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The Lopingian tetrapod ichnoassociation from Italy, a key for the understanding of low-latitude faunas before the end-Permian crisis

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ABSTRACT - The tetrapod footprints from the Lopingian of Italy are worldwide known and were the subject of a number of studies. They come mostly from the Dolomites and especially from the Bletterbach gorge, other occurrences are known from the Venetian Prealps and the Carnic Alps. The track-bearing unit is the alluvial and marginal marine Arenaria di Val Gardena Formation, deposited under a semi-arid climate during the late Lopingian. In the last comprehensive revision, the tetrapod ichnoassociation includes abundant and diverse tracks attributed to eureptiles (cf. *Dromopus* isp., *Rhynchosauroides pallinii*, *Paradoxichnium problematicum*, cf. *Protochirotherium* isp.), abundant tracks attributed to parareptiles (*Procolophonichnium tirolensis, Pachypes dolomiticus*), uncommon but diverse tracks attributed to therapsids (*Capitosauroides* isp., *Dicynodontipus* isp., *Dolomitipes accordii*) and rare tracks attributed to anamniotes (cf. *Batrachichnus* isp.). The occurrence of further ichnotaxa, such as *Contiichnus* and *Merifontichnus*, is currently debated. This is the most abundant, diverse and best-preserved tetrapod ichnoassociation of the Lopingian all over the world, thus it is a reference for tetrapod ichnotaxonomy. It is characterized by a strong affinity to Triassic ichnofaunas and includes the earliest ichnological evidence of an archosauriform radiation and some of the earliest clues of parasagittal locomotion in therapsids and archosauriforms. This low-latitude tetrapod ichnoassociation is similar to contemporary faunas from mid- and high-palaeolatitudes, but it seems to be more diverse. In tetrapod footprint biochronology, it is currently the reference for the Bletterbach Ichnofaunal Unit and the *Paradoxichnium* tetrapod footprint biochron. Also, it may include the base of the *Protochirotherium* tetrapod footprint biochron.

Key words: tetrapod footprints; Lopingian; Permian; Bletterbach; Dolomites.

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1. INTRODUCTION

Tetrapod tracks from the late Lopingian of Italy come exclusively from the Arenaria di Val Gardena (Grödner Sandstein) Formation, and are known since the first description of a specimen from the Dolomites area by Abel (1929), previously reported by Kittl (1891). The first study of tetrapod tracks from the most famous site of the Dolomites, the Bletterbach gorge, is by Leonardi (1951). Nevertheless, it is in the 70s and the 80s, after intensive field work in the Bletterbach (Butterloch) gorge and nearby localities, that the Dolomites tetrapod ichnoassociation became the most important of the Lopingian, because of abundance, quality and diversity of the material. Several new ichnogenera and ichnospecies have been introduced, and the ichnofauna was compared with the contemporary tetrapod track and body-fossil record, evidencing noteworthy similarities with Lopingian associations from South Africa and Russia (e.g. Leonardi et al., 1975; Conti et al., 1975, 1977, 1979, 1980, 1981, 1987; Ceoloni et al., 1988a, 1988b). During these years, some additional material has been found in the Venetian Prealps (Mietto, 1975, 1981) and in the Carnic Alps (Mietto and Muscio, 1987). The stratigraphic value of the Dolomites tetrapod ichnoassociation was evidenced by Conti et al. (1997) and Avanzini et al. (1999, 2001), who first applied the concept of Faunal Units (e.g. Walsh, 1998) to the tetrapod footprints and introduced the Bletterbach Ichnofaunal Unit. New discoveries from the Dolomites area were described by Wopfner (1999) and Nicosia et al. (2001). Comprehensive revisions of the lacertoid and pareiasaurian tracks of the Dolomites, including remarks on the potential trackmakers, were proposed by Valentini et al. (2007, 2008, 2009). During the last decade, the Lopingian tetrapod ichnoassociation from Italy has been interested by a large number of new studies. Tetrapod footprint palaeoecology and ichnotaphonomy have been discussed by Citton et al. (2016), Kustatscher et al. (2017) and Bernardi et al. (2017a). The ichnofaunal composition, with special consideration of assumed archosauriform tracks, has been discussed by Bernardi et al. (2015, 2017a). New ichnotaxonomic revisions have been proposed, focusing on single ichnotaxa (Citton et al., 2019a) or on the whole tetrapod ichnoassociation (Marchetti et al., 2017, 2019a). The biostratigraphic value of the ichnoassociation was re-discussed by Petti et al. (2015), Voigt and Lucas (2018), Marchetti et al. (2019a, 2019b) and Schneider et al. (2020).

The scope of this contribution is to describe the state-of-the-art of the studies on Lopingian tracks from Italy and the value of this ichnoassociation for ichnotaxonomy, palaeoecology, palaeobiogeography, biochronology and studies on the tetrapod fauna, otherwise unknown from the Lopingian skeletal record of this area. Eventually, possible directions for future research are provided.

2. GEOLOGICAL SETTING AND STRATIGRAPHY-DOLOMITES

All fossil tetrapod footprints from the Lopingian of western Dolomites region in NE Italy come from several localities in the Trentino-Alto Adige/Südtirol autonomous region (Fig. 1; Tab. 1). The larger, more diverse and significant part of the studied material comes from the Bletterbach gorge (e.g. Leonardi, 1951; Leonardi et al., 1975; Conti et al., 1977; Ceoloni et al., 1988a; Nicosia et al., 2001; Citton et al., 2016; Bernardi et al., 2017a; Marchetti et al., 2019a). This site, declared as the UNESCO World Heritage Site The Dolomites, is characterized by a complete and well-exposed succession of the alluvial Arenaria di Val Gardena Formation (about 180 m-thick) that grades upwards into the shallow marine *Bellerophon* Formation (about 60 m-thick) (Fig. 2). The track-bearing strata belong to the Arenaria di Val Gardena Formation, which in this site unconformably overlies the Ora Formation of the Athesian Volcanic Group. The stratigraphy and sedimentology of this site has been thoroughly analysed by Accordi (1958) and subsequently by Massari et al. (1988, 1994), who identified an overall fining- and thinning-upwards trend from alluvial red beds to coastal sabkha and shallow marine deposits, in a semi-arid palaeoenvironment, because of the occurrence of calcisols and vertisols in the red beds and of evaporites in the shallow marine facies. The sequence is characterized by three superimposed transgressive-regressive cycles, which seem to affect the preservation and composition of the fossil biota (Kustatscher et al., 2017). The earliest recorded marine ingression is represented by the so-called Cephalopod Bank ("Banco a Cefalopodi", e.g. Conti et al., 1977), a thick limestone level within the Arenaria di Val Gardena Formation, at the top of the waterfall that topographically separates the upper and lower part of the Bletterbach gorge (Fig. 2). The second recorded marine ingression is documented by the first layers of the *Bellerophon* Formation, named Nautiloid Horizon A ("Orizzonte a Nautiloidi", e.g. Posenato, 2010). The third marine ingression is represented by the lower part of the *Bellerophon* Formation, including the Nautiloid Horizon B, that represents the definitive establishment of marine conditions after the deposition of the Arenaria di Val Gardena Formation (Posenato, 2010). The Arenaria di Val Gardena Formation of the Dolomites is characterized by a very variable thickness, between 0-500 m. It documents alluvial fan, proximal to distal floodplain, sabkha-like, lagoon and shallow-marine palaeoenvironments (Perwanger, 1946; Bosellini and Hardie, 1973; Massari et al., 1988, 1994; Posenato, 2010; Kustatscher et al., 2017). Besides the abundant vertebrate and invertebrate trace fossil content (e.g. Conti et al., 1977; Marchetti et al., 2019a), palaeosols and plants remains are fairly common (Wopfner and Farrokh, 1988; Kustatscher et al., 2012, 2017), and testify to a warm to hot, sub-humid to semi-arid climate with strong seasonality (Cassinis et al., 1999; Kustatscher et al., 2017). In the Dolomites, the Arenaria di Val Gardena Formation is topped by the *Bellerophon* Formation, which documents the marine ingression of the Palaeo-Tethys Ocean in this area, from East to West.

The age of the Arenaria di Val Gardena Formation is well-constrained in its upper part whereas there are more uncertainties on its lower part. Radiometric dating (U/Pb) indicates an age of 274.1±1.4 Ma (Kungurian) for the top of the underlying volcanic Ora Formation in the Dolomites area (Marocchi et al., 2008). The base of the Arenaria di Val Gardena Formation is characterized by an angular unconformity corresponding to a gap of at least 14 Ma of duration, according to some authors (Cassinis et al., 1999; Morelli et al., 2007). Palaeomagnetic studies in the western Dolomites and Carnia highlight a reversal that was recorded about 20 m above the base of the Arenaria di Val Gardena Formation and was initially referred to the Guadalupian Illawarra reversal (Mauritsch and Becke, 1983; Dachroth, 1988). Nevertheless, sporomorphs sampled about 20 m above the base of the formation in the Bletterbach gorge section indicate a Lopingian age (Vyatkian = late Wuchiapingian-Changhsingian; Pittau, 2001), so the palaeomagnetic reversal mentioned above is probably Lopingian (Posenato, 2010). Sporomorphs found at the base (Bletterbach gorge) or 15 m below the Nautiloid Horizon A (Seceda locality) indicate a Changhsingian age (Pittau, 2001). The oldest worldwide occurrence of chirotheriid tracks (cf. *Protochirotherium*) within the Arenaria di Val Gardena Formation (e.g. Conti et al., 1977; Petti et al., 2015) may suggest a Changhsingian age for at least part of the formation, because the body fossils of their trackmakers, the archosauriform archosaurs, appeared

