

Crouching theropod at the seaside. Matching footprints with metatarsal impressions and theropod autopods: a morphometric approach

M. ROMANO*[‡] & P. CITTON^{‡‡}

*Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstr 43, Berlin, Germany

^{‡‡}Dipartimento di Scienze della Terra, 'Sapienza' Università di Roma, Piazzale Aldo Moro, 5, 00185, Rome, Italy

(Received 11 December 2015; accepted 18 May 2016)

Abstract – We compare theropod footprints with elongate metatarsal prints from central Italy with known autopod structures in major theropod groups, in order to more accurately define the trackmaker attribution. Our work, using morphometric analysis, shows the considerable potential of explorative methods such as PCA (principal component analysis) and cluster analysis when describing important characters for a given taxonomic group (body and ichnofossils) and identifying important anatomical regions. Moreover, the results of the analysis suggest that the putative trackmaker is likely a member of Ornithomimosauria, with significant affinities in the posterior autopod structure with the genus *Struthiomimus*. The fundamental importance of integrating both osteological and ichnological data, when investigating locomotor and behavioural hypotheses, is highlighted. This approach could also contribute positively to the complex cognitive process of trackmaker identification and be favourable for the attainment of a more natural definition of ichnotaxa.

Keywords: dinosaurs, footprints, Cretaceous, Ornithomimosauria, Italy, palaeobiogeography .

1. Introduction

The recent finding of mesaxononic tridactyl footprints referable to a theropod dinosaur (see Citton *et al.* 2015), preserving a well-marked and complete trace of the right and left metatarsus, gave the chance to perform a morphometric and quantitative analysis in order to establish the best fit between the analysed tracks and well-known non-avian theropod pes morphologies.

Elongated traces are well reported in the dinosaurian ichnological record. Metatarsal impressions have been ascribed to theropod dinosaurs (Gierliński 1994, 1996; Romero-Molina *et al.* 2003; Farlow *et al.* 2015; ichnogenera *Kayentapus*, *Eubrontes*, *Gigandipus* in Lockley, Matsukawa & Li, 2003); tentatively to a theropod (Lockley *et al.* 1998); ornithischian dinosaurs (i.e. ichnogenus *Anomoepus* in Avanzini, Gierliński & Leonardi, 2001); Oviraptorosauria (Nicosia *et al.* 2007); a small theropod (Milàn, Loope & Bromley, 2008); a quadruped small non-theropod with a theropod-like pes (i.e. *Silesaurus* in Gierliński, Lockley & Niedzwiedzki, 2009); a ceratosaurian theropod (Gierliński Lockley & Niedzwiedzki, 2009); a large *Dilophosaurus*-like theropod (Milner *et al.* 2009); a basal ornithischian (Wilson, Marsicano & Smith, 2009); and an ?ornithomimosaur (Farlow *et al.* 2015).

The studied footprints were identified on a calcareous block in the pier of Porto Canale-Riomartino, a small harbour located a few kilometres southeast of

Latina (Latium, Central Italy, see Citton *et al.* 2015, fig. 1, p. 2). The track-bearing block comes from the Ausoni Mountains, which are part of the Volsci Range (Centamore, Di Manna & Rossi, 2007), the innermost portion of the 'Apenninic Carbonate Platform' (i.e. the Latium-Abruzzi and Campania Carbonate Platforms considered as a unitary domain – *sensu* Mostardini & Merlini, 1986; Pescatore *et al.* 1999; Cosentino *et al.* 2002). In this domain, the typical sedimentary succession includes neritic carbonate sediments of a shelf environment (Accordi *et al.* 1988) undergoing short emersion events (Chiocchini *et al.* 1994; Chiocchini, Pampaloni & Pichezzi, 2012).

The rock on which the footprints are preserved is made of hazel mudstone–wackestone with evidence of surface emersion at the time of dinosaur trampling. The microfaunal assemblage, characterized by the occurrence of *Cuneolina sliteri* Arnaud Vanneau & Premoli Silva, 1995 (Chiocchini, Pampaloni & Pichezzi, 2012), suggests a late Aptian – ?early Albian age. The faunal composition also includes *Nezzazata isabellae* and *Arenobulimina gr. cochleata*, shell fragments, subordinate ostracods and very rare oncoids (Citton *et al.* 2015).

The studied tracks were attributed to a medium-sized, non-avian theropod on the basis of the features characterizing the metatarsal impressions and, in general, for the relative proportions of the preserved anatomical elements, more resembling the osteological structure of theropods rather than that of ornithopods (Citton *et al.* 2015). The footprint F3 (following the subdivision in

[‡]Author for correspondence: paolo.citton@uniroma1.it

Citton *et al.* 2015), which was qualified as a true track (*sensu* Lockley, 1991; Marty, Strasser & Meyer, 2009), preserves several anatomical details that can be used as topographical reference points for the identification of the osteological elements that have left the impressions.

On the basis of the available evidence, two different hypothetical pes morphologies were reconstructed, and the lengths obtained in the two models were analysed morphometrically. In the study, several pedal morphologies of avian and non-avian theropods were included. Analyses comparing footprints and theropod autopods using PCA (principal component analysis) or other morphometric methods are not new in tetrapod ichnology and are all focused on the phalangeal portion of the digit and, in some cases, on the metatarsals (e.g. Farlow & Lockley, 1993; Dalla Vecchia & Tarlao, 2000; Smith & Farlow, 2003; Farlow *et al.* 2013, 2014; Castanera *et al.* 2015). Given the preservation of mirrored anatomical details, the material considered in the present study allows us to tentatively match the footprints with elongated metatarsal traces to the theropod pedal morphologies morphometrically.

A more refined attribution to a putative trackmaker will allow a better appraisal of dinosaurian diversity in the carbonate platforms of the central Mediterranean area, with implications for macroevolutionary models and palaeobiogeography.

2. Material and methods

The footprint F3 (Fig. 1) was selected as the reference track. Starting from the impression, two hypothetical foot structures and anatomical constraints derived from the type of impression were reconstructed.

The first anatomical constraint, considered the most solid for the morphometric analysis, is the proximal termination of the metatarsus impression. In this portion, the footprint is countersunk, reaching its maximum width at the proximal edge (this structure is clearly visible in the footprint F2, Fig. 1).

This structure corresponds to the area of articulation between the metatarsus and distal tarsal and can be considered in all probability as the proximal limit of the metatarsals. Distally, the second probable constraint is the terminal tip of the three digits. *In vivo* experiments (i.e. *Homo sapiens* and *Gallus gallus*, pers. obs.) show that the proximal and distal extremities anatomically related to a footprint (imprinted in the first moment of touchdown and in the last moment of the kick-off phase) remain largely unchanged in position on a cohesive substrate, during locomotion and, more reasonably, during a resting phase. This might not be the case in loose and granular media, as experimentally shown by Falkingham & Gatesy (2014) for a guinea fowl walking through dry and granular material. However, in the studied material we do not deal with loose sediment at the time of track formation but with a cohesive carbonate mud; both these conditions represent two of the many possible surface layer and substrate conditions on which a fossil footprint can be made, and are differently

preserved, in the fossil record. In this specific case, and taking into account that footprint F3 is a 'true track' not showing relevant extra morphological substrate-related features, the two identified areas can be used as quite stable biometric constraints and homologous points. In contrast, the footprint width seems to show a greater amount of variation, which can be ascribed both to the development of expulsion rims and/or the collapse of sediments under waterlogged conditions.

The choice of homologous reference points with regards to the position of the joint between the metatarsus and the proximal phalanges is a more subjective approach. In particular, the variability affecting the distal arrangement of the metatarsus in different theropod groups must be carefully taken into account. In this regard, two general patterns were identified. In the first, from here on referred to as Type I, the terminations of the third and fourth metatarsal coincide more or less distally, while the second is shorter, with a more proximal termination. This morphology can be observed, for example, in *Struthiomimus altus*, *Tochisaurus nemegtensis* and *Ornitholestes hermanni* (see Holtz, 1994, fig. 1, p. 481). The second arrangement (Type II) is characterized by a longer, distally more developed third metatarsal, while metatarsals II and IV are shorter and more or less equal in length (thus ending approximately at the same point distally, a condition considered typical of primitive theropods in Holtz, 1994). This more widespread condition is observed in a large number of theropods, including *Albertosaurus libratus*, *Elmisaurus rarus*, *Avimimus portentosus*, *Coelophysis bauri*, *Dilophosaurus wetherilli*, *Ceratosaurus nasicornis*, *Allosaurus fragilis*, *Chilantaisaurus tashuikouensis*, *Elaphrosaurus bambergi* and *Deinonychus antirrhopus* (see Holtz, 1994, fig. 1, p. 481). The two recognized patterns (Type I and Type II) were used to identify the homologous points for measurements, as reported in Figure 2.

In order to take the measurements, the metatarsophalangeal joints of digits III and IV for Type I, and that of digit III for Type II, were considered coincident with the deepest footprint portion, subcircular in shape, which is located proximally to the hypex between digits III and IV. The measurements selected for the morphometric analysis are the total length of the metatarsus (measured along the metatarsal III (MTL)) and the lengths of the phalangeal portions of digits II–IV.

Osteological reference material for body fossils was taken and measured from published photographs and drawings (Fig. 3). Thirty-seven theropod taxa were selected, representing Abelisauridae, Allosauridae, Avialae, Coelophysoidea, Coelurosauria *incertae sedis*, Deinonychosauria, Neoceratosauria, Ornithomimosauria, Oviraptorosauria and Tyrannosauridae (see Table 1).

The second digit in *Daspletosaurus* and *Sinovenator* is little known and incomplete, so this was coded with a question mark. In contrast, the ungual phalanx in digit III in *Aucasaurus* is not preserved distally, but the reconstruction provided by Coria, Chiappe & Dingus

