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Stratigraphic and geographic distribution of dinosaur tracks in the UK

Abbreviated title: UK dinosaur tracks

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Abstract

Dinosaur tracks are a key means of determining the palaeoecology and distribution of dinosaurs through time. They provide a highly complementary information source to the body (skeletal) fossil record but differ in preserving direct evidence of animals' interactions with their environment. The UK has a rich history of ~200 yrs of dinosaur track discovery but no recent synthesis exists. Here, we present a new dataset of dinosaur tracks in the UK. This dataset shows a close correlation between the distribution of terrestrial sediments and the preservation of dinosaur tracks through the Mesozoic, providing discrete snapshots into dinosaur communities in the Upper Triassic, Middle Jurassic and Lower Cretaceous. The dinosaur track record shows similar broad patterns of diversity and relative abundance of the major dinosaur groups (Theropoda, Sauropodomorpha, Ornithopoda, and Thyreophora) through time to the body fossil record, although differs in that body fossils are found (albeit infrequently) in marine sediments. There is a broad trend towards higher numbers of track occurrences through time and a notable increase in the relative abundance of ornithopod tracks following the Jurassic-Cretaceous boundary. The track record remains an underutilised resource with the potential to provide a much fuller view of Mesozoic dinosaur ecosystems.

Keywords: Dinosaur, UK, track, footprint, Mesozoic

Dinosaurs were a hugely successful group of vertebrates with a wide array of morphologies and ecologies that dominated terrestrial ecosystems globally during much of the Mesozoic (Brusatte 2012; Benson 2018). They are best and most famously known from their skeletal remains (body fossils) which provide key evidence of their life and appearance. However, skeletal material is often incomplete, and can be difficult to find, collect, prepare, and study, leading to large uncertainties in the appearance or palaeobiology of some species (e.g., Lee *et al*. 2014; Brusatte 2021) or long-time lags between fossil discovery and publication (e.g., Forster *et al*. 2022). A highly complementary source of information is that provided by the tracks that dinosaurs left behind (e.g., trace or ichno-fossils), which provide direct evidence of behaviour and of an animal living in a particular environment, given that unlike bones, tracks are rarely transported. Dinosaur tracks and trackways have therefore provided major insights into aspects of dinosaur distribution and palaeobiology such as mode and speed of locomotion, anatomy, behaviour, life histories and interactions (e.g., Thulborn & Wade 1979; Thulborn 1990; Lockley 1991; Day *et al*. 2002a,b; Falkingham & Gatesy 2014; Falkingham *et al*. 2016). Furthermore, tracks are often more abundant than body fossils given that organisms only possess one skeleton but may leave many millions of tracks in their lifetime, which often occur in stratigraphic levels where bone is rarely fossilised, filling key gaps in the fossil record (Crimes & Droser 1992; Lockley 1998; Carrano & Wilson 2001).

Whilst highly useful for reconstructing past life and environments, tracks also present some challenges. Dinosaur tracks can often be assigned to a broad taxonomic group, e.g., Theropoda or Ornithopoda, relatively easily but can rarely (if ever) be definitively attributed to an individual species or even genus. This is in part because of similarities in the anatomy of the foot skeleton within different dinosaur groups as well as that the final track morphology is the product of multiple factors including the original foot anatomy, preservation mode, environment, and sediment characteristics (e.g., Jackson *et al*. 2009, 2010; Falkingham & Gatesy 2014; Turner *et al*. 2020). Whilst early workers (e.g., Hitchcock, 1945) tended to refer to and name the trackmakers rather than the tracks themselves, in time a separate ichnotaxonomy was developed for track morphotypes that was not directly tied to morphological species (Lockley 2007; review in Gatesy and Falkingham, 2020).

The field of dinosaur ichnology saw an initial surge in interest in the mid-19th century, including the earliest scientific report of tracks by Hitchcock (1836), prior to the recognition and naming of Dinosauria as a distinct group (Owen 1842). These early discoveries were followed by a long period of little research during the late 19th and early to middle 20th century (e.g., Romano & Whyte, 2003). However, since the 1980s there has been somewhat of a “dinosaur track renaissance”, in part driven by a shift from simply reporting track morphologies to directly using these as a source of important palaeoecological and palaeobiological information on dinosaurs as well as wider recognition of the value of the ichnological record (Thulborn 1990; Lockley 1991; Gillette & Lockley 1991; Falkingham *et al*. 2016). Indeed, the field has expanded dramatically, with new track sites regularly now reported globally (e.g., Falkingham *et al*. 2022; Klein *et al*. 2022; Lallensack *et al*. 2022a; Romilio *et al*. 2022; Xing *et al*. 2022) and increasingly diverse approaches applied to extract value from this record (e.g., McCrea *et al*. 2015; Bernardi *et al*. 2018; Falkingham *et al*. 2020; Turner *et al.* 2020; Lockley & Schumacher 2021).

There is a long history of dinosaur tracks being reported and studied in the UK, from the mid-19th century to the present day, reflecting the excellent exposure of Mesozoic rocks through many parts of the UK and a long history of public and scientific interest in fossils (Beckles 1851; Sarjeant 1974; Delair & Sarjeant 1985; Benton & Spencer 1995). Perhaps most notably, this includes the first direct link in the scientific literature between dinosaurs and their tracks made based on the attribution of tridactyl tracks from the Isle of Wight to the ornithopod *Iguanodon* (Beckles, 1862). Reviews of the UK vertebrate track record were produced by Sarjeant (1974) and Delair and Sarjeant (1985), and information on significant sites was also summarised as part of the Geological Conservation Review Series (Benton & Spencer 1995). However, these records were largely reports of individual track occurrences, covering a wide range of vertebrates including dinosaurs, and lacked a wider and integrated analysis of the size, shape, and value of the dinosaur track record. Since these works there has been a wealth of new tracks discovered across the UK, including in Wales (e.g., Lockley *et al*. 1996; Falkingham et al. 2022), southern England (e.g., Radley *et al.* 1998; Lockwood *et al*. 2014; Pond *et al.* 2014; Lockwood 2016; Shillito & Davies 2019; Hadland *et al*. 2021), Oxfordshire (e.g., Day et al. 2002a, b, 2004), North Yorkshire (e.g., Whyte & Romano 1993, 2001a,b; Romano & Whyte 2003; Whyte *et al*. 2007; Romano *et al*. 2018) and Scotland (e.g., Clark *et al*. 2004, 2005; Brusatte *et al*. 2016; dePolo *et al*. 2020). However, most research has continued to focus on regional syntheses and/or reporting of individual sites. Hence, here we present an up-to-date review of UK dinosaur tracks drawing explicit comparisons with the body fossil record, allowing us to assess: [1] the stratigraphic and geographic distribution of UK dinosaur tracks and the biases present within that record; and [2] the contribution of the ichnological record to our understanding of UK dinosaur communities.

Methods

We compiled a database of the UK non-avian dinosaur track record based on a comprehensive review of the published literature. We downloaded data on UK occurrences of non-avian dinosaur ichnotaxa from the Paleobiology Database (PBDB; paleobiodb.org) in July 2021. These data were then checked and verified against the original primary literature. The PBDB is missing many ichnological records because these have presumably received less attention for data entry than the dinosaur body fossil record. As a result, we supplemented this with comprehensive literature searches.

