A MULTIVARIATE TAXONOMIC ANALYSIS OF THE LATE CARBONIFEROUS VERTEBRATE ICHNOFAUNA OF ALVELEY, SOUTHERN SHROPSHIRE, ENGLAND

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ABSTRACT. A diverse Late Carboniferous (Westphalian D; Moscovian) vertebrate ichnofaunal assemblage from the Alveley Member (Salop Formation, Warwickshire Group) of Alveley, southern Shropshire, UK, is a significant example of an early, transitional tetrapod community. Positive tetrapod footprint casts (convex hyporeliefs) within fine- and medium-grained sandstone red-beds were formed subaqueously in an alluvial floodplain setting. A statistical analysis of this material, the first using multivariate techniques on Late Palaeozoic trackways, has been undertaken to determine the ichnospecific diversity and morphological variation within the ichno-assemblage. Nine ichnotaxa have been identified, following a study of more than 200 trackways. These include the amniote ichnogenera *Dimetropus* Romer and Price, 1940, *Ichniotherium* Pohlig, 1885 and *Hyloidichnus* Gilmore, 1927, but there is a dominance of trackways of the ichnogenus *Limnopus* Marsh, 1894, which represent stem-lissamphibian 'temnospondyls'. Following statistical analysis, the ichnogenera *Limnopus* and *Batrachichnus* are subsumed as ichnosubgenera under the senior available name *Limnopus*. The Alveley ichnofaunal assemblage provides significant range extensions for a number of amniote and stem-lissamphibian trackmakers from the latest Carboniferous or Permian down into the mid-Late Carboniferous. It also marks a key transitional stage in the evolution of tetrapod communities, from the 'amphibian' grade assemblages of the Carboniferous to the more terrestrial, amniote-dominated communities of the Early Permian.

KEY WORDS: Amniota, Carboniferous, stem-Lissamphibia, taxonomy, tetrapod, trackway.

VERTEBRATE trackways provide a considerable amount of data that are not supplied by skeletal material. Ichnofossils are the only animal remains that are undoubtedly *in situ* and give evidence of behaviour during life, such as living environment or precise mode of locomotion. Together with data from vertebrate skeletal assemblages, they have the potential greatly to enhance our understanding of early vertebrate life.

The tetrapod ichnofauna of Alveley, southern Shropshire, is the only vertebrate trackway assemblage of Late Carboniferous age in Europe. The material is representative of the Late Carboniferous to Early Permian transition within vertebrate communities, from the dominance of amphibians to that of amniotes, as it includes trackways made by a variety of primitive tetrapods of amphibian and reptilian grades. The numerous specimens of exceptionally well-preserved vertebrate trackways can be readily compared with Early Permian vertebrate ichno-assemblages from Germany, France and northern Italy.

Preliminary studies of the Alveley ichnofauna were undertaken by Haubold and Sarjeant (1973, 1974), who recognised six ichnospecies within five ichnogenera (*Ichniotherium willsi*, *Dimetropus salopensis*, *Limnopus rawi*, *Batrachichnus alveleyensis*, *Anthichnium major* and *A. salamandroides*), based upon a selection of the better preserved material. However, due to advances in the understanding of vertebrate ichnology over the last 30 years, the ichnofauna is in need of revision. This study utilises all the available material, amounting to over 2400 individual footprints within 203 trackways, to build on Haubold and Sarjeant's initial work and provide a comprehensive review of the ichno-assemblage.

One of the greatest problems in utilising vertebrate trackway data stems from unsatisfactory ichnotaxonomy. Due to the range of preservational variants arising from differences, for example, in slope angle, method of preservation and trackmaker behaviour, traditional taxonomic methods have frequently produced unstable ichnotaxonomies, with a tendency towards oversplitting. The phenetic

method reported here provides a multivariate, statistical, non-biased approach to vertebrate ichnotaxon identification, which is repeatable and as stable and objective as possible. Ichnotaxon diagnoses can hence be revised and tightened, and the placement of undescribed trackways into certain groups is controlled. This stabilization of vertebrate ichnotaxonomy, together with the resulting assessment of ichnotaxonomic diversity, enables a clearer palaeoecological interpretation, and more accurate comparisons with other vertebrate ichnofaunas and known skeletal assemblages.

THE ALVELEY ICHNO-ASSEMBLAGE

The extensive vertebrate and invertebrate ichnofauna of Butts Quarry, Alveley, southern Shropshire (SO 7556 8298; Text-fig. 1A), was discovered by Dr F. Raw in 1914. A preliminary collection was made upon their discovery, although most of the material was collected during the Easter and September of 1919 (Lapworth Museum Archive, Miscellaneous Collection 60). The material has since been housed in the Lapworth Museum at the University of Birmingham. The specimens were found within the Alveley Member of the Salop Formation (Warwickshire Group; Text-fig. 1B), and consist predominantly of tetrapod trackways and isolated footprints, although trackways of myriapods, the characteristic terrestrial invertebrate fauna of this period, occur on the bedding plane surfaces of some specimens. These have been identified as *Diplichnites gouldi* Gevers, thought to represent the biotaxon *Arthropleura* Jordan, and are indicative of alluvial and shallow lacustrine palaeoenvironments (Briggs *et al*. 1979; Trewin and McNamara 1995). Specimens showing vertebrate resting traces are also present in the assemblage, as well as sedimentary structures useful as environmental indicators (rippled beds, sun cracks and rain-pitted surfaces). Typical Late Carboniferous plant fossils (Lycopsida and Sphenopsida) are found locally in the Alveley Member, for example, at Hall Close Quarry (SO 7605 8375).

Palaeoenvironments and sedimentology

The Halesowen and Salop formations of the Warwickshire Group were deposited on the southern margin of the Pennine Basin, which occupied a region near the palaeoequator during the Late Carboniferous and Early Permian (Cope *et al*. 1992; Johnson *et al*. 1997; Woodcock and Strachan 2000). The Halesowen Formation represents an ephemeral stage of coal-forming swamp conditions, with caliche palaeosols indicative of an increasingly arid environment (Johnson *et al*. 1997), whilst the Salop Formation is principally composed of oxidised, well-drained, alluvial floodplain red-beds, typical of the Upper Westphalian D and lowest Permian strata across Europe (Anderton *et al*. 1979). Depositional environments represented by Upper Westphalian sediments are predominantly fluvio-deltaic, and the sediments of the Warwickshire Group in the British Midlands are primarily alluvial red-beds with a lack of well-defined marker beds or biostratigraphical elements (Powell *et al*. 2000).

Stratigraphy and sedimentology of the Alveley Member. The unit, formerly part of the Keele Formation (Powell *et al*. 2000), is the lowest stratigraphical division of the Salop Formation of the Warwickshire Group (formerly the 'Barren Coal Measures') in the Staffordshire and Shropshire area (Text-fig. 1B; Powell *et al*. 2000). The type area contains 152–247 m of Westphalian D (Moscovian) sediments (Besly and Cleal 1997; Johnson *et al*. 1997; Powell *et al*. 2000), described by Whitehead and Pocock (1947) as those of an alluvial floodplain. Interbedded red mudstones and red to red-brown, fine- and medium-grained sublitharenitic sandstones, interspersed with thin, white and black *Spirorbis* limestone horizons form the bulk of the succession, in association with clay bands comprising illite and kaolinite (Besly and Cleal 1997). The presence of minor caliche palaeosols is indicative of the proposed semi-arid climatic conditions of the Late Carboniferous (Johnson *et al*. 1997). Two facies associations were recognized within the Alveley Member by Glover and Powell (1996), and interpreted to be the result of fluctuating water levels across the alluvial plain. The first represents a floodplain environment dominated by the persistence of a high water table. Deposition occurred predominantly within localized shallow ponds and lakes, in the form of channel and sheet-flood sandstones. These are interspersed with weakly developed ferruginous and gley palaeosols, and clay horizons with rain-pits, together signifying periods of emergence and drying. The
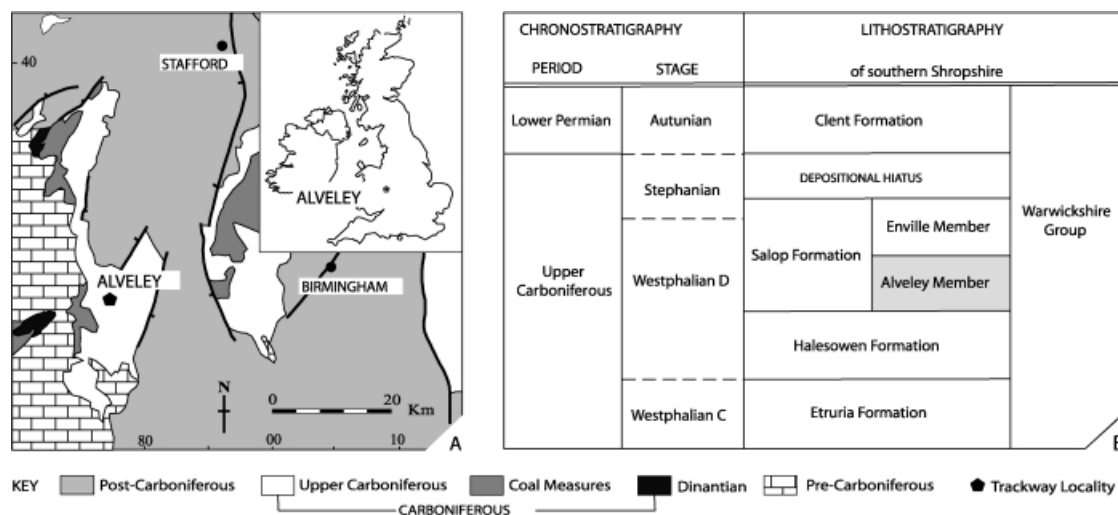
TEXT-FIG. 1. A, Geological map of the South Staffordshire Coalfield, UK, showing the geographical position of the Alveley trackway locality (after Glover and Powell 1996). B, stratigraphical classification of the Warwickshire Group in southern Shropshire (after Powell *et al*. 2000).

second facies association is indicative of slow sedimentation and low water levels, marked by well-developed caliche horizons. Thin sheet-flood sandstones, formed by occasional flash floods, are traceable over several kilometres. Minor, thick sandstone bodies represent high-sinuosity fluvial-system deposits.

At Butts Quarry, where the Alveley ichno-assemblage was collected, the succession at outcrop measures only 8 m and is at present poorly exposed, although Raw did log the fresh section in 1919 (Lapworth Museum Archive, Miscellaneous Collection 60). Sediments here represent the first facies association of Glover and Powell (1996). Soft, unconsolidated red mudstone and clay horizons alternate with fine- to medium-grained, red and grey sheet and channel sandstones. The sharp, planar bases of these sandstones are marked with positive casts of rain pits, sun cracks and fluted tool marks, indicative of a periodic emergence of the underlying mudstone and clay horizons. The ichnological material also occurs as positive casts upon the bases of these sandstone beds, although the 100-mm interval of alternating sandstone beds and clay horizons within which the material was found (Raw, unpublished manuscript, Lapworth Museum Archive, Miscellaneous Collection 60) is no longer well exposed.

NUMERICAL TAXONOMY AND STATISTICAL ANALYSIS OF *LIMNOPUS*

Ninety-five per cent of the Alveley ichno-assemblage comprises trackways hitherto assigned to the ichnogenera *Limnopus* Marsh, 1894, *Batrachichnus* Woodworth, 1900 and *Anthichnium* Nopsca, 1923, of which 66 per cent are exceptionally well-preserved, surface-level traces. These trackways afford an opportunity to examine ichnospecific diversity and morphological variation within this assemblage using multivariate techniques.

Numerical taxonomy

Numerical taxonomy in this context can be defined as the classification of taxonomic units into taxa based upon the numerical analysis of a number of pre-defined characters and character states. The concepts upon which this definition is based trace back to the French botanist Michel Adanson (1727–1806) and are hence termed 'neo-Adansonian', as reviewed by Sneath and Sokal (1973, p. 5). These principles are: (1) the greater the content of information in the taxa of a classification and the more characters on which it is

based, the better a given classification will be; (2) *a priori*, every character is of equal weight in creating natural taxa; (3) overall similarity between any two entities is a function of their individual similarities in each of the many characters in which they are being compared; (4) distinct taxa can be recognized because correlations of characters differ in the groups of organisms under study; (5) taxonomy is viewed and practiced as an empirical science; (6) classifications are based on phenetic similarity.

Numerical methods were applied to the large number of exceptionally well-preserved trackways noted above in order to determine ichnotaxonomic divisions present in the Alveley ichno-assemblage. The principal method employed utilizes data from an undescribed or problematic vertebrate ichno-assemblage and evaluates the phenetic (morphological) similarity of the trackways using multivariate cluster analysis. The resulting phenogram splits the trackway 'data cases' (each case associated with a single manus–pes set), or the 'trackway mean' values (the mean value of the sum of the data cases of a single trackway) into morphologically distinguishable groups, which may then be assigned to ichnospecies or ichnogenus level by comparison with type material. This technique provides an objective and repeatable basis for the identification and classification of further trackways into established ichnotaxa, thereby stabilizing the ichnotaxonomy whilst giving an accurate, functional picture of ichnospecies diversity.

Whilst ternary analyses and bivariate plots *sensu* Weems (1990) show a degree of clustering within the dataset used in this study, the level of cluster overlapping was such that bivariate and ternary plots alone could not be accurately used for reliable ichnotaxon classification. However, as increasing numbers of variables (characters) were considered, clusters became more discrete. Multivariate clustering enables a potentially infinite number of variables to be included in the analysis and thereby provides a more accurate basis for ichnotaxon differentiation and classification. The successful use of multivariate cluster analysis in distinguishing vertebrate ichnotaxa demonstrates that their description should be based upon as many characters as possible, with ichnogenera defined by a unique set of diagnostic characters, backed up with a comprehensive description of all other variables.

In order for the analysis to be successful, the trackway material should be studied in detail before analyses are attempted. It is important that only established type and exceptionally well-preserved specimens from surface-level trackways are used for the stabilisation of vertebrate ichnotaxonomy. In order for ichnodiversity to reflect biodiversity rather than sediment mechanics, those trackway characters known to represent merely extra-morphological features, that are not directly preserved due to the anatomy of the trackmaker, should be excluded from the initial multivariate analysis (see Appendix). Once the taxonomy of the groups under study has been resolved, less well-preserved trackways can be identified with the use of the revised ichnotaxon diagnoses and with direct comparison to type material.

It should be noted that these phenetic methodologies do not aim to produce an outline of evolutionary relationships between taxa, for which phylogenetic analysis is the appropriate tool, but do provide a method for grouping and distinguishing taxa dependent upon their morphological characteristics.

Previous use of numerical methods

Numerical methods have been used previously to aid discrimination between tridactyl dinosaur footprints and trackways (Demathieu 1990; Weems 1990). Approaches involved the use of numerical parameters and mean character value ratios to explore the morphological variability within trackways, with the aim of estimating biological species diversity (Weems 1990) and to aid identification of poorly preserved footprint specimens by comparison with a well-preserved ichno-assemblage (Demathieu 1990). Moratalla *et al.* (1988) used bivariate plots, Factor Analysis and Discriminate Analysis, to distinguish successfully ornithopod and theropod trackways, whilst Farlow and Lockley (1993) employed osteometric ratios from a range of bipedal dinosaurs in comparison with equivalent footprint measurements, in order to match tracks to trackmakers. A number of authors (e.g. Haubold 1970, 1973; Conti *et al.* 1977; Fichter 1994, 1998) have used direct numerical values taken from the trackway specimens, in conjunction with calculated figures of glenoacetabular length, forelimb length and hindlimb length to aid identification of Early Permian ichnological material. Conti *et al.* (1977) utilized data from single ichnotaxa to yield bivariate biometric analyses, exploring the variation within these ichnotaxa. However, analyses at a level higher than bivariate, examining the relationships between separate ichnotaxa, have never before been undertaken on vertebrate trackways.

