

Outline of a Permian tetrapod footprint ichnostratigraphy

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Abstract: Tetrapod footprints are among the most common fossil remains in continental Permian strata and thus are of biostratigraphic interest. Based on the vertical distribution of the 13 best-known Permian tetrapod ichnotaxa, three footprint biochrons are suggested for the period: (1) *Dromopus* – latest Carboniferous (approximately Gzhelian) to late Early Permian (approximately Artinskian), representing ichnoassemblages dominated by tracks of temnospondyls, reptiliomorphs, pelycosaurs and early diapsids; (2) *Erpetopus* – late Early Permian (approximately Kungurian) to late Middle Permian (approximately Capitanian), representing ichnoassemblages dominated by tracks of non-diapsid eureptiles; and (3) *Paradoxichnium* – Late Permian (Wuchiapingian and Changhsingian), representing ichnoassemblages dominated by tracks of medium- and large-sized parareptiles, non-diapsid eureptiles and early saurians. This is the most conservative ichnostratigraphic concept, and it may be possible to refine it to almost stage-level resolution by future comprehensive analysis, especially of Permian captorhinomorph and therapsid footprints. Other major tasks to improve Permian tetrapod footprint ichnostratigraphy include enhanced knowledge of Middle Permian tetrapod footprints, and clarification of the palaeoenvironmental factors that may control the distribution of tetrapod footprints in space and time.

Permian tetrapod footprints play a key role in the history of vertebrate ichnology and were the subject of the first published account of vertebrate ichnofossils almost 200 years ago (Anon. 1828; Pemberton *et al.* 1996; Lockley & Meyer 2000). Since then, tetrapod footprints have been found in Permian stratal successions of 21 countries on six continents (Fig. 1): (1) Africa – Morocco (Voigt *et al.* 2010, 2011a, b; Hminna *et al.* 2012), Niger (Smith *et al.* 2015), South Africa (De Beer 1986; Smith 1993; De Klerk 2002) and Tunisia (Newell *et al.* 1976); (2) Asia – Turkey (Gand *et al.* 2011); (3) Europe – Austria (Niedermayr & Scheriau-Niedermayr 1980; Voigt & Marchetti 2014), the Czech Republic (Geinitz 1861; Holub & Kozur 1981), France (Gand 1988; Gand *et al.* 2000; Gand & Durand 2006), Germany (Pabst 1908; Haubold 1984; Voigt 2005, 2012), the UK (Haubold & Sarjeant 1973, 1974), Hungary (Kaszap 1968; Barabás-Stuhl 1975; Haas 2001), Italy (Conti *et al.* 1977; Ceoloni *et al.* 1988; Marchetti 2014), Poland (Czyżewska 1955; Voigt *et al.* 2012), Russia (Schneider *et al.* 1992; Tverdokhlebov *et al.* 1997; Lucas *et al.* 1999; Gubin *et al.* 2003; Surkov *et al.* 2007), Serbia (Jovanovic 2012, 2013) and Spain (Gand *et al.* 1997; Voigt & Haubold 2015); (4) North America – Canada (Mossman & Place 1989; Calder *et al.* 2004; van Allen *et al.* 2005) and the USA (Cotton *et al.*

1995; Haubold *et al.* 1995; Lucas & Hunt 2005; Voigt & Lucas 2015a); (5) Oceania – Australia (Warren 1997); and (6) South America – Argentina (Melchor & Sarjeant 2004; Krapovickas *et al.* 2015) and Brazil (Costa da Silva *et al.* 2012).

The abundance of Permian tetrapod footprints disguises their uneven distribution in space and time, as the vast majority of tracks come from Early Permian (Cisuralian) beds that almost exclusively represent equatorial regions of Pangaea (Figs 1 & 2). Apart from the imbalanced record, Permian tetrapod footprints have a great potential to become a useful tool in stratigraphic analyses of continental deposits because the period experienced several major steps in the evolution of terrestrial tetrapods. In particular, these are the descent of anamniote reptiliomorphs (Lucas 2005, 2006; Kessel 2010; Clack & Milner 2015), the transition from ‘pelycosaur’- to non-mammalian therapsid-dominated synapsids (Kemp 2006, 2012), and the diversification and increasing body size of parareptiles (Tsuji & Müller 2009), as well as the radiation of non-diapsid (=‘captorhinomorph’) (O’Keefe *et al.* 2006) and diapsid eureptiles (Müller & Reisz 2006; Reisz *et al.* 2011) that are reflected in late Palaeozoic terrestrial tetrapod ichnoassemblages. A number of vertebrate ichnologists have tried to take advantage of this fact by proposing from simple

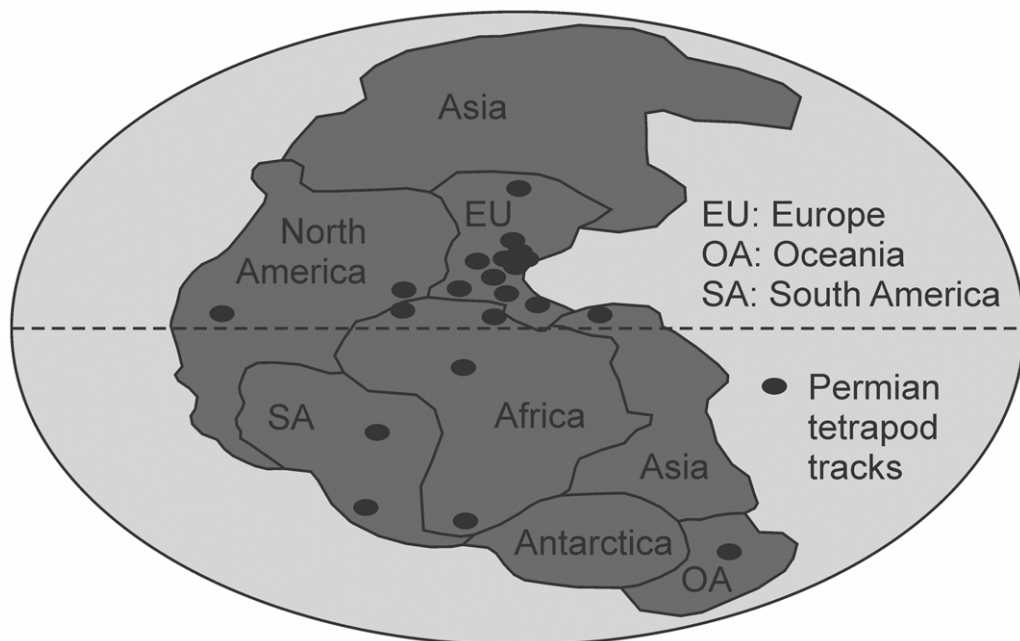


Fig. 1. Permian Pangaea and the distribution of Permian tetrapod tracksites.

to detailed schemes for subdividing Permian strata using fossil tetrapod footprints (Pabst 1908; Schmidt 1959; Haubold & Katzung 1972; Boy & Fichter 1988; Gand 1988; Voigt 2005; Gand & Durand 2006; Lucas 2007; Avanzini *et al.* 2011; Voigt & Lucas 2013). Most of the previous work suffers from ichnotaxonomical oversplitting and the overvaluation of local footprint records. By focusing on widely distributed and well-documented ichnotaxa, we intend to reboot the analysis of Permian tetrapod footprints for stratigraphic purposes.