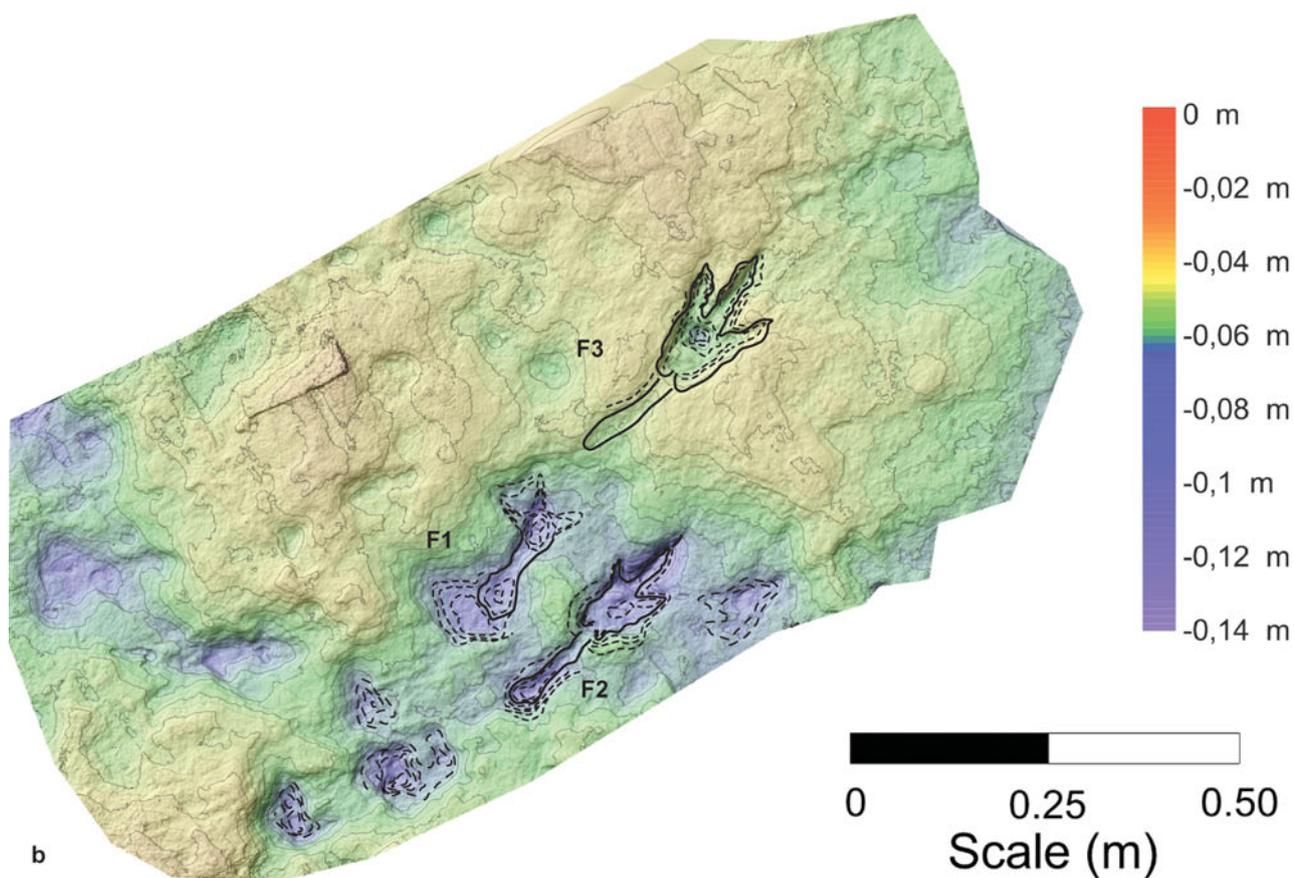
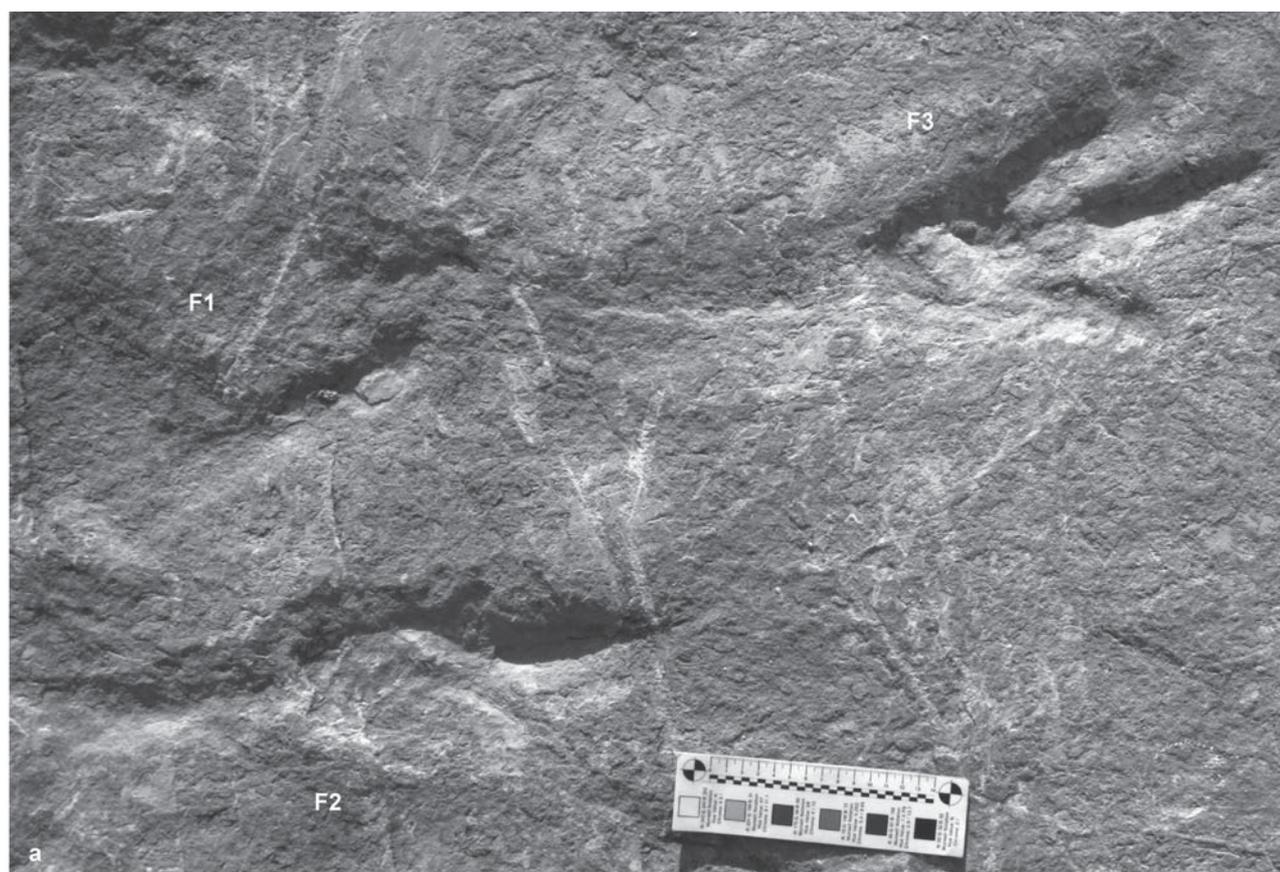


Figure 1. (Colour online) Riomartino tracks. (a) Footprints F1, F2 and F3. Scale in the photograph = 15 cm; (b) Shaded coloured photogrammetric model of the track-bearing block with superimposed interpretative drawing (drawn on the actual track-bearing block). Slightly modified from Citton *et al.* (2015).

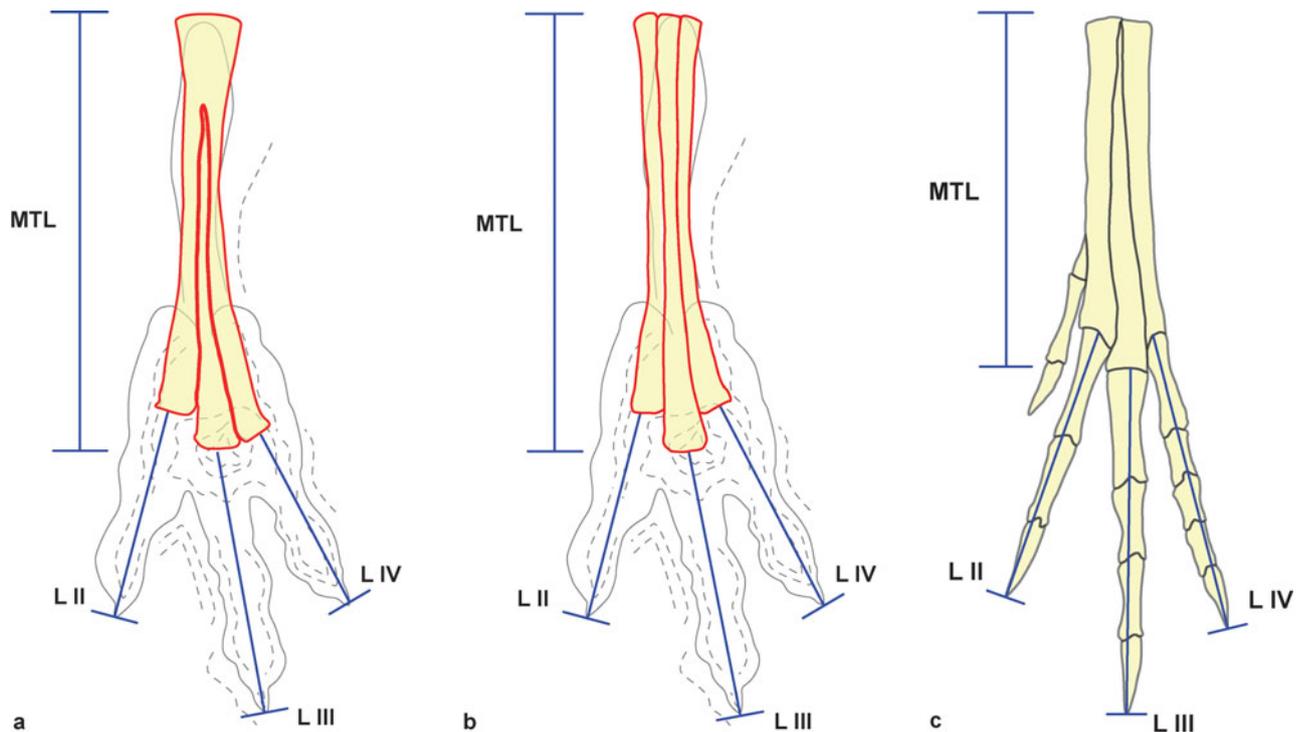


Figure 2. (Colour online) Homologous points chosen for the measurements in the footprints and autopods. (a) Type I interpretation; (b) Type II interpretation; (c) foot in *Chirostenotes pergracilis* redrawn from Weishampel, Dodson & Osmólska (1990, fig. 3.11, p. 63, fig. 9.2, p. 247). MTL – metatarsus length; LII – digit II length; LIII – digit III length; LIV – digit IV length.

(2002, fig. 4, p. 464) was considered sufficiently accurate for inclusion here. In *Harpymimus* digits III and IV are incomplete, but we tentatively consider the reconstruction provided by Makovicky, Kobayashi & Currie (2004, fig. 6.5, p. 145) as realistic. In *Gallimimus* the unguis phalanx of digit II was reconstructed using average dimensions of the unguis phalanges in digits III and IV. The second phalanx of digit II in *Ajancingenia yanshini* ('*Ingenia*' in Weishampel, Dodson & Osmólska, 2004) was reconstructed using the length of the second phalanx in digit III of the same taxon. The length of these two phalanges is comparable and more or less equal in a wide range of theropods, including *Allosaurus*, *Coelophysis*, *Compsognathus*, *Dilophosaurus*, *Majungasaurus*, *Megapnosaurus* and *Tyrannosaurus*. In *Tyrannosaurus rex*, a cast of FMNH PR 2081 was used for reference; in this specimen the penultimate and unguis phalanges are missing and have been reconstructed. For the foot in *Saurophaganax* we considered the holotype OMNH 01307, which is partly reconstructed (first and second phalanges of digit II; third phalanx of digit III; third and fourth phalanges of digit IV). The unguis phalanx in digit II of *Sinornithosaurus millenii* was reconstructed using the average dimensions of the unguis phalanges of digits III and IV in Xu, Wang & Wu (1999, fig. 4, p. 265). Because the software used replaces question marks with values derived from an algorithm applied to the whole dataset, we chose instead to reconstruct missing parts using the available osteological data and the wide-ranging phalangeal formulae for the three phalanges for digit II.

The Deinonychosauria (*sensu* Senter, 2007) *Bambiraptor*, *Deinonychus*, *Sinornithoides* and *Sinovenator* are characterized by the classic modified raptorial digit II, which is retractable and characterized by a hypertrophied sickle-shaped claw. It follows that such taxa could be excluded *a priori* as the putative trackmaker of the footprints studied in the present work, since they were made by a trackmaker with three functional digits during locomotion. Didactyl footprints referred to Deinonychosauria are well known and described in the literature (Sarjeant, 1971; Zhen *et al.* 1995; Lockley *et al.* 2004; Li & Lockley, 2005; Li *et al.* 2006; Kim *et al.* 2008, 2012; Li *et al.* 2008; Mudroch *et al.* 2011). A wide range of taxa was considered in the morphometric analysis, including morphotypes that are incompatible with the Italian material, in order to provide a more comprehensive overview of the pedal type morphospace occupied by major groups of theropods. The selected lengths are shown in Figure 2 and total measurements are reported in Table 1.

The values obtained from the footprints (Type I and II) and from the osteological record were subjected to PCA using the software Paleontological Statistics 3.06 (PAST, Hammer, 2015). The raw data were log-transformed in order to fit linear models and for the correspondence of the log-transform to an isometric null hypothesis (see Chinnery, 2004; Cheng *et al.* 2009; Romano & Citton, 2015). Finally, a hierarchical cluster analysis was performed, again via the software PAST 3.06 using the pair-group algorithm (UPGMA) and the