Each entry in our new database (Supp. Table 1) represents a particular track morphology at a single stratigraphic horizon and geographically restricted locality (e.g., quarry or short section of coastline). Thus, this does not represent the total number of reported tracks in the UK—some sites, particularly coastal sites dominated by finds in fallen blocks from the cliff face, have the same morphologies regularly reported such as from the coastal section exposing the Burniston Footprint Bed in Burniston, North Yorkshire (e.g., Black 1929, Whyte *et al*. 2006) and we record this as a single occurrence in our database. Data was recorded on modern geography (locality name, county, country, latitude and longitude), original geographic setting of the find (coastal, inland quarry, other inland settings such as river cuttings), published ichnotaxonomy identification, major clade to which the tracks belong (e.g., Theropoda, Sauropodomorpha, Ornithopoda, Thyreophora), whether the tracks are tridactyl or not, litho- and chronostratigraphy, sedimentology (mudstone, sandstone, conglomerate, limestone), depositional setting (using classification terms from the Paleobiology Database), and the key publication describing the occurrence. Analysis and visualisation of this dataset were conducted in R version 4.1.2 (R Core Team 2022). R code is available in the Supplementary Information. Time series plots were created using functions from the package geoscale 2.0.1 (Bell 2022).

In order to draw comparisons between the track and body fossil records for UK dinosaurs, occurrences of dinosaur body fossils were also downloaded from the PBDB and supplemented with 13 body fossil records from the recent literature, resulting in 454 occurrences in total (Supp. Table 2). Taxonomic data were added to classify these records into the same major clades as used for our track data (see above). Minor edits were made to stratigraphic age, location or environment as required for consistency with the track fossil record, obvious errors or based on more recent literature (these changes are highlighted in Supp. Table 2).

We made comparisons between the numbers of occurrences of tracks and body fossils through time (binned at stage level) for the major taxonomic groups that can be distinguished using the track record. To make comparisons between the track record and major patterns in the relative proportions of marine versus non-marine rocks (driven primarily by sea level changes), we drew on data from Smith & McGowan (2007; Supp. Table 3). Their dataset includes information on absolute geological map outcrop area for marine versus non-marine rocks at stage level through the Phanerozoic of England and Wales, allowing us to calculate relative proportions of marine versus non-marine rock outcrop area from the Upper Triassic to Upper Cretaceous.

To compare time series, we used generalized least-squares regression (GLS) with a first-order autoregressive model (corARMA) fitted to the data using the R package nlme (version 3.1-160; Pinheiro *et al*. 2022). GLS reduces the chance of overestimating the statistical significance of regression lines due to serial correlation. Time series were transformed prior to analysis by taking the natural log. We calculated likelihood-ratio-based pseudo-R^2 using the R package MuMIn (version 1.47.1; Bartoń 2022).

Results

Our new database contains 260 occurrences of dinosaur tracks or trackways in the UK. Summary data are provided in Figures 2-4 with detailed breakdowns by time interval, lithological and taxonomic group in Supplementary Figures 1-14. Dinosaur tracks are known from England, Scotland and Wales but are currently unknown from Northern Ireland (Figs 1, 2A, and Supp. Table 1). Dinosaur tracks have been identified in rocks from the Upper Triassic through to the Lower Cretaceous (Figs 2B, 3A). Over half (61.9%) of occurrences are from the Cretaceous, followed by the Jurassic (31.9%) and the Triassic (6.2%) (Figs 2B, 3A). The majority (85.8%) of the occurrences are in England with much smaller and approximately equal contributions from Scotland (8.1%) and Wales (6.2%) (Fig. 2A), reflecting the small geographic distribution of tracks in the latter two countries (Fig. 1). The geographic distribution can be broken up into four key areas: the Upper Triassic of South Wales, representing the Mercia Mudstone Group; the Middle Jurassic through Lower Cretaceous of southern England (Dorset, Oxfordshire, Isle of Wight, East Sussex, West Sussex, Surrey, Buckinghamshire, Kent), representing the Great Oolite, Purbeck, Wealden, and Lower Greensand groups; the Middle Jurassic of North Yorkshire, northern England, representing the Ravenscar Group; and the Middle Jurassic of the Isle of Skye in Scotland, representing the Great Estuarine Group. The geological units with the most abundant track occurrences are the Wealden (32.3%), Purbeck (26.9%) and Ravenscar (22.7%) groups (Fig. 2C). The vast majority of track occurrences (75.5%) are found in modern coastal settings (e.g., coastal bedding plane exposures, cliff sections, loose blocks), with a smaller number coming from quarries 20.1%) and other inland settings (e.g., rivers; 4.4%) (Fig. 2D).

UK dinosaur tracks are most commonly preserved in sandstones (59.6%) followed by limestones (28.7%) (Fig. 2E). Preservation in mudstones (9%) and conglomerates (2.7%) is much less frequent. The most common palaeoenvironmental setting is fluvial (39%) followed by coastal, incorporating environments described generally as coastal plus lagoonal (32.7%). Other terrestrial settings (alluvial, lacustrine) are much less frequent (Fig. 2F).

Approximately three-quarters (76%) of occurrences are of tridactyl tracks (produced by theropods and ornithopods), with non-tridactyl tracks (produced by most sauropodomorphs and thyreophorans) being much less common (24%) (Fig. 2G). Of our defined taxonomic groups, occurrences are dominated by Ornithopoda (38.8%) followed by Theropoda (19.2%) and Sauropodomorpha (15.4%), with the smallest proportion made up by Thyreophora (6.5%). A substantial proportion of tracks are either only described as tridactyl and could be produced by either theropods or ornithopods (5.4%) or are not identified beyond the level of Dinosauria (Fig. 2H).

Track occurrences through time (Fig. 3A) show three intervals of occurrences in the Upper Triassic (Norian stage; Mercia Mudstone Group), the Middle Jurassic (with greatest numbers of occurrences in the Aalenian and Bathonian stages; Ravenscar, Great Estuarine and Great Oolite groups) and the Lower Cretaceous (greatest numbers of occurrences in the Berriasian, Barremian and Albian; Purbeck, Wealden, and Lower Greensand groups). There are no tracks known for the Upper Triassic (Carnian), Lower Jurassic, latest Middle–Upper Jurassic (Callovian–Tithonian) or Upper Cretaceous. The highest peak of occurrences is in the Berriasian (resulting from the Purbeck Group and lowermost Wealden Group tracks) followed by smaller but similar peak numbers of occurrences in the Barremian, the Bathonian, and the Aalenian. Even smaller occurrence peaks are present in the Norian and the Albian. Sauropodomorphs and theropods dominate the record during the Triassic, when ornithopods and thyreophorans are absent from the track record. All four groups are present in the Middle Jurassic, although sauropodomorphs and theropods remain the most abundant and thyreophoran occurrences are rare. In the Lower Cretaceous, by contrast, there is a shift in the composition with assemblages dominated by ornithopods and sauropodomorphs proportionately rarer. Thyreophorans are present in Lower Cretaceous assemblages but remain rare.

