

Permian tetrapod footprints: biostratigraphy and biochronology

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Abstract: Permian tetrapod footprints are known from localities in North America, South America, Europe and Africa. These footprints comprise four ichnofacies, the *Chelichnus* ichnofacies from aeolianites and the *Batrachichnus*, *Brontopodus* and *Characichnos* ichnofacies from water-laid (mostly red-bed) strata. Permian track assemblages of the *Chelichnus* ichnofacies are of uniform ichnogenetic composition and low diversity, range in age from Early to Late Permian, and thus are of no biostratigraphic significance. Footprints of the *Batrachichnus* and *Brontopodus* ichnofacies represent two biostratigraphically distinct assemblages: (1) Early Permian assemblages characterized by *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Limnopus* and *Varanopus*; and (2) Middle to Late Permian assemblages characterized by *Brontopus*, *Dicynodontipus*, *Lunaepes*, *Pachypes*, *Planipes*, and/or *Rhynchosauroides*. Few Permian footprint assemblages are demonstrably of Middle Permian (Guadalupian) age, and there is a global gap in the footprint record equivalent to at least Roadian time. Permian tetrapod footprints represent only two biostratigraphically distinct assemblages, an Early Permian pelycosaur assemblage and a Middle to Late Permian therapsid assemblage. Therefore, footprints provide a global Permian biochronology of only two time intervals, much less than the ten time intervals that can be distinguished with tetrapod body fossils.

The global record of Permian tetrapod footprints encompasses localities in North America, South America, Europe and Africa (Fig. 1). Permian tetrapod footprints can be assigned to four ichnofacies, an aeolian *Chelichnus* ichnofacies and water-laid (red-bed) *Batrachichnus*, *Brontopodus* and *Characichnos* ichnofacies (Hunt & Lucas 2006). Various biostratigraphical schemes employing tetrapod footprints have been proposed, particularly for the Early Permian *Batrachichnus* ichnofacies, especially in Europe. For the purposes of a global Permian tetrapod footprint biostratigraphy, the operational taxonomic unit is the ichnogenus, as almost all ichnospecies are variants confined to a single locality and thus of little biostratigraphical value. Here, we rely primarily on the ichnotaxonomy of Haubold (1996, 2000) and McKeever & Haubold (1996) to review the biostratigraphical distribution of Permian tetrapod footprints to argue that on a global basis they only discriminate two intervals of Permian time.

Ichnotaxonomy

Biostratigraphy and biochronology are strongly dependent on taxonomy. This is because index taxa – those used to indicate age equivalence (correlation) – must be taxa with a well-founded and agreed taxonomy. Disagreements about

correlations are often based on disagreements about taxonomy that undermine the identification of index taxa.

Prior to the mid-1990s, about 150 ichnogenera of Permian tetrapod footprints had been named (most of them of Early Permian age) (Haubold 2000). Many of these ichnogenera (and their ichnospecies) were based on small samples that appeared to demonstrate distinctive footprint structures and therefore seemed to justify the naming of many ichnotaxa. However, in 1994, the discoveries of Jerry MacDonald, an outstanding amateur footprint collector, in the Lower Permian strata of southern New Mexico, United States, became available for study (see articles in Lucas & Heckert 1995). MacDonald's collection consisted of more than 2000 slabs with footprints from a mega-tracksite in the Robledo Mountains of southern New Mexico, and localities in the field included many more. Most importantly, large surfaces were available for study that showed many footfalls of individual animals (trackways) in different substrate and gait conditions.

Peabody (1948) articulated much of the basis of the methodology that we (with Haubold and others) have employed to interpret the footprint variation in this huge sample. Like almost all other vertebrate ichnologists, we regard vertebrate ichnotaxa as proxies of biotaxa. In

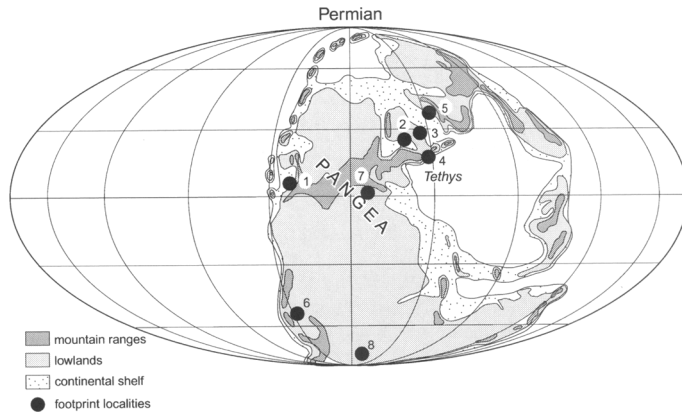


Fig. 1. Distribution of principal Permian tetrapod tracksites on Permian Pangea. Locations are: 1, western United States; 2, France; 3, Germany; 4, Italy; 5, Russia; 6, Argentina; 7, Morocco; 8, South Africa.

other words, we want different tetrapod ichnotaxa to correspond to discrete biotaxa, although we realize that the biotaxon equivalent to an ichnogenus is likely to be a family, suborder or order. To achieve this, we examine the various footprints, looking for what might be considered optimal tracks with a structure that best reflects the actual foot morphology. This optimal track structure is identified by matching the track to a presumed trackmaker. We consider other track structures that do not reflect the actual foot structure as suboptimal and regard them as extramorphological variants (Peabody's term). In other words, we judge the reason why the sub-optimal tracks do not match the foot structure to be the result of differences in substrate, gait or other factors (especially taphonomy) that prevented an optimal footprint from being preserved. By looking at a wide range of variation in individual trackways and across multiple trackways, we separated what we concluded are many extramorphological variants from the optimal tracks (Fig. 2). The result has been the elimination of numerous ichnogenera that were demonstrably based on extramorphological variants of a valid ichnogenus based on optimal track morphology. The most striking example is the small temnospondyl track ichnogenus *Batrachichnus*, which includes tracks that have been called *Anthichnium*, *Crenipes*, *Dromillopus*, *Nanopus*, *Salichnium*, *Saurichnites* and many others (Haubold 1996; Haubold & Lucas 2001a).

Lucas (2005a) called this approach to tetrapod footprint ichnotaxonomy the 'fusion method' because it eliminates many names applied to extramorphological variants and recognizes as valid only one name based on an

optimal track structure and its extramorphological variants (it thus fuses many names into one). The result, in popular parlance, has been ichnotaxonomic 'lumping' of the many Permian tetrapod footprint ichnogenera into a much smaller number of ichnogenera (e.g. Haubold 1996, 2000; McKeever & Haubold 1996; Voigt 2005). An easy measure of this is to compare Schult (1995), who recognized 23 ichnogenera in the Robledo Mountains megatracksite by attaching names to many extramorphological variants, with Hunt *et al.* (1995), who, using the fusion method, recognized only seven ichnogenera in the same sample.