Analysis of the Alveley ichno-assemblage

Firstly, all material (68 well-preserved surface-level *Limnopus*, *Batrachichnus* and *Anthichnium* track-ways) was sorted *a priori* into ichnotaxa, based upon major morphological variations. The material, including other, less well-preserved specimens, was also sketched and described in order to increase familiarisation with the range of variance amongst specimens. An exhaustive list of both quantitative and qualitative characters was compiled, with which to describe numerically and analyse each well-preserved trackway (consisting of a number of trackway data cases) for taxonomic classification (see Appendix). The chosen variables aimed to reflect all possible features of each individual footprint, and of each trackway as a whole. Characters that describe both morphological and extra-morphological features were recorded, in order to determine variation within ichnotaxa, but only those characters directly affected by trackmaker morphology were used for multivariate cluster analysis. Quantitative measurements were made to the nearest millimetre or degree, with an error of no greater than ± 1 mm/degree, whilst qualitative measurements used binary notations, e.g. tail trace absent (0), present (1) (see Appendix). Any appropriate alterations to the original *a priori* sorting were subsequently based upon all available data, following cluster analysis.

Among the measured specimens, only those that recorded a value for every character were suitable for use in the multivariate analyses. Those specimens that could not be included in the analyses were identified afterwards by the comparison of their recorded characters with those describing the pre-identified ichnotaxa. Within the trackway dataset, some measurements were unobtainable, for example, due to obscured or poorly preserved footprints or absent prints (beyond the margin of the measured slab). This reduced the number of trackway data cases for which the data set is complete and, in order to utilize as much of the trackway data as possible, the initial cluster analyses were run using the mean values, or 'trackway mean', for each quantitative variable within each trackway. This use of means was additionally useful as the number of cases was particularly high (up to 1000 data cases), and a reduction provided a more manageable phenogram. In addition, trackways that were not made at original surface level (i.e. not 'true' ichnotaxa, but undertracks and overtracks) were omitted from the initial analyses. This ensured that only surface-level trackways were used in the stabilisation of the ichnotaxonomy of the assemblage, and consequently increased the resolution of this analysis by eliminating taxa that cannot be resolved as 'true' ichnotaxa. Separate analyses were run to help resolve the ichnotaxonomy of these specimens once the surface-level ichnotaxonomy had been resolved. Measurements from a single trackway of *Ichniotherium willsi* were used to provide an 'outgroup' ichnotaxon.

The data were subjected to phenetic multivariate cluster analysis within MVSP (Multi Variate Statistical Package, Kovach 1999), using a number of different linkage methods and distance algorithms. These repeatedly demonstrate that the clusters found within each phenogram remain consistent throughout various combinations, indicating a high level of stability within the clustering. In the descriptions and figures below, which illustrate the results useful in resolving the ichnotaxonomy of the 'true', surface-level trackways, the distance algorithm used is the Manhattan, or city-block, metric. The Sequential Agglomerative Hierarchical Nonoverlapping (SAHN) clustering linkage method used is the Weighted Pair-Group Method using Arithmetic averages, or WPGMA (Sneath and Sokal 1973; Abbott *et al.* 1985; Kovach 1999). Sixty-eight of the best-preserved surface-level specimens were analysed, and, using 54 characters, a phenetic dendrogram (phenogram) was produced (Text-fig. 2), in conjunction with a distance matrix and a clustering report. For comprehensive reviews of the use of various multivariate clustering methods the reader is referred to Sneath and Sokal (1973), Dunn and Everitt (1982) and Abbott *et al.* (1985).

Each of the clusters was defined in conjunction with continual comparisons with the trackway material and constant referral back to the original data set, and the trackways were named by reference to the type specimens as described in the literature (Geinitz 1861; Butts 1891; Woodworth 1900; Nopsca 1923; Gilmore 1927; Baird 1952; Haubold 1970, 1971*a*, 1973; Haubold *et al.* 1996; Schult 1996), and by comparison with the type specimens of *Batrachichnus plainvillensis* and *Limnopus vagus*. Where trackway dimensions of the type specimens had been given by these authors (e.g. Woodworth 1900; Haubold 1970, 1973), the measurements were included in a separate cluster analysis, run using only these selected characters.
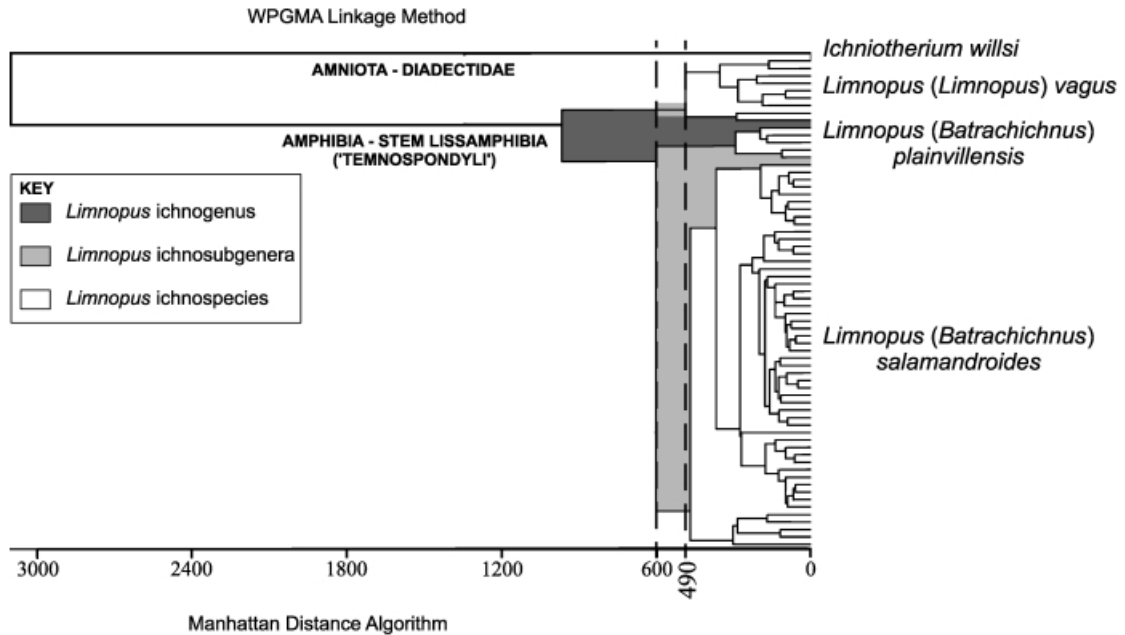
TEXT-FIG. 2. Phenogram illustrating results of a multivariate cluster analysis carried out upon 68 well-preserved *Limnopus* trackways, with a single specimen of *Ichniotherium willsi* as an 'outgroup' ichnotaxon.

Further cluster analyses were then run in order to explore the trends within the data, and to aid identification of the remaining specimens. Characters reflecting size were omitted from the analysis, and this demonstrated that although ichnotaxa are indeed based heavily upon size, some ichnotaxa are distinguishable based upon shape differences, and this was confirmed by Principal Components Analysis. In order to identify the trackways with indistinctly preserved digits, characters related to the digits were also omitted; this enabled the identification of a further 29 specimens. Multivariate analyses additionally gave an indication of the ichnotaxa to which undertrack specimens could be attributed, lending support to *a priori* identifications. As a consequence of these multivariate cluster analyses, the diagnoses of the amphibian ichnotaxa found in the Alveley ichno-assemblage have been revised, and partial trackways not included in the phenetic cluster analysis have been identified accordingly.

Results

1. Following the multivariate cluster analysis of 68 well-preserved surface-level trackways previously attributed to the ichnogenera *Limnopus*, *Batrachichnus* and *Anthichnium*, three ichnospecies are recognised that fall into two distinct size groupings (Text-fig. 3). In the interests of taxonomic resolution and stability, and because they have slightly different stratigraphic ranges, the well-established ichnogeneric names *Limnopus* and *Batrachichnus* are retained. The ichnotaxon *Anthichnium* is interpreted as a junior synonym of the latter ichnogenus (see below). However, as no clear, morphologically based, diagnostic boundary can be drawn between *Limnopus* and *Batrachichnus*, and they differ only in terms of size, it is proposed that the two ichnogenera should be reduced to ichnosubgeneric rank under the senior available name *Limnopus*. In consequence, the 'amphibian' ichnospecies within the Alveley assemblage have been identified as *Limnopus* (*Limnopus*) *vagus* (20 specimens), *L.* (*Batrachichnus*) *salamandroides* (157 specimens) and *L.* (*B.*) *plainvillensis* (26 specimens). The ichnospecies *Limnopus rawi*, *Batrachichnus alveleyensis* and *Anthichnium major*, erected by Haubold and Sarjeant (1973, 1974), are considered to be junior synonyms of the ichnospecies *Limnopus* (*L.*) *vagus*, *Limnopus* (*B.*) *plainvillensis* and *Limnopus* (*B.*) *salamandroides* respectively. In total, 97 *Limnopus* trackways have been identified to ichnospecies level.
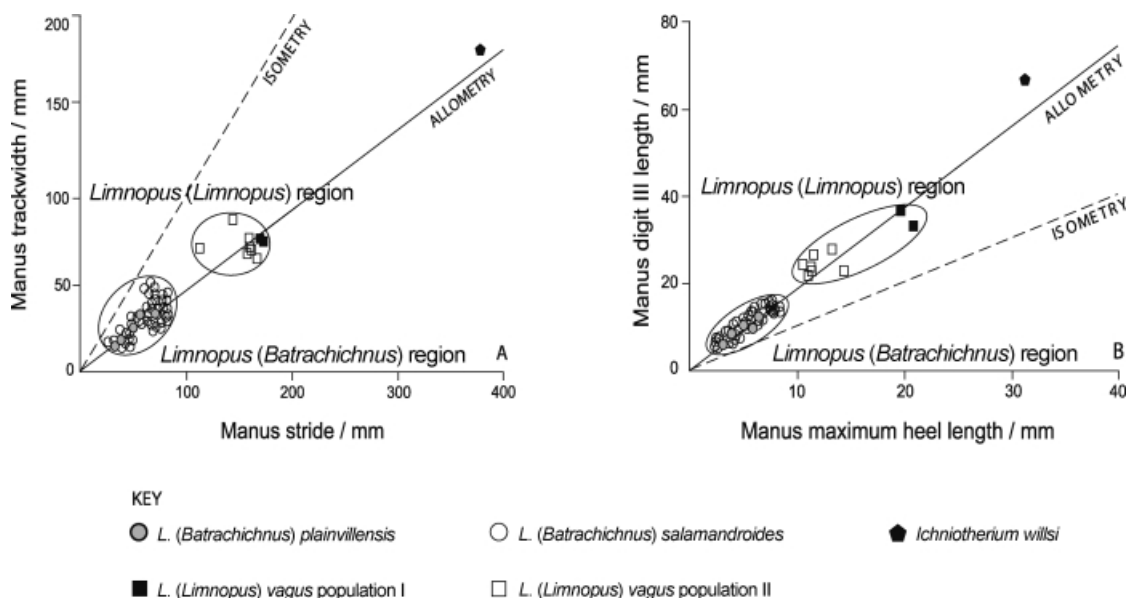
TEXT-FIG. 3. Bivariate scatter plots illustrating size divergence between the ichnospecies of *Limnopus*, in terms of trackway pattern (A) and foot morphology (B). The trend of size increase indicates allometrical growth within the associated biospecies. A, scatter plot of manus trackwidth onto manus stride. B, scatter plot of manus digit III length onto manus maximum heel length.

2. The representatives of *Limnopus* (*Batrachichnus*) within the assemblage, *L.* (*B.*) *plainvillensis* and *L.* (*B.*) *salamandroides*, are consistently discrete ichnospecies, differentiated by trackway pattern and the proportion of digit length to sole length. Whilst trackway pattern can vary according to trackmaker behaviour (Peabody 1959), digit lengths are anatomically controlled features, and it is therefore hypothesized that these two ichnospecies represent two distinct biotaxa.

3. Specimens that clustered together under the ichnospecies *L.* (*B.*) *salamandroides* could be further split into a number of separate groups, according to size. However, analysis of manus footlength (Text-fig. 4) indicate that these groupings have no taxonomic significance, as they demonstrate a continuous size range amongst the *L.* (*B.*) *salamandroides* specimens and not separate groupings that may reflect distinct family generations or different biotaxa. Indeed, it is suggested that *L.* (*B.*) *salamandroides*, in exhibiting this continuous size range, represents a single discrete population that comprises members of a single biotaxon. Nevertheless, a wide range of preservational styles is exhibited within this ichnospecies (Text-fig. 5), and this is attributed to differences in substrate consistency at the time of imprinting, or differences in trackmaker behaviour. In contrast, the range of preservational style present in *L.* (*B.*) *plainvillensis* is attributable only to variations in substrate consistency, not trackmaker size (Text-fig. 6).

4. *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*) are morphologically very similar, but show considerable size variation (Text-fig. 7). However, a variety of bivariate plots of morphological characters (Text-fig. 3A–B) indicate that the two ichnosubgenera are distinct and plot as discrete clusters on an allometric trend. The plot of manus digit III length against manus maximum heel length (Text-fig. 3B) also shows two statistical populations within the *Limnopus* (*Limnopus*) region, but this is based on a small number of specimens and is not reflected in other bivariate plots (Text-fig. 3A). In the absence of further material, it is not possible to develop firm conclusions about this latter distribution and a conservative taxonomic approach is adopted here, with all specimens assigned to *Limnopus* (*Limnopus*) *vagus*.

5. *Limnopus* (*Limnopus*) *vagus* is represented by trackways exhibiting two dominant preservational styles, related to the size of the trackmaker (Text-fig. 8B, D). However, these can be demonstrated to pertain to the
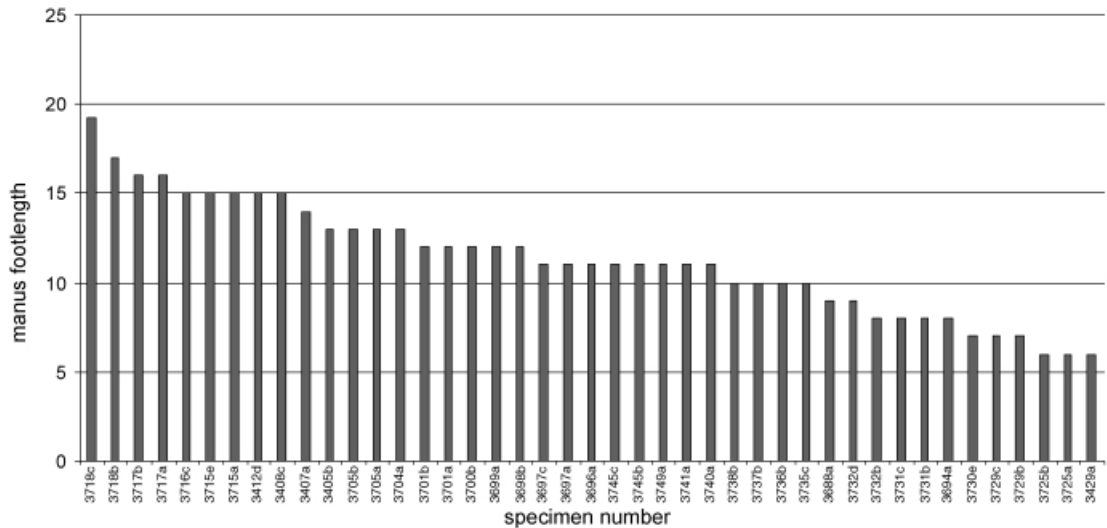
TEXT-FIG. 4. Plot of manus footlength within *Limnopus* (*Batrachichnus*) *salamandroides*, illustrating the continuous size range within this ichnospecies.

same type of trackmaker by specimens showing a transitional preservational stage (Text-fig. 8C).
6. It is clear that *Limnopus* (*Limnopus*) *vagus* could represent the traces of an adult version of the *Limnopus* (*Batrachichnus*) trackmaker. However, it is also highly possible that *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*) could be the representatives of two different biotaxa of two discrete size ranges. Retaining separate binomina emphasises this possibility, enables a more detailed taxonomic description of specimens, and helps to stabilise ichnotaxonomy by maintaining frequently used, well-established names.