There are notable differences in the relative distribution of dinosaur body and track fossils within the UK. For instance, body fossils are found throughout Mesozoic units with a high proportion of occurrences in modern inland settings (particularly in the Jurassic) in contrast to the track record which is dominated by occurrences in modern coastal settings (Fig. 1). Like the track record, body fossils are predominantly known from England. All four taxonomic groups considered are represented in the English fossil record, with smaller numbers of occurrences in Scotland and Wales and correspondingly lower taxonomic diversity. However, body fossils are also reported from Northern Ireland where no dinosaur tracks are currently known (Fig. 1). In terms of the relative proportion of each taxonomic group, body fossils of ornithopods, sauropodomorphs and theropods have similar numbers of occurrences in the UK (~27-30%) whereas in the track record, ornithopod occurrences are roughly twice that of the two other groups. Thyreophorans consistently comprise the smallest proportion of identified track and body fossil occurrences (Supp. Table 2). Whilst the Welsh body and track fossil records indicate similar patterns in terms of the relative abundance of sauropodomorphs and theropods (Triassic, Mercia Mudstone Group), the very limited Scottish body fossil record indicates the presence of sauropodomorphs, thyreophorans and theropods in the Great Estuarine Group (Middle Jurassic) but the track record suggests that ornithopods were also present (Fig. 4). Comparison of the body fossil record with the main track-bearing areas in England show that whilst the Ravenscar Group (Middle Jurassic) in North Yorkshire is very well known in terms of track abundance and diversity (all four taxonomic groups are represented), the body fossil record is very poor, with only three reported occurrences in total (Supp. Table 2) and no body fossil record of thyreophorans (Fig. 4). The south coast of England has the highest number of body fossil occurrences in the Wealden, Purbeck and Great Oolite groups (Supp. Table 2). All four taxonomic groups are represented in the Lower Greensand and Great Oolite groups, but the track record of the former lacks sauropodomorphs, and ornithopod and thyreophoran tracks are unknown in the latter (Fig. 4).

In contrast to the dinosaur track record, body fossils are more consistently present in the fossil record (Fig. 3B), with occurrences known in every stage from the Carnian through to the Cenomanian, although no occurrences are known from the rest of the Upper Cretaceous (Turonian–Maastrichtian). Peaks in occurrences are present in the Rhaetian in the Triassic, the Sinemurian, Bathonian, and Kimmeridgian in the Jurassic, and the Barremian in the Cretaceous. The highest body fossil occurrence numbers are in the Barremian followed by the Bathonian. In general, there is an increase in occurrence numbers through time, with much higher numbers for the Cretaceous versus earlier time intervals. Taxonomically, the Triassic record is dominated by sauropodomorphs and theropods (Fig. 3B). Thyeophorans become a more substantial component of the record in the Lower Jurassic, whereas ornithopods only appear in the Middle Jurassic but remain a very minor component of diversity prior to the end of the Jurassic. The Cretaceous record contrasts substantially with the Jurassic, with ornithopods making up the greatest proportion of occurrences (Fig. 3B).

Direct comparison of the body and track occurrence records show some similarities in their overall pattern (Fig. 3C), including higher abundances of both during the Cretaceous, but are also distinct in some aspects. Statistical comparisons using GLS recover a weak but significant correlation between the body and track records ($p = 0.006$; $R^2 = 0.286$). The track record shows peaks in the Norian and Aalenian stages where body fossils are very poorly known. The track record also shows very high abundance in the Berriasian, where body fossil occurrences are relatively low compared to later stages of the Cretaceous. The track record is more discontinuous than the body fossil record with fewer geological units and stages represented (Figs 3, 4).

The track record is correlated ($p < 0.001$; $R^2 = 0.58$) with the outcrop area of terrestrial (i.e., non-marine) sedimentary rocks in the UK through time (Fig. 3D). Terrestrial sedimentary rocks are highly abundant in the Carnian and Norian of the Upper Triassic and the Berriasian through the Barremian of the Lower Cretaceous. A smaller peak in the abundance of terrestrial sedimentary rocks is present in the Aalenian through Bathonian of the Middle Jurassic. Marine sediments overwhelmingly dominate the Lower and Upper Jurassic and Upper Cretaceous. The body fossil record also shows similarities to the abundance of terrestrial sedimentary rocks, although body fossils also occur in the time intervals when marine rocks are dominant (e.g., Lower and Upper Jurassic). The similarities between the body fossil record and the abundance of terrestrial sedimentary rocks are not significant ($p = 0.33$; $R^2 = 0.58$). When the Triassic, which has very low numbers of body fossil occurrences prior to the Rhaetian despite a very high proportion of outcropping terrestrial sedimentary rocks, is excluded, a significant correlation is recovered for the remainder of the Mesozoic data ($p = 0.026$; $R^2 = 0.71$).

Discussion

Controls and biases on the UK track record

Our results demonstrate a number of biases operating within the UK dinosaur track record. First, we found a strong positive correlation between the relative abundance of terrestrial sedimentary rocks and the number of dinosaur track occurrences. This relationship is to be expected: unlike body fossils, tracks are unlikely to be transported far from their source and are therefore most commonly found in fully terrestrial and coastal palaeoenvironments in which the animals lived (for at least some part of their lifespan). As a result, changes in the abundance of non-marine sedimentary settings in the UK rock record, driven primarily by changes in sea level, exert a first-order influence on the UK dinosaur track record (Fig. 3). Thus, in intervals of high sea level represented by deposition of marine sedimentary rocks (e.g., Lower Jurassic, Upper Cretaceous) there is an absence of dinosaur tracks. Although the dinosaur body fossil record is also significantly correlated with the abundance of terrestrial sedimentary rocks, this correlation is weaker than for tracks because body fossils can be transported into marine sedimentary settings (e.g., Martill *et al.* 2006). This means that dinosaur body fossils are known from fully marine sedimentary sequences in the Lower and Upper Jurassic and Upper Cretaceous (Benton & Spencer 1995; Naish & Martill 2007, 2008). The close correlation between the track record and the abundance of non-marine sediments may also explain the current absence in the UK track record of taxonomic groups such as ceratopsian dinosaurs and birds, which had their greatest diversity and abundance in the Upper Cretaceous.

The dominance of dinosaur tracks in non-marine sediments is also consistent with their relative abundance in siliciclastic lithologies, the most abundant lithological group deposited on land (Amiotte Suchet *et al*., 2003). Of the siliciclastic sediments, sandstones are the most common lithology in which UK tracks are found. Tracks found in sandstones are commonly preserved as casts on the bottom of infilling sediments or where the rock has split along the original track-bearing surface exposing infilling sediments within the track made in another lithology, both preservation styles are common on the North Yorkshire coastline (e.g., Romano and Whyte, 2003). Thus, the recorded lithology in our database does not necessarily represent the original morphology in which the track was made. The original track-bearing horizon is often a mudstone, which if the substrate is firm enough, preserve tracks and detail well but are often relatively weakly consolidated compared to other lithologies and thus, suspectable to erosion. Few tracks are preserved in conglomerates likely because the sediment make-up is relatively coarse and deposition occurs in a relatively high energy environment, neither of which are conducive to track preservation. The sediment type may also influence the size range of taxa recorded in the ichnological record, e.g., bias towards larger forms although that's unlikely to have impacted the group level analysis here. Because most tracks are made in wet sediments near bodies of water, e.g., lakes, rivers, lagoons, coastline, there is also a bias towards certain lithologies and thus palaeoenvironments, and this must be considered when making palaeoecological inferences.

