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The Permo-Triassic Tetrapod Faunal Diversity in the Italian Southern Alps

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1. Introduction

The Permian and Triassic palaeogeography of the Alpine region originated a peculiar geological situation, now well exposed in several sections, in which marine sediments, continental deposits, and volcanites interfinger. The study of the resulting mixed sections allowed to build a framework of biostratigraphic and chronological data in which tetrapod footprints play a key role (e.g., Avanzini & Mietto, 2008).

Global track record is much more abundant than the skeletal record and, although suffering from problems related to a correct attribution to the trackmakers, provides data as reliable as those obtained from skeletal remains (Carrano & Wilson, 2001 and references therein).

During the Permian and the Early-Middle Triassic, tetrapods, and especially reptiles, radiated and entire new land-dwelling groups originated (e.g., the archosaurs). Consequently, in this temporal interval the tetrapod track record shows a huge increase in variability reflecting the morphological diversity spanning from a stem-reptile to a 'mammalian' foot, from basal crocodylomorph to a dinosauromorph foot. How is this pattern documented in the Dolomites region and surrounding areas (Southern Alps, NE Italy)?

In this geographical sector the recent discovery of many new tetrapod footprint-bearing outcrops has yielded to a phase of renewed interest for ichnological data. As a result, the stratigraphical, palaeoecological and palaeogeographical importance of tetrapod footprints in this geographical sector is becoming more and more widely acknowledge.

In this contribution we provide an overview of Permian and Triassic tetrapod faunal composition as deduced from the study of several ichnosites located in the Italian Southern Alps with special reference to the pattern exhibited around the PT boundary.

2. Geological setting

In the Permian succession of the Southern Alps tetrapod tracks are found within two tectonosedimentary cycles. The lower cycle is represented by the alluvial-lacustrine continental deposits of the Collio and Tregiovo Formations while the upper cycle is represented by clastic red-beds of the Verrucano Lombardo Formation and Val Gardena Sandstone (Trentino Alto Adige). Towards the top, the latter interfingers with the sulphate evaporites and shallow-marine carbonate sequences of the Bellerophon Fm. The two cycles are put in contact by a regional unconformity documented by erosional surfaces and

palaeosol horizons. Floristic and radiometric data (Cassinis & Doubinger, 1991, 1992; Cassinis et al., 1999, 2002; Schaltegger & Brack, 1999) indicate that the lower cycle is Artinskian-Kungurian in age (Early Permian). The upper cycle has been dated by means of sporomorphs and foraminifers and is considered Wuchiapingian in age (Late Permian, Cassinis et al., 2002).

Triassic units follow. The precise position of the PT boundary in the Southern Alps has been debated for long time (see Broglio Loriga & Cassinis, 1992 for a review). Although some early works put the boundary at or very close to the Bellerophon-Werfen Formation limit (Bosellini, 1964; Assereto et al., 1973; Posenato, 1988), the PT boundary is now thought to lie within (Pasini, 1985; Broglio Loriga et al., 1986; Visscher & Brugman, 1988; Farabegoli & Perri, 1998; Farabegoli et al., 2007) or at the top (Wignall et al., 1996) of the Tesero Member, the lowermost part of the Werfen Fm. The first Triassic tetrapod tracks are found within the terrigenous and terrigenous-carbonate units of the Werfen Fm. and are Olenekian in age (Early Triassic). Several terrigenous and terrigenous-carbonate units of Anisian age (Middle Triassic) follow: Gracilis Fm., Voltago Cgl., Richthofen Cgl., Morbiac dark Limestones. All were deposited in lagoonal-peritidal to continental environments and have yielded well preserved ichnoassociations. No tetrapod tracks are known from the Dolomites' Ladinian (Middle Triassic) which is represented mainly by basinal units (Buchenstein Fm. and Wengen Group) and carbonate platform deposits (Sciliar Dolomite).

3. Permian and Triassic ichnoassociations

Permian and Triassic ichnoassociations in the Southern Alps have been documented since the XIX century (e.g., Curioni, 1870). Recent reviews have been published by Conti et al. (1997), Conti et al. (1999), Conti et al. (2000), Avanzini et al. (2001), Avanzini & Mietto (2008). Here we provide an updated overview on these studies focusing on the contribution that tetrapod ichnology can give to the debates concerning the large scale patterns of extinction and subsequent recovery on lands near the PT boundary (Benton & Twitchett, 2003; Twitchett et al., 2001; Retallack et al., 2006; Sheldon & Chakrabarti, 2010).

In the Alpine area several different types of bioevents were recognized (Conti et al., 2000; Ronchi et al., 2005). According to their relative importance, they had different degrees of utility for correlation. The first-appearance datum (FAD) and last appearance datum (LAD) concern a taxon, at either genus and species level, and are important at the regional level. The first occurrence (FO) and last occurrence (LO) as well as the disappearance event (DE) concern a faunal complex and have very high correlation power.

Here, ichnoassociations have been grouped in four discrete time bins: Artinskian-Kungurian (Early Permian) (Fig. 1), Wuchiapingian (Late Permian) (Fig. 2), Olenekian (Early Triassic) and Anisian (Middle Triassic) (Fig. 3). Traditionally, these discrete associations have been considered 'Faunal Units' (FU) (Conti et al., 1997; Conti et al., 1999; Conti et al., 2000; Avanzini et al., 2001; Ronchi et al., 2005).