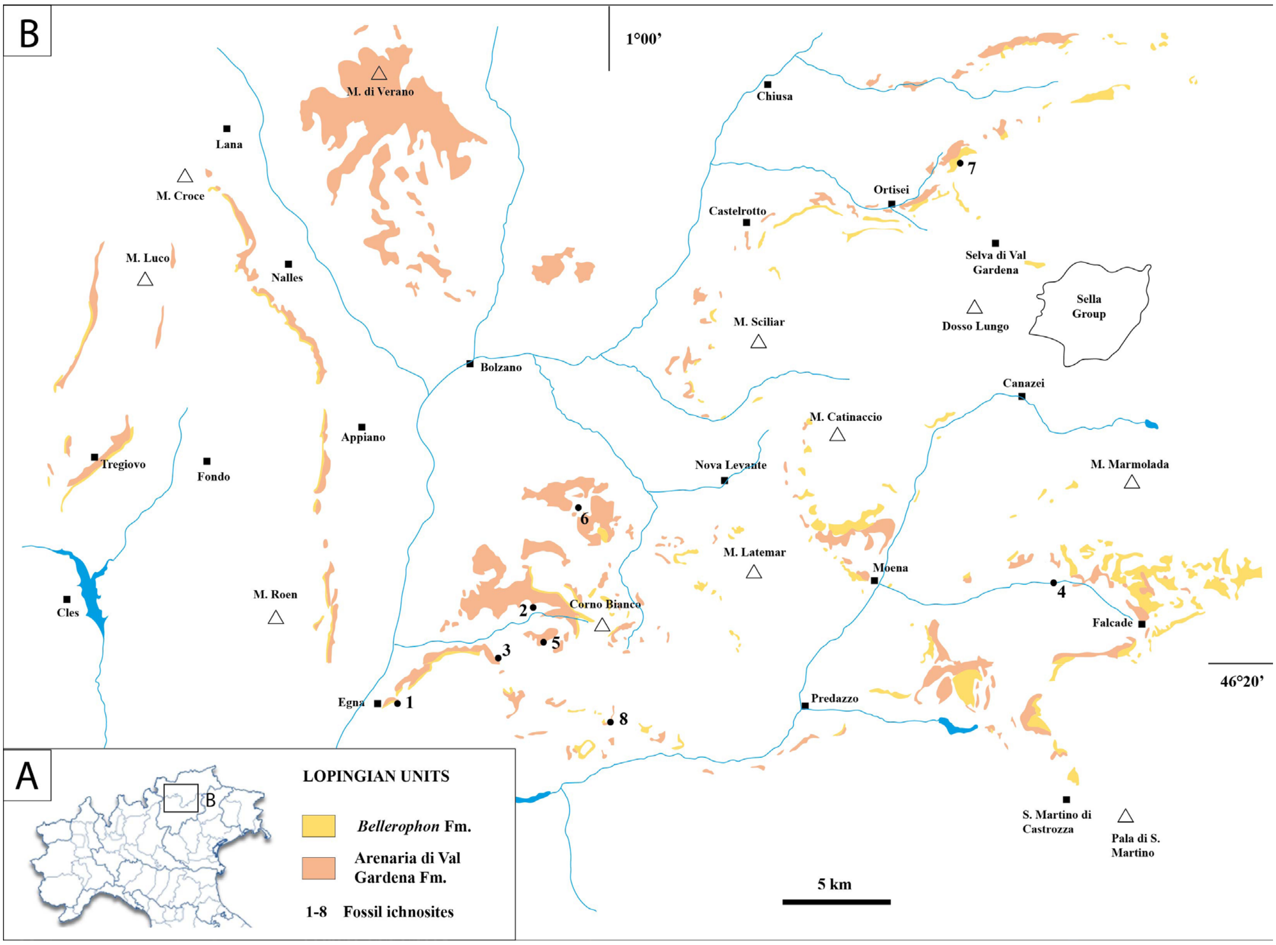

Fig. 1 - Simplified geological map and localities of the Dolomites area (1-8). 1 - Egna/Neumarkt, 2 - Bletterbach, 3 - Pausa, 4 - S. Pellegrino pass, 5 - Redagno di Sopra/Oberreiden, 6 - Nova Ponente/Deutschnofen, 7 - Seceda Mount, 8 - Daiano.

in the Changhsingian of Russia (*Archosaurus rossicus* tetrapod zone: Sennikov and Golubev, 2017). A possible archosauriform (*Eorasaurus*) is known from older units (late Capitanian-Wuchiapingian), but its phylogenetic position is non-decisive (e.g. Ezcurra et al., 2014; Ezcurra, 2016). A conodont fauna found in correspondence of the Nautiloid Horizon B in the lower part of the *Bellerophon* Formation, indicates a late Changhsingian age (Posenato, 2010), whereas the base of the overlying Werfen Formation includes the PT boundary based on micro- and macrofossils of marine invertebrates (e.g. Posenato, 2019). Therefore, the age of the Arenaria di Val Gardena Formation is probably Lopingian, and more specifically late Wuchiapingian-early Changhsingian.

3. THE DOLOMITES VERTEBRATE ICHNOASSOCIATION

3.1. HISTORICAL OVERVIEW

The first description of tetrapod footprints from the Lopingian of Italy is by Abel (1929), who described and figured an isolated track preserved in convex hyporelief from the locality of Egna/Neumarkt, near Bolzano/Bozen. He assigned the specimen to *Herpetichnium acrodactylum*. This specimen was previously reported by Kittl (1891), when this area was part of the Austro-Hungarian Empire.

The first detailed studies date back to the 1950s and were prompted by Piero Leonardi, the first holder of the chair of geology at Ferrara University, who began studying the world famous Bletterbach gorge site in the Dolomites region (Leonardi, 1951, 1952, 1953, 1955, 1957, 1960, 1967). He found several new specimens in the lower part of the Bletterbach gorge in 1948. Leonardi (1951) assigned these specimens to: *Eumechichnium gampsodactylum*, *Ichnium* cf. *brachydactylum*, *Nanopus*? *grimmi*, cf. *Onychichnium escheri*, *Ornithoidipus*? *perwangeri*, *Prochirotherium permicum* and *Thecodontichnus* isp. He therefore introduced a new ichnogenus, *Prochirotherium*, and three new ichnospecies, *N. grimmi, O. perwangeri* and *P. permicum*. Further research in this area was led by Piero Leonardi between 1951-1960. The new material was later described by Leonardi (1974), who assigned these tracks to *Dromopus lacertoides* and to undetermined tetrapod tracks of anamniotes, sphenacodont synapsids, lepidosauromorphs/procolophonids and archosauromorphs.

Starting in 1972, a research team including Maria

Tab. 1 - The fossiliferous localities. Note that the coordinates may refer to recognizable places near the outcrops. The question mark means uncertain occurrence. Note that the occurrences of *Contiichnus* and *Merifontichnus* are currently debated.

geographic area	locality name	coordinates	further indications	references	Ichnotaxa											
					Batrachichnus	*Capitosauroides*	*Contiichnus*	*Dicynodontipus*	*Dolomitipes*	*Dromopus*	*Merifontichnus*	*Pachypes*	*Paradoxichnium*	*Protochirotherium*	*Rhynchosauroides*	tetrapod tracks indet.
Dolomites	Egna/ Neumarkt	46°18'44.1"N 11°16'19.2"E	Western slope of Cislon mount, between Gleno and Montagna/Montan	Kittl, 1891; Abel, 1929; Marchetti et al., 2019a									X?			
Dolomites	Bletterbach gorge	46°21'28.18"N 11°26'03.09"E	In the gorge below the waterfall and in the valley above the waterfall	Leonardi P., 1951; Conti et al., 1975, 1977; Ceoloni et al., 1988 a,b; Valentini et al., 2007, 2009; Bernardi et al., 2017 a,b; Citton et al., 2019a; Marchetti et al., 2019a	X?	X	X	X	X	X?		X	X	X?	X	X
Dolomites	Pausa	46°20'05.31"N 11°21'35.73"E	Aside the road n° 48, between Doladizza/ Kalditsch and Pausa	Leonardi P., 1957; Leonardi G., 1974; Conti et al., 1977; Marchetti et al., 2019a									X?			
Dolomites	San Pellegrino pass	46°22'41.88"N 11°47'38.4"E	On the slopes NE of San Pellegrino pass, immediately north of the Cima Uomo chalet	Leonardi G., 1974; Valentini et al., 2007; Marchetti et al., 2019a											X	
Dolomites	Redagno di sopra/ Oberradein	46°20'54.7"N 11°24'22.4"E	Aside the provincial road 130, about 700 m E of the Geological Museum of Redagno di Sopra/ Oberrradein	Conti, 1987; Valentini et al., 2007, 2009; Marchetti et al., 2019a								X			X	X
Dolomites	Nova Ponente/ Deutschnofen	46°23'29.5"N 11°24'49.7"E	In the woods immediately south of Pietralba/ Weissenstein	Leonardi P., 1960; Wopfner, 1999; Bernardi et al., 2015; Marchetti et al., 2019a										X?		
Dolomites	Seceda mount	46°36'02.4"N 11°43'32.4"E	Near Ortisei	Ceoloni et al., 1988b												X
Dolomites	Daiano	46°18'03.2"N 11°26'54.4"E	Between Cugola pass and Daiano, immediately east of Pra di Ronco	Unpublished, reported by Marco Spezzamonte												X
Venetian Prealps	Merendaore	45°43'06.1"N 11°11'46.9"E	Along the road SP 9, north of Merendaore	Mietto, 1975											X	X
Venetian Prealps	Ulbe	45°42'54.4"N 11°12'14.2"E	North-east of Merendaore, known also as Brunialti	Mietto, 1981, 1995; Marchetti et al., 2017		X?					X?	X	X			X
Venetian Prealps	Cortiana	45°45'59.6"N 11°14'37.7"E	Southern slopes of Monte Alba	Marchetti et al., 2017		X?			X?							
CarnicAlps	Valdajer	46°32'51.9"N 13°05'06.9"E	Between the Valdajer castle and the Valdajer alm	Mietto and Muscio, 1987; Dalla Vecchia et al., 2012								X				X