One result of the sweeping ichnotaxonomic revisions of Haubold, Hunt and Lucas is to recognize that there is one tetrapod footprint assemblage (ichnofauna) in Lower Permian water-laid (usually red-bed) strata in the United States, Canada, Argentina, Germany, France, Italy, Russia and some other places in Europe (Hunt & Lucas 1998). In other words, the tetrapod footprints in Early Permian red beds are a single assemblage of broad, uniform composition. The following ichnogenera dominate: *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Ichniotherium*, *Limnopus* and *Varanopus*. This assemblage is composed mostly of the tracks of temnospondyls, diadectomorphs, seymouriamorphs, procolophonids and pelycosaurs (Table 1). The North American record demonstrates that most (if not all) of these ichnogenera have long stratigraphical ranges through most or all of Early Permian time (Haubold & Lucas 2001a, b, 2003; Lucas 2002b). Furthermore, at the Robledo Mountains mega-tracksite in southern New Mexico, almost

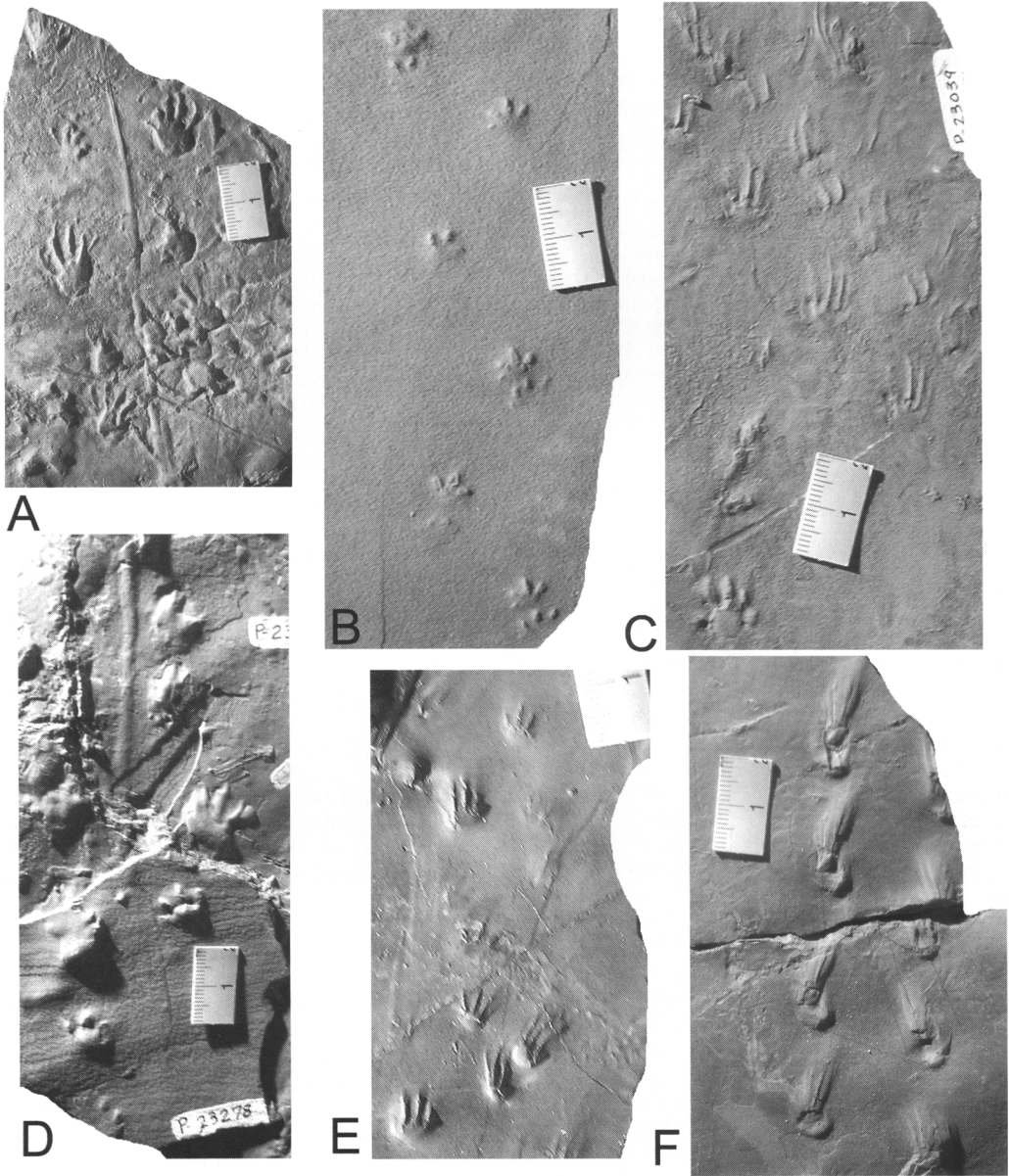


Fig. 2. Examples of small temnospondyl tracks from the Lower Permian Robledo Mountains megatracksite in southern New Mexico. All specimens are assigned to *Batrachichnus delicatulus* (Lull) and are in the collection of the New Mexico Museum of Natural History (NMMNH). They demonstrate nearly optimal footprint structure (A) and a variety of suboptimal extramorphological variants. The specimen in D is particularly interesting because it shows near optimal footprint structures with a median tail or body drag on the underside of one bedding plane (above), and the underside of a lower bedding plane (below) with underprints and no median drag. A, NMMNH P-23001; B, NMMNH P-23174; C, NMMNH P-29039-040; D, NMMNH P-23277-78; E, NMMNH P-23952; F, NMMNH P-23432.

Table 1. Common Permian tetrapod footprint ichnogenera and the inferred trackmakers (based largely on Haubold 1996)

Ichnofacies	Ichnogenera	Trackmaker
<i>Batrachichnus</i> (Early Permian)	<i>Amphisauropus</i>	seymouriamorph
	<i>Batrachichnus</i>	temnospondyl
	<i>Dimetropus</i>	pelycosaur
	<i>Dromopus</i>	araeoscelid
	<i>Erpetopus</i>	captorhinomorph
	<i>Hyloidichnus</i>	captorhinomorph
	<i>Ichniotherium</i>	diadectomorph
	<i>Limnopus</i>	temnospondyl
	<i>Tambachichnium</i>	araeoscelid
	<i>Varanopus</i>	captorhinomorph
<i>Chelichnus</i>	<i>Chelichnus</i>	pelycosaur
<i>Batrachichnus</i> (Mid- to Late Permian)	<i>Brontopodus</i>	therapsid
	<i>Dicynodontipus</i>	therapsid
	<i>Lunaepes</i>	therapsid
	<i>Merifontichnus</i>	therapsid
	<i>Pachypes</i>	pareiasaur
	<i>Rhynchosauroides</i>	eosuchian

all of these ichnogenera co-occur in a single, narrow stratigraphical interval. This suggests that local biostratigraphical zonation based on these ichnotaxa, especially those proposed in Germany and France, are not of global applicability and may also be of questionable utility, even at the local or regional scale.

A similar, broad-based ichnotaxonomic review of tracks of the *Chelichnus* ichnofacies has greatly simplified ichnotaxonomy, reducing ichnogenetic diversity to simply *Chelichnus* (Morales & Haubold 1995; McKeever & Haubold 1996). There has not, however, been a similar broad ichnotaxonomic revision of the Middle to Late Permian footprints attributed to pareiasaurs and therapsids. Because of this, we use the current names, although we are skeptical of the validity of some of them. Thus, our purpose here is not to revise ichnotaxonomy, so we list ichnogenera as reported by what we consider the most reliable source. Ichnogenetic names that we have placed in quotation marks are those we consider to be questionable identifications.

Ichnofacies

Permian tetrapod footprints have previously been assigned to two principal ichnofacies: an

aeolian *Chelichnus* ichnofacies and a water-laid (red-bed) *Batrachichnus* ichnofacies (Hunt & Lucas 2005b, 2006; Hunt *et al.* 2005c, d). Hunt & Lucas (2006) have also assigned Mid- to Late Permian track assemblages from water-laid strata to the *Brontopodus* and *Characichnus* ichnofacies. Swanson & Carlson (2002) described Early Permian tetrapod footprints from dolomitic strata in Oklahoma and suggested that they may represent another, little known ichnofacies, but we regard this footprint assemblage as a poorly preserved example of the *Batrachichnus* ichnofacies.

The *Batrachichnus* ichnofacies encompasses ichnoassemblages in which the majority of tracks are of quadrupedal carnivores with a moderate to high diversity (four to eight ichnogenera). This ichnofacies represents tidal flat through fluvial plain environments from the Devonian to the Middle Triassic. The *Batrachichnus* ichnofacies encompasses one previously named ichnocoenosis, originally named as an ichnofacies: *Batrachichnus* from the Early Carboniferous to Early Permian, which is separable into sub-ichnocoenoses:

- (1) inland/distal alluvial fan settings characterized by an abundance of *Ichniotherium* and a paucity of *Dimetropus*, the *Ichniotherium* sub-ichnocoenosis;
- (2) alluvial plain settings characterized by the presence of *Amphisauropus*, the *Amphisauropus* sub-ichnocoenosis;
- (3) coastal/tidal flat settings characterized by the relative abundance of *Batrachichnus* and *Dimetropus*, the *Dimetropus* sub-ichnocoenosis (Hunt & Lucas 2005b, 2006) (Fig. 3).

