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Late Permian (Lopingian) terrestrial ecosystems: A global comparison with new data from the low-latitude Bletterbach Biota

Massimo Bernardi[a,b,*], Fabio Massimo Petti[a,c], Evelyn Kustatscher[d,e], Matthias Franz[f], Christoph Hartkopf-Fröder[g], Conrad C. Labandeira[h,i,j], Torsten Wappler[k], Johanna H.A. van Konijnenburg-van Cittert[l], Brandon R. Peecook[m], Kenneth D. Angielczyk[m]

[a] MUSE - Museo delle Scienze di Trento, Corso del Lavoro e della Scienza 3, 38123 Trento, Italy
[b] School of Earth Sciences, University of Bristol, Bristol, BS81RJ, UK
[c] PaleoFactory, Dipartimento di Scienze della Terra, Sapienza Università di Roma, Piazzale Aldo Moro, 5I-00185 Rome, Italy
[d] Museum of Nature South Tyrol, Bindergasse/Via Bottai 1, 39100 Bozen/Bolzano, Italy.
[e] Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität and Bayerische Staatssammlung für Paläontologie und Geobiologie, Richard-Wagner-Straße 10, 80333 München, Germany.
[f] Geowissenschaftliches Zentrum der Universität Göttingen, Abteilung Angewandte Geologie, Goldschmidtstraße 3, 37077 Göttingen, Germany
[g] Geologischer Dienst Nordrhein-Westfalen, De-Greiff-Straße 195, 47803 Krefeld, Germany
[h] Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA
[i] Department of Entomology and BEES Program, University of Maryland, College Park, MD 20742, USA
[j] College of Life Sciences, Capital Normal University, Beijing 100048, China
[k] Hessisches Landesmuseum Darmstadt, 64283 Darmstadt, Germany
[l] Laboratory of Palaeobotany and Palynology, Budapestlaan 4, 3584 CD Utrecht and Naturalis Biodiversity Center, PO Box 9517, 2300RA Leiden, The Netherlands
[m] Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605-2496, USA

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ABSTRACT

The late Palaeozoic is a pivotal period for the evolution of terrestrial ecosystems. Generalised warming and aridification trends resulted in profound floral and faunal turnover as well as increased levels of endemism. The patchiness of well-preserved, late Permian terrestrial ecosystems, however, complicates attempts to reconstruct a coherent, global scenario. In this paper, we provide a new reconstruction of the Bletterbach Biota (Southern Alps, NE Italy), which constitutes a unique, low-latitude record of Lopingian life on land. We also integrate floral, faunal (from skeletal and footprint studies), and plant–insect interaction data, as well as global climatic interpretations, to compare the composition of the 14 best-known late Permian ecosystems. The results of this ecosystem-scale analysis provide evidence for a strong correlation between the distribution of the principal clades of tetrapod herbivores (dicynodonts, pareiasaurs, captorhinids), phytoprovinces and climatic latitudinal zonation. We show that terrestrial ecosystems were structured and provincialised at high taxonomic levels by climate regions, and that latitudinal distribution is a key predictor of ecosystem compositional affinity. A latitudinal diversity gradient characterised by decreasing richness towards higher latitudes is apparent: mid- to low-latitude ecosystems had the greatest amount of high-level taxonomic diversity, whereas those from high latitudes were dominated by small numbers of higher taxa. The high diversities of tropical ecosystems stem from their inclusion of a mixture of late-occurring holdovers from the early Permian, early members of clades that come to prominence in the Triassic, and contemporary taxa that are also represented in higher latitude assemblages. A variety of evidence suggests that the Permian tropics acted as both a cradle (an area with high origination rates) and museum (an area with low extinction rates) for biodiversity.

1. Introduction

The late Palaeozoic is a pivotal time interval for the evolution of terrestrial ecosystems. A generalised aridification trend, best documented in Europe and North America (Chumakov and Zharkov, 2002; Roscher and Schneider, 2006), shows a transition from hygrophytic,

everwet communities to xerophytic, seasonally dry ones (e.g., DiMichele et al., 2001; Looy et al., 2014). For plants, this transition triggered a replacement of older Palaeozoic lineages by more modern Mesozoic groups (e.g., DiMichele et al., 2001; Looy et al., 2014), and the development of the four phytogeographic provinces of Gondwana, Cathaysia, Euramerica and Angara (Meyen, 1982; Archangelsky, 1990; Ziegler, 1990; Wagner, 1993). Tetrapod faunas experienced a major changeover, most famously with the gross compositional change from those dominated by basal synapsids ('pelycosaurs') to those dominated by non-mammalian therapsids, such as Anomodontia, Gorgonopsia, and Cynodontia (e.g., Brocklehurst et al., 2017; Angielczyk and Kammerer, in press and ref. therein). Moreover, this period saw the diversification of parareptiles (Tsuji and Müller, 2008; Ruta et al., 2011; Benton, 2016), and the radiation of diapsid reptiles (Müller and Reisz, 2006; Reisz et al., 2011), including the emergence of archosauriforms (Ezcurra et al., 2014; Bernardi et al., 2015).

Late Permian ecosystems generally are considered to be more ecologically integrated than those of the early Permian, at least in terms of the number of trophic levels (Olson, 1966; Benton, 2012). However, the dynamics of both floral and faunal turnover are still poorly understood. The transition from Palaeozoic to Mesozoic plant groups, for example, seems to be globally diachronous (Knoll, 1984; DiMichele et al., 2001; Looy et al., 2014), and late Permian vertebrate communities have been described as highly homogeneous across the whole of Pangaea (Sues and Boy, 1988; Rage, 1988; Milner, 1993; Dilkes and Reisz, 1996; Sues and Munk, 1996) to moderately endemic (Modesto et al., 1999; Modesto and Rybczynski, 2000; Angielczyk and Kurkin, 2003; Sidor et al., 2005; Angielczyk, 2007). Although new discoveries (e.g., Angielczyk and Sullivan, 2008; Smith et al., 2015; Huttenlocker et al., 2015; Benton, 2016; Huttenlocker and Sidor, 2016) and macroevolutionary studies (e.g., Fröbisch, 2009; Sidor et al., 2013) are contributing to a new and more comprehensive picture of late Permian terrestrial life, the geographic patchiness of well-preserved Lopingian ecosystems complicates attempts to outline a coherent, global scenario. Furthermore, a deep understanding of Permian terrestrial ecosystems is especially relevant because this time interval precedes the most severe biotic crisis of Earth history, the end-Permian mass extinction (Benton and Twitchett, 2003).

Lopingian tetrapod faunas, yielding skeletal and/or footprint remains, are known from Scotland (Benton and Walker, 1985), Great Britain and Germany (Benton and Walker, 1985; Sues and Boy, 1988), Poland (Ptaszyński and Niedźwiedzki, 2004; though its age is controversial, see Bachman and Kozur, 2004; Nawrocki et al., 2005; Racki, 2005), Italy (Conti et al., 1977), Morocco (Jalil and Dutuit, 1996; Voigt et al., 2010; Hminna et al., 2012), Tunisia (Newell et al., 1976), Malawi (Haughton, 1926; Jacobs et al., 2005; Kruger et al., 2015), Mozambique (Latimer et al., 1995; Castanhinha et al., 2013), Tanzania (Gay and Cruickshank, 1999; Sidor et al., 2010; Angielczyk et al., 2014a), Zimbabwe (Bond, 1973; Gaffney and Mc Kenna, 1979), Zambia (Drysdall and Kitching, 1963; Kemp, 1976; Lee et al., 1997; Angielczyk et al., 2014b), Niger (Sidor et al., 2005; Smith et al., 2015), South Africa (MacRae, 1990; Smith, 1993a, 1993b; De Klerk, 2002; Ward et al., 2005; Rubidge, 2005; Smith et al., 2012; Rubidge et al., 2016), Madagascar (Mazin and King, 1991; Schoch and Milner, 2000), Brazil (Battail, 2000; Langer, 2000; Dias-da-Silva, 2012; Costa da Silva et al., 2012; Boos et al., 2013), India (Kutty, 1972; Ray, 1999, 2000; Ray and Bandyopadhyay, 2003; Kammerer et al., 2016), China (Li and Cheng, 1995a, 1995b; Lucas, 2001; Metcalfe et al., 2009; Liu, 2013; Liu et al., 2014), Laos (Battail, 2000, 2009) and Russia (Ivakhnenko et al., 1997; Gubin et al., 2003; Benton et al., 2004; Surkov et al., 2007). Plant fossil assemblages have been described from the Germanic Basin (mostly Germany and England; e.g., Stoneley, 1958; Haubold and Schaumberg, 1985; Schweitzer, 1986; Uhl and Kerp, 2002 and ref. therein), Italy (e.g., Visscher et al., 2001; Kustatscher et al., 2012, 2014); Oman and Jordan (Berthelin et al., 2003; Kerp, 2006; Hamad et al., 2008), China (Sun, 2006; Deng et al., 2009), Brazil (Archangelsky, 1986; Rohn and

Rösler, 1989, 2000; Langer et al., 2008), Antarctica (McLoughlin et al., 1997; Manus et al., 2002), South Africa (Anderson and Anderson, 1985; Prevec et al., 2009, 2010), Laos (Bercovici et al., 2012), and Australia (Beattie, 2007). Notably, the lack of plant and animal fossil co-occurrence, or alternatively their extremely low diversity, prevents the full reconstruction of terrestrial ecosystems for most of these sites. Complex and structured terrestrial ecosystems have been reconstructed so far only from South Africa (Karoo Basin; e.g., Gastaldo et al., 2005; Prevec et al., 2009, 2010; Nicolas and Rubidge, 2010; Smith et al., 2012), Russia (Southern Urals; e.g., Benton et al., 2004; Sahney and Benton, 2008) and China (Ordos and Yunggur Basins; Lucas, 2001), although co-occurring plant and animal remains are available also from other sites (see below).

Even when floral and faunal data are available for ecosystem reconstruction, vertebrates have generally received considerably more attention and more integrated studies have seldom been performed. For example, an approach developed by Roopnarine and colleagues (Angielczyk et al., 2005; Roopnarine et al., 2007; Roopnarine, 2009; Roopnarine and Angielczyk, 2012, 2015, 2016) focuses on trophic interactions between animals while reducing primary producers to units of productivity necessary to support the system. Perhaps the most direct research on Permian plant–animal interactions comes from studies of the trophic relationships between herbivorous terrestrial arthropods and vascular plants. These studies span the early Permian of Texas (Schachat et al., 2014, 2015; Schachat and Labandeira, 2015); the early and middle Permian of southeastern Brazil (Adami-Rodrigues et al., 2004a, 2004b); the late Permian to late Triassic of the Karoo Basin of South Africa (Prevec et al., 2009, 2010; Labandeira et al., 2017) and the early Permian to Middle Triassic of the Dolomites, northeastern Italy (Wappler et al., 2015; Labandeira et al., 2016). The patterns emerging from this research provide an important baseline for understanding changes in plant-animal interactions across the Permo-Triassic transition.

The palaeogeographic configuration of the late Permian identifies three great continental masses that are principally distributed at the mid-latitudes (Gondwana, Laurussia and Siberia), joined together into a quasi-continuous supercontinent (Pangaea), bordered to the east by a series of islands (Cathaysia) and the Tethys Ocean (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). Climate has been suggested as the main controlling factor of biogeographic and phytogeographic distributions under this continental configuration (Ziegler, 1990; Rees et al., 2002; Sidor et al., 2005), and long- and short-term climate changes have been investigated for this interval using fossil floras, climate-sensitive rocks, and modelling (Cuneo, 1996; Fluteau et al., 2001; Rees, 2002; Rees et al., 2002; Roscher et al., 2008, 2011; Wopfner and Jin, 2009; Schneebeli-Hermann, 2012).

In this paper we provide a new, comprehensive reconstruction of the Bletterbach Biota (Lopingian of Southern Alps, NE Italy), and we review and discuss the other 13 best-known Lopingian terrestrial associations containing both vertebrate (documented by skeletal and footprint data) and plant remains, with the ultimate goal of providing the most complete analysis of late Permian ecosystems worldwide. Given the limited amount of data available on Lopingian low latitude terrestrial ecosystems (cf. Sidor et al., 2005), we suggest that the Bletterbach ecosystem constitutes a unique record that is a key reference for global studies. By integrating floral, faunal and climatic global interpretations, we discuss the composition of late Permian ecosystems and provide evidence for a strong correlation between the distribution of the main herbivorous tetrapod groups (dicynodonts, pareiasaurs, captorhinids), phytoprovinces and climatic latitudinal zonation.

2. Late Permian climates and terrestrial ecosystems

The progressive trend towards drier climates during the late Palaeozoic had its most dramatic effect in the continental interior and

at mid-latitudes, resulting in semi-arid to arid conditions and strongly seasonal precipitation patterns (e.g., Kerp, 2000; Roscher and Schneider, 2006; Montañez et al., 2007; Roscher et al., 2008, 2011). This is well expressed in the geological record, such as by the thick evaporite sequences of the German Zechstein Basin and the redbed sequence of the Lodève Basin (Schneider et al., 2006). However, the aridification process did not affect all landmasses the same way. In the tropics, for example, this trend was interrupted by several wet phases during the Cisuralian (early Permian) and at least one major wet interval in the Lopingian (Wuchiapingian: Roscher et al., 2008; Schneider et al., 2006). Furthermore, Pangaea was divided into different palaeo-climatic zones. Palaeofloristic data from the Wordian (middle Permian) (Rees et al., 1999, 2002) testify to the presence of a tropical "summerwet" area (in their terminology – here we will refer to "wet" or "dry" climates in the tropics given the absence of true seasons) on both sides of the equator and along the southern margin of the northern arm of Pangaea. This climate zone was surrounded by a desert zone extending slightly beyond 30° north and south. To the north followed the winterwet zone, the warm temperate zone, the cool temperate zone (up to 60°N) and finally the cold temperate zone. Proceeding south from the desert zone was the mid-latitude desert zone, the warm temperate zone, the cool temperate zone and finally the cold temperate zone. Late Permian climate models (Kutzbach and Ziegler, 1993; Fluteau et al., 2001; Roscher and Schneider, 2006; Roscher et al., 2008, 2011) depict similar scenarios with Central Pangaea dominated by arid climate zones (Desert hot). Conditions in the equatorial and subtropical areas were potentially extreme with estimated summertime high temperatures of 40–50 °C (Looy et al., 2016 and ref. therein). A warm temperate belt subject to monsoon circulation (Tropics seasonal) was proposed by Roscher et al. (2008, 2011) along the eastern and western coasts of equatorial to subtropical areas. Arid and cold temperate conditions at

higher latitudes (Desert cold) were followed by steppe cold and boreal seasonal climates in the polar regions (Fig. 1).

These climate zones, and the peculiar palaeogeography of late Palaeozoic Pangaea, gave rise to characteristic floristic associations that display increasing endemism from the early to the late Permian (Ziegler, 1990; Rees et al., 1999; Willis and McElwain, 2002). The Gondwanan flora occurred throughout the southern hemisphere (today's Africa, Madagascar, India, Antarctica, Australia, and South America) and was mainly composed of glossopterids, sphenophytes and ferns, although lycophytes and cordaitaleanes also were significant during the Cisuralian in this area (e.g., Archangelsky, 1990; Cuneo, 1996; Willis and McElwain, 2002). The Cathaysian flora developed in a tropical wet/humid climate of equatorial to tropical latitudes, and was characterised by the dominance of sphenophytes, ferns, and pteridosperm-grade seed plants, including gigantopterids. Records of this association are found in China, Laos, Korea, Japan, Thailand, Indonesia and Malaysia (Glasspool et al., 2003; Booi et al., 2009). The Euramerican flora, dominated by conifers, ginkgophytes and ferns (DiMichele et al., 2008), evolved in tropical to seasonally tropical climates, and is best documented in Europe and North America. The Angaran flora, subject to temperate climatic conditions of the middle latitudes for the Northern Hemisphere (Russia, North China), was composed of cordaitaleans, sphenophytes, ferns and peltasperms (Meyen, 1982). Mixed floras characterise boundary areas, such as the southeastern parts of Russia, where the local floras have many elements in common with both the Euramerican and Cathaysian floras. These climatic belts and floral provinces resulted in semi-discrete biomes that, in turn, drove the diversification of invertebrate and tetrapod communities (Sidor et al., 2005; Smith et al., 2015).
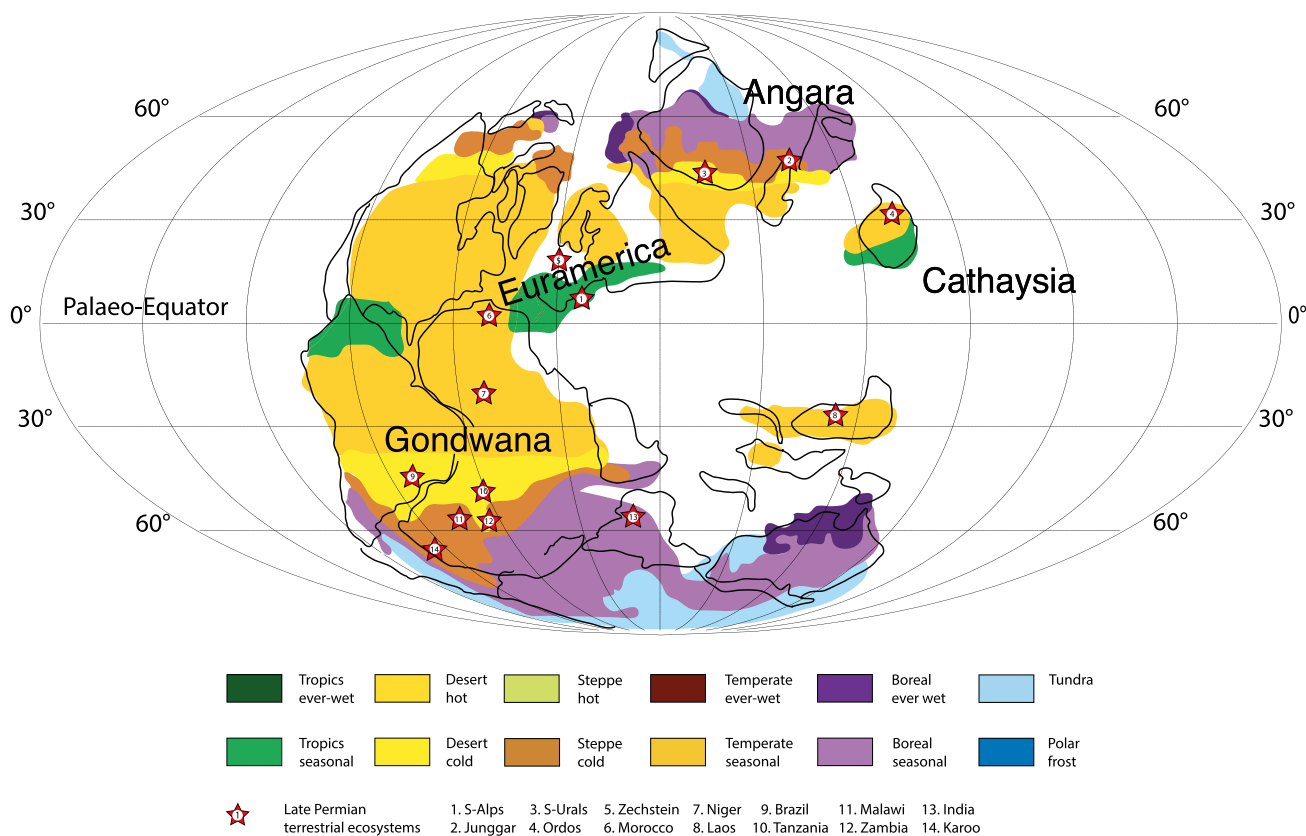

Fig. 1. Lopingian climatic zones (colours) and phytoprovinces (bold text) (modified after Roscher et al., 2008, 2011). Stars mark the 14 best-documented late Permian terrestrial ecosystems discussed in the text.