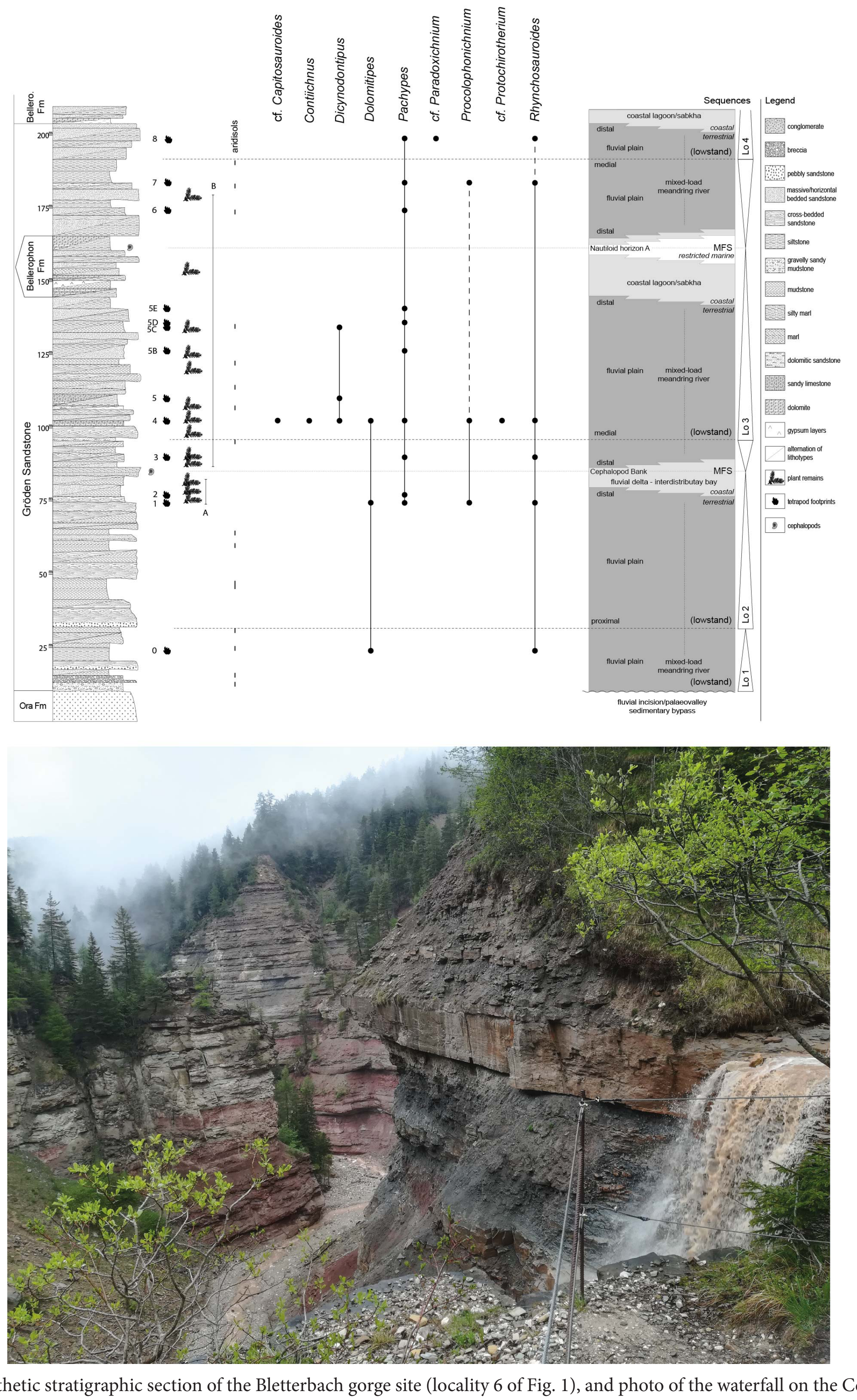

Fig. 2 - Synthetic stratigraphic section of the Bletterbach gorge site (locality 6 of Fig. 1), and photo of the waterfall on the Cephalopod Bank from the same site. The scheme shows the stratigraphic occurrences of tetrapod ichnogenera, plant remains and palaeosols; lithofacies and sequence stratigraphy. Note that the occurrence of *Contiichnus* is currently debated. A-B: flora types. 0-8: ichnofossil sites (numbers 1, 2, 3, 4, 5, 6, 7, 8 correspond to those provided by Ceoloni et al. 1988a). Actual track occurrences are represented by dots, lines represent the supposed stratigraphic distribution, dashed lines uncertain stratigraphic distribution.

Alessandra Conti, Giuseppe Leonardi, Nino Mariotti and Umberto Nicosia started intensive field work in the Bletterbach gorge and in nearby localities of the Dolomites. The largest part of the material came from the Bletterbach gorge, and constitutes the bulk of the present-day collection of about 900 specimens. In a first phase of the research campaign, until 1975, the specimens were not precisely placed in the stratigraphic section of the Bletterbach gorge and a large part was found in debris. The first results of these discoveries were published by this research group in a series of papers in the 70s.

Leonardi and Nicosia (1973) described a pentadactyl imprint preserved in convex hyporelief found in 1972 and attributed to temnospondyl anamniotes. Leonardi et al. (1975) described a large pentadactyl *pes* imprint preserved in convex hyporelief, found at the base of the waterfall in 1973 (Fig. 3). They introduced the ichnogenus *Pachypes* and the ichnospecies *Pachypes dolomiticus* and attributed these tracks to pareiasaurid parareptiles, because of the large size, the ectaxony, the reduction of lateral digits, consistent with forms such as *Bradysaurus*. Conti et al. (1975) described several specimens found in 1973 and attributed them to different groups of anamniotes, synapsids and reptiles. Among the reptile tracks, the ichnogenera *Dromopus* and *Notalacerta* were identified. They also described, for the first time from Bletterbach gorge, remains of fishes and bivalves. Also, the cephalopods were described, although their first mention is by Perwanger (1946), and they were reported also by Leonardi (1967). One of the most important works on Italian ichnology of the 20th century is Conti et al. (1977). This work described the large quantity of material found during field work in the Bletterbach gorge and nearby localities between 1972-1976, including also material found in the same area between 1951-1960. Conti et al. (1977) assigned these specimens to: *Amphisauropus* aff. *latus*, *Limnopus*, *Notalacerta* and rachitomous anamniote tracks indet. (attributed to anamniotes); *Dimetropus* isp., *Ichniotherium cottae* and *Laoporus* isp. (attributed to pelycosaur-grade synapsids); *Dicynodontipus geinitzii*, anomodont and theriodont tracks indet. (attributed to therapsid synapsids); *Phalangichnus perwangeri*, *Varanopus* aff. *curvidactylus*, *Pachypes dolomiticus* (attributed to anapsid reptiles); *Dromopus lacertoides*, *Rhynchosauroides palmatus*, *Rhynchosauroides pallinii* and lepidosaur tracks indet. (attributed to non-archosauromorph diapsid reptiles) and *Chirotherium* isp., *Synaptichnium* isp., ?*Thecodontichnus* cf. *verrucae*, *Tridactylichnium leonardii* and proterosuchian tracks indet. (attributed to archosauromorph diapsid reptiles). Other tracks, such as ?*Pseudobradypus* isp., were attributed to reptiles. A new ichnogenus (*Tridactylichnium*) and three new ichnospecies (*T. leonardii, P. perwangeri* and *R. pallinii*) were erected. Other trace fossils, including vertebrate coprolites, invertebrate burrows (*Rhizocorallium* and burrows indet.) and invertebrate traces (?*Kouphichnium*) were preliminarily described. A review of the other fossils found in the Bletterbach gorge including fishes, cephalopods, plant remains and sporomorphs was also part of this work.