Institutional abbreviations. BU, Lapworth Museum, University of Birmingham, UK; DM, Staatliches Museum für Mineralogie und Geologie, Dresden, Germany; MNG, GN, Museum der Natur, Gotha, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts, USA; USNM, United States National Museum, Smithsonian Institution, Washington, USA; WVU, West Virginia University, USA; YPM, Yale Peabody Museum, Yale University, New Haven, USA. All material described below, unless stated, is from Butts Quarry, Alveley, Shropshire, UK, from the Alveley Member of the Salop Formation (Warwickshire Group), and is housed at the Lapworth Museum of Geology, University of Birmingham, UK.

Dataset. A copy of the dataset upon which the numerical analysis is based is deposited in the Lapworth Museum of Geology, University of Birmingham, UK.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus LIMNOPUS Marsh, 1894

Type ichnospecies. By monotypy; *Limnopus vagus* Marsh, 1894. Upper Pennsylvanian (Kasimovian–Gzelian), Virgil Series, Howard Limestone, Osage County, Kansas, USA. Type specimen YPM 532.

Included ichnosubgenera. Limnopus (*Limnopus*) Marsh, 1894; *Limnopus* (*Batrachichnus*) Woodworth, 1900.

Diagnosis (emended after Haubold 1971*a*). Quadrupedal trackway with pes pace angulation of 74–96 degrees. Pes impression commonly placed closely behind the manus impression. Stride:footlength ratio varies from 3·1 to 7·6. Tetradactyl manus, with short, broad digits; lengths progress from I–II–III, IV equal to II. Digit III is directed parallel to or curves towards the trackway midline. Pentadactyl pes, up to 135 mm

BU 3736

BU 3688

BU 3432a

BU 3398a
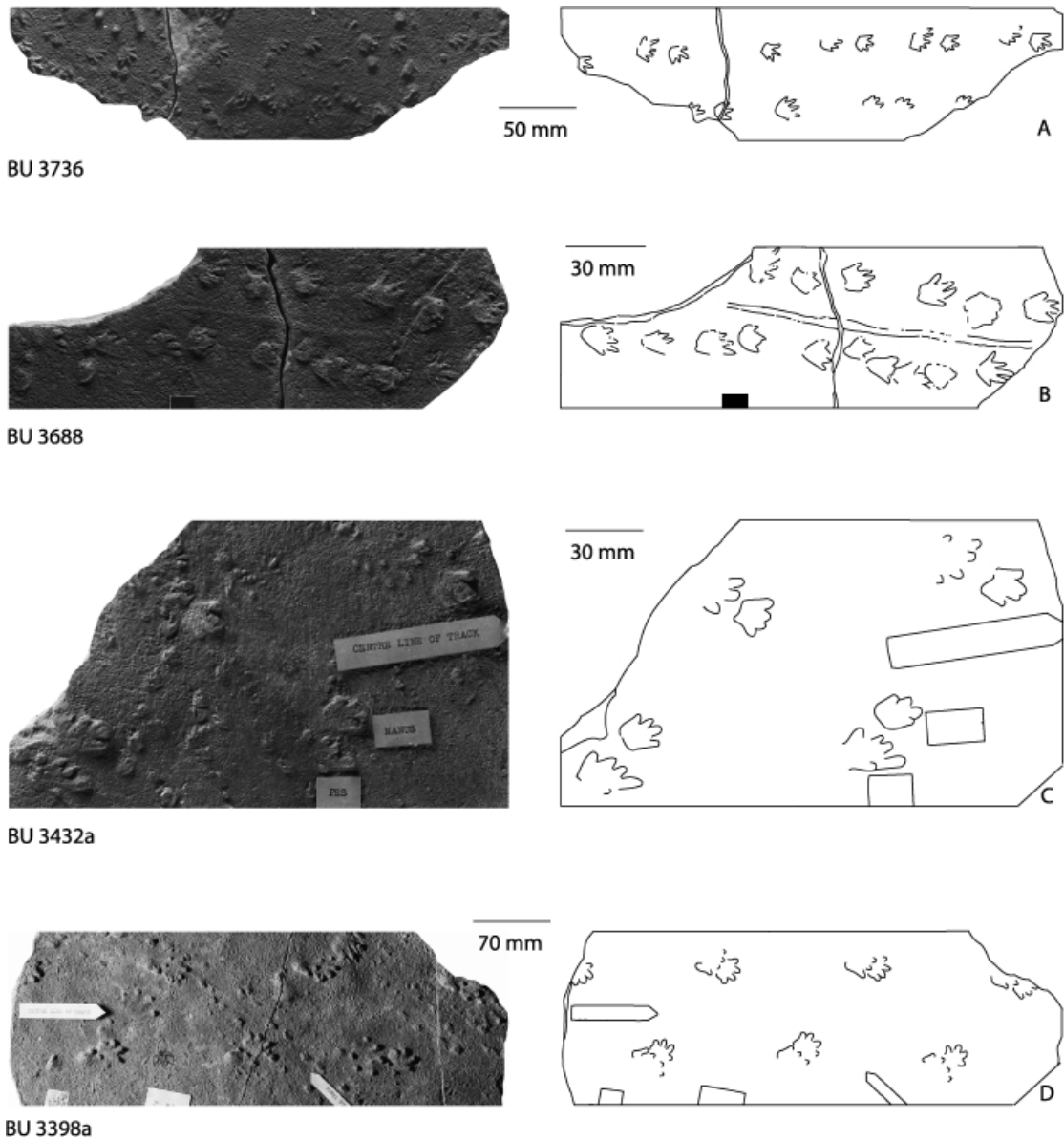
TEXT-FIG. 5. *Limnopus* (*Batrachichnus*) *salamandroides* (Geinitz, 1861); Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. Selected trackways illustrating range of preservational styles within the ichnospecies. A, BU 3736. B, BU 3688. C, BU 3432a. D, BU 3398a, type specimen of *Anthichnium major* Haubold and Sarjeant, 1973.

long, with digit V frequently missing. Digit lengths increase I–II–III–IV, V equal to II. Sole pad is proximally broadly rounded in well-preserved tracks, although extra-morphological influences may produce a U-shaped heel. The basal pads of digit I of both the manus and the pes are usually impressed. Manus and pes digits with rounded tips.

Remarks. The ichnogenus *Limnopus* was erected by Marsh (1894), in conjunction with the ichnotaxa *Baropus lentus* and *Allopus littoralis*. These three ichnogenera were synonymized and refigured by Baird (1952), who chose *Limnopus* as the available name and synonymized the ichnospecies *Allopus littoralis* and *Baropus lentus*, with the original specimen of *A. littoralis* (YPM 207) as the type. Haubold (1971*b*) subsequently synonymized *L. littoralis* with *L. waynesburgensis* (Tilton 1931), which had first been assigned by Tilton (1931) to the ichnogenus *Baropus*. In addition, Haubold (1971*a*) noted the similarity between *Limnopus* and *Nanopus*, although he did not synonymize the two. *Limnopus zeilleri* (Delage, 1912) is not considered to belong to the ichnogenus *Limnopus*, as reference to the original figured specimens, which are unclear (Delage 1912; Haubold 1971*a*), suggests that *L. zeilleri* is very distinct from the type ichnospecies, *L. vagus*. *Limnopus* is a stable ichnogenus, which may represent the large (possibly adult) form of *Batrachichnus*. Haubold (1971*a*) first recognized the similarity between these two ichnogenera, noting that the digit arrangements closely correlate with the anatomy of the Eryopoidea (stem-lissamphibia of Ruta and Coates 2004). Haubold (pers. comm. 2002) argues that it is possible for *Limnopus* and *Batrachichnus* to represent trackmakers of different biotaxa and therefore that separate ichnotaxa should be retained. In agreement with this statement, and in order to retain taxonomic stability whilst recognizing the obvious similarities between *Limnopus* and *Batrachichnus*, *Limnopus* is here divided into two ichnosubgenera, *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*). This is based upon the numerical, multivariate analysis of a large number of *Batrachichnus* and *Limnopus* specimens, as outlined above. Whilst in terms of foot size *Limnopus* splits into three groups (Text-fig. 3B), the intermediate size group is included under *Limnopus* (*Limnopus*) *vagus*, as these specimens fit within the diagnosis of this ichnospecies. Bivariate plots based upon trackway pattern (Text-fig. 3A) clearly illustrate the distinction between *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*). Principal Components Analysis confirms that the principal component of dissimilarity (96 per cent) between these two ichnosubgenera is one of size (Text-fig. 7), which varies within a continuous range across the measured specimens. The second component (3·9 per cent) is based upon digit and print angulations, which were shown by Peabody (1959) to vary widely within biospecies as a result of trackmaker speed and substrate consistency. Other components have negligible significance. Therefore, as size is not considered an ichnogenerically diagnostic character, and digit/print angulations are variable dependent upon environmental factors, *Limnopus* Marsh, 1894 and *Batrachichnus* Woodworth, 1900 are here classified as ichnosubgenera of the senior name. In addition, *Batrachichnus* is synonymous with *Anthichnium* Nopsca, 1923. Haubold (1971*a*) assigned *Limnopus* to either the Edopsoidea or the Eryopoidea, based upon the fact that there are few other large terrestrial amphibians of that age with tetradactyl manus morphology and ossified tarsals, suggested by the distinct sole impression of *Limnopus*. Both of these families were interpreted as stem-lissamphibian clades in the analysis of Ruta and Coates (2004). The lack of abundant skeletal remains of large, terrestrial, Upper Palaeozoic amphibians renders generic identification of the trackmaker difficult; nevertheless, recent work has led Haubold (2000) to suggest the genus *Eryops* as the most likely trackmaker of *Limnopus*. The appearance of *Limnopus* in the Alveley ichno-assemblage extends the stratigraphical range of this ichnogenus from the mid-Kungurian (Lower Rotliegendes, mid-Permian) back to the Upper Moscovian (lower Pennsylvanian, Upper Carboniferous).

Stratigraphical range. Upper Moscovian to mid-Kungurian.

Ichnosubgenus LIMNOPUS (LIMNOPUS) Marsh, 1894

Included ichnospecies. Limnopus cutlerensis Baird, 1965, from the Lower Permian Cutler Formation of San Miguel County, Colorado, USA; *L. haussei* (Schmidt, 1959), from the Lower Permian (Lower Rotliegend) of the Döhlen Basin, Dresden, Sachsen; *L. regularis* (Heyler and Lessertisseur, 1963) from the Lower Permian of Lodève, Herault, France.

Type ichnospecies. As for ichnogenus.

Limnopus (*Limnopus*) *vagus* Marsh, 1894

Text-figures 7C, 8A–D

* v 1894 *Limnopus vagus* Marsh, p. 82, pl. 2, fig. 2; pl. 3, fig. 2.
 v 1894 *Baropus lentus* Marsh, p. 83, pl. 2, fig. 5.
 v 1894 *Allopus littoralis* Marsh, p. 83, pl. 2, figs 4–4a.
 v 1926 'stegocephalian or reptile' Tilton, pp. 389–391, pl. 11, figs A–E.
 v 1927 *Baropus lentus* Marsh; Gilmore, p. 23, text-fig. 10.
 v 1927 *Baropus coconinoensis* Gilmore, pp. 24–26, text-fig. 9, pl. 7.
 v 1931 *Baropus waynesburgensis* Tilton, pp. 551–555, text-fig. 4, table 2.
  1952 *Limnopus vagus* Marsh; Baird, pp. 834–836, pl. 122, text-figs 1–2, table 1.
  1952 *Limnopus littoralis* (Marsh); Baird, pp. 836–837, pls 123–124, figs 1–3, text-fig. 3.
 v 1952 *Limnopus waynesburgensis* (Tilton); Baird, pp. 837–838, pl. 124, fig. 4, text-fig. 4.
  1965 *Limnopus cutlerensis* Baird, p. 47, text-fig. 14B–C.
  1970 *Limnopus vagus* Marsh; Haubold, p. 96, text-fig. 5B [*kop.* Baird 1952, text-fig. 2].
  1970 *Limnopus cutlerensis* Baird; Haubold, p. 96, text-fig. 5D.
  1970 *Limnopus littoralis* (Marsh); Haubold, p. 96, text-fig. 5H [*kop.* Baird 1952, text-fig. 3].
  1970 *Limnopus waynesburgensis* (Tilton); Haubold, p. 96, text-fig. 5G [*kop.* Baird 1952, text-fig. 4].
 v 1971*a* *Limnopus vagus* Marsh; Haubold, p. 17, text-fig. 12.5.
 ? 1971*a* *Amphisauroides minor* (Heyler and Lessertisseur); Haubold, p. 21, text-fig. 14.3.
 v 1973 *Limnopus rawi* Haubold and Sarjeant, pp. 899–900, pl. 3, text-fig. 2.4.
 v 1974 *Limnopus rawi* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 2.
  1987 *Limnopus zeilleri* (Delage); Gand, p. 98, pl. 2E (*non* pl. 2A–D, 2F), text-figs 28–30, tables 43–50.
 v 1990 *Limnopus vagus* Marsh; Hunt *et al.*, p. 292, text-figs 3B, 4F.
  1996 *Limnopus vagus* Marsh; Hunt *et al.*, p. 264, text-fig. 2F (*non* text-fig. 2E).
 v 1996 *Limnopus* sp.; Haubold *et al.*, pp. 143–145, text-fig. 7B–C.

Material. BU 2471b; 3397a; 3400a; 3402–3403; 3405c; 3410c; 3689a; 3706b; 3707a; 3714a.

Diagnosis (emended from Baird 1952). Species of *Limnopus* (*Limnopus*) with pes slightly longer than wide, print angulation 39–100 degrees, pes print angulation 70–123 degrees. Pes impressed posterior and somewhat lateral to manus, occasionally overlapping it slightly. Manus footlength 26–41 mm, pes footlength 29–48 mm.

Description

Manus morphology. Tetradactyl, fully plantigrade to semi-digitigrade. Footwidth (26–41 mm) greater than footlength (21–40 mm). All four digits distinct; impression strength increases distally along digits, and in some specimens (BU 3397a, 3689a) decreases medially. Digits short, broad and distally tapering, with rounded tips and medial curvature. Digit III, the longest digit, 8–18 mm from hypex, is the most curved; digits I and IV almost straight. Total digit angulation 65–95 degrees. Sole appears uniformly padded, but digits of overlapping pes obscure heel imprint, which is relatively short (10–27 mm), broad (8–28 mm) and convex, or with square base.

Pes morphology. Pentadactyl, plantigrade to digitigrade, although digits IV–V may not always be preserved. Footlength (29–48 mm) greater than footwidth (18–47 mm). Impression strength increases distally along digits. Digits relatively long and slender, and taper distally to a rounded tip. Digits I to IV strongly impressed, with medial increase in impression strength. Digit V represented by faint digit tip outline only, giving total digit angulation of 70–86 degrees, whilst angulation between digits I–IV varies from 48–79 degrees. Digit I is most strongly impressed, with oval, broad sole pad at base. Digit IV is longest, 12–25 mm long from hypex. Digits I, II and V straight, whilst digits III and IV curve slightly laterally. Sole uniformly padded, with extended, elongate heel (10–32 mm long) that tapers distally (heel width 3 mm from posterior termination equals 10–20 mm).

