

Linking tetrapod tracks to the biodynamics, paleobiogeography, and paleobiology of their trackmakers: *Pachypes dolomiticus* Leonardi *et al.*, 1975, a case study

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SUMMARY - *Linking tetrapod tracks to the biodynamics, paleobiogeography, and paleobiology of their trackmakers: Pachypes dolomiticus Leonardi et al., 1975, a case study* - Case studies on features of definite ichnotaxa enabling the identification of their trackmakers are very rare, and those concerning Paleozoic footprints are virtually absent. Here, taking as an example the Late Permian ichnospecies *Pachypes dolomiticus* Leonardi *et al.*, 1975, assigned to pareiasaurs, we provide a data source of characters which are virtually linked to possible biodynamic skills of its trackmaker. The ichnological data support dual-gait locomotion, a semiplantigrade hand and a digitigrade foot for the *Pachypes* trackmaker. Furthermore, paleontological data suggest that some differences might occur within hypothetical pareiasaurian footprints, linked to different morphological features of the biotaxa. The latter data also let us hypothesize that the *Pachypes* trackmaker belong to a pareiasaur of the clade Therischia. The data employed here also provide paleobiogeographical and paleobiological information not yet determined from body fossils. They support, for instance, the hypothesis that juvenile and adult trackmakers of *P. dolomiticus* shared, at least partially, the same habitat.

RIASSUNTO - *Relazione tra orme di tetrapodi, biodinamica, paleobiogeografia e paleobiologia dei trackmaker: Pachypes dolomiticus Leonardi et al., 1975, un caso di studio* - Gli studi sui caratteri di specifici icnotaxa riconducibili ai loro trackmaker sono molto rari, e quelli riguardanti orme paleozoiche sono virtualmente inesistenti. In questo lavoro, prendendo come esempio *Pachypes dolomiticus* Leonardi *et al.*, 1975, un'icnospecie del Permiano superiore attribuita a pareiasauri, forniamo un insieme di caratteri virtualmente correlabili a possibili aspetti biodinamici del suo trackmaker. I dati paleoicnologici fanno ipotizzare, per il trackmaker di *Pachypes*, una locomozione del tipo dual-gait, una mano semiplantigrada e un piede digitigrado. Inoltre, i dati paleontologici suggeriscono la possibile presenza di leggere differenze all'interno di ipotetiche orme di pareiasauri, legate a differenze morfologiche dei biotaxa. Queste ultime ci inducono anche ad ipotizzare che il trackmaker di *Pachypes* sia un pareiasauro del clado Therischia. I dati analizzati in questo lavoro forniscono anche informazioni di tipo paleobiogeografico e paleobiologico non ancora ricavate dallo studio delle ossa. Ad esempio, essi ci permettono di ipotizzare che esemplari giovanili e adulti del trackmaker di *P. dolomiticus* condividessero, almeno parzialmente, lo stesso habitat.

Key words: Paleoichnology, *Pachypes*, Pareiasaurs, Biodynamics, Paleobiology

Parole chiave: Paleoicnologia, *Pachypes*, Pareiasauri, Biodinamica, Paleobiologia

1. INTRODUCTION

Today, vertebrate ichnotaxa are almost universally accepted to correspond to biotaxa proxies, but the former usually represent higher taxonomic ranks, having therefore a larger temporal range. Indeed, autopodia are usually rather more conservative with respect to other skeletal structures. However, differences and trends among higher taxa exist, and they can help in assigning tracks to a trackmaker, though usually not at genus (nor at species) rank. Carrano & Wilson (2001) suggested a synapomorphy-based track identification, but this methodology has never been applied later. Indeed, autopodia are more rarely preserved with respect to other skeletal remains and are not as studied as other skeletal structures in systematic and phylogenetic analyses; those on Permian bodyfossil taxa, for example, are still broadly "skull-centric". As a result, tetrapod ichnotaxa are often only vaguely referred to higher rank biotaxa, as also pointed out by Voigt *et al.* (2007). Indeed, both case studies on

anatomical features of definite biotaxa allowing a clear discrimination among a cluster of footprints, and studies on features of definite ichnotaxa allowing the identification of their trackmakers, are very rare, and those concerning Paleozoic footprints are virtually absent.

Here, taking as an example the Late Permian ichnospecies *Pachypes dolomiticus* Leonardi *et al.*, 1975 (Leonardi *et al.* 1975; Conti *et al.* 1977), which has been recently revised by Valentini *et al.* (2008), we provide data which allow an evaluation of possible biodynamic skills of Paleozoic trackmakers. The re-examination of the *P. dolomiticus* distinctive features eventually allowed to assign it unequivocally to pareiasaurs (Valentini *et al. op. cit.*). While the taxonomy and phylogenetic relationship of pareiasaurs have been recently revised (Lee 1997a, 1997b; Jalil & Janvier 2005), up-to-date studies on anatomical features and differences within the clade related to stance and locomotor skills are missing. This paper might therefore trigger a cross investigation, aimed at finding correspondences between the ichnofossil and body-

fossil features. Moreover, the ichnological data, as will be discussed later, shed light on some paleobiological aspects of pareiasaurs not yet determined from bodyfossils.

The *P. dolomiticus* specimens figured here are housed in the following institutions: Museo di Paleontologia e Preistoria "Piero Leonardi" (University of Ferrara), Museo Civico di Predazzo (MGP), Museo di Paleontologia of the University "Sapienza", Rome (N.S. 34).

2. CHARACTERS OF *PACHYPES* AND INFERRED BIODYNAMICS OF ITS TRACKMAKER

Valentini *et al.* (2008) have ascribed three ichnospecies to the ichnogenus *Pachypes* Leonardi *et al.*, 1975, namely: *Pachypes dolomiticus*, *Pachypes primus* (Gubin & Boulanov in Gubin *et al.* 2003) and *Pachypes* isp. (= *Brontopus giganteus* Heyler & Lessertisseur, 1963 in Surkov *et al.* 2007). Exhaustive new description and diagnosis of the type ichnospecies *P. dolomiticus* from the Upper Permian Arenaria di Val Gardena (Northeastern Italy) have been provided therein as

well. The *P. dolomiticus* type material, as well as the pes and manus principal features, are shown here in figures 1 and 2. For a geological frame of the Arenaria di Val Gardena, see Neri (2007 *cum biblio*). *Pachypes*, amongst the largest Paleozoic tetrapod footprints, has been referred to pareiasaurs by means of comparison with the skeletal features of several Paleozoic reptilian biotaxa (Valentini *et al.* 2008). *Pachypes* exhibits pentadactyl and heteropod autopodia, with the pes larger than the manus. The pes still exhibits the basal reptilian structure (digit lengths ratio I<II<III<IV), whilst the manus displays a more symmetrical overall morphology (I<II~III~IV). Both the pes and the manus are massive, with short and sturdy digits. The pes is characterized by a very short and thin digit V. Within Paleozoic tetrapods, this pattern of characters matches only with that of pareiasaurs (Fig. 3).

