, 1995), there is a section of trackway which shows manus prints three to four times further away from the trackway axis than the pes prints. Only an animal with forelimbs much longer than hind limbs could produce such a trackway, and pterosaurs are the only animals yet known from the Mesozoic which fit this description. The small rounded impressions on the track surface could be beak prod marks.

Pterosaur remains have been found in the Purbeck Limestone Formation (Howse & Milner, 1995), but represent smaller individuals than those which made the prints. On the basis of comparison with large, well preserved pterosaur remains from the Santana Formation of Brazil, we estimate that the pterosaur responsible for *Purbeckopus* had a wingspan of about 6 m. The oldest skeletal remains of pterosaurs of this size, from the Hastings Beds of England (Owen, 1874) are currently dated as Valanginian (Lower Cretaceous) in age. The Purbeck tracks are only slightly older (Berriasian) and show that very large pterosaurs had already appeared by the end of the Jurassic.

6. PREVIOUS WORK

Tracks attributed to pterosaurs were first described by Stokes in 1957 when he named a set of tracks from the Salt Wash Member of the Morrison Formation in the Carrizo Mountains, Arizona as *Pteraichnus saltwashensis*. Subsequent workers followed his example when they came across similar tracks (Logue, 1977; Stokes, 1978; Stokes & Madsen, 1979). More recently, Padian and Olsen (1984) disputed the pterosaurian origin of such tracks, arguing instead that they were more likely to have been made by a crocodile, and supporting their claim with trackway experiments performed with *Caiman*. This produced a rash of reassignments of tracks, from a pterosaurian, to a crocodilian origin (Conrad, Lockley & Prince, 1987; Prince & Lockley, 1989; Unwin, 1989; Lockley, 1991). More recently Lockley *et al.* (1995), Mazin *et al.* (1995) and Unwin (1997) have concluded, on the basis of new evidence that *Pteraichnus* and similar tracks are in fact pterosaurian in origin, as originally proposed.

7. DISCUSSION

With the identification of *Purbeckopus* and *Pteraichnus* as the tracks of pterosaurs a number of inferences may be made.

These tracks indicate that pterosaurs adopted a semi-erect, quadrupedal mode of locomotion on land, as many have argued (Pennycuick, 1986; Unwin, 1987a, 1987b, 1989; Wellnhofer, 1988, 1991; Wellnhofer & Vahldiek 1986), though this may not have been their only means of terrestrial locomotion.

The shape of the pes and manus impressions is quite consistent, but the width of the trackways varies a great deal. The manus impressions may lie in the same line as the pes impressions, or may be up to four times further away from the trackway axis. This implies that when moving about quadrupedally on land the forelimbs of pterosaurs were folded to varying degrees.

In addition, pterosaurs obviously could, and regularly did, rotate the forelimb to such a degree that the long axis of the manus print was parallel to the movement direction.

The presence of possible beak marks may indicate that the maker of *Purbeckopus* was feeding, and similar marks have been found in association with other pterosaur tracks (Parker & Balsey, 1989; Lockley *et al.*, 1995).

The degree of curvature of the toes of the pes of *Purbeckopus* may be due to the yielding nature of the trackway surface. Stokes (1957) suggested, based on the evidence of the type trackway of *Pteraichnus*, that the tracks which seemed to have been made on a softer surface showed a more pronounced curvature. The *Purbeckopus* tracks were made in an unconsolidated comminuted shell sand on the shore of a large shallow lagoon; the shells may have compacted rather than been displaced.

8. CONCLUSIONS

The *Purbeckopus* tracks are preserved in a biomicrosparrudite deposited in intertidal to supratidal flats. Such an area would provide abundant food for pterosaurs, both in the seas and in the organic-rich estuarine muds.

Purbeckopus pentadactylus is a pterosaur track. No other group of animals (apart from bats) could make tracks where the fore feet are consistently a considerable distance outside the tracks made by the hind feet. In addition, pterosaurs are the only taxon in which the pes contains an elongate penultimate phalanx as displayed in these tracks. The evidence of these tracks suggests that the preferred mode of terrestrial locomotion for pterosaurs was a semi-erect quadrupedal gait.

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