Another potential bias relates to morphology. Our results show that the recorded and reported UK dinosaur track record is overwhelmingly dominated by tridactyl tracks made primarily by theropod and ornithopod dinosaurs (Fig. 2G). While this may in part reflect true patterns of abundance of these groups (see below) it is also the case that tridactyl tracks are highly familiar and more readily identifiable to palaeontologists and the public alike. By contrast, sauropodomorph tracks are often preserved as bowl-like depressions with few morphological features, and if not obviously aligned within trackways may be difficult to recognise. Similarly, thyreophoran tracks are also less familiar and less readily identifiable than tridactyl impressions. Indeed, in a number of cases in the UK (in the Great Estuarine and Purbeck groups) and more widely these have upon initial discovery (particularly when poorly preserved) been initially assigned to other quadrupedal dinosaurs especially sauropods before being revised (e.g., Ensom, 1987, Lockley, 1991; Whyte and Romano, 1994, Milàn & Chiappe 2009). Together this may explain why in many areas, sauropodomorph and thyreophoran tracks have only been discovered relatively recently, e.g. sauropodomorph tracks in Scotland (Brusatte *et al*., 2016) and South Wales (Lockley *et al*. 1996) or sauropod and thyreophoran tracks in North Yorkshire (e.g. Whyte & Romano 1993, 2001b), whereas discoveries of tridactyl tracks have a much longer history, dating back to the early 19th century (e.g., Beckles 1851, 1862; Sollas 1879; Brodrick 1908).

Most dinosaur tracks in the UK are found on coastal sections (e.g., Romano *et al.* 2018; Ensom 2006; Falkingham *et al.* 2022), which are sites of active erosion with new tracks and trackways becoming exposed over time, and often also sites that are frequently visited by fossil collectors, academics, and the public. Historically, dinosaur tracks have been also recovered from inland sites primarily within active working quarries (e.g., summary in Ensom 2006), but the number of such quarries has reduced over time and so discoveries are now infrequent. This bias towards coastal discoveries may play into the predominance of both English and Cretaceous records in our database, given the more extensive coastal exposures of terrestrial and coastal/marginal Cretaceous deposits in England when compared to other time intervals and countries (Fig. 1). The bias towards Cretaceous records is also likely influenced by the extensive historical and present-day quarrying for building stone of the Purbeck Group that occurs in Dorset.

Reporting bias may also play a role in the patterns observed in our data. For some geological sequences, there has been very extensive reporting of track occurrences, whereas for others published data are less systematic and comprehensive. For example, Ensom (1995) published a complete catalogue of dinosaur track occurrences from the Purbeck Group, drawing on both literature and museum collections and Romano and Whyte (2003) undertook a similar task in North Yorkshire and including verified reports from non-published local sources. By contrast, Wealden Group track occurrences lack a similarly comprehensive synthesis (e.g., Radley *et al*. 1998; Pond *et al*. 2014; Lockwood 2016; Shillito & Davies 2019). Such variation in reporting patterns will inevitably feed through into our dataset.

The scientific value of the track record

The scientific value of the dinosaur track record lies primarily in two main areas: (i) its potential to provide validation of patterns derived from the more intensively studied body fossil record; (ii) its potential to provide novel and distinct insights into aspects of dinosaur evolution, biogeography, biomechanics and palaeoecology compared to those generated from body fossils. The major limitations of the track record are in the difficulties around taxonomic identification: tracks can normally only be identified to the level of major clades (e.g., Sauropoda, Ornithopoda) and not to lower-level clades or genus/species level (Lockley, 1991). Moreover, even identifying tracks to the level of major clade may be challenging: it is not always possible to determine if tridactyl tracks were made by ornithopods or theropods (Castanera *et al*. 2013; Hurum *et al*. 2016), and even the tracks typically identified as made by ornithopods may actually have been produced by a broader set of ornithischian taxa with similar foot morphologies, such as basal ornithischians like *Lesothosaurus* and heterodontosaurids (Butler *et al*. 2008). In recent years, experimental digital and statistical methods have been implemented to correctly, and more efficiently, identify track makers (e.g., Belvedere *et al*. 2018; Lallensack *et al*. 2022a; 2022b). These new methods could remove a lot of the ambiguity in identifying track makers but typically require a high-level of technical and computational expertise, often (but not exclusively) rely on 3D track data and are time consuming to implement so not yet widely utilised. As a result of these uncertainties, the taxonomic categories used in our dataset and analyses are deliberately very coarse.

Nevertheless, the UK dinosaur track record does show patterns that are very similar to and support inferences from the UK body fossil record (e.g., Fig. 3). Both records show similar broad increases in the number of occurrences and the diversity of different taxonomic groups represented through the Mesozoic, with low numbers of occurrences dominated by sauropodomorphs and theropods in the Triassic to much higher numbers of occurrences and multiple taxonomic groups (sauropodomorphs, theropods, thyreophorans, and ornithopods) in the Cretaceous. Both show a similar transition around the Jurassic–Cretaceous boundary, with a major increase in the relative abundance of ornithopods. This increase has been recognised globally and is noted to coincide with an apparent decline in sauropod diversity and abundance from the Jurassic to the Cretaceous (Mannion *et al*. 2011; Chiarenza *et al*. 2022) although the latter is not clear from the UK body or track data. This is likely because we do not have non-marine (terrestrial) rocks during the Upper Jurassic when we might expect to see a maximum in sauropod diversity as seen elsewhere, most prominently the Morrison Formation, USA (e.g., Mannion *et al*. 2021). In the UK, thyreophoran body fossil and track records have the lowest number of occurrences relative to the other taxonomic groups recognised here but the broad patterns of change in both body fossil and track records are similar. The relatively low number of thyreophoran tracks relative to other dinosaur groups is a globally recognised phenomenon (e.g., Porchetti *et al*. 2016, Thulborn, 1990) and at a global scale, thyreophorans are also substantially underrepresented in the track record compared to their body fossil record (e.g., McCrea *et al*. 2001; Milàn & Chiappe, 2009). Whether the body fossil or the track record is more reflective of true relative abundance for thyreophorans is unclear; however, tracks were only comparatively recently identified (e.g., McCrea *et al*. 2001; Whyte and Romano, 2003; Milàn & Chiappe 2009; Pond *et al*. 2014; Shillito and Davies, 2019, DePolo *et al*. 2020).

The UK dinosaur track record also adds information in some areas that is distinct from that provided by the body fossil record. For example, dinosaur body fossil records are scarce or absent from the Norian stage of the Late Triassic and the Aalenian stage of the Middle Jurassic, and thus the track record provides our best information on the composition of UK dinosaur faunas in these time intervals. UK dinosaur tracks are highly abundant and provide the primary information on faunal composition in areas and geological sequences in which dinosaur body fossils are rare or unknown, such as the Middle Jurassic Ravenscar Group of North Yorkshire (Whyte & Romano 1993, 2001a,b; Romano & Whyte 2003; Whyte *et al*. 2007; Romano *et al*. 2018) or the Great Estuarine Group of Scotland (Clark *et al*. 2004, 2005; Brusatte *et al*. 2016; dePolo *et al*. 2020). Thus, the regional significance of dinosaur tracks for understanding faunal composition and evolution is high particularly when coupled with the body fossil record (e.g., Bernardi *et al*. 2018). The UK dinosaur track record also provides novel palaeoecological and palaeobiological insights. These include insights into sauropod and theropod locomotion including the first dual gait track (Day et al. 2002a,b; 2004), dinosaur swimming behaviour (Whyte & Romano 2001a), skin impressions and dinosaur-landscape interactions (e.g., Shillito & Davies 2019), potential evidence for parental care in theropods (Clark *et al*. 2006), and maximum and minimum sizes for dinosaurs falling outside of the range represented by body fossils (e.g., Clark *et al*. 2006; Lockwood 2016).