Conti et al. (1977) was the first work to describe an extensive Lopingian tetrapod ichnoassociation from floodplain and marginal marine environments. For the first time in Permian units, typical Triassic chirotheriid tracks were recognised (*Chirotherium* and *Synaptichnium*). The occurrence of these archosauromorph ichnotaxa suggested a Triassic affinity of the tetrapod ichnoassociation, thus for the first time a Lopingian age for the upper part of the Arenaria di Val Gardena Formation in the Bletterbach gorge was proposed. In fact, previous studies considered

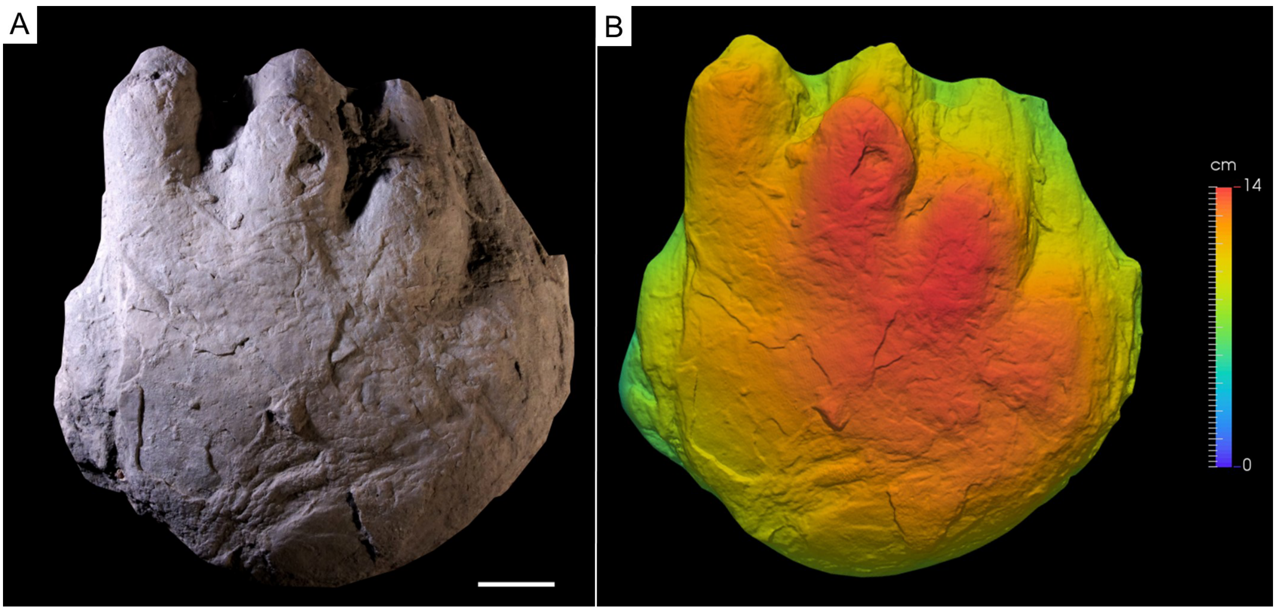

Fig. 3 - IGPF 73-111. Holotype of *Pachypes dolomiticus*, right *pes* imprint, convex hyporelief. A) photograph. B) False-colour depth map of the 3D model. IGPF-Paleontological Museum "Piero Leonardi", Ferrara. Scale bar = 5 cm.

this formation as Cisuralian or Guadalupian (e.g. Accordi, 1958). Conti et al. (1977) made also a detailed comparison of the Dolomites ichnoassociation with the Permian-Triassic faunas all over the world, highlighting a strong similarity with Lopingian assemblages from Russia and South Africa. Conti et al. (1977) evaluated also the palaeoecology of the tetrapod ichnoassociation, estimating a decrease of anamniote forms in the upper part of the stratigraphic section and an overall low relative abundance of herbivores.

Leonardi (1979) and Conti et al. (1981) revised the tetrapod footprints previously described by Leonardi (1951) and re-assigned them to *Dromopus lacertoides*, *Rhynchosauroides* cf. *schochardti* and *Prochirotherium permicum*. The ichnotaxa *N. grimmi* and *O. perwangeri* were considered *nomina dubia*.

In a second phase of the research campaign in the Bletterbach gorge, starting in 1976, all the specimens were searched *in situ*, in order to be precisely placed in the stratigraphic section. The new data were published in a series of papers between the 1970s and the 1980s (e.g. Conti et al., 1979, 1980; Ceoloni et al., 1988a). Conti et al. (1979) discussed preliminarily the tetrapod footprint biostratigraphy of the Bletterbach gorge section based on the new data. The occurrence of typical Triassic forms such as *Chirotherium*, *Dicynodontipus* and *Rhynchosauroides* in the upper part of the section confirmed the Lopingian age of this stratigraphic interval. The lower part of the section was considered not older than late Guadalupian, according to thickness and depositional rate. Conti et al. (1987) described tetrapod footprints from a new site, near the village of Redagno di Sopra/Oberradein. They identified *Pachypes dolomiticus*, indeterminate lacertoid tracks, indeterminate anomodont tracks and possible swimming traces. Ceoloni et al. (1988a) built a new stratigraphic scheme highlighting the track occurrences at eight different levels within the Bletterbach gorge section. Based on the study of two large slabs coming from level 4, they erected one new ichnogenus (*Janusichnus*) and five new ichnospecies (*Chelichnus tazelwürmi, Hyloidichnus tirolensis, Ichniotherium accordii, Janusichnus bifrons* and ?*Paradoxichnium radeinensis*). *C. tazelwürmi* and *I. accordii* were attributed to pelycosaur-grade synapsids, *H. tirolensis* to anapsid reptiles, *P. radeinensis* to lepidosauromorph reptiles and *J. bifrons* to reptiles. The Dolomites ichnoassociation was compared to the Assemblage IV from Russia and the *Daptocephalus* Assemblage Zone from South Africa, both of latest Permian age. Ceoloni et al. (1988b) considered the Dolomites tetrapod ichnoassociation slightly younger than those from the Lopingian of Germany and Scotland. Massari et al. (1988) analysed the stratigraphy of the Bletterbach gorge section based on sporomorphs, foraminiferans, algae and tetrapod footprints found in the Arenaria di Val Gardena and *Bellerophon* formations, assigning to this stratigraphic interval a ?latest Capitanian-Changhsingian age.

During the 1990s, few studies analyzed the Lopingian tracks of the Dolomites. Nevertheless, it is remarkable the work by Conti et al. (1997), who for the first time in tetrapod ichnology applied the concept of Faunal Units (e.g. Walsh, 1998) to the tetrapod footprint record. These are informal units delimited by isochronous events. Conti et al. (1997) introduced the Bletterbach Faunal Unit based on the tetrapod ichnoassociation from the Dolomites. These units were later named Ichnofaunal Units by Avanzini et al. (2001). Wopfner (1999) described two new tracks from the locality Nova Ponente/Deutschnhofen and assigned them to *Chirotherium* isp. Massari et al. (1999) listed the tetrapod footprint of the Dolomites in a description of the stratigraphy and fossil content of the Bletterbach gorge.

The new century started with a series of reviews of the Dolomites tetrapod ichnoassociation, discussing its ichnotaxonomic, faunistic, palaeoecologic and stratigraphic significance (Conti et al., 2000; Avanzini et al., 2001; Cassinis et al., 2002; Avanzini and Tomasoni, 2004; Nicosia et al., 2005; Leonardi, 2008). New data were provided by Nicosia et al. (2001), who described *Rhynchosauroides* cf. *palmatus* from about 20 m above the base of the Arenaria di Val Gardena Formation in the Bletterbach gorge section. A comprehensive revision of the lacertoid tracks from the Lopingian of the Dolomites was provided by Valentini et al. (2007). They identified: *Ganasauripus ladinus*, *Rhynchosauroides pallinii*, *Rhynchosauroides* isp. 1 and *Rhynchosauroides* isp. 2. The ichnogenus *Ganasauripus* and the ichnospecies *G. ladinus* were erected in this paper. Valentini et al. (2008) provided a detailed functional study and track-trackmaker correlation for *Pachypes dolomiticus*. The *manus* tracks resulted more completely impressed and inwards-directed than *pes* tracks, suggesting a dual gait of the trackmaker, which would be consistent with contemporary therischian pareiasaurs such as *Scutosaurus*. Valentini et al. (2009) comprehensively revised *Pachypes dolomiticus* from the Dolomites describing, for the first time, incomplete step cycles of this ichnospecies. They also re-assigned the material from the Lopingian of Russia originally described by Gubin et al. (2003) and Surkov et al. (2007) to the new combination *Pachypes primus* and to *Pachypes* isp., respectively. The material from the Guadalupian of France and South Africa assigned to *Brontopus* and *Planipes* was instead considered clearly different from *Pachypes* and of probable therapsid origin.

The last 10 years were initially characterized by reviews of the Dolomites tetrapod ichnoassociation (Avanzini et al., 2011). Subsequently, several papers with a large amount of new data were published. The chirotheriid footprints from the Lopingian of the Dolomites, initially studied and assigned to *Chirotherium* isp. by Conti et al. (1977) and Wopfner (1999), were re-analysed by Bernardi et al. (2015), who assigned these specimens and some new material to cf. *Protochirotherium* isp. This was considered the earliest record of mesaxonic *pes* footprints of archosauromorphs thus preceeding of about 10 Ma the earliest record of mesaxonic *pes* skeletons within this group. These footprints permitted to infer a size range and morphology analogue to the Early Triassic forms, thus suggesting an earlier radiation and diversification of archosauriforms. Bernardi et al. (2017a) proposed a study of the Lopingian biotas from 14 different localities all around the world, with an integration of data from tetrapod footprints and skeletons, plant remains and insect damage on plant remains. The Dolomites biota was chosen as the main reference for the low palaeolatitudes. The results highlighted a biota composition strongly dependent by palaeolatitude, and a higher taxonomic diversity at low palaeolatitudes. Bernardi et al. (2018) studied the palaeobiogeographic distribution of tetrapod faunas and ichnofaunas across the Permian-Triassic boundary, including the Dolomites ichnofauna, and noted a shift of the faunas towards higher palaeolatitudes during the Early Triassic.

Kustatscher et al. (2017) analysed the effects of sea-level change on the Bletterbach gorge biota, after a reconstruction of the transgressive-regressive cycles along the section. The tetrapod footprint diversity seems to increase during the transgressive phases, reaching its maximum at the beginning of the regressive phases. This was interpreted as a taphonomic effect due to rapid burial rather than an actual increase of diversity. Another palaeoecologic study of the Bletterbach ichnofauna was conducted by Ronchi et al. (2018), who described, for the first time from the Arenaria di Val Gardena Formation, trace fossils attributed to swimming behaviour of fishes (*Undichna* cf. *quina* and *Undichna bina*) associated with the tetrapod tracks cf. *Procolophonichnium* isp. and *Rhynchosauroides* isp. Further reviews of the Bletterbach gorge biotas were proposed by Bernardi et al. (2017b) and Marchetti et al. (2017).