Permian tetrapod footprint ichnotaxa and trackmaker relationships

Almost 400 different scientific names were introduced and used for Permian tetrapod footprints

during the first two centuries of research (Haubold 2000). This count includes a huge number of synonyms that result from naming footprints based on extramorphological variations, the stratigraphic age of the track-bearing beds or even the geographical position of track localities (Haubold 1996, 2000; Voigt 2005). Instead, tetrapod footprint ichnotaxa should be named on the basis of anatomically controlled characters of the imprint morphology and trackway pattern only. Following this ichnotaxonomic concept, there are currently 13 valid ichnogenera of Permian tetrapod footprints. For the purpose of the present paper, we designate an ichnogenus to be valid if there is representative material known from at least three different localities. Here, we briefly characterize the 13 valid ichnogenera of Permian tetrapod footprints.

Permian	Africa	Asia	Europe	North America	Oceania	South America
Late	Morocco, Niger, South Africa, Tunisia		France, Germany, Great Britain, Hungary, Italy, Poland, Russia		Australia	Brazil
Middle			France			
Early	Morocco	Turkey	Austria, Czech Republic, France, Germany, Great Britain, Hungary, Italy, Poland, Russia, Serbia, Spain	Canada, USA		Argentina

Fig. 2. Generalized stratigraphic distribution of Permian tetrapod tracks.

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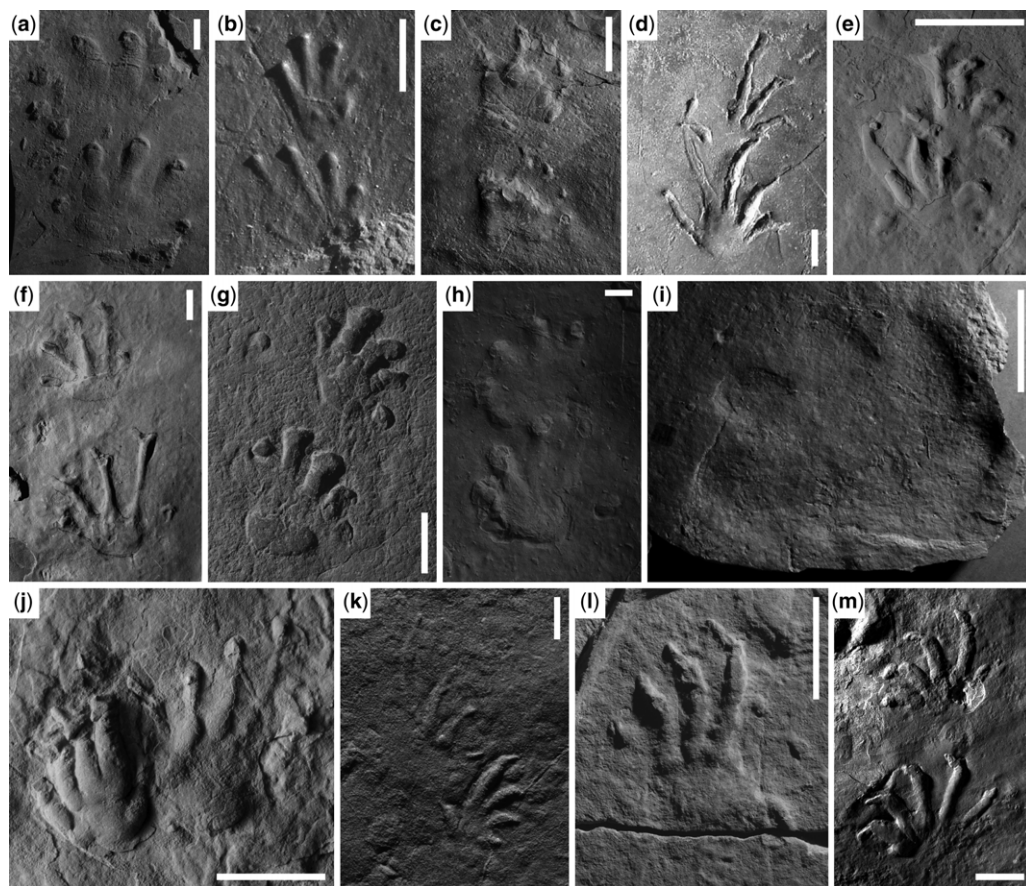


Fig. 3. Permian tetrapod footprint ichnotaxa: (a) *Amphisauropus* Haubold, 1970; (b) *Batrachichnus* Woodworth, 1900; (c) *Dimetropus* Romer & Price, 1940; (d) *Dromopus* Marsh, 1894; (e) *Erpetopus* Moodie, 1929; (f) *Hylodichnus* Gilmore, 1927; (g) *Ichniotherium* Pohlig, 1892; (h) *Limmopus* Marsh, 1894; (i) *Pachypes* Leonardi *et al.*, 1975; (j) *Paradoxichnium* Müller, 1959; (k) *Rhynchosauroides* Maidwell, 1911; (l) *Tambachichnium* Müller, 1954; (m) *Varanopus* Moodie, 1929. Photographed tracks show manus-pes couples, except for (i) and (l), which illustrate imprints of an isolated manus and pes, respectively. Scale bars are 1 cm (in a, b, d–f, h & m), 5 cm (in c, g, j & l) and 10 cm (in i).

Amphisauropus Haubold, 1970

Pentadactyl manus and pes imprints up to 70 mm long (Fig. 3a). Manus one-quarter shorter than pes imprints, distinctly wider than long. Manual digits short, digit length increases from I to IV, digit V a little bit longer than I; palm more than half as long as imprint length. Pes imprint as long as wide, IV is the longest digit and V is slightly longer than II. Manus and pes imprints with distinct pads at the base of digit I. Trackways often with manus strongly rotated inwards and pes imprints rotated outwards; digit and tail/body traces common. Potential trackmakers are anamniote reptiliomorphs, especially Seymouriamorpha (Haubold 2000; Voigt 2005).

Batrachichnus Woodworth, 1900

Tetrapod track with pentadactyl pes and tetradactyl manus imprints less than 40 mm in length (Fig. 3b). Both imprints with indistinctly impressed proximal margin and distally rounded, straight digits. Manus imprints as long as wide, digits short with III the longest and IV shorter than II. Pes imprints longer than wide, digit length increases from I to IV, and V is shorter than II. Pedal digit IV about 1.5–2 times as long as the sole. Manus imprints often slightly turned inwards, pes imprints usually subparallel to the trackway midline. Tail/body traces may be present. Tracks of this ichnogenus are referred to small anamniote tetrapods, especially temnospondyls (Haubold 1996; Voigt 2005; Stimson *et al.* 2012).

Dimetropus Romer & Price, 1940

Tracks of quadrupedal tetrapods with pentadactyl manus and pes imprints that may exceed 200 mm in length (Fig. 3c). Imprints with relatively short digits, and proximally extended palm and sole. Digits increase in length from I to IV, V as long as III in the pes imprint, and V is as long as II in the manus imprint. Manus imprints as long as wide, pes imprints about one-quarter longer than wide. Imprints often show semi-spherical impressions of the metatarsal and metacarpal phalangeal pads. Digit tips more or less acute; trackways with imprints either aligned parallel to the trackway midline or slightly turned outwards. Tail/body traces common. *Dimetropus* seems to be the track of most 'pelycosaurs', except for varanopids and derived caseids (Haubold 1971b, 1973, 1984, 2000; Fichter 1979, 1983b; Voigt 2005).