Trackway structure. Manus–pes overlap variable (from 14 mm overlap of manus by pes, to 16 mm distance between manus heel and pes digit tip III). Manus prints turned slightly medially (manus print angulation 39–100 degrees), whilst pes prints range from medially facing to slightly laterally facing (pes print angulation 70–123 degrees). Pes trackwidth narrow in comparison to pes footwidth (pes trackwidth 84–114 mm), but greater than manus

trackwidth (50–101 mm). Manus pace angulations 74–109 degrees and pes pace angulations 65–95 degrees. Manus stride:footlength 3·9–7·6, pes stride:footlength 3·4–5·7. Manus stride 112–179 mm, manus pace 83–123 mm; pes stride 132–182 mm, pes pace 116–152 mm.

Remarks. Haubold and Sarjeant (1973, 1974) erected a new ichnospecies, *Limnopus rawi*, to describe the specimens of *Limnopus* (*Limnopus*) within the Alveley ichno-assemblage. However, this ichnospecies was erected purely to refer to specimens of *Limnopus* (*Limnopus*) from Shropshire, UK, and was not based upon significant morphological traits. Consequently, *Limnopus rawi* is here considered to be a junior synonym of *L.* (*L.*) *vagus*. The ichnospecies is represented within the Alveley ichno-assemblage predominantly by two styles of preservation (Text-figs 8B, D), related to trackmaker size, with one specimen (BU 3405c, Text-fig. 8c) exhibiting a transitional stage. This enables the two preservational styles to be attributed to the same type of trackmaker and therefore the same ichnospecies. Larger specimens (Text-fig. 8B) are more deeply impressed than smaller trackways, and therefore preserve the entire length of the digits, whilst in smaller specimens these may appear as tip marks only (Text-fig. 8D). This shallower style of preservation is similar to that of the type specimen of *L.* (*L.*) *vagus*. Comparison of *L.* (*L.*) trackways with those of *L.* (*B.*) demonstrates that the most significant difference between these ichnotaxa is one of size (Text-fig. 7). In terms of foot morphology, *L.* (*L.*) *vagus* can be split into three statistical populations according to size difference (Text-fig. 3B), but in terms of trackway pattern (Text-fig. 3A), *L.* (*L.*) *vagus* separates clearly from *Limnopus* (*Batrachichnus*).

Ichnosubgenus LIMNOPUS (BATRACHICHNUS) Woodworth, 1900

Type ichnospecies. *Batrachichnus plainvillensis* Woodworth, 1900. Upper Carboniferous, Narragansett Basin, Plainville, Wrentham, Massachusetts, USA. Type specimen MCZ 1052.

Included ichnospecies. *Limnopus* (*Batrachichnus*) *salamandroides*, from the Lower Permian of Thüringer Wald, Germany.

Diagnosis (emended after Haubold 1971*a*). Manus footlength generally up to 26 mm. Pace angulation not greater than 108 degrees. Plantigrade pes, digit IV longest, I of equal length to V. Sole relatively slender and gently rounded at the back. Manus plantigrade to semi-plantigrade and tetradactyl, Digit III longest. Pes trackwidth equals, or slightly exceeds, manus trackwidth. A clear tail trace is frequently present.

Remarks. The ichnogenus *Batrachichnus* was erected and described by Woodworth (1900) and diagnosed by Gilmore (1927, p. 36) as 'small forms, quadrupedal, with four and five toes on manus and pes respectively. With or without median groove. Toes slender, radially arranged'. This ichnogenus remained monospecific until the erection of *B. celer* (Matthew 1903), now assigned to *Dromillopus* (Haubold 1971*a*). The ichnospecies *L.* (*Batrachichnus*) *delicatula*, also known as *B. delicatulus*, was first described by Lull (1918) as *Exocampe? delicatula*, and assigned to *Batrachichnus* by Gilmore (1927), based upon the similar size and digital formula to *B. plainvillensis*. Haubold *et al.* (1996) noted that *Dromillopus parvus* Gilmore, 1927, assigned to *Batrachichnus* by Haubold (1971*a*), is a preservational variant of *L* (*B.*) *delicatulus*, as is *B. obscurus* Gilmore, 1927, which is a name pertaining to very small trackways with a pes length of less than 5 mm. After study of the type specimens of *D. parvus*, *E.? delicatula* and *B. obscurus*, these ichnospecies are here considered to belong to *L.* (*B.*) *plainvillensis*.

Stratigraphical range. Upper Moscovian to mid-Kungurian.

Limnopus (*Batrachichnus*) *plainvillensis* Woodworth, 1900

Text-figure 6A–F

   ? 1891   *Notalacerta jacksonensis* Butts, p. 18, text-fig. 2.
   v 1918   *Exocampe? delicatula* Lull, pp. 344–346, text-fig. 4, pl. 3, fig. I.
* v 1900   *Batrachichnus plainvillensis* Woodworth, pp. 452–453, pl. 40, fig. 1, text-fig. 2.
   v 1912   *Ichnium dolichodactylum* Pabst; Hardaker, pp. 669–670, text-fig. 22.
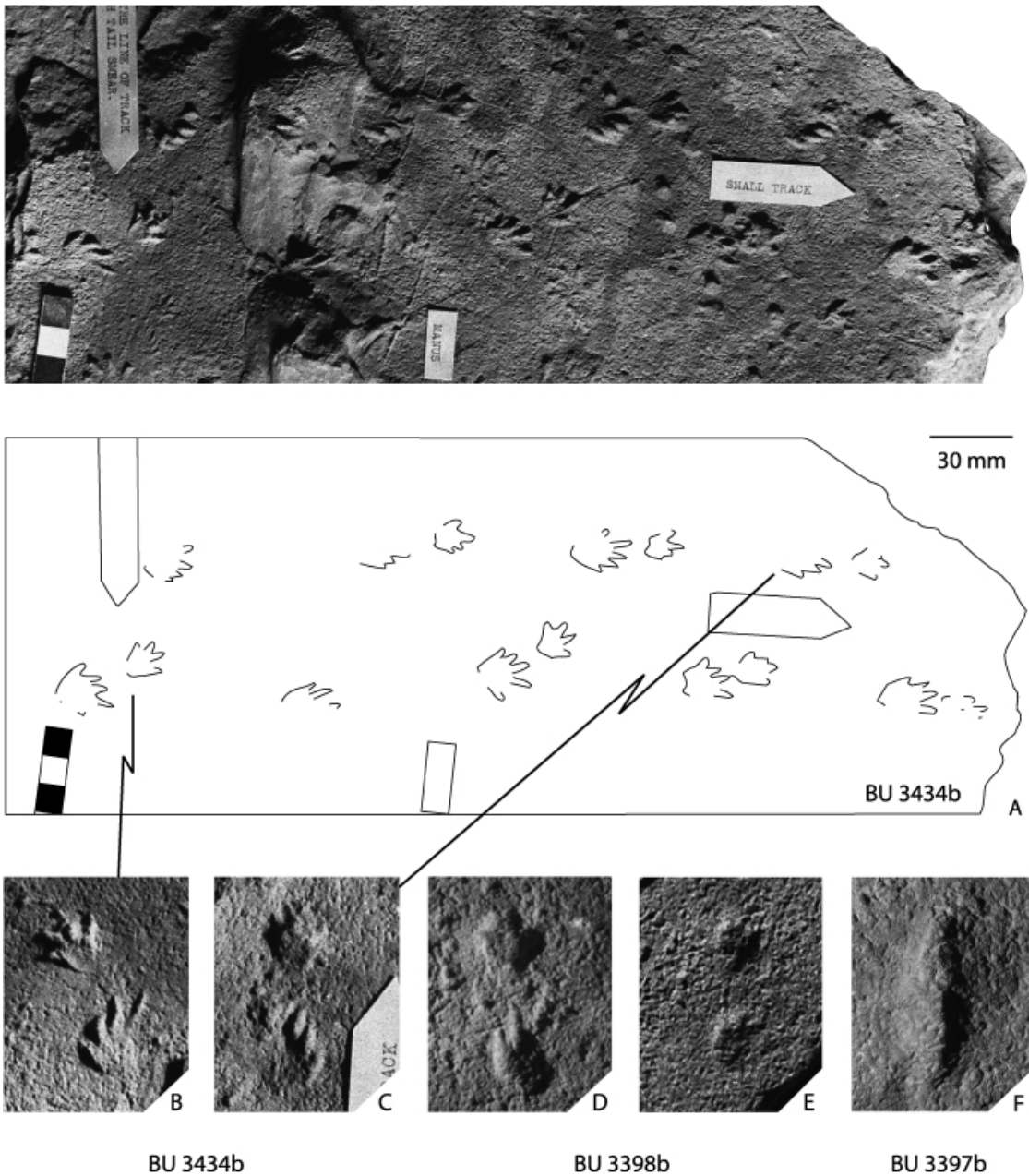
TEXT-FIG. 6. *Limnopus* (*Batrachichnus*) *plainvillensis* Woodworth 1900; Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. A, BU 3434b with interpretative drawing. B–F, selected manus-pes sets illustrating preservational variation within the ichnospecies. Scale: manus footlength is 8 mm. B–C, BU 3434b. D–E, BU 3398b, type specimen of *Batrachichnus alveleyensis* Haubold and Sarjeant, 1973. F, BU 3397b.

v 1927   *Batrachichnus delicatula* (Lull); Gilmore, pp. 36–40, text-figs 15–16 [*kop*. Lull 1918, text-fig. 4],
            pl. 12.
  1927   *Batrachichnus obscurus* Gilmore, pp. 40–42, text-figs 17–18 [kop. Woodworth 1900], pl. 12.
v 1927   *Dromillopus parvus* Gilmore, pp. 42–45, text-figs 19–20, pl. 14.
v *1970*   *Batrachichnus plainvillensis* Woodworth; Haubold, p. 92, text-fig. 3A [*kop*. Woodworth 1900, text-
            2].
v 1970   ?*Batrachichnus parvus* (Gilmore); Haubold, p. 92, text-fig. 3B [*kop*. Gilmore 1927, text-fig. 19].
  1970   *Amphisauroides* sp.; Haubold, p. 104, text-fig. 7E.
v 1971*a*   *Batrachichnus plainvillensis* Woodworth; Haubold, p. 14, text-fig. 10.8 [*kop*. Woodworth 1900,
            text-fig. 2].
? 1971*a*   *Nanipes delicatus* Gilmore; Haubold, p. 14, text-fig. 10.5.
v 1971*a*   *Batrachichnus parvus* (Gilmore); Haubold, p. 14, text-fig. 10.9.
v 1973   *Batrachichnus alveleyensis* Haubold and Sarjeant, p. 899, pl. 1, text-figs 2–3.
v 1974   *Batrachichnus alveleyensis* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 1.
  1981   *Batrachichnus hunecki* Holub and Kozur, pp. 166–167, pl. 6, figs 1, 3.
v 1996   *Batrachichnus delicatulus* (Lull); Hunt *et al*., pp. 168–171, text-fig. 2.
  1996   *Batrachichnus plainvillensis* Woodworth; Schult, p. 117, text-fig. 5.
? 1996   *Dromillopus quadrifidus* Matthew; Schult, p. 118, text-fig. 9.
  1996   *Batrachichnus salamandroides* (Geinitz); Haubold, pp. 37–48, text-fig. 8A.

Material. BU 3398b; 3403b; 3413a; 3434b; 3693a.

Diagnosis. An ichnospecies of *Limnopus* (*Batrachichnus*) with manus and pes stride up to 74 mm. Relatively low trackwidth (manus trackwidth up to 37 mm; pes trackwidth up to 41 mm), with correspondingly low pace angulation, up to 108 degrees.

Description

Manus morphology. Tetradactyl manus, footlength (5–15 mm) slightly greater than footwidth (7–12 mm). Deep, plantigrade impressions may render digits indistinguishable, but well-preserved specimens show relatively short, slender, distally tapering digits with rounded tips. Digit III longest (up to 13 mm), and total digit divarification is 48–102 degrees. Digits vary from straight to slightly medially curved; this curvature decreases from digits I to IV. Stride 29–74 mm; pace 21–51 mm. Well-preserved heel is square with concave base and uniformly padded with strongly imprinted sole. Alternatively, heel may appear more strongly impressed at bases of digits I and IV. Impression strength increases distally along digits.

Pes morphology. Pentadactyl, although digit V often not preserved along entire length. Pes is slightly larger than manus; footlength (8–19 mm) greater than footwidth (5–13 mm). Tracks deeply imprinted, yet pes digits more frequently distinctly preserved than those of manus. Digit I frequently best preserved, with elongate sole pad at base. Long, slender digits with mean total angulation of 71 degrees (Digits I–V), whilst digits I–IV have mean angulation of 57 degrees. Digit IV is longest (up to 20 mm). Digits may taper distally or maintain constant breadth along length; all digits vary from straight to slightly medially curved. In less well-preserved specimens, only digits I–III may be impressed. Stride 29–74 mm, pace 22–63 mm. Strongly imprinted, uniformly padded, elongate sole with rounded heel, which may appear pointed in less well-preserved specimens.

Trackway structure. There is no evidence for the characteristic *Limnopus* (*Batrachichnus*) tail trace in any of the surface trackway specimens of *L.* (*B.*) *plainvillensis* from the Alveley ichno-assemblage. Both manus and pes prints frequently face forward in alignment with trackway midline, although manus occasionally has slight inward (medial) turn towards trackway midline. Overlapping of manus by pes is rare, occurring in only 6 per cent of manus–pes sets, although manus–pes distance is variable (distance between manus heel and pes digit tips from 0–10 mm). Pes trackwidth (20–41 mm) greater than manus trackwidth (12–37 mm), fitting with original description of *Batrachichnus plainvillensis* and contrary to first description of *B. alveleyensis* (Haubold and Sarjeant 1973). Pace angulation characteristically low (61 to 108 degrees). Regular manus–pes set pattern.

Undertracks. Material: BU 3397b; 3400c, d; 3408a; 3430a; 3690a; 3692b; 3695a; 3708b; 3709b; 3711a; 3712b, c; 3715b, d; 3716c, d; 3719a; 3726a, b; 3728a; 3730c, d; 3731d; 3733c; 3735a; 3736a; 3738c; 3739b; 3742a; 3743a; 3744a; 3745a; 3746a; 3748b; 3750b. *Limnopus* (*Batrachichnus*) is also preserved as numerous undertracks, represented by deep impressions peaking at footprint centre with indistinguishable digits. Manus–pes sets regularly

placed, although distance between manus and pes is variable, accordant with above description. Pes larger than manus (mean size of pes tracks 6–10 mm, manus tracks 4–5 mm), and preserves longer, more elongate heel impression. Prints appear to face forward with respect to trackway midline. Pes trackwidth may be slightly greater than, or equal to manus trackwidth. Deeper undertracks appear as elongate ovals where manus and pes impressions have merged.