3. The Bletterbach ecosystem, Southern Alps

We provide here a complete description of the Bletterbach ecosystem, recorded in the continental deposits of Bletterbach Gorge (Southern Alps, northern Italy), and based on newly-collected primary data (see Supplementary Material), a thorough literature review, and the taphonomic and preservational insights provided by Kustatscher et al. (2017). During the late Permian, this region was positioned very close to the palaeoequator, at about 0–5°N latitude (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008; Kustatscher et al., (2017). At this site, a long and nearly-complete succession of the Gröden/Val Gardena Sandstone crops out along a deeply incised gorge. Radiometric dating (U/Pb) suggests an age of 274.1 (± 1.4) million years for the top of the underlying Auer/Ora Formation (Avanzini et al., 2007; Marocchi et al., 2008). Palynology, tetrapod occurrences, and dating of the overlying Bellerophon Formation based on nautiloids and brachiopods (Ceoloni et al., 1988; Posenato, 2010) suggest a Wuchiapingian age for the Gröden/Val Gardena Sandstone (Pittau, 2001, 2005; Avanzini et al., 2011; Kustatscher et al., 2012, 2017).

Our study focuses on an approximately 10 m thick interval that comprises the so-called 'Cephalopod Bank' of Mutschlechner (1933) and strata immediately above and below this important marker horizon (Fig. 2). It represents the maximum flooding surface of Lopingian T–R sequence Lo2 (Massari et al., 1988, 1994; Massari and Neri, 1997; Posenato, 2010), and the marine-terrestrial facies shifts related to this sea-level highstand are considered responsible for the high preservation potential of this interval (Kustatscher et al., 2017). This interval includes 'site 4' of Ceoloni et al. (1988), the 'cuticle horizons' of Clement-Westerhof (1984, 1986, 1987), and the 'megafossil horizon' of Kustatscher et al. (2017). Considering the high sedimentation rate hypothesised for the Gröden/Val Gardena Sandstone at this site (Massari et al., 1994, Avanzini and Tomasoni, 2004; see also discussion below), this interval can be considered penecontemporaneous (i.e. it represents a very short interval of time), therefore allowing a meaningful reconstruction of the biotic interactions within the associated biome.

3.1. Depositional environment

The studied interval (see details in Supplementary Materials) is characterised by pronounced marine-terrestrial facies shifts from a channel-floodplain system to a deltaic system and a subsequent reversal back to a channel-floodplain system (e.g., Conti et al., 1986; Massari and Neri, 1997; Posenato, 2010; Kustatscher et al., 2017). The strata below the Cephalopod Bank are formed predominantly by fining-upward cycles of overbank environments, laterally associated with a mixed-load meandering river (Ori, 1986; Massari et al., 1994; Massari and Neri, 1997; Kustatscher et al., 2017). A set of laterally accreting point bar sheets represents the fill of a high-sinuosity meandering channel. Both the mixed-load channel fill and the floodplain deposits suggest noteworthy variation in discharge rate within a perennial river system. During stages of high discharge, sediment was introduced to overbank environments, which were subject to pedogenic modifications during stages of low discharge (Kustatscher et al., 2017).

Towards the Cephalopod Bank, the successively decreasing thicknesses of fining-upward cycles suggest a retrogradational pattern of strata architecture. In the Bletterbach, the short-term marine transgression from the east and continued sediment input from the west resulted in the formation of a deltaic plain (Kustatscher et al., 2017). The dark and heterolithic shales, which are bioturbated and rich in plant fragments, originated from interdistributary bays and delta-plain wetlands. Suspension load and plant fragments were introduced into these low-energy environments by crevassing of distributaries. The most prominent feature of the transgression interval is the Cephalopod Bank itself. The sheet-like architecture, horizontally laminated to low-angle cross-bedded sandstone lithofacies, and random orientation of the cephalopod shells, suggest a storm- or flood-generated high-energy event (e.g. Massari et al., 1994; Massari and Neri, 1997; Prinoth, in press). Above the Cephalopod Bank, the regression resulted in progradation of a channel-floodplain system closely resembling the lithofacies exposed below the Cephalopod Bank.
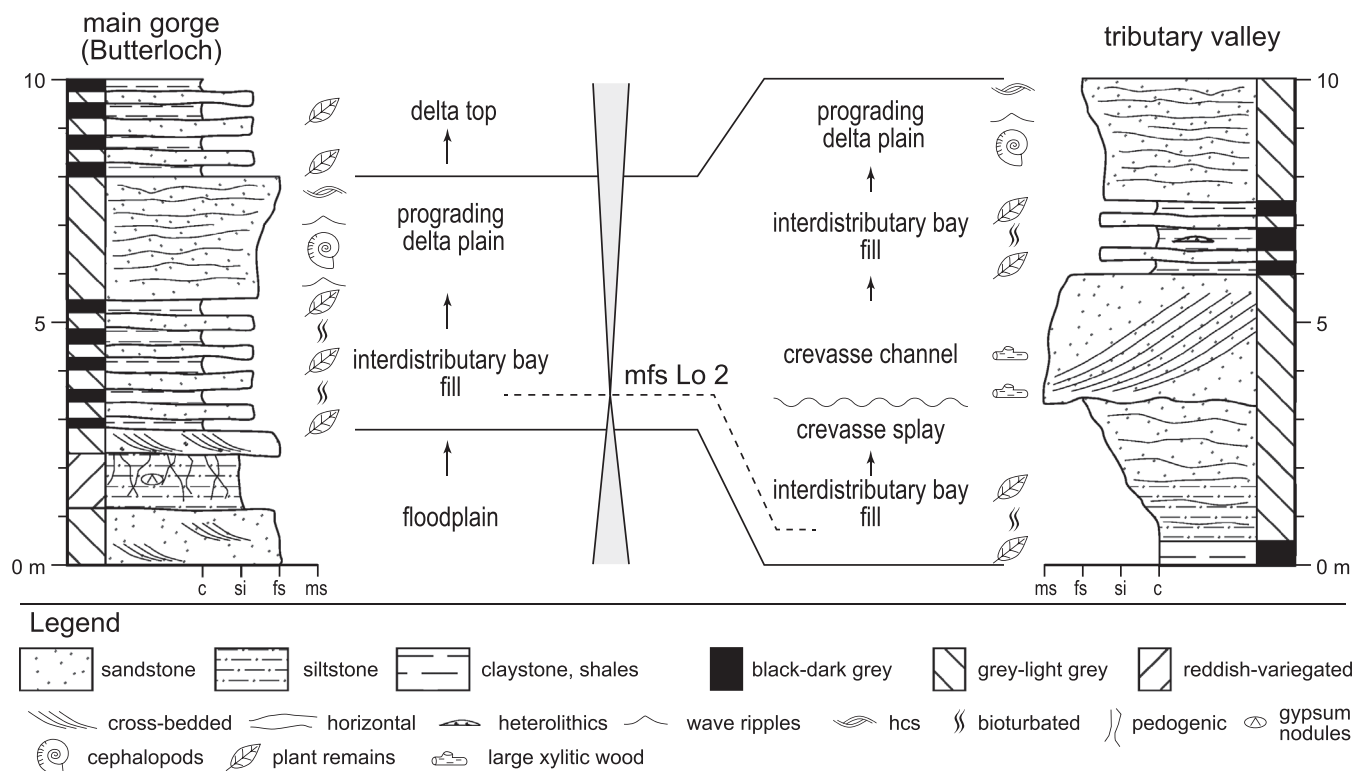

Fig. 2. Simplified logs of the interval around the Cephalopod Bank exposed at the Butterloch (main gorge) of the Bletterbach and a tributary valley showing delta plain lateral facies shifts.

3.2. Palynology

The miospore assemblage is well preserved and dominated by *Lueckisporites virkkiae* Potonié et Klaus, 1954, *Klausipollenites schaubergeri* (Potonié et Klaus) Jansonius, 1962, *Jugasporites delasaucei* (Potonié et Klaus) Leschik, 1956, *Lunatisporites* spp. and the monosaccate prepollen *Nuskoisporites dulhuntyi* Potonié et Klaus, 1954 (also see Supplementary Information). In addition, *Perisaccus* sp., multitaeniate bisaccates (e.g., *Protohaploxypinus* spp., *Striatopodocarpites* sp.) and alete bisaccates (e.g., *Alisporites* spp.) are minor components. Trilete spores are extremely rare. The association is very similar in all samples except in the uppermost, which was collected from a thin grey mudstone horizon approximately 6 m above the top of the Cephalopod Bank (at 81.75 m in the Bletterbach litholog of Massari et al., 1994, p. 140). It is noteworthy that this assemblage differs by the presence of acanthomorph acritarchs (ca. 3% of all palynomorphs) whereas the average percentages of miospores are almost the same as in all other samples.

The miospore assemblages are very similar to Association A of Massari et al. (1988), with the majority of the pollen produced by conifers and probably peltasperms. *Cycadopites*, the pollen of ginkgophytes, cycadophytes and perhaps some seed fern groups, was not found in the studied samples. Trilete spores of lycophytes, sphenophytes and ferns are very rare; these hygrophytic floral elements were probably restricted to small areas with high water table levels. In most cases, assemblages which are dominated by *Lueckisporites virkkiae* and multitaeniate bisaccates are interpreted as derived from a minimally mesophytic, but more likely xerophytic, flora that flourished in dry habitats (e.g., Foster, 1979; Massari et al., 1994).

Rare occurrences of the acritarch genus *Micrhystridium* Deflandre, 1939 have been recorded from the Gröden/Val Gardena Sandstone before, but without any data on their stratigraphic distribution (Massari et al., 1994; Pittau, 2005). The Bletterbach acritarch assemblage is of very low diversity (Fig. 3). Palynomorph assemblages from nearby Zechstein strata of the Southern Permian Basin regularly yield acritarchs (e.g., Schaarschmidt, 1963; Jachowicz, 1997; for a comprehensive review see Hartkopf-Fröder and Heunisch, in press). Most Permian acritarchs have been recorded from nearshore (lagoonal) to proximal shelf facies. However, the presence of acritarchs indicates at least some marine influence or a brackish water environment, such as along the lower delta plain to the prodelta area. Previously, only the 'Cephalopod Bank' was interpreted as representing a marine environment in the lower part of the Bletterbach section. Our discovery of acritarchs approximately 6 m above the top of this bed indicates that the studied interval, which yielded the diverse macroflora and vertebrate tracks discussed below, was deposited close to the coast.
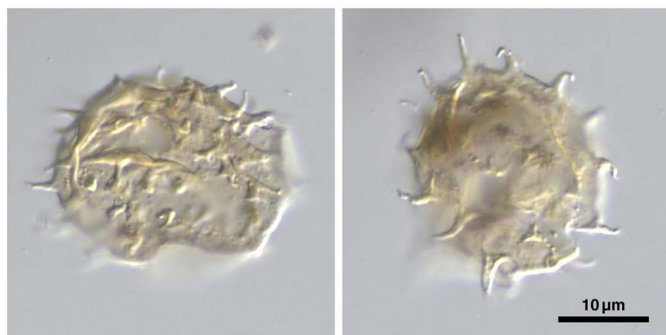

Fig. 3. Newly-described acanthomorph acritarchs (*Micrhystridium* complex) from a thin grey mudstone horizon approximately 6 m above the top of the Cephalopod Bank in the Bletterbach Gorge (Southern Alps) provide evidence that the ecosystem described here developed in a coastal environment (sample 114,936 Geol. Surv. NRW).

3.3. Plant macrofossils

The studied interval yielded plant remains from two different horizons, below and above the maximum flooding surface, with the most productive horizon being the one below the marine bed (Fig. 2; 'Flora A' in Kustatscher et al., 2017). About 1870 plant specimens were assigned to 30 fossil taxa. This plant material includes well-preserved, decimetre-long foliage, shoots, stem fragments, fructifications, cuticle sheets and dispersed seeds. The plant taxa consist of ginkgophytes (50%: *Baiera* Braun, 1843, *Sphenobaiera* Florin, 1936), conifers (40%: *Ortiseia* Florin, 1964, *Quadrocladus* Schweitzer, 1960, *Pseudovoltzia* Florin, 1927, *Dolomitia* Clement-Westerhof, 1987), taeniopterids (2%: *Taeniopteris* Brongniart, 1828), seed ferns (1%: *Germaropteris* Kustatscher et al., 2014, *Sphenopteris* (Brongniart) Sternberg, 1825), and sphenophytes (< 1%) (Clement-Westerhof, 1984, 1986, 1987; Poort and Kerp, 1990; Visscher et al., 2001; Bauer et al., 2014; Kustatscher et al., 2012, 2014, 2017). The fossiliferous horizon above the marine horizon ('Flora B' in Kustatscher et al., 2017) yielded fragmentary plant remains (debris), but with exceptionally well-preserved cuticles mostly of gymnosperms (conifers, seed ferns). The conifers are the dominant group in this flora; seed ferns are common, and ginkgophytes rare. Horsetails, ferns and cycadophytes are not preserved.

Ginkgophytes and conifers grew near their depositional settings and on adjacent uphill slopes. *Ortiseia*, having the most coriaceous leaves, might have occupied drier environments whereas *Quadrocladus*, which has thinner, more elongate leaves probably lived closer to water bodies. The cuticles of taeniopterids and ginkgophytes are thin, and the laminae are expanded (megaphylls), suggesting that they may have grown close to water sources as well. Among the seed ferns, *Germaropteris* shows thick, leathery pinnules, partially imbricated with thick cuticles and well-protected, sunken stomata, whereas the leaves of *Sphenopteris* are thin, dissected, with a wide lamina and thin, poorly protected cuticles (Kustatscher et al., 2012, 2014, 2017). This disparity in cuticle structure suggests that *Germaropteris* was probably present in slightly drier or more xerophytic substrates characterised by higher salinity, nutrient deficiency and better-drained soils, among other features within a broader environmental setting (Vörding and Kerp, 2008). By contrast, *Sphenopteris* likely grew closer to water bodies and/or in the more humid understorey. Sphenophytes also would have grown proximal to water bodies. The presence of charcoal remains indicates that wildfires were present (Uhl et al., 2012).

Conifers and ginkgophytes are probably over-represented in the flora because of their higher preservation potential, reflected also by the mass occurrences of ginkgophyte leaves or dispersed conifer leaves on several bedding planes (Kustatscher et al., 2012; Kustatscher et al., 2017; Bauer et al., 2014). The macroflora differs strikingly from the composition of the miospore assemblage. This difference could buttress the hypothesis that the ginkgophytes shed their leaves seasonally, as does modern *Ginkgo*, and that monolete pollen grains were not transported over a long distance. The dominance of ginkgophytes, however, is exceptional among all known Lopingian floras. Ginkgophytes generally are rare elements in late Permian plant assemblages (Bauer et al., 2014), and have been related to a humid phase during the middle Wuchapingian or to more humid local environmental conditions within areas broadly characterised by semiarid to arid climates (Kustatscher et al., 2017).