Dromopus Marsh, 1894

Pentadactyl manus and pes imprints up to 80 mm in length (Fig. 3d). Palm/sole short, digits long, slender and distally tapered. Manus and pes imprints very similar in shape; both imprints are about one-third longer than wide, but manus about one-quarter shorter than the pes imprint. Digit length increases from I to IV, IV is highly elongated and V is about as long as II. Primary marginal overstepping of the manus imprint by the pes common. Digit dragging and tail/body traces only in tracks that were made on slippery ground. *Dromopus* is probably the track of various lizard-like Permian parareptiles and eureptiles, such as bolosaurids and araeoscelids (Haubold 1971b, 1973, 1984, 2000; Fichter 1979, 1983a; Voigt 2005).

Erpetopus Moodie, 1929

Pentadactyl manus and pes imprints up to 30 mm in length, average length 10–12 mm (Fig. 3e). Digit length increases from I to IV, and V is as long as I or II. Digits are thin, long and straight with acute terminations. Distal parts of digits I–IV are curved inwards, the distal part of digit V is curved outwards. Subrectangular palm/sole reaches about one-third of the total imprint length. Wide range of trackway pattern and orientation of imprints with respect to the trackway midline. Most likely trackmakers are small captorhinomorphs (Haubold 1971b; Haubold & Lucas 2001, 2003; Bernardi & Avanzini 2011; Voigt *et al.* 2013a).

Hyloidichnus Gilmore, 1927

Tracks of quadrupedal tetrapods with pentadactyl imprints up to 80 mm in length (Fig. 3f). Manus

and pes imprints similar in size and digit proportions. Both imprints are about as long as wide with long, straight and slender digits. Digits increase in size from I to IV, V is about as long as I. Digits have tapering tips that are curved inwards in digits I–IV, but rotated outwards in digit V. Bifurcated digit tips (I–IV) are common. Short, indistinct palm/sole impression. Pes imprints slightly and manus imprints usually strongly rotated inwards with respect to the trackway midline. Tail or body traces not observed. Tracks of *Hyloidichnus* are referred to captorhinids (Haubold 1971b; Gand 1988; Gand & Durand 2006) or, even more specifically, to moradisaurine caphorinids (Voigt *et al.* 2009, 2010).

Ichniotherium Pohlig, 1892

Pentadactyl manus and pes imprint with enlarged, blunt digit tips (Fig. 3g). Pes imprints up to 200 mm in length, about as long as wide, and the sole characterized by large, oval to circular shaped pad. Manus imprints distinctly wider than long and about one-fifth shorter than the pes imprints. Digit length increases from I to IV, V shorter than II or as long as III depending on ichnospecies. Trackways with pes imprints rotated outwards to positioned forwards, manus imprints subparallel to the trackway midline or slightly to moderately rotated inwards. Primary marginal overstepping may occur. Tail or body traces very rare and always discontinuous. Based on the excellent vertebrate body and trace fossil record of the Early Permian Tambach Formation of central Germany, *Ichniotherium* is unambiguously referred to diadectomorph trackmakers (Berman *et al.* 1998, 2004; Fichter 1998; Voigt & Haubold 2000; Voigt 2005; Voigt *et al.* 2007).

Limnopus Marsh, 1894

Tracks of quadrupedal tetrapods with tetradactyl manus imprints (Fig. 3h). Tracks are identical to *Batrachichnus* except for the fourth digit of the manus imprint, which is about as long as digit II in *Limnopus*, but about as long as digit I in *Batrachichnus*. In addition, digits are relatively shorter in *Limnopus*. Total pes imprint length may reach up to 200 mm. Potential trackmakers are large-size temnospondyls, such as eryopids of Early Permian time (Haubold 1971b, 1973, 1984, 2000; Fichter 1979, 1983a; Tucker & Smith 2004; Voigt 2005; Voigt & Lucas 2015b).

Pachypes Leonardi et al., 1975

Tracks of quadrupedal tetrapods with pentadactyl manus and pes imprints up to 400 mm in length

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(Fig. 3i). Manus and pes imprints differ in size and shape. Both imprints with short and sturdy, distally rounded digits, as well as well-developed sole and palm. Pes imprints about as long as wide; digits increase in length from I to IV, and V is about as long as I. Manus imprints about one-quarter wider than long; digits I–IV almost sub-equal in length, V significantly shorter. Trackways with pes imprints directed forwards and manus imprints rotated inwards. No tail or body traces. *Pachypes* is usually referred to pareiasaurian trackmakers (Leonardi *et al.* 1975; Conti *et al.* 1977; Haubold 2000; Valentini *et al.* 2008, 2009; Voigt *et al.* 2010).

Paradoxichnium Müller, 1959

Lacertoid tracks with pentadactyl manus and pes imprints up to 110 mm in length (Fig. 3j). Manus imprints more than one-third shorter than pes imprints. Both imprints morphologically similar, except for a relatively shorter digit IV in the manus imprint. Digit length increases moderately from I to IV, V about as long as II. Low interdigital angles, I–V range from about 30° to 40°. Trackways with manus imprints rotated slightly inwards and pes imprints rotated outwards. Potential trackmakers are relatively large-sized neodiapsids, especially basal archosauromorphs, such as Protorosauridae (Haubold 1971*b*, 1973, 2000; Voigt 2012).

Rhynchosauroides Maidwell, 1911

Tracks of quadrupedal tetrapods with pentadactyl manus and pes imprints up to about 80 mm in length (Fig. 3k). Imprints are typical lacertoid and morphologically very similar to *Dromopus* except for three features: (1) the manus imprint is relatively smaller in *Rhynchosauroides*; (2) *Rhynchosauroides* has a digitigrade pes imprint and a plantigrade manus imprint, which is the exact opposite of *Dromopus*; and (3) *Rhynchosauroides* includes trackways that show a lateral overstep of the manus imprint by the pes, whereas the pes imprint has never been observed to be placed in front of the manus imprint in *Dromopus*. Potential trackmakers of Permian *Rhynchosauroides* are Pre-Mesozoic saurians: that is, basal lepidosauromorphs and archosauromorphs (Haubold 1966, 1971*a, b*; Avanzini & Renesto 2002; Klein *et al.* 2010).

Tambachichnium Müller, 1954

Quadrupedal trackway with pentadactyl manus and pes imprints up to 90 mm in length (Fig. 3l). Manus and pes imprints with similar proportions, both imprints longer than wide, showing slender digits with distinct claw impressions. The relative lengths of digits correspond to $I < II \approx$

$V < III < IV$. Digits I and V are often incompletely preserved. Trackway pattern highly variable, pes may be impressed behind the manus, partially overstepping the manus or even is placed in front of the manus imprint. Pes imprint is often rotated slightly outwardly; manus imprint set is in the direction of movement. No accessories such as digit dragging or tail/body traces are known. Digit and imprint proportions are most similar to the autopods of varanopid synapsids (Voigt 2005; Voigt & Lucas 2015*b*).

Varanopus Moodie, 1929

Tracks of quadrupedal tetrapods with pentadactyl manus and pes imprints up to 45 mm in length (Fig. 3m). Manus imprint is slightly wider than long, pes imprint as long as wide and about one-fifth longer than the manus imprint. Digit length increases from I to IV, V is as long as II or III in the pes imprint, but shorter than II in the manus imprint. All digits have acute distal ends (distinct claw impressions). Palm/sole remarkably short, measures about one-fifth of the total imprint length. Pes imprints more or less parallel to the trackway midline, manus imprints are usually turned slightly inwards. Marginal primary overstepping may occur; tail/body traces have never been observed. Based on the digit proportions and the short sole/palm, early captorhinomorphs with a relatively long pedal digit V are the most likely *Varanopus* trackmakers (Fichter 1979; Voigt 2005; Voigt *et al.* 2009).