Remarks. Notalacerta jacksonensis Butts, 1891, is here tentatively assigned to *L. (B.) plainvillensis*, based upon the original description and figured specimen (Butts 1891). *N. jacksonensis* has previously been considered by various authors (e.g. Gilmore 1927; Haubold 1971*a*) to bear no resemblance to the type specimen of *Notalacerta*, *N. missouriensis* Butts, 1891. However, the original specimen of *N. jacksonensis* is not figured well enough to render the present assignment to *L. (B.) plainvillensis* certain. *Batrachichnus alveleyensis* Haubold and Sarjeant 1973 (BU 3398, Text-fig. 6D–E), is assigned to *L. (B.) plainvillensis*, as the original diagnosis of *B. alveleyensis* rests upon the lack of tail trace in the type specimen. However, Gilmore (1927) noted (after Matthew 1903) that *B. plainvillensis* may also lack a 'median groove'. Therefore, *B. alveleyensis* is here assigned to *L. (B.) plainvillensis*, as the absence of a tail trace in *B. alveleyensis* is the only significant difference between the two species, and this absence may be simply due to substrate conditions (Peabody 1959). Indeed, the preservational style of *L. (B.) plainvillensis* within the Alveley ichno-assemblage is highly variable due to differences in substrate conditions (Text-fig. 6B–F). This re-assignment of *B. alveleyensis* is additionally supported by results of the multivariate statistical analysis carried out on a number of trackways from the Alveley ichno-assemblage, including numerical data on the holotype specimen (MCZ 1052) of *B. plainvillensis*, as given by Woodworth (1900) and Haubold (1973). *Dromillopus* Matthew, 1904, as represented by the type ichnospecies, *Dromillopus quadrifidus*, is recognized as an ichnogenus similar to, yet distinct at an ichnogeneric level, from *Limnopus (Batrachichnus)*. This similarity led some subsequent authors to attribute specimens of *B. plainvillensis* to *D. quadrifidus* (e.g. Schult 1996). However, the ichnotaxonomic assignments of Schult (1996) cannot be checked with certainty, as specimen numbers were not supplied. In his description of *Batrachichnus*, Woodworth (1900) proposed that 'stegocephalians' might be the responsible biotaxa, and suggested *Amphibamus* (Carboniferous, Ohio), or an unknown form with a tetradactyl manus, of similar size and shape to *Melanerpeton* from the Permian of Germany, as possible trackmakers. Haubold (1971*a*) assigned *Batrachichnus* to the Superfamily Edopoidea (stem-lissamphibia, or 'temnospondyls'), due to the similar tetradactyl manus morphology. He suggested *Dendrerpeton* as a possible trackmaker; however, this generic designation was based only upon a lack of morphological features providing evidence to the contrary. More recent work has led Haubold (2000) to attribute *Batrachichnus*, as a possible juvenile form of *Limnopus*, to *Eryops*.

<div align="center">

Limnopus (Batrachichnus) salamandroides (Geinitz, 1861)

Text-figures 5A–D, 7A–B

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* 1861	*Saurichnites salamandroides* Geinitz, p. 4, pl. 1.	
1897	*Ichnium tetradactylum* Pabst, p. 87, text-figs 3–4.	
1900	*Ichnium anakolodactylum* Pabst, pp. 55, 60.	
1905	*Ichnium rhopalodactylum* Pabst, p. 10.	
1905	*Ichnium kalnanum* Pabst, p. 10.	
1908	*Ichnium anakolodactylum* Pabst; Pabst, p. 93, pl. 23, figs 2–3, text-fig. 31.	
1923	*Anthichnium anacolydactylum* Nopsca, p. 135.	
1970	*Anthichnium salamandroides* (Geinitz); Haubold, pp. 89–92, pl. 14, text-fig. 3E.	
?1970	*Amphisauropus imminutus*; Haubold, pp. 103–104, pl. 20, text-fig. 7D.	
1971*b*	*Anthichnium salamandroides* (Geinitz); Haubold, pp. 19–20, pl. 5, fig. 1.	
1972	*Anthichnium salamandroides* (Geinitz); Haubold and Katzung, pp. 889–895, text-fig. 2.1.	
v 1973	*Anthichnium salamandroides* (Geinitz); Haubold and Sarjeant, pp. 897–899, text-fig. 2.1.	
1973	*Anthichnium salamandroides* (Geinitz); Haubold, p. 7, pls 6–7.	
v 1973	*Anthichnium major* Haubold and Sarjeant, pp. 898–900, text-fig. 2.2.	
v 1974	*Anthichnium salamandroides* (Geinitz); Haubold and Sarjeant, p. 260, text-fig. 1 (left).	
v 1974	*Anthichnium major* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 1 (centre).	
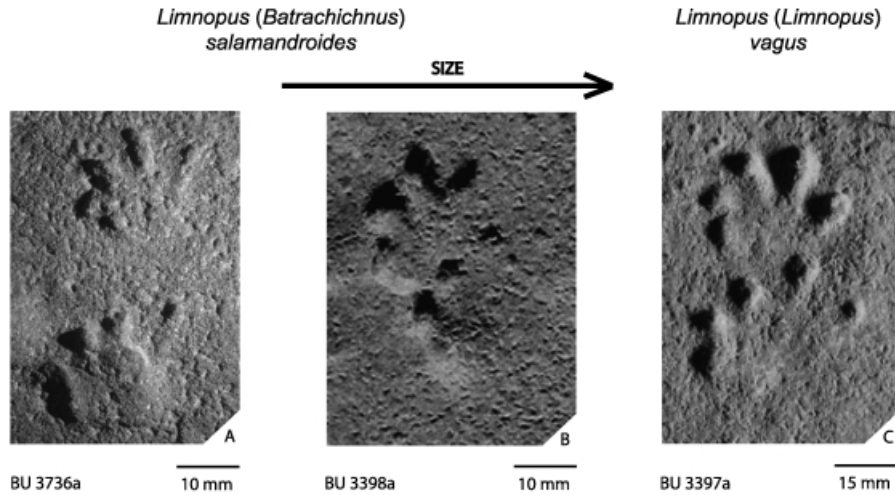
TEXT-FIG. 7. *Limnopus* Marsh 1894; Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. Selected manus-pes sets illustrating morphological similarity between *Limnopus* (*Batrachichnus*) and *Limnopus* (*Limnopus*). A, *L.* (*Batrachichnus*) *salamandroides*, BU 3736. B, *L.* (*Batrachichnus*) *salamandroides*, BU 3398a. C, *L.* (*Limnopus*) *vagus*, BU 3397a.

1981	*Saurichnites salamandroides* Geinitz; Holub and Kozur, pp. 152–154, pls 1, 6, fig. 4.
1982	*Anthichnium salamandroides* (Geinitz); Fichter, pp. 90–91, text-fig. 1.
1983*b*	*Saurichnites salamandroides* Geinitz; Fichter, pp. 13–26, text-figs 3A–B, 4A–B, 5.
? 1983*b*	*Saurichnites intermedius* Fritsch; Fichter, pp. 39–45, text-fig. 23.
1985	*Anthichnium salamandroides* (Geinitz); Haubold, pp. 93–94.
1987	*Anthichnium salamandroides* (Geinitz); Gand, pp. 75–98, pl. 3A–D, F (*non* 3E), text-figs 20–23, tables 25–42.
v 1990	*Anthichnium* sp. Hunt *et al.*, p. 292, text-fig. 3A.
v 1990	cf. *Nanopus* sp. Hunt *et al.*, p. 295, text-figs 3C, 4E.
v 1990	*Gilmoreichnus* sp. Hunt *et al.*, pp. 295–297, text-figs 3J, 5E.
? 1992	*Anthichnium salamandroides* (Geinitz); Demathieu and Gand, pp. 22–26, text-fig. 4E.
1995	*Anthichnium salamandroides* (Geinitz); Gand *et al.*, pp. 103–107, pl. 2, text-fig. 6B–C.
v 1996	*Batrachichnus delicatula* (Lull); Haubold *et al.*, pp. 137–143, text-fig. 2A, C.
v 1996	*Batrachichnus delicatula* (Lull); Hunt *et al.*, pp. 168–171, text-fig. 2A [*kop.* Haubold *et al.* 1996, text-fig. 2C], C.
v 1996	*Limnopus* sp. Haubold *et al.*, pp. 143–145, text-fig. 7A.
1996	*Batrachichnus salamandroides* (Geinitz); Haubold, pp. 37–48, text-figs 6A–B, 8B, 10A.

Material. BU 3407a; 3408c; 3412d; 3429a; 3688a; 3694a; 3696a; 3697a, c; 3698b; 3699a; 3700b; 3701a, b; 3704a; 3705a, b; 3710d; 3711a; 3712b, c; 3713b; 3715a, e; 3716c; 3718b; 3720b, c; 3723c, d; 3724a; 3725b; 3729b, c; 3730e; 3731b, c; 3732b, d; 3735c; 3736b; 3737b; 3738b; 3740a; 3741a; 3745b, c. Incomplete and not identified in cluster analysis: 2471c, f; 3398c; 3413c; 3430a; 3432a; 3689b, c; 3690a; 3692a, b, d; 3698a; 3708b, d; 3715b, d; 3716c, d; 3719a; 3721c; 3722c; 3723a, b; 3726a; 3727a; 3728a; 3729a; 3730c, d; 3731d; 3733c; 3735a; 3736a; 3738c; 3739b; 3742a; 3743a; 3744a; 3745a; 3746a; 3747b–d; 3748b, c; 3749a; 3750b.

Diagnosis. An ichnospecies of *L.* (*Batrachichnus*) with a large stride (manus stride up to 158 mm, pes stride up to 159 mm) and trackwidth (manus trackwidth up to 68 mm, pes trackwidth up to 94 mm) in relation to footlength (between 5 and 32 mm; manus length generally up to 26 mm). Pace angulation is correspondingly high (manus pace angulation up to 128 degrees, pes pace angulation up to 110 degrees). Digits are slightly longer in proportion to heel length than in *L.* (*B.*) *plainvillensis*.

Description

Manus morphology. Tetradactyl, plantigrade manus, impressed along length, with impression strength slightly increasing distally towards digit tips. Footlength approximates footwidth (footlength 5–26 mm, footwidth 4–28 mm). Digits long (digit III longest, 2–14 mm from hypex to digit tip, length approximates 50 per cent footlength), and slender, with rounded tips. Digits straight, or very slightly medially curving. Heel square, slightly wider than long (width 2–18 mm, length 2–11 mm) with concave base. On less well-preserved specimens, imprinted only where sole extends back from base of digit I; sole appears to form rounded, bulbous pad at back of heel, altering preserved shape of the distal heel. Otherwise, sole is uniformly padded. Total digit angulation measures 50–121 degrees. Print angulation 40–116 degrees (i.e. manus may face inwards or outwards towards trackway midline, and can lie with long axis parallel to trackway midline).

Pes morphology. Pentadactyl pes; impression strength varies from sub-digitigrade to sub-plantigrade so that in less well-preserved specimens, digits IV and V are absent, or only tips are preserved (digitigrade preservation). Digit I impressed along entire length, including where sole extends from base of digit, but remainder of sole is unimpressed. Digits long (Digit IV longest, 4–19 mm from hypex to digit tip) and slender, with constant breadth and rounded tips. Curvature ranges from very slightly medial to straight; curvature decreases from digit I to V. Heel often faint or completely unimpressed; on well-preserved trackways appears rounded and slightly tapering, with a uniformly padded sole. Heel equidimensional, with length 3–12 mm, and width 2–17 mm. Footlength 6–32 mm, footwidth 4–32 mm. Total digit angulation 32–81 degrees; digit angulation between digits I–IV 64–89 degrees.

Trackway structure. Distance between manus heel and pes digit III tip within a single set up to 19 mm; overlap of manus by pes is up to 8 mm. Both manus and pes prints are variable in inclination (medially or laterally facing, or in alignment with trackway midline), although inclination is predominantly medial; manus values 43–106 degrees, pes values 65–112 degrees. Pace angulations 51–128 degrees for manus and 39–110 degrees for pes. Accordingly, pes trackwidth (14–94 mm) is greater than manus trackwidth (12–68 mm). Manus stride 31–158 mm, manus pace 20–109 mm, with stride:footlength 2·9 to 9·2. Pes stride 27–159 mm, pes pace 23–128 mm; stride:footlength 2·4 to 7·0.

Remarks. Limnopus (*Batrachichnus*) *salamandroides* was formerly classified under the ichnogenus *Anthichnium*, erected by Nopsca (1923) with the description of the ichnospecies *Anthichnium anacolodactylum*. However, the type specimen of *Anthichnium* was described by Geinitz (1861) under the name *Saurichnites salamandroides*, assigned to *Anthichnium* by Haubold (1970). A number of forms were described under the ichnogenus *Ichnium* by Pabst (1897, 1900, 1905, 1908), the species names of which were supposed to illustrate the preservational form of the digits. These forms have since been recognized as morphological variants of the *Anthichnium* type ichnospecies, *A. salamandroides*. Haubold (1971*a*) recognized the similarity of *Anthichnium* and *Dromillopus* Gilmore, 1927, and *Dromillopus parvus* Gilmore, 1927, was subsequently re-assigned to *Batrachichnus* by Haubold *et al.* (1996), highlighting the similarity between *Anthichnium* and *Batrachichnus*. Indeed, Haubold (1996) suggested that *Anthichnium* is synonymous with *Batrachichnus*, and observed that the type specimen of *Anthichnium* is itself an undertrack and therefore not taxonomically stable. *Anthichnium salamandroides* is here accommodated under the ichnosubgenus *Limnopus* (*Batrachichnus*). The ichnotaxon *Anthichnium major*, erected by Haubold and Sarjeant (1973, 1974; BU 3398, Text-fig. 5D) to describe *Limnopus* (*Batrachichnus*) trackways of intermediate size from Shropshire, is different from *Limnopus* (*Batrachichnus*) *salamandroides* only in terms of size, not morphology. This ichnospecies is, therefore, synonymized with *Limnopus* (*Batrachichnus*) *salamandroides*, following numerical analysis of the type specimen. The range of preservational styles within *Limnopus* (*Batrachichnus*) *salamandroides* is variable, dependent upon both trackmaker size and substrate conditions at time of imprinting (Text-fig. 5), whereas *L.* (*Batrachichnus*) *plainvillensis* is variable only due to substrate conditions (Text-fig. 6).

Ichnogenus DIMETROPUS Romer and Price, 1940

Type ichnospecies. Dimetrodon berea Tilton, 1931. Lower Permian, Waynesburg Sandstone, Washington Formation, Dunkard Group, Berea, Ritchie County, West Virginia, USA. Type specimen WVU Permian Number 147.
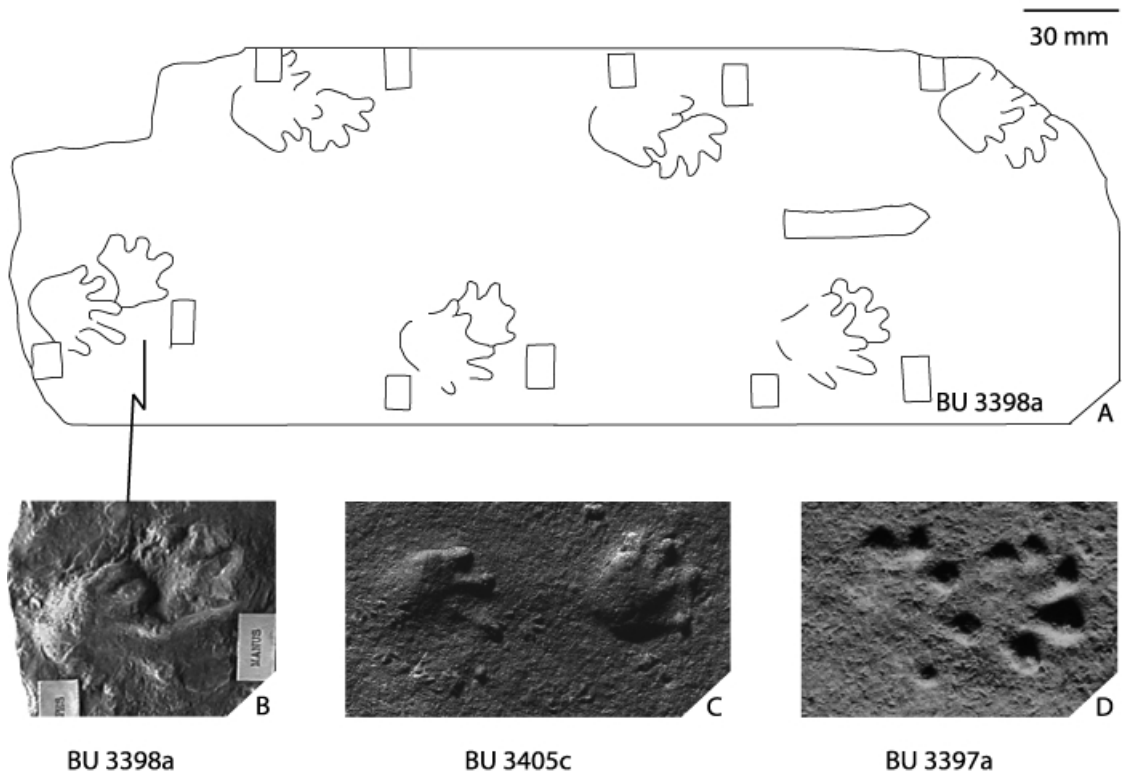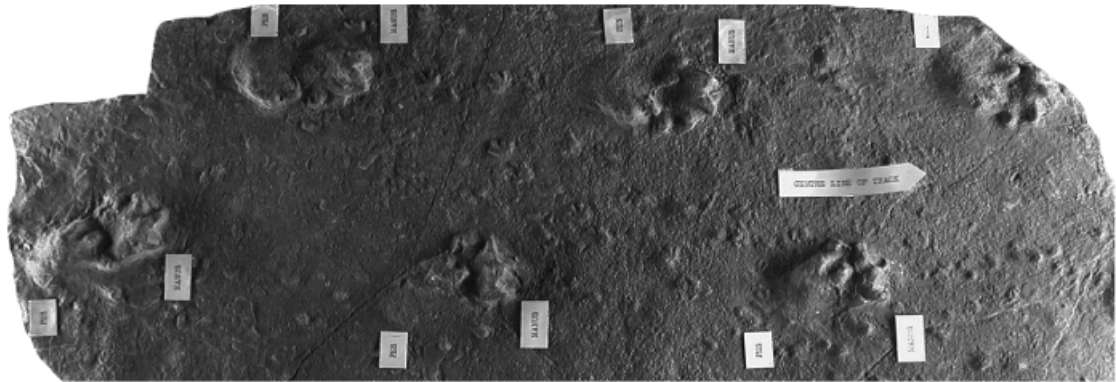
TEXT-FIG. 8. *Limnopus* (*Limnopus*) *vagus* Marsh, 1894; Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. A, BU 3403a, type specimen of *Limnopus rawi* Haubold and Sarjeant, 1973, with interpretative drawing. B–D, selected manus-pes sets illustrating preservational variation within the ichnospecies. B, BU 3398a, manus footlength is 24 mm. C, BU 3405c, manus footlength is 22 mm. D, BU 3397a, manus footlength is 20 mm.