The *Chelichnus* ichnofacies encompasses ichnofaunas that have a low diversity (less than five ichnogenera) of tetrapod tracks in which manus and pes tracks are subequal in size and equant in shape, with short digit impressions. This ichnofacies is recurrent in dune faces of aeolian environments, and it extends from the Early Permian to the Early Jurassic. The *Chelichnus* ichnofacies encompasses two named ichnocoenoses (originally named as ichnofacies). These are the *Chelichnus* (= *Laoporus*) ichnocoenosis of Early Permian age (Lockley *et al.* 1994; Hunt & Lucas 2005b) and the *Brasilichnium* ichnocoenosis of Late Triassic to Early Jurassic age (Lockley *et al.* 1994, 2004; Schultz-Pittman *et al.* 1996).

The *Brontopodus* ichnofacies encompasses medium diversity ichnoassemblages in which the majority of tracks are of terrestrial herbivores with a small quantity (generally

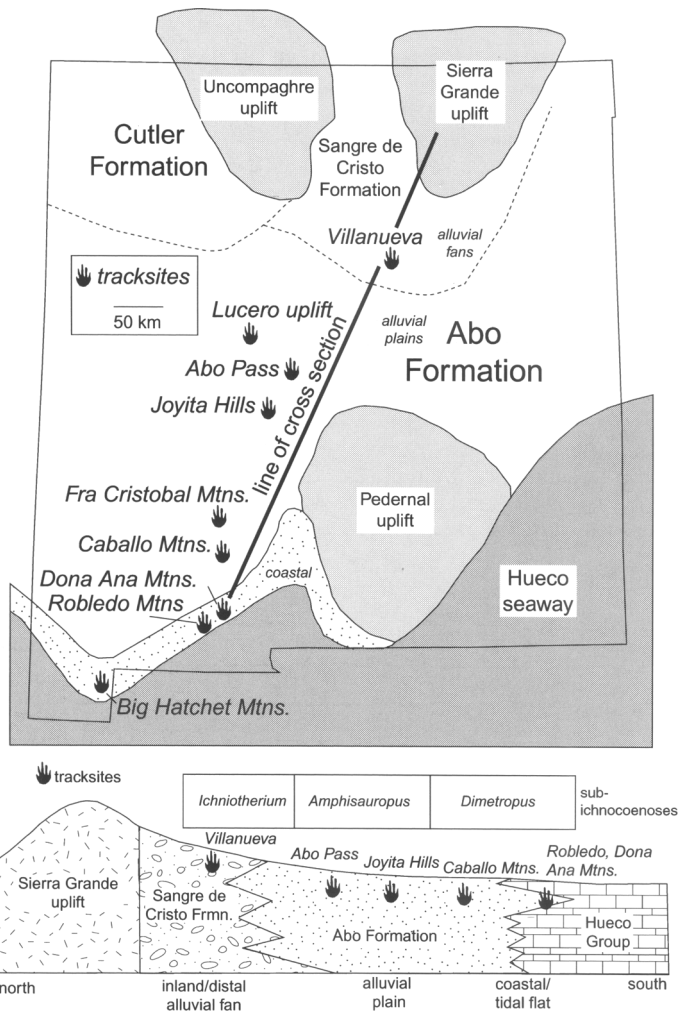


Fig. 3. Palaeogeographic map of New Mexico during the Early Permian and north-south transect of Early Permian red beds in New Mexico showing distribution of possible tetrapod sub-ichnocoenoses (from Lucas 2005a).

> 10%) of terrestrial carnivore tracks. This ichnofacies includes coastal plain-marine shoreline environments and some lacustrine shorelines and ranges from Middle Permian to Recent in age (Hunt & Lucas 2006). It includes the *Pachypes* ichnocoenosis of Middle to Late Permian age.

The *Characichnos* ichnofacies of Hunt & Lucas (2006) encompasses medium diversity ichnofaunas in which the majority of tracks are swimming traces (parallel scratch marks) and fish swimming trails (*Undichna*). This ichnofacies represents shallow lacustrine (and tidal) environments.

Footprint-based biostratigraphy is often confined to a given ichnofacies largely because each ichnofacies has its own ichnotaxonomy. Thus, although the same trackmakers may have made tracks in different lithofacies, the tracks are so different morphologically that they receive different ichnotaxonomic names. For this reason, we do not attempt footprint-based correlations between ichnoassemblages of the temporally overlapping aeolian *Chelichnus* and the water-laid *Batrachichnus* and *Brontopodus* ichnofacies. The *Characichnos* ichnofacies consists of swimming traces and is of no biostratigraphic significance.

Permian footprint distribution in space and time

North America

United States

In North America, tetrapod footprints of Permian age are found primarily in the western United States in Arizona, New Mexico and Texas, and some important sites are also known in the adjoining states of Utah, Colorado and Oklahoma (Fig. 4).

The *Chelichnus* ichnofacies in North America is best known from aeolian strata of the Coconino Sandstone in Arizona, although some other Permian aeolianites also yield tracks in Arizona, Utah, Colorado and New Mexico (Hunt & Lucas 2005a). Lull (1918) and Gilmore (1926, 1927, 1928) first described the Coconino tracks from the Grand Canyon of Arizona (where the widely used name *Laoporus* was introduced, although it is now recognized as a junior subjective synonym of *Chelichnus*), and Middleton *et al.* (1990) and Hunt *et al.* (2005a) provide a recent summary. The Coconino Sandstone is of late Leonardian age (Fig. 5). Note that it is directly overlain by marine strata of the late Leonardian Kaibab Formation (Hopkins 1990), and that the Coconino is homotaxial to the Leonardian Glorieta Sandstone of New Mexico and the San Angelo Formation of Texas (Middleton *et al.* 1990). In effect, Coconino dune fields were landward of the shorelines and coastal plains that deposited the Glorieta and San Angelo sediments during late Leonardian time.

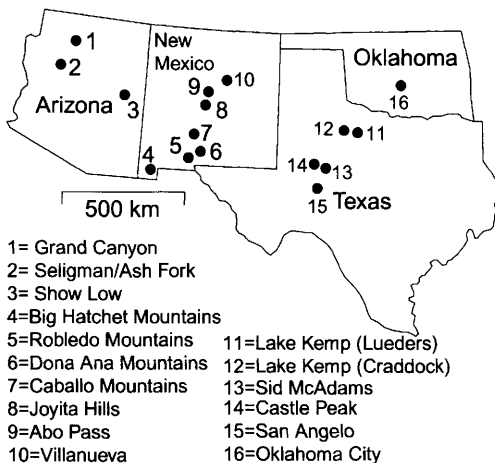


Fig. 4. Distribution of principal Permian tracksites in the western United States.

In the Lake Powell area of Utah, *Chelichnus* is known from the Wolfcampian Cedar Mesa Sandstone (Loope 1984; Lockley & Madsen 1993; Hunt & Lucas 2006), and in the Colorado Front Range it is known from the Leonardian Lyons Sandstone (e.g. Lockley & Hunt 1995). In Arizona, the early Leonardian DeChelly Sandstone (Blakey & Knepp 1989) yields *Chelichnus* and *Dromopus* (McKee 1934; Lockley *et al.* 1994, 1995; Morales & Haubold 1995; Haubold *et al.* 1995b). However, in New Mexico, mixed aeolian-fluvial facies of the DeChelly Sandstone yield *Amphisauropus*, *Dimetropus* and *Limnopus* (Lucas *et al.* 2005c).