In the present study: i) no vertical differences within a single bin have been considered even though some are well known; and, ii) only species-level determinations have been considered except where a genus or a higher-level taxon is represented by an undetermined species only (e.g., *Procolophonichnium* isp.), or in the case of *Rhynchosauroides* isp.1 and *Rhynchosauroides* isp.2 of Valentini et al. (2007) which underwent a formal revision and, although not yet renamed, can be considered as distinct ichnospecies.

3.1 Artinskian-Kungurian (Early Permian)

The Permian first cycle ichnoassociation is documented within the Collio and Tregiovo Formations. Data have been recorded in the Collio basin (Geinitz, 1869; Curioni, 1870; Cassinis, 1966; Berruti, 1969; Ceoloni et al., 1987; Conti et al., 1991) and from sediments cropping out in other localities of the Orobie basin (Gümbel, 1880; Dozy, 1935; Casati, 1969; Casati & Forcella, 1988; Nicosia et al., 2000; Santi, 2003, 2005; Santi & Krieger, 2001) and in the Tregiovo and Luco basins (Conti et al., 1997; Avanzini et al., 2008).

The ichnoassociation includes the following ichnospecies (after Conti et al., 1997; Conti et al., 2000, updated) (Fig. 1).

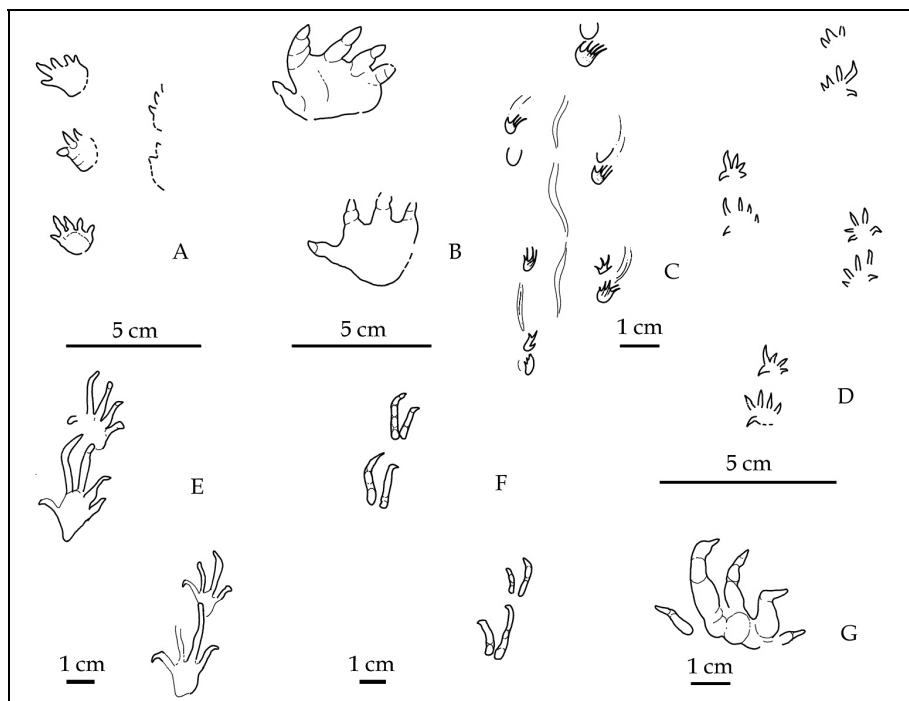


Fig. 1. Artinskian and Kungurian (Early Permian) tetrapod tracks from the Southern Alps. A) *Amphisauropus imminutus* Haubold, 1970; B) *Amphisauropus latus* Haubold, 1970; C) *Batrachichnus salamandroides* (Geinitz, 1861); D) *Camunipes cassinisi* Ceoloni et al., 1987; E) *Dromopus lacertoides* (Geinitz, 1861); F) *Dromopus didactylus* (Moodie, 1896); G) *Varanopus curvidactylus* Moodie, 1929. From Santi & Krieger (1999), Ceoloni et al. (1987), Avanzini et al. (2008).

Amphisauropus imminutus Haubold, 1970

Amphisauropus latus Haubold, 1970

Batrachichnus salamandroides (Geinitz, 1861)

Camunipes cassinisi Ceoloni et al., 1987

Dromopus lacertoides (Geinitz, 1861)

Dromopus didactylus (Moodie, 1896)

Ichnoterium cottae (Pohlig, 1885)

Varanopus curvidactylus Moodie, 1929

Santi (2007) has clearly shown that *Camunipes cassinisi* Ceoloni et al., 1987 is a junior synonym of *Erpetopus* Moodie, 1929.