Included ichnospecies. *Dimetropus leisnerianus* (Geinitz, 1863) from the Upper Rotliegend of the Thüringer Wald, Germany; *D. nicolasi* Gand and Haubold, 1988, from the Lower Permian of the Lodève and St. Affrique basins, southern France.

Diagnosis. Quadrupedal trackway with pes footlength up to 220 mm. Depending on the stride length, pace angulation 80–100 degrees; stride:footlength ratio averages 3:1 (range 2·5:1–4·2:1). Manus and pes long

axes lie approximately parallel to the trackway midline. Plantigrade, pentadactyl impression, digit IV longest. Pes heel length comprises over half the total footlength. Digits relatively slender, with sharp, robust claws directed towards the trackway midline. Pes digit divarification between digits I–IV up to 80 degrees, with strongly impressed heel proximal to digits III–V. Manus smaller than pes, total digit divarification (from I–V) 90 degrees on average, with a narrower heel than that of pes. Possible tail trace running straight along trackway midline.

Remarks. *Dimetropus* was first described by Geinitz (1863) under the name of *Saurichnites leisnerianus*, followed by Pabst (1895), who erected the junior synonym *Ichnium acrodactylum* from the Early Permian (Rotliegend) Tambach Formation of Thüringen, central Germany. The type ichnospecies of *Dimetropus*, *Dimetrodon berea* Tilton, was described by Tilton (1931) based upon a specimen from the Lower Permian Waynesburg Sandstone (Washington Formation, Dunkard Group) of West Virginia, USA. However, as he used the name *Dimetrodon*, which is the name referring to skeletal material of the proposed trackmaker and therefore not appropriate to describe the ichnotaxon, the name *Dimetropus* of Romer and Price (1940) takes priority. *Dimetropus* has been associated with the carnivorous 'pelycosaur' *Dimetrodon* since the recognition of the type ichnospecies, *Dimetropus berea* (Tilton, 1931), based upon comparisons with skeletal material made by Tilton (1931). It was argued by Haubold (1971a) that *Dimetrodon* is only one of a number of possible 'pelycosaurian' *Dimetropus* trackmakers, including *Haptodus* and *Sphenacodon*, based upon the skeletal morphology of the manus and pes. Indeed, Haubold and Sarjeant (1973) attributed *D. salopensis* to a sphenacodontid 'pelycosaur', despite a lack of corresponding Upper Carboniferous body fossils at the time, and this attribution is supported in a recent review of Permian trackmakers by Haubold (2000). The appearance of *Dimetropus* in the Late Carboniferous Alveley ichno-assemblage marks the first occurrence of this ichnotaxon outside the Permian.

Stratigraphical range. Upper Moscovian to mid-Kungurian.
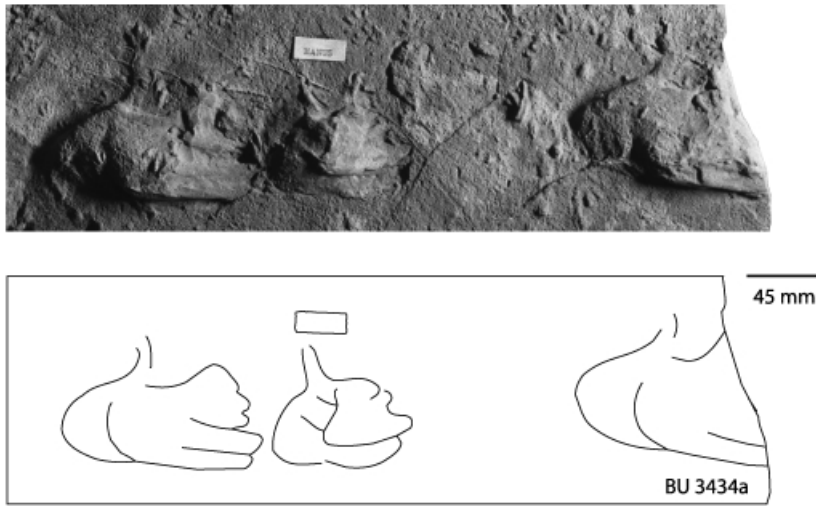
Dimetropus leisnerianus (Geinitz, 1863)

Text-figure 9

1863	*Saurichnites leisnerianus* Geinitz, p. 389, pl. 4, fig. 5.
v 1895	*Ichnium acrodactylum* Pabst, p. 575.
* v 1971a	*Dimetropus leisnerianus* (Geinitz); Haubold, p. 34.
1971b	*Dimetropus leisnerianus* (Geinitz); Haubold, pp. 32–33, text-fig. 9.
v 1973	*Dimetropus salopensis* Haubold and Sarjeant, pp. 905–906, text-fig. 3.2.
v 1974	*Dimetropus salopensis* Haubold and Sarjeant; Haubold and Sarjeant, p. 260, text-fig. 3 (right).
1973	*Dimetropus leisnerianus* (Geinitz); Haubold, pp. 20–21, pls 36–39, table 5.
1982	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 100–103, text-figs 6–7.
1983a	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 153–159, text-figs 14A–D, 15.
? 1983c	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 141–142, text-figs 27–28.
? 1984	*Dimetropus leisnerianus* (Geinitz); Fichter, pp. 222–223, text-fig. 15.
p 1987	*Dimetropus leisnerianus* (Geinitz); Gand, p. 167, pl. 6A (*non* 6C), text-figs 47–51, tables 86–92.
1996	*Dimetropus leisnerianus* (Geinitz); Hunt *et al.*, p. 177, text-fig. 7B.
v 1996	*Dimetropus leisnerianus* (Geinitz); Haubold, pp. 53–54, pl. 14–15, table 6.
1998	*Dimetropus leisnerianus* (Geinitz); Haubold, p. 10, pl. 5, table 1.
2000	*Dimetropus leisnerianus* (Geinitz); Haubold, p. 11.

Material. BU 3413; 3434; 3691a; 3706a; 3730a; 3734x.

Description

Manus morphology. Pentadactyl, deeply impressed, plantigrade manus 64–66 mm (length) by 41–50 mm (width). Digits long, slender, taper distally. Digits I–III curve slightly laterally; Digit IV lies at 56 degrees (mean) and tip of Digit V curves round medially to lie at 90 degrees with respect to trackway midline. Digit IV is longest, up to 63 mm.

TEXT-FIG. 9. *Dimetropus leisnerianus* (Geinitz, 1863); Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. BU 3434a, specimen of the type series of *Dimetropus salopensis* Haubold and Sarjeant, 1973. Only the left side of the trackway is preserved.

Total digit angulation 79 degrees. Broad, rounded heel exhibits deep sole pad, extending from Digits II to V and reaching half-way along sole. Claws may be evident on Digits IV and V, although this is an extra-morphological feature.

Pes morphology. Pentadactyl, plantigrade pes of length 90–94 mm, width 50–57 mm. Deeply impressed, so that Digits I–II are not distinctly separate. Digits long (II longest, up to 91 mm), slender and distally tapering. Digits I–III slightly laterally curving, Digit IV lies at 40 degrees and tip of Digit V lies at 90 degrees to trackway midline. Mean total digit angulation 66 degrees. Heel broad, elongate, and tapering, with deep, rounded sole pad extending from Digits I–III, reaching halfway along sole. Claws are evident on Digits IV and V. Pes pace measured at 28 mm.

Trackway structure. Manus–pes overlap is variable (1–7 mm). Both manus and pes prints face forwards with respect to trackway midline. Faint, straight tail trace, 10 mm wide, runs at 35 mm from interior extent of manus. Trackwidth (107–132 mm) is approximately three times manus footwidth. Manus stride 92 mm, manus pace 19 mm.

Remarks. Dimetropus leisnerianus was first described by Geinitz (1863) under the name *Saurichnites leisnerianus*, and later by Pabst (1895) under the name *Ichnium acrodactylum*. Whilst the type specimens of *S. leisnerianus* and *I. acrodactylum* appear superficially different, they are now considered to be variants of the trackways of a single type of trackmaker. Haubold (1971a) re-assigned *S. leisnerianus* to *Dimetropus*, and drew up a list of criteria with which to identify the new ichnotaxon *Dimetropus leisnerianus*, and a list of possible extra-morphological features. Consequently, *D. leisnerianus* encompasses a large variation within specimens, and includes undertracks. The specimens figured in Fichter (1983b, c, 1984) are considered to be possible undertracks, although they are not figured sufficiently to enable certain identification. *Dimetropus salopensis* (Haubold and Sarjeant 1973, 1974; Text-fig. 9) is here re-assigned to *D. leisnerianus*, as the morphological variance of *D. salopensis* is encompassed by that of *D. leisnerianus*.

Ichnogenus HYLOIDICHNUS Gilmore, 1927

1927   *Hyloidichnus* Gilmore, p. 51.
1927   *Hylopus* Gilmore, pp. 45–51.
1996   *Gilmoreichnus* Haubold, pp. 33–34.

Type ichnospecies. Hyloidichnus bifurcatus Gilmore, 1927. Lower Permian, Hermit Shale, Hermit Gorge, Grand Canyon National Park, Arizona, USA. Type specimen USNM 11518.

Included ichnospecies. Hyloidichnus major (Heyler and Lessertisseur, 1963), from the Lower Permian of Lodève, Herault, France.

Diagnosis (emended from Gilmore 1927; Haubold 1971*a*). Narrow, quadrupedal trackway. Pace angulation over 100 degrees on average, but manus pace angulation higher than pes pace angulation. Partial primary manus–pes overlap. Both manus and pes impressions pentadactyl and semi-plantigrade with narrow sole. Digit lengths increase I–II–III–IV, V equal to I, digits IV and V usually shallow and incompletely impressed. Digits are straight and slender; digit tips frequently have bifurcated ends (extramorphological feature). Pes length up to 66 mm, pes stride:footlength ratio between 4:1 and 5:1.

Remarks. Hyloidichnus was erected by Gilmore (1927, p. 51) with the type ichnospecies, *H. bifurcatus*, described as 'quadrupedal, semi-digitigrade. Both manus and pes have five digits. Manus smaller than pes and placed in front of hindfoot. Toes terminated either with pellets or having bifurcated ends'. The bifurcated digit tips of *H. bifurcatus* are characteristic of *Hyloidichnus* but not always present, and may be present on the longer digits of other ichnotaxa, such as *Dromopus* (Haubold *et al*. 1996). The resemblance of *H. bifurcatus* to *Hylopus hermitanus* was noted by Gilmore (1927), and *H. hermitanus* was later selected as the type ichnospecies of *Gilmoreichnus* (Haubold 1971*a*). Subsequent authors (e.g. Haubold 1971*b*) have also recognized the similarity, which had previously led to the 'lumping' of *Hyloidichnus* and *Gilmoreichnus* into a single ichnogenus. Despite claims that *Hyloidichnus* and *Gilmoreichnus* are in fact distinct ichnogenera (e.g. Haubold *et al*. 1996), many authors have assigned specimens of *Hyloidichnus bifurcatus* to *Gilmoreichnus hermitanus*, due to the similarity between these ichnospecies (e.g. Haubold 1971*b*; Haubold *et al*. 1996; Lucas *et al*. 1996). The two ichnogenera are here considered synonymous. Haubold (1971*a*) also noted the similarity between *Hyloidichnus* and the ichnogenera *Amphisauroides* and *Amphisauropus*, and originally attributed these tracks to the Seymouriamorpha stem-amniotes, suggesting that the trackmaker could be any of the biotaxa *Phanerosaurus*, *Diadectes*, *Diasparactus*, *Discosauriscus* or *Melanerpeton*. Here, *H. arnhardti* Haubold, 1973, is considered to be a specimen of *Amphisauropus*, after viewing the type specimen. However, recent work (Haubold 2000) has indicated that *Hyloidichnus* is most likely to have been produced by a representative of either a pelycosaurian group or, most likely, the Eothyrididae, a basal synapsid group. The appearance of *H. bifurcatus* in the Upper Carboniferous Alveley ichno-assemblage extends the known range of *Hyloidichnus* from the mid-Gzelian back into the Upper Moscovian.

Stratigraphical range. Upper Moscovian to Upper Artinskian.

Hyloidichnus? *bifurcatus* Gilmore, 1927

Text-figure 10

* v	1927	*Hyloidichnus bifurcatus* Gilmore, pp. 52–53, pl. 16, text-fig. 25.
v	1927	*Hylopus hermitanus* Gilmore, pp. 46–51, text-fig. 21, pl. 15.
v ?	1927	*Collettosaurus pentadactylus* Gilmore, pp. 60–63, text-fig. 32, pl. 19, fig. 1.
v	1928	*Hyloidichnus whitei* Gilmore, pp. 5–7, pl. 3, figs 1–2, text-fig. 3.
	1954	'*Procolophonichnium*'? *microdactylum* (Pabst); Müller, pp. 190–195, pl. 16, figs 1–2, text-fig. 1.
v	1971*a*	*Hyloidichnus bifurcatus* Gilmore; Haubold, p. 22, text-fig. 18.9.
v	1971*a*	*Hyloidichnus whitei* Gilmore; Haubold, p. 22, text-fig. 18.7 [*kop*. Gilmore 1928, text-fig. 3].
?	1971*a*	*Hyloidichnus major* Heyler and Lessertisseur; Haubold, p. 22, text-fig. 18.8.
	1971*b*	*Varanopus microdactylus* (Pabst 1896); Haubold, pp. 27–28, pl. 7, fig. 2; pl. 17.
	1971*b*	*Gilmoreichnus hermitanus* (Gilmore); Haubold, pp. 33–34, text-figs 20.1, 21A, 22A–B.
?	1971*a*	*Varanopus microdactylus* Moodie; Haubold, p. 30, text-fig. 19.1.
	1971*b*	*Hyloidichnus* sp. nov.; Haubold, p. 24, pl. 2, fig. 2.