In North America, the *Batrachichnus* ichnofacies is best understood in New Mexico, where numerous and extensive red-bed track assemblages of Early Permian age are known (see articles in Lucas & Heckert 1995; Lucas *et al.* 1998; Lucas *et al.* 2004; Hunt *et al.* 2005b) (Fig. 3). These assemblages are from red-bed ichnofacies of the Earp Formation (Big Hatchet Mountains), the Robledo Mountains Formation of the Hueco Group (Robledo, Doña Ana and San Andres Mountains), the Abo Formation (Caballo and Fra Cristobal Mountains, Joyita Hills, Abo Pass) and the Sangre de Cristo Formation (Villanueva) (Fig. 3). Relative abundances of the ichnotaxa vary between sites, but *Dromopus* and *Batrachichnus* dominate the ichnoassemblages, and co-occur primarily with *Dimetropus*, *Hyloidichnus* and *Limnopus* (e.g. Haubold 2000; Haubold & Lucas 2001a; Lucas *et al.* 2005a, c). Lucas *et al.* (2001) reported *Amphisauropus* and *Varanopus* from the Abo Pass tracksite, which is stratigraphically low in the Abo Formation (Fig. 5). *Ichnotherium* is present in some of the 'inland' assemblages in central and northern New Mexico (Hunt *et al.* 2005e).

Tracksites in the Sangre de Cristo and Abo formations are of Wolfcampian age, but a complete precise correlation and stratigraphical ordering of these sites has not yet been completed. Nevertheless, tracksites in the Robledo Mountains Formation in southern New Mexico are close in age to the Wolfcampian–Leonardian boundary (Kietzke & Lucas 1995; Lucas *et al.* 1995), whereas tracksites in the Caballo and Fra Cristobal Mountains and at Abo Pass are stratigraphically low in the Abo Formation and thus are of Mid-Wolfcampian age (Lucas *et al.* 2001, 2005a, b).

Various ichnogenera do vary stratigraphically. For example, *Batrachichnus* dominates tracksites stratigraphically low in the Abo Formation (Lucas *et al.* 2005a, b), whereas it is co-dominant with *Dromopus* at stratigraphically

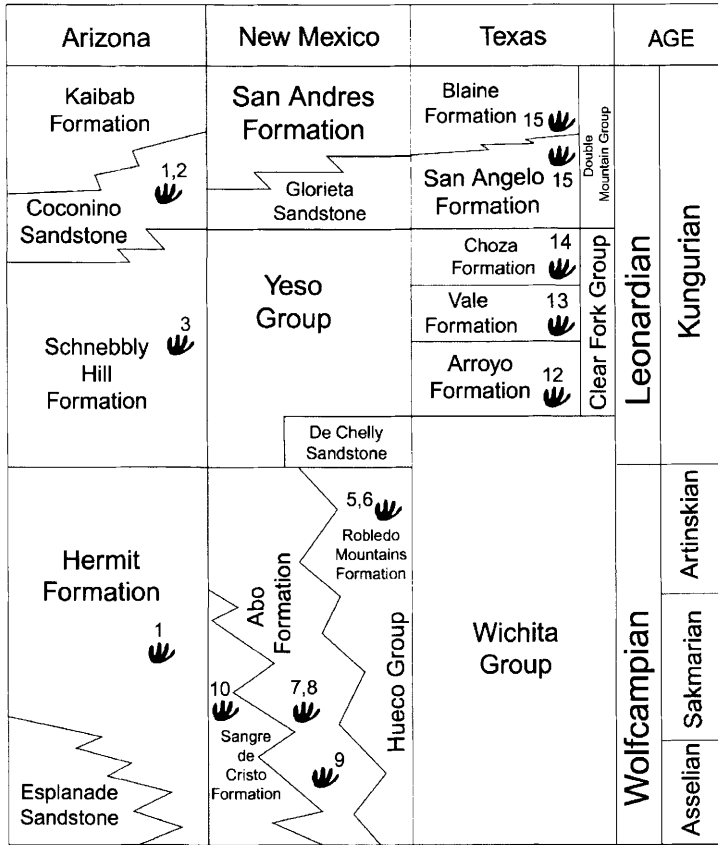


Fig. 5. Correlation of principal North American Permian tracksites.

higher sites. However, ichnogenic composition does not vary significantly through the Abo Formation. The New Mexican red-bed track record thus encompasses most or all of Wolfcampian time and belongs to a single biostratigraphic assemblage.

In Arizona, the Wolfcampian Hermit Formation (Shale) (Blakey & Knepp 1989) yields tetrapod tracks assigned to the ichnogenera *Batrachichnus*, *Hyloidichnus*, *Ichniotherium* and *Limnopus* (Haubold *et al.* 1995a; Hunt & Santucci 1998; Hunt & Lucas 2005a; Hunt *et al.* 2005a). The stratigraphically higher Wolfcampian Organ Rock Shale in Monument Valley, Arizona, yields *Dromopus* and '*Gilmoreichnus*' (Vaughn 1964; Haubold *et al.* 1995a). In central Colorado, the Wolfcampian Maroon Formation yields *Dimetropus*, *Ichniotherium*, *Tambachichnium*, and *Varanopus* (Voigt *et al.* 2005). Also, in the San Juan Mountains of Colorado, Wolfcampian strata of the Cutler Formation yield *Limnopus* (Baird 1965).

Much less is known of Leonardian-age tracks in North America. A single specimen of *Dimetropus* is known from the Leonardian Schnebbly Hill Formation near Show Low in Arizona (Haubold *et al.* 1995a). A locality in the lower part of the Hennessey Formation at Oklahoma City yields *Amphisauropus* and possible *Dromopus* (Lucas & Suneson 2002). In Texas, *Dimetropus* is known from the Leonardian Vale Formation at the Sid McAdams locality in Taylor County (Olson & Mead 1982; Lucas & Hunt 2005), and Dalquest (1963) reported large amphibian tracks (*Limnopus*?) from the Leonardian Lueders Formation near Lake Kemp in Baylor County.

The classic North American Leonardian tracksite is in the upper part of the Choza Formation at Castle Peak near Abilene, Texas (Moodie 1929, 1930). Haubold & Lucas (2001b, 2003) revised the ichnotaxonomy at Castle Peak, and it comprises *Erpetopus*, *Varanopus* and *Dromopus*. We have recently collected a tracksite

in the Arroyo Formation at Lake Kemp in Baylor County, Texas, and *Batrachichnus* dominates this assemblage, with fewer numbers of *Dromopus* and possible *Amphisauropus* (Lucas & Hunt 2005). Indeed, it might be tempting to suggest that *Erpetopus* and abundant *Varanopus* are characteristic of the Leonardian, although too few Leonardian age tracksites are known to confirm this. Furthermore, the Castle Peak and Lake Kemp tracksites are in playa and mudflat deposits of a broad, low relief coastal plain, quite different from the Wolfcampian tracksites in New Mexico, which come from strata that represent both inland floodplains (Sangre de Cristo and Abo formations) and coastal tidal flats (Robledo Mountains and Earp formations). Thus, the differences now perceived between Wolfcampian and Leonardian tetrapod tracks may be due to facies differences and not temporally significant.

The stratigraphically highest Permian tetrapod footprints from North America are in the San Angelo and Blaine formations at San Angelo, Tom Green County, Texas. Pittman *et al.* (1996) and Lucas & Hunt (2005) provided preliminary data on these tracks, which are large, indistinct tracks, possibly of a caseid pelycosaur, and rare *Amphisauropus*. The San Angelo and Blaine are late Leonardian in age (Fig. 5), and these youngest North American Permian tracks mirror the abundance of caseid pelycosaur seen in the San Angelo Formation body fossil fauna (e.g. Olson 1962). It is also interesting that the common Coconino (correlative to the San Angelo) ichnogenus *Chelichnus* has been thought by some to be a caseid track, so this may provide a link between the *Chelichnus* and *Batrachichnus* ichnofacies.

In the eastern United States, tetrapod footprints are known from the Wolfcampian interval of the Dunkard Group in southeastern Ohio (*Dromopus* and *Limnopus*: Haubold 1971; Cotton *et al.* 1995) and in northwestern West Virginia (Waynesburg Sandstone, *Dimetropus* and *Limnopus*: Tilton 1926, 1931; Romer & Price 1940; Baird 1952).