Other characters displayed by *P. dolomiticus* which are possibly linked to morphofunctional skills of its trackmaker are discussed next. The *P. dolomiticus* pattern of features is also compared with those of *P. primus* and *Pachypes* isp., in order to assume the stance and locomotion of the *Pachypes* trackmaker.

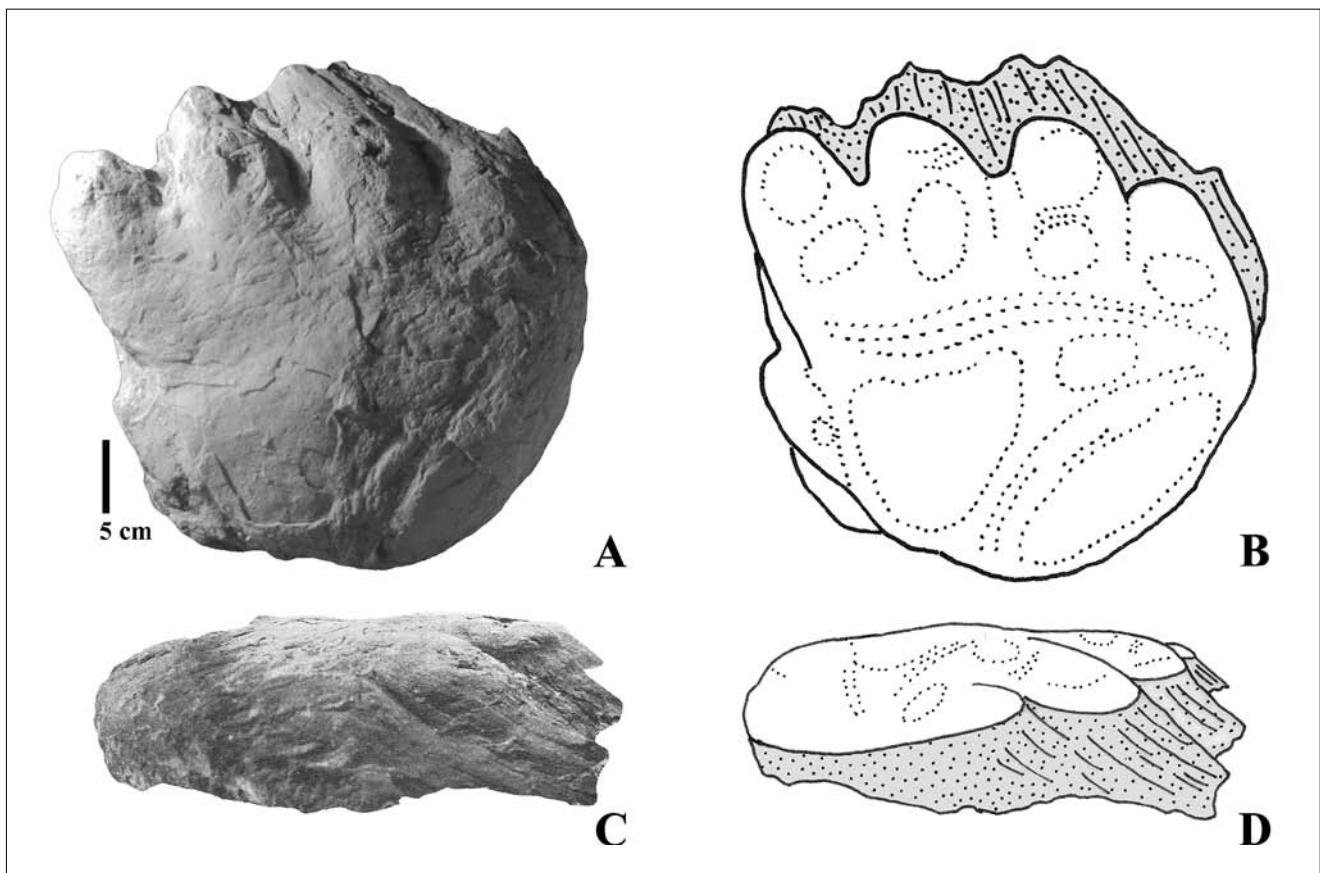


Fig. 1 - Holotype of *Pachypes dolomiticus* Leonardi *et al.*, 1975, specimen 73/111, natural cast of a right pes. Museo di Paleontologia e Preistoria "Piero Leonardi", University of Ferrara. Photographs and drawings of the holotype from above and lateral view. Photograph in C from Conti *et al.* (1977), drawings in B and D modified from Conti *et al.* (1977). Sliding traces in grey.

Fig. 1 - Olotipo di *Pachypes dolomiticus* Leonardi *et al.*, 1975, esemplare 73/111, controimpronta di pes destro. Museo di Paleontologia e Preistoria "Piero Leonardi", Università di Ferrara. Fotografie e disegni dell'olotipo visto dall'alto e in vista laterale. Fotografia in C da Conti *et al.* (1977), disegni in B e D modificati da Conti *et al.* (1977). Le tracce di scivolamento sono indicate in grigio.

Fig. 2 - Manus and pes of *Pachy-
pypes dolomiticus* Leonardi et
al., 1975. A. N.S. 34/10, natural
cast of a right manus. B. N.S.
34/23a-b, natural cast of a left
manus. C. N.S. 34/79/3, natural
cast of a left pes. D. N.S. 34/22,
natural cast of a left pes.

Fig. 2 - Manus e pes di Pa-
chypyes dolomiticus Leonardi
et al., 1975. A. N.S. 34/10, con-
troimpronta di manus destra. B.
N.S. 34/23a-b, controimpronta
di mano sinistra. C. N.S.
34/79/3, controimpronta di pes
sinistro. D. N.S. 34/22, con-
troimpronta di pes sinistro.