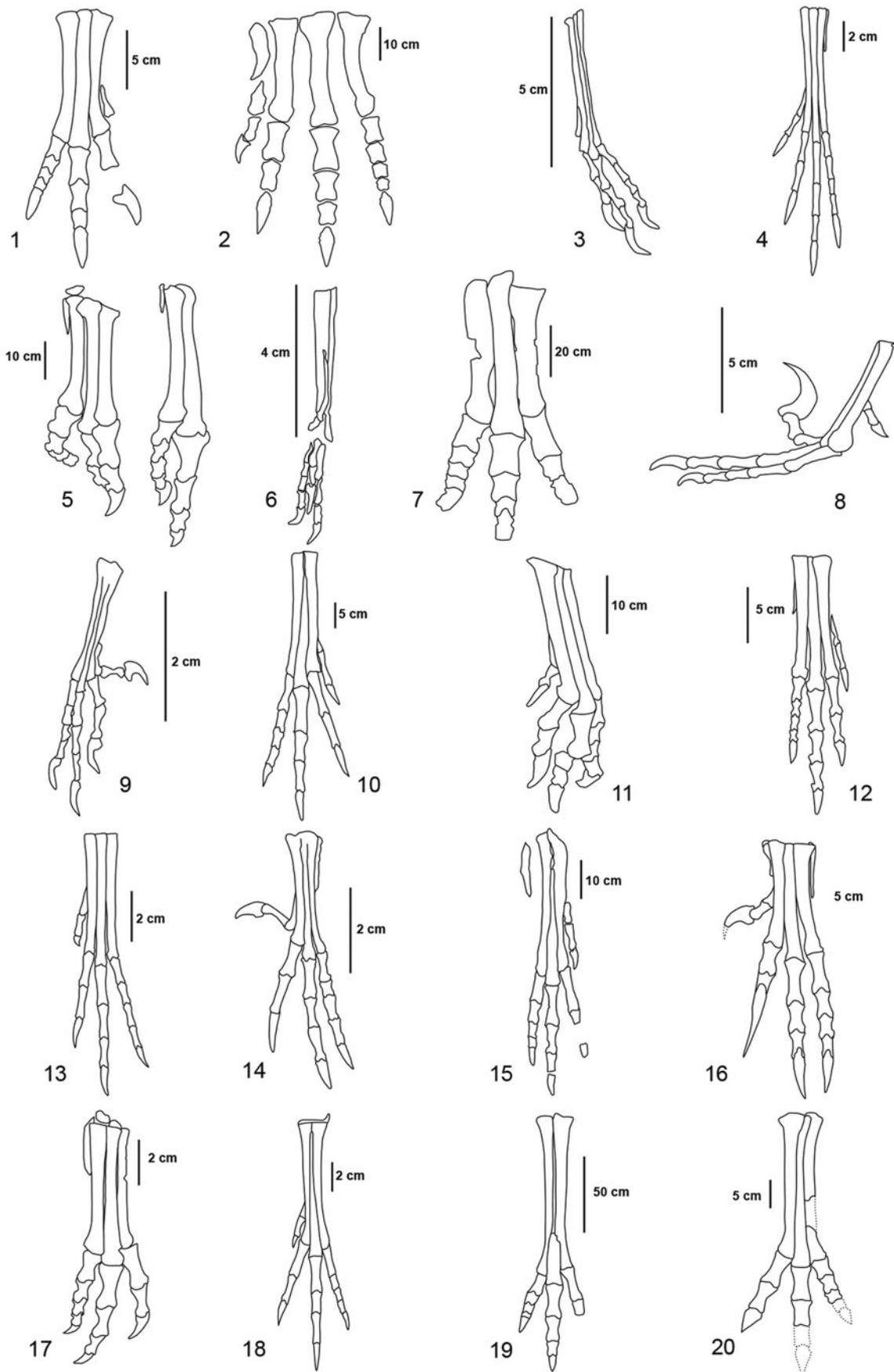


Figure 3. Foot outlines of the selected theropod taxa. 1 – *Ajancingenia*; 2 – *Allosaurus*; 3 – *Anchiornis*; 4 – *Archaeopteryx*; 5 – *Aucasaurus*; 6 – *Aurornis*; 7 – *Deinocheirus*; 8 – *Bambiraptor*; 9 – *Changchengornis*; 10 – *Chirostenotes*; 11 – *Citipati*; 12 – *Coelophysis*; 13 – *Compsognathus*; 14 – *Confuciusornis*; 15 – *Daspletosaurus*; 16 – *Deinonychus*; 17 – *Dilophosaurus*; 18 – *Elmisaurus*; 19 – *Gallimimus*; 20 – *Harpyimimus*.

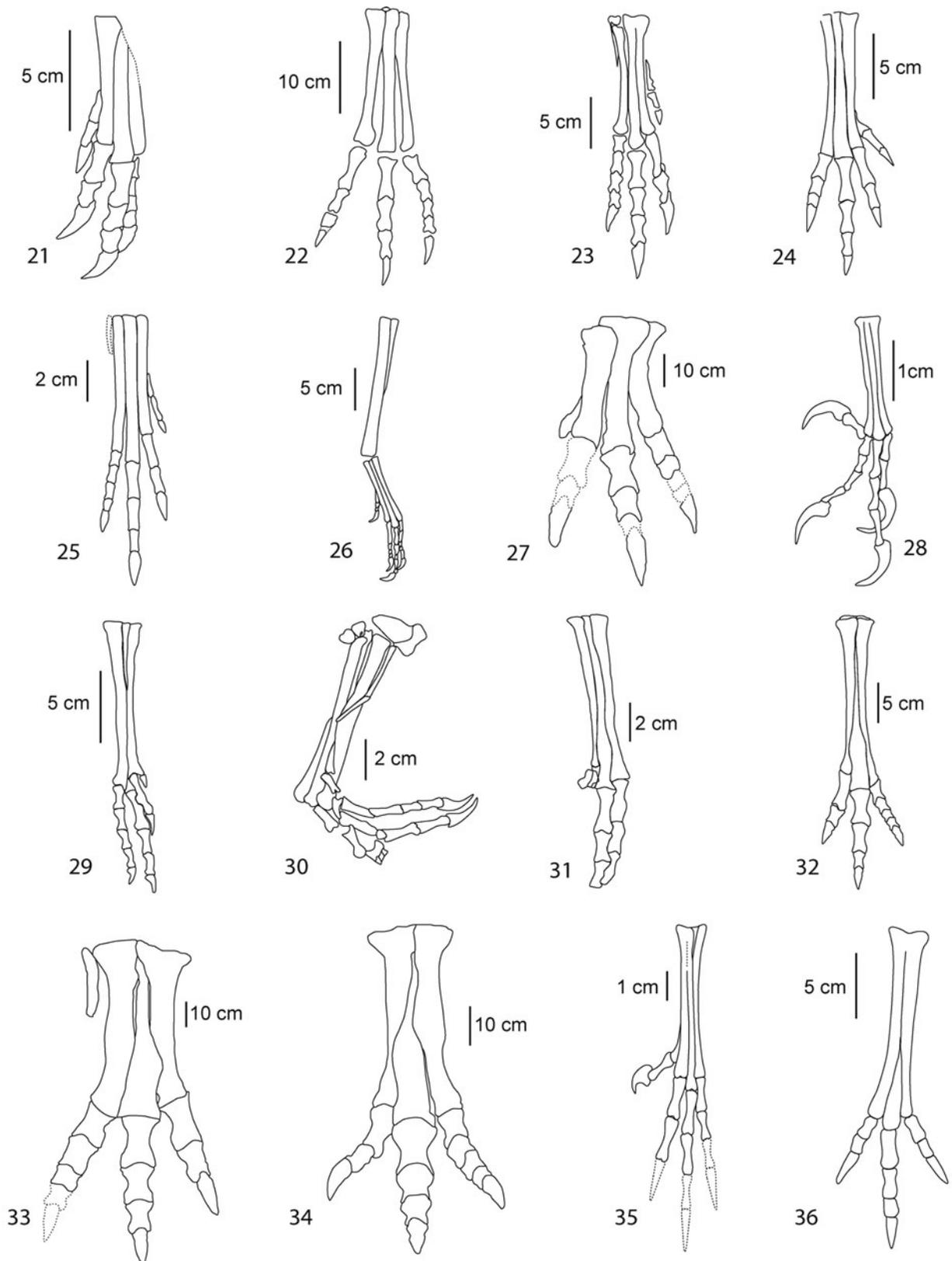


Figure 3. (Continued) Foot outlines of the selected theropod taxa. 21 – *Khaan*; 22 – *Liliensternus*; 23 – *Syntarsus*; 24 – *Nedcolbertia*; 25 – *Procompsognathus*; 26 – *Protarchaeopteryx*; 27 – *Saurophaganax*; 28 – *Sinornis*; 29 – *Sinornithoides*; 30 – *Sinornithosaurus*; 31 – *Sinovenator*; 32 – *Struthiomimus*; 33 – *Tyrannosaurus*; 34 – *Tarbosaurus*; 35 – *Wellnhoferia*; 36 – *Avimimus*; T1 – Type I; T2 – Type II. Specimens redrawn from the original figures reported in Table 1.

Table 1. List, measurements and references for the theropod taxa selected for the present study

Considered Taxa	MT-III	D-II	D-III	D-IV	Source
<i>Ajancingenia</i>	118	85	103	74	Weishampel, Dodson & Osmólska (2004, p. 176, fig. 8.3)
<i>Allosaurus</i>	346	293	350	257	Madsen (1993, p. 159, plate 53)
<i>Anchiornis</i>	49	31	43	37	Hu <i>et al.</i> (2009, p. 2, fig. 2)
<i>Archaeopteryx</i>	64	47	60	56	Osmólska (1981, p. 91, fig. 6)
<i>Aucasaurus</i>	380	225	280	220	Coria, Chiappe & Dingus (2002, p. 464, fig. 4)
<i>Aurornis</i>	40	21	27	24	Godefroit <i>et al.</i> (2013, p. 359, fig. 1)
<i>Avimimus</i>	156	53	85	54	Vickers-Rich, Chiappe & Kurzanov (2002, p. 68, fig. 3.1)
<i>Bambiraptor</i>	80	58	85	78	Burnham <i>et al.</i> (2000, p. 9, fig. 7)
<i>Changchengornis</i>	22	15	19	17	Qiang, Chiappe & Shu'An (1999, p. 4, fig. 3)
<i>Chirostenotes</i>	167	141	166	246	Weishampel, Dodson & Osmólska (1990, p. 247, fig. 9.2)
<i>Citipati</i>	259	159	177	164	Senter (2007, p. 435, fig. 3)
<i>Coelophysis</i>	122	81	113	78	Lucas <i>et al.</i> (2006, p. 91, fig. 8)
<i>Compsognathus</i>	53	38	52	45	Weishampel, Dodson & Osmólska (1990, p. 291, fig. 13.15)
<i>Confuciusornis</i>	30	25	30	28	Martin & Zhou (1998, p. 288, fig. 2)
<i>Daspletosaurus</i>	394	?	274	232	Carr & Williamson (2000, p. 122, fig. 8)
<i>Deinocoelurus</i>	605	373	409	355	Lee <i>et al.</i> (2014, p. 258, fig. 3)
<i>Deinonychus</i>	143	141	167	171	Weishampel, Dodson & Osmólska (2004, p. 205, fig. 10.8)
<i>Dilophosaurus</i>	302	205	237	185	Weishampel, Dodson & Osmólska (1990, p. 63, fig. 3.11)
<i>Elmsaurus</i>	70	46	58	44	Osmólska (1981, p. 91, fig. 6)
<i>Gallimimus</i>	116	77	94	68	Weishampel, Dodson & Osmólska (2004, p. 145, fig. 6.5)
<i>Harpymimus</i>	205	143	96	116	Weishampel, Dodson & Osmólska (2004, p. 145, fig. 6.5)
<i>Khaan</i>	73	40	63	48	Clark, Norell & Barsbold (2001, p. 211, fig. 2)
<i>Liliensternus</i>	202	148	177	148	Lucas <i>et al.</i> (2006, p. 91, fig. 8)
<i>Majungasaurus</i>	134	110	110	87	Carrano (2007, p. 174, fig. 11)
<i>Nedcolbertia</i>	112	63	90	61	Kirkland <i>et al.</i> (1998, p. 246, fig. 9)
<i>Procompsognathus</i>	72	43	59	40	Farlow & Lockey (1993, p. 126, fig. 1)
<i>Protarchaeopteryx</i>	87	58	72	57	Qiang <i>et al.</i> (1998, p. 775, fig. 1)
<i>Saurophaganax</i>	417	340	398	290	OMNH 01307
<i>Sinornis</i>	20	15	23	21	Weishampel, Dodson & Osmólska (2004, p. 222, fig. 11.5)
<i>Sinornithoides</i>	122	46	77	71	Senter (2007, p. 435, fig. 3)
<i>Sinornithosaurus</i>	93	43	74	68	Xu, Wang & Wu (1999, p. 265, fig. 4)
<i>Sinovenator</i>	90	?	51	56	White (2009, p. 8, fig. 5)
<i>Struthiomimus</i>	218	94	123	84	Weishampel, Dodson & Osmólska (2004, p. 145, fig. 6.5)
<i>Syntarsus</i>	128	97	122	69	Lucas <i>et al.</i> (2006, p. 91, fig. 8)
<i>Tyrannosaurus</i>	775	505	623	587	FMNH PR 2081
<i>Tarbosaurus</i>	510	309	399	332	Weishampel, Dodson & Osmólska (2004, p. 126, fig. 5.20)
<i>Wellnhoferia</i>	49	38	47	39	Elzanowski (2001, p. 525, fig. 2)
<i>Type I</i>	260	121	152	108	
<i>Type II</i>	260	121	152	125	

Euclidean Similarity index. The results of the analysis are discussed in the following sections.

2.a. Institutional abbreviations

FMNH – Field Museum of Natural History, Chicago, Illinois; OMNH – Oklahoma Museum of Natural History, Norman, Oklahoma.