A study on the registration and preservation of tetrapod tracks has been proposed by Citton et al. (2016), who analysed a slab from the level 4 of the Bletterbach gorge section with 11 trackways belonging to *Pachypes dolomiticus, Chelichnus tazelwürmi, Ganasauripus ladinus* and *Janusichnus bifrons*. Through interpretive drawings, photos and 3D models, the sequence of ripple formation and trackway registration was reconstructed based on the principle of cross-cutting relationships, highlighting a variable morphological preservation through time. A peculiar case of track interference was observed, indicating that caution must be kept when establishing the timeline of passages only from overprinting. Citton et al. (2019a) revised the ichnotaxon *Chelichnus tazelwürmi* and, after a comparison with the type material of *Chelichnus* from Scotland, concluded that this ichnospecies should not be classified as *Chelichnus*. They introduced the ichnogenus *Contiichnus* (previously informally named *Latentitherichnus*) and assigned this ichnospecies to the new combination *Contiichnus tazelwürmi*. Through a study of the 3D models of *C. tazelwürmi*, Citton et al. (2019a) highlighted a more deeply-impressed medial part of *pes* imprints, whereas the weight was more evenly-distributed in the *manus* imprints. These tracks were attributed to an indeterminate group of therapsids.

Voigt et al. (2015) revised the slab studied by Abel (1929), which contains the material assigned to *Tridactylichnium* by Conti et al. (1977) and a new specimen, and assigned this material to *Paradoxichnium problematicum*. Voigt and Lucas (2019) introduced the *Paradoxichnium* Tetrapod Footprint Biochron for the Lopingian. The main reference is the Dolomites tetrapod ichnoassociation. As representative ichnotaxa from the Arenaria di Val Gardena Formation they figured: *Hyloidichnus, Pachypes, Paradoxichnium* and *Rhynchosauroides*.

The first comprehensive revision of the tetrapod ichnoassociation from the Dolomites after Conti et al. (1977) was written by Marchetti et al. (2019a). These authors analysed about 900 specimens, selecting those showing the best morphological preservation and revising the ichnotaxonomy according to the most recent studies on Permian-Triassic ichnofaunas. They identified: cf. *Batrachichnus* isp. (temnospondyl anamniote), *Capitosauroides* isp. (reptiliomorph anamniote), *Dicynodontipus* isp. (cynodont therapsid), *Dolomitipes accordii* (dicynodont therapsid), cf. *Dromopus* isp. (neodiapsid), *Pachypes dolomiticus* (pareiasaurian parareptile), *Paradoxichnium problematicum* (archosauromorph neodiapsid), *Procolophonichnium tirolensis* (procolophonoid parareptile), cf. *Protochirotherium* isp. (archosauriform neodiapsid) and *Rhynchosauroides pallinii* (neodiapsid). The ichnogenus *Dolomitipes* was introduced in the new combination *Dolomitipes accordii*. The new combination *Procolophonichnium tirolensis* was proposed. *Ganasauripus ladinus* has been synonymized with *Rhynchosauroides pallinii*. This tetrapod ichnoassociation, dominated by neodiapsid and parareptile footprints and with less abundant therapsid and anamniote tracks, resulted as the most diverse, best-preserved and abundant ichnoassociation of the Lopingian, sharing similarities with contemporary ichnoassociations from North Africa and Europe and in a lesser degree, South Africa and Russia, but with a stronger Triassic affinity because of the more common and diverse neodiapsid tracks.

In tetrapod track stratigraphy, the Dolomites tetrapod ichnoassociation is the reference for the *Paradoxichnium* tetrapod footprint biochron (Voigt and Lucas, 2018; Schneider et al., 2020), although some dissimilarities exist with older Lopingian ichnofaunas (e.g. Petti et al., 2015). Petti et al. (2015), because of the possible occurrence of *Protochirotherium* in the Arenaria di Val Gardena Formation, suggested to move to the late Lopingian (Changhsingian) the base of the Triassic *Protochirotherium* tetrapod footprint biochron. The Dolomites tetrapod ichnoassociation is also the reference for the Bletterbach Ichnofaunal Unit (Conti et al., 1977; Avanzini et al., 2001). Marchetti et al. (2019b) re-discussed preliminarily the Ichnofaunal Units from the Southern Alps, and updated the Bletterbach Ichnofaunal Unit.

3.2. ICHNOASSOCIATION STRUCTURE

The tetrapod ichnoassociation from the Arenaria di Val Gardena Formation of the Dolomites, in the most recent revision by Marchetti et al. (2019a), includes the following ichnogenera (Tab. 2): cf. *Batrachichnus*, *Capitosauroides*, *Dicynodontipus*, *Dolomitipes*, cf. *Dromopus*, *Pachypes*, *Paradoxichnium*, *Procolophonichnium*, cf. *Protochirotherium* and *Rhynchosauroides*. The occurrence of a further ichnotaxon, *Contiichnus*, is currently debated because it is considered a junior synonym of *Procolophonichnium* by Marchetti et al. (2019a).

The ichnogenus *Batrachichnus* (Figs. 4A, 5A) is a rare ichnotaxon (one specimen) at the Lopingian of the Dolomites. It has been described as cf. *Batrachichnus* isp. by Marchetti et al. (2019a). The only specimen known is a trackway. It is considered a small track (*pes* length <2 cm) of temnospondyl anamniotes, mostly based on the tetradactyl *manus* (Voigt, 2005).

The ichnogenus *Dolomitipes* (Figs. 4B, 5B) is a fairly common ichnotaxon (12 specimens) from the Arenaria di Val Gardena Formation of the Dolomites. It has been erected by Marchetti et al. (2019a) in the new combination *D. accordii*, based on material from the Bletterbach gorge. This material includes two trackways and several *pes-manus* couples and isolated tracks. Material assignable to this ichnogenus has been first described by Conti et al. (1977) as *Limnopus* isp. and *Ichniotherium cottae*. *Dolomitipes* differs from *Limnopus* because of the pentadactyl *manus* and from *Ichniotherium* because of the relatively shorter digit IV and the well-impressed basal pads of digits II-V. The ichnospecies *D. accordii* has been originally introduced by Ceoloni et al. (1988a) as *Ichniotherium accordii*, based on a trackway found in level 4 of the Bletterbach gorge section. *Dolomitipes* is considered by Marchetti et al. (2019a, 2019c) a medium-sized track (*pes* length of about 9-12 cm) of dicynodont therapsids, mostly based on the *pes* mesaxony, the broad sole, the digit tips separated from the palm/sole, the *manus* wider than long, more impressed and more inward-rotated than the *pes*.

The ichnogenus *Capitosauroides* (Fig. 4C) is a relatively uncommon ichnotaxon (six specimens) from the Lopingian of the Dolomites. It has been described as *Capitosauroides* isp. by Marchetti et al. (2019a). It is known from *pes-manus* couples and isolated tracks, trackways were not recognized. Material assigned to this ichnogenus has been first described by Leonardi and Nicosia (1973) and Conti et al. (1977) as undetermined anamniote tracks. The specimen assigned to *Hyloidichnus* by Voigt and Lucas (2018) has been re-assigned to cf. *Capitosauroides* isp. by Marchetti et al. (2019a). *Capitosauroides,* according to Marchetti et al. (2019c), is considered a medium- to relatively large-sized track (*pes* length of about 5-20 cm) of therocephalian therapsids, mostly based on the semi-circular arrangement of digit bases, the relatively short and concave palm/sole, the medial-lateral increase in relief and the weak ectaxony.

The ichnogenus *Dicynodontipus* (Fig. 4D) is a rare ichnotaxon (four specimens) from the Arenaria di Val Gardena Formation of the Dolomites. The known material includes a *pes-manus* couple and few isolated tracks. It has been first described as *Dicynodontipus geinitzii* by Conti et al. (1977), although some of this material was previously described as undetermined therapsid tracks by Conti et al. (1975). It is considered a medium-sized track (*pes* length of about 5-10 cm) of cynodont therapsids, mostly based on the broad palm/sole separated from the digit tips, the digit proportions and the trackway pattern (e.g. Haubold, 1966, 1971; Marchetti et al., 2019c).

The ichnogenus *Procolophonichnium* (Figs. 4E, 5C) is a fairly common ichnotaxon (11 specimens) from the Lopingian of the Dolomites. It is known from at least six trackways and several *pes-manus* couples and isolated imprints. It has been described in the new combination *P. tirolensis* by Marchetti et al. (2019a). The ichnospecies has been originally introduced by Ceoloni et al. (1988a) as *Hyloidichnus tirolensis*, based on a trackway found in the Level 4 of the Bletterbach gorge section. Marchetti et al. (2019a) considered the ichnospecies ?*Paradoxichnium radeinensis* and *Contiichnus tazelwürmi* (described by Ceoloni et al., 1988a) as junior synonyms of *P. tirolensis*, and the ichnogenus *Contiichnus* (described by Citton et al., 2019a) as junior synonym of *Procolophonichnium* (described by Nopcsa, 1923). In fact, all this material shows the diagnostic features of *P. tirolensis*, including a proximal *pes* digit V and a *manus* imprint slightly longer than wide. The ichnotaxa *Prochirotherium permicum*, *Nanopus*? *grimmi* and *Janusichnus bifrons* (described by Leonardi, 1951 and Ceoloni et al., 1988a, respectively) were instead considered *nomina dubia* and assigned to cf. *Procolophonichnium* isp. (Marchetti et al., 2019a). *P. tirolensis* is considered a relatively small- to medium-sized track (*pes* length of about 2-8 cm) of small parareptiles such as procolophonoids, mostly based on the parallel and grouped digit imprints, the weak ectaxony, the short palm/sole and the medial-lateral decrease in relief (Marchetti et al., 2019a, 2019c).