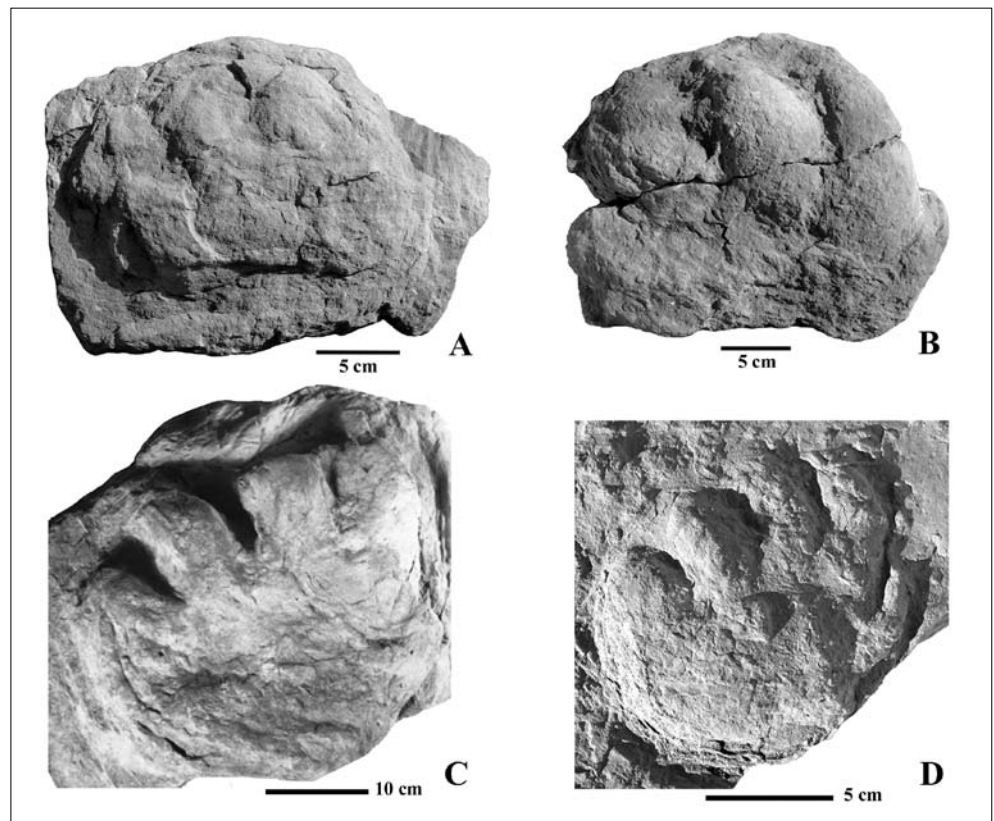
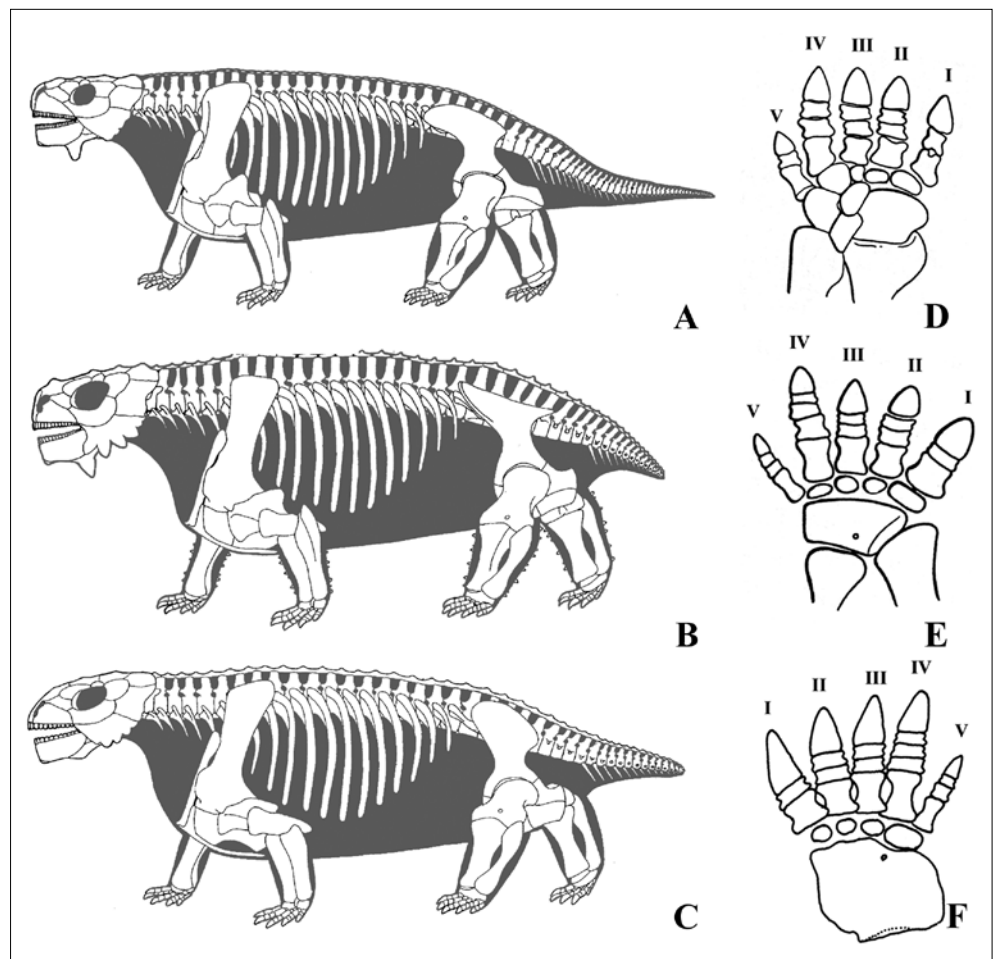


Fig. 3 - Skeletal reconstructions
of A. *Bradysaurus* (modified
from Lee 1997b) B. *Scutosau-
rus* (modified from Lee, 1997b)
C. *Anthodon* (modified from
Lee 1997b), and dorsal view
of D. left hand of *Bradysaurus*
(modified from Romer 1976) E.
left foot of *Bradysaurus* (modi-
fied from Romer 1976) F. right
foot of *Embrithosaurus* (modi-
fied from Lee 1997b).

Fig. 3 - Ricostruzione schele-
trica di A. *Bradysaurus* (mo-
dificato da Lee 1997b), B.
Scutosaurus (modificato
da Lee 1997b), C. *Anthodon* (mo-
dificato da Lee 1997b) e vista
dorsale di D. mano sinistra di
Bradysaurus (modificato da
Romer 1976) E. piede sinistro
di *Bradysaurus* (modificato da
Romer 1976) F. piede destro di
Embrithosaurus (modificato da
Lee 1997b).



2.1. *Manus and pes characters*

The *P. dolomiticus* manus and pes are semiplantigrade, the sole being proportionally larger than the palm. The latter terminates backward in a straight or concave shape connecting the digits I-V, indicating that the carpus of the *P. dolomiticus* trackmaker was held off the ground. Instead, the sole terminates backward in a rounded-oval shape. As it does not extend much backwardly with respect to the external digits, it can be inferred that the tarsus of the trackmaker was not completely impressed. A ridge connecting the proximal ends of digits I-IV, at the inferred phalangeal-metatarsal area, characterizes most of the preserved pedes. Two bean-shaped sole pads, at the inferred tarsal/metatarsal area, are also frequently impressed. The first one is on the inner side of the sole, the second extends from the base of digit V to digit IV. These pads are frequently connected to one another. *P. primus* and *Pachypes* isp. display manus and pes shape and grady consistent with those of *P. dolomiticus*. It is worth mentioning that Valentini *et al.* (2008) assumed an opposite attribution of the *Pachypes* isp. morphotypes as interpreted by Surkov *et al.* (2007). That is, they presumed that the manus *sensu* Surkov *et al.* (2007) might correspond to the pes and vice versa.