These fossil footprint ichnotaxa cover a wide range of potential trackmakers among Permian terrestrial tetrapods: temnospondyls, seymouriamorph and diadectomorph reptiliomorphs, 'pelycosaurian-grade' synapsids, and small-sized and large-sized parareptiles, as well as non-diapsid and diapsid eurentiles (Fig. 4). Nevertheless, there is a significant lack of knowledge with regard to the tetrapod footprint record of Permian lepospondyls, therapsids and procolophonids. As footprints of supposed Permian lepospondyls are rare and small (e.g. Voigt & Lucas 2015*a, b*), their ichnological characters have not yet been satisfyingly determined. Supposed therapsid tracks seem relatively common in Middle–Late Permian deposits (e.g. Newell *et al.* 1976; Conti *et al.* 1977; De Beer 1986; Ceoloni *et al.* 1988; Smith 1993; Fichter 1994; Gand *et al.* 2000; De Klerk 2002; Gand & Durand 2006), but the material currently lacks a comprehensive and comparative analysis. Tracks of Permian procolophonids are still obscure (Klein *et al.* 2015), although there is potential material among undescribed Lopinigian tracks from Germany, Morocco and Poland.

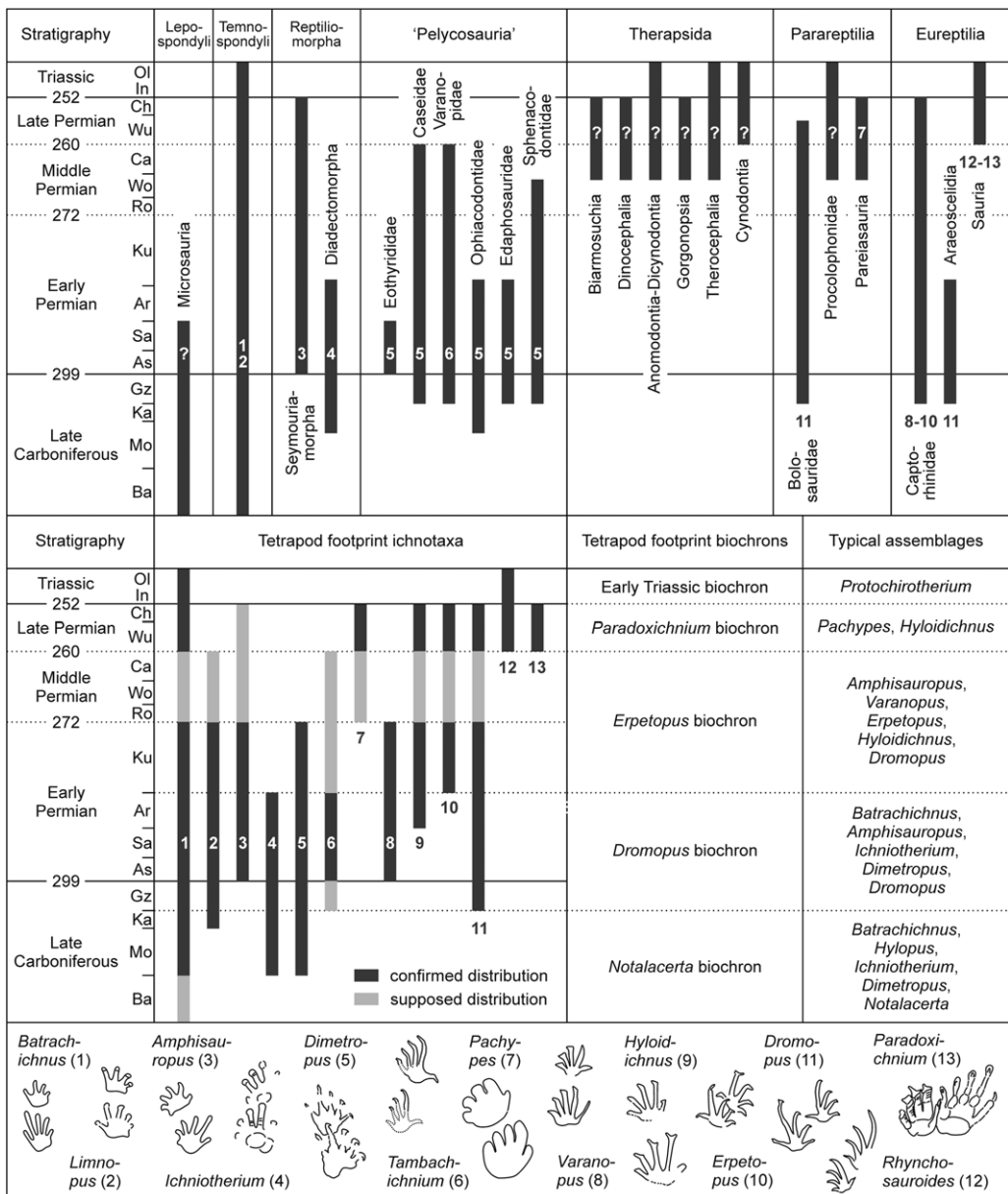


Fig. 4. Stratigraphic distribution of Permian terrestrial tetrapod taxa and related footprint ichnotaxa (compiled from Tsuji & Müller 2009; Reisz *et al.* 2011; Huttenlocker & Rega 2012; Kemp 2012; Ezcurra *et al.* 2014; Schoch 2014). The three suggested Permian tetrapod footprint biochrons – *Dromopus*, *Erpetopus* and *Paradoxichnium* – approximately correspond to the chronostratigraphic series early (Cisuralian), middle (Guadalupian) and late (Lopingian) Permian. For abbreviations of the chronostratigraphic stages see ICS (2015).

Stratigraphic distribution of Permian tetrapod footprints

The stratigraphic ranges of the valid Permian tetrapod footprint ichnotaxa are difficult to assess

because the precise age of the footprint-bearing strata is often poorly constrained. Despite these problems, we will shortly discuss the first and last occurrences of the valid ichnotaxa and, wherever possible, compare it to the stratigraphic range

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of the body fossils of the inferred trackmakers (Fig. 4).

Batrachichnus tracks have been described from Carboniferous strata of North America and Europe (Butts 1891; Woodworth 1900; Matthew 1905; Haubold & Sarjeant 1973, 1974; Voigt 2005, 2012; Stimson *et al.* 2012). The same morphotype of tetrapod tracks is also known from Late Permian strata of Russia (Tverdokhlebov *et al.* 1997) and Morocco (Voigt *et al.* 2015), and there are even similar tracks known from Early Triassic beds (Klein & Lucas 2010, fig. 57). Thus, *Batrachichnus* is expected to range through the entire Permian Period. The apparent morphological stasis is not surprising, considering that this kind of tetrapod footprint refers to a plesiomorphic autopodial structure of a diverse and long-lived group, the temnospondyls (Schoch 2014).

Limnopus first occurs in the Late Carboniferous (Marsh 1894; Haubold & Sarjeant 1973, 1974; Voigt 2005, 2012). Its stratigraphically youngest record comprises unquestionable material from the late Early Permian of Italy (Marchetti *et al.* 2013, 2015; Marchetti 2014) and ambiguous material from the Middle Permian of France (Gand & Durand 2006). A Late Carboniferous–Middle Permian distribution of *Limnopus* is in accordance with the stratigraphic range of the most likely trackmakers, eryopids (Werneburg & Berman 2012; Schoch 2014).