The ichnogenus *Pachypes* (Figs. 3, 4F, 5D) is the second most common ichnotaxon (26 specimens) from the Arenaria di Val Gardena Formation of the Dolomites. A trackway and two incomplete step cycles are known, the majority of occurrences are isolated tracks. It has been originally described as *Pachypes dolomiticus* by Leonardi et al. (1975) and comprehensively revised by Valentini et al. (2009). Some material previously assigned to relatively large undetermined therapsid tracks (e.g. Conti et al., 1977; Avanzini et al., 2011) has been re-assigned to cf. *Pachypes* isp. by Marchetti et al. (2019a). *Pachypes* is considered a medium- to large-sized track (*pes* length of about 6-37 cm) of pareiasaurian parareptiles, probably therischian forms such as *Scutosaurus*, based on the broad and grouped digit imprints, the weak ectaxony and the marked reduction of lateral digit imprints (Valentini et al., 2008).

The ichnogenus *Dromopus* (Figs. 4G, 5E) is a rare ichnotaxon (two specimens) in the Lopingian of the

Tab 2. Current and previous ichnotaxonomic assignments of the tetrapod tracks from the Lopingian of Italy.

	Current assignment	Previous assignments	References
Dolomites	cf. *Batrachichnus* isp.		Marchetti et al. 2019a
Dolomites	*Dolomitipes accordii*	*Limnopus* isp., *Ichniotherium cottae*, *Ichniotherium accordii*	Conti et al. 1977; Ceoloni et al. 1988a; Marchetti et al. 2019a
Dolomites	*Capitosauroides* isp.	Undetermined anamniote track, *Hyloidichnus* isp.	Leonardi and Nicosia 1973; Conti et al., 1977; Voigt and Lucas, 2018; Marchetti et al. 2019a
Dolomites	*Dicynodontipus* isp.	Undetermined therapsid track, *Dicynodontipus geinitzi*	Conti et al. 1975, 1977; Marchetti et al. 2019a
Dolomites	*Procolophonichnium tirolensis*	*Hyloidichnus tirolensis*, ?*Paradoxichnium radeinensis*	Ceoloni et al. 1988a; Marchetti et al. 2019a
Dolomites	cf. *Procolophonichnium* isp.	*Prochirotherium permicum*, *Nanopus? grimmi*, *Janusichnus bifrons*	Leonardi 1951; Ceoloni et al. 1988a; Marchetti et al. 2019a
Dolomites	*Pachypes dolomiticus*		Leonardi et al. 1975; Conti et al. 1977; Valentini et al. 2009; Marchetti et al. 2019a
Dolomites	cf. *Pachypes* isp.	Undetermined therapsid track	Conti et al. 1977; Avanzini et al. 2011; Marchetti et al. 2019a
Dolomites	cf. *Dromopus* isp.	*Rhynchosauroides* isp. 1	Valentini et al. 2007; Marchetti et al. 2019a
Dolomites	*Rhynchosauroides pallinii*	*Ganasauripus ladinus*	Conti et al. 1997; Valentini et al. 2007; Marchetti et al. 2019a
Dolomites	cf. *Rhynchosauroides* isp.	*Ornithodipus? perwangeri; Phalangichnus perwangeri*	Leonardi et al. 1951; Marchetti et al. 2019a
Dolomites	*Paradoxichnium problematicum*		Voigt et al. 2015; Marchetti et al. 2019a
Dolomites	cf. *Paradoxichnium* isp.	Undetermined tetrapod track, *Tridactylichnium leonardii*	Abel 1929; Conti et al. 1977; Marchetti et al. 2019a
Dolomites	cf. *Protochirotherium* isp.	*Chirotherium* isp.	Conti et al. 1975; Wopfner, 1999; Bernardi et al. 2015; Marchetti et al. 2019a
Dolomites	*Contiichnus tazelwürmi*/ *Procolophonichnium tirolensis*	*Chelichnus tazelwürmi*	Ceoloni et al. 1988a; Citton et al. 2019a; Marchetti et al. 2019a
Venetian Prealps	cf. *Capitosauroides* isp.	Procolophonomorpha tracks	Mietto 1995; Marchetti et al. 2017
Venetian Prealps	Undetermined therapsid track		Marchetti et al. 2017
Venetian Prealps	*Pachypes* isp.	*Pachypes dolomiticus*	Mietto, 1981; Marchetti et al. 2017
Venetian Prealps	cf. *Merifontichnus* isp./undetermined track		Marchetti et al. 2017; Citton et al. 2019b
Venetian Prealps	*Rhynchosauroides* isp.	*Eumechichnium gampsodactylum*	Mietto 1975; Marchetti et al. 2017
Venetian Prealps	*Paradoxichnium* isp.		Marchetti et al. 2015; 2017
Carnic Alps	*Pachypes* isp.		Dalla Vecchia et al. 2012
Carnic Alps	Undetermined tracks	*Prochirotherium permicum*	Mietto and Muscio 1987; Marchetti et al. 2019a

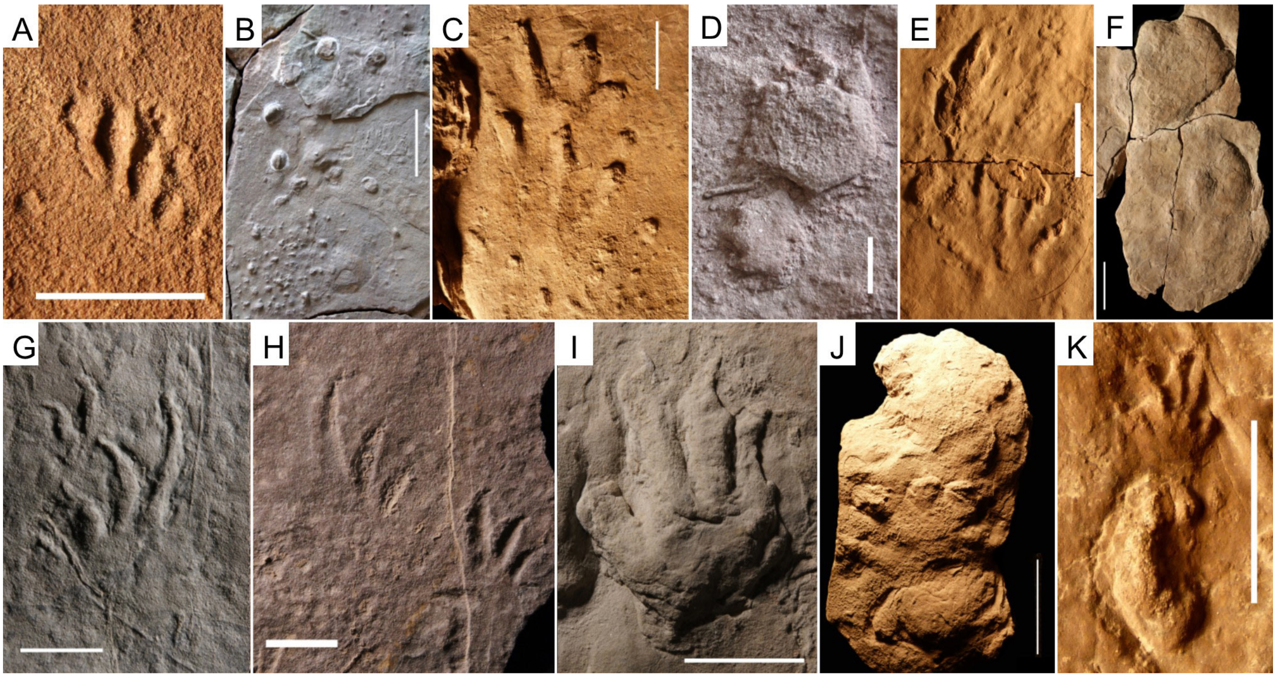

Fig. 4 - Tetrapod tracks from the Dolomites. A) NMS-NN 1. cf. *Batrachichnus* isp., right *pes-manus* couple, convex hyporelief. B) UR-NS 34/19. *Dolomitipes accordii*, left *pes-manus* couple, convex hyporelief. C) UR-NN 1. *Capitosauroides* isp., right *pes-manus* couple, convex hyporelief. D) UR 73/64. *Dicynodontipus* isp., left *pes-manus* couple, convex hyporelief. E) NMS-NS 34/26. *Procolophonichnium tirolensis*, right *pes-manus* couple, convex hyporelief (holotype). F) NMS-NS 34/27. *Pachypes dolomiticus*, left *pes-manus* couple, convex hyporelief. G) NMS-NS 34/51. cf. *Dromopus* isp., left *pes-manus* couple, convex hyporelief. H) UR-NN 28. *Rhynchosauroides pallinii*, left *pes-manus* couple, concave epirelief. I) MGR 0027. *Paradoxichnium problematicum*, right *manus*, convex hyporelief. J) UR 75/2. cf. *Protochirotherium* isp., right *pes-manus* couple, convex hyporelief. K) UR-NS 34/28. *Contiichnus tazelwürmi*/*Procolophonichnium tirolensis*, left *pes-manus* couple, convex hyporelief (holotype of *C. tazelwürmi*). MGR-Geoparc Bletterbach, GeoMuseum, Redagno, Italy; MNS-Museum of Nature South Tyrol, Bolzano, Italy; UR-Palaeontological Museum, SAPIENZA Università di Roma, Italy. Scale bar A=1 cm. Scale bar C, D, E, G, H, K=2 cm. Scale bar B, I, J=5 cm. Scale bar F=10 cm.