The Early Permian ichnoassociation is bounded by the *Amphisauropus latus* FO and *Ichnotherium cottae* FO at the base and by the *Dromopus didactylus* LO at the top. This association is very similar to those found in the Permian of various European countries. It is named Collio FU and it can in turn be subdivided into two subunits. The lower subunit (Pulpito subunit) is characterized by the presence of *Amphisauropus latus* Haubold, 1970, *Dromopus lacertoides* (Geinitz, 1861) and *Ichnotherium cottae* (Pohlig, 1885). The upper subunit (Tregiovo subunit) is bounded by the disappearance event (DE) for all but one of the preceding forms, yielding a drastic reduction of faunal diversity; indeed the subunit is monotypic being represented by very frequent specimens of the only relict species *Dromopus didactylus* (Moodie, 1896). This pattern was interpreted as a bioevent, given the relatively unchanged sedimentation conditions.

3.2 Wuchiapingian (Late Permian)

The Permian second cycle ichnoassociation has been recorded in the Bletterbach section (Ceoloni et al., 1988; Conti et al., 1975; 1977; 1980; Leonardi & Nicosia, 1973; Leonardi et al., 1975; Nicosia et al., 1999) and other quasi-coheval outcrops (SS. 48, Col Frattón (Kittl, 1891; Abel, 1926); S. Pellegrino Pass (Conti et al., 1977), Seceda (Valentini et al., 2009), Nova Ponente (Wopfner, 1999), Recoaro (Mietto, 1975; 1981) San Genesio-Meltina Plateau in the Adige basin (Avanzini, unpublished).

The ichnoassociation includes the following ichnospecies (after Avanzini et al., 2001; Conti et al. 2000; Valentini et al., 2007, updated) (Fig. 2).

Chelichnus tazekwurmi Ceoloni et al., 1988

Dicynodontipus geinitzi (Hornstein, 1876)

Ganasauripus ladinus Valentini et al., 2007

Hyloidichnus tirolensis Ceoloni et al., 1988

Ichnotherium accordii Ceoloni et al., 1988

Ichnotherium cottae (Pohlig, 1885)

Janusichnus bifrons Ceoloni et al., 1988

Pachypes dolomiticus Leonardi et al., 1975

Paradoxichnium radeinensis Ceoloni et al., 1988

Protochirotherium isp.

Rhynchosauroides pallinii Conti et al., 1977

Rhynchosauroides isp.1 of Valentini et al., 2007

Rhynchosauroides isp.2 of Valentini et al., 2007

Therapsida indet.

Note that the specimens from Val Gardena Fm. ascribed to *Chelichnus tazekwurmi* Ceoloni et al., 1988 and *Ichnotherium cottae* (Pohlig, 1885) are currently under revision and that their nomenclature is expected to change in the near future.

The Upper Permian tetrapod footprint complex is characterized by a diversified fauna almost completely new as compared with other Permian faunas (Ceoloni et al., 1986). Bounded in its lower part by the *Rhynchosauroides* and *Protochirotherium* FAD, its records also the *Dicynodontipus* FAD and the *Ichnotherium* LAD. It is named the Bletterbach FU.