1983*a*	*Varanopus microdactylus* (Pabst); Fichter, pp. 136–147, text-figs 6A–D, 7B, 8A–B, 9A–B.
? 1983*b*	*Hyloidichnus arnhardti* Haubold; Fichter, pp. 97–108, text-figs 68A–B, 69A–B.
p 1987	*Hyloidichnus major* (Heyler and Lessertisseur); Gand, p. 139, pl. 4B, D (*non* C), text-figs 38–42, tables 66–79.
1996	*Gilmoreichnus hermitanus* (Gilmore); Haubold *et al.*, pp. 149–154, text-figs 17A–C, 18C.
v 1996	*Hyloidichnus bifurcatus* Gilmore; Lucas *et al.*, p. 273, text-fig. 4D.
v non 1996	*Gilmoreichnus hermitanus* (Gilmore); Lucas *et al.*, p. 273, text-fig. 5C.
1996	*Hyloidichnus bifurcatus* Gilmore; Hunt *et al.*, p. 296, text-fig. 3C.
v 1996	*Hyloidichnus bifurcatus* Gilmore; Schult, p. 145, text-figs 8A–B, 9A.
v non 1996	*Hyloidichnus bifurcatus* Gilmore; Schult, p. 145, text-fig. 9D.
1998	'*Varanopus*' *microdactylus* (Pabst); Haubold, pp. 10–11, text-fig. 6A–C.

Material. BU 3702.

Description

Pes morphology. Pentadactyl, plantigrade pes; square heel of 39 mm wide. Impression strength equal across footprint, with deeper sole pads preserved at digit bases, where digits meet heel. Digits long and slender, with bifurcating tips, an acknowledged extra-morphological feature. Digit lengths increase from I to IV (Digit IV 35 mm in length from hypex to digit tip); Digit V approximately equal in length to Digit I. Digits straight, with total digit angulation of 104 degrees. Footlength 66 mm, footwidth 56 mm.

Remarks. Gilmore (1928) erected *H. whitei* (holotype specimen USNM 11692), from the Hermit Shale of Arizona, based on the appearance of bifurcated digits upon the manus (*H. bifurcatus* exhibits bifurcated tips only on the pes). However, experiments with modern amphibians and reptiles (Peabody 1959) have shown that this bifurcation is a purely extra-morphological feature, and therefore *H. whitei* is considered to be synonymous with *H. bifurcatus*. Although *H. major* Heyler and Lessertisseur, 1963 is considered to be a separate ichnospecies, the specimen figured by Haubold (1971) is *H. bifurcatus*. The ichnospecies *H. major* was mentioned in a review of Early Permian ichnotaxa by Haubold and Katzung (1972), although it was not formally described by Haubold until 1973.


Ichnogenus ICHNIOTHERIUM Pohlig, 1892

Type ichnospecies. Saurichnites cottae Pohlig, 1885. Lower Permian, Tambach Formation, Thüringer Wald, Germany. Type specimen GN 1351.

Included ichnospecies. Possibly *Saurichnites rittlerianum* (Hochstetter, 1868), from the Lower Permian Braunau Formation of Oslavan and Semil, Czech Republic. *I. aequalis* (Heyler and Lessertisseur, 1963), from the Lower Permian of Lodève, southern France; *I. willsi* Haubold and Sarjeant, 1973, from the Upper Carboniferous of Alveley, southern Shropshire, UK.

Diagnosis. Quadrupedal trackway with a narrow trackwidth. Depending on the stride length, pes pace angulation 80–135 degrees, with an average value of 90–100 degrees. Stride:footlength ratio normally 3·5:1, with a maximum value of 5:1. Manus impression further turned towards trackway midline than pes. Manus and pes both pentadactyl and plantigrade. Pes and manus digits are robust and sturdy, IV longest, V almost as long. Pes length approximately equal to width, with an oval, inwards extending heel, usually deeply impressed and sharply defined. Pes footlength up to 140 mm. Manus smaller than pes, but relatively broader. Manus sole less strongly defined than heel.

Remarks. Ichniotherium has recently been attributed to the Diadectidae (Haubold 2000), following the discovery of diadectid skeletal material in conjunction with the ichnospecies *Ichniotherium cottae* at the Bromacker locality, Thüringen, Germany (Eberth *et al.* 2000). The blunt claws, strong digits and small sole (representative of the carpus) are, however, more characteristic of the Edaphosauria (Haubold 1971*a*). Based upon the foot morphology of *Casea*, *Cotylorhynchus* and *Ennantosaurus*, Haubold (1971*a*)
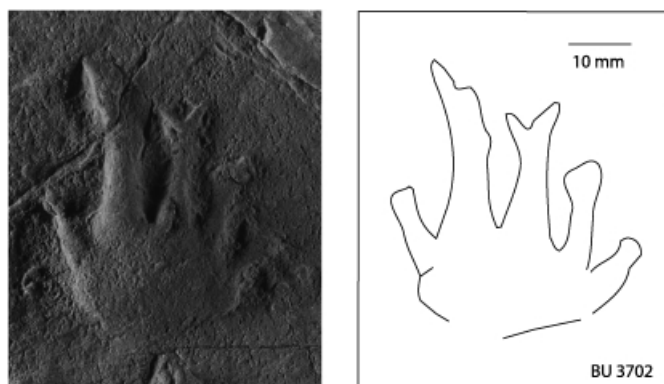
TEXT-FIG. 10. *Hyloidichnus*? *bifurcatus* Gilmore, 1927; Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. BU 3702, isolated pes impression.

suggested that *Ichniotherium* may have been produced by Early Permian members of the Caseidea. However, the most recent attribution of *Ichniotherium* to the biotaxon *Diadectes* will be followed here. There is some debate over the genus-level taxonomy of *Saurichnites* and *Ichniotherium*, but *Ichniotherium* is retained here in the interests of stability.

Stratigraphical range. Upper Moscovian to mid-Kungurian.

Ichniotherium willsi Haubold and Sarjeant, 1973

Text-figure 11

v * 1973   *Ichniotherium willsi* Haubold and Sarjeant, pp. 900–904, text-fig. 3.1.
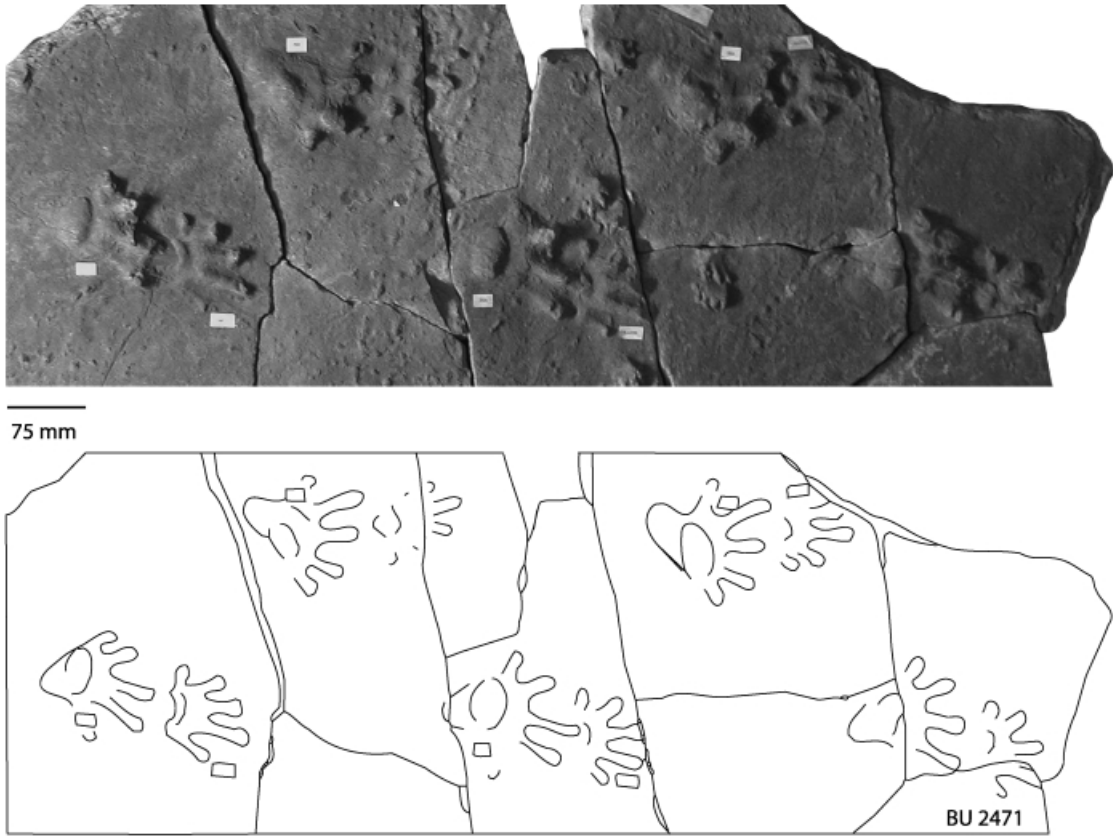 v 1974   *Ichniotherium willsi* Haubold and Sarjeant; Haubold and Sarjeant, p. 262, text-fig. 3 (left).

Material. BU 2471a; 3703a.

Diagnosis. Ichnospecies of *Ichniotherium* that is plantigrade with an elongate, laterally extended sole bearing small, deep pad. Sole in two sections, the first extending from the digits I to IV, the second extending from digit V. Digit lengths increase I–II–III–IV, V equals II.

Description

Manus morphology. Pentadactyl, plantigrade manus with slight increase in impression strength distally along digits. Digits II, III and IV deeply impressed, especially at base where digits meet sole; I and V fainter. Digits straight, relatively long in proportion to footlength (75–83 mm, footwidth 78–96 mm), tips enlarged. Longer digits (IV longest, up to 49 mm from hypex to digit tip) appear slender, whilst shorter digits appear broader, as digit breadth remains fairly consistent (8–15 mm at digit bases). Some digits show very faintly defined phalanges. Mean total digit angulation 141 degrees (range 126–152 degrees). Sole characterized by lunate pad at base of digits, curving convexly towards digit tips. No other sole pads impressed, heel obscured by overlapping pes. Heel 23–45 mm long, 23–28 mm wide.

Pes morphology. Pentadactyl, plantigrade pes. Impression strength greater than manus; also larger than manus (footlength 121–128 mm, footwidth 91–95 mm). Digits short in proportion to footlength, broad and straight, tips enlarged. Digit V often represented only by enlarged tip. Digit III longest (up to 43 mm from hypex to digit tip). Mean total digit angulation 86 degrees, range 80–93 degrees. Deep imprinting of digits gives impression of intra-digital webbing. Although this is consistent throughout the trackway, it is likely to be an extra-morphological feature. The

75 mm

BU 2471

TEXT-FIG. 11. *Ichniotherium willsi* Haubold and Sarjeant, 1973; Alveley Member, Salop Formation, Warwickshire Group; Westphalian D, Shropshire, UK. A, BU 2471. B, selected manus-pes set, BU 2471.

presence of claws suggested by ridged, sloped imprint at front of each digit tip, although this may also be an extra-morphological feature. Sole is marked by large, oval pad, placed half-way down sole, width approximating to footwidth, impressed as deeply as digit tips. Remainder of sole elongate with rounded heel, laterally inclined, faintly imprinted. Heel length 84–87 mm, heel width 16–18 mm.

Trackway structure. Distance between manus and pes varies throughout trackway length, with maximum overlap value of 12 mm; maximum distance between manus heel and pes digit III tip 14 mm. Trackwidth very low in comparison to footlength (manus trackwidth 177–192 mm, pes trackwidth 158–174 mm), mean interior trackwidth of 75 mm measures less than mean pes width of 93 mm, with relatively high stride:trackwidth (mean manus value 2·0, mean pes value 2·3). Manus prints forward facing or medially inclined (manus print angulation 80–87 degrees), pes prints laterally inclined (pes print angulation 97–104 degrees). Manus pace angulation 91–94 mm, pes pace angulation 94–111 mm. Manus stride 372–385 mm, manus pace 309–312 mm, stride:footlength 4·5 to 4·8. Pes stride 392–395 mm, pes pace 244–270 mm.

Remarks. Ichniotherium willsi shows considerable morphological differences from *I. cottae* of the Lower Permian of Germany. Digit arrangement and heel shape vary considerably between the two ichnospecies. Although the characteristic extension to the heel seen in *I. willsi* is seen on a small number of specimens of *I. cottae* from the Lower Permian Tambach Formation of Germany, the heel of *I. willsi* extends to a much greater extent. Whilst this may be a purely extra-morphological feature, the difference in digit morphology is such that *I. willsi* is not considered to be synonymous with *I. cottae*.

## COMPARISON WITH OTHER EUROPEAN MATERIAL

The Alveley ichno-assemblage is one of a number of Late Palaeozoic terrestrial tetrapod localities found along the southern margin of the ancient Euramerican continent (Panchen 1980), forming a belt that stretches across present day North America, through Britain into northern Europe. This distribution coincides with the Early Permian palaeoequator, which may indicate that terrestrial tetrapods had a principally palaeotropical distribution throughout this period. However, as different terrestrial environments within the Late Carboniferous – Early Permian are demonstrably characterized by different ichnogenera, it is appropriate to compare the ichnofauna from Alveley with ichno-assemblages from comparable sedimentary settings, as outlined below.

The major Early Permian tracksites of Europe occur predominantly within the Upper Rotliegend of the Tambach, Oberhof, Goldlauter, Manebach and Gehren formations, Thüringen, and the Kreuznach and Standenbühl formations in the Saar-Nahe Basin region of Germany (Haubold 1970, 1971*b*, 1973, 1998, 2000; Haubold and Katzung 1975; Fichter 1983*a, b*, 1994; Boy and Fichter 1988; Haubold and Stapf 1998; Eberth *et al.* 2000). Other, less extensive material occurs in the sedimentary basins of the Massif Central, southern France (Rabejac Formation, Lodève and Saint-Affrique; Haubold 1971*a*, 2000; Haubold and Katzung, 1975; Gand 1985; Demathieu and Gand 1992; Gand *et al.* 1995), the Alps of northern Italy (Collio Formation, Tregiovo; Boy and Fichter 1988; Gand *et al.* 1995; Haubold 2000), the Krkonose Basin, Czech Republic, and the Inner Sudeten basins of Russia and Poland (Haubold and Katzung 1975). These localities typically comprise fine-grained, siliciclastic sediments, although minor dune ichnofacies are present. The reported ichno-assemblages include the principal components *Limnopus (Batrachichnus)*, *Limnopus (Limnopus)*, *Amphisauropus, Dimetropus, Dromopus, Hyloidichnus* and *Ichniotherium*, which are all widely distributed across the Lower Permian of Europe (Haubold 1970, 1971*a*, 1971*b*, 1973, 1998, 2000; Haubold and Katzung 1975; Conti *et al.* 1977; Holub and Kozur 1981; Fichter 1983*a*, 1983*b*, 1994; Gand 1985; Boy and Fichter 1988; Demathieu and Gand 1992; Haubold and Stapf 1998). Other, minor components vary between sites, and ichnogenera such as *Chelichnus, Tambachichnium* and *Varanopus* may or may not be present, depending upon the quality of preservation and extent of excavation.