3. Results

A first PCA was conducted on the total dataset. The analysis, conducted on a correlation matrix, showed that 97.2% of the variance was resolved into the first principal component and 1.45% into the second one. Thus, the first two principal components account for about 98.65% of the variance for the considered dataset. In Figure 4a the bivariate scatter plot of the first two principal components is shown. The second and third principal components account together only for 1.31% of the total variance. For this reason scatter plots of components 2 and 3 were not considered significant for the present study and are simply given for completeness in the online Supplementary Material available at <http://journals.cambridge.org/geo>. The taxa are

connected via convex hulls according to the particular group they belong to. The analysis of the loadings for the first principal component (Fig. 4b) shows that the four variables considered are all positively correlated with comparable loads.

This indicates, in all probability, that the first principal component largely indicates the absolute size and substantial isometric growth (see Hammer & Harper, 2006). The distribution in the scatter plot along the first principal component describes the differences in size, from very small autopods as in the Avialae *Changchengornis* and *Sinornis* (metatarsus length about 2 cm) to giant pedal proportions as in *Tyrannosaurus rex* (metatarsus length about 78 cm). In the central position we find taxa of intermediate size such as *Gallimimus*, *Harpymimus*, *Coelophysis* and *Avimimus*. On the basis of the loadings (Fig. 4c), the second component is essentially a linear inverse combination between the length of the metatarsal and the length of the second digit (conventionally regarded as informative loading greater than 0.3 and smaller than -0.3). This means that, as the metatarsal length increases, the second digit (responding to the great part of the variance for principal component II) decreases and vice versa. On the basis of loading, the lengths of the third and fourth

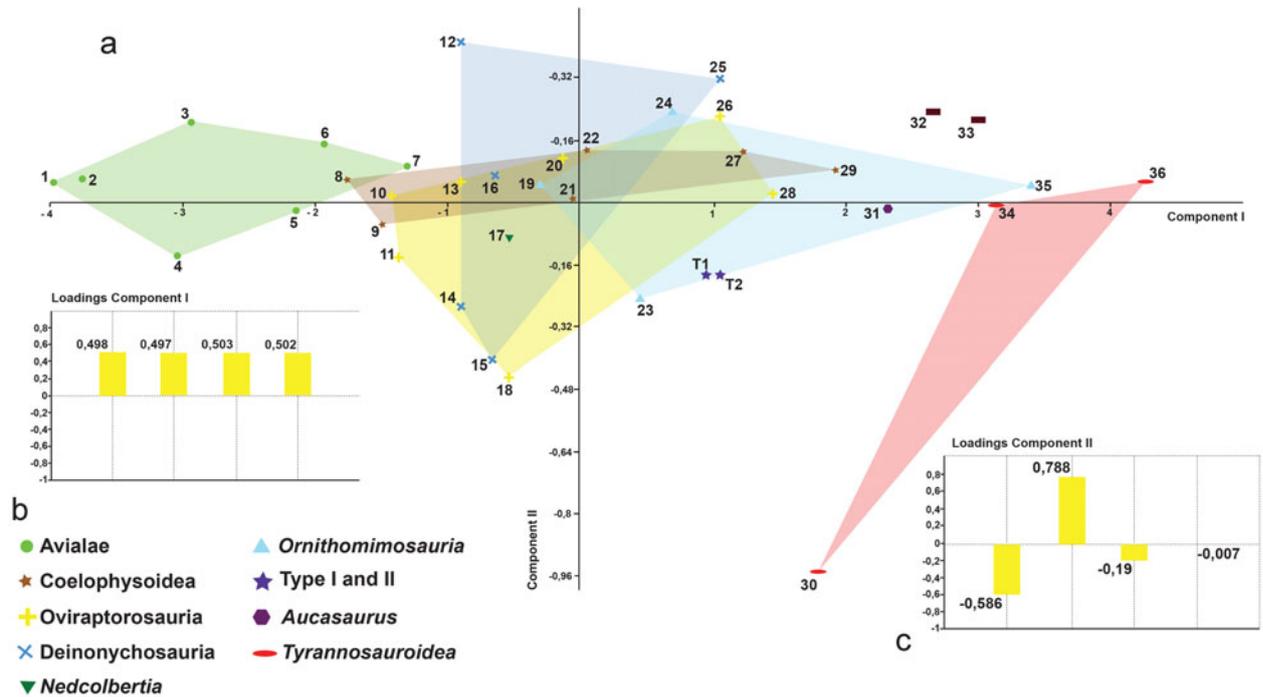


Figure 4. (Colour online) (a) Bivariate scatter plot of the first two principal components; (b) loadings of component I; (c) loadings of component II. 1 – *Changchengornis*; 2 – *Sinornis*; 3 – *Confuciusornis*; 4 – *Aurornis*; 5 – *Anchiornis*; 6 – *Wellnhoferia*; 7 – *Archaeopteryx*; 8 – *Compsognathus*; 9 – *Procompsognathus*; 10 – *Elmisaurus*; 11 – *Khaan*; 12 – *Sinovenator*; 13 – *Protarchaeopteryx*; 14 – *Sinornithosaurus*; 15 – *Sinornithoides*; 16 – *Bambiraptor*; 17 – *Nedcolbertia*; 18 – *Avimimus*; 19 – *Gallimimus*; 20 – *Ajancingenia*; 21 – *Coelophysis*; 22 – *Syntarsus*; 23 – *Struthiomimus*; 24 – *Harpymimus*; 25 – *Deinonychus*; 26 – *Chirostenotes*; 27 – *Liliensternus*; 28 – *Citipati*; 29 – *Dilophosaurus*; 30 – *Daspletosaurus*; 31 – *Aucasaurus*; 32 – *Allosaurus*; 33 – *Saurophaganax*; 34 – *Tarbosaurus*; 35 – *Deinocheirus*; 36 – *Tyrannosaurus*; T1 – Type I; T2 – Type II.

digit are not significant when it comes to detecting the variance and for the discrimination of morphometric patterns from the analysed dataset.

Members of Avialae form a fairly circumscribed cluster in the left portion of the graph (therefore small absolute size). The convex hull for Coelophysoidea shows an area of existence developed essentially along the principal component I, while definitely restricted along the second component. This indicates that the group is conservative with regard to the general arrangement and morphometric ratios of the feet, however, with a relatively broad range of dimensions, ranging from the smallest *Compsognathus* (metatarsus 53 mm in length) to the largest *Dilophosaurus* at the right end of the convex hull (metatarsus about 302 mm in length).

The convex hulls in Deinonychosauria, Ornithomimosauria and Oviraptorosauria show considerable areal extent along both components I and II. This suggests that, in addition to covering a considerable range of absolute size, taxa within these three groups are also characterized by consistent morphometric differences in pedal anatomy (in particular in the inverse relationship between the length of the metatarsus and the length of the second digit). The convex hulls in these groups (also including Coelophysoidea) are widely overlapping in the central portion of the graph.

Therefore, this area of morphospace is largely occupied by non-avian theropods. In the right portion of the scatter plot the convex hull is occupied by large members of Tyrannosauroidae. The extension along component I is very limited, and is shaped by taxa of comparably large dimensions.

When considering morphometric features (component II), *Tyrannosaurus* and *Tarbosaurus* are close, and share a common and consistent structural pattern. The tyrannosaurid *Daspletosaurus*, however, is far removed when component II is considered, revealing a distinctive and autapomorphic character within the group. It is worth noting, however, that the pes in *Daspletosaurus* it is not complete and digit II was coded with a question mark (this can affect the position of the taxon in the scatter plot, considering that digit II is crucial for the description of the total variance observed).

The two hypotheses based on the footprints studied in this paper fall very close to each other (Fig. 4). This indicates that, even when two alternative arrangements for the termination of the metatarsals and for the metatarsal–phalangeal articular region (Type I and II) are considered, the morpho-structural pattern remains consistent and solid. The two hypotheses fall within the convex hull area (Ornithomimosauria) and especially close to *Struthiomimus*. Using the software option ‘Min. span tree’ (linking morphometrically close

taxa), the two hypotheses are connected to each other and in turn connect to both *Struthiomimus* and to *Harpymimus*, thus emphasizing a great affinity with Ornithomimosauria.

To further test this hypothesis a hierarchical cluster analysis was performed. The dendrogram obtained through the pair-group algorithm and the Euclidean Similarity measure is shown in Figure 5.

The two hypotheses are combined in a sister group relationship and are connected by a pectinate arrangement to *Struthiomimus* and *Harpymimus*, recovering the *Harpymimus* + *Struthiomimus* + Type I + Type II cluster and indicating an affinity of the Italian footprints to Ornithomimosauria. Based on these empirical results, the foot of *Struthiomimus* (taxon resulted as sister group of the footprints in the cluster analysis) was superimposed on the new footprints to test the match.

3.a. Matching the foot of *Struthiomimus* with the analysed footprints

When comparing foot morphology to the footprint, the arthral interpretation was preferred, so that the plantar pads and interphalangeal articulations are arranged accurately. This arrangement has recently been supported by Cuesta *et al.* (2015), describing the preserved podotheca (scales covering the foot in extant birds) in *Concavenator corcovatus* as the basal condition in Tetanurae. Here, this configuration is tentatively applied to Ornithomimosauria, specifically to the foot of *Struthiomimus*. In Figure 6 the pes is statically superimposed on the footprint, while the formation of a footprint necessarily implies a dynamic conception of the impression-making process (Baird, 1980; Thulborn, 2013; Romano, Citton & Nicosia, 2016).

During this process, different parts of the foot contact the substrate in different and diachronic ways and many observed structures result from the interference of movements (with complex multiphasic download of body weight) at different stages of locomotion (see Thulborn & Wade, 1989; Avanzini, 1998; Gatesy *et al.* 1999; Falkingham & Gatesy, 2014; Romano, Citton & Nicosia, 2016).

The foot of *Struthiomimus* matches the reference footprint rather well, with a close correspondence between the anatomical constraints and the shape and differential depth of impressions in the footprint (Fig. 6). Minor differences and discrepancies are likely a consequence of missing soft tissue regions (e.g. skin) and corneous unguis sheaths; these parts contribute to the impression but did not fossilize (except in rare cases, see below). According to Cuesta *et al.* (2015), in *Concavenator corcovatus* the impressions of corneous unguis sheaths extend beyond the tip of the unguis phalanx by 41.27% and 31.78% of the total claw length in relation to digits III and IV.

These percentages differ from those seen in extant birds (see Manning *et al.* 2009 and discussion in Cuesta *et al.* 2015) and are on average lower in extinct avian theropods, where they range from 12% to 30% (Pu

et al. 2013; Cuesta *et al.* 2015). Cuesta *et al.* (2015) suggested the higher percentage observed in *Concavenator* is caused by a taphonomic displacement of the skin and sheath with respect to their original anatomical position.

An additional character that makes the new Italian footprints compatible with a struthiomimid-like trackmaker is the complete absence of a hallux impression. Considering that the metatarsals were completely laid on the ground with an approximately horizontal final position (the depth of the straight portion of the metatarsal traces is fairly constant), the impression of the first digit might be expected, as observed in several published records (e.g. Lockley, Meyer & Faria dos Santos, 1998; Lockley, Matsukawa & Li, 2003; Conti *et al.* 2005; Nicosia *et al.* 2007; Gierliński, Lockley & Niedzwiedzki, 2009). Within Ornithomimosauria, *Struthiomimus* is characterized by the derived absence of the first toe in the foot. In particular, the derived group within Ornithomimosauria formed by *Anserimimus*, *Archaeornithomimus*, *Gallimimus*, *Struthiomimus* and *Ornithomimus* (constituting the Ornithomimididae *sensu* Makovicky, Kobayashi & Currie, 2004) are identified by the loss of the first pedal digit, an unambiguous synapomorphy, in addition to a proximally reduced metatarsal III (Makovicky, Kobayashi & Currie, 2004). In the same way, the absence of the imprint of the first digit in footprints with metatarsal traces led Farlow *et al.* (2015) to ascribe to ornithomimosaurians some elongated tracks from the classic Paluxy River site (Farlow *et al.* 2015, p. 21, figs 5D and 5E).

Other morphological features of the metatarsus in the Ornithomimosauria are worth mentioning. In *Garudimimus* and *Harpymimus* metatarsal III separates metatarsals II and IV for the entire length of the metapodium; in ornithomimids metatarsals II and IV exclude metatarsal III in cranial view (along the extensor surface of the proximal portion) resulting in complete contact proximally (Makovicky, Kobayashi & Currie, 2004). Such a configuration results in a proportionally very narrow metatarsal (typical condition of arctometatarsalia, see Holtz, 1994), compatible with the long and narrow traces of the metatarsals in the Italian specimens. Based on the dimensions of a complete skeleton of *Struthiomimus altus* figured in Longrich (2008, fig. 6, p. 985) the putative trackmaker would have had a hip height of about 1.06 m and a total body length of about 2.8 m.