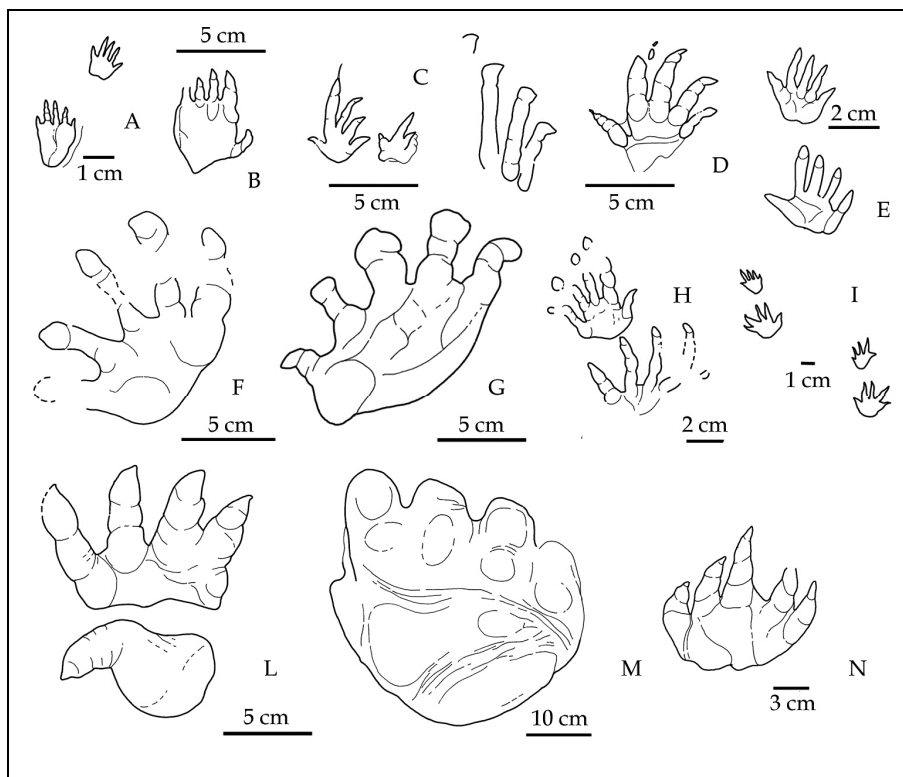


Fig. 2. Wuchiapingian (Late Permian) tetrapod tracks from Southern Alps. A) *Chelichnus tazekwurmii* Ceoloni et al., 1988; B) *Dicynodontipus geinitzi* (Hornstein, 1876); C) *Ganasauripus ladinus* Valentini et al., 2007; D) *Rhynchosauroides pallinii* Conti et al., 1977; E) *Hyloidichnus tirolensis* Ceoloni et al., 1988; F) *Ichniotherium accordii* Ceoloni et al., 1988; G) *Ichniotherium cottae* (Pohlig, 1885); I) *Janusichnus biffons* Ceoloni et al., 1988; M) *Pachypes dolomiticus* Leonardi et al., 1975; H) *Paradoxichnus radeinensis* Ceoloni et al., 1988; L) cf. *Protochirotherium* isp.; M) Therapsida indet. From Conti et al. (1977, 2000), Valentini et al. (2007).

Early Permian and Late Permian associations of the Southern Alps are separated by a stratigraphic break that correspond to a time-gap of 14-27 Ma (Italian IGCP 203 Group, 1986; Cassinis et al., 1988; Cassinis et al., 1999). A similar hiatus, equivalent to part of the Middle Permian, has been recognized in the global Permian tetrapod fossil record and has been termed Olson's gap (Lucas and Heckert, 2001). The gap is thought to be associated with a significant remodelling of the global Permian tetrapod fauna (Lucas and Heckert, 2001; Lucas, 2004). As stated before, the two Southern Alpine FUs have been considered two different 'evolutionary stages' (Conti et al., 2000).

3.3 Olenekian (Early Triassic)

In the studied sector, the Early Triassic is represented by the Werfen Fm.: a complex succession of carbonate, terrigenous and mixed sediments. The formation is divided into

nine members and tracks are present in the upper three (Campil Member, Cencenighe Member and San Lucano Member).

Tracks have been found near Recoaro, in Val Gardena (Bulla/Pufels), and Val Travnigolo (Conti et al., 2000; Mietto, 1986). Olenekian tracks are generally poorly preserved and some, as those signaled by Leonardi (1967, p. 118, 119), are here discarded. Furthermore (*contra* e.g. Avanzini & Mietto, 2008) levels bearing *Capitosauroides* and *Procolophonichnium* ichnogenera (e.g., cropping out in the Monte Marzola) previously considered to be part of the Werfen Fm. are here reconsidered within the 'Gracilis Formation' which is Anisian (Middle Triassic) in age. The ichnoassociation includes the following ichnospecies (after Avanzini et al., 2001; Conti et al. 2000, updated) (Fig. 3):

Rhynchosauroides palmatus (Lull, 1942)

Rhynchosauroides schochardti (Rühle von Lilienstern, 1939)

Both *R. palmatus* (Lull, 1942) and *R. schochardti* (Rühle von Lilienstern, 1939) have not been validated by Valentini et al. (2007) in their review of the ichnogenus *Rhynchosauroides* from the Val Gardena Sandstone. No review has been conducted of this ichnogenus in the Werfen Formation. We acknowledge that both ichnospecies could follow in an undetermined *Rhynchosauroides* isp., this is however nearly irrelevant (i.e., Early Triassic ichnodiversity could be 1 instead of 2) to the data analyses presented here.

The Lowermost Triassic of the Southern Alps is characterized by the scarce presence of vertebrates, a factor that is undoubtedly linked to environmental conditions (palaeogeography) which did not favor the permanence in this region of complex and consistent faunal associations. The ichnoassociations are dominated by *Rhynchosauroides* forms that are likely mainly Permian survivor.

3.4 Anisian (Middle Triassic)

Several Anisian ichnoassociations have been found in the Dolomites and surrounding areas. These are found within several formations (Gracilis Fm., Voltago Cgl., Richthofen Cgl., Morbiac dark Limestones) which document transitional continental to marine environments. Tracksites are located in the Braies Dolomites (Northern Dolomites), in the eastern Dolomites, in the upper Val di Non and Val d'Adige, and in the Recoaro-Vallarsa area (Abel, 1926; Brandner, 1973; Mietto, 1987; Avanzini, 1999, 2000, 2002; Avanzini et al., 2001; Avanzini & Leonardi, 2002; Avanzini & Lockley, 2002; Avanzini & Neri, 1998; Avanzini & Mietto, 2008; Todesco et al., 2008; Todesco & Bernardi, 2011).

The ichnoassociation includes the following ichnospecies (after Avanzini & Mietto, 2008, updated) (Fig. 3):

Brachychirotherium paeneparvum Demathieu & Leitz, 1982

Brachychirotherium circaparvum Demathieu, 1967

Capitosauroides cf. *bernbургensis* Haubold, 1971

Chirotherium barthii Kaup, 1835

Chirotherium rex Peabody, 1948

Isochirotherium infernense Avanzini & Leonardi, 2002

Isochirotherium delicatum Courel & Demathieu, 1976

Parasynaptichnium gracilis Mietto, 1987

Procolophonichnium isp.