It is extremely important that much of the Permian tetrapod footprint record in the western United States can be cross-correlated with marine biostratigraphy with great confidence (e.g. Lucas 2002b; Haubold & Lucas 2003). Thus, intercalated or bracketing marine strata in southern New Mexico and Texas contain biostratigraphical indicators (fusulinaceans, conodonts and/or ammonoids) that allow the track record to be readily correlated to the North American provincial stages Wolfcampian and Leonardian (Fig. 5).

Canada

Early Permian track records of the *Batrachichnus* ichnofacies are known in Canada from Nova Scotia and Prince Edward Island. At Brule in Nova Scotia, red beds of the Cape John Formation (Pictou Group) yield an extensive assemblage that comprises *Amphisauropus*, *Dimetropus*, *Dromopus*, '?*Gilmoreichnus*', *Limnopus* and *Varanopus* (Van Allen *et al.* 2005). Fossil plants indicate an age of Stephanian–Autunian for the Cape John Formation.

Red beds of the Hillsborough Formation on Prince Edward Island yield assemblages that comprise *Amphisauropus*, '*Gilmoreichnus*', '*Ichniotherium*' and *Varanopus* (Mossman & Place 1989; Calder *et al.* 2004). Based on associated fossil plants, these are of late Autunian age. The Canadian record thus encompasses characteristic ichnogenera of the *Batrachichnus* ichnofacies in Lower Permian strata.

Europe

The European Permian tetrapod footprint record (Fig. 6) comes principally from three countries – Germany, France and Italy – although Lower Permian tracks are also known from the United Kingdom, Spain, Poland, and the Czech Republic (e.g. Haubold 1973, 1984). Most of these records, including those from the United Kingdom, Spain, Poland and the Czech Republic, are of characteristic ichnogenera of the *Batrachichnus* ichnofacies of Early Permian age (e.g. Haubold 1970, 1971, 1973; Haubold & Sarjeant 1973; Cassinis & Santi 2005) and are not reviewed here.

Recently described footprints from the Tumlin Sandstone in Poland of supposed Late Permian age (Ptaszyński & Niedźwiedzki 2004) are actually of Early Triassic age (Racki 2005). In Scotland, footprints of the *Chelichnus* ichnofacies are known from the Corncockle, Hopeman and Lochabriggs formations (e.g. McKeever & Haubold 1996). These units predate the Zechstein transgression and are probably of late Capitanian or early Wuchiapingian age.

Here, we focus on the three track records – from Germany, France and Italy – of greatest importance to building a Permian footprint biostratigraphy and biochronology. An important aspect of the European track record is how poorly most of it can be correlated to the standard global stratigraphic scale (SGCS). In general, age control is based on fossil plants, and we consider it imprecise and questionable in places.

Germany

In Germany, the most extensive Permian track records are from the Thuringian and the

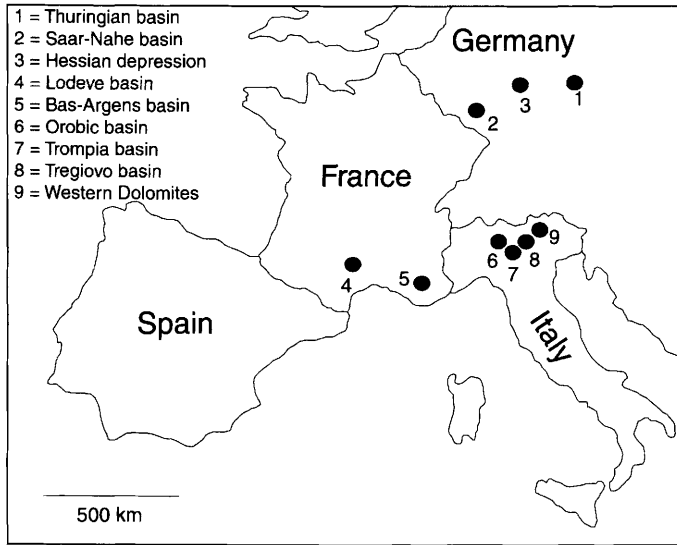


Fig. 6. Distribution of principal Permian tracksites in western Europe.

Saar–Nahe basins (Fig. 6). The Thuringian record, which is all assigned to the *Batrachichnus* ichnofacies, is of some historical significance, as one of the first known records of Permian footprints. Voigt (2005) has recently revised this record, and his revision indicates an essentially consistent tetrapod footprint assemblage from the Georgenthal through the Tambach formations, that is, from Late Pennsylvanian to Artinskian time (Fig. 7). This assemblage consists of *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus* and *Ichnoterium*. In Thuringia, the LO (lowest occurrence) of *Varanopus* is in the Oberhof Formation, whereas the LO of *Tambachichnium* is in the Goldlauter Formation. The Georgenthal–Tambach interval is assigned to the Gzhelian–Artinskian based on cockroach, selachian and amphibian biostratigraphy as well as Ar/Ar ages which indicate that the Oberhauf and Goldlauter formations are about 287–288 Ma (Roscher & Schneider 2005). The Thuringian record thus parallels the North American record by indicating an essentially uniform ichnoassemblage characteristic of the *Batrachichnus* ichnofacies from Late Pennsylvanian through most (or all) of the Early Permian.

In the Saar–Nahe Basin, tracks of the *Batrachichnus* ichnofacies are well known from the Glan and Nahe subgroups and have been extensively described by Fichter (1976, 1982, 1983a, b, 1984). The ichnogenera present are essentially the same as those in the

Thuringian Basin, and include *Amphisauropus*, *Batrachichnus*, *Hyloidichnus* and *Varanopus*.

Boy & Fichter (1988a, b) used the footprint record from the Saar–Nahe Basin as the principal basis for recognition of six successive tetrapod footprint zones that spanned the Permian (Fig. 8). These are the (in ascending order) *Protritonichnites lacertoides*, *Saurichnites incurvatus*, *Varanopus microdactylus*, *Anhomoiichnium*, *Harpagichnus* and *Rhynchosauroides* zones. Boy & Fichter (1988b, p. 882) claimed that ‘the biostratigraphic zonation of tetrapod tracks is not based on ecological and local climatic changes . . . but on large-scale faunal interchange across wide areas of Pangea’. Nevertheless, the biostratigraphical zonation of Boy & Fichter has been invalidated by taxonomic revision and further understanding of the stratigraphical distribution of Permian tetrapod footprint ichnogenera. Thus, their *Protritonichnites* is *Dromopus*, and what they termed *Anhomoiichnium* includes tracks now termed *Dromopus* and *Batrachichnus* (Haubold 1996). *Saurichnites incurvatus* of Boy & Fichter also is *Batrachichnus* (Haubold 1996). The zones are thus based on *Dromopus*, *Batrachichnus* and *Varanopus*, ichnogenera that routinely co-occur and have long stratigraphical ranges in the North American and the Thuringian Lower Permian sections. Furthermore, ‘*Harpagichnus*’ (= *Chelichnus*) is the dominant ichnogenus of the *Chelichnus* ichnofacies and is found in Permian aeolianites

Varanopus. Conchostracans and insects, as well as a U/Pb age of 284 ± 4 Ma from the Octon Member suggest it is either Artinskian or Kungurian in age (Gand *et al.* 1997; Bethoux *et al.* 2002; Roscher & Schneider 2005).

In contrast, the track assemblage of the La Lieude Formation (or member of the Salagou Formation of some authors), which is stratigraphically higher, above the Merifons Member of the Salagou Formation (Fig. 7), is quite distinctive. It encompasses the ichnogenera *Brontopus*, *Dromopus*, *Lunaepes*, *Merifontichnus*, and *Planipes*, which are mostly the tracks of therapsids. Roscher & Schneider (2005) assign the La Lieude Formation a Wuchiapingian age, linking it to the Zechstein and Bellerophon transgressions. Indeed, the footprint assemblage of the La Lieude Formation has much in common with that of the Wuchiapingian Val Gardena Sandstone in Italy (see below), so we assign it a Wuchiapingian age (Fig. 7).