Amphisauropus is almost exclusively known from Early Permian strata (Voigt 2015). The first occurrence might be coincident with the base of the Permian Period by track records from the Brule Formation of Nova Scotia, eastern Canada (van Allen *et al.* 2005) and the Ilmenau Formation of the Thuringian Forest, central Germany (Voigt 2005, 2012). *Amphisauropus* has been mentioned based on a single manus–pes imprint from the supposed latest Permian Ikakern Formation of Morocco (Hminna *et al.* 2012). If correct, this would be the only non-Early Permian record of the ichnotaxon. Terrestrial seymouriamorphs, the most likely trackmakers of *Amphisauropus*, are known from Early, as well as Late, Permian deposits (Berman *et al.* 2000; Klembara 2011).

The record of *Ichniotherium* extends down almost to the early Late Carboniferous (Voigt & Ganzewski 2010), whereas the stratigraphically youngest occurrences come from late Early Permian deposits of New Mexico (Voigt & Lucas 2015b). This kind of track has also been reported from the Late Permian Val Gardena Sandstone Formation of Italy (Conti *et al.* 1977; Ceoloni *et al.* 1988; Avanzini *et al.* 2001), but, according to ongoing revisions, the related material most probably represents therapsid tracks that do not fit the characteristics of *Ichniotherium*. Diadectomorphs as probable

trackmakers of *Ichniotherium* are only known from Late Carboniferous and Early Permian strata (Berman *et al.* 2004; Reisz 2007; Kennedy 2010; Kissel 2010). The recently proclaimed diadectid *Alveusdectes* from the Late Permian of China (Liu & Bever 2015) does not interfere with this view, as the advanced and differentiated dentition with canines of this taxon relates the Chinese specimen to therapsids rather than to diadectomorphs.

Dimetropus is well known from Late Carboniferous deposits in Africa (Lagnaoui *et al.* 2014) and Europe (Haubold & Sarjeant 1973, 1974; Voigt 2005, 2012; Voigt & Ganzewski 2010). The stratigraphically youngest occurrence of the ichnotaxon is from the late Early Permian Wellington Formation of Oklahoma, USA (Sacchi *et al.* 2014). A Late Carboniferous–Early Permian range of *Dimetropus* largely coincides with the stratigraphic distribution of potential trackmakers (i.e. eothyridids, basal caseids, ophiacodontids, edaphosaurids and sphenacodontids: Kemp 2006, 2012; Huttenlocker & Rega 2012).

Tambachichnium is hitherto only known from Early Permian strata of France (undescribed material from the Rabejac Formation of the Lodève Basin), Germany (Müller 1954; Haubold 1971b; Haubold & Stapf 1998; Voigt 2005, 2012), Colorado (Voigt *et al.* 2005) and New Mexico (Lucas *et al.* 2013b; Voigt & Lucas 2015b). This ichnotaxon is also expected to be found in Middle Permian ichnoassemblages (see Gand *et al.* 1995 for an ambiguous record from SE France), as skeletal remains of the supposed varanopid trackmakers have been recorded in strata of Late Carboniferous–late Guadalupian age (Campione & Reisz 2010).

Pachypes has been reported from the Late Permian type locality in Italy (Leonardi *et al.* 1975; Conti *et al.* 1977; Valentini *et al.* 2009), and the Late Permian of Morocco (Voigt *et al.* 2010) and Niger (Smith *et al.* 2015). Moreover, Valentini *et al.* (2009) synonymized Late Permian tracks from Russia (Gubin *et al.* 2003; Surkov *et al.* 2007) with *Pachypes*. Thus, the ichnotaxon is relatively well known from uppermost Permian strata. As pareiasaurians, the most likely trackmakers of *Pachypes*, have a temporal range from the Middle to Late Permian (Tsuji 2011; Tsuji *et al.* 2013), a future discovery of these tracks in Guadalupian tetrapod ichnoassemblages is to be expected.

Varanopus is known from basal Permian deposits of Canada (van Allen *et al.* 2005) and the Czech Republic (unpublished specimen in the collection of the Natural History Museum Vienna, Austria), and is a common track in Early Permian deposits of Europe (Gand 1988; Haubold & Stapf 1998; Voigt 2005, 2012; Gand & Durand 2006; Marchetti 2014; Marchetti *et al.* 2015; Voigt & Haubold 2015) and North America (Gilmore 1927, *Hylopus*

hermitanus = *Varanopus*; Lucas *et al.* 2001, 2013a, b; Voigt *et al.* 2005). Among the last occurrences of the ichnogenus seem to be tracks from the late Early Permian of France (Gand 1988; Gand & Durand 2006), Spain (Voigt & Haubold 2015) and Italy (Marchetti 2014; Marchetti *et al.* 2015). The supposed trackmakers, basal captorhinomorphs with a relatively long pedal digit V (Voigt *et al.* 2009), may have existed beyond the Early Permian, but at present there is no relevant skeletal record to demonstrate this.

Hyloidichnus is known from Early Permian (Gand 1988; Gand *et al.* 1997; Gand & Durand 2006; Marchetti *et al.* 2013, 2015; Marchetti 2014; Voigt & Haubold 2015; Voigt & Lucas 2015a), as well as Late Permian, strata (Ceoloni *et al.* 1988; Voigt *et al.* 2010). All mentioned Early Permian records are from beds of probable Artinskian–Kungurian age. There is, however, a single record from the lower part of the Abo Formation in the Fra Cristobal Mountains of southern New Mexico (Lucas *et al.* 2012) that could be older and thus shift the first appearance of the ichnotaxon to the early Early Permian. The first peak abundance of *Hyloidichnus* in the late Early Permian is in accordance with the radiation of moradisaurine captorhinids, which are the most likely trackmakers of this kind of tetrapod footprint (O’Keefe *et al.* 2006; Voigt *et al.* 2009).

Erpetopus is known from Early Permian strata of France (Haubold & Lucas 2001, 2003), Italy (Haubold & Lucas 2001, 2003; Santi 2007; Marchetti *et al.* 2013, 2015; Marchetti 2014) and the USA (Haubold & Lucas 2001, 2003; Lucas *et al.* 2013a), as well as Late Permian deposits of Morocco (Hminna *et al.* 2012; Voigt *et al.* 2015). Tracks of this ichnogenus first appear almost simultaneously in the late Early Permian (for a more detailed discussion see below: *Erpetopus* biochron). *Erpetopus* is very generally referred to small captorhinomorph trackmakers (Haubold 1971b; Haubold & Lucas 2001, 2003; Bernardi & Avanzini 2011; Voigt *et al.* 2013a), so that the body fossil record in this case does not help to constrain the temporal range of these tracks.

Dromopus is the most common and most widely distributed kind of Permian tetrapod track, with numerous reports from strata of Cisuralian, as well as Lopingian, age (Haubold 1971b; Gand 1988; Haubold *et al.* 1995; Haubold 1996, 2000; Voigt 2005, 2012; Marchetti *et al.* 2015). Although there is just one ambiguous record from possible Middle Permian deposits (Gand 1988; Gand & Durand 2006), the diversity and temporal range of potential trackmakers among lacertoid parareptiles and eurentiles raises the expectation that *Dromopus* will be found in Permian strata of any age (Reisz *et al.* 2011; Modesto *et al.* 2015).

Palaeozoic *Rhynchosauroides* is only known from the Late Permian Val Gardena Sandstone Formation of the Southern Alps, Italy (Conti *et al.* 1977; Haubold 2000; Avanzini *et al.* 2001; Valentini *et al.* 2007), although the ichnogenus has very extensive Triassic records. A Late Permian distribution of the ichnogenus is in agreement with the temporal range of potential trackmakers (i.e. basal lepidosauromorphs and archosauromorphs: Ezcurra *et al.* 2014).