Rhynchosauroides tirolicus Abel, 1926

Rhynchosauroides peabodyi Faber, 1958

Rotodactylus cf. *cursorius* Peabody, 1948

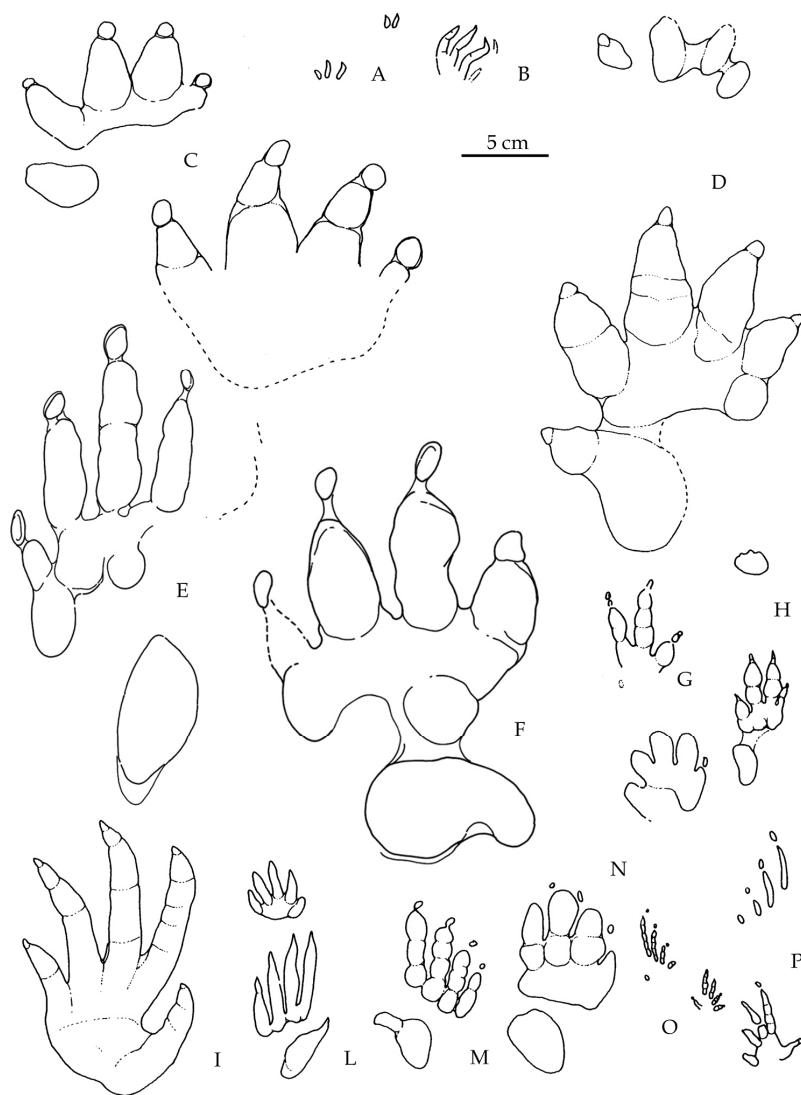


Fig. 3. Olenekian (A, B) and Anisian (C-P) (Early and Middle Triassic) tetrapod tracks from Southern Alps. A) *Rhynchosauroides palmatus* (Lull, 1942); B) *Rhynchosauroides schochardti* (Rühle von Lilienstern, 1939); C) *Chirotherium rex* Peabody, 1948; D) *Isochirotherium infernense* Avanzini and Leonardi, 2002; E) cf. *Sphingopus* isp.; F) *Chirotherium barthii* Kaup, 1835; G) tridactyl footprint, possible dinosauriformes; H) *Isochirotherium delicatum* Courel & Demathieu, 1976; I) *Parasynaptichnium gracilis* Mietto 1987; L) *Synaptichnium pseudosuchoides* Nopcsa, 1923; M) *Synaptichnium cameronense* (Peabody, 1948); N) *Brachychirotherium* aff. *Parvum*; O) *Rhynchosauroides tirolicus* Abel, 1926; P) *Rhynchosauroides peabodyi* Faber, 1958. From Avanzini (2003), Avanzini & Mietto (2008).

Rotodactylus lucasi Demathieu & Gand, 1973

Sphingopus isp.

Synaptichnium cameronense (Peabody, 1948)

Synaptichnium pseudosuchoides Nopcsa, 1923

Synaptichnium diabloense Peabody, 1948

Therapsida indet.

In the considered sector, tetrapod tracks are not recorded from Ladinian deposits, in correspondence of a great rise of the sea level. Well documented associations reappear only in the Late Triassic (Tuvanian).

In the Anisian, a progressive increase in the complexity of the ichnoassociations and the size of the taxa from the Bithynian to the Illyrian is documented in the Southern Alps.

The analysis of the stratigraphic distribution of ichnofaunas crossed with sequence stratigraphy and the ammonite biostratigraphy has led to the identification, within the Pelsonian - Illyrian interval of several taxa characterized by a narrow vertical distribution (Avanzini & Mietto, 2008).

While the Aegean-Bithynian interval is characterized by several lizard-like ichnotaxa and small archosauriform (*Parasynaptichnium gracilis* and *Synaptichnium pseudosuchoides* FAD), the middle Pelsonian and the Illyrian are mainly dominated by medium-large chirotheroids (i.e., *Chirotherium barthii*, *C. cf. rex*, *Isochirotherium herculis*).