3.4. Plant-insect interactions

On the examined 1870 plant remains, 47 plant–arthropod interactions were recorded (see Supplementary Materials), corresponding to 2.5% of the Bletterbach samples. Except for mining, all the fundamental interaction types are represented: i) external foliage feeding, consisting of margin feeding, hole feeding, skeletonization and surface feeding; ii) piercing and sucking; iii) oviposition; iv) galling; v) seed predation; and vi) wood boring (Wilf and Labandeira, 1999; Labandeira et al., 2007)
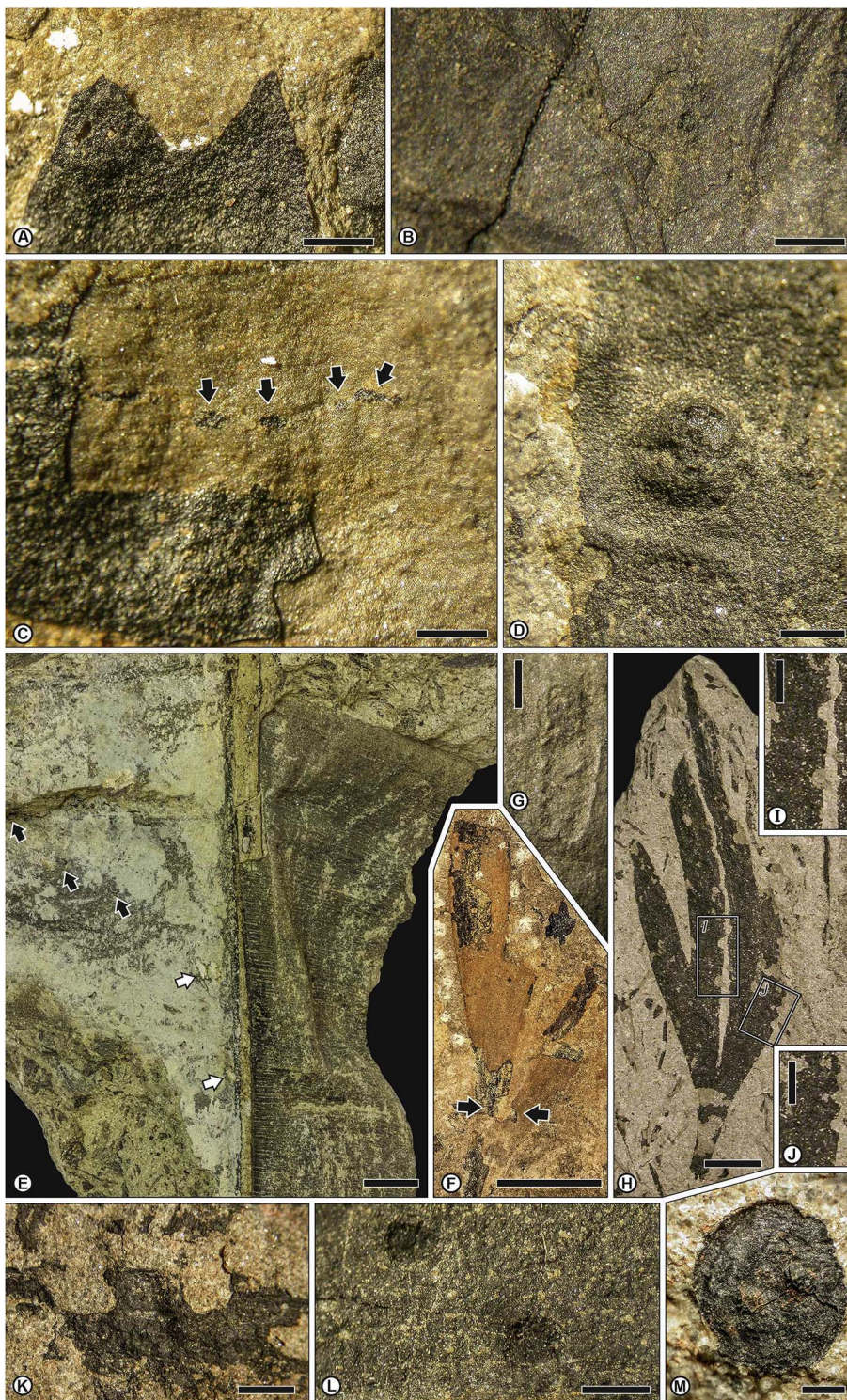
Fig. 4. Insect-mediated damage at the Bletterbach Gorge. A–D. Insect interactions on conifers. A. Excision of leaf apex (DT13) on *Ortiseia leonardii* (PAL 2020); scale bar = 1 mm. B. Circular to ellipsoidal galls on the primary vein (DT33) on *Pseudovoltzia* sp. (PAL859); scale bar = 1 mm. C. Cluster of elliptical piercing-and-sucking scars (DT48; black arrows) on *Quadrocladus* sp. (PAL 1448); scale bar = 1 mm. D. Woody spheroidal leaf gall on *Quadrocladus* sp. (PAL 1464); scale bar = 1 mm. E. Insect interactions cycadophytes with extensive oviposition on the midvein (DT76; white arrows) and on the lamina (DT101; black arrows) on *Taeniopteris* sp. (PAL 1532); scale bar = 10 mm. F–J. Insect interactions ginkgophytes. F. Margin feeding (DT12; black arrows) at the margin of an unaffiliated ginkgophyte (PAL 821); scale bar = 5 mm. G. Window feeding (DT130) with a distinct callus on an unaffiliated ginkgophyte (PAL 1455); scale bar = 2 mm. H. Margin feeding (DT12) at the margin of an unaffiliated ginkgophyte (PAL 1445); scale bar = 10 mm; enlarged in I. and J., scale bars = 5 mm. K. Margin feeding (DT12) of a *Dicranophyllum*-like leaf (PAL 997); scale bar = 3 mm. L. Wood boring (DT160) on an unidentified axis (PAL 2016); scale bar = 1 mm. M. Seed predation (DT74) on PAL 1088; scale bar = 1 mm.

(Fig. 4). There is evidence for host specificity, as already established for the Cisuralian and Lopingian localities of north-central Texas and South Africa (Beck and Labandeira, 1998; Prevec et al., 2009; Schachat et al., 2014, 2015). At Bletterbach, taeniopterid-like leaves exhibit a sixfold higher damage frequency (9%) than their frequency in the flora would indicate (1.5%). By contrast, ginkgophytes, which constitute 51% of the flora, show a sixfold lower incidence of herbivory (8.3%). The second most commonly herbivorised group are conifers. The data indicate a frequency of herbivore attack of 6.7% for *Pseudovoltzia*, 1.9% for *Quadrocladus*, and 0.7% for *Ortiseia*. Unaffiliated *Dicranophyllum*-like

leaves reveal a 3.5% herbivore attack level. Seed ferns (*Sphenopteris*, *Germaropteris*) and sphenophytes display no signs of insect-mediated herbivory. This absence of herbivory on this group is atypical, as other groups of seed plants such as Wuchiapingian glossopterids from the Karoo Basin of South Africa (Prevec et al., 2009), Guadalupian-Lopingian glossopterids from Argentina (Cariglino and Gutiérrez, 2011) and Kungurian gigantopterids from Texan Euramerica display the highest herbivory levels compared to other plant groups in their respective floral assemblages (Beck and Labandeira, 1998; Labandeira, 2006; Schachat et al., 2014, 2015). It could be that the low abundance

of seed ferns in the Bletterbach sites did not reach the threshold of systemic herbivory that was evident in the South African and Texan sites, where seed fern taxa were much more abundant. Such a consequence is explained by the apparency hypothesis of Feeny (1976), whereby high herbivory levels are triggered by host-plant conspicuousness, as a result of elevated host-plant abundance.

The Bletterbach damage frequency (3.5%) is comparable, within a factor of three, to analyses of bulk floral damage values on coeval palaeofloras from Euramerica (Beck and Labandeira, 1998; Labandeira and Allen, 2007; Vasilenko, 2007), Cathaysia (Glasspool et al., 2003), and other Gondwanan sites (e.g., Adami-Rodrigues et al., 2004a, 2004b; Prevec et al., 2009; Gallego et al., 2014). Consequently, the Bletterbach level of overall herbivory is typical for Permian wetland floras. The observed plant–insect associational data indicate two patterns. First is that mostly ectophytic and generalised interactions were the major patterns of herbivory worldwide for Permian terrestrial communities; endophytic and more specialised interactions were considerably rarer. Second, several different, major, gymnosperm lineages (such as sphenopterids, Glossopteridales, Gigantopteridales and Peltaspermales) were the most herbivorised group of plants throughout the Permian (Labandeira and Currano, 2013), although the Lopingian Bletterbach locality lacks elevated seed fern herbivory probably due to the rarity of peltasperms and sphenopterids in its flora. Instead, elevated herbivory levels and host specificities predominated on cycadophytes and ginkgophytes at Bletterbach.

3.5. Vertebrate fauna

The Bletterbach has long been known for abundant tetrapod footprints (Kittl, 1891; Abel, 1929) that constitute the most diverse late Permian ichnoassociation known (Lockley and Meyer, 2000; Lucas and Hunt, 2006). Based on data from the literature, the Bletterbach ichnoassemblage includes 10–13 ichnotaxa belonging to various groups of parareptiles (mostly pareiasaurs) and basal neodiapsids, followed by therapsids, archosauriforms and captorhinids. Pareiasaurs, documented by *Pachypes dolomiticus* (Leonardi et al., 1975; Valentini et al., 2009; Voigt et al., 2010; Smith et al., 2015), make up 38% of the faunal association. Carnivorous therapsids, documented by unnamed ichnotaxa, constitute 4% of the association. Other therapsids (2–3%) are documented by the presence of *Contiichnus tazelwurmi* (Citton et al., 2017), *Dicinodontypus geinitzi* (Hornstein 1876) and the enigmatic 'Ichniotherium' footprints. The tracks assigned to *Hyloidichnus tirolensis* by Ceoloni et al. (1988) has been repeatedly attributed to a captorhinid producer (Haubold, 1996, 2000; Voigt et al., 2009, 2010; Avanzini et al., 2011) and constitute 5% of the association. A recent review (L. Marchetti pers. comm. 2017) suggests these tracks should be assigned to the ichnogenus *Procolophonichnium*, in which case the attribution would range from captorhinid to small therapsid (following Klein et al., 2015), or to a parareptile. In the absence of new definitive assignment we rely here on the most commonly accepted interpretation. The presence of lacertoid (basal neodiapsid) early saurians is evidenced by the classical *Rhyncosauroides–Dromopus* group (Maidwell, 1911; Abel, 1929; Conti et al., 1977; Valentini et al., 2007; Avanzini et al., 2011), which makes up 42% of the association. Archosauriformes, documented by Chirotheriidae indet., cf. *Protochirotherium* Fichter and Kunz, 2004 and the archosauriform-related *Paradoxichnium radeinensis* Ceoloni et al., 1988 constitute 2% of the association (Conti et al., 1977; Ceoloni et al., 1988; Bernardi et al., 2015; Voigt et al., 2015).

The Bletterbach ichnoassociation documents a numerical dominance of pareiasaurs and small lacertoid neodiapsids – early saurians, with their footprints far outnumbering all others (Kustatscher et al., 2017). In particular, pareiasaur and captorhinid tracks are markedly more abundant than dicynodont footprints. Captorhinid, dicynodont and indeterminate small therapsid tracks are similarly sized (pes length < 10 cm) and therefore have similar preservational potential, allowing meaningful comparisons of abundances. The absence or

extreme rarity of anamniote footprints seems to reflect a common feature of Lopingian ichnoassociations worldwide (Tverdokhlebov et al., 1997; Voigt and Lucas, 2016).

3.6. Trophic network

Although insect body fossils have not been found at Bletterbach, the ecologically relevant deposit of insect body fossils in the nearly coeval Salagou Formation of the Lodève Basin (Béthoux, 2008) can be used as a proxy for part of the community. The Lodève insect fauna is composed of several orders of insects, belonging to the palaeopterous lineages Odonatoptera, Diaphanopterodea, and Palaeodictyoptera, as well as orthopterans and early representatives of modern holometabolan clades (Béthoux, 2008). In contrast, the insect assemblages of the Guadalupian to Lopingian of European Russia are significantly more diverse (Aristov et al., 2013), and broadly include diverse archaeorthopterans, orthopterans and early representatives of several extant holometabolous lineages. Accordingly, we tentatively propose that the Bletterbach ecosystem supported a herbivorous insect fauna containing taxa as diverse as mandibulate orthopteroids, piercing-and-sucking hemipteroids and the likely exophytic and endophytic larvae of basal holometabolous lineages. As demonstrated by plant-arthropod interactions, this entomofauna preferentially fed on taeniopterids, conifers and ginkgophytes, and was probably preyed upon by the small secondary consumers documented by footprints, such as lizard-like insectivores (Fig. 5). Some of the plant damage could be ascribed to orthopteroid, hemipteroid and holometabolous insects, although assignments to specific lineage remain uncertain.

Pareiasaurs, small to medium herbivorous therapsids and captorhinids would have been the high-fibre herbivores in this ecosystem. Their feeding mechanisms differ in a number of details, suggesting that they might have had different food preferences, although this is difficult to ascertain. Pareiasaurs, for example, had leaf-shaped, cuspidate marginal teeth for puncturing and tearing apart fibrous plants (Munk and Sues, 1993; Lee, 1997; Reisz and Sues, 2000). Although no direct evidence exists, crosschecking abundance data suggest that pareiasaurs might have fed upon ginkgophytes and conifers in the Bletterbach flora. Other primary consumers, such as dicynodonts, might have fed on sphenophytes and ferns, as discussed below. Captorhinids, which had broad dentaries, multiple rows of peg-like teeth and highly developed chewing mechanisms (Dodick and Modesto, 1995; Sues and Reisz, 1998; Reisz and Sues, 2000), would have been able to pierce or grind tough plant material such as sphenophytes and some seed plants (Benton, 2015). Herbivorous therapsids, captorhinids and neodiapsids probably were preyed upon by large secondary consumers such as archosauriforms and therapsids, which constitute the majority of large-sized faunivorous tetrapods represented in the track assemblage. Curiously, plant remains of conifer and seed fern ovules (Munk and Sues, 1993) were found within the abdominal cavity of *Protorosaurus*, suggesting a mixed diet at least for some late Permian archosauriformes.

Using the classification proposed by Olson (1966), which groups ecological communities into three types based on the relative diversities of tetrapod herbivores and whether sources of primary productivity were dominantly terrestrial or aquatic, the Bletterbach community seems to represent a Type II community with fully terrestrial tetrapod herbivores, and to a lesser degree herbivorous insects, forming the primary link between primary producers and tetrapod secondary consumers. This general structure is comparable to what is seen in the dicynodont-dominated ecosystems of southern Gondwana (Olson, 1966).