The features displayed by *P. dolomiticus* support a digitigrade posture of its trackmaker's foot. We here hypothesize that, during the step-cycle, the foot touched the ground with the digits and the distal metatarsal area, along with a pad of soft tissue on the tarsal area, the tarsus being held off the ground. Accordingly, given the postulated stance, the longest pedal digit IV of the *P. dolomiticus* trackmaker would bend (crescent-like shape imprint) in order to reach an anatomically more favorable position. Since the manus and pes of *P. primus* and *Pachypes* isp. exhibit a similar overall morphology to those of *P. dolomiticus*, we assume that the *Pachypes* trackmaker exhibited a posture characterized by a semiplantigrade hand and a digitigrade foot.

2.2. *Trackway characters*

The following features characterize the *P. dolomiticus* trackway: the pes and manus are differently oriented with respect to the midline, the former being sub-parallel to it, the latter being turned inward (Fig. 4, A); the pes usually exhibits sliding traces (Fig. 1, 5) related to the medial digits, whereas no such traces are seen in the manus; a deep internal displacement rim is also frequently exhibited by the pes. Also, the depth of impression of the manus and pes is nearly

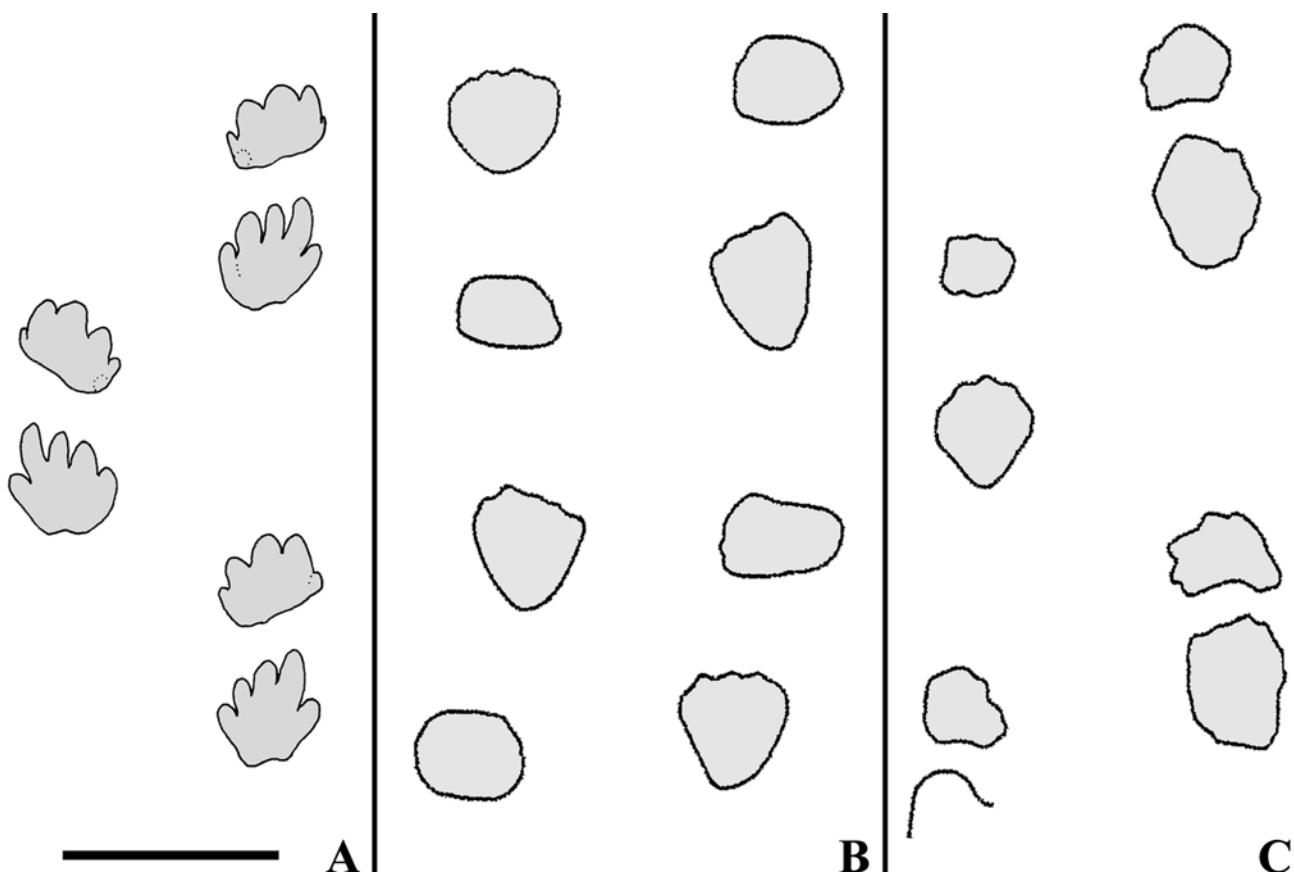


Fig. 4 - Trackways of *Pachypes* Leonardi *et al.*, 1975. A. Restored trackway of *P. dolomiticus*. B. Trackway of *P. primus* TW-1 (modified from Gubin *et al.* 2003). C. Trackway of *P. primus* TW-2 (modified from Gubin *et al.* 2003). Trackways at the same scale. Scale bar = 50 cm.

Fig. 4 - Piste di *Pachypes* Leonardi *et al.*, 1975. A. Ricostruzione della pista di *P. dolomiticus*. B. Pista TW-1 di *P. primus* (modificato da Gubin *et al.* 2003). C. Pista TW-2 di *P. primus* (modificato da Gubin *et al.* 2003). Piste riportate alla stessa scala. Unità di misura = 50 cm.

the same. Moreover, no tail-drag traces are preserved. Besides the manus and pes characters, *P. primus* and *Pachypes* isp. exhibit also a similar pattern of trackway features with respect to *P. dolomiticus*, that will be discussed here.