Dolomites. It is currently known from two trackways. It has been described as cf. *Dromopus isp.* by Marchetti et al. (2019a). This ichnogenus has been described from this area since Leonardi (1974). It is considered a relatively small to large (0.5-7 cm) track of diapsid eureptiles or bolosaurid parareptiles, based on the thin, slender, clawed digit I-IV imprints superimposed at their base, the semidigitigrady and the marked ectaxony (e.g. Voigt, 2005).

The ichnogenus *Rhynchosauroides* (Figs. 4H, 5F) is the most common ichnotaxon (59 specimens) in the Arenaria di Val Gardena Formation of the Dolomites. It is known from about 20 trackways and a large amount of incomplete step cycles, *pes-manus* couples and isolated tracks. It has been first described with the new ichnospecies *Rhynchosauroides pallinii* by Conti et al. (1977), although material later assigned to *Rhynchosauroides* has been known since Leonardi (1951). A comprehensive revision of the lacertoid tracks from the Arenaria di Val Gardena Formation has been proposed by Valentini et al. (2007), who identified *R. pallinii*, *Rynchosauroides* isp. 1, *Rhynchosauroides* isp. 2 and introduced the ichnotaxon *Ganasauripus ladinus*. Marchetti et al. (2019a) considered *R. pallini* the only valid *Rhynchosauroides* ichnospecies from the Lopingian of the Dolomites. These authors considered *G. ladinus* a junior synonym of *Rhynchosauroides pallinii*, and *O. perwangeri* and *P. perwangeri* (described by Leonardi, 1951 and Conti et al., 1977, respectively) as *nomina dubia*. The Lopingian *Rhynchosauroides* is considered a small- to medium-sized (*pes* length <9 cm) track of Archosauromorpha or Younginiformes mostly based on the thin, slender, clawed digit I-IV imprints superimposed at their base, the semidigitigrady, the marked ectaxony and the relatively short *pes* digit V (Marchetti et al., 2019a).

The ichnogenus *Paradoxichnium* (Fig. 4I) is a rare ichnotaxon (one specimen) in the Lopingian of the Dolomites. It is known from few isolated footprints. It has been described as *Paradoxichnium problematicum* by Voigt et al. (2015). The material first described by Abel (1929) and the ichnotaxon *Tridactylichnium leonardii* (Fig. 5G), described by Conti et al. (1977), have been re-assigned to cf. *Paradoxichnium* isp. by Marchetti et al. (2019a). An incomplete step cycle and some isolated footprints have been assigned to cf. *Paradoxichnium* isp. in the same paper. *Paradoxichnium* is considered a relatively large track (*pes* length of about 15 cm) of archosauromorph diapsids, such as *Protorosaurus,* mostly based on the long, clawed and tightly grouped digit imprints and the relatively long *pes* digit V (Marchetti et al., 2019a).

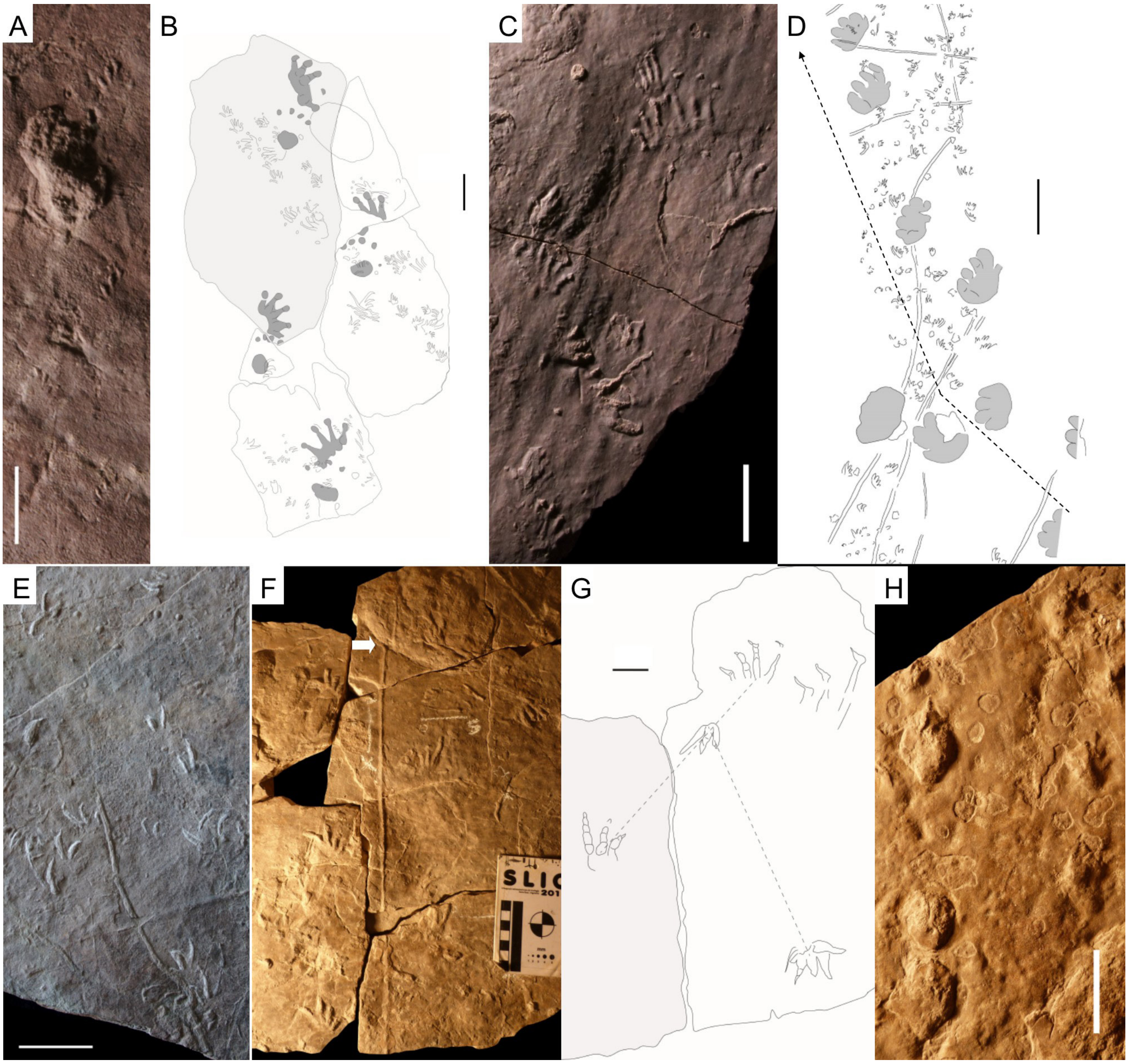

Fig. 5 - Tetrapod trackways from the Dolomites. A) NMS-NN 1. cf. *Batrachichnus* isp., trackway, convex hyporelief. B) UR/NMS-NS 34/26. *Dolomitipes accordii*, trackway, interpretive drawing (holotype). The grey part of the slab has not been relocated. C) NMS-NS 34/26. *Procolophonichnium tirolensis*, trackway, convex hyporelief (holotype). D) UR-NS 34/28. *Pachypes dolomiticus*, trackway showing a change in direction, interpretive drawing. E) UR-NS 34/33. cf. *Dromopus* isp., trackway with possible tail impression, convex hyporelief. F) UR-NS 34/28. *Rhynchosauroides pallinii*, trackway with continuous tail impression, superimposed and dislocated (arrow) by a *Pachypes dolomiticus pes-manus* couple, convex hyporelief. G) IGPF 73/92. cf. *Paradoxichnium* isp., two incomplete step cycles including the holotype of *Tridactylichnium leonardii*, interpretive drawing. The grey part of the slab has not been relocated. H) UR-NS 34/28. *Contiichnus tazelwürmi*/*Procolophonichium tirolensis*, trackway, convex hyporelief (holotype of *C. tazelwürmi*). IGPF-Paleontological Museum "Piero Leonardi", Ferrara University, Italy; MNS-Museum of Nature South Tyrol, Bolzano, Italy; UR-Palaeontological Museum, SAPIENZA Università di Roma, Italy. Scale bar A,H=2 cm. Scale bar C, E, G=5 cm. Scale bar B, D=10 cm.

The ichnogenus *Protochirotherium* (Fig. 4J) is a rare ichnotaxon (three specimens) in the Arenaria di Val Gardena Formation of the Dolomites. It is known from few isolated but well-preserved tracks, including a possible *pes-manus* couple. It has been described as cf. *Protochirotherium* isp. by Bernardi et al. (2015). This includes the material originally assigned to *Chirotherium* isp. by Conti et al. (1977) and Wopfner (1999). It is considered a relatively large track (*pes* length up to 28 cm) of archosauriform diapsids because of the *pes* mesaxony and the *pes* digit V imprint proximal, in abduction, and clearly separated from the *pes* digit I-IV group (Bernardi et al., 2015).