4. Ichnodiversity trends through the Permo-Triassic

The likely producer of an ichnospecies is generally uncertain; tracks and trackmakers can only be associated with certainty when found in association (e.g., Voigt et al., 2007). However, for most studies the identity of the trackmaker does not need to be (and cannot be) determined at a specific or generic level. The range of the possible producers can be constrained within the least inclusive group that bounds all the taxa sharing similar morphological characteristics that fit with the features of the studied tracks (Carrano & Wilson, 2001). In the case of the track record here analysed this implies that different ichnogenera can be attributed to trackmakers belonging to different taxonomic categories. Furthermore, acknowledging that different substrates, behaviours and even different ichnotaxonomic traditions can bias our palaeobiodiversity and abundance estimates, the here suggested taxonomic designations are based on: i) the most conservative found in literature (i.e., broad), and ii) the most widely acknowledged (i.e., some single alternative hypothesis have been discarded) (Tab. 1).

For example the ichnogenus *Procolophonichnium* has been attributed to different biological groups such as procolophonids (Anapsida), therapsids (Synapsida) and basal amniotes (see Klein & Lucas, 2010; Klein et al., in press). The least inclusive group that bounds these taxa is the Amniota and *Procolophonichnium* is here conservatively considered as produced by an indeterminate stem group amniote (i.e., basal amniote). A coarse assignment of trackmaker identity has been shown to be still useful for evolutionary studies (e.g., Wilson and Carrano, 1999; Carrano & Wilson, 2001).

Although possibly unsafe, a link between ichnofaunal and faunal record in the Dolomites area is the only possible source of information about tetrapod life on lands in Permian and Triassic since, as state above, the bony record is nearly absent.

Ichnodiversity and faunal composition through time are shown in Figs. 4 and 5. Taken at face value, available data show that diversity (shear number of ichnospecies) grows through

the Permian, then suddenly drops in (or until) the Olenekian and then reaches its maximum in the Anisian. A finer stratigraphic and temporal resolution would show that lowest and highest diversity are separated by circa 6 million years only (Avanzini & Mietto, 2008).

Ichnotaxon	Attribution
<i>Amphisauropus</i>	Seymouriamorpha
<i>Batrachichnus</i>	Stem group Amphibia
<i>Brachychirotherium</i>	Archosauria
<i>Capitosauroides</i>	Stem-group Amphibia
<i>Chelichnus</i>	Non-therapsid Eupelycosauria
<i>Chirotherium</i>	Archosauriformes
<i>Dicynodontipus</i>	Non-mammalian Therapsida
<i>Dromopus</i>	Araeoscelida
<i>Erpetopus</i>	Captorhinidae
(<i>Camunipes</i>)	
<i>Ganasauripus</i>	Lepidosauromorpha
<i>Hyloidichnus</i>	Captorhinidae
<i>Ichniotherium</i>	Diadectomorpha
<i>Isochirotherium</i>	Archosauriformes
<i>Janusichnus</i>	Stem-group Amniota
<i>Pachypes</i>	Pareiasauridae
<i>Paradoxichnium</i>	Lepidosauromorpha
<i>Parasynaptichnium</i>	Archosauriformes
<i>Procolophonichnium</i>	Stem-group Amniota
<i>Protochirotherium</i>	Archosauriformes
<i>Rhynchosauroides</i>	Lepidosauromorpha/Eosuchia
<i>Rotodactylus</i>	Dinosauromorpha
<i>Sphingopus</i>	Dinosauromorpha
<i>Synaptichnium</i>	Archosauriformes
<i>Varanopus</i>	Captorhinomorpha

Table 1. Permian-Triassic tetrapod ichnogenera and their inferred trackmakers (mainly after Haubold, 1996, 2000; Klein et al., 2011)

The Artinskian-Kungurian (Early Permian) ichnoassociation (Fig. 1) is comparable with coeval associations around the World (the so-called *Batrachichnus* ichnofacies; Lucas & Hunt, 2006) and document the presence of 5 different groups: amphibians, seymouriamorphs, diadectomorphs, captorhinomorphs and araeoscelids (Fig. 4). These are represented, in similar proportion, by 8 different ichnospecies. The most notable difference with other Lower Permian tracksites is the absence of tracks ascribed to large non-therapsid Eupelycosaur grade trackmakers (e.g. *Dimetropus*).

The richer Wuchiapingian (Late Permian) ichnoassociation (Fig. 2) is constituted of 14 ichnospecies which document the presence of 6 groups: diadectomorphs and captorhinomorphs are still present, together with lepidosauromorphs, pareiasaurs, synapsids and archosauriforms (Fig. 4). This ichnoassociation, according to Lucas and Hunt (2006, p. 152), “the most characteristic ichnofauna being that of the Val Gardena Formation” allowed

defining a *Pachypes* ichnocoenosis in the *Brontopodus* ichnofacies (Lucas and Hunt, 2006). As widely acknowledge, however, Southern Alps Late Permian ichnoassociation is far richer than elsewhere and, although ichnodiversity-based estimates can be misleading for the problems acknowledge before, it is interesting to note that, on a global scale, Wuchiapingian land vertebrate life experienced a dramatic drop in diversity (the end-Guadalupian crisis; see Benton, 1995; King, 1991; Retallack et al., 2006; Sahney & Benton, 2008).