4. Discussion

The new Italian footprints allow a morphometric–quantitative approach to test the correspondence and compatibility between theropod tracks with metatarsal impressions and the osteological structures of autopods in the principal groups of theropods.

The preliminary results of the PCA indicate that the relative length of the second digit can be a useful diagnostic character within theropods, with repercussions for the study of body fossils and the interpretation of

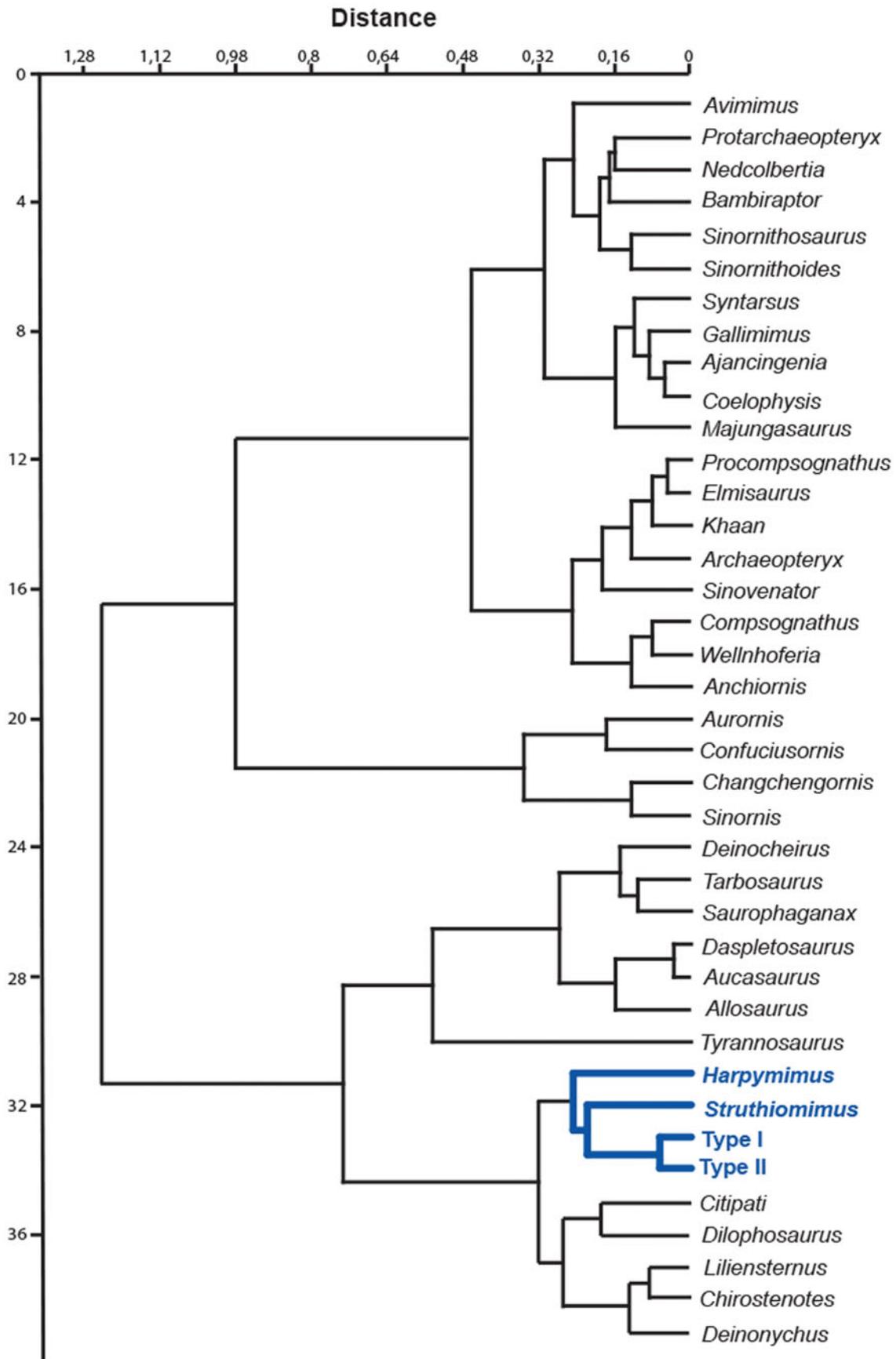


Figure 5. (Colour online) Cluster analysis dendrogram obtained using the pair-group algorithm and the Euclidean Similarity. The two hypotheses obtained from the footprints (Type I and II) are properly combined in a sister group relationship and are connected by a pectinate arrangement to *Struthiomimus* and *Harpymimus*.

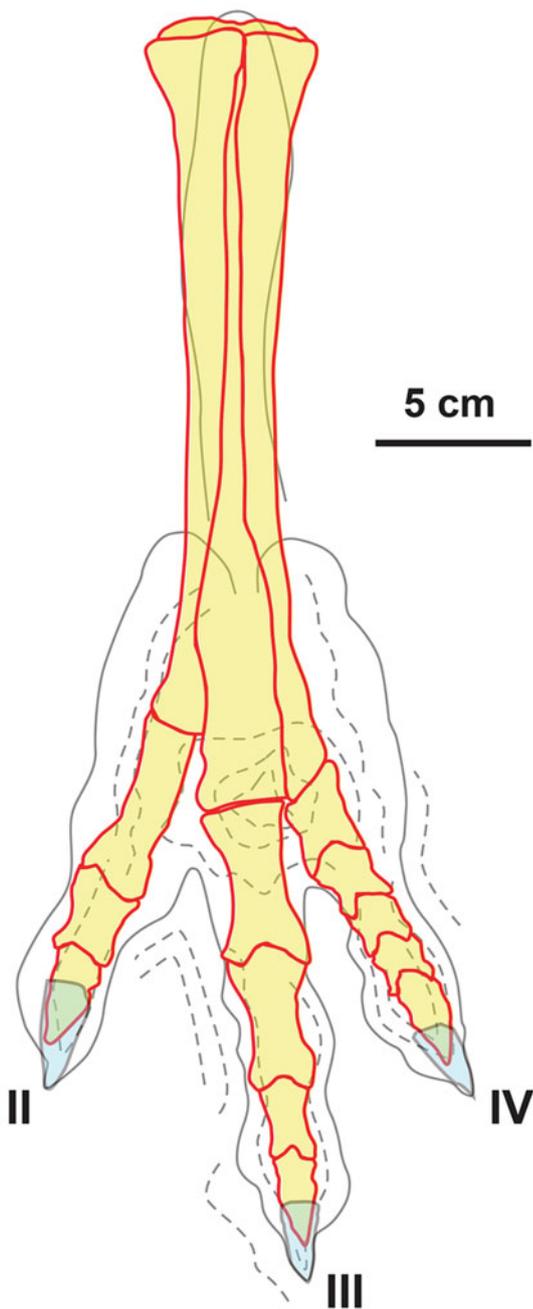


Figure 6. (Colour online) Static superimposition of the foot of *Struthiomimus* on analysed footprint. Corneous unguual sheath were assumed and shown in the illustration.

the ichnological record. The third digit appears to be less variable (loading equal to -0.1899 , therefore not significant for the variance), with a more stable relationship with the metatarsus, even with a substantial increase in size. This could be related to the strictly mesaxonic functionality in both large and small theropods (at least in the weight-bearing phase). In this interpretation, the more functional structures, with a crucial role in locomotion, are less variable and more conservative.

In a cluster analysis dendrogram Avialae are combined in one group, demonstrating a stable and compact morphometric pattern for the foot in that clade,

with the exception of *Wellnhoferia* and *Anchiornis*, which may have acquired a pes structure more similar to that of *Compsognathus*. The large theropods *Tyrannosaurus*, *Tarbosaurus*, *Daspletosaurus*, *Allosaurus*, *Saurophaganax* and *Deinocheirus* are gathered in a cluster, hinting at a similar pedal structure. Similar results have been also obtained by Farlow *et al.* (2013) and Farlow *et al.* (2014). These authors used different homologous measures (particularly the length and width of pedal phalanges) in their cluster analyses, obtaining a gathering of the genera *Tyrannosaurus*, *Allosaurus* and *Daspletosaurus* in the same group on a morphometric basis (Farlow *et al.* 2013, p. 117, fig. 5.18), as well as *Allosaurus*, *Gorgosaurus* and *Tyrannosaurus* (Farlow *et al.* 2014, p. 1035, fig. 9). Considering that all these taxa reached very large body sizes, the result of the cluster analysis might highlight a common convergence of the pes reflecting the need to support a large body during locomotion and in the resting phase (see also Farlow *et al.* 2013). New and ongoing morphometric studies consider RMA slopes, Landmark and finite elements analysis in major non-avian theropods in an attempt to identify possible allometric trends with increasing absolute size; these efforts will likely shed light on these issues.

Both in the PCA and in the cluster analysis the two morphological hypotheses (e.g. Type I and Type II) fall very close to each other, indicating a well-defined and stable general structure, despite the two different interpretations for the metatarsus distal end. However, based on the differential depth analysis of the footprints, and in particular the identification of the medio-laterally moved metatarsal–phalangeal pad of digits III and IV, the Type I hypothesis results are decidedly more plausible. This model includes a shorter second metatarsal with the third and fourth metatarsal more or less coincident and more developed distally, thus similar to the foot structure of *Struthiomimus* that is characterized by a shorter metatarsal II.

The analysis suggests that the putative trackmaker is a member of Ornithomimosauria, with a greater morphometric affinity with *Struthiomimus* and *Harpyimimus*. Considering the lack of a hallux track, and the arctometatarsalian structure of the metatarsal, the putative trackmaker is very likely a member of the Ornithomimidae (*sensu* Makovicky, Kobayashi & Currie, 2004) with noteworthy affinities with *Struthiomimus*.

This present ichnological study also sheds light on the behaviour of the putative trackmaker. Ornithomimosauria are a group of lightly built theropods, medium to large in size. Because of the particular conformation of the hindlimb (well developed, with proportionately long distal elements) in this group, they have been considered among the most cursorial of theropods (e.g. Holtz, 1994; Makovicky, Kobayashi & Currie, 2004). According to Makovicky, Kobayashi & Currie (2004) ornithomimids were characterized by a well-developed sense of balance and had to be fast runners. Thulborn (1990) has estimated a maximum running speed for ornithomimosauria of 35 to 60 km hr⁻¹.