3.7. Biome characterisation

The Bletterbach flora fits the tropical wet biome of Rees et al. (2002), which is characterised by a depauperate flora composed mainly of ginkgophytes and voltzialean conifers with some cordaitaleans (see
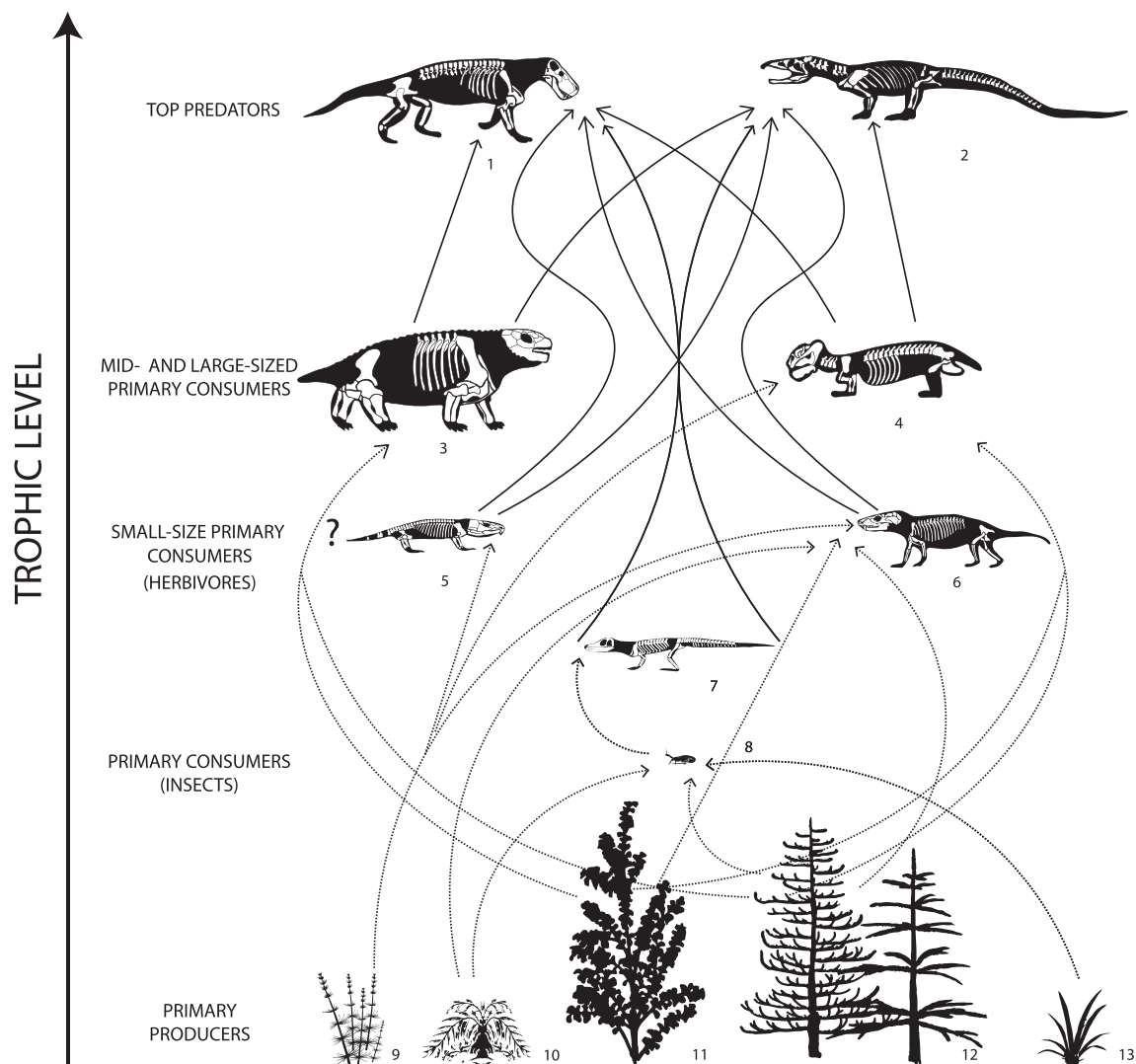
Fig. 5. Simplified trophic network architecture of the Bletterbach biota (Southern Alps), showing the inferred complex interactions of floral and faunal communities; 1) faunivorous therapsids; 2) archosauromorphs; 3) pareiasaurs; 4) herbivorous therapsids; 5) possible captorhinids; 6) indet. therapsids; 7) basal neodiapsids; 8) insects; 9) sphenophytes; 10) seed ferns; 11) ginkgophytes; 12) conifers; 13) taeniopterids.

also Willis and McElwain, 2002). The flora and the sedimentary record from the entire Lopingian Bletterbach succession (Kustatscher et al., 2017) also shows some features of the geographically proximal (poleward) 'subtropical desert biome' (Rees et al., 2002; Willis and McElwain, 2002). This is characterised by an arid environment with a scarce vegetation of cycadophytes, ginkgophytes, and voltzialean conifers that would grow along the coast. The marine influence as shown by the nautiloids washed onto the delta plain, the flora and the palynomorphs, but also by the microclimate created by the proximity of the ocean appears to be a key feature of Bletterbach sequence. The climatic model proposed by Roscher et al. (2008) showed that, although the Bletterbach latitudinal belt would have experienced a 'desert hot' climate, the influence of the Palaeotethys on this region would have resulted in a more humid 'tropical seasonal' microclimate. Moreover, Kustatscher et al. (2017) demonstrated that the environmental conditions throughout the Bletterbach sequence were deeply influenced by sea-level changes.

4. Other late Permian terrestrial ecosystems

The composition of the other 13 best-known late Permian terrestrial ecosystems is reviewed below in latitudinal order, from North to South

(Fig. 1). For each ecosystem, we provide a quantitative characterisation of the fauna, considering both the skeletal and footprint records, the relative abundance of the floral groups, and climatic and palaeolatitudinal settings. Compositional percentages of faunal associations are the sum of skeletal and (when available) footprint data (see Supplementary Materials for further details).

4.1. Junggar Basin, China

The Junggar Basin, today within Xinjiang Province (NW China), is characterised by heterogeneous lithologies that reflect a variety of depositional environments and flow regimes including alluvial, braided, and meandering fluvial, and shallow lacustrine types (Wartes et al., 2000 and ref. therein). During the Lopingian, the basin was located at a palaeolatitude of about 40˚N (Bykadorov et al., 2003; Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008; Shuang et al., 2014). The Junggar experienced periodic dry-wet fluctuations, as well as yearly seasonal changes (Zhu et al., 2005; Wan et al., 2014), within a generally semi-arid climate (Ouyang et al., 2003; Zhu et al., 2005). Palaeoclimatic models attribute the Junggar ecosystem to the 'steppe cold' zone (Rees et al., 2002; Sidor et al., 2005; Roscher et al., 2008; Smith et al., 2015).

The majority of tetrapod fossils were discovered in lacustrine deposits of the Cangfanggou Group (Quanzijie, Wutonggou and Guodikeng formations; Wartes et al., 2000), that we here assume to be part of a single fauna. Dicynodonts, such as *Jimusaria* and *Turfanodon*, represent the vast majority of the association (80%, 8 specimens), followed by amphibians and therocephalians (10%) (Lucas, 2001, 2005; Kammerer et al., 2011; Liu and Abdala, 2017). The dicynodonts of the Junggar Basin exhibit mixed affinities to those of Russia and Gondwana (e.g., Kammerer et al., 2011). The Guodikeng Formation is also noteworthy in recording an overlap in the stratigraphic ranges of the dicynodontoid *Jimusaria* and *Lystrosaurus* (e.g., Young, 1939; Cheng, 1993; Lucas, 1993, 2001; Metcalfe et al., 2009). This relationship resembles the overlapping stratigraphic ranges of *Lystrosaurus* and the dicynodontoids *Dicynodon*, *Daptocephalus*, and *Dinanomodon* in the latest Permian of the Karoo Basin (e.g., Smith, 1995; Smith and Botha-Brink, 2014; Viglietti et al., 2016).

Very few data are available on the Junggar flora, with only ferns and seed ferns documented by macrofloral remains (Wang, 1985; Wartes et al., 2000). Plant fossils are characteristic of a transitional flora dominated by Angaran taxa with some Euramerican and endemic elements; Cathaysian elements are absent or rare (Wang, 1985). The Guodikeng Formation also has yielded a *Lueckisporites virkkiae–Klausipollenites schaubergeri* Assemblage dominated by pollen of "mesophytic" affinity (73%; sensu Zhu et al., 2005). Wan et al. (2014, 2016) described a gymnosperm, *Septomedullopitys* (Wan et al., 2014), consisting of a stem with coprolites and borings evidencing well-developed plant–animal and plant–fungus interactions.

4.2. South Urals, Russia

The upper Permian (Tatarian) continental succession of the Moscow Basin in the South Urals is best known for its abundant tetrapod fauna. It is dominated by fluvial deposits of four lithofacies representing mud flat, sandy distributary, small gravelly-channel and large gravelly-channel deposits (Newell et al., 1999; Benton et al., 2004). Newell et al. (2010) recognised a muddy playa–lacustrine depositional system in the uppermost part of the succession (Vyazniki and Gorokhovets sections), similar to that at the top of the Karoo sequence (Smith and Botha-Brink, 2014; although see Gastaldo et al., 2017; Li et al., 2017). During the late Permian, the South Urals were located around latitude 28–34˚N (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). Sedimentological data indicate an arid environment for this sector (Newell et al., 1999), though no severe desertic conditions are thought to have developed over the area (Tverdokhlebov et al., 2005). The palaeoclimatic model of Rees et al. (2002) attributed the Southern Urals to the 'mid latitude desert' zone, while Roscher et al. (2008, 2011) considered the area a 'desert cold' zone.

This succession has yielded numerous and diverse terrestrial tetrapods (Tverdokhlebov et al., 2003; Benton et al., 2004) that testify to a rich and complex trophic network (e.g., Sennikov and Golubev, 2006). The succession often is subdivided into two different assemblages related to the Severedovinian (Capitanian *pro parte* and Wuchiapingian) and Vyatkian (Changhsingian) time intervals. During the Severedovinian, the fauna was dominated by small-sized, piscivorous amphibians and stem amniotes (Dvinosauridae, Chroniosuchidae, 60%), followed by small and large pararreptiles (procolophonids and pareiasaurs, 19%), anomodonts (dicynodonts and venyukovioids, 10%), carnivorous therapsids (gorgonopsians, 2%), and seymouriamorphs (2%). During the Vyatkian the major representatives of the Russian faunal assemblage still persisted, with stem-amniotes (chroniosuchids, 39%), followed by seymouriamorphs (kotlassiids, 17%), small and large pararreptiles (procolophonids and pareiasaurs, 14%), temnospondyl amphibians (dvinosaurids, 8%), medium-sized therocephalians (scylacosaurids and moschorhinids, 6%), medium- to large sized gorgonopsians (8%), dicynodonts (5%), rare cynodonts (1%) and small reptiliomorphs (1%). The latest Permian vertebrate fauna additionally

includes the gracile piscivorous reptile *Archosaurus* Tatarinov, 1960, the oldest member of the Archosauriformes (Gower and Sennikov, 2000; Ezcurra et al., 2014). Surkov et al. (2007) described putative dicynodonts tracks that they referred to *Brontopus giganteus* Heyler and Lessertisseur, 1963. However these were later reinterpreted as pareiasur tracks (Valentini et al., 2009).

The late Permian flora of European Russia has become known as 'Tatarian' based on the dominance of the peltaspermalean genus *Tatarina* Meyen, 1969 (Meyen and Gomankov, 1980). During the Vyaznikovian, the flora was dominated by peltasperms (50–80%), followed by ginkgophytes and conifers. Ferns were rare and sphenophytes only locally present (Newell et al., 1999; Naugolnykh, 2005; Karasev and Krassilov, 2006; Lozovsky et al., 2016). As such, this plant assemblage includes typical elements of the East European platform and the Zechstein flora of Europe. The Vyaznikovian fossil assemblage also shows abundant evidence for plant–arthropod interactions (Krassilov and Karasev, 2008), as well as a rich insect fauna including Thysanoptera (Lophoneurida), Neuroptera, Mecoptera, Hemiptera, Paleomanteida, Coleoptera, Trichoptera, Blattida, Grylloblattida, Orthoptera, and Dermaptera (Protelytroptera). Cockroaches (Blattida) dominate (65% of insect remnants); leafhoppers (Hemiptera) and grylloblattids (Grylloblattoda), consisting of 17% and 8%, respectively, are less common (Aristov et al., 2013; Lozovsky et al., 2016).

Finally, we note that additional late Permian fossil localities are present farther north on the Russian platform, such as the Sokolki faunal subassemblage known primarily from outcrops along the Northern Dvina River near the city of Kotlas (e.g., Modesto and Rybczynski, 2000). These areas have a long history of study dating to the late nineteenth century (see reviews in Ochev and Surkov, 2000; Modesto and Rybczynski, 2000), including work examining faunal composition and palaeoecology (e.g., Sennikov, 1996; Ivakhnenko et al., 1997; Ivakhnenko, 2001, 2003, 2015). We have not included these localities in our analyses here because of the lack of abundance data comparable to that available for the southern Urals region.

4.3. Ordos Basin, China

In the Ordos Basin, mostly located within Shaanxi Province of northeastern China, Lopingian deposits mainly consist of red fluvial deltaic and shallow lacustrine clastic rocks (Yang et al., 1986; Zhai, 1990; Yang et al., 2005), which were deposited at about 27–34˚N (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). Tetrapod fossils were discovered in various North China Block localities in Gansu, Henan, Hubei, Shanxi Provinces and Inner Mongolia Autonomous Region (Cheng et al., 1995; Cheng and Ji, 1996; Cheng and Li, 1997; Li, 2001; Liu, 2013; Benton, 2016), and have been correlated with the Severodvinian-Vyatkian of Russia and the *Cistecephalus* and *Daptocephalus* assemblage zones of South Africa (Benton, 2016). During the late Permian, the Ordos Basin was characterised by a warm-humid climate (DiMichele and Phillips, 1996; Rees, 2002), although it became progressively drier (Sun, 2006). Palaeoclimatic models assign it to the 'tropical everwet' zone (Rees et al., 2002; Sidor et al., 2005; Smith et al., 2015) or to the 'seasonal tropics' climate belt (Roscher et al., 2008, 2011).

The late Permian (late Wuchiapingian) Henan fossil fauna (Jiyuan Fauna, Upper Shihezi Formation) is represented by numerous teeth and a few skeletal remains of scutes and vertebrae of pareiasaurs (47%), gorgonopsians (40%), chronosuchians (7%), cynodonts and few undetermined therapsids (Liu et al., 2014; Xu et al., 2015; Benton, 2016). The Shanxi (Wuchiapingian) vertebrate fauna is dominated by pareiasaurs and originates from the overlying Sunjiagou Formation (Liu et al., 2015). Only one dicynodont has been found in the Lopingian deposits of the Ordos Basin, the cryptodont *Daqingshanodon limbus* Zhu, 1989, from the Naobaogou Formation of Inner Mongolia (Zhu, 1989; Lucas, 2001, 2005; Li, 2001; Kammerer et al., 2011; Li and Liu, 2013). The Sunjiagou Formation of Shanxi, Henan, and Shaanxi provinces

and the Ningxia Huizu Autonomous Region, has yielded a rich flora of sphenophytes, *Noeggerathiopsis*, ferns, seed ferns, ginkgophytes and conifers, as well as taeniopterids. Seed ferns and conifers are the dominant group in the flora, sphenophytes are common (15%), whereas ginkgophytes and ferns are rare (Wang and Wang, 1986). Megaspores attributed to lycophytes suggest that this group played a major role in the late Permian floras of North China (Feng et al., 2011). The flora of the Shischenfeng Group in the Ordos Basin is characterised by a mixture of Euramerican, principally Zechstein-type vegetation, and Cathaysian elements (e.g., Wang, 1985; Wang and Wang, 1986; Sun, 2006). The presence of mixed floras in northern China is corroborated by the nearby flora of southwestern Mongolia, dominated by Angaran elements with occasional Cathaysian elements (Shen et al., 2006). Other regions, such as the Weibei Coalfield of Shaanxi Province, are characterised by a typical late Cathaysian flora. The Weibei Coalfield flora is particularly rich and diverse (209 species from 66 genera), and is divided into four plant assemblages. Abundant gigantopterids (*Gigantoclea*, *Fascipteris*) and sphenophytes (*Sphenophyllum*, *Lobatannularia*, *Annularia*) are found in between the coaly layers of the succession, with an increase in Euramerican taxa only in the upper part of the succession, where the coaly levels decrease in number with a corresponding a decrease in diversity. This could indicate a shift to an increasingly seasonal climatic regime (Wang, 2010). The peculiar composition of the Ordos Flora was attributed to the Middle Eurasian belt or the Eurasian arid Province (Durante, 1983; Wang, 1985).

From the Changhsingian Stage of the Ningxia Huizu Autonomous Region, the oldest complex gallery of a wood engraving insect and a network of borings and larval tunnels has been described recently (Feng et al., 2017). Several of these tunnel and gallery structures have been documented on the conifer host *Ningxiaites specialis*, of uncertain taxonomic relationships, and consist of an entrance tunnel into bark wood, a mother gallery expansion within cambial tissue, and subsequent development of several parallel larval tunnels that bore through cambium, into secondary xylem (wood) tissue, and finally emerge from the bark surface. This was followed by closure of the wound formed by the gallery system by enrolled wood and bark. This highly stereotyped wood boring indicates a complex social structure, including fungal symbioses, and probably agriculture made by male and female polyphagan beetles and their larvae. The borings also housed a microcommunity that included two species of beetles, oribatid mites, fungi, chelicerate arthropod predators and other organisms that evidently were extinguished at the end of the Permian. This occurrence is reminiscent of bark beetle and ambrosia beetle communities that separately evolved approximately 120 million years later during the Early Cretaceous (Farrell et al., 2001).

4.4. Central Europe

During the Lopingian, the European Zechstein Basin extended from the British Isles, through the North Sea into the Baltic region, Poland, Germany and the Netherlands. Marginal marine facies, linked with the marine transgression of the Zechstein Sea, prevailed, although aeolian-fluvial/lacustrine sediments were dominant in the northernmost sectors (Peacock et al., 1968), represented by the Hopeman Sandstone Formation (Glennie, 2002). The German and British sectors of the Zechstein Basin during the Lopingian were at latitudes 15–20°N (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). These ecosystems are considered to have been developed under semi-arid climate conditions and to belong to the 'desert' zone of Rees et al. (2002).

The Kupferschiefer localities (Hesse, Saxony Anhalt and Thuringia in Germany), the correlative Marl Slate of England, and the Cutties Hillock and Hopeman Sandstone formations of Scotland have yielded several pareiasaur and dicynodont remains, followed by archosauromorphs and rare captorhinids, cynodonts and temnospodyls (Newton, 1893; Rowe, 1980; Benton and Walker, 1985; Haubold and Schaumberg, 1985; Evans and Haubold, 1987; Sues and Boy, 1988; Sues

and Munk, 1996; Cruickshank et al., 2005; Witzmann, 2005; Schaumberg et al., 2007; Tsuji and Müller, 2008). Vertebrate ichnofaunas, discovered in Scotland (Corncockle and Locharbriggs sandstones; McKeveer and Haubold, 1996), Devon (Warrington and Scrivener, 1990), Poland (Tumlin Sandstone; Ptaszyński and Niedźwiedzki, 2004), France (La Lieud Formation, Lodève Basin; Gand et al., 2000) and Germany (Rotliegend; Müller, 1959; Haubold, 1984; Fichter, 1994; Voigt, 2012) include several ichnogenera. These were produced mostly by basal neodiapsids – early saurians, parareptiles and temnospondyl amphibians.