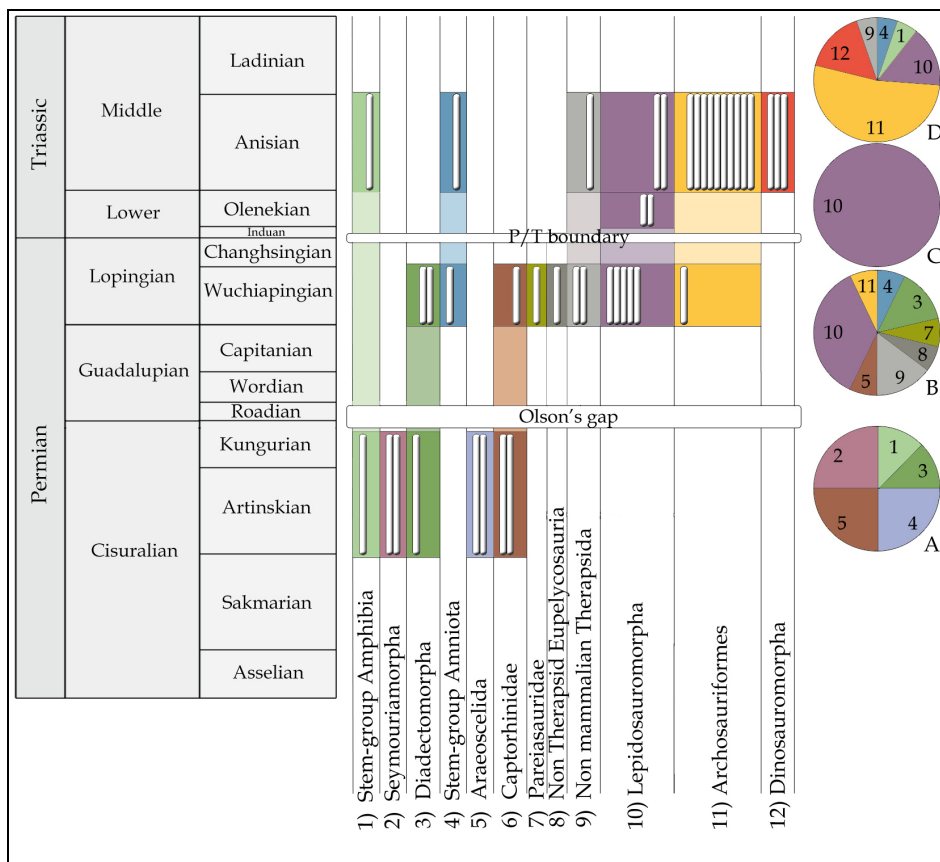


Fig. 4. Tetrapod ichnodiversity and faunal composition through the Permian and Triassic in the Dolomites region (Southern Alps, NE Italy). White bars represent the ichnospecies listed in the text for each of the four studied ichnoassociation: A) Artinskian-Kungurian (Early Permian), B) Wuchiapingian (Late Permian), C) Olenekian (Early Triassic), and D) Anisian (Middle Triassic). Each color, corresponding to the cardinal numbers 1-12, represent any least inclusive group to which the ichnospecies are referred.

Olenekian (Early Triassic) tracks (Fig. 3) are all found isolated and poorly preserved. This surely has to do with the low preservation potential for tracks in the Southern Alps formations. However the few track-bearing levels within the three upper members of the Werfen Fm. undoubtedly record transitional continental-marine environments with high

preservation potential: where tracks could be preserved a monotypic lepidosauromorph fauna is documented (2 ichnospecies). The interpretation of this datum in the considered geographical sector is however poorly supported: both an “ecological bias” (e.g., only the coast dwellers who were able to live on the ephemeral emerged lands left their footprints), or a real “evolutionary pattern” (e.g., recovery in diversity from PT mass extinction was extremely slow) would produce the observed pattern of diversity.

Anisian (Middle Triassic) ichnoassociation is very diverse being constituted by 18 ichnospecies. 5 groups are represented: lepidosauromorphs, stem amphibians, “synapsids”, archosauriforms and dinosauromorphs (Fig. 4). It is interesting to note that as soon as the Anisian, nearly 70% of the ichnodiversity in the considered geographical sector documents the presence of archosaurs (10 archosaur-produced + 3 dinosauromorph-produced ichnospecies). The pattern is consistent with those observed in Germany, France and Arizona (USA) (see Hunt and Lucas, 2007 and references therein).

5. Discussion and conclusions

Our analysis of the Permo-Triassic faunal composition in the Dolomites region as deduced from the track record well matches the skeletal record with the obvious exclusion of few, very rare forms, dubiously referred to high level taxonomic groups too inclusive to be meaningful (Amphibia, Amniota). In this way, incidentally, the footprint reliability for evolutionary studies was, once again, confirmed. This is in particular true when data are collected from rich and deeply studied ichnoassociations. Once stated the reliability of data, we can analyse the impact of two well known biological crises that have been documented world-wide in the Middle and Late Permian (see Hallam & Wignall, 1997; Retallak et al. 2006; Sheldon, 2006 and references therein) on mid Early Permian to late Early Triassic faunas in the Dolomites.