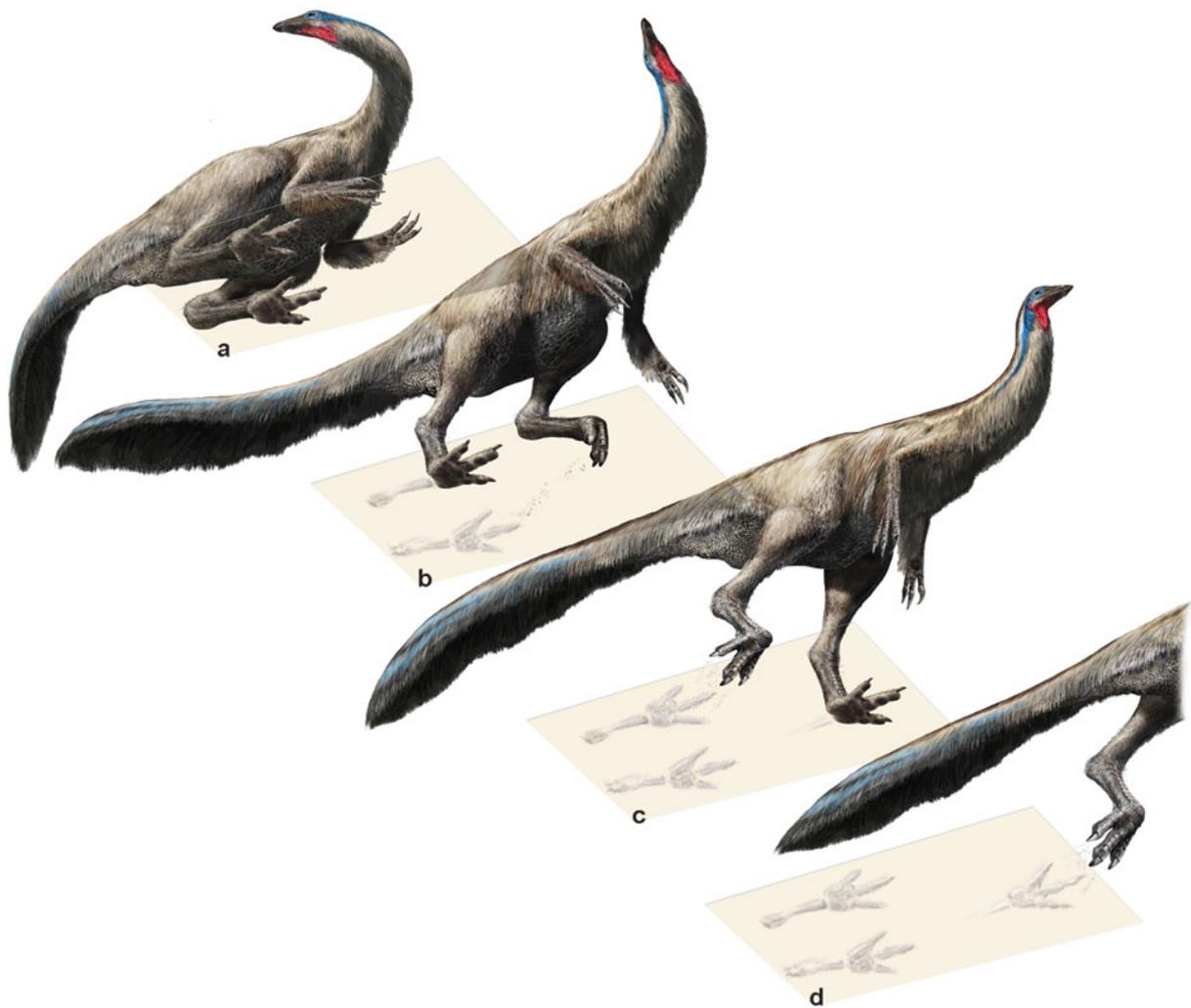


Figure 7. (Colour online) Main phases of the movement made by the Riomartino trackmaker. (a) Resting phase in 'crouched' position; (b) the trackmaker walks in a 'crouched position', while the right footprint is being definitively impressed; (c) initial rising up and definitive impression of the second left footprint; (d) final kick-off. Artwork created by Davide Bonadonna (<http://www.davidebonadonna.it>).

The recently re-described heavily built *Deinocheirus mirificus* (Lee *et al.* 2014) departs from this trend. It is the largest member of the Ornithomimosauria and has been interpreted as a non-cursorial theropod.

Our work focused on 'crouching' postures in ornithomimosaur (for a discussion of the meaning of 'crouching' see Citton *et al.* 2015). This particular behaviour may be related to a resting position during a locomotor cycle, or squatting for foraging. Prey stalking or careful walking during locomotion on unstable or waterlogged substrates has also been suggested in the literature (see Kuban, 1989; Romero-Molina *et al.* 2003; Nicosia *et al.* 2007; Petti *et al.* 2008).

It is not known if theropods substantially modified their locomotion pattern when walking on different substrates. Wilson, Marsicano & Smith (2009) suggested that basal theropods did not change their mode of locomotion substantially on different sediment and substrate conditions, unlike ornithopods for example. In extant taxa, Milàn (2006) described and figured long metatarsal tracks from the large cursorial taxon

Dromaius novaehollandiae, which were left by the animal during feeding on the ground. In this case, the metatarsus made complete contact with the substrate. In the new Italian ichnofossils it is worth noting that in this 'crouching' position, traces of the manus are not preserved, in contrast to other similar finds (see Milner *et al.* 2009 and references therein). According to Makovicky, Kobayashi & Currie (2004), *Struthiomimus* is peculiar in having the proportionally longest hand among ornithomimosaur. With this configuration, once the theropod was crouching on the metatarsals, the front limb would have likely interacted with the substrate. Therefore, it is possible that the Italian trackmaker, although having affinities with *Struthiomimus* in the pedal skeleton, differed in the length and overall osteology of the forelimb. The main movements made by the trackmaker, involving a resting phase in a 'crouched' position followed by squatted walking and final rising up, are shown in Figure 7.

Regarding the age, there is a good match between the identified taxonomic group and the age of the trampled

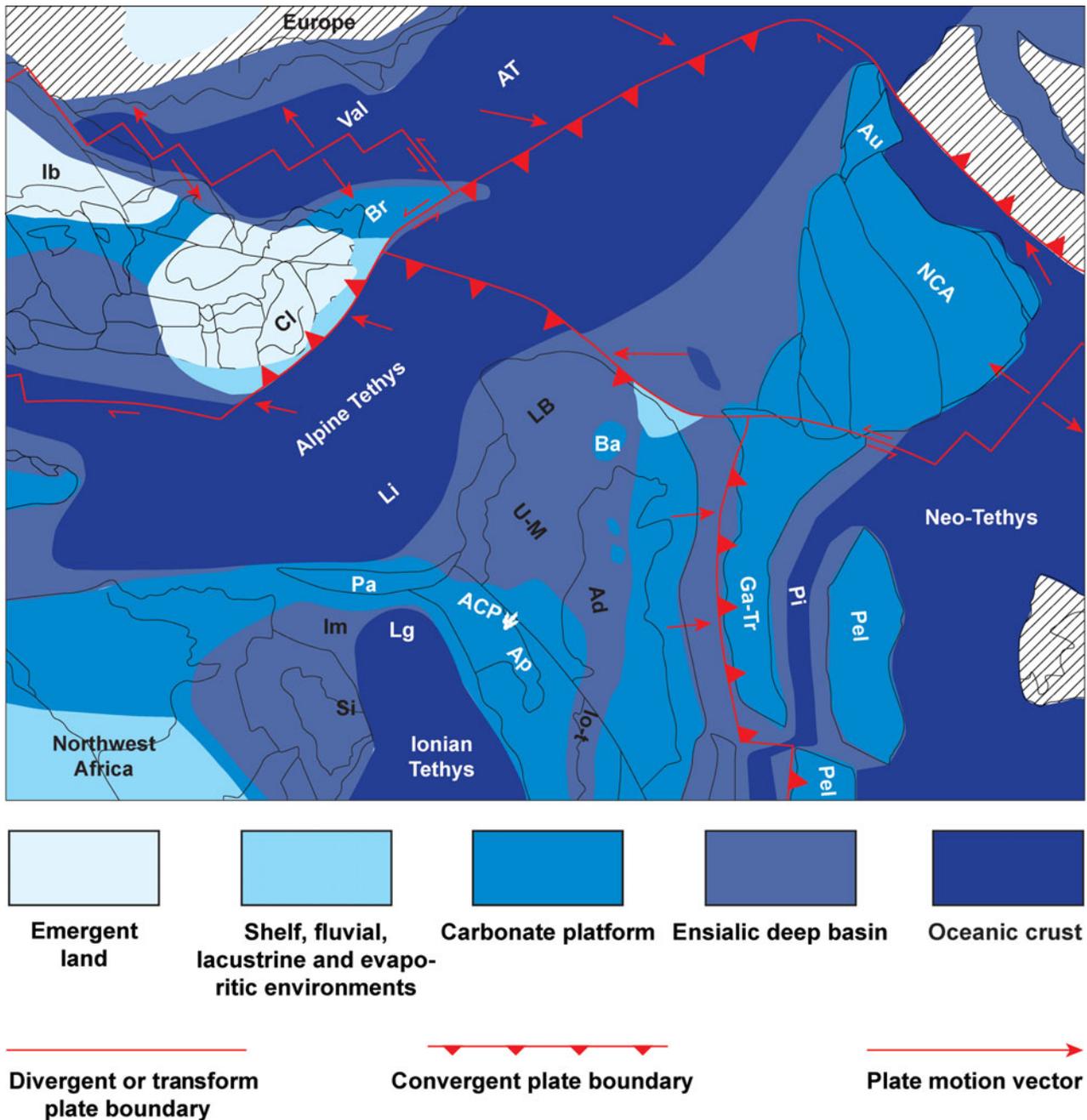


Figure 8. (Colour online) Palaeogeographic map of the peri-Mediterranean region during the Aptian (from Turco *et al.* 2007, redrawn and modified). Ad – Adriatic–Dinaric Carbonate Platform; ACP – Apenninic Carbonate Platform; Ap – Apulian Platform; AT – Alpine Tethys Ocean; Au – Australpine; Ba – Bagnolo Carbonate Platform; Br – Briançonnais; Cl – Calabria; Ga-Tr – Gavrovo-Tripoliza; Io-t – Ionian trough; Ib – Iberia; Im – Imerese Basin; LB – Lombard Basin; Li – Ligure-Piemontese Ocean; Lg – Lagonegro Basin; NCA – Northern Calcareous Alps; Pa – Panormide Carbonate Platform; Pel – Pelagonian; Pi – Pindos; Si – Sicilian Basin; U-M – Umbria-Marche Basin; Val – Valais Ocean. White footprint highlights the location of the Apenninic Carbonate Platform, from which the tracks in study come from.

block. The block can be attributed a late Aptian – ?early Albian age. Ornithomimosauria have a late Barremian to late Maastrichtian distribution; *Harpymimus* is known from upper Albian deposits while *Struthiomimus* has a temporal range from the late Campanian to the early Maastrichtian (Makovicky, Kobayashi & Currie, 2004). Elongated tracks of metatarsals in theropod footprints from central Italy (Sezze ichnosite, Cenomanian) and southern Italy (Borgo Celano, late Hauterivian – early Barremian) have been considered

compatible with an Ornithomimosauria and Oviraptorosauria trackmaker (Nicosia *et al.* 2007; Petti *et al.* 2008). At the Sezze ichnosite, the authors considered the second trackmaker more likely, based on the narrow trace of a claw, which appears to be more compatible with the laterally compressed ungual phalanges in oviraptorosaurs. The large theropod tracks from Witt Ranch (Dakota Group, Union County, New Mexico) preserve an elongated posterior impression, doubtfully referable to the metatarsals, and were assigned by

Lockley, Matsukawa & Witt (2006) to an ornithomimid or struthiomimid theropod, such as the most common Dakota Group theropod ichnotaxon *Magnoavipes*; according to the authors such attribution is corroborated and supported by the complete absence of a hallux trace.

The attribution of tracks to a struthiomimid-like theropod requires some palaeobiogeographical considerations, in the light of the current discussion about the palaeogeography of the central Mediterranean area. The Riomartino tracks can be easily included in the second association of the dinosaur track record of Italy (late Tithonian – late Cenomanian), recently discussed by Citton, Nicosia & Sacchi (2015). According to these authors, during the late Tithonian – late Cenomanian time interval a northern origin of the dinosaurian fauna making up this association can be discarded owing to the existence of a large oceanic area called the Vardar Ocean (Channel & Kozur, 1997); similarly, a provenance from the east can be excluded because of the presence of the Ionian trough (Aubouin, 1959) separating the Italian carbonate platforms from the Dinaric region, and in addition, migration from western areas (Iberian region, Canudo *et al.* 2009) can be rejected since the Umbro-Marchean succession was sedimented in a wide and deep depositional basin, most likely not allowing any passage. Back to the putative trackmaker, Ornithomimosauria are predominantly known from Central Asia, North America (e.g. *Shenzhousaurus*, *Harpymimus*, *Garudimimus*) and Spain (i.e. *Pelecanimimus*) (Makovicky, Kobayashi & Currie, 2004). Thus, taking into account the palaeogeographic framework of the peri-Mediterranean area in Middle Cretaceous time (Aptian, Fig. 8), dinosaurs could have reached the ‘Apenninic Carbonate Platform’ through migration routes from Gondwana via Adria (Sacchi *et al.* 2009; Zarcione *et al.* 2010). Apart from skeletal remains referred to *Nqwebasaurus thwazi* from the Kirkwood Formation (Lower Cretaceous) of South Africa, regarded as the basalmost known ornithomimosaur (Choiniere, Forster & de Klerk, 2012), these theropods have never been further reported from southern continents.

5. Conclusions

Our work highlights the great potential of morphometric methods to describe specific characters of a given taxonomic group (both in body fossils and in footprints) more objectively, as already convincingly pointed out recently in the literature (Castanera *et al.* 2015).

These approaches integrate morphometric analysis with footprint morphology and differential impression depth (‘footprint holomorphy’ *sensu* Romano, Citton & Nicosia, 2016), and may shed light on taxonomically relevant characters but also on the biomechanical properties and importance of selected anatomical regions. The latter, cross-checked and plotted on a phylogenetic analysis, can be pivotal for understanding in which particular node and branch a specific morphology, or

even a particular behavioural trait, has been acquired. Such integrative approaches also shed light on the dispersal of different clades and different palaeobiogeographical models. In this study, we consider it likely that dinosaurs could reach the Apenninic Carbonate Platform only through migration routes from Gondwana through the Adria region. The identification of a struthiomimid-like theropod as the putative trackmaker of the new Italian material further supports that putative Ornithomimosauria were present in Gondwana, as previously suggested by other Italian tracks and skeletal material from South Africa. Ichnological data proved to be once again a crucial source of evidence, especially in cases where the body-fossil record results are virtually absent. As we have experienced in recent years, ichnology has passed, in all respects, from a mere curiosity or corollary of vertebrate palaeontology, to a critical mass of ‘pawing’ often unique evidences and inferences.