Plant assemblages in the Zechstein Basin are almost completely restricted to the marine Kupferschiefer. Classical Kupferschiefer floras come from the Lower Rhine region, Thuringia, Hesse, and Saxony in Germany, as well as England and Poland (e.g., Germar in Kurtze, 1839; Solms-Laubach, 1884; Gothan and Nagelhard, 1923; Weigelt, 1928, 1930; Stoneley, 1958; Schweitzer, 1960, 1986; Ullrich, 1964; Brandt, 1997; Uhl and Kerp, 2002, in press). Additional elements have been found in the Balearic Isles (Bercovici et al., 2009) and the Esterel Massif of Southern France (e.g., Visscher, 1968). This widespread plant assemblage is characterised by an absolute dominance of conifers (e.g., Weigelt, 1928, 1930; Stoneley, 1958; Ullrich, 1964; Schweitzer, 1960, 1986; Uhl and Kerp, 2002; Bödige, 2007; Bauer et al., 2013). Seed ferns are common, whereas putative taeniopterids, ginkgophytes and sphenophytes are rare. Lycophytes have never been encountered as macrofossils, but they are evidenced by the palynological record, including megaspores. A very small Zechstein flora of conifers has been reported from Belgium (Florin, 1954). Late Permian floras from Poland and Hungary are dominated by conifers (Heer, 1876; Czarnocki and Samsonowicz, 1913; Pajchlowa and Wagner, 2001). Rare cycad leaf fragments have been documented in the Spanish flora (Bercovici et al., 2009).

The palynoflora of the Zechstein of the Southern Permian Basin has recently been summarised by Hartkopf-Fröder and Heunisch (in press). The distinctive miospore assemblage of the Zechstein is characterised by saccate pollen grains. In most cases, the morphologically variable, widespread *Lueckisporites virkkiae* is most abundant. In some areas, e.g. in the Lower Rhine region, *Jugasporites delasaucei/moersensis* and *Klausipollenites schaubergeri* each can constitute up to 40% of the miospore assemblage (Grebe and Schweitzer, 1964) while *Nuskoisporites dulhuntyi* is rare. In situ pollen *Nuskoisporites*, *Jugasporites*, *Lueckisporites* and *Lunatisporites* have been described from male structures of voltzialean conifers such as *Ullmannia frumentaria* and *Ortiseia* (Potonié and Schweitzer, 1960; Clement-Westerhof, 1984). Typical of the Zechstein palynoflora are also multitaeniate, haploxylonoid and diploxylonoid pollen grains such as *Protohaploxypinus* spp., *Striatopodocarpites* and *Striatoabieites*. Only very few monolete and trilete spores have been recorded (e.g., Rebelle and Doubinger, 1988; Fijałkowska, 1994). The scarce occurrence of well-preserved spores and rare megaspores indicates that lycophytes (Selaginellaceae), sphenophytes and ferns were very minor constituents of the Zechstein macroflora. Broadly speaking, the palynoflora mirrors the composition of the Zechstein macroflora, characterised by low diversity, and the dominance of conifers accompanied by only a few seed ferns and very rare lycophytes, sphenophytes and ferns, some of which probably flourished on moist to wet soils and near bodies of water.

4.5. Morocco

The Argana Basin is located between Marrakech and Agadir in southern Morocco. An excellently-exposed Permian–Triassic redbed succession crops out in this basin and consists of alluvial, fluvial, lacustrine, aeolian and playa deposits, which were laid down in a continental rift basin during the initial opening phase of the central Atlantic (Manspeizer, 1988; Zühlke et al., 2004). The Ikakern Formation consists of alluvial fan conglomerates fining upwards and laterally into alluvial plain conglomerates, sandstones, and mudstones (Hmich

et al., 2006; Voigt et al., 2010). The Argana Basin was located at approximately latitude 0–5˚S during the late Permian (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). Although the late Permian Argana Basin overall was characterised by semiarid climatic conditions (Hmich et al., 2006), the deposition of the Tourbihine Member of the Ikakern Formation, where most tetrapod fossils have been found, has been correlated with the onset of the (middle) Wuchiapingian wet phase that interrupted the overall drying trend of the Permian climatic curve (Roscher and Schneider, 2006). In the palaeoclimatic model of Rees et al. (2002), this region is part of the tropical wet biome (Roscher et al., 2008; Smith et al., 2015).

The Ikakern Formation of the Argana Basin has yielded both vertebrate remains and fossil tracks (Dutuit, 1976, 1988; Jalil and Dutuit, 1996; Jalil and Janvier, 2005; Hmich et al., 2006; Steyer and Jalil, 2009; Voigt et al., 2010). The assemblage is dominated by small-sized captorhinids (36.4%), followed by basal neodiapsids (18.2%), and large-sized pararereptiles (pareiasaurs, 18.2%). Rare elements, but with comparable percentages, are lepospondyl and temnospondyl amphibians (diplocaulid nectrideans, 9%; indeterminate temnospondyl amphibians, 9.2%), and archosauromorphs (9.1%). De Koning (1957) reported the presence of *Voltzia heterophylla* from Jebel Tafilalt, which currently is the only documented plant taxon from the Ikakern Formation (Hminna et al., 2012).

4.6. Niger

The upper Permian Moradi Formation of northern Niger is a continental redbed succession deposited in the Tim Mersoi and Iullemeden basins that has yielded numerous vertebrate, invertebrate, plant and trace fossils (Sidor et al., 2005; Damiani et al., 2006; Smiley et al., 2008; Smith et al., 2015; Looy et al., 2016; Sidor pers. comm., 2016). It documents a floodplain lake environment subjected to an arid climate with a high water table in an evaporative setting (Looy et al., 2016). During the late Permian these basins were located around latitude 10–20˚S (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008; Smith et al., 2015; Looy et al., 2016), in a transitional regime between the 'desert' and the 'tropical summer-wet' biomes of Rees et al. (2002) (see also Sidor et al., 2005; Poulsen et al., 2007; Peyser and Poulsen, 2008; Tabor et al., 2011; Smith et al., 2015). Interpretations of climate suggest warm and hyperarid with a highly seasonal monsoonal rainfall (Smith et al., 2015; Looy et al., 2016).

The tetrapod record is represented by both skeletal remains and well-preserved footprints. Large-sized pareiasaurs prevail in the faunal assemblage (38.6%), followed by captorhinids (36.8%), small- and large-sized therapsids (10.6%) and temnospondyl amphibians (10.5%). Small neodiapsids (4%) are rare elements in the fauna. The macrofossil flora documents a low-diversity association representative of sparsely-vegetated lake margins in a gymnosperm-dominated woodland. Preserved plant material includes leaves, ovuliferous dwarf shoots of primitive voltzialean conifers, conifer shoots and logs and *Agathoxylon*-type woody stems (Looy et al., 2016). Looy et al. (2016) concluded that voltzialean conifers were not restricted to arid environments in the equatorial tropics during the late Permian, but extended into the northern and southern paratropical regions.

4.7. Laos

The Luang Prabang Basin of northern Laos contains three distinct upper Permian continental formations that have yielded both fossil tetrapods and plants (Bercovici et al., 2012). The informally named 'Red Claystone Formation' is characterised by facies interpreted as an alluvial plain with interbedded fluvial sandstone bars. The 'Limestone and Sandstone Formation' is typified by a change from marine deposits to a claystone rich in terrestrial plant fossils and additional marine sediments. The 'Purple Claystone Formation' shows a vertical evolution from braided river to an alluvial plain with sheet flood sand-bed and

bed-load river deposits. During this time, the Luang Prabang Basin was located around latitude 15˚S (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). The Luang Prabang ecosystem developed in a tropical wet/humid climate (Sun, 2006) and has been placed in the 'tropical everwet' biome of Rees et al. (2002) and in the 'temperate seasonal' climate belt by Roscher et al. (2008).

Only a few fragmentary remains of dicynodonts have been retrieved from the 'Red Claystone Formation', whereas the 'Purple Claystone Formation' has yielded specimens of dicynodonts and rare stem amniotes such as chroniosuchians (Counillon, 1896; Battail, 1995, 2009; Battail et al., 1995; Steyer, 2009). Although the dicynodonts have not been fully described, Battail (2009) suggested that multiple species may be present and that this fauna might display a very high degree of endemism. The Limestone and Sandstone formation also has yielded an abundant but low diversity, transported macrofloral assemblage. The flora is primarily composed of Cathaysian taxa, with sphenophytes, ferns, seed ferns and leaves resembling *Glossopteris*, similar to those described from the upper Permian deposits of the Chahe and Tucheng sections in Guizhou, South China (Bercovici et al., 2012).

4.8. Brazil

In the Paraná Basin, the lower Lopingian (Wuchiapingian) traditionally has been considered to be represented by the Morro Pelado Member of the Rio do Rasto Formation, which crops out in the municipalities of Aceguá, Serra do Cadeado and São Gabriel. Correlations among these localities, and to strata in other basins, are obscure because of uncertainties in the exact stratigraphic relationships of the individual fossiliferous outcrops, and the fact that they preserve largely distinct faunal assemblages that include taxa with contradictory biostratigraphic implications (see reviews in Boos et al., 2013, 2015). The Serra do Cadeado localities frequently have been considered to be Lopingian in age, based on the presence of the dicynodont *Endothiodon* (Barberena et al., 1985; Langer, 2000; Cisneros et al., 2005; Dias-da-Silva, 2012; Boos et al., 2013), which is found in the Lopingian *Pristerognathus*, *Tropidostoma*, and *Cistecephalus* Assemblage Zones of the Karoo Basin (e.g., Smith et al., 2012; Day et al., 2015). However, this correlation is complicated by the discovery at Serra do Cadeado of a tapinocephalid dinocephalian (Boos et al., 2015), which is a clade largely thought to occur only in the Guadalupian. The discovery of an *Endothiodon* species in likely Guadalupian strata in Tanzania (Angielczyk et al., 2014a; Cox and Angielczyk, 2015) and radiometric dates from the Karoo Basin suggest that the lower *Pristerognathus* zone is Guadalupian in age (Day et al., 2015). These issues raise questions about the Lopingian age assignment of the tetrapod-bearing horizons, given that they would imply the existence of a late-surviving dinocephalian, and also whether the localities sample a single fauna. We included the Rio do Rasto assemblage in our analyses because of the possibility that at least part of the fauna is Lopingian in age, and also because it is our sole data point for the South American portion of Gondwana. However, we acknowledge the possibility that the assemblage may be older and/or represent a collection from a greater stratigraphic range than the others we considered. Consequently, this part of our dataset may need to be reassessed as research on the Rio do Rasto Formation proceeds.

During the Lopingian, the Paraná Basin was located at a palaeolatitude of about 35˚S (Scotese, 2003; Stampfli and Borel, 2004; Zhu et al., 2005; Blakey, 2008), and the Morro Pelado Member documents the transition from delta front to delta top environments (Milani et al., 2007), deposited under an arid to extremely arid climate (Langer et al., 2008; Rohn and Rösler, 2000), with an extended dry season (Cuneo, 1996). Rees et al. (2002) attributed the Rio do Rastro ecosystem to the 'mid latitude desert' zone (see also Sidor et al., 2005; Smith et al., 2015).

The tetrapod fauna is represented by the temnospondyl amphibians *Australerpeton* and '*Rastosuchus*' of the Rhinesuchidae, the dicynodonts

Endothiodon and *Rastodon*, the non-dicynodont anomodont *Tiarajudens*, anteosaurid dinocephalians such as *Pampaphoneus*, and indeterminate taphinocephalids (Barberena and Araújo, 1975; Barberena and Dias, 1998; Dias and Schultz, 2003; Langer et al., 2008; Cisneros et al., 2011, 2012; Boos et al., 2013, 2015, 2016). Several vertebrate ichnotaxa were also documented from supposed Lopingian strata of the Rio do Rasto Formation, including *Chelichnus* Jardine, 1850, *Procolophonichnium* Nopcsa, 1923, and *Dicynodontipus* von Lilienstern, 1944, all of which are attributed to dicynodonts and other therapsids; *Rhynchosauroides* Maidwell, 1911, a neodiapsid – early saurian; and unnamed footprints tentatively attributed to amphibians (Costa da Silva et al., 2012).

The very scarce vegetation of this region includes plant macrofossils from the upper Rio do Rasto Formation and from the partially coeval Teresina Formation (e.g., Rösler, 1978; Rohn et al., 1984; Rösler and Rohn, 1984; Rohn and Rösler, 1986a, 1986b, 1997; Langer et al., 2008). The flora is dominated by glossopterid leaves and ferns with rare sphenophytes and lycophytes. Bortoluzzi (1975) also mentioned *Ginkgo*-like leaves and lycophyte remains from the upper Permian Serra Alta Formation. Glossopterids probably occupied the floodplains and channel levees while the herbaceous hygrophytic elements represented the understorey of a woodland (Cuneo, 1996). Rare insect remains also have been found in this basin (Langer et al., 2008).

4.9. Tanzania

Late Permian tetrapod fossils are preserved in two rock units, the Ruhuhu and Usili formations, in the Ruhuhu Basin of Tanzania (Angielczyk et al., 2014a). Tetrapods occur at multiple stratigraphic horizons in each formation, three in the Ruhuhu Formation and five in the Usili Formation (Sidor et al., 2010; Simon et al., 2010; Angielczyk et al., 2014a; Cox and Angielczyk, 2015). Of these, the five Usili horizons and the uppermost Ruhuhu horizon appear to be Lopingian in age, whereas the lower two Ruhuhu horizons are more likely Guadalupian in age (Angielczyk et al., 2014a). Precise interbasinal biostratigraphic correlation for the Ruhuhu and Usili formations is complicated by the fact that the Ruhuhu Basin includes a mix of endemic and widespread taxa, and the stratigraphic ranges of some widespread taxa may not correspond exactly with those in better studied areas such as the Karoo Basin (Angielczyk, 2007; Sidor et al., 2010; Angielczyk et al., 2014a, 2014b; Huttenlocker et al., 2015). Based on current understanding of stratigraphic ranges in the Ruhuhu Basin, it seems that the uppermost Ruhuhu and Usili horizons sample a single faunal assemblage (Gay and Cruickshank, 1999; Sidor et al., 2010; Angielczyk et al., 2014a), which can be correlated with the upper *Cistecephalus* and/or lower *Daptocephalus* assemblage zones of the Karoo Basin (Sidor et al., 2010; Angielczyk et al., 2014a, 2014b).

The uppermost Ruhuhu and Usili formations record a transition in depositional environment from nearshore lacustrine, through a prograding alluvial fan and, eventually, playa flat and floodplain settings, reflecting changes in subsidence and sedimentation rates in response to the regional tectonics of the basin (e.g., Kreuser and Markwort, 1988; Kreuser et al., 1990; Kaaya, 1992; Catuneanu et al., 2005; Sidor et al., 2010; Angielczyk et al., 2014a). The Ruhuhu Basin is attributed to a Permian palaeolatitudinal position of 55°S (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008; Wopfner and Jin, 2009). Reconstructed late Permian climates for the Ruhuhu Basin vary significantly. Large scale modelling has predicted cool to cold, semi-arid to arid climates (Rees et al., 2002; Roscher et al., 2008, 2011), whereas sedimentological investigations suggest a warm, dry climate (Kreuser and Markwort, 1988; Kreuser et al., 1990; Kaaya, 1992; Wopfner and Jin, 2009). The fauna is dominated by dicynodonts consisting of endothiodonts, emydopoids, cryptodonts, and dicynodontoids (52%), followed by gorgonopsians, therocephalians, cynodonts and notably abundant biarmosuchians (35%), pareiasaurs (5.5%) and amphibians (6.6%) (Peecook, 2016; see also Sidor et al., 2010).

Plant remains are largely absent from the Usili Formation, with the exception of in situ trunks of 'Palauroxylon', which are common in the lower portion of the formation (Wopfner and Jin, 2009; Angielczyk et al., 2014a). A more extensive plant record is known from the Ruhuhu Formation. Of particular note in the context of this paper is that the uppermost, tetrapod-bearing horizon of the Ruhuhu Formation falls within the *Glossopteris* beds of Kaaya (1992). These strata have produced fossils of *Glossopteris*, *Vertebraria*, *Gangamopteris*, sphenophytes, and silicified wood (Kaaya, 1992). This flora provides a useful snapshot of the plant community that was contemporaneous with the Ruhuhu and Usili tetrapods.

4.10. Malawi

The late Permian fauna from Malawi is documented in the fluviolacustrine deposits of the Chiweta Beds in northern Malawi, which are considered to be age-equivalent to the *Cistecephalus* Assemblage Zone (Fröbisch, 2009). Northern Malawi was positioned at a palaeolatitude of 55°S during the late Permian (Yemane, 1994; Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). Climate models suggest a temperate to cool, seasonal climate (Yemane, 1994; Rees et al., 2002; Roscher et al., 2008). The faunal assemblage is dominated by dicynodonts (47%) that consist of endothiodonts, emydopoids, cryptodonts, and dicynodontoids, and gorgonopsians (35%), with rare temnospondyls (9%), and a single biarmosuchian and a single therocephalian (Haughton, 1926; Keyser, 1975; Jacobs et al., 2005; Fröbisch, 2009; Kurkin, 2011; Sidor et al., 2013; Kruger et al., 2015). Plant macroremains are mostly represented by *Glossopteris* leaves, *Vertebraria* roots and *Paracalamites* stems. Palynomorphs are dominated by striate bisaccate, polyplicate and monosaccate pollen (e.g., *Densipollenites*, *Guttulapollenites*, *Striatopodocarpites*, *Vittatina*), characteristic elements of the late Permian *Glossopteris* flora in Gondwana, whereas spores are under-represented and constitute < 5% of the palynoflora (Yemane, 1994).