Dinosaur tracks are a valuable component of our geoheritage (Page, 2018) and are increasingly recognised as such, forming the basis for, or contributing to various regional (e.g., Regionally Important Geosites in the UK), national (e.g., Bien de Interés Cultural in Spain or Sites of Special Scientific Interest in the UK) or international (e.g., World Heritage List or Global Geopark) protections and recognition (Alcalá *et al*. 2016). They are also one of the most common ways in which the public can encounter dinosaur fossils in the natural world. Thus, beyond their scientific value, they provide key aesthetic and pedagogic opportunities in the tourism and public education sectors. Indeed, the close relationship between palaeontological heritage and tourism is exemplified in locations such as South Korea, which has well-developed and protected fossil geosites (Paik *et al*. 2010), or Dinosaur Stampede Quarry in Australia (Thulborn and Wade, 1979; Agnew and Demas, 2014). Today in the UK, dinosaur tracks are mostly found as fallen blocks in coastal settings. As a result, there are few well-developed sites where tracks are easy to identify and guaranteed, paired with accompanying interpretative aids to support, and encourage visitors. Currently the most accessible dinosaur track site with some (albeit limited) interpretative aids in the UK is likely Spyway Quarry, Dorset, where >100 sauropod tracks are exposed on a bedding plane within the Lower Cretaceous Purbeck Group (Wright, 1998; Edgar *et al*. 2023). Thus, the *in-situ* UK dinosaur track record is heavily underutilised at present and a comprehensive review of the current conservation, management and communication plans in place is required to leverage the greatest value and longevity from these sites.

Conclusion

Here we present a new comprehensive database of UK dinosaur track fossils containing 260 unique occurrences reported over the last >150 years. Dinosaur tracks are reported from across the UK, through the Late Triassic to Early Cretaceous from intervals characterised by non-marine rocks. Tridactyl tracks from Ornithopoda and Theropoda are the most commonly reported, followed by non-tridactyl tracks from Sauropoda and Thyreophora, the latter of which is relatively rare throughout the record. In contrast, body fossils are known from a more continuous series of time intervals and are found in both marine and non-marine rocks, although considerably less frequently in the former. Despite these differences, the trace and body fossil records overall show similar patterns throughout the Mesozoic in terms of intervals of number of occurrences and the relative abundance of major taxonomic groups. One of the most notable features of both records is the major increase in absolute and relative abundance of Ornithopoda in the Cretaceous and the relative rarity of thyreophorans throughout the record. This suggests that despite the different biases operating on the body and track records, they provide similar representations of the evolution of dinosaur communities through time in the UK, at least at a broad taxonomic scale. For some intervals, particularly parts of the Early Cretaceous, the UK record is among the most informative worldwide for understanding dinosaur evolution.

Looking forward, many UK dinosaur tracks are known only from 2D images or line drawings, and detailed morphological and biometric information is often patchy. The increasing ease of generating high-resolution 3D models, the increasing application of computational and experimental approaches including biomechanical modelling, as well as more wholesale collection of biometric and morphological data alongside new discoveries makes it highly probable that the UK dinosaur track record will continue to provide key insights into how, where and when this charismatic group of organisms lived and what they looked like. To optimise the value of the track record for the current and future, particularly considering difficulties with removal and long-term storage of tracks, we strongly support collection and reporting of as much metadata as possible, including 3D models of tracks and the raw images in an open repository.

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Data availability: Our new UK dinosaur track database, the PBDB body fossil record and relative abundance of non-marine/marine rocks in England and Wales used in this study are provided in Supplementary Tables 1-3, respectively. R-code used to analyse the data and generate Figures 2 and 3, and Supplementary Figures 1-14 is given in Supplementary Information 1 and 2.

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Figures Captions

Figure 1: UK map showing the distribution of Mesozoic rocks by epoch and locations of (A) trace and (B) body dinosaur fossil locations.

Figure 2. Summary of UK dinosaur track record showing relative proportions of track occurrences in the database. A) Occurrences by country. B) Occurrences by geological time period. C) Occurrences by lithological group. D) Occurrences by modern geographical setting. E) Occurrences by lithology in which tracks are preserved. F) Occurrences by palaeoenvironmental setting. G) Occurrences by morphology, using a simple morphological division into tridactyl versus non-tridactyl tracks. H) Occurrences by dinosaur group. The category 'Dinosauria' includes tracks not identified in published literature beyond having been made by dinosaurs. The category 'Ornithischia/Theropoda' represents tridactyl tracks that have not been identified as either those of ornithopods or theropods.

Figure 3. UK dinosaur track and body fossil occurrences through time and relative to depositional environment. A) Track record. Indet=indeterminate. B) Body fossil record. Other dinosaur groups =primarily material from basal ornithischian dinosaurs and to a lesser extent Dinosauria indeterminate. C) Comparison of total occurrences of track and body fossil records. D) Relative proportion of terrestrial units in the UK through time. Dinosaur body silhouettes are from Phylopic: Sauropodomorpha=*Cetiosaurus oxoniensis* (Mike Taylor); Theropoda=*Baryonyx walker* (Scott Hartman); Ornithopods= *Mantellisaurus atherfieldensis* (Matthew Dempsey); Thyreophora=*Polacanthus foxii* (the funkmonk).

Figure 4. Stratigraphic range chart of UK dinosaur body fossils versus tracks through geological time. The base of the Mercia Mudstone is diachronous and extends down into the Lower Triassic not shown here. Thyreophoran body fossils(s) recorded in the Hastings Group incorporates the lower three formations of the current Wealden Group and thus, is grouped with the Wealden Group. The Cromer Knoll Group overlies the Humber Group, of which the Kimmeridge Clay Formation is the uppermost unit, as in the Ancholme Group in the south of the UK, and it underlies the Chalk/Shetland Group. Mid Jurassic units vary by geographic region: the Ravenscar Group outcrops in the Cleveland Basin, Yorkshire, the Inferior Oolite Group throughout south and central England and the Great Estuarine Group in the Hebrides Basin and Scotland. The Corallian Group is laterally equivalent and interfingers with the Ancholme Group and occurs within it. Dinosaur body silhouettes are from Phylopic (see Fig. 3 caption for details).

Figure 5. Palaeoenvironmental reconstructions for discrete timeslices of the Mesozoic of the UK where dinosaur tracks are found. A) Bendricks Rocks, Mercia Mudstone Group, South Wales (Late Triassic) showing an early sauropodomorph and small (*Grallator* trackmaker) and larger (*Anchisauripus* trackmaker) theropod dinosaurs in an alluvial plain setting. B) Spyway Quarry, Purbeck Group, Dorset (earliest Cretaceous) showing large sauropod dinosaurs walking along a shelly beach next to a lagoon. Small heterodontosaurid ornithischians and pterosaurs are also shown although neither are known from Spyway Quarry and heterodontosaurids are only known to date from body fossils. C) Lee Ness, lower Wealden Group, East Sussex (Early Cretaceous), showing a diverse ecosystem including the large iguanodontian *Barilium*, a smaller iguanodontian, an ankylosaur, sauropods, a tyrannosauroid, and small theropods. All images copyright Mark Witton.