The pes of *P. primus* is parallel to the midline whereas the manus is turned inward as in *P. dolomiticus*, but these ichnotaxa slightly differ in the degree of rotation of the manus with respect to the midline (see Fig. 4). Indeed, according to Gubin *et al.* (2003) the axis of the *P. primus* holotype manual digit III is inclined of 70° toward the midline, whereas the manus is rotated of nearly 30° on average in *P. dolomiticus*. As for *Pachypes* isp., Valentini *et al.* (2008) interpreted footprints 7-9 (Surkov *et al.* 2007: 645, fig. 4) as a possible right manus-pes couple, where track 7 corresponds to the pes and track 9 to the manus. Though the state of preservation of the mentioned footprints and the lack of a trackway do not allow to determine their exact inclination with respect to the midline, the axis of the manus seems apparently a little more turned inward than the pes axis.

As already mentioned, *P. dolomiticus* displays sliding traces associated to the pes only (Figs 1, 5). These are related to the pes digits I-IV (most commonly II-IV), being as large as the width of the digits and inclined toward the internal part of the footprint. Also, their depth decreases from the proximal to the distal part, but the traces never are as deep as the footprint. Two ridges parallel to one another and to the axis of the sliding trace itself are in some cases impressed on the latter (see Fig. 5, A, G). Owing to their morphology, the pes sliding traces are here related to blunt unguals of the trackmaker, that possibly exhibited hooves. Also, together with the deep internal displacement rim usually exhibited by the pes, they suggest slight inside-out rotation of the trackmaker's foot during the propulsive phase of the step cycle, before the foot was raised off the ground. As for *P. primus* and *Pachypes* isp., they exhibit a similar pattern of sliding marks to *P. dolomiticus*. According to Gubin *et al.* (2003), the pes of *P. primus* exhibits anterior and posterior drag traces, whereas the manus displays an anterior ridge shifted forward and no carpal ridges. Gubin *et al.* (*op. cit.*: 521), grounded on the characters of the drag traces, interpret the foot of the *P. primus* trackmaker as moving from the rear to the front, first falling from the postero-external direction, then rising forward at lowering and rise. Instead, according to them, the hand was possibly applied in a lateral-medial direction and raised off the ground frontward. The sliding traces of *Pachypes* isp. are described by Surkov *et al.* (2007) as being directed outwards with respect to the midline in footprint 7 – possibly a pes according to Valentini *et al.* (2008) – thus reflecting posterolateral limb retraction, whereas footprint 3 – possibly a manus according to the same authors – does not display traces of backward pushing and scratching. Surkov *et al.* (2007) have linked these features respectively to a sprawling gait (trace 7) and a parasagittal gait (trace 3). Also, the morphotype B of Surkov *et al.* (2007), i.e. the pes *sensu* Valentini *et al.* (2008), is characterized according to the former authors by blunt digit tips and

scratch marks possibly linked to horny hooves, as the *P. dolomiticus* pes. Thus, based on a rather similar pattern of sliding traces to *P. dolomiticus*, Gubin *et al.* (2003) and Surkov *et al.* (2007) give a different interpretation of the fore- and hindlimb gait of the *P. primus* and *Pachypes* isp. trackmaker, respectively.

The *P. dolomiticus* depth of impression of the manus and pes is nearly the same, as in *Pachypes* isp. (Surkov *et al.* 2007). No information concerning the *P. primus* relative manus and pes depth is given in Gubin *et al.* (2003). All these three forms are characterized by trackways showing no tail-drag marks.

2.3. Assumed stance and locomotion of the *Pachypes* trackmaker

The characters discussed above allow to infer possible morphofunctional and locomotor skills of the *Pachypes* trackmaker. For instance, the different orientation of the *Pachypes* manus and pes with respect to the midline – the manus being turned inward with respect to it whereas the pes is subparallel to the midline – suggests different stance of the *Pachypes* trackmaker fore- and hindlimbs. As already mentioned, *Pachypes* has been assigned to pareiasaurs, which were characterized by heavy and armoured skulls. Thus, theoretically, we could assume that their hand imprints must have been deeper than the foot imprints because of the considerable load discharged on the forelimbs, that had to sustain the weight of the anterior trunk. Instead, the depth of impression of the *P. dolomiticus* manus and pes is nearly the same, both in juvenile and adult specimens. The divergence from the theoretical model is possibly related to different roles of the fore- and hindlimbs during locomotion as well.

According to us, the presence of sliding traces in the *Pachypes* pes and their absence in the manus (at least in the carpal region), gives further strength to the hypothesis of a different posture of its trackmaker fore- and hindlimbs. Indeed, the pes sliding traces might be related to the forward thrust of the trackmaker's hindlimb, whereas the absence of sliding traces in the manus might be linked to a sprawling gait of the trackmaker's forelimb that contributed little to the forward thrust. A dual-gait is here hypothesized as the most likely locomotor behaviour of the *Pachypes* trackmaker: this type of locomotion, which has been described for several Permian therapsids (see for example Kemp 1978 and Blob 2001), is characterized by forelimbs exhibiting a somewhat sprawling gait and hindlimbs held in an erect or semi-erect position. The forelimbs of the *Pachypes* trackmaker had primarily the role of sustaining the heavy anterior trunk, while its hindlimbs produced the forward thrust.

The *Pachypes* trackway characters could also be explained or strengthened by different mobility of the trackmaker's joint connecting the epipodials to the proximal tarsal/carpal elements – the former being more mobile – a feature seen in diadectids and Paleozoic amniotes (Berman & Henrici 2003; Voigt *et al.* 2007). The low degree of mo-