The effects of the first crisis, the so-called Olson's extinction, are documented in the considered geographical sector by: i) the progressive disappearance of long ranging taxa, typical of the Early Permian (and Carboniferous) as the Seymouriamorpha and the Araeoscelidia; ii) the persistence of groups as the Diadectids and the Captorhinomorphs; iii) the appearance of groups that will have their explosion during the Late Permian (Pareiasaurs and non-mammalian Therapsids). Contemporaneously it is worth of note the appearance of the first Lepidosauromorphs and of rare Archosauromorphs. On the contrary, the events recorded between Late Permian and late Early Triassic, across the end-Permian crisis, suggest a very low survival, and only of the groups that appeared during the Late Permian (Lepidosauromorph, non Mammalian Therapsid, Archosauromorphs). Noticeably, an early appearance and the abundant presence of *Rotodactylus* and *Sphingopus* in the Southern Alps also supports the hypotheses of an early origin, soon after the PT boundary, for the Dinosauroomorpha (e.g., Brusatte et al., 2011).

The recognized trends, suggest different controlling factors for the two Permian crises (Fig. 5). The end-Guadalupian “crisis” (Benton, 1995, 1989; King, 1991; Retallack et al., 2006), or “extinction” (Sahney & Benton, 2008) seems to show the typical feature of the depletion of a long-lived association, mainly characterized by ecological replacement of the old taxa with new ones (famous examples, based on bone remains, are the replacement of Caseids with Pareiasaurs in the niche of large plant-eaters and of large Sphenacodontids with the non-mammalian Therapsid among carnivorous), and thus an event controlled by normal

environment changes, more or less slow and gradual. The end-Permian crisis, instead, is recorded by the termination of short lived taxa, just appeared during the same Late Permian and can be better interpreted as the result of a mass-extinction, connected to a series of catastrophic events.

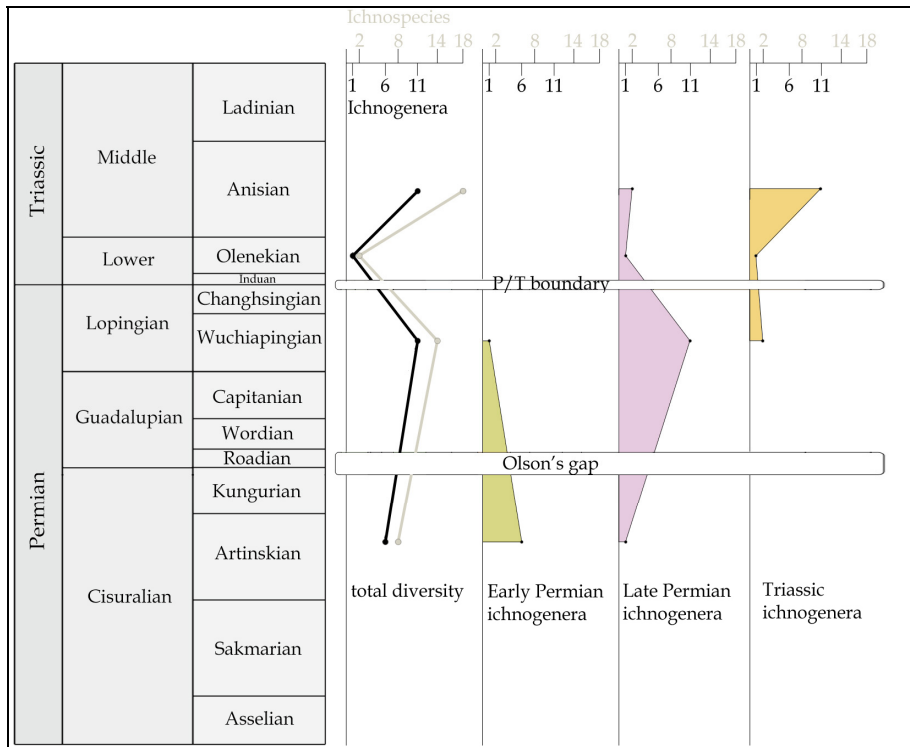


Fig. 5. Tetrapod ichnodiversity through time in the Southern Alps. Colored polygons represent the duration of each of the studied ichnoassociations.

Thus, paradoxically, it may have been the end-Guadalupian, slow speed, crisis that, anticipating the substitution of obsolescent anatomical and ecological 'models' and forcing the appearance of entirely new taxa, allowed some land-animal groups overcoming the following and much more acute, end-Permian crisis.

6. Acknowledgments

We thank F.M. Petti and R. Todesco (Science Museum, Trento) for constructive discussions and M.C. Deflorian (Science Museum, Trento) for assistance with figures. This study is part of the project "The Permian-Triassic ecological crisis in the Dolomites: extinction and recovery dynamics in Terrestrial Ecosystems" financed by the Promotion of Educational Policies, University and Research Department of the Autonomous Province of Bolzano - South Tyrol. The research was supported also by the Science Museum, Trento and the Sapienza University of Rome.

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