The other biostratigraphically important French track record comes from the Bas-Argens Basin in southeastern Provence (Gand *et al.* 1995). Low in this section, a few tracks (*Dromopus*, *Varanopus*) are known from the Bayonne Formation, which is of probable Artinskian or Kungurian age. The overlying Pradinaux Formation yields a much more extensive track assemblage of the ichnogenera '*Chelichnus*', *Hyloidichnus*, *Lunaepes*, *Planipes*, *Pseudosynaptichnium*, *Tambachichnium* and *Varanopus*. The stratigraphically highest track assemblage is from the La Motte Formation: *Batrachichnus*, *Dromopus*, '*Dimetropus*', *Hyloidichnus*, '*Laoporus*', *Limnopus* and *Varanopus*.

The key age indicator in this succession is the so-called 'A7 rhyolite', which is unconformably overlain by the Pradinaux Formation. The latest and most reliable age estimate for the rhyolite is an Ar/Ar age of 272.5 ± 0.3 Ma (Zheng *et al.* 1992), which is Late Kungurian on the standard global chronostratigraphic scale. Durand (2006) reviews age indicators for the Pradinaux Formation, which are megafossil plants, palynomorphs and ostracodes, to conclude that a Wordian age is most likely, although our reading of the age data indicates it could be younger. The overlying LeMuy Formation appears on a palaeobotanical basis to be of Zechstein (Wuchiapingian?) age.

Thus, in France, the Lower Permian strata produce track assemblages dominated by *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Limnopus* and *Varanopus*. A stratigraphically much higher level in the Lodève Basin at La Lieude yields therapsid tracks, among others, and compares well with the Upper Permian ichnoassociation from Italy (see below).

The Pradinaux Formation footprint assemblage may be of Wordian or slightly younger age, but an Artinskian age, as claimed by Haubold & Lucas (2003) seems highly unlikely. This means that the oldest Permian footprint assemblage with therapsid tracks is the Pradinaux assemblage.

Italy

In the Southern Alps of northern Italy (Fig. 6), Permian tetrapod tracks are found at two disparate stratigraphic intervals. The lower interval encompasses the Collio and Tregiovo formations in the Orobic, Val Trompia and Tregiovo basins. The younger interval is the Val Gardena (Gröden) Sandstone in the Western Dolomites. Avanzini *et al.* (2001) and Cassinis & Santi (2005) provide the most recent reviews of these assemblages in their stratigraphic context.

The Collio Formation in the Orobic basin yields *Amphisauropus*, *Batrachichnus*, *Dromopus* and *Varanopus* as well as '*Camunipes*' and '*Ichniotherium*' (Nicosia *et al.* 2000; Santi & Krieger 2001). In the Val Trompia Basin, the Collio Formation tracks have been assigned to *Amphisauropus*, *Batrachichnus*, '*Camunipes*', *Dromopus*, *Ichniotherium* and *Varanopus* (Geinitz 1869; Curioni 1870; Berruti 1969; Ceoloni *et al.* 1987; Conti *et al.* 1991; Avanzini *et al.* 2001). Megafossil plant and palynomorph data indicate that the Collio Formation is of Early Permian age, either Artinskian or Kungurian. Furthermore, in the Val Trompia Basin, Schaltegger & Brack (1999) reported U–Pb zircon ages of 283 ± 1 Ma and 280.5 ± 2 Ma for the rhyolitic ignimbrites that bracket the Collio Formation. These are Artinskian ages on the current time scale (Fig. 7).

In the Tregiovo Basin, *Dromopus* has been reported from stratigraphically low in the Tregiovo Formation. Age assignments for the Tregiovo Formation based on megafossil plants and palynomorphs range from Kungurian to Ufimian. Thus, Italian ichnologists perceive the Tregiovo Formation tracks to be slightly younger than those of the Collio Formation, but to still represent one 'ichnoassociation' (e.g. Conti *et al.* 1997; Avanzini *et al.* 2001). We agree, and conclude the data best support an Artinskian–Kungurian age for this ichnoassociation.

In the Western Dolomites, an extensive track assemblage of the *Brontopodus* ichnofacies is known from the Val Gardena Sandstone (principal locality is Bletterbach Gorge) (Leonardi & Nicosia 1973; Leonardi *et al.* 1975; Conti *et al.* 1977, 1991; Nicosia *et al.* 2001). The principal ichnogenera documented are *Pachypes*, *Dicynodontipus*, *Rhynchosauroides* and *Varanopus*. The Val Gardena Sandstone interfingers with and is

overlain by the marine Bellerophon Formation, which is of Wuchiapingian age (Ceoloni *et al.* 1988). This is a rare European example where a direct correlation of the tracks to the SGCS is possible. Thus, the upper 'ichnoassociation' of the Italian section (Avanzini *et al.* 2001) is fundamentally different from the lower 'ichnoassociation' in having tracks of therapsids and pareiasaurs. There is also a substantial temporal gap between the two ichnoassociations, equal to at least the entire Guadalupian (e.g. Cassinis *et al.* 2002; Lucas 2002b).

Russia

Despite the extensive outcrop area of non-marine Permian strata in Russia, few tetrapod track records have been documented. Lucas *et al.* (1999) reported a handful of tetrapod footprints (assigned to cf. *Dromopus* and cf. *Dimetropus*) from Early Permian red beds of the Caucasus. Tverdokhlebov *et al.* (1997) described red-bed tracks assigned to *Batrachichnus* from the Upper Tatarian of Russia, and Gubin *et al.* (2001) mentioned apparent pareiasaur tracks, also from the Upper Tatarian.

South America

Brazil

Leonardi (1987, 1994) reported tetrapod swimming traces (*Characichnos* ichnofacies) from the Rio do Rastro Formation at Tonetti in Paraná State, Brazil. This record, which Leonardi (1994, p. 46) correctly termed 'unclassifiable', is of Mid- or Late Permian age (the age of the Rio do Rastro Formation: Cisneros *et al.* 2005), but is of no biostratigraphical significance at present

Argentina

Melchor (2001) described Permian tetrapod footprints from Argentina in the Carapacha Basin (*Batrachichnus* ichnofacies tracks assigned to *Batrachichnus*, *Hylodichnus* and 'cf. *Gilmoreichnus*') and the eastern Permian basin (*Chelichnus* ichnofacies tracks assigned to *Chelichnus*). Melchor (2001) suggested these records are of Late Permian age, but both records are more probably older. The Argentinian track record is significant because it suggests the presence in southern Gondwana during the Early to early Middle Permian of some of the characteristic ichnogenera of the *Batrachichnus* and *Chelichnus* ichnofacies.

In the Carapacha Basin of La Pampa Province, tetrapod footprints of the *Batrachichnus* and *Characichnos* ichnofacies are found in the Urre-Lauquen Member of the Carapacha Formation (Melchor 2001; Melchor & Sarjeant

2004). These have been assigned to *Batrachichnus*, *Hylodichnus*, cf. *Amphisauropus* and cf. *Varanopus* and also include swimming traces assigned to *Characichnos*. Melchor (2001) and Melchor & Sarjeant (2004) claimed that the associated palaeoflora indicates an 'early Late Permian age', which means Kazanian on the time scale that they used. However, this palaeoflora lacks any tie to a marine time scale and, as Melchor & Cesari (1997, p. 628) stated, it 'could have been deposited during the Late Permian' (our italics). Indeed, this is the 'Golondrinian' palaeoflora of Archangelsky & Cúneo (1984), which is younger than their 'Lubeckian' palaeoflora of Argentina. The Lubeckian palaeoflora has some direct ties to marine biostratigraphy that indicate it ranges in age from about Asselian to Sakmarian. However, the Golondrinian palaeoflora lacks such ties and is thought to begin in the Artinskian with an uncertain upper age limit (Archangelsky & Cúneo 1984).