4.11. Zambia

In Zambia, the Lopingian is represented by the Upper Madumabisa Mudstone Formation in the Luangwa Basin, a rift basin that was active during the Permian and Triassic (Banks et al., 1995; Catuneanu et al., 2005). Depositional environments include alluvial plains with low to high sinuosity river channels and ponds, as well as facies that likely represent subaqueous deposition in an axial lake (Drysdall and Kitching, 1963; Yemane and Kelts, 1990; Banks et al., 1995). Tetrapod fossils appear to have accumulated during episodic flooding events of a vegetated floodplain (Drysdall and Kitching, 1963; Angielczyk et al., 2014b). It was long thought that multiple, discrete Permian faunal assemblages were preserved in the Upper Madumabisa Mudstone (see reviews in Fröbisch, 2009; Angielczyk et al., 2014b), but comparisons of dicynodont occurrences in different parts of the basin suggest that a single assemblage is present (Angielczyk et al., 2014b). The ecosystem developed at a palaeolatitude of about 50–60°S in the continental interior of Gondwana (Yemane et al., 2002). Different ecological models have produced different climatic hypotheses: Yemane et al. (2002) suggested a cool to moderately warm climate with abundant moisture, Rees et al. (2002) attributed Zambia to the cold temperate zone, and Roscher et al. (2011) advocated that the region was a cold desert to cold steppe region. The Upper Madumabisa Mudstone Formation assemblage is dominated by a diverse dicynodont fauna of pylaecephalids, endothiodonts, emydopoids, cryptodonts, and dicynodontoids (80%), followed by faunivorous therapsid groups (gorgonopsians, therocephalians, cynodonts, biarmosuchians, 16%), pareiasaurs (2.7%), amphibians (0.4%), and a single specimen referred to Capthorinidae (0.1%) (Peecook, 2016). Angielczyk et al. (2014b) correlated the fauna with the *Cistecephalus* Assemblage Zone of the Karoo Basin. Taking into account the biostratigraphic revision of Viglietti et al. (2016), which moved the lower boundary of the *Daptocephalus* Assemblage Zone of the Karoo Basin downwards, it is now likely that the Upper Madumabisa

Mudstone Formation fauna correlates with parts of the *Cistecephalus* and lower *Daptocephalus* zones.

The Upper Madumabisa Mudstone Formation also has yielded an extensive record of fossil plants, pollen and wood suggestive of a rich glossopterid woodland (Barbolini et al., 2016). The palynoassemblage discovered in the Luangawa Basin is dominated by *Lueckisporites nya-kapendensis, Vittatina africana, Guttulapollenites hannonicus, Densipolle-nites indicus* (Utting, 1970, 1976; Barbolini et al., 2016). A *Glossopteris* macroflora was reported in the Luangwa area by Bond (1954), Gair (1959, 1960) and Drysdall and Kitching (1963), who described *Glos-sopteris indica* (Brongniart) Schimper, 1869, *Gangamopteris cyclopter-oides* Feistmantel, 1876, *Noeggerathiopsis hislopi* Feistmantel, 1879, *Sa-maropsis* sp. and fossil wood attributed to cf. *Dadoxylon bougheyi* Williams (Utting, 1970; Barbolini et al., 2016).

4.12. India

The red mudstones of the Kundaram Formation that crop out in the Pranhita-Godavari Valley document the formation of channel–interch-annel deposits in an extensive floodplain setting (Sengupta, 1970; Ray, 1999). The environment represented by the Kundaram Formation de-veloped at a palaeolatitude of about 55–60˚S (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008; Wopfner and Jin, 2009). The climate of this region during the Lopingian has been reconstructed as warm and moist, with seasonal rainfall (Behrensmeyer and Hook, 1992). Ac-cording to Rees et al. (2002), the Kundaram ecosystem sits within the 'cool temperate' zone (see also Sidor et al., 2005; Smith et al., 2015), and based on the work of Roscher et al. (2008, 2011), well within a 'cool' boreal area at the border between 'everwet' and 'seasonal' cli-matic zones.

The fauna is dominated by small, medium and large sized dicyno-donts (85.5%), followed by gorgonopsians (9.7%) and captorhinids (4.8%) (Kutty, 1972; Ray, 2000, 2001; Ray and Bandyopadhyay, 2003; Kammerer et al., 2016). The recent recognition that specimens pre-viously referred to *Emydops* and *Cistecephalus* actually represent a new cistecephalid genus (*Sauroscaptor tharavati*; Kammerer et al., 2016), has increased the level of endemism displayed by the Kundaram Formation assemblage. A correlation with the *Tropidostoma* and *Cistecephalus* As-semblage Zones of the Karoo Basin (Fröbisch, 2009; Kurkin, 2011) has been proposed, albeit most of the taxa in the assemblage are either endemic or stratigraphically long-ranging in the Karoo, making an exact correlation difficult. The Kundaram Formation also preserves a typical *Glossopteris* flora (Pascoe, 1959; Robinson, 1970; Ray, 1999), reconstructed as a glossopterid forest with an abundant fern under-storey. The coeval Raniganj Formation yielded a *Glossopteris*-rich plant assemblage with additional sphenophytes (Ray, 1999). The slightly younger Handapa Flora from the Kamthi Formation of the Godavari Basin is a rich and diverse fossil-plant assemblage (Chandra and Singh, 1992; Chandra et al., 2008; Joshi et al., 2014), and is dominated by glossopterids (up to 60%), followed by sphenophytes (~7%), ferns (~5%), cycadophytes (3%), corystosperms (3%), ginkgophytes (2%), peltasperms (1%), cordaitaleans (1%), conifers (1%) and lycophytes (< 1%).

4.13. South Africa

The upper Permian portion of the Permo-Triassic Beaufort Group of the Karoo Basin in South Africa represents by far the best-known por-trait of late Permian terrestrial ecosystems and their geological context (e.g., Anderson and Anderson, 1985; Rubidge, 2005; Catuneanu et al., 2005; Roopnarine et al., 2007; Prevec et al., 2009; Smith et al., 2012; Rubidge et al., 2013, 2016). This vast basin covers more than half of the surface area of South Africa, and it contains a near-continuous strati-graphic record of the late Permian. Here we focus on the four bios-tratigraphic assemblage zones spanning the latest Capitanian to Changhsingian (Rubidge et al., 2013; Day et al., 2015; Gastaldo et al.,

2015), at which time the Karoo was located around 60–65˚S latitude (Scotese, 2003; Stampfli and Borel, 2004; Blakey, 2008). The deposi-tional environment varies from large meandering channel belts to a network of numerous smaller channels with low sinuosity, punctuated by episodes of overbank sedimentation (e.g., Smith et al., 1993; Catuneanu et al., 2005; Prevec et al., 2010; Smith and Botha-Brink, 2014). The late Permian Karoo climate is generally reconstructed as arid (Retallack et al., 2003, 2006; Ward et al., 2005), although Cuneo (1996) suggested a temperate climate with a strong dry season, based on the absence of peat-forming horizons. However, the diversity of the Lopingian floras of KwaZulu-Natal, which grew in huge meandering river systems (Gastaldo et al., 2005), suggests a slightly wetter en-vironment (Lacey et al., 1975; Anderson and Anderson, 1985; Prevec et al., 2009; Li et al., 2017; Gastaldo et al., 2017). New sedimentolo-gical, palaeopedological and palaeobotanical analyses support at least seasonally moist to possible waterlogged edaphic conditions in some areas (Tabor et al., 2007; Prevec et al., 2010). Rees et al. (2002) at-tributed the Karoo Basin to the 'cool temperate' zone, whereas the numerical model of Roscher et al. (2008, 2011) assigned it to the 'cold steppe' biome.

An exceptional number of late Permian vertebrate remains has been collected from the Beaufort Group (Nicolas and Rubidge, 2010; Smith et al., 2012). The diversity and abundance of these fossils, combined with the lithological homogeneity of Beaufort Group strata, has led to a long history of subdivision of the group into biostratigraphic zones (Day, 2013). In the context of this paper, the faunal assemblages pre-sent in the currently-recognised biostratigraphic assemblage zones are useful units for ecological comparisons.

The oldest late Permian assemblage is the *Pristerognathus* Assemblage Zone of late Capitanian to earliest Wuchiapingian age, re-presented principally by medium-sized dicynodont herbivores (87.5%), and subordinately by the small-sized therocephalian carnivores (7.5%) and large sized parareptiles herbivores (3%) (Smith et al., 2012). The *Tropidostoma* Assemblage Zone of early Wuchiapingian age is almost completely dominated by medium-sized dicynodont herbivores (96%), whereas the remaining 4% consist of large-sized gorgonopsian carni-vores (1.9%), parareptiles (0.6%), small-sized amphibians, reptiles and synapsids such as the fish-eating temnospondyls, plant-eating captor-hinids, and flesh-eating therocephalians (Smith et al., 2012). The *Cis-tecephalus* Assemblage Zone of Wuchiapingian *pro parte* age is still marked by the clear predominance of medium-sized, herbivorous di-cynodonts (92%), with low percentages of small and large carnivores that include gorgonopsians (4%), therocephalians (1.2%), and small carnivorous to large herbivorous parareptilians (1.7%). The remaining 1% is subdivided among medium-sized carnivores (cynodonts and biarmosuchians), small-sized fish-eating amphibians (temnospondyls), and neodiapsids (Smith et al., 2012). Smith et al. (2012) tabulated data for the then-current *Dicynodon* Assemblage Zone, which corresponds to the lower *Daptocephalus pro parte* and upper *Daptocephalus* Assemblage Zones of Viglietti et al. (2016), assigned to late Wuchiapingian to Changhsingian time. This assemblage, in comparison to that of the *Cistecephalus* Assemblage Zone, has fewer medium-sized herbivores such as dicynodonts (77%), but higher percentages of small and large carnivores such as gorgonopsians (3%); therocephalians (9%), and comparable numbers of large herbivorous parareptilians (3%), and medium-sized carnivorous cynodonts (5%). The remaining 3% is sub-divided among medium-sized carnivorous and small fish-eating am-phibians such as temnospondyls and neodiapsids (Smith et al., 2012). Eleven vertebrate footprint specimens, consisting of single prints or trackways, have been attributed to dicynodonts and pareiasaurs (MacRae, 1990; Smith, 1993b; De Klerk, 2002).

The macroflora of the southern Karoo Basin is less diverse than the tetrapod assemblages, an observation that likely is due to taphonomic factors and, possibly, low sampling levels in certain areas. In KwaZulu-Natal preservation is better and diversity is higher (Lacey et al., 1975; Anderson and Anderson, 1985; Gastaldo et al., 2005; Prevec et al.,

2009, 2010). Although most available data for the southern Karoo Basin originates from the highest part of the Permian succession, the flora is generally dominated by glossopterids (both leaves and reproductive organs). Additional elements are stem and leaf remains of sphenophytes and gymnosperm wood (*Agathoxylon*). Rare, allochthonous elements are sphenopterid fragments during the late Permian (Gastaldo et al., 2005; Prevec et al., 2009, 2010). The dominance of glossopterids also is reflected in the palynoflora, but the microflora also includes intrabasinal elements such as sphenophytes, ferns and conifers and extrabasinal elements such as peltasperms and corystosperms (Gastaldo et al., 2005; Prevec et al., 2009). The environment therefore can be reconstructed as a low-diversity glossopterid-dominated woodland, with the understorey predominantly populated by sphenophytes and ferns and additional peltasperms, corystosperms and conifers as either subsidiary or non-local elements, some during the latest Permian (Prevec et al., 2009). The Karoo (and Karoo-type; see below) floras show a clear Gondwanan affinity.

Plumstead (1963) examined patterns of plant–insect interactions at the Vereeniging locality, immediately south of Johannesburg. The rich record of plant–insect interactions primarily consist of external foliage feeding by mandibulate orthopteroid insects, with lower incidences of piercing and sucking and oviposition presumably by palaeodictyopteroid and odonatopteroid taxa, respectively. Evidence for galling and seed predation is rare. Likely because of their dominance in the flora, glossopterid taxa are the most intensively herbivorised plants, primarily by external foliage feeders and ovipositing insects. However, qualitatively insect damage on glossopterid foliage appears to exceed that predicted by floristic abundance alone, demonstrating a preferential targeting of seed ferns at Vereeniging and Clouston Farm localities (Plumstead, 1963; Prevec et al., 2009, 2010). Lopingian insect body fossil remains are scarce and include a variety of early appearing orthopteroid taxa such as the Liomopteridae, stenorrhynchian nymphs of the Hemiptera and archostematan beetles (Coleoptera) (Riek, 1974, 1976; Van Dijk, 1981, 1998; Geertsema and van den Heever, 1996; Van Dijk and Geertsema, 1999; Geertsema and van Dijk, 1999; Prevec et al., 2010).

5. Late Permian biogeography

It has generally been assumed that terrestrial vertebrate faunas were homogeneous during the late Permian (Sues and Boy, 1988; Rage, 1988; Milner, 1993; Dilkes and Reisz, 1996). Dicynodonts, for example, achieved a Pangaean distribution during this time (King, 1988, 1992); their remains are found in Gondwana and Laurussia (Fröbisch, 2009; Kurkin, 2011). Basal dicynodontoids, that is *Dicynodon*-grade species, have been reported from South Africa, Zambia, Tanzania, Laos, China, Scotland, and Russia, and a similar distribution has been documented for Pylaecephalidae, with the iconic species *Diictodon feliceps* being reported from South Africa, Zambia and China (Angielczyk and Sullivan, 2008; Fröbisch, 2009). Cryptodont remains have been found in South Africa, Madagascar, India, Zambia, Malawi, China, Russia and Scotland (Fröbisch, 2009; Kammerer et al., 2011; Kurkin, 2011). Recent phylogenetic analyses have shown close relationships between dicynodont genera across Gondwana and Laurussia (Angielczyk and Kurkin, 2003; Kammerer et al., 2011; see also Huttenlocker et al., 2015). Likewise, pareiasaur faunas exhibit close similarities among China, Russia, South Africa and Western Europe, with an absence of geographically restricted subclades, providing additional evidence for cross-Pangaean dispersal (Benton, 2016). The nearly global distribution of cynodonts, such as *Procynosuchus*, led Sues and Munk (1996) to conclude that there were 'no major topographic and climatic obstacles for faunal exchange between the northern and southern regions of Pangaea' during this time interval (Sues and Munk, 1996, p. 221; see also Sues and Boy, 1988). The gorgonopsian *Sauroctonus* was present in both Russia and Tanzania (Gebauer, 2014), and several pairs of therocephalian sister genera existed between Russian and African basins

(Huttenlocker et al., 2015; Huttenlocker and Sidor, 2016). Sidor et al. (2013) supported the idea of a homogeneous and broadly distributed fauna in southern Gondwana during the late Permian. This pattern seems to have continued into the earliest Triassic, with the cosmopolitan dicynodont *Lystrosaurus* being present throughout much of Gondwana, as well as Russia and China (e.g., King, 1990; Battail and Surkov, 2000; Lucas, 2001; Surkov et al., 2005; Fröbisch, 2009).

Other authors provided evidence for provincialism, with or without endemism, among terrestrial faunas during the Lopingian (Modesto et al., 1999; Modesto and Rybczynski, 2000; Angielczyk and Kurkin, 2003; Abdala and Allinson, 2005; Angielczyk, 2007; Germain, 2010; Sidor et al., 2013; Angielczyk et al., 2014b; Huttenlocker and Sidor, 2016; Huttenlocker et al., 2015). Many of these authors concluded that late Permian faunal homogeneity probably is an oversimplified concept (Sidor et al., 2005). Indeed, temnospondyls and lepospondyls developed high levels of endemism (Sidor et al., 2005; Steyer et al., 2006; Germain, 2010), and emydopoid and endothiodont dicynodonts were restricted to the Gondwanan regions of South Africa, Tanzania, Zambia, India, Mozambique, and Brazil (Fröbisch, 2009; Kurkin, 2011). If comparisons are made at the species and genus levels, it turns out that none of the Russian Permian dicynodonts are found in Gondwana, and vice versa (Angielczyk and Kurkin, 2003; Kammerer et al., 2011). Endemism probably was low during the early Permian, at least in the tropics (Cisneros et al., 2015), and increased during the middle and late Permian as a consequence of warming and aridification across Pangaea (Steyer et al., 2006), when the distribution of faunas became more strongly controlled by latitudinal differentiation of climatic regions (Sidor et al., 2005). A similar pattern was proposed for floral associations (Willis and McElwain, 2002).

How do ecosystem-scale comparisons add to or modify these conclusions? Our focus here is on the overall composition of the ecosystems, particularly the relative abundances of higher clades, and not genus or species (alpha level) taxonomic similarity, which has been investigated in other studies (e.g., Fröbisch, 2009; Sidor et al., 2013; Benton, 2016). The choice to use higher taxonomic groups is driven by the scale of the goals and by the resolution of our source data. For example, ichnological data can be used reliably only at high taxonomical levels, and dietary hypotheses are available in the literature for coarse-grained groups only (Munk and Sues, 1993; Dodick and Modesto, 1995; Lee, 1997; Cox, 1998; Sues and Reisz, 1998; Wilson and Carrano, 1999; Reisz and Sues, 2000; Carrano and Wilson, 2001; Roopnarine et al., 2007; Smith et al., 2012; Smith et al., 2015; Bernardi et al., 2016).