Paradoxichnium has long been known just from the holotype, a trackway with well-preserved imprints from the terrestrial marginal facies of the Late Permian Zechstein of central Germany (Müller 1959; Haubold 1971b; Voigt 2012). Ceoloni *et al.* (1988) assigned some tracks from the Late Permian Val Gardena Sandstone Formation with a question mark to the ichnogenus *Paradoxichnium*. According to preliminary results of an ongoing revision of the Val Gardena tetrapod ichnoassemblage, these tracks are much more similar to *Hyloidichnus* than *Paradoxichnium*. The Val Gardena tetrapod ichnoassemblage includes, however, a few tracks that can unambiguously be assigned to the latter ichnogenus. The most recent record of *Paradoxichnium* is from marginal-marine red beds of the Zechstein in SW Germany (Voigt *et al.* 2015). Thus, *Paradoxichnium* seems to be restricted to Late Permian deposits. This is in accordance with the temporal range of the most likely trackmakers (i.e. protorosauroid archosauromorphs: Gottmann-Quesada & Sander 2009; Voigt 2012).

Permian tetrapod footprint biochronology

Based on the vertical distribution of the 13 best-known Permian tetrapod ichnotaxa, we suggest a subdivision of the period into three footprint biochrons (Figs 4–7). From base to top these are the *Dromopus*, *Erpetopus* and *Paradoxichnium* biochrons. The bases of these biochrons are defined by the first appearances of the respective ichnogenus.

The *Dromopus* biochron lasts for about 20 myr and covers the stratigraphic interval of the latest Carboniferous (approximately Gzhelian) up to the late Early Permian (approximately Artinskian) (Lucas 2007). *Dromopus* was introduced for tracks from the Virgilian Howard Limestone Formation of the Wabaunsee Group of Kansas, USA (Marsh 1894; Haubold 1971b). This assemblage is considered to be the stratigraphically earliest record of the ichnogenus and thus defines the base of the *Dromopus* biochron. Tetrapod footprint assemblages of the *Dromopus* biochron are the most common and best documented of all Permian vertebrate trace fossils. They are dominated by temnospondyl (*Batrachichnus*, *Limnopus*), reptiliomorph anamniote

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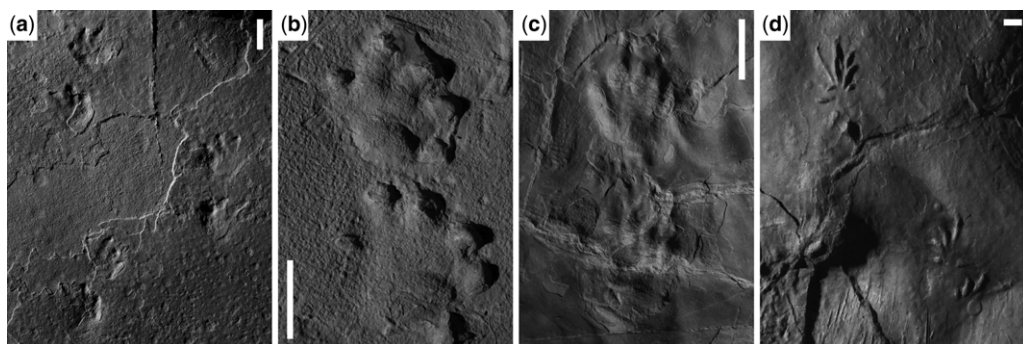


Fig. 5. Tetrapod footprints from the early Early Permian of the Intra-Sudetic Basin in southern Poland illustrating a typical ichnoassemblage of the *Dromopus* biochron (after Voigt *et al.* 2012): (a) *Amphisauropus*, trackway of three manus-pes sets; (b) *Ichnoterium*, left manus-pes set; (c) *Dimetropus*, left manus-pes set; and (d) *Dromopus*, two manus-pes sets. Scale bars are 1 cm (in a & d) and 5 cm (in b & c).

(*Amphisauropus*, *Ichnoterium*), ‘pelycosaurian’-grade synapsid (*Dimetropus*, *Tambachichnium*) and lacertoid tracks of small parareptiles or early diapsids (*Dromopus*) (Figs 4 & 5). Tracks of early captorhinomorphs (*Varanopus*, *Hyloidichnus*) are a minor component. Among others, this biochron includes some famous late Carboniferous–Early Permian tetrapod footprint-bearing sections, such as those of the Boskovice, Krkonose-Piedmont and Intra-Sudetic basins of the Czech Republic and

Poland (Geinitz 1861; Pabst 1908; Czyzewska 1955; Holub & Kozur 1981; Haubold 1984; Voigt *et al.* 2012), the French Lodève Basin (Tuilières-Loiras and Viala formations: Gand 1988; Gand & Durand 2006), the Thuringian Forest Basin of central Germany (Georgenthal–Tambach formations: Haubold 1985; Voigt 2005, 2012), the Cantabrian and Pyrenean basins of Spain (Peranera and Sagra formations: Gand *et al.* 1997; Voigt & Haubold 2015), the Souss, Khenifra and Tiddas basins in

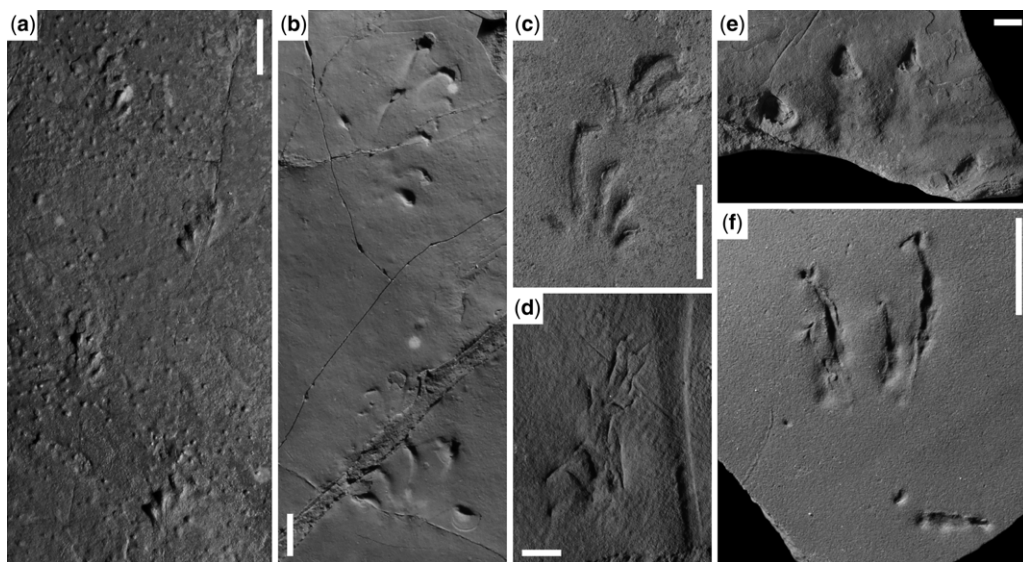


Fig. 6. Tetrapod footprints from the late Early Permian Arroyo de Alamillo Formation in central New Mexico, USA, illustrating a typical ichnoassemblage of the *Erpetopus* biochron (after Lucas *et al.* 2013a): (a) *Batrachichnus*, trackway of four manus-pes sets; (b) *Varanopus*, incomplete trackway of two manus-pes sets; (c) *Erpetopus*, left manus-pes set; (d) & (e) captorhinomorph tracks indet., left manus-pes set and incomplete imprint of right pes or manus; and (f) *Dromopus*, right manus-pes set. Scale bars are 1 cm.