In the eastern Permian basin of Mendoza Province, footprints of *Chelichnus* are present in the Areniscas Atigradas Member of the Yacimiento Los Reyunos Formation (Melchor 2001). A tuff below the tracks has been $^{40}\text{Ar}/^{39}\text{Ar}$ dated at ~266 Ma, although the scatter of single crystal ages from the tuff ranges from 263 to 269 Ma (Melchor 2000). Based on the age, Melchor (2001) concluded that the tracks are no older than Wordian (Kazanian). However, given the scatter of single crystal ages they could be as old as Roadian. If these tracks actually are Roadian or Wordian (they could be younger), they are one of the few known Middle Permian track records (Fig. 9).

Africa

Morocco

One Pennsylvanian and three Permian footprint records have been documented from Morocco. Hmich *et al.* (2006) report *Batrachichnus* and *Dromopus* from the El Menizla Formation of the Ida Ouzal Sub-Basin of the Souss Basin. Based on cockroach biostratigraphy, they assign this record a Stephanian B (late Kasimovian/middle Gzhelian) age.

Hmich *et al.* (2006) also document *Limmopus*, cf. *Batrachichnus* and *Dromopus* from 'unit B' in the Khenifra Basin. Based on the palaeoflora (Broutin *et al.* 1998), this occurrence is assigned a Kungurian (Autunian) age.

The 'upper formation' in the Tiddas Basin yielded tetrapod tracks assigned to 'Amphisauroides', 'Gilmoreichnus' and *Hylodichnus* (El Wartiti *et al.* 1986; Broutin *et al.* 1987; Larhrib

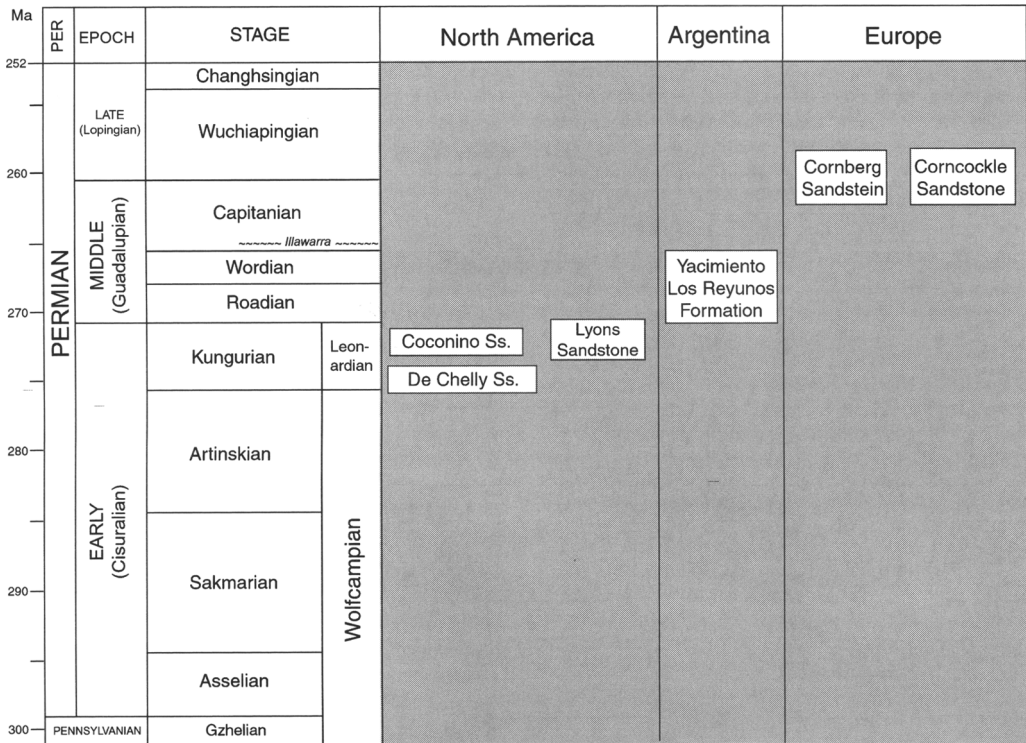


Fig. 9. Global correlation of selected Permian tetrapod tracksites of the *Chelichnus* ichnofacies.

1996). However, only the record of *Hyloidichnus* can be confirmed (Hmich *et al.* 2006). This record is also assigned a Kungurian age based on palaeoflora (Broutin *et al.* 1998).

Tracks assigned to *Synaptichnium* and *Rhynchosaurooides* have been reported from the Tourbihine Member (T2) of the Ikakern Formation in the Argana Basin (Jones 1975; Hmich *et al.* 2006). Tetrapod body fossils from this unit have been assigned a Kazanian age (Jalil & Dutuit 1996), but Hmich *et al.* (2006) correlate this record to the Wuchiapingian 'wet phase', which essentially equates it to the Val Gardena Sandstone in northern Italy.

Thus, the Moroccan record indicates typical *Batrachichnus* ichnofacies in Upper Pennsylvanian to Lower Permian strata. A much younger ichnoassemblage is present in strata of probable Wuchiapingian age.

South Africa

A substantial record of tetrapod footprints apparently is present but largely undocumented in Mid-Upper Permian strata in the Karoo Basin of South Africa (e.g. Seeley 1904; Smith 1993; Ward 2004). These are primarily tracks of

pareiasaurs, dinocephalians and dicynodonts and should be further studied and compared to the Middle and Upper Permian tracks from France and northern Italy, which they resemble. The track record from South Africa, once documented, should fill much of the Middle Permian global gap in the tetrapod footprint record.

Correlations

Chelichnus ichnofacies

The Permian *Chelichnus* ichnofacies is of the same ichnogeneric composition at all sites. The fact that Permian units of disparate ages, such as the Coconino and DeChelly formations in the United States, the Corncockle and Lochabriggs sandstones in Scotland, the Cornberg Sandstein in Germany and the Yacimiento Los Reyunos Formation in Argentina, have similar tetrapod ichnofossils is a reflection of shared ichnofacies, not of precise age equivalence (Fig. 9). Tetrapod footprints of the aeolian ichnofacies are thus of no biostratigraphical value as presently understood.

The aeolian trackmakers may have been some of the same animals as the red-bed trackmakers, and indeed one ichnogenus, *Dromopus*, is found in both ichnofacies. Furthermore, lithofacies transitional between aeolian and fluvial of the DeChelly Sandstone in central New Mexico yield typical *Batrachichnus* ichnofacies tracks, such as *Amphisauropus*, *Dimetropus* and *Limnopus* (Lucas *et al.* 2005a). But, in general, the aeolian track assemblages cannot be directly compared and correlated with the red-bed tracks: the tracks of both ichnofacies are too different in morphology.

Early Permian *Batrachichnus* ichnofacies

Tetrapod footprints of the Early Permian *Batrachichnus* ichnofacies are of broad, uniform composition, and ichnodiversity is much higher than in the *Chelichnus* ichnofacies. The following ichnogenera dominate: *Amphisauropus*, *Batrachichnus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Ichniotherium*, *Limnopus* and *Varanopus*. This assemblage is the tracks of temnospondyls, diadectomorphs, seymouriamorphs, captorhinomorphs and pelycosaur (Table 1). The North American record demonstrates that most (if not all) of these ichnogenera have long stratigraphical ranges through most or all of Wolfcampian and Leonardian time (Haubold & Lucas 2001a, b; Lucas 2002b). Furthermore, at the Robledo Mountains megatracksite in southern New Mexico, all of these ichnogenera (except *Varanopus* and *Ichniotherium*) co-occur in a single, short stratigraphical interval. This suggests that local biostratigraphical zonations based on these ichnotaxa, especially those proposed in Germany and France, are not of global applicability and may also be of questionable local or regional utility. Thus, the Early Permian *Batrachichnus* ichnofacies yields a single biostratigraphical assemblage of tetrapod footprints found in the United States, Canada, Argentina, Germany, France, Italy, Russia and some other places in Europe (Fig. 10).