By plotting faunal composition against latitude, some trends can be observed (Fig. 6). The most diverse assemblages are those at mid to low latitudes, whereas those at higher latitudes (Junggar and Karoo), although rich in fossils, are much less diverse. This pattern emerges because higher latitude communities are heavily dominated by a small number of therapsid higher taxa, such as Dicynodontia, Gorgonopsia and Therocephalia, whereas low latitude communities are composed of a mixture of therapsids, late-surviving members of clades better known from the early Permian (especially captorhinids and some temnospondyls), and early members of taxa that become more common in the Triassic communities following the end-Permian mass extinction (illustrated by archosauriforms represented by footprints in the Bletterbach assemblage). Maximum floral diversity has been hypothesised to have shifted from low latitudes during the early Permian to middle to high latitudes in the late Permian (Rees, 2002). Given the comparatively poor sampling of many important late Permian terrestrial ecosystems, it is difficult to fully resolve whether these geographic shifts in diversity are true empirical patterns or stem from preservation bias or a lack of adequate sampling (as observed by Prevec et al., 2010). However, growing knowledge of the diversity of the Niger fauna (Sidor et al., 2005; Smith et al., 2015) and the Bletterbach biota, provide evidence for higher diversity in low-latitude ecosystems (cf. Rees, 2002), suggesting that additional research efforts focused on low-latitude regions
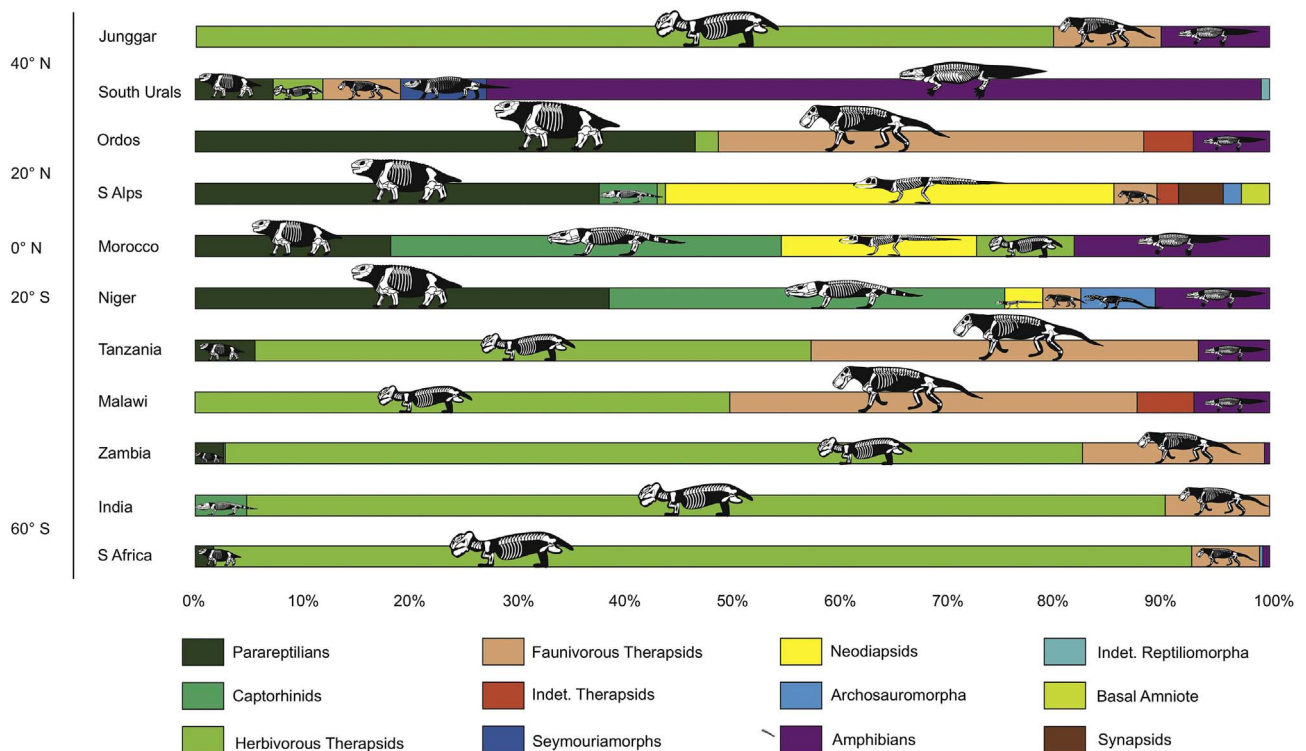
Fig. 6. Faunal composition and relative abundances in the 14 best-documented late Permian terrestrial ecosystems, plotted against palaeolatitudes. Lopingian latitudinal gradient shows poleward decline in tetrapod richness at high taxonomic levels.

might result in key discoveries.

The relative abundances of three major groups of herbivores, dicynodonts, pareiasaurs and captorhinids, is clearly structured. The highest percentage of herbivorous dicynodonts in the associations is at high palaeolatitudes: 80% in the Junggar Basin of China, 92% in India, and 75–95% in South Africa. By contrast, the lowest percentage, including complete absences, occur in tropical and subtropical regions, with few exceptions, such as possible dicynodont tracks from the Bletterbach (2%), and a few specimens from Scotland, South China and Laos (Conti et al., 1977; Newton, 1893; Benton and Walker, 1985; Bercovici et al., 2012). King (1992) suggested that dicynodonts were adapted to exploiting components of the Gondwanan flora, but their occurrence in Laurussia, particularly Russia and China, indicates that this was not the sole factor for determining their distribution (Angielczyk and Sullivan, 2008). However, when superimposed on late Permian floral palaeobiogeography, the distribution and relative abundance of dicynodonts does indeed appear to mirror the distribution of Gondwanan- and Angaran-dominated floras (Cuneo, 1996; Cox, 1998). Rees et al. (2002) proposed that the relatively dominant *Glossopteris* (Gondwana) and 'Cordaites' (Angara) taxa might represent possible ecological analogues, though the taxonomic confusion surrounding late Permian 'Cordaites' (Taylor et al., 2009) complicates testing this hypothesis. Alternatively, if a more specialised diet for dicynodonts is postulated, the lowest common denominator could be sought for all floral assemblages associated with their presence. In this case, ferns and sphenophytes have a common presence (see also Rees et al., 2002), a correlation that echoes Rayner's (1992) proposed association of dicynodonts and sphenophytes. This association is indicated when abundances are considered: where ferns and sphenophytes were more abundant in the Gondwanan and Angaran floras, dicynodonts also were dominant; in contrast, where ferns and sphenophytes were less abundant, as in the Euramerican flora, dicynodonts were rarer. The high variety of sphenophytes and ferns in the Cathaysian flora however clashes with this hypothesis, since only few dicynodonts have been discovered in this area, mostly in northern China and Laos (Bercovici et al., 2012). However, these areas

are understudied compared to other, better researched regions such as southern Africa or Russia, so their dicynodont diversity may be underestimated. Nevertheless, a climatic constraint appears crucial: dicynodonts were best adapted to cool-temperate climates, for example the 'desert cold' and 'steppe cold' of Roscher et al. (2008), where glossopterid or conifer dominated woodlands with a sphenophyte and fern understorey were present.

Pareiasaurs display a global distribution ranging from South Africa (2–3%) to Russia (14–19%), but they are most abundant in tropical and equatorial ecosystems such as the Ordos Basin of north-central China (47%), Bletterbach of northeastern Italy (38%), Morocco (18%) and Niger (55%) (Fig. 6). As noted above, pareiasaurs may have fed on high-fibre vegetation (Munk and Sues, 1993; Lee, 1997; Reisz and Sues, 2000). Smith et al. (2015) hypothesised that Karoo pareiasaurs probably grazed the lycopods and sphenophytes that flourished along and within floodplain channels. However, these two plant groups are poorly represented at low-latitude sites of central Pangaea, such as Niger, Morocco and the Southern Alps, where pareiasaurs dominated the ecosystems. In these geographical regions, a Euramerican flora prevailed, where ginkgophytes and conifers would have constituted the majority of high-fibre plants. Conifers and ginkgophytes are absent in several sites where pareiasaurs have been found, namely in the Ordos (DiMichele and Phillips, 1996) and Karoo (Prevec et al., 2010) basins, and are minor floral constituents of the southern Urals (Wang, 1985, 1996). If the distribution and abundance of pareiasaur remains versus floral assemblages is plotted, the lowest common denominator is again represented by ferns, but they are nearly or completely absent in the Niger and Bletterbach floras (Looy et al., 2016; Kustatscher et al., 2012, 2014, 2017). In summary, pareiasaur distribution best – although not perfectly – correlates with the distribution of conifer and ginkgophyte woodlands that developed in tropical wet and warm temperate climates of equatorial to sub-equatorial Pangaea, ('tropics seasonal' and 'temperate seasonal' of Roscher et al., 2008).

The captorhinid distribution pattern is similar to that of the pareiasaurs (Fig. 6), with captorhinids contributing appreciable faunal

diversity in the Moroccan (36%), Nigerian (21%) and Bletterbach (5%) ecosystems. Like pareiasaurs, captorhinids preferentially may have fed on highly fibrous plant material (Dodick and Modesto, 1995; Hotton et al., 1997; Reisz and Sues, 2000), such as sphenophytes and seed ferns (Benton et al., 2004). Seed ferns are well represented in the Bletterbach, but not in the Nigerian and Moroccan floral associations, although the latter are still poorly known. Notably, pareiasaurs and captorhinids show a similar pattern of relative abundance in these ecosystems. Their co-occurrence in appreciable numbers in the same low-latitude ecosystems might suggest the occupancy of different niches in these environments. By contrast, captorhinids are always more abundant than dicynodonts and other therapsids in these ecosystems, suggesting a possible competitive displacement or preference for different plants. When superimposed on climatic zones, captorhinid distribution best correlates with the semi-arid to arid conditions of the tropical wet biome, the 'tropics seasonal' and 'desert hot' of Roscher et al. (2008), where they might have fed on seed ferns and conifers.

Carnivorous tetrapods, presumably less dependent on the distribution of floral types, exhibit a less clear pattern of distribution (Fig. 6). Faunivores, including those specialising in tetrapods, fish or insects, are much more abundant in low-latitude ecosystems. The herbivore-to-carnivore ratio is about 1:1 in the Morocco, Ordos and Southern Alps ecosystems and ca. 3:1 in the Niger ecosystem. The herbivore-to-carnivore ratio greatly increases in high latitude ecosystems reaching, for example, a 5:1 ratio in the *Cistecephalus* Assemblage Zone of the Karoo Basin, and an 8:1 ratio in the Junggar and Upper Madumabisa Mudstone faunas. Being dominated by amphibians, the Russian records show a large predominance of fish eaters. The low abundances of herbivores compared to carnivores in the low latitude ecosystems resemble those of early Permian ecosystems (Olson, 1966; Hotton et al., 1997; Reisz and Sues, 2000). The transition to modern community structure, characterised by very abundant tetrapod herbivores, generally has been posited to have occurred during the late Permian (e.g., Olson, 1966). Our results, as well as other observations of early Permian communities with abundant tetrapod herbivores (Eberth et al., 2000; Berman et al., 2014), suggest that this transition was protracted and that our picture of 'typical' community types for different time intervals is strongly influenced by patterns of geographical sampling.

By compiling both tetrapod skeletal and footprint data at family and (sub)order levels for the ecosystems discussed above, we also tested correlations between floral and faunal associations as well as their patterns of geographical variability. For each of the 14 ecosystems, we coded the relative abundance of the principal plant groups of lycophytes, sphenophytes, ferns, peltasperms, glossopterids, other seed ferns, taeniopterids, ginkgophytes and conifers, as well as the major tetrapod groups of dicynodonts, gorgonopsians, pareiasaurs, and captorhinids. Through cluster analysis (see Supplementary Material for details), we produced three dendrograms that were plotted on Lopingian palaeomaps for: i) abundance of faunal groups in the ecosystems (Fig. 7), ii) abundance of plant groups in the ecosystems (Fig. 8), and iii) whole ecosystems that include faunal and flora data (Fig. 9).

Faunal and flora abundances do not show the same pattern. Faunas, as discussed above and first presented by Sidor et al. (2005), display a latitudinal correlation with Austral mid- to high-latitude associations of the Karoo-type and Laos being compositionally more similar to high-latitude boreal associations such as the Junggar Basin than to low-latitude Gondwanan faunas. A Euramerican association constitutes a single cluster, and low-latitude (inter-tropical) associations form another distinct cluster, with a Niger and Morocco association clustering with the Southern Alps Bletterbach assemblage. Floral data, by contrast, produces a dendrogram that highlights the affinity of Austral mid- to high-latitude associations such as the Karoo Basin and Laos, which form a single cluster to the exclusion of all boreal and low-latitude Gondwanan associations. The Euramerican and north Gondwana assemblages cluster together, and support the close affinity of the Niger and

Morocco floras with those from Europe and Russia. Caution should be used, given the paucity of floral data for northern Gondwana, although this pattern is supported by both floral and faunal data.

The dendrogram based on whole-ecosystem composition data (Fig. 9) shows two main clusters. One cluster includes ecosystems of the Southern Hemisphere only [(((Zambia, Malawi), Laos) Karoo) (India, Brazil), Tanzania)], whereas the other groups boreal ecosystems + Niger: [(((Morocco, Niger) ((South Urals, Zechstein), Southern Alps)), (Ordos, Junggar))]. The ((Zambia, Malawi), Laos) cluster is mainly bounded by faunal affinity, especially Malawi and Zambia, which are united by the dominance of dicynodonts. The scarcity of floral data available for all three regions adds little information to the cluster analysis beyond a general *Glossopteris* affinity with secondary sphenophytes. Brazil and India are grouped both for their faunal similarities, expressed as dicynodont-dominated with secondary gorgonopsids, and floral similarities, expressed as *Glossopteris* dominance with secondary ferns, and sphenophytes. Tanzania and the Karoo Basin are closely related to the former cluster by similar faunal elements, with dicynodonts dominant, and secondarily dominant gorgonopsians and rare pareiasaurs. This austral cluster groups all ecosystems from the cold steppe biome of Malawi, Zambia and the Karoo Basin; the boreal seasonal biome of India; the mid-latitude desert biome of Brazil and Tanzania; and the desert tropical wet biome of Laos. The other major cluster shows Morocco and Niger mainly united by their similar faunas with dominant captorhinids and pareiasaurs. While the floral records are scarce and do not provide definitive data for further analysis, the two are marked by the presence of conifers. The ((Southern Urals, Zechstein), Southern Alps) cluster is mainly grouped on the basis of floral similarity, with abundant peltasperms, conifers, and well-represented ginkgophytes (e.g., Schweitzer, 1986; Uhl and Kerp, 2002; Naugolnykh, 2005; Karasev and Krassilov, 2006; Lozovsky et al., 2016; Kustatscher et al., 2017). The relative abundance of pareiasaurs also links the Southern Alps, South Urals and the Zechstein, although the latter two are characterised by the presence of dicynodonts in higher abundance compared to the Southern Alps. This low to mid latitude boreal cluster is then associated with Morocco and Niger to form the (((Morocco, Niger) ((South Urals, Zechstein), Southern Alps)) cluster. This larger group is conifer- and pareiasaur-dominated, and the two sub-groups share the abundance of captorhinids in the Southern Alps, Morocco and Niger, which provides a strong clustering attractor in the analysis.

Traditionally, floras from the Zechstein, South Urals and Southern Alps have been described as similar, comprising a 'European' biome (Gothan, 1930; Ziegler, 1990; Rees et al., 2002). However, the single Moroccan record (Hminna et al., 2012), and the recent discoveries in Niger (Looy et al., 2016), also provide evidence for the affinity of these two African sites with the European ones. Together, these assemblages all share the common presence of voltzialean conifers, allowing the recognition of a 'paratropical' biome, as suggested by Looy et al. (2016). Faunal data strongly support this hypothesis, with strong compositional similarities between assemblages from Morocco, Niger (Sidor et al., 2005; Voigt et al., 2010; Smith et al., 2015) and the Southern Alps (this study).

The Ordos and Junggar biotas are grouped by their floral similarity, and are linked to the ((Morocco, Niger) ((South Urals, Zechstein), Southern Alps)) cluster by the presence of conifers and pareiasaurs (Wang, 1985; Wang and Wang, 1986; Schweitzer, 1986; Uhl and Kerp, 2002; Sun, 2006; Hminna et al., 2012; Kustatscher et al., 2017). This boreal + Niger cluster exclusively includes two biomes: the desert hot and the cold steppe, which have aridity as a common feature. The affinity of boreal and austral high latitude faunas, however, does not hold when the whole-ecosystem analysis is performed, implying that latitudinal affinity is stronger than climatic relatedness.