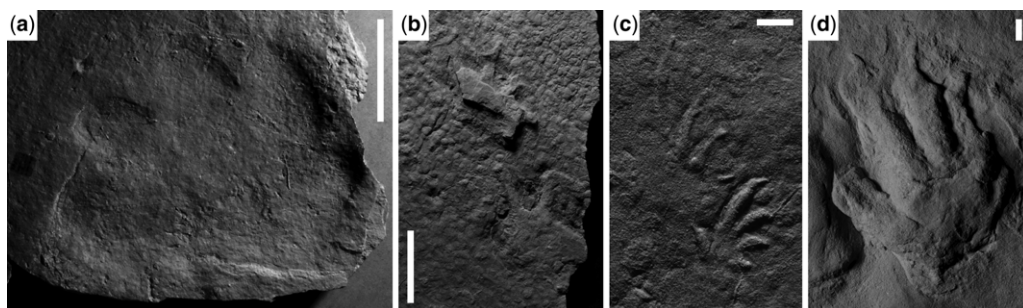


Fig. 7. Tetrapod footprints from the Late Permian Val Gardena Sandstone Formation of the Southern Alps, Italy, illustrating a typical ichnoassemblage of the *Paradoxichnium* biochron: (a) *Pachypes*, right manus; (b) *Hyloidichnus*, left manus-pes set; (c) *Rhynchosauroides*, left manus-pes set; and (d) *Paradoxichnium*, left manus. Scale bars are 5 cm (in a & b) and 1 cm (in c & d).

central Morocco (Hmich *et al.* 2006; Voigt *et al.* 2011a, b), and the late Carboniferous–Early Permian red beds of Nova Scotia and Prince Edward Island of maritime Canada (Mossman & Place 1989; Calder *et al.* 2004; van Allen *et al.* 2005; Brink *et al.* 2012), as well as numerous localities in the American Southwest (Hermit Formation, Arizona; Abo, Robledo Mountains and Sangre de Cristo formations, New Mexico; Maroon Formation, Colorado; Cotton *et al.* 1995; Haubold *et al.* 1995; Lucas & Hunt 2005; Voigt *et al.* 2005; Voigt & Lucas 2015a, b) (Fig. 8).

The *Erpetopus* biochron lasted for about 24 myr and covers the stratigraphic interval of the late Early Permian (approximately Kungurian) up to the late Middle Permian (approximately Capitanian).

Erpetopus was introduced for tracks from the Choza Formation of the Clear Fork Group of Texas, USA (Moodie 1929; Haubold & Lucas 2001, 2003). The type locality and several other late Early Permian occurrences of *Erpetopus* in southern France (Rabejac Formation: Haubold & Lucas 2001, 2003), Italy (Collio and Pizzo del Diavolo formations: Marchetti *et al.* 2013, 2015; Marchetti 2014) and New Mexico (Arroyo de Alamillo Formation: Lucas *et al.* 2013a) compete for the first appearance of the ichnogenus (Figs 6 & 8). The only available direct radioisotopic age for these strata (283.1 ± 0.6 – 279.8 ± 1.1 Ma for the Collio Basin of the Italian Southern Alps: Schaltegger & Brack 2007) indicates a Kungurian age. A similar age is provided by recent radioisotopic

Stratigraphy	Czech Republic	France	Germany	Italy	Russia	Spain	Morocco Niger	South Africa	Tunisia	Canada USA	Footprint Biochron
Late Permian	Ch Wu	Zechstein La Lieude	Zechstein	Val Gardena	Russian Platform	Ribera d'Urgellet	Ikakern Moradi	Karoo Basin	Cheguim		<i>Paradoxichnium</i>
Middle Permian	Ca Wo Ro	Salagou									<i>Erpetopus</i>
Early Permian	Ku Ar	Rabejac		Collio s.l.						Choza/ A.d.A.	
	Sa As	Viala T.-Loiras	Thuringian Forest Basin		Northern Caucasus	Peranera Sagra	Tiddas Khenifra Souss			Hermit Abo Brule	<i>Dromopus</i>
Carboniferous	Gz	Sudetes Bohemia Moravia									

Fig. 8. Approximate stratigraphic range of Permian tetrapod footprint-bearing strata that may help to refine the Permian tetrapod footprint ichnostratigraphic scheme. Explanation: Czech Republic/Poland – Sudetes, Bohemia, Moravia (Intra-Sudetic, Krkonoše-Piedmont, Boskovice basins); France – T.-Loiras (Tuilières-Loiras Formation); Germany – Zechstein (marginal terrestrial facies); Italy – Collio s.l. (Collio, Pizzo del Diavolo and Tregiovo formations); Morocco – Tiddas, Khenifra and Souss basins; Russia – Russian Platform (Kirov, Orenburg and Vologda regions); Canada/USA – A.d.A. (Arroyo de Alamillo Formation). For abbreviations of the chronostratigraphic stages, see ICS (2015).

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dating of volcanic ash layers 150 m above the Rabec Formation of the French Lodève Basin (284.4 ± 0.13 Ma; Michel *et al.* 2015).

In New Mexico, USA, footprint assemblages of the *Dromopus* and *Erpetopus* biochrons are stratigraphically superposed (e.g. Voigt & Lucas 2015a). These are footprint assemblages from the Robledo Mountains Formation and the bulk of the Abo Formation (*Dromopus* biochron) overlain by the uppermost Abo Formation and lower Yeso Group (Arroyo de Alamillo Formation) assemblages of the *Erpetopus* biochron. Marine strata that intertongue with and overlie these assemblages contain age-diagnostic foraminiferans which indicate that the boundary of the *Dromopus* and *Erpetopus* biochrons is very close to the base of the Kungurian (Lucas *et al.* 2015; Vachard *et al.* 2015).

Based on these data, we propose the base of the Kungurian as the approximate first appearance date of *Erpetopus*. The *Erpetopus* biochron is characterized by ichnoassemblages with abundant and diverse tracks of non-diapsid eureptiles (at least two different ichnospecies of *Varanopus*, *Hyloidichnus* and *Erpetopus*; Haubold & Lucas 2001, 2003; Lucas *et al.* 2013a; Marchetti 2014; Marchetti *et al.* 2015; Voigt & Haubold 2015) distinct from lacertoid tracks of small parareptiles or diapsids (*Dromopus*) (Figs 4 & 6). Seymouriamorph (*Amphisauropus*) and 'pelycosaurian'-grade synapsid tracks (*Dimetropus*) are less abundant, and temnospondyl tracks (*Batrachichnus*, *Limnopus*) extremely rare. Therapsid, huge parareptile and varanopid synapsid tracks (*Tambachichnium*) may be part of the supposedly Middle Permian tetrapod ichnoassemblages of the Lodève and Esterel basins of France (Gand 1988; Gand *et al.* 1995; Gand & Durand 2006), but this material is difficult to evaluate without careful revision and, especially, additional material for comparative analysis. Therefore, the knowledge of ichnoassemblages of the *Erpetopus* biochron is currently restricted to occurrences of probably exclusive latest Early Permian (Kungurian) age in France, Italy and the USA (Fig. 8).