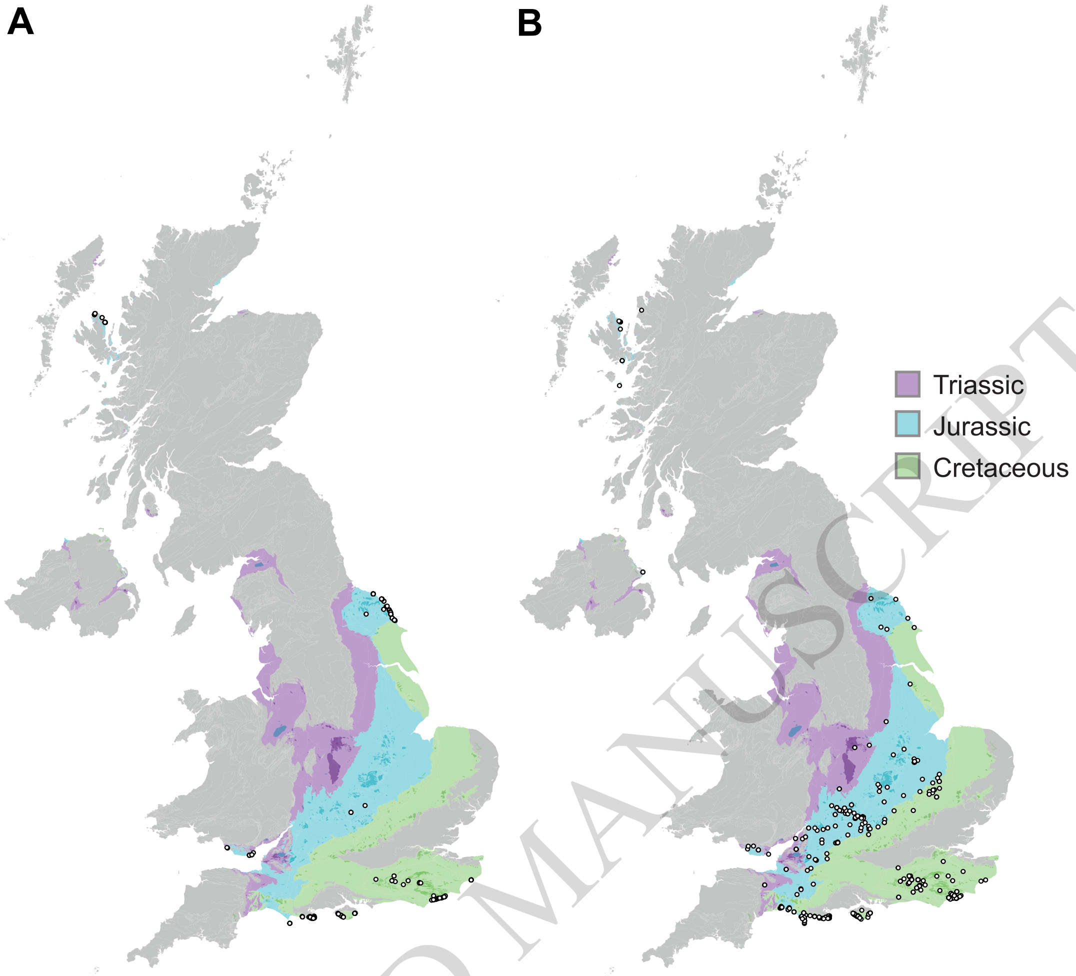

Figure 1

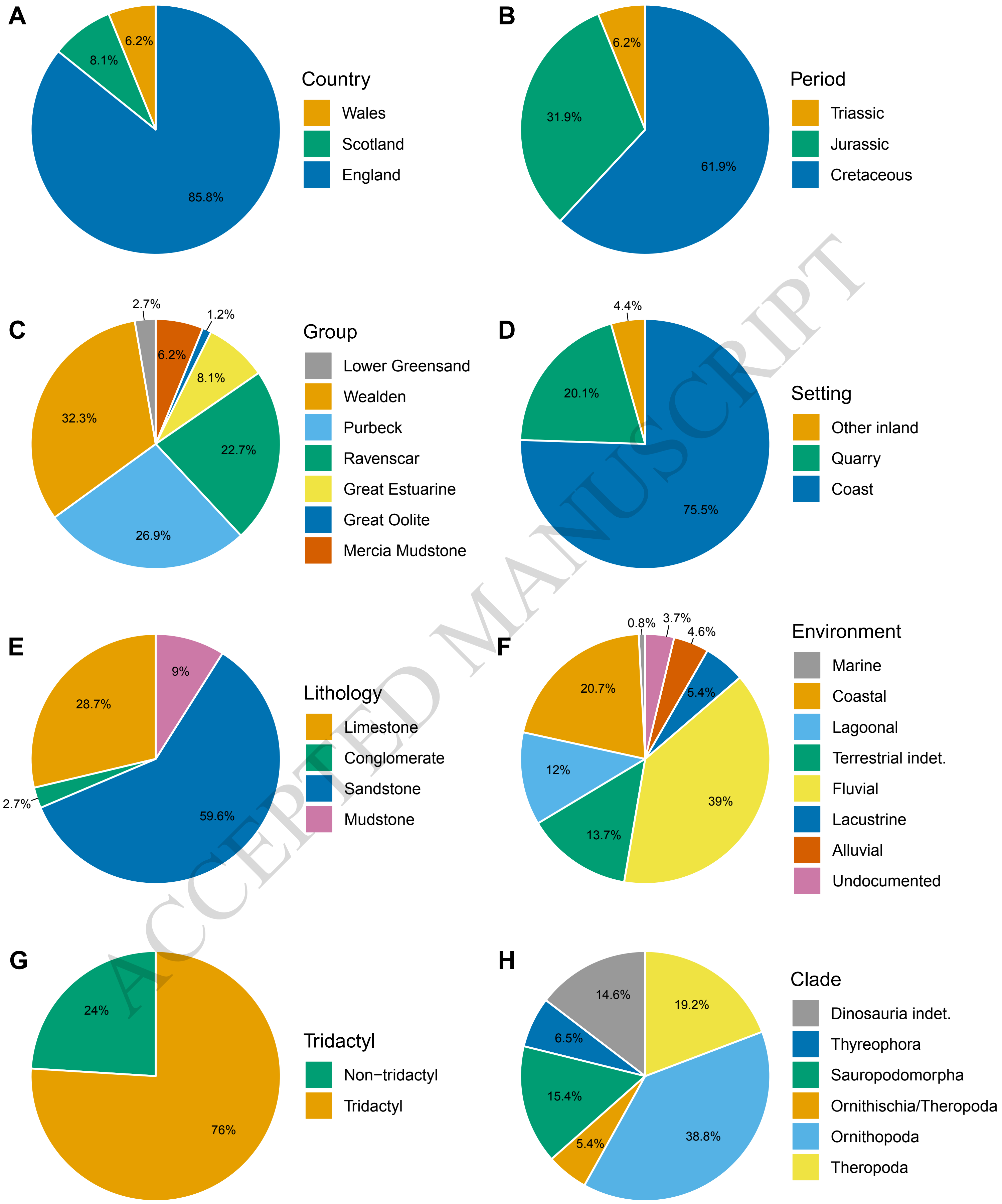
A
6.2%
8.1%
85.8%
Country
Wales
Scotland
England
B
6.2%
31.9%
61.9%
Period
Triassic
Jurassic
Cretaceous
C
2.7%
1.2%
6.2%
8.1%
32.3%
22.7%
26.9%
Group
Lower Greensand
Wealden
Purbeck
Ravenscar
Great Estuarine
Great Oolite
Mercia Mudstone
D
4.4%
20.1%
75.5%
Setting
Other inland
Quarry
Coast
E
9%
28.7%
2.7%
59.6%
Lithology
Limestone
Conglomerate
Sandstone
Mudstone
F
0.8%
3.7%
4.6%
20.7%
5.4%
12%
39%
13.7%
Environment
Marine
Coastal
Lagoonal
Terrestrial indet.
Fluvial
Lacustrine
Alluvial
Undocumented
G
24%
76%
Tridactyl
Non−tridactyl
Tridactyl
H
14.6%
19.2%
6.5%
15.4%
5.4%
38.8%
Clade
Dinosauria indet.
Thyreophora
Sauropodomorpha
Ornithischia/Theropoda
Ornithopoda
Theropoda