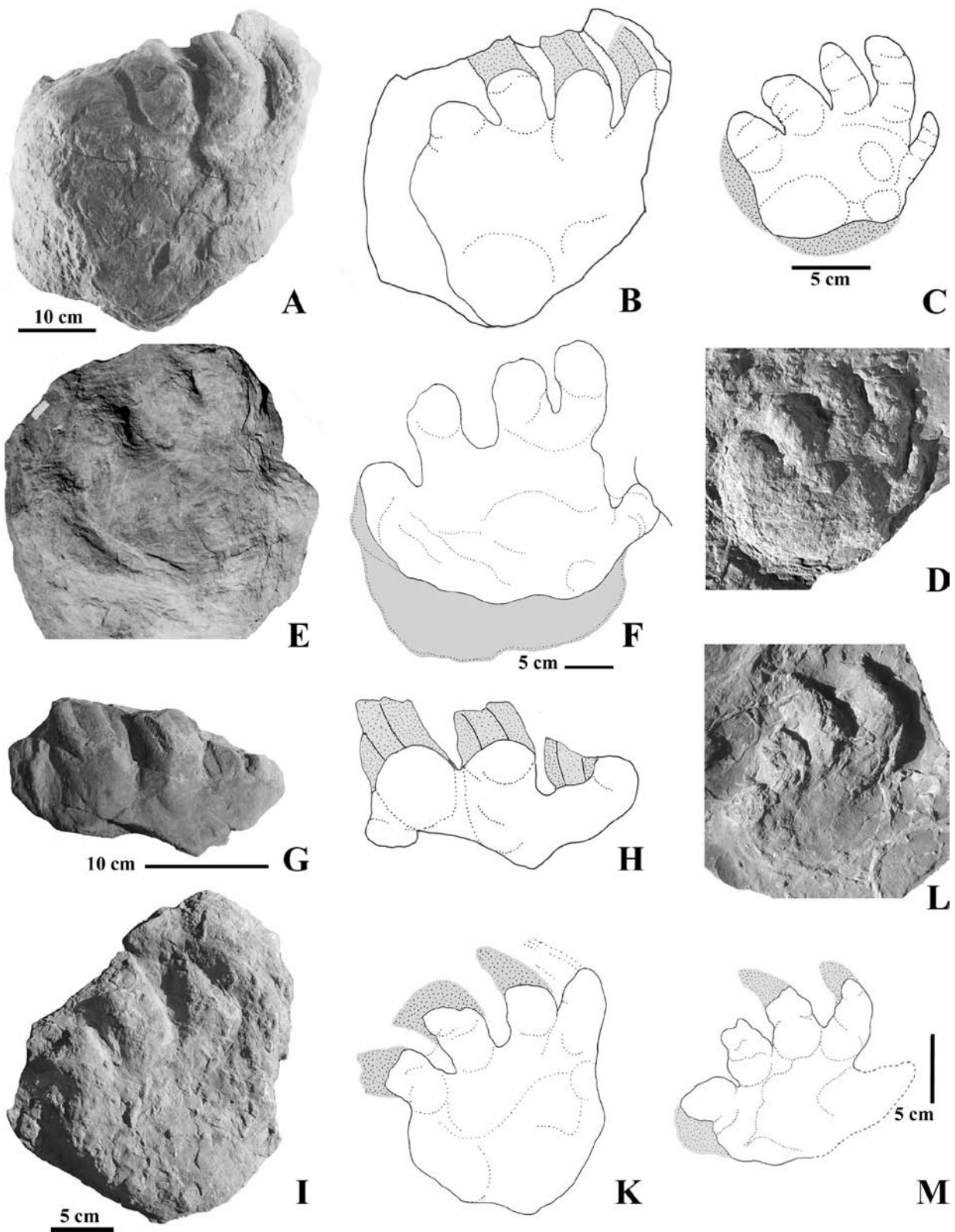


Fig. 5 - Sliding traces of the pes of *Pachypes dolomiticus* Leonardi *et al.*, 1975. A-B. MGP 9/17, natural cast of a left pes. C-D. N.S. 34/22, natural cast of a left pes. E-F. N.S. 34/24, natural cast of a left pes. G-H. N.S. 34/18, natural cast of three digits of a left pes. I-K. N.S. 34/48, natural cast of a left pes. L-M. N.S. 34/25, natural cast of a left pes. Sliding traces in grey.

Fig. 5 - Tracce di scivolamento del pes di *Pachypes dolomiticus* Leonardi *et al.*, 1975. A-B. MGP 9/17, controimpronta di pes sinistro. C-D. N.S. 34/22, controimpronta di pes sinistro. E-F. N.S. 34/24, controimpronta di pes sinistro. G-H. N.S. 34/18, controimpronta di tre dita di pes sinistro. I-K. N.S. 34/48, controimpronta di pes sinistro. L-M. N.S. 34/25, controimpronta di pes sinistro. Le tracce di scivolamento sono indicate in grigio.

bility of the *Pachypes* trackmaker wrist-joint is suggested by the sharp impression of the palm proximal end of the *P. dolomiticus* manus, together with the absence of any extra-morphological trace (as displacement rims or scratch marks) linked to the movement of the trackmaker's hand, thus indicating little if any rotation of the latter during the step-cycle. Given the assumed sprawling gait of the *Pachypes* trackmaker forelimb, such a feature would also be consistent with an inward rotation of the manus, which presumably had only little freedom of movement during the step-cycle. On the contrary, the forward to lateral movement of the foot of the *Pachypes* trackmaker during the step-cycle (testified by the sliding traces) could be related to higher mobility of the ankle-joint.

3. THE *PACHYPES* TRACKMAKER WITHIN PAREIASAURS: AN OVERVIEW

According to Lee (1997a, 1997b), in pareiasaurs the postcranium is diversified and postcranial features are at least as diagnostic as cranial features. Early pareiasaurs such as *Bradysaurus* Watson, 1914 are large, heavily ossified, with a dermal armour restricted to the dorsal midline, large anterior expansion of sacral blade of ilium and wide postaxial flange extending all the way down shaft of femur (Lee 1997b). These early pareiasaurs are morphologically distinct from all later forms, called velosaurs (*sensu* Lee 1997b). The Russian *Deltavjatia* Ivachnenko, 1987 is important because it exhibits a pattern of characters that bridge that gap (Lee *op. cit.*). More derived forms (Velosauria *sensu* Jalil & Janvier 2005), such as *Scutosaurus* Hartmann-Weinberg, 1930, *Pareiasuchus* Broom & Haughton, 1913 and *Elginia* Newton, 1893 are characterized by a very "mammal-like" pelvis and a loose covering of osteoderms over the entire dorsum (Lee 1997b). Finally, the late, dwarf pareiasaurs *Nanoparia* Broom, 1936, *Anthodon* Owen, 1876 and *Pumiliopareia* Lee, 1997a, exhibit a rigid dermal armour over the entire dorsum, expanded flattened ribs, great reduction of humeral torsion, greatly developed trochanter major, offset femoral head and reduced cnemial crest of the tibia (Lee 1997b). As to the body size the latter forms, as well as *Elginia* and *Provelosaurus* Lee, 1997a, have a snout-vent length of 50-100 cm, while this length exceeds 150 cm in the other pareiasaurs. In conclusion, data from Lee (1997b), in agreement with those in Jalil & Janvier (2005), allow to identify three main groups within pareiasaurs (Fig. 6): the early forms, a small group of highly derived, dwarf pareiasaurs (Pumiliopareiasauria in Jalil & Janvier 2005) and the remnant forms which correspond almost completely to the Therischia (Jalil & Janvier 2005). It is worth mentioning that the earliest known taxa and most basal forms *Bradysaurus*, *Embrithosaurus* Watson, 1914 and *Nochelesaurus* Haughton & Boonstra, 1929 occur in the South African *Tapinocephalus* Assemblage Zone (Beaufort Group, Karoo Basin).