Middle to Late Permian Brontopodus ichnofacies

The Middle to Late Permian record of tetrapod footprints in water-laid facies is less extensive than but shows significant differences from the Early Permian record. This is a record dominated by the tracks of therapsids. Pareiasaur (*Pachypes*) and eosuchian tracks (*Rhynchosauroides*) also are diagnostic of this record. It is best known from Italy and France, and South African and Russian records demonstrate a

broad distribution of this biostratigraphical assemblage. Its oldest occurrence appears to be Wordian, but most records are younger, of Capitanian–Wuchiapingian age.

Global gap

There is a stratigraphical gap in the global Permian tetrapod footprint record. This is the gap between the youngest Early Permian track records, which are as young as Kungurian, and the oldest well-documented Late Permian records, which are no older than Wordian. This gap, approximately equivalent to the Roadian, is approximately the same duration as the corresponding mid-Permian gap in the tetrapod body fossil record, which also approximately equals Roadian time (Lucas 2001, 2002c, 2004).

There are only a few described footprint assemblages that may fill this gap. The Pradinaux Formation assemblage in France is the key assemblage, as it documents the LO of therapsid tracks. We now accept the Pradinaux Formation assemblage as tentatively of Wordian age. Older age assignments (e.g. Haubold & Lucas 2003) seem unlikely, but an age as young as Wuchiapingian cannot be ruled out.

Global biostratigraphy and biochronology

An important question to ask of the Permian footprint record is how many useful biostratigraphic datum points can be identified? On a global basis, we believe there are only two: (1) the highest occurrence (HO) of pelycosaur tracks; and (2) the LO of therapsid tracks. Thus, we see no important biostratigraphical datum points within the Lower Permian record, as it consists of tracksites that yield the standard Early Permian ichnogenera that form a single, Lower Permian biostratigraphical assemblage that actually occurs in the Pennsylvanian as well. The HO of pelycosaur tracks is in assemblages that are no younger than Kungurian on the SGCS. Therefore, note that we reject the identification as *Dimetropus* by Demathieu *et al.* (1992) of some tracks from Middle Permian strata in the French Bas-Argens Basin.

The LO of therapsid tracks appears to be in the Pradinaux Formation of the Bas-Argens Basin in France. If this unit is of Wordian age, not younger, then the LO of therapsids in the track and body fossil record is essentially synchronous, or Wordian (Lucas 2004).

If we construct a global biochronology based on tetrapod footprints, it contains only two time intervals (Fig. 10). Lucas (2002b) recognized these same intervals, but believed the gap

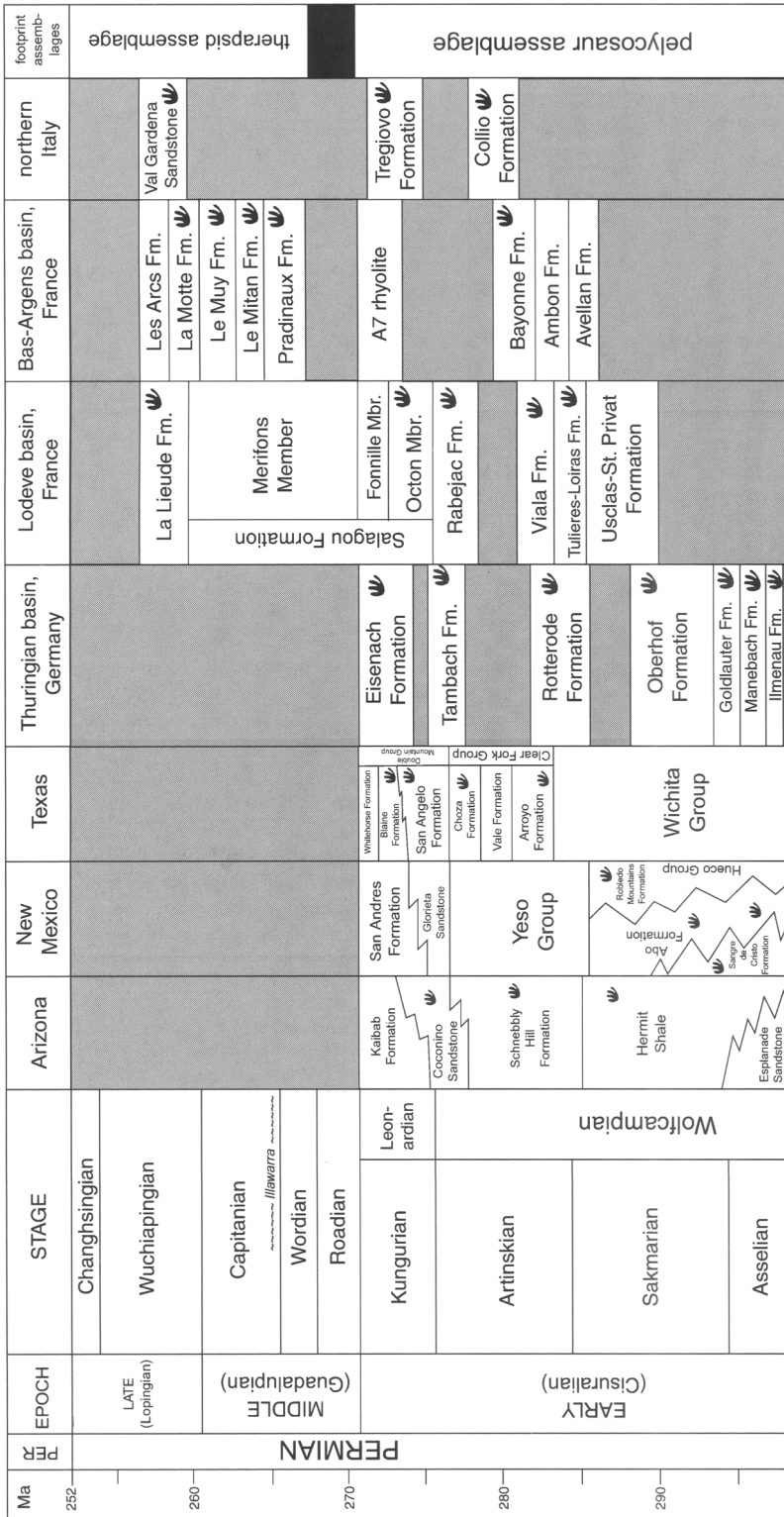


Fig. 10. Global correlation of selected Permian tetrapod tracksites of the *Batrachichnus* and *Brontopodus* ichnofacies.

between them to be longer than we indicate here. He named these two intervals the *Dromopus* and *Rhynchosauroides* biochrons, and noted that the *Dromopus* biochron has a temporal range of Pennsylvanian through Early Permian, and *Rhynchosauroides* has a temporal range of Late Permian through Late Triassic. However, this needs to be modified, as *Dromopus* does have records in the Middle and possibly Late Permian. Furthermore, *Rhynchosauroides* has its LO in Wuchiapingian strata, much younger than the LO of therapsid tracks. Therefore, we propose to identify a global Permian footprint biostratigraphy as consisting of a Lower Permian pelycosaur assemblage and a Middle–Upper Permian therapsid assemblage. Tetrapod footprints thus only discriminate two intervals of Permian time (Fig. 10).

In contrast, tetrapod body fossils can be used to discriminate about ten intervals of Permian time (Lucas 2002a, 2005b, 2006). Therefore, the tetrapod track record only resolves Permian time about 20% as well as does the tetrapod body fossil record. It thus represents an excellent example of the low biochronological resolution provided by tetrapod footprints (Lucas 1998).

We have benefited immensely in our studies of Permian tetrapod footprints from the collaboration and advice of J. Calder, H. Haubold, A. Lerner, M. Lockley and J. MacDonald. Reviews by J. Calder, M. Lockley, S. Voigt and an anonymous reviewer improved the content and clarity of the manuscript.

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