In summary, our ecosystem-scale investigation highlights that late Permian terrestrial associations were structured and provincialised at high taxonomic levels, principally because they show clear compositional trends and zonation patterns. The evolution of both floral and
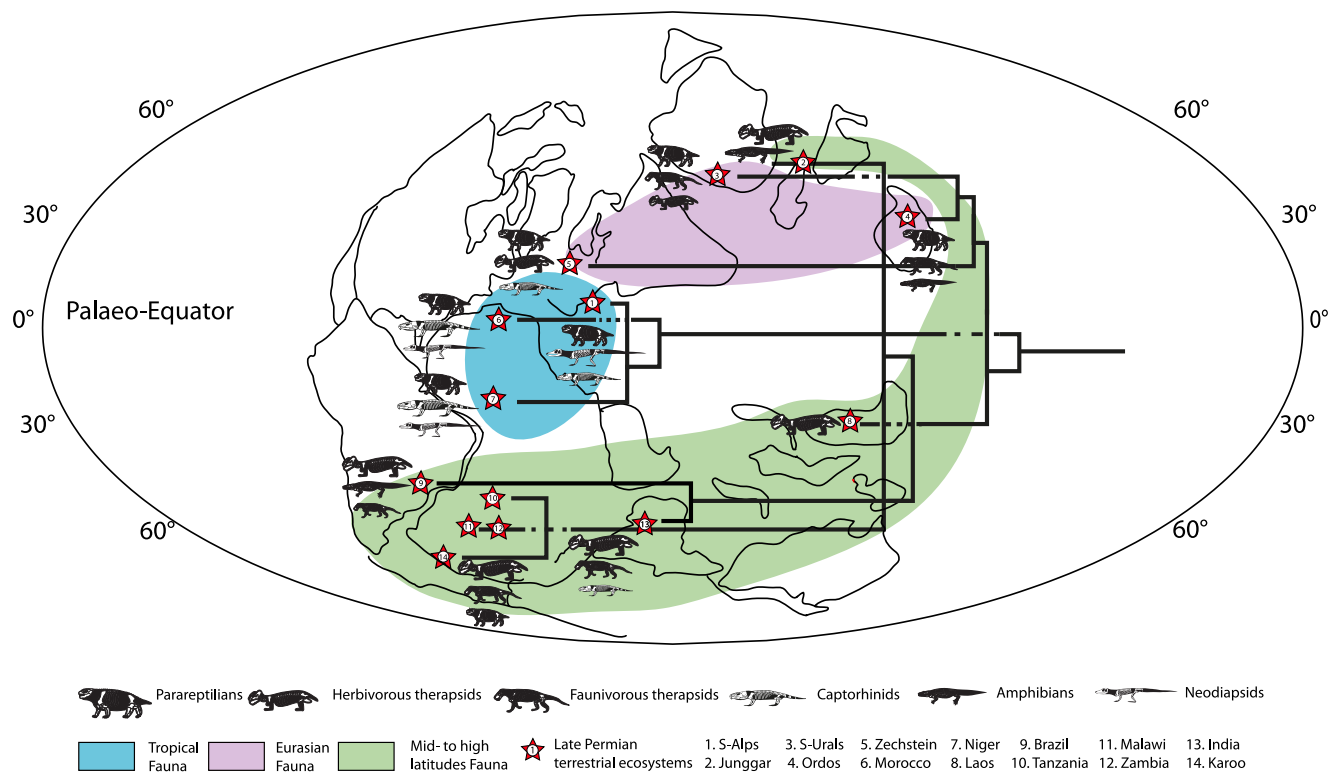
Fig. 7. Faunal affinities of the 14 best-documented Lopingian ecosystems based on relative abundance of the main tetrapod groups. Cluster analysis highlights a three-fold subdivision of tetrapods into tropical, Eurasian, and mid- to high-latitude faunas.
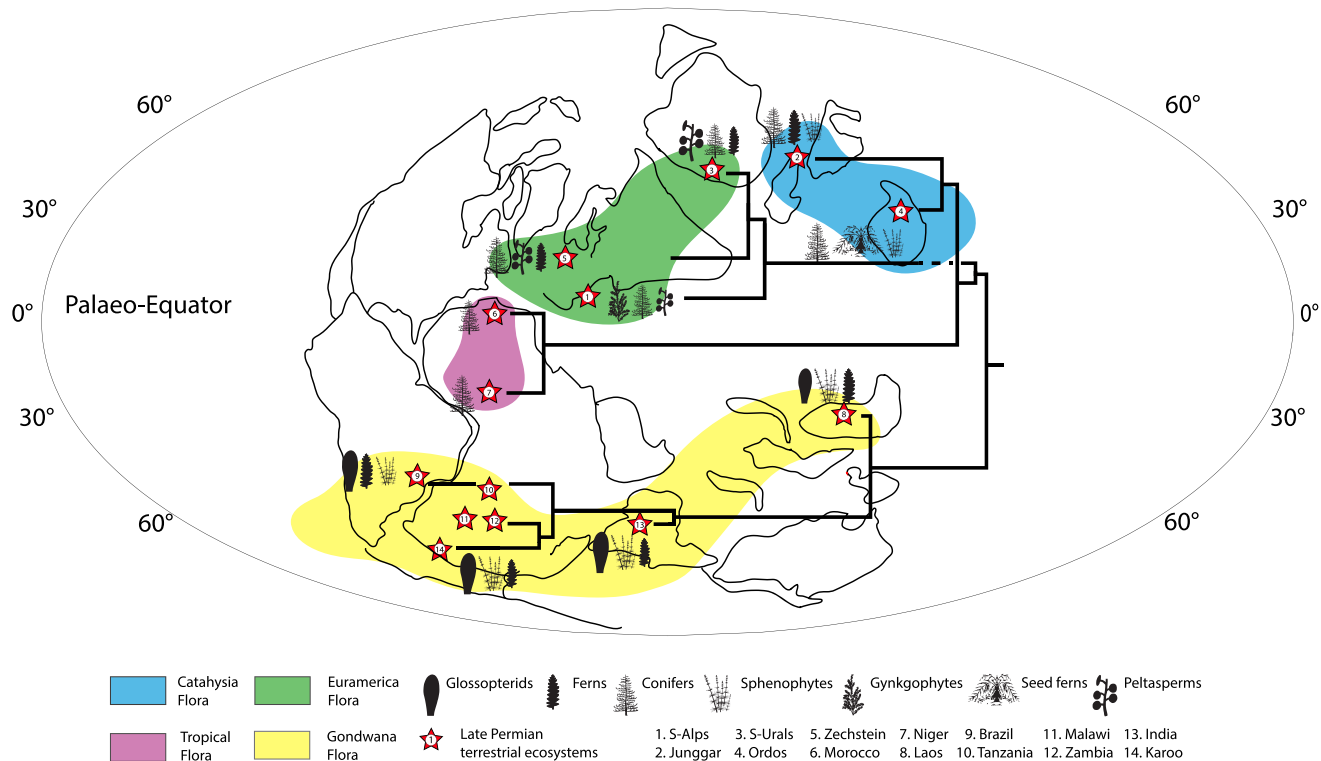

Fig. 8. Floral affinities of the 14 best-documented Lopingian ecosystems based on relative abundance of the main plant groups. Cluster analysis recovers a deep dichotomy between boreal and austral associations, but highlights the Eurasian affinity of northern Gondwana floras.
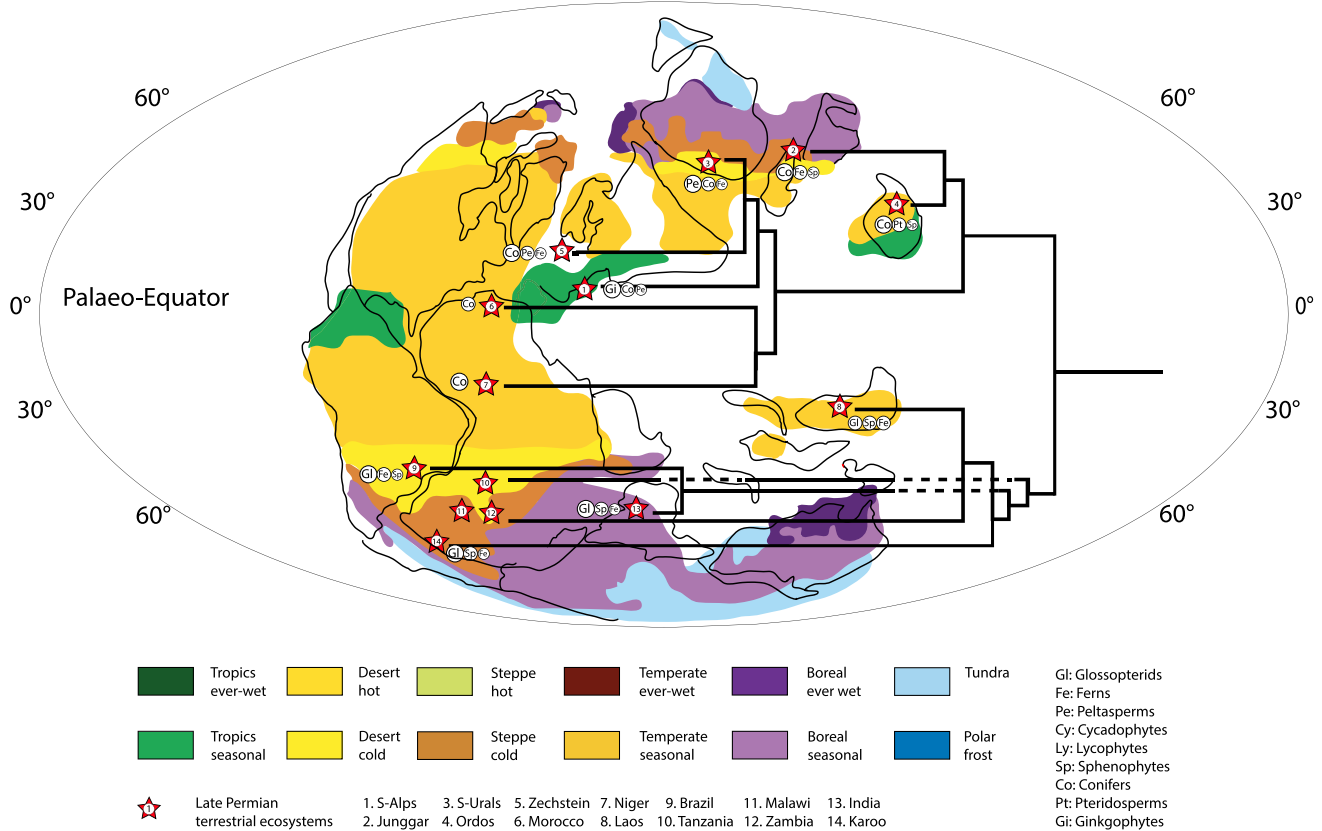
Fig. 9. Whole ecosystem affinities based on relative abundance of the main faunal and floral groups. Climate, latitude and tectonic history control the affinity of the 14 best-documented Lopingian ecosystems. Note in particular the Eurasian affinity of north Gondwana ecosystems and the southern affinity of south Cathaysian (Laos) ecosystems.

faunal bioprovinces (Milner, 1993; Sidor et al., 2005) was probably driven by the development of climate regimes (Rees, 2002; Sidor et al., 2005; Roscher et al., 2008), although latitudinal distribution was a strong predictor of ecosystem compositional affinity. North Gondwanan ecosystems (Morocco, Niger) had closer affinities with Euramerican ecosystems (Southern Alps, Zechstein, South Urals) than to south Gondwanan (Karoo Basin, India, Brazil) ecosystems. The presence of communities with mixed compositions along the northern Pangaean coast had been observed already for the plant assemblages; for example, in Turkey, the Arabian Peninsula, New Guinea, central Tibet, and China (Durante, 1983; Wang, 1985; Berthelin et al., 2003; Kerp, 2006; Abu Hamad et al., 2008; Srivastava and Agnihotri, 2010; Wang, 2010). The Laos ecosystem shows affinity with Karoo-type ecosystems, a condition probably inherited before the northward migration of the various continental blocks of southeastern Asia from the northeastern margin of Gondwana (Metcalfe, 2013).

A long-standing question in biogeography is whether the high levels of diversity observed in the modern tropics arise from the tropics serving as a cradle of biodiversity, that is an area with elevated origination rates, or alternatively a museum, an area with low extinction rates (Stebbins, 1974). A vast literature has developed attempting to test these hypotheses. Studies on various taxa suggest that this dichotomy is likely an oversimplification, with the tropics having both cradle-like and museum-like aspects (e.g., Jablonski, 1993; McKenna and Farrell, 2006; Jablonski et al., 2006, 2013; Ricklefs, 2006; Diniz-Filho et al., 2007; Moreau and Bell, 2013). Furthermore, there is evidence to suggest that the modern latitudinal biodiversity gradient, characterised by high diversity in the tropics that declines towards the poles, has not been a stable pattern over the Phanerozoic (Mannion et al., 2014).

Two recent studies of Permian tetrapod diversity at low taxonomic levels came to opposite conclusions regarding latitudinal biodiversity gradients: one is similar to a modern poleward decline in diversity (Benson and Upchurch, 2013); the other displays a temperate peak in diversity (Brocklehurst et al., 2017). Rees et al. (2002) suggested a temperate peak in plant diversity during the late Permian. The results of our higher-level analysis come down firmly on the side of a poleward decline in tetrapod richness in the Lopingian. They also indicate that this pattern stems from the tropics acting as both a cradle and museum, with tropical assemblages including a mixture of late-occurring hold-overs from the early Permian, for example some temnospondyls and captorhinids, in addition to early members of clades that come to prominence during the Triassic, principally Archosauriformes, and contemporary taxa that also are represented in higher latitude assemblages, such as therapsids and pareiasaurs. We note that our approach captures a different aspect of latitudinal diversity patterns than counts of species or genera, but we assert that this aspect tells us something important about late Permian tetrapod distributions and community structures that is more obscure when only total species richness is considered.

Finally, sampling issues are an important consideration when interpreting our results. The late Permian tetrapod record is very patchily distributed, and many assemblages are extremely undersampled when compared to well-studied areas such as the Karoo Basin. Nevertheless, the fact that the distinct compositions of the low latitude assemblages are apparent, despite their generally poor sampling, provides some reason to think the observed patterns are real. Further work in traditionally understudied high and low latitude Permian assemblages, perhaps employing groups such as plants and insects, is needed to test the hypotheses presented here. Such analyses would improve our understanding of the role of the Permian tropics in generating and/or preserving tetrapod biodiversity.

6. Conclusions

In this paper we studied the overall composition of the 14 best-documented late Permian terrestrial ecosystems. We examined these ecosystems by comparing the relative abundances of high-level plant and animal taxa against their palaeogeographical distributions. We found that terrestrial ecosystems were structured and provincialised at high taxonomic levels. The evolution of both floral and faunal bioprovinces was driven by the development of climate regions and latitudinal distributions, which were significant controlling factors for ecosystem compositional affinity. We concluded that:

1) The Bletterbach Biota of the Southern Alps provides a unique window on equatorial life in the late Permian. Together with the Morocco and Niger ecosystems, the Bletterbach Biota provides evidence that the most diverse assemblages are those at mid to low latitudes. Fossil-rich, higher latitude ecosystems, such as northern China and South Africa are much less diverse at comparable taxonomic levels. High-latitude communities are dominated by a small number of therapsid higher taxa, whereas the low-latitude communities are composed of a mixture of therapsids, captorhinids, temnospondyls, and archosauriforms.

2) Climatic constraint appears crucial in shaping the distribution of the three principal groups of Lopingian herbivores. Dicynodonts were best adapted to cool temperate climates where glossopterid/conifer-dominated woodlands with a sphenophyte/fern understorey were present. Pareiasaur distribution best correlates with conifer- and ginkgophyte-rich woodlands that developed in the warm temperate climate of equatorial to sub-equatorial Pangaea. Captorhinid distribution shows a pattern similar to the pareiasaurs and correlates well with the semi-arid to arid conditions of the tropical wet biome, where they might have fed on pteridosperms and conifers.

3) Climate, latitude and tectonic history controlled the nature of the different ecosystems. Northern Gondwanan ecosystems (Morocco, Niger) show closer affinities with Euramerican ecosystems (Southern Alps, Zechstein, South Urals) than to southern Gondwanan (Karoo-type, India, Brazil) ecosystems. The Laotian ecosystem shares affinities with Karoo-type ecosystems, probably inherited from their original geographical position, before the northward migration of the various continental blocks that now constitute SE Asia.

4) The Lopingian latitudinal diversity gradient shows poleward decline in tetrapod richness at high taxonomic levels. Tropical assemblages include a mixture of late-occurring holdovers from the early Permian (e.g., temnospondyls, captorhinids), early members of clades that come to prominence in the Triassic (e.g., Archosauriformes), and contemporary taxa that also are represented in higher latitude assemblages (e.g., therapsids, pareiasaurs), suggesting that the tropics acted as both as cradle (i.e., an area with elevated origination rates) and museum (i.e., an area with low extinction rates) for biodiversity.

5) Considerable progress is being made towards understanding the biogeographical patterns of Permian plants, insects and their associations. The most prominent of these continental-wide patterns of plant distribution are Gondwanan floras to the south and east and Euramerican floras to the north and west, with mixed floras occurring sporadically at their intersection along a general equatorial trend. More recently, insect faunas have been characterised regionally within these two great floral provinces, although robust patterns of association have yet to emerge. New studies on plant–insect interactions have documented a "baseline" for the diversity and intensity of Permian herbivory as well as degrees of host-specialisation. These latter studies, as in the plant and tetrapod studies, are partly motivated by a need to understand the effects of the end-Permian ecological crisis.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2017.10.002.

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M. Bernardi et al. *Earth-Science Reviews 175 (2017) 18–43*

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43