Acknowledgements. Kenneth Angielczyk of the Field Museum of Natural History (Ill, USA) and Kyle Davis of the Sam Noble Museum of Natural History (Ok, USA) are warmly thanked for providing useful photographic material of *Tyrannosaurus* and *Saurophaganax*. Umberto Nicosia is specially thanked for discussions during the study and the preparation of the manuscript. We are also grateful to Nizar Ibrahim, for his suggestions and correction of an early version of this manuscript, and to Simone Maganuco, for important tips on the final version. The artist Davide Bonadonna (<http://www.davidebonadonna.it>) is warmly thanked for having created the artworks. We further thank Peter Falkingham, an anonymous reviewer and the Executive Editor Paul Upchurch for suggestions and comments that greatly improved the manuscript. This work was made possible by financial support to MR from the Alexander von Humboldt-Foundation (Sofja Kovalevskaja-Award to Jörg Fröbisch ‘*Early Evolution and Diversification of Synapsida*’ of the German Federal Ministry of Education and Research). This study was conducted within the ‘PalaeoWorks’ Project (<https://www.facebook.com/pages/PalaeoWorks/1444856609165872>).

Supplementary material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0016756816000546>.

References

- AUBOUIN, J. 1959. Contribution à l'étude géologique de la Grèce Septentrionale: les confins de l'Épire et de la Thessalie. *Annales Géologiques des Pays Helléniques* **10**, 1–525.
- ACCORDI, G., CARBONE, F., CIVITELLI, G., CORDA, L., DE RITA, D., ESU, D., FUNICIELLO, R., KOTSAKIS, T., MARIOTTI, G. & SPOSATO, A. 1988. Note illustrative della carta delle litofacies del Lazio-Abruzzo ed aree limitrofe. C.N.R.-P.F. Geodinamica: sottoprogetto 4. *Quaderni della Ricerca Scientifica* **114**, 1–223.
- ARNAUD VANNEAU, A. & PREMOLI SILVA, I. 1995. Biostratigraphy and systematic description of benthic foraminifers from mid-Cretaceous shallow-water carbonate platform sediments at sites 878 and 879 (Mit

- and Takuyo-Daisan Guyots). In *Proceedings of the Ocean Drilling Program, Scientific Results, vol. 144* (eds J. A. Haggerty, I. Premoli Silva, F. Rack & M. K. McNutt), pp. 199–219. College Station, Texas.
- AVANZINI, M. 1998. Anatomy of a footprint: bioturbation as a key to understanding dinosaur walk dynamics. *Ichnos* **6**, 129–39.
- AVANZINI, M., GIERLIŃSKI, G. & LEONARDI, G. 2001. First report of sitting *Anomepus* tracks in European Lower Jurassic (Lavini di Marco site – Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* **107**, 131–6.
- BAIRD, D. 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. In *Aspect of Vertebrate History: Essay in Honor of Harris Colbert* (ed. L. L. Jacobs), pp. 219–230. Flagstaff, Arizona: Museum of Northern Arizona Press.
- BURNHAM, D. A., DERSTLER, K. L., CURRIE, P. J., BAKKER, R. T., ZHOU, Z. & OSTROM, J. H. 2000. Remarkable new bird-like dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. *University of Kansas Paleontological Contributions* **13**, 1–14.
- CANUDO, J. I., BARCO, J. L., PEREDA-SUBERBIOLA, X., RUIZ-OMEÑACA, J. I., SALGADO, L., FERNÁNDEZ-BALDOR, F. T. & GASULLA, J. M. 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. *Bulletin de la Société géologique de France* **180**, 5–11.
- CARR, T. D. & WILLIAMSON, T. E. 2000. A review of Tyrannosauridae (Dinosauria, Coelurosauria) from New Mexico. *New Mexico Museum of Natural History and Science Bulletin* **17**, 113–45.
- CASTANERA, D., COLMENAR, J., SAUQUÉ, V. & CANUDO, J. I. 2015. Geometric morphometric analysis applied to theropod tracks from the Lower Cretaceous (Berriasian) of Spain. *Palaeontology* **58**, 183–200.
- CENTAMORE, E., DI MANNA, P. & ROSSI, D. 2007. Kinematic evolution of the Volsci Range: a new overview. *Italian Journal of Geosciences* **126**, 159–72.
- CARRANO, M. T. 2007. The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **27**, 163–79.
- CHANNEL, J. E. T. & KOZUR, H. W. 1997. How many oceans? Meliata, Vardar and Pindos oceans in Mesozoic Alpine paleogeography. *Geology* **25**, 183–86.
- CHENG, Y. N., HOLMES, R., WU, X. C. & ALFONSO, N. 2009. Sexual dimorphism and life history of *Keichosaurus hui* (Reptilia: Sauropterygia). *Journal of Vertebrate Paleontology* **29**, 401–8.
- CHINNERY, B. 2004. Morphometric analysis of evolutionary trends in the ceratopsian postcranial skeleton. *Journal of Vertebrate Paleontology* **24**, 591–609.
- CHIOCCHINI, M., FARINACCI, A., MANCINELLI, A., MOLINARI, V. & POTETTI, M. 1994. Biostratigrafia a foraminiferi, dasicladali e calpionelle delle successioni carbonati che mesozoiche dell'Appennino centrale. *Studi Geologici Camerti, Volume Speciale* **1994A**, 9–130.
- CHIOCCHINI, M., PAMPALONI, M. L. & PICHEZZI, R. M. 2012. *Microfacies e Microfossili delle Successioni Carbonatiche Mesozoiche del Lazio e dell'Abruzzo (Italia Centrale) – Cretacico*. Memorie per servire alla descrizione della Carta Geologica d'Italia. Volume 17. Roma: ISPRA, Servizio Geologico d'Italia, Dipartimento Difesa del Suolo, 269 pp.
- CHOINIERE, J. N., FORSTER, C. A. & DE KLERK, W. J. 2012. New information on *Nqwebasaurus thwazi*, a coelurosaurian theropod from the Early Cretaceous Kirkwood Formation in South Africa. *Journal of African Earth Sciences* **71**, 1–17.
- CITTON, P., NICOSIA, U., NICOLOSI, I., CARLUCCIO, R. & ROMANO, M. 2015. Elongated theropod tracks from the Cretaceous Apenninic Carbonate Platform of southern Latium (central Italy). *Palaeontologia Electronica* **18.3.49a**, 1–12.
- CITTON, P., NICOSIA, U. & SACCHI, E. 2015. Updating and reinterpreting the dinosaur track record of Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **439**, 117–125.
- CLARK, J. M., NORELL, M. A. & BARSBOLD, R. 2001. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. *Journal of Vertebrate Paleontology* **21**, 209–13.
- CONTI, M. A., MORSILLI, M., NICOSIA, U., SACCHI, E., SAVINO, V., WAGENSOMMER, A., DI MAGGIO, L. & GIANOLLA, P. 2005. Jurassic dinosaur footprints from Southern Italy: footprints as indicators of constraints in paleogeographic interpretation. *Palaios* **20**, 534–50.
- CORIA, R. A., CHIAPPE, L. M. & DINGUS, L. 2002. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* **22**, 460–5.
- COSENTINO, D., CIPOLLARI, P., DI DONATO, V., SGROSSO, I. & SGROSSO, M. 2002. The Volsci Range in the kinematic evolution of the northern and southern Apennine orogenic system. *Bollettino della Società Geologica Italiana, Special Issue* **1**, 209–18.
- CUESTA, E., DÍAZ-MARTÍNEZ, I., ORTEGA, F. & SANZ, J. L. 2015. Did all theropods have chickenlike feet? First evidence of a non-avian dinosaur podotheca. *Cretaceous Research* **56**, 53–9.
- DALLA VECCHIA, M. & TARLAO, A. 2000. New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia). Part II – Paleontology. *Memorie di Scienze* **52**, 227–93.
- ELŻANOWSKI, A. 2001. A new genus and species for the largest specimen of *Archaeopteryx*. *Acta Palaeontologica Polonica* **46**, 519–32.
- FALKINGHAM, P. L. & GATESY, S. M. 2014. The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences (PNAS)* **111**, 18279–84.
- FARLOW, J. O., BATES, K. T., BONEM, R. M., DATTILO, B. F., FALKINGHAM, P. L., GILDNER, R., JACEN, J., KUBAN, G. J., MARTIN, A. J., O'BRIEN, M. & WHITCRAFT, J. 2015. Dinosaur footprints from the Glen Rose Formation (Paluxy River, Dinosaur Valley State Park, Somervell County, Texas). In *Early- and Mid-Cretaceous Archosaur Localities of North-Central Texas, Field Trip Guidebook* (ed. C. Noto), pp. 14–37. Dallas, Texas: Society of Vertebrate Paleontology.
- FARLOW, J. O., HOLTZ, T. R., WORTHY, T. H. JR. & CHAPMAN, R. E. 2013. Feet of the fierce (and not so fierce): pedal proportions in large theropods, other non-avian dinosaurs, and large ground birds. In *Tyrannosaurid Biology* (eds J. M. Parrish, R. E. Molnar, P. J. Currie & E. B. Koppelhaus), pp. 88–132. Bloomington, Indiana: Indiana University Press.
- FARLOW, J. O. & LOCKLEY, M. G. 1993. An osteometric approach to the identification of the makers of early Mesozoic tridactyl dinosaur footprints. *New Mexico Museum of Natural History and Science Bulletin* **3**, 123–31.
- FARLOW, J. O., SCHACHNER, E. R., SARRAZIN, J. C., KLEIN, H. & CURRIE, P. J. 2014. Pedal proportions