The relative diversity and frequency of ichnotaxa at any one site is heavily influenced by environmental factors, in particular geographical and sedimentological setting. However, no Early Permian ichno-assemblage displays such a marked dominance of temnospondyl amphibian trackways of a single ichnogenus, in conjunction with an exceptionally low diversity and number of amniote trackways, as that found within the Alveley ichno-assemblage. It is possible that amniotes were present in Late Carboniferous environments to the same extent as in Early Permian communities, but are not represented within the Alveley ichno-assemblage due to sedimentological factors or an unsuitable environmental setting. However, Late Carboniferous skeletal assemblages from similar sedimentary environments, such as the Westphalian D material from Nýřany, Czech Republic, exhibit a dominance of one or two biospecies of small, semi-aquatic stem-lissamphibia, with a reduced number of amniotes (Milner 1980). Therefore, it is hypothesized that the prominence of *Limnopus* within the Alveley assemblage is non-artefactual.

CONCLUSIONS

1. Phenetic analysis has been used to identify ichnotaxa within a hitherto partially described assemblage. The use of numerical methods increased the accuracy of ichnofaunal identification, with the intention of providing a stable ichnotaxonomy upon which further classifications, predictions and comparisons can be based. Using this method, the validity of previous vertebrate trackway designations is open to investigation under phenetic multivariate analysis with the use of the corresponding type specimens. In addition, undescribed trackways from other problematical ichno-assemblages can be more reliably classified by numerical comparison of their character morphology with that of type specimens associated with the ichnotaxa identified during *a priori* sorting. Phenetic analysis is a useful tool with which to rigorously test and refine ichnotaxonomic groupings, as exemplified by the numerical study of the Alveley ichno-assemblage. With the aid of such statistical, objective methods, the ichnotaxonomy of this assemblage has
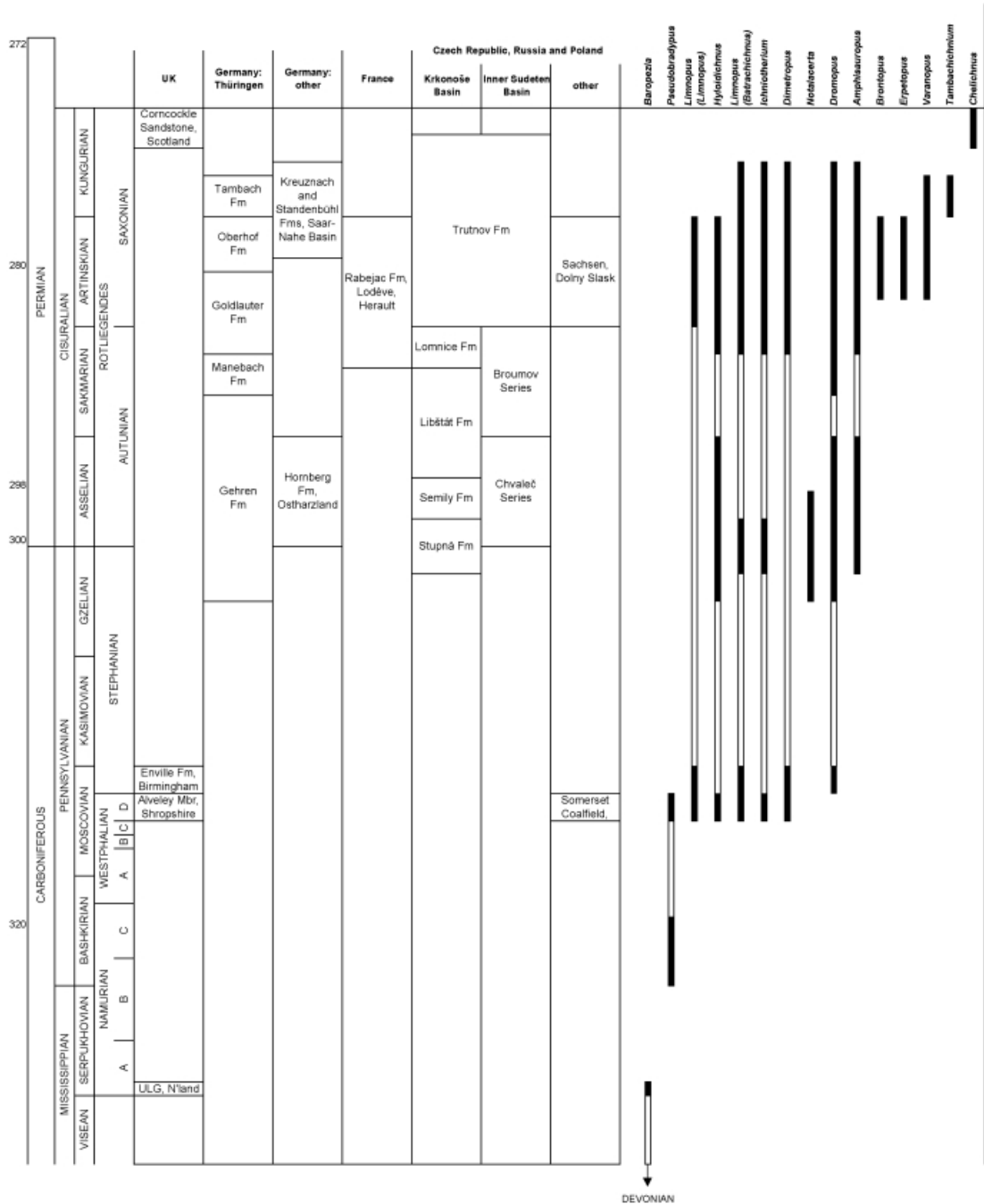
TEXT-FIG. 12. Stratigraphical distribution of tetrapod ichnotaxa through the Late Carboniferous and Early Permian of Europe, illustrating the age of major trackway-bearing formations. The Alveley ichno-assemblage extends the stratigraphical ranges of a number of predominantly Permian ichnotaxa back into the mid-Late Carboniferous. Solid black lines indicate ichnotaxon appearance, white lines indicate ghost ranges, grey lines indicate uncertain ranges due to indeterminate ichnotaxon classification. Mbr, Member; Fm, Formation; Gp, Group; ULG, Upper Limestone Group; N'land, Northumberland; *L.* (*Limnopus*), *Limnopus* (*Limnopus*); *L.* (*Batrachichnus*), *Limnopus* (*Batrachichnus*). Data sources for individual columns: Haubold 1971*a*, *b*, 1998, 2000; Haubold and Katzung 1975; Boy and Fichter 1988; Milner 1994; Scarboro and Tucker 1995; McKeever and Haubold 1996; Clack 1997; Haubold and Stapf 1998.

been stabilized, enabling an accurate estimation of ichnospecies diversity, under which clear comparisons may be made with Early Permian ichnofaunas. Importantly, however, as with the use of all numerical methods in palaeontology, multivariate analysis must not be relied upon in isolation for vertebrate trackway identification and classification. Ichnotaxonomic schemes must always be founded upon detailed study of the original material with the *support* of statistical, numerical evidence.

2. Close examination of the results of multivariate cluster analyses shows that the difference between ichnospecies can often be based predominantly upon size, particularly within *Limnopus*. Whilst this is a useful character with which to describe morphological trends within the entire dataset, it is not suitable as an ichnotaxonomically diagnostic character. Ichnogenera, however, are more congruent with biotaxa. This agrees with similar statements made by workers on other trackway groups (e.g. Baird 1952; Weems 1990). Therefore, although the concept of trackway ichnospecies is essential for accurate specimen description, ichnogenera alone should be used for working comparisons with skeletal and other ichnological material.

3. The ichnofauna of the Late Carboniferous assemblage from Alveley, Shropshire, UK, is dominated by trackways of the ichnogenus *Limnopus* (95 per cent of the total ichnofauna), which is here redefined to incorporate two ichnosubgenera, *Limnopus* (*Limnopus*) and *Limnopus* (*Batrachichnus*). These ichnosubgenera are introduced here as a means of expressing the significant morphological similarity between *Limnopus* and *Batrachichnus*, whilst recognising that they are most likely of different trackmaker origin.

4. This study shows that the material from Alveley comprises six ichnospecies within four ichnogenera. These have been identified as *Ichniotherium willsi* (1 specimen), *Hyloidichnus*? *bifurcatus* (1 specimen), *Dimetropus leisnerianus* (8 specimens), *Limnopus* (*Batrachichnus*) *plainvillensis* (26 specimens), *L.* (*Batrachichnus*) *salamandroides* (157 specimens) and *L.* (*Limnopus*) *vagus* (20 specimens). The ichnotaxa recognized represent an early marginal freshwater–terrestrial tetrapod community, developed shortly after the appearance of the amniotes during the early Westphalian (Upper Bashkirian–Lower Moscovian). The ichnofauna is characterised by a high frequency and low diversity of stem-lissamphibian tetrapods of the paraphyletic group Temnospondyli (95 per cent of the trackways), as represented by the ichnogenus *Limnopus*. The ichnogenera *Dimetropus*, *Ichniotherium* and *Hyloidichnus* represent a smaller, relatively low diversity amniote assemblage (5 per cent) of inferred sphenacodontids, diadectids and eothyrids respectively (Haubold 2000). These are typical Late Carboniferous–Early Permian red-bed ichnotaxa, as recognized by Haubold and Stapf (1998). In comparison, typical dune facies ichno-assemblages of the period are composed predominantly of *Chelichnus* and *Dromopus* trackways (Morales and Haubold 1995; Haubold *et al*. 1996; Haubold and Stapf 1998).

5. The Alveley marginal-terrestrial ichno-assemblage extends knowledge of Palaeozoic ichnofaunas back into the mid-Late Carboniferous, a period for which little is known regarding terrestrial tetrapod communities, in comparison with well-documented Permian and Triassic faunas. Most of the ichnogenera in the Westphalian D (mid-Late Carboniferous) Alveley assemblage are otherwise restricted to the latest Carboniferous and Permian, and the assemblage produces significant stratigraphic range extensions in the amniote and stem-lissamphibian trackway record (Text-fig. 12).

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APPENDIX

Definition of continuous and binary characters
#, suspected extra-morphological features not used in multivariate cluster analysis.

Continuous (quantitative) characters

1. MFL, PFL: footlength (manus, pes). Length of foot from centre of base of heel to level of tip of longest digit. Measured along line of digit III.

2. MFW, PFW: footwidth (manus, pes). Width of foot between tips of two outer digits.

3. MS, PS: stride (manus, pes). Distance between tip of digit III of a footprint and tip of digit III of preceding, corresponding print of foot on the same side of the body. Represented in locomotion by 'a pendular movement of the leg, which is completed when the foot regains its starting position' (Leonardi 1987, p. 65). The distance covered during this movement is the distance measured upon the resulting trackway. Hence, the value of stride is directly proportional to trackmaker velocity.

4. MP, PP: pace (manus, pes). Distance between tip of digit III of a footprint and tip of digit III of corresponding print of foot on other side of body. In other words, the distance between impression of the right and left manus, or right and left pes.

5. M–PD: manus–pes distance. Distance between tip of digit III of manus and tip of digit III of pes, within a single manus–pes set.

6. MTW, PTW: trackwidth (manus, pes). Width of trackway measured between tip of digit III of a footprint and line joining tips of digit III of corresponding print of foot on other side of body.

7. Mα, Pα: pace angulation (manus, pes). Angle between two consecutive measurements of pace. This value is directly proportional to trackmaker velocity. Observations on modern species have shown that pace angulation may vary according to age, sex, health (especially bone fractures) and gait. Therefore pace angulation is not reliable as a taxonomically diagnostic character. Note that manus pace angulation is greater than pes pace angulation if manus prints are closer to the trackway midline than the pes prints.

8. Mγ, Pγ: print angulation (manus, pes). Angle nearest trackway midline, between line cutting trackway midline perpendicularly and meeting footprint at heel base, and line dissecting digit III, passing through tip of digit III and heel base. The precise value of print angulation may vary with the speed of the trackmaker. However, the general direction of print angulation (prints facing towards the trackway midline, away from the trackway midline, or parallel with the trackway midline) may still be used diagnostically.

9. M–PO: manus–pes overlap. The overlap of the manus print by the succeeding pes print. Calculated using manus footlength − manus–pes distance. Negative number indicates no overlap, i.e. a positive distance between manus heel and pes digit III.

10. MθI, MθII, MθIII, PθI, PθII etc.: digit divarification (manus, pes, digits I–IV/V). Angle between consecutive digits. Angle focus at base of digit I. Known to vary widely across groups (Peabody 1959) and therefore not suitable as a diagnostic character.

11. MDI, MDII, MDIII, PDI, PDII etc.: digit length (manus, pes, digits I–IV/V). Length of digit from base at heel to tip, measured along centre of digit.

12. MHXI, MHXII, MHXIII, PHXI, PHXII, etc.: digit hypex lengths (manus, pes, digits I–IV/V). Also known as the 'free length'. Length of digit from mid-point of the distance between two adjacent hypices to the digit tip.

13. # MBI, MBII, MBIII, PBI, PBII, etc.: basal digit width (manus, pes, digits I–IV/V). Width of digit at line passing through two adjacent hypices, with the measured digit at the centre. Values are easily altered by extra-morphological features. This can be particularly misleading in smaller trackways, as any extra-morphological differences are more noticeable, occupying a larger proportion of the total value.

14. # MDTI, MDTII, MDTIII, PDTI, PDTII, etc.: digit tip width (manus, pes, digits I–IV/V). Width of digit measured 2 mm from digit tip. As above, values are easily altered by extra morphological features, and this can be particularly misleading in smaller trackways.

15. MHL, PHL: heel length (manus, pes). Length of heel from base to horizontal line passing through lowest observed bifurcation points between digits II and III, and digits III and IV (in five digit prints), or to lowest observed bifurcation between digits II and III in four digit prints. Used only for plantigrade prints.

16. MHW, PHW: heel width (manus, pes). Width of heel at base, measured 2 mm from heel base if heel has a tapering or pointed morphology. Used only for plantigrade prints.

17. ST:FL: stride: footlength ratio (manus, pes)

Binary (qualitative) characters
Note that absences (due to poor preservation or absent sections of trackway) are not indicated by (0), but are instead not recorded. This is to prevent the clustering of characters recording a state of (1) together with absent characters.

1. NO: digit number. Number of digits preserved and distinguishable: three (3); four (4); five (5).

2. # GRD: footprint grade. Reflects the extent to which the heel is used in locomotion, but may be affected by consistency of substrate and level of preservation of footprint. Tracks may be digitigrade (digit preserved only), semi-digitigrade (hypex length of digits and proximal part of heel preserved only) or plantigrade (entire foot preserved, including heel): digitigrade (1); semi-digitigrade (2); plantigrade (3).

3. # CRV: digit curvature. Measured for each digit on a print. May be affected by consistency of substrate or speed of trackmaker. Known to vary widely across groups (Peabody 1959): curved towards trackway midline (1); straight (2); curved outwards from trackway midline (3).

4. # DTM: digit tip morphology. Amphibians tend to have rounded digit tips whilst amniote trackways often show pointed digit tips. However, digit tip morphology is externally affected by substrate consistency, and the shape of the print may be altered as the foot is removed from the ground: rounded (1); pointed (2).

5. # DBM: digit breadth morphology. Observed along digit length, from hypex to digit tip. Easily altered in appearance by extra-morphological features: tapering (1); uniform (2); widening (3).

6. # HM: heel morphology. Shape of heel at base. May be affected by level of preservation of footprint, trackmaker speed and substrate consistency: rounded (1); tapering (2); square (3).

7. # SPM: sole pad morphology. Amniote tracks often preserve sole pads, associated with protection of ossified carpals and tarsals; this feature is absent in amphibians. However, varying levels of preservation and substrate consistency may lead to the appearance of sole pads in amphibian tracks: absent (1); present (2).

8. # SM: sole morphology. Refers to length of sole. Values may be affected by speed of trackmaker, substrate condition and method of preservation: short (1); elongate (2).

9. TAIL: tail trace: absent (0); present (1).

10. TRK: trackway pattern: regular (1); irregular (2).