As for the pareiasaurian locomotion, although Surkov *et al.* (2007) report that they were fore- and aft-sprawlers, it is generally believed that they featured the most upright limb postures of any Paleozoic reptile group (Romer 1976; Carroll 1988; Sumida & Modesto 2001). According to Romer (1976: 338) "In the pareiasaurs the structure of the girdle and limb elements indicates that the elbow had been rotated backward to some degree, the knee forward, and the limbs had thus been brought close to the body, so that much of the weight could be vertically supported by the limb bones". Moreover, the relatively short vertebral column of pareiasaurs, together with gradual spreading and fusion of the dorsal dermal osteoderms from the basal forms to the most derived ones (Lee 1997b) is consistent with a low mobility of the trunk. In contrast, sprawling locomotion involves lateral undulation of the trunk, that is flexibility of it. Thus, it is unlikely that pareiasaurs had a fully sprawling locomotor habits. The ichnological data, as previously discussed, support at least a dual-gait locomotion.

The angle between the proximal and distal expansions of the humerus in pareiasaurs is variable. It is of nearly 60° in *Bradysaurus* and approximately 45° in all other pareiasaurs with the exception of the advanced forms *Anthodon* and *Provelosaurus* (Lee 1997a, 1997b), which display an angle of nearly 20°. Jalil & Janvier (2005) include the latter feature among the synapomorphic characters of the Pumiliopareiasauria. Thus, the three states (respectively 0, 1, 2) form a morphocline. According to Lee (1997a), the humerus in *Anthodon* and *Provelosaurus* is superficially "therapsid-like": it exhibits entepicondylar foramen not visible in distal dorsal view, ectepicondylar foramen located very proximally, as well as radial condyle located distally. A feeble humerus "twist" is related, according to Romer (1976), to a more vertical position of the forelimb. According to us, it would also probably involve a parallelization of the hand to the direction of movement and consequently, from a paleoichnological point of view, a parallelization of the manus imprint with respect to the midline. Indeed, assuming that the more vertical forelimb contributed more extensively to the forward thrust during locomotion, and also that it had to sustain the heavy anterior trunk, it is functionally unlikely that the hand was turned inward.

Consequently, we can exclude as possible *Pachypes* trackmakers both the generalized taxa from South Africa (*Bradysaurus*, *Nochelesaurus* and *Embrithosaurus*) and the Pumiliopareiasauria (*Provelosaurus*, *Anthodon*, *Pumiliopareia*) with an angle torsion of the humerus of nearly 20°. The former are excluded on the ground of stratigraphic criteria, since the basal forms have been uncovered, as said above, from the *Tapinocephalus* Assemblage Zone which is Middle Permian in age, whereas *Pachypes* is Late Permian in age (Valentini *et al.* 2008). Gubin *et al.* (2003), on the basis of a comparison between the *P. primus* features and Russian pareiasaurian skeletal material, argue that the most likely *P. primus* trackmaker was close to *Deltavjatia*.

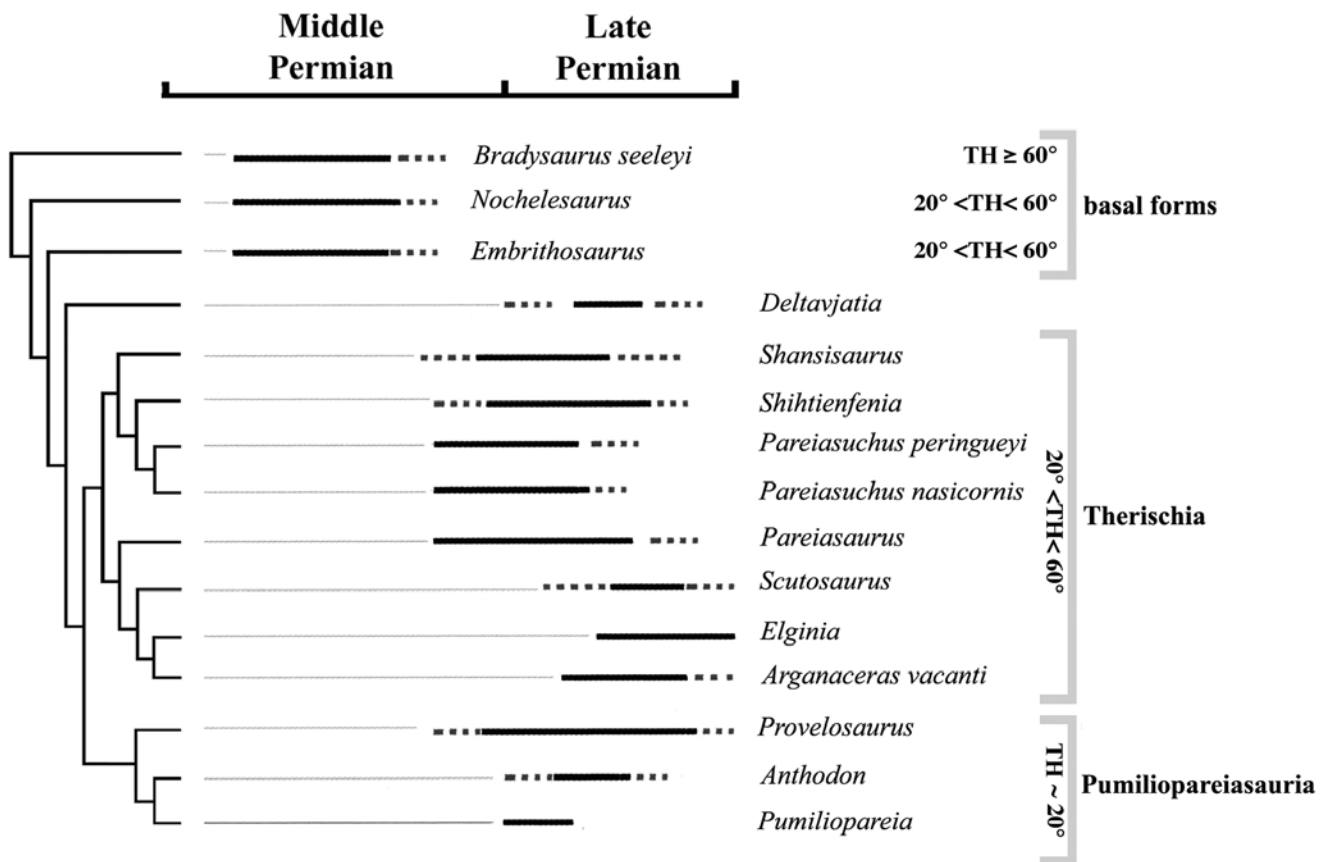


Fig. 6 - Phylogenetic relationship and stratigraphic distribution of several genera of pareiasaurs (simplified and modified from Jalil & Janvier 2005). Three main groups can be recognized: the early forms from the *Tapinocephalus* Assemblage Zone of South Africa, the Therischia and the Pumiliopareiasauria (see discussion in the text). TH= angle torsion of the humerus.