Figure 2

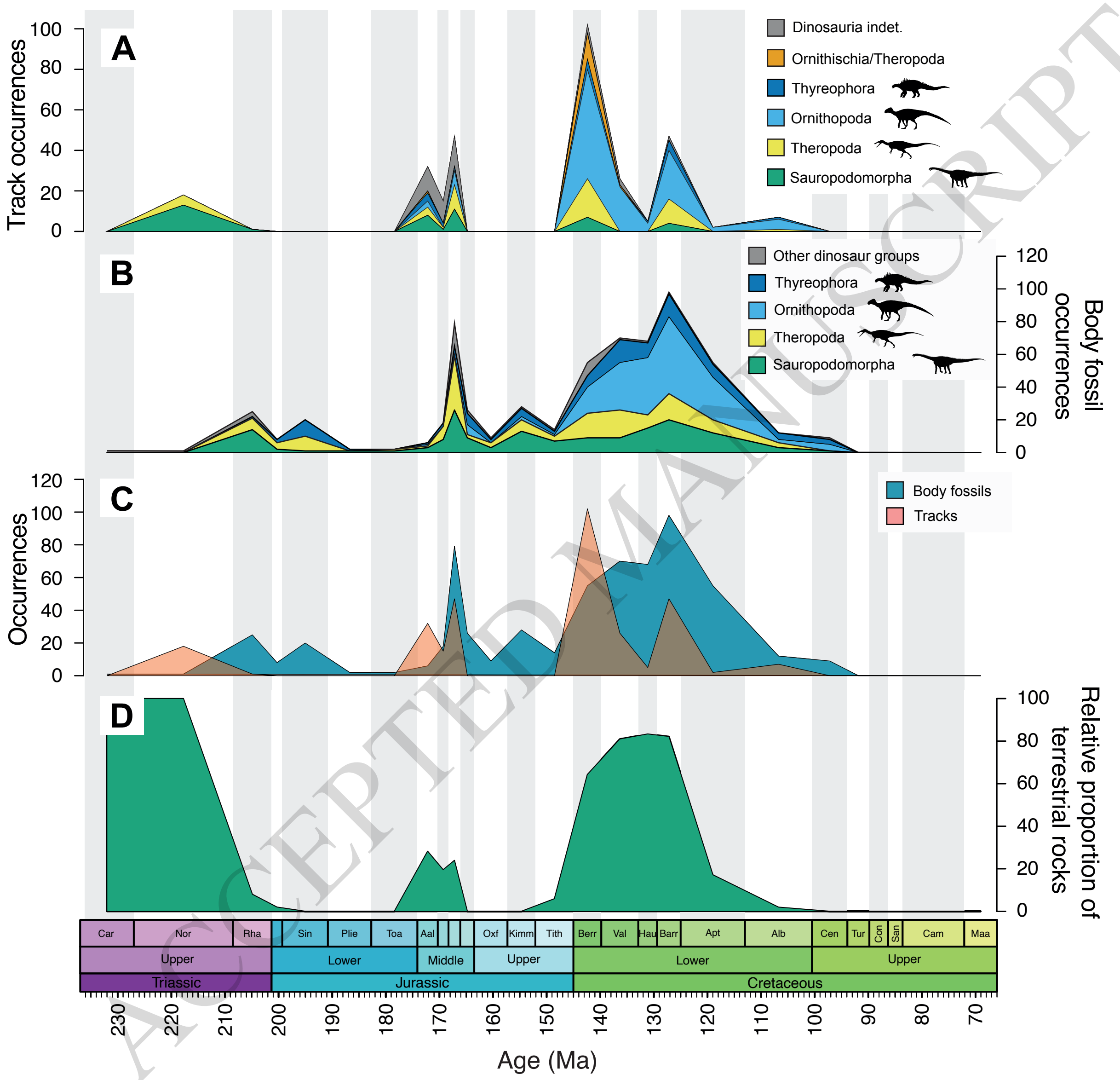
A
Track occurrences
100
80
60
40
20
0
Dinosauria indet.
Ornithischia/Theropoda
Thyreophora
Ornithopoda
Theropoda
Sauropodomorpha
B
Other dinosaur groups
Thyreophora
Ornithopoda
Theropoda
Sauropodomorpha
Body fossil occurrences
120
100
80
60
40
20
0
C
Occurrences
120
100
80
60
40
20
0
Body fossils
Tracks
D
Relative proportion of terrestrial rocks
100
80
60
40
20
0
Car
Nor
Rha
Sin
Plie
Toa
Aal
Oxf
Kimm
Tith
Berr
Val
Hau
Barr
Apt
Alb
Cen
Tur
Con
San
Cam
Maa
Upper
Lower
Middle
Upper
Lower
Upper
Triassic
Jurassic
Cretaceous
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
Age (Ma)