The *Paradoxichnium* biochron lasts for about 8 myr and covers the Late Permian (Wuchiapingian and Changhsingian). *Paradoxichnium* has been introduced for tracks from marginal-marine deposits of the German Zechstein, more precisely in a horizon correlated with the second most basal evaporation cycle of the Southern Permian Basin (Staßfurt Formation, Z2; Müller 1959; Ullrich 1964). The Staßfurt Formation is considered to be late Wuchiapingian in age (Szurlies 2013). The recent find of *Paradoxichnium* from marginal-marine Zechstein red beds of the Annweiler Formation in SW Germany may be approximately the same age (Voigt *et al.* 2015). The third occurrence of *Paradoxichnium* is in the Val Gardena Sandstone Formation

of the Italian Southern Alps, for which palynological analyses have suggested a late Capitanian–Changhsingian age (Pittau 2005) or just a Lopingian age (Posenato 2010; Kustatscher *et al.* 2012).

Owing to these age constraints, we propose the base of the Late Permian as the approximate first appearance date of *Paradoxichnium*. The *Paradoxichnium* biochron is dominated by pareiasaurian (*Pachypes*), captorhinomorph (*Hyloidichnus*, *Erpetopus*) and parareptilian–neodiapsid lacertoid (*Dromopus*), as well as early saurian tracks (*Rhynchosauroides*, *Paradoxichnium*) (Figs 4 & 7). Anamniote tracks are extremely rare (Tverdokhlebov *et al.* 1997; Voigt *et al.* 2015), whereas therapsid tracks play a key role, although most of the material is not yet adequately studied or even part of a valid ichnotaxonomy (Newell *et al.* 1976; Conti *et al.* 1977; Ceoloni *et al.* 1988; Smith 1993; Gand *et al.* 2000; De Klerk 2002; Voigt *et al.* 2015). Most typical ichnoassemblages of the *Paradoxichnium* biochron have been known from Italy (Val Gardena Sandstone Formation: Conti *et al.* 1977; Ceoloni *et al.* 1988), Morocco (Ikakern Formation: Voigt *et al.* 2010, 2015; Hminna *et al.* 2012) and Niger (Smith *et al.* 2015) (Fig. 8). Several other horizons and places hitherto provided just low-diversity ichnoassemblages (Müller 1959; Newell *et al.* 1976; Smith 1993; Tverdokhlebov *et al.* 1997; De Klerk 2002; Gubin *et al.* 2003; Surkov *et al.* 2007; Fortuny *et al.* 2011; Voigt *et al.* 2015) or diverse ichnoassemblages that need further study in order to allow conclusive comparisons (Gand *et al.* 2000).

Perspectives

The proposed Permian tetrapod footprint biochronozonation represents a conservative ichnostratigraphic concept that, following future analysis, provides scope for significant refinement. For example, the *Dromopus* biochron provides potential for subdivision by fixing the first appearance of *Amphisauropus*, *Hyloidichnus* and two distinct *Varanopus* ichnospecies (Lucas *et al.* 2013a; Marchetti 2014; Marchetti *et al.* 2015; Voigt & Haubold 2015). Totally unexplored is the stratigraphic value of Permian therapsid tracks. Other potential time markers are the first appearance of procolophonid and chirotheriid tracks in the Middle and Late Permian (Bernardi *et al.* 2015; Klein *et al.* 2015). Subject to sufficient data, a stage-level stratigraphic resolution of the Permian by tetrapod footprints would appear realistic. At present, biochronological organization of the Permian tetrapod-body-fossil record recognizes 10 biochrons (Lucas 2005, 2006), whereas there are nine marine stages recognized for the Permian. If our prediction is correct, Permian

footprint biochronology thus could subdivide the Permian about as well as do tetrapod body fossils, although much work lies ahead to reach this ambitious goal.

In order to be able to develop a more effective Permian ichnostratigraphic scale, it is vital to both enhance the knowledge of Middle Permian tetrapod footprints and to apply an ichnotaxonomy that is solely based on anatomically controlled features of the imprint morphology and trackway pattern (Haubold 1996). The latter will be a key for understanding the abundant record of supposed therapsid footprints already known from France, Italy, Tunisia, South Africa and other countries (e.g. Newell *et al.* 1976; Conti *et al.* 1977; Ceoloni *et al.* 1988; Smith 1993; Gand *et al.* 2000; Voigt *et al.* 2015). Moreover, this will provide a reliable basis to revise the numerous occurrences with late Early Permian–Late Permian tetrapod footprints preserved in aeolian sandstones, such as the Coconino Sandstone of Arizona (Gilmore 1926, 1927, 1928), the Cornberg Sandstone of Germany (Schmidt 1959; Fichter 1994), the sandstones of the Yacimiento Los Rayunos Formation in Argentina (Melchor 2001; Krapovickas *et al.* 2015), and the Corncockle and Lochabriggs sandstones of Scotland (McKeever & Haubold 1996). It is ironic that these first scientifically reported fossil tetrapod footprints on Earth (Anon. 1828; Pemberton *et al.* 1996; Lockley & Meyer 2000) might be the last we will understand in terms of their faunistic and stratigraphic meaning.

Finally, it is a major task to increase the knowledge of the influence of the palaeoenvironment (e.g. climate, facies, vegetation, topography and latitude) as a controlling factor for the distribution of tetrapod footprints in space and time. Basic studies with respect to Permian tetrapod footprints focus especially on the geographical distribution of seymouriamorph, diadectomorph and ‘pelycosaurian’-grade synapsid tracks (Haubold & Katzung 1978; Hunt & Lucas 1998, 2006; Voigt & Lucas 2012; Voigt *et al.* 2013*b*). Future progress on Permian tetrapod ichnofacies will hopefully help to understand apparently isolated footprint records (e.g. *Robledopus macdonaldi* from the late Early Permian of New Mexico: Voigt *et al.* 2013*a*) in an otherwise remarkably uniform Permian tetrapod ichnofauna.

Conclusions

Based on the above, we offer the following conclusions:

- Tetrapod footprints are among the most common and widespread fossils in continental Permian strata, and have a great potential for Permian biostratigraphy and biochronology.

- Based on the vertical distribution of the 13 best-known Permian tetrapod ichnotaxa, three Permian footprint biochrons can be recognized: the *Dromopus* (oldest), *Erpetopus* and *Paradoxichnium* (youngest) biochrons.
- The *Dromopus* biochron is latest Carboniferous (approximately Gzhelian) to late Early Permian (approximately Artinskian), and it encompasses ichnoassemblages dominated by tracks of temnospondyls, reptiliomorphs, pelycosaurs and early diapsids.
- The *Erpetopus* biochron is late Early Permian (approximately Kungurian) to late Middle Permian (approximately Capitanian), and encompasses ichnoassemblages dominated by tracks of non-diapsid eureptiles.
- The *Paradoxichnium* biochron is Late Permian (Wuchiapingian and Changhsingian), and it includes ichnoassemblages dominated by tracks of medium- and large-sized parareptiles, non-diapsid eureptiles and early saurians.
- This conservative biochronology may be refined to almost stage-level resolution by future comprehensive analysis, especially of Permian captorhinomorph and therapsid footprints.
- Other major tasks to improve Permian tetrapod footprint ichnostratigraphy include augmenting our knowledge of Middle Permian tetrapod footprints and clarification of the palaeoenvironmental factors that control the distribution of tetrapod footprints in space and time.

This work is based on the study of approximately 20 000 Palaeozoic tetrapod footprints in more than 120 public and private collections worldwide. We are grateful to numerous colleagues in Argentina, Austria, Canada, the Czech Republic, France, Germany, Hungary, Italy, Morocco, Russia, South Africa, Spain, Tunisia, the UK and the USA who supported us by providing access to collections, the organization of joint fieldwork and many inspiring discussions. Special thanks go to two anonymous reviewers for their constructive comments.

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