- of *Poposaurus gracilis*: convergence and divergence in the feet of archosaurs. *The Anatomical Record* **297**, 1022–46.
- GATESY, S. M., MIDDLETON, K. M., JENKINS, F. A. JR. & SHUBIN, N. H. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature* **399**, 141–4.
- GIERLIŃSKI, G. 1994. Early Jurassic theropod tracks with the metatarsal impressions. *Przegląd Geologiczny* **42**, 280–4.
- GIERLIŃSKI, G. 1996. Feather-like impressions in a theropod resting trace from the Lower Jurassic of Massachusetts. In *The Continental Jurassic* (ed. M. Morales), pp. 179–84. Museum of Northern Arizona Bulletin Volume 60.
- GIERLIŃSKI, G. D., LOCKLEY, M. G. & NIEDZWIEDZKI, G. 2009. A distinctive crouching theropod trace from the Lower Jurassic of Poland. *Geological Quarterly* **53**, 471–6.
- GODEFROIT, P., CAU, A., DONG-YU, H., ESCUILLIÉ, F., WENHAO, W. & DYKE, G. 2013. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* **498**, 359–62.
- HAMMER, Ø. 2015. *Paleontological Statistics (PAST) 2.06*. Oslo, Norway: University of Oslo. <http://folk.uio.no/ohammer/past/>.
- HAMMER, Ø. & HARPER, D. A. T. 2006. *Paleontological Data Analysis*. Oxford: Blackwell Publishing Ltd, 351 pp.
- HOLTZ, T. R. 1994. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *Journal of Vertebrate Paleontology* **14**, 480–519.
- HU, D., HOU, L., ZHANG, L. & XU, X. 2009. A pre-*Archaeopteryx* troodontid theropod from China with long feathers on the metatarsus. *Nature* **461**, 640–3.
- KIM, J. Y., KIM, K. S., LOCKLEY, M. G., YANG, S. Y., SEO, S. J., CHOI, H. I. & LIM, J. D. 2008. New didactyl dinosaur footprints (*Dromaeosauripus hamanensis* ichnogen. et ichnosp. nov.) from the Early Cretaceous Haman Formation, south coast of Korea. *Palaeogeography, Palaeoclimatology, Palaeoecology* **262**, 72–8.
- KIM, J. Y., LOCKLEY, M. G., WOO, J. O. & KIM, S. H. 2012. Unusual didactyl traces from the Jinju Formation (Early Cretaceous, South Korea) indicate a new ichnospecies of *Dromaeosauripus*. *Ichnos* **19**, 75–83.
- KIRKLAND, J. I., BRITT, B. B., WHITTLE, C. H., MADSEN, S. K. & BURGE, D. L. 1998. A small coelurosaurian theropod from the Yellow Cat Member of the Cedar Mountain Formation (Lower Cretaceous, Barremian) of Eastern Utah. In *Lower and Middle Cretaceous Terrestrial Ecosystems* (eds S. G. Lucas, J. I. Kirkland & J. W. Estep), pp. 239–48. New Mexico Museum of Natural History and Science Bulletin no. 14.
- KUBAN, G. 1989. Elongate dinosaur tracks. In *Dinosaur Tracks and Traces* (eds D. D. Gillette & M. G. Lockley), pp. 57–79. Cambridge: Cambridge University Press.
- LEE, Y. N., BARSBOLD, R., CURRIE, P. J., KOBAYASHI, Y., LEE, H. J., GODEFROIT, P., ESCUILLIÉ, F. & CHINZORIG, T. 2014. Resolving the long-standing enigmas of a giant ornithomimosaur *Deinocheirus mirificus*. *Nature* **515**, 257–60.
- LI, D., AZUMA, Y., FUJITA, M., LEE, Y. N., ARAKAWA, Y. 2006. A preliminary report on two new vertebrate track sites including dinosaurs from the early Cretaceous Hekou Group, Gansu Province, China. *Journal of the Paleontological Society of Korea* **22**, 29–49.
- LI, R. & LOCKLEY, M. G. 2005. Dromaeosaurid trackways from Shandong Province China. *Journal of Vertebrate Paleontology* **25**, 84A.
- LI, R., LOCKLEY, M. G., MAKOVICKY, P. J., MATSUKAWA, M., NORELL, M. A., HARRIS, J. D. & LIU, M. 2008. Behavioral and faunal implications of Early Cretaceous deinonychosaur trackways from China. *Naturwissenschaften* **95**, 185–91.
- LOCKLEY, M. G. 1991. *Tracking Dinosaurs: A New Look at an Ancient World*. Cambridge: Cambridge University Press, 238 pp.
- LOCKLEY, M. G., HUNT, A. P., MEYER, C., RAINFORTH, E. C. & SCHULTZ, R. J. 1998. A survey of fossil footprint sites at Glen Canyon National Recreation Area (western USA): a case study in documentation of trace fossil resources at a national preserve. *Ichnos* **5**, 177–211.
- LOCKLEY, M. G., MATSUKAWA, M. & LI, J. 2003. Crouching theropods in taxonomic jungles: ichnological and ichnotaxonomic investigations of footprints with metatarsal and ischial impressions. *Ichnos* **10**, 169–77.
- LOCKLEY, M. G., MATSUKAWA, M. & WITT, D. 2006. Giant theropod tracks from the Cretaceous Dakota Group northeastern New Mexico. *New Mexico Museum of Natural History & Science Bulletin* **35**, 83–7.
- LOCKLEY, M. G., MEYER, C. A., FARIA DOS SANTOS, V. 1998. *Megalosauripus* and the problematic concept of *Megalosaurus* footprints. *Gaia* **15**, 313–37.
- LOCKLEY, M. G., WHITE, D., KIRKLAND, J. & SANTUCCI, V. 2004. Dinosaur tracks from the Cedar Mountain Formation (Lower Cretaceous), Arches National Park, Utah. *Ichnos* **11**, 285–93.
- LONGRICH, N. 2008. A new, large ornithomimid from the Cretaceous Dinosaur Park Formation of Alberta, Canada: implications for the study of dissociated dinosaur remains. *Palaeontology* **51**, 983–97.
- LUCAS, S. G., KLEIN, H., LOCKLEY, M. G., SPIELMANN, J. A., GIERLIŃSKI, G. D., HUNT, A. P. & TANNER, L. H. 2006. Triassic–Jurassic stratigraphic distribution of the theropod footprint ichnogenus *Eubrontes*. In *The Triassic–Jurassic Terrestrial Transition* (eds J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, A. R. C. Milner & J. I. Kirkland), pp. 86–93. New Mexico Museum of Natural History and Science Bulletin Volume 37.
- MADSEN, J. H. 1993. *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin* **109**, 1–163.
- MAKOVICKY, P. J., KOBAYASHI, Y. & CURRIE, P. J. 2004. Ornithomimosauria. In *The Dinosauria. Second Edition* (eds D. B. Weishampel, P. Dodson & H. Osmólska), pp. 137–50. Berkeley: University of California Press.
- MANNING, P. L., MARGETTS, L., JOHNSON, M. R., WITHERS, P. J., SELLERS, W. I., FALKINGHAM, P. L., MUMMERY, P. M., BARRETT, P. M. & RAYMONT, D. R. 2009. Biomechanics of dromaeosaurid dinosaur claws: application of X-ray microtomography, nano-indentation, and finite element analysis. *The Anatomical Record* **292**, 1397–405.
- MARTIN, L. D. & ZHOU, Z. 1998. *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. *Naturwissenschaften* **85**, 286–89.
- MARTY, D., STRASSER, A. & MEYER, C. A. 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* **16**, 127–42.
- MILÁN, J. 2006. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: ichnotaxonomic implications. *Palaeontology* **49**, 405–20.
- MILÁN, J., LOOPE, D. B. & BROMLEY, R. G. 2008. Crouching theropod and *Navahopus* sauropodomorph tracks from

- the Early Jurassic Navajo Sandstone of USA. *Acta Palaeontologica Polonica* **53**, 197–205.
- MILNER, A. R. C., HARRIS, J. D., LOCKLEY, M. G., KIRKLAND, J. I. & MATTHEWS, N. A. 2009. Birdlike anatomy, posture, and behavior revealed by an Early Jurassic theropod dinosaur resting trace. *PLoS ONE* **4**, e4591. doi: [10.1371/journal.pone.0004591](https://doi.org/10.1371/journal.pone.0004591).
- MOSTARDINI, F. & MERLINI, S. 1986. Appennino centro-meridionale: sezione geologiche e proposta di modello strutturale. *AGIP, 73rd Congresso della Societa Geologica Italiana, Roma*, 59 pp.
- MUDROCH, A., RICHTER, U., JOGER, U., KOSMA, R., IDÉ, O. & MAGA, A. 2011. Didactyl tracks of paravian theropods (Maniraptora) from the ?Middle Jurassic of Africa. *PLoS ONE* **6**, e14642. doi: [10.1371/journal.pone.0014642](https://doi.org/10.1371/journal.pone.0014642).
- NICOSIA, U., PETTI, F. M., PERUGINI, G., D'ORAZI PORCHETTI, S., SACCHI, E., CONTI, M. A., MARIOTTI, N. & ZARATTINI, A. 2007. Dinosaur tracks as paleogeographic constraints: new scenarios for the Cretaceous geography of the periadriatic region. *Ichnos* **14**, 69–90.
- OSMÓLSKA, H. 1981. Coossified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. In *Results of the Polish–Mongolian Palaeontological Expeditions—Part IX* (ed. Z. Kielan-Jaworowska), pp. 79–95. *Palaeontologia Polonica* **42**.
- PETTI, F. M., CONTI, M. A., D'ORAZI PORCHETTI, S., MORSILLI, M., NICOSIA, U. & GIANOLLA, P. 2008. A theropod dominated ichnocoenosis from the Late Hauterivian–Early Barremian of Borgo Celano (Gargano promontory, Apulia, Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* **114**, 3–17.
- PESCATORE, T., RENDA, P., SCHIATTARELLA, M. & TRAMUTOLI, M. 1999. Stratigraphic and structural relationship between Meso-Cenozoic Lagonegro basin and coeval carbonate platforms in Southern Apennines, Italy. *Tectonophysics* **315**, 269–86.
- PU, H., CHANG, H., LÜ, J., WU, Y., XU, L., ZHANG, J. & JIA, S. 2013. A new juvenile specimen of *Sapeornis* (Pygostylia: Aves) from the Lower Cretaceous of Northeast China and allometric scaling of this basal bird. *Paleontological Research* **17**, 27–38.
- QIANG, J., CHIAPPE, L. M. & SHU'AN, J. 1999. A new Late Mesozoic confuciusornithid bird from China. *Journal of Vertebrate Paleontology* **19**, 1–7.
- QIANG, J., CURRIE, P. J., NORELL, M. A. & SHU-AN, J. 1998. Two feathered dinosaurs from northeastern China. *Nature* **393**, 753–61.
- ROMANO, M. & CITTON, P. 2015. Reliability of digit length impression as a character of tetrapod ichnotaxobase: considerations from the Carboniferous–Permian ichnogenus *Ichniotherium*. *Geological Journal* **50**, 827–38.
- ROMANO, M., CITTON, P. & NICOSIA, U. 2016. Corroborating trackmaker identification through footprint functional analysis: the case study of *Ichniotherium* and *Dimetropus*. *Lethaia* **49**, 102–16.
- ROMERO-MOLINA, M., SARJEANT, W., PÉREZ-LORENTE, F., LOPEZ, A. & REQUETA, E. 2003. Orientation and characteristics of theropod trackways from the Las Losas Palaeoichnological Site (La Rioja, Spain). *Ichnos* **10**, 241–54.
- SACCHI, E., CONTI, M. A., D'ORAZI PORCHETTI, S., LOGOLUSO, A., NICOSIA, U., PERUGINI, G. & PETTI, F. M. 2009. Aptian dinosaur footprints from the Apulian platform (Bisceglie, Southern Italy) in the framework of periadriatic ichnosites. *Palaeogeography, Palaeoclimatology, Palaeoecology* **271**, 104–16.
- SARJEANT, W. A. S. 1971. Vertebrate tracks from the Texas of Castle Peak, Texas. *The Texas Journal of Science* **22**, 343–66.
- SENDER, P. 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* **5**, 429–63.
- SMITH, J. B., FARLOW, J. O. 2003. Osteometric approaches to trackmaker assignment for the Newark Supergroup ichnogenera *Grallator*, *Anchisauripus*, and *Eubrontes*. In *The Great Rift Valley of Pangea in Eastern North America. Sedimentology, Stratigraphy and Paleontology Volume 2* (eds P. M. LeTourneau & P. E. Olsen), pp. 273–92. New York: Columbia University Press.
- THULBORN, R. A. 1990. *Dinosaur Tracks*. London: Chapman and Hall, 410 pp.
- THULBORN, R. A. 2013. Lark Quarry revisited: a critique of methods used to identify a large dinosaurian trackmaker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. *Alcheringa* **37**, 312–30.
- THULBORN, R. A. & WADE, M. 1989. A footprint as a history of movement. In *Dinosaur Tracks and Traces* (eds D. D. Gillette & M. G. Lockley), pp. 51–6. Cambridge: Cambridge University Press.
- TURCO, E., SCETTINO, A., NICOSIA, U., SANTANTONIO, M., DI STEFANO, P., IANNACE, A., CANNATA, D., CONTI, M. A., DEIANA, G., D'ORAZI PORCHETTI, S., FELICI, F., LIOTTA, D., MARIOTTI, N., MILIA, A., PETTI, F. M., PIERANTONI, P. P., SACCHI, E., SBRESCIA, V., TOMMASETTI, K., VALENTINI, M., ZAMPARELLI, V. & ZARCONI, G. 2007. Mesozoic paleogeography of the Central Mediterranean Region. *Geoitalia 2007, VI Forum Italiano di Scienze della Terra. Epitome* **2**, 108.
- VICKERS-RICH, P., CHIAPPE, L. M. & KURZANOV, S. 2002. The enigmatic bird-like dinosaur *Avimimus portentosus*. In *Mesozoic Birds* (eds L. M. Chiappe & L. M. Witmer), pp. 65–86. Berkeley: University of California Press.
- WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (eds) 1990. *The Dinosauria*. Berkeley: University of California Press, 733 pp.
- WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (eds) 2004. *The Dinosauria. Second Edition*. Berkeley: University of California Press, 861 pp.
- WHITE, M. A. 2009. The subarctometatarsus: intermediate metatarsus architecture demonstrating the evolution of the arctometatarsus and advanced agility in theropod dinosaurs. *Alcheringa* **33**, 1–21.
- WILSON, J. A., MARSICANO, C. A. & SMITH, R. M. H. 2009. Dynamic locomotor capabilities revealed by early dinosaur trackmakers from Southern Africa. *PLoS ONE* **4**, e7331. doi: [10.1371/journal.pone.0007331](https://doi.org/10.1371/journal.pone.0007331).
- XU, X., WANG, X. L., WU, X. C. 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* **401**, 262–6.
- ZARCONI, G., PETTI, F. M., CILLARI, A., DI STEFANO, P., GUZZETTA, D. & NICOSIA, U. 2010. A possible bridge between Adria and Africa: new palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. *Earth-Science Reviews* **103**, 154–62.
- ZHEN, S., LI, J., ZHANG, B., CHEN, W. & ZHU, S. 1995. Dinosaur and bird footprints from the Lower Cretaceous of Emei County, Sichuan. *Memoirs of Beijing Natural History Museum* **54**, 105–20.