Figure 3

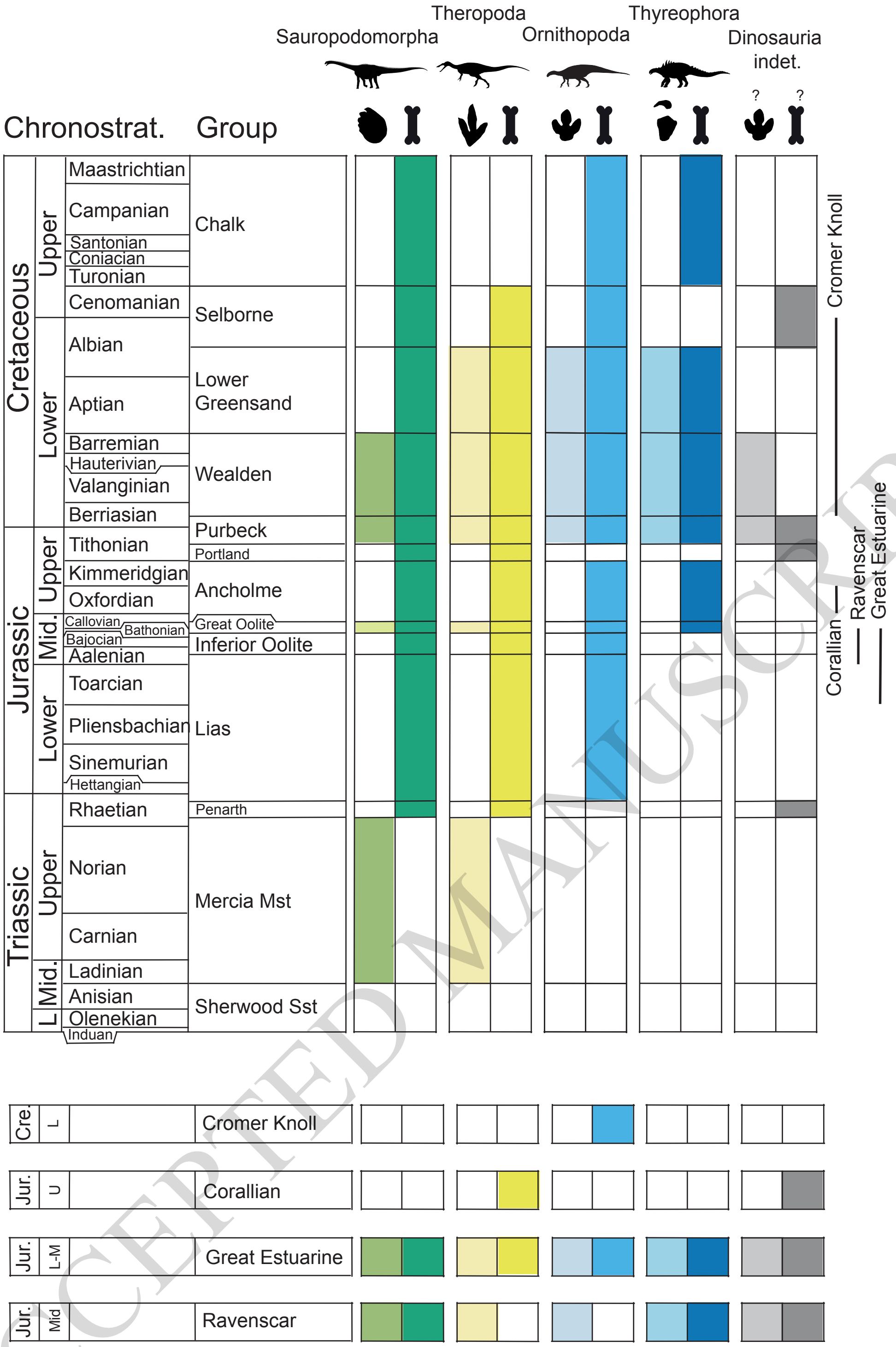
Theropoda
Thyreophora
Sauropodomorpha
Ornithopoda
Dinosauria indet.
?
?
Chronostrat.
Group
Cretaceous
Upper
Lower
Jurassic
Upper
Mid.
Lower
Triassic
Upper
Mid.
L
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Aalenian
Toarcian
Pliensbachian
Sinemurian
Hettangian
Rhaetian
Norian
Carnian
Ladinian
Anisian
Olenekian
Induan
Chalk
Selborne
Lower Greensand
Wealden
Purbeck
Portland
Ancholme
Great Oolite
Inferior Oolite
Lias
Penarth
Mercia Mst
Sherwood Sst
Cromer Knoll
Corallian
Ravenscar
Great Estuarine
Cre.
L
Cromer Knoll
Jur.
U
Corallian
Jur.
L-M
Great Estuarine
Jur.
Mid
Ravenscar

Figure 4

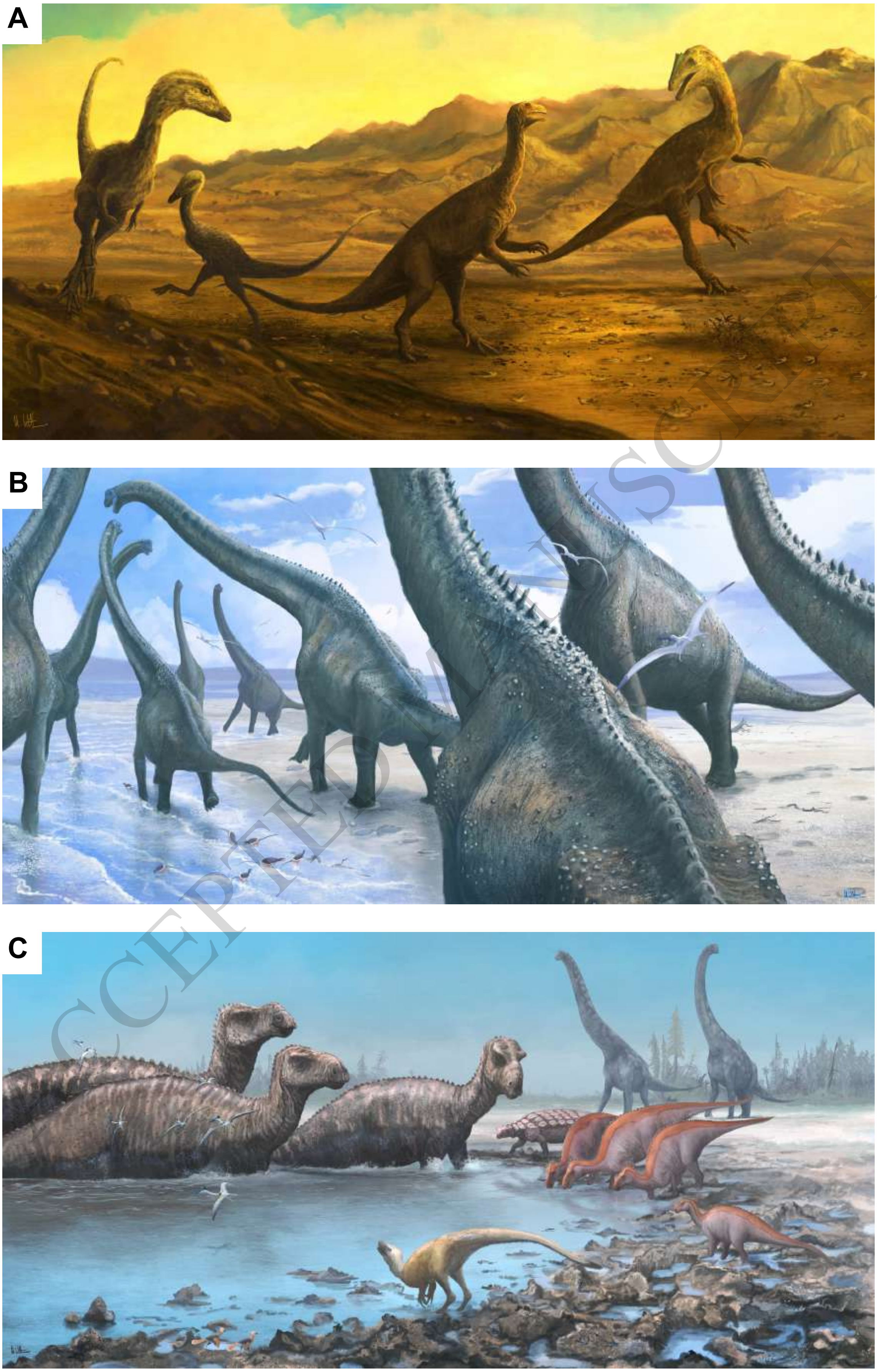

Figure 5