Fig. 6 - Relazioni filogenetiche e distribuzione stratigrafica di diversi generi di pareiasauri (semplificato e modificato da Jalil & Janvier 2005). Si possono riconoscere tre gruppi principali: le forme basali della *Tapinocephalus* Assemblage Zone del Sud Africa, i Therischia e i Pumiliopareiasauria (vedi discussione nel testo). TH= angolo di torsione dell'omero.

As for the foot of *Scutosaurus*, these authors report that it exhibits short digits as in *P. primus* but displays more resemblance to the pes of *P. dolomiticus*, without providing any additional morphological argument. Comparisons in Gubin *et al.* (2003), however, are based almost solely on manual remains. According to these authors the hand of *Deltavjatia*, based on specimen MS n° 5324, is characterized by digit I being perpendicular to the axis of the hand, digit II being the longest, and digits III-IV of decreasing size. In contrast, the hand of *Bradysaurus* is characterized by digits II and IV of nearly the same length, and by the digit I being much larger with respect to the other digits. Finally, the hand of the *Scutosaurus* type specimen exhibits shorts digits of nearly the same length (Gubin *et al.* 2003). These authors (*op. cit.*: 520, fig. 6e) do also figure the hand of the abovementioned *Deltavjatia* specimen MS n° 5324; on the basis of that drawing, it appears that the hand exhibits a phalangeal formula inconsistent with that of pareiasaurs which is 2:3:3:3:2, but Gubin *et al.* (2003) do not argue this incongruence. Thus, the phalangeal count of the manus of *Deltavjatia* should be re-confirmed on the basis of

the available specimens. Indeed, according to Lee (1997b) and Jalil & Janvier (2005) the pareiasaurian manual phalangeal formula is 2:3:3:3:2 in all specimens providing evidence of it, including *Deltavjatia*. Notwithstanding this uncertainty, we cannot exclude *a priori* that a pareiasaur near to *Deltavjatia* could be the *P. primus* trackmaker. According to Lee (1997b) *Deltavjatia* is an important taxon which exhibits a pattern of characters that bridge the morphological gap between the basal forms and all later forms. However, according to this author its postcranium, such as the rotation of the humerus, is incompletely known (Lee 1997b): indeed, presumably because of distortion, one humerus in specimen UMZC T1321 exhibits a rotation of approximately 45°, the other one of approximately 20°. Instead, owing to the arguments discussed above, we are inclined to hypothesize that the *Pachypes* trackmaker belongs to the clade Therischia, which comprises according to Jalil & Janvier (2005) the Chinese forms (*Shansisaurus* Cheng, 1980, *Shihtienfenia* Young & Yeh, 1963, *Sanchuansaurus* Gao, 1989) and European forms (*Elginia*, Kupferschiefer pareiasaur), the Russian *Scutosaurus*, as well as the South

African *Pareiasaurus* Owen, 1876 and *Pareiasuchus*, and *Arganaceras* Jalil & Janvier, 2005 from Morocco.

4. PAREIASAURIAN PALEOBIOGEOGRAPHY AND PALEOBIOLOGY: DATA INFERRED FROM *PACHYPES*

So far, pareiasaurs have been uncovered from Middle to Upper Permian deposits of South America (Brazil), Africa (Morocco, Niger, Zambia, Tanzania, South Africa), Europe (Scotland, Germany), Russia and China. The pareiasaurs from the *Tapinocephalus* Assemblage Zone of South Africa are the most basal forms, thus suggesting that the group had Gondwanian origins. However, the geographic radiation of pareiasaurs is still poorly known (Lee 1997a). The European taxa form a clade, but are not closely related to the other forms from the Northern hemisphere, that is the Russian and Chinese taxa. Moreover, the latter do not represent discrete radiations, thus allowing to suppose several dispersions between hemispheres (Lee *op. cit.*). New pareiasaurian remains were found recently in Morocco and Niger and have been attributed, respectively, to *Arganaceras vacanti* Jalil & Janvier, 2005 and *Bunostegos akokanensis* Sidor *et al.*, 2003. The former is closely related, according to Jalil & Janvier (2005), to the European *Elginia mirabilis* Newton, 1893.

Following the ichnotaxonomic revision of *Pachypes*, pareiasaurian footprints are now recorded from Upper Permian deposits of both Northeastern Italy and Russia (Valentini *et al.* 2008). Thus, if we link the paleoichnological record to the bodyfossil record, pareiasaurs appear to completely surround the Late Permian Palaeotethys Ocean embayment.

Furthermore, *Pachypes* offers some interesting clues concerning the paleobiology of pareiasaurs which have not yet been determined from skeletal remains. For instance, the *P. dolomiticus* manus and pes length/width ratio indicates little if any allometric growth of the hand and foot linear characters of its trackmaker (Valentini *et al.* 2008). According to Spencer & Lee (2000), pareiasaurian small individuals (either small species or juveniles of large species) are extremely rare, though large adults are abundant in many deposits. According to them this bias is not entirely taphonomic, since small specimens of other taxa are common in at least some deposits yielding abundant large pareiasaurs. Spencer & Lee (2000) suggest therefore that pareiasaurs either had a rather short juvenile period compared to adulthood, or that juveniles frequented habitats which were less amenable to preservation than those occupied by adults. Data derived from *P. dolomiticus* indicate that juvenile and adult specimens are proportionally fewer than subadult ones. Moreover, juveniles have been uncovered from the same levels of subadult and adult specimens, thus indicating that they shared, at least partially, the same habitat.

Gubin *et al.* (2003) have pointed out that the *P. pri-*

mus trackways – TW-1 and TW-2 – could belong to individuals of different sexes on the ground of, namely, the different size of the footprints with respect to the glenoacetabular distance and the different size of the manus with respect to the pes. The *P. dolomiticus* material can neither confirm nor reject this assumption, since the restored trackways do not exhibit a clear separate ratio of the footprint size vs the glenoacetabular distance.

5. CONCLUSIONS

We have suggested here some hypotheses on the biodynamics and paleobiology of pareiasaurs, grounded on the analysis of the *Pachypes* ichnospecies (*Pachypes dolomiticus*, *Pachypes primus* and *Pachypes* *isp.*). The ichnological data support dual-gait locomotion, a semiplantigrade hand and a digitigrade foot for the *Pachypes* trackmaker. In addition, variation within pareiasaurs of some postcranium features such as the degree of rotation of the humerus suggest on the one hand that differences possibly occur within hypothetical pareiasaurian trackways and, on the other hand, that the trackmaker of *Pachypes* presumably belongs to the *Therischia*. Moreover, from the data on *P. dolomiticus* we can infer at least partial shearing of the same habitat between adult and juvenile trackmakers.

Altogether, the information and inferences on pareiasaurs provided here on the basis of the ichnological data confirm that footprints can add to our knowledge of bodyfossil taxa by extrapolating information that is not always directly readable from bones, as already pointed out by Lockley & Hunt (1995).

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