The ichnogenus *Contiichnus* (Figs. 4K, 5H) is a rare ichnotaxon (one specimen) in the Lopingian of the Dolomites. This specimen includes three trackways from the same stratigraphic surface, the level 4 of the Bletterbach gorge section. It has been introduced by Citton et al. (2019a) in the new combination *C. tazelwürmi*. The ichnospecies was originally described as *Chelichnus tazelwürmi* by Ceoloni et al. (1988a). Citton et al. (2019a) attributed these small tracks (*pes* length <2 cm) to an unknown group of therapsids mostly based on the supposed large sole and sub-equal length of *pes* digit II-IV imprints. Marchetti et al. (2019a) assigned these footprints to *Procolophonichium tirolensis* and attributed the latter ichnotaxon to a parareptile trackmaker mostly based on the medial-lateral decrease in relief and a different interpretation of the *pes* track morphology and orientation.

The tetrapod footprints from the Arenaria di Val Gardena Formation of the Dolomites show remarkable abundance, diversity and morphological preservation (*sensu* Marchetti et al., 2019d). The ichnoassociation, as revised by Marchetti et al. (2019a), is characterized by a marked abundance and diversity of tracks attributed to neodiapsids such as *Dromopus, Rhynchosauroides, Paradoxichnium* and *Protochirotherium* (52% of specimens, 40% of ichnogenera). Tracks attributed to parareptiles, represented by *Pachypes* and *Procolophonichnium*, were also abundant (30% of specimens, 20% of ichnogenera). Less abundant but quite diverse were the tracks attributed to therapsids, including *Capitosauroides, Dicynodontipus* and *Dolomitipes* (18% of specimens, 30% of ichnogenera). Tracks attributed to anamniotes were instead very rare, with the only possible occurrence of *Batrachichnus* (1% of specimens, 10% of ichnogenera). Differently from this revision, Citton et al. (2019a) identified a further ichnotaxon attributed to therapsids, *Contiichnus*.

This is the most diverse, best-preserved and most abundant tetrapod ichnoassociation from the Lopingian all over the world, thus it is a reference for ichnotaxonomic and chronostratigraphic studies of this time interval. It is a marginal marine, low latitude tetrapod ichnoassociation compositionally similar to other Lopingian ichnoassociations, including those from eolian palaeoenvironments and from the mid-high palaeolatitudes (e.g. Hminna et al., 2012; Smith et al., 2015; Marchetti et al., 2019c, 2019e). Nevertheless, evaluating both the track and the skeletal records, the faunal diversity seems higher than the contemporary faunas from the mid-high palaeolatitudes of South Africa and Russia, suggesting high origination and low extinction rates at low palaeolatitudes (Bernardi et al., 2017a). The abundance and diversity of tracks attributed to neodiapsids and especially the first occurrence of mesaxonic tracks attributed to archosauriforms typical of the Triassic (cf. *Protochirotherium* isp.) pushes back the archosauriform radiation of about 10 Ma compared with the skeletal record (Bernardi et al., 2015).

The occurrence of ichnotaxa usually showing evidence of parasagittal gait, such as *Dicynodontipus* and cf. *Protochirotherium* (Lucas, 2019), is in agreement with the acquisition of such trait during the late Lopingian for cynodont therapsids and archosauriform neodiapsids, respectively. In fact, a *Dicynodontipus* trackway with narrow gauge, long stride and complete primary *pes-manus* overstep has been observed in Lopingian units of Scotland (Marchetti et al., 2019e). However, no *Protochirotherium* trackways are known from the Lopingian and no trackways of these two ichnotaxa have been recorded from the Dolomites, so far. So, more material is needed to eventually confirm this hypothesis.

The Dolomites tetrapod ichnoassociation, especially as regards the Bletterbach gorge site, offers the unique opportunity to study the palaeoecology of the biota. The occurrence of tetrapod and invertebrate traces, plant remains, damage caused by herbivore insects, fishes and bivalves, allows a detailed reconstruction of the trophic network (Bernardi et al., 2017a). After the revision by Marchetti et al. (2019a, 2019c), this trophic network would include: top predators such as archosauromorphs (*Paradoxichnium, Protochirotherium*); mid- and large-sized primary consumers such as pareiasaurids (*Pachypes*), dicynodont therapsids (*Dolomitipes*) and theriodont therapsids (*Capitosauroides*); small-sized primary consumers such as non-archosauromorph diapsids (*Dromopus, Rhynchosauroides*), cynodont therapsids (*Dicynodontipus*), procolophonids (*Procolophonichnium*) and anamniotes (*Batrachichnus*). Would the trackmaker of the ichnotaxon *Contiichnus* be a small therapsid as revised by Citton et al. (2019a), this would fit the small-sized primary consumers group.

4. GEOLOGICAL SETTING AND STRATIGRAPHY-VENETIAN PREALPS

Compared to the Dolomites, the Lopingian stratigraphic succession that crops out in the Recoaro area (Vicenza, Veneto) is similar but significantly less thick; the Arenaria di Val Gardena Formation, which has a thickness of 20-50 m, lies directly and uncomformably on the metamorphic basement (Barbieri et al., 1980). As noted by Marchetti et al. (2017), the lower half of the formation is characterised by alluvial red beds arranged in upward fining- and thinning-cycles constituted of discontinuous conglomeratic lenses with an erosive base, passing upwards to coarse-grained m-thick sandstone, red to grey in colour, with cross stratification and dm-thick fine-grained sandstone and cm-thick laminated mudstone. The upper half of the formation is characterized by well-stratified and laterally continuous dm-thick laminated mudstone red, yellow, or grey in colour. The mudstones are characterized by pedogenic horizons and are interbedded to dark or light grey dolostone in strata 10-80 cm thick with irregular bedding and arranged in upward-thickening sequence, representing the basal lithofacies of the *Bellerophon* Formation. The upper contact of the Arenaria di Val Gardena Formation with the *Bellerophon* Formation is transitional (Fig. 6); the stratigraphic limit between these two formations corresponds conventionally to the last siliciclastic layer.

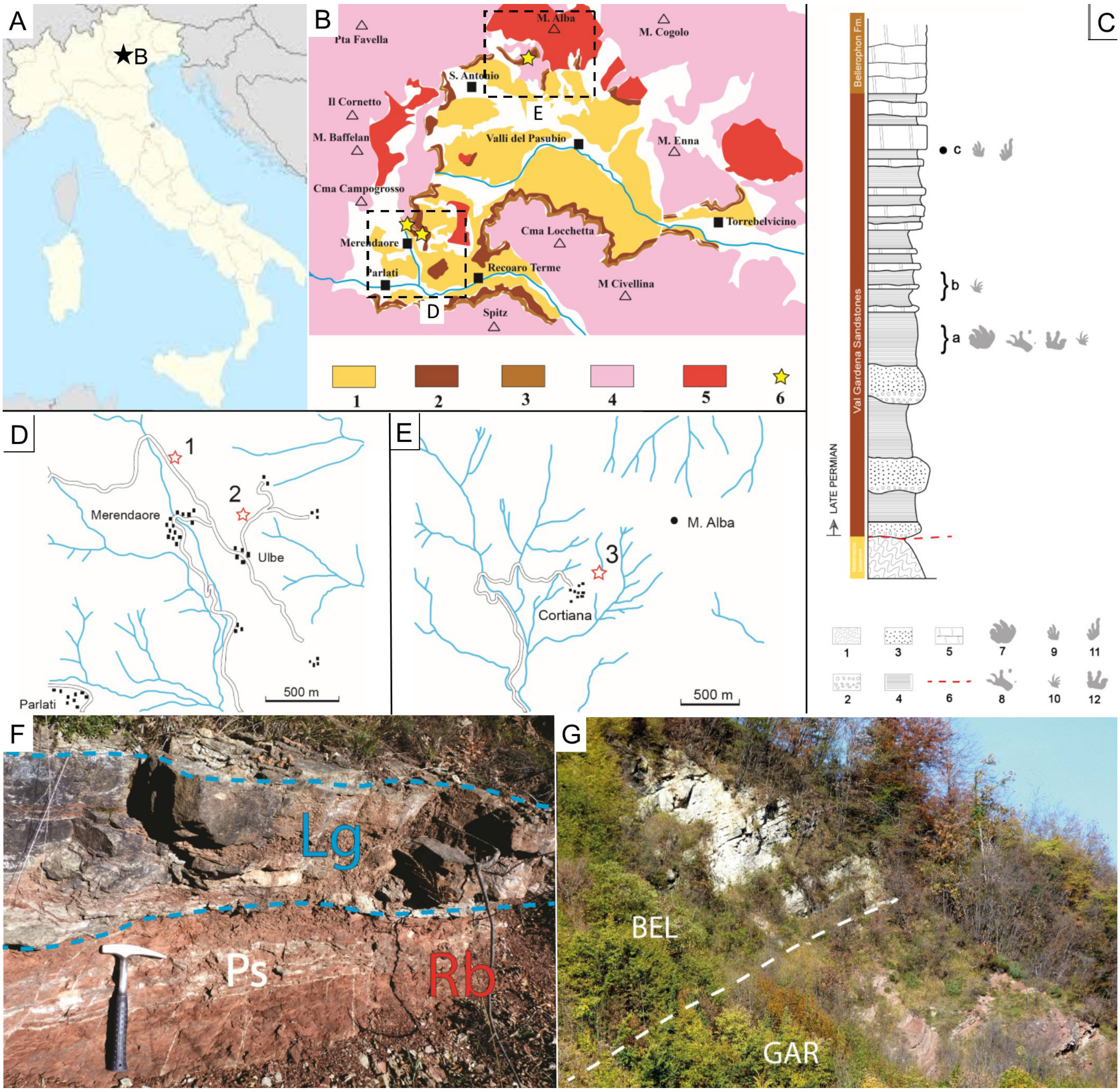

Fig. 6 - Geological setting and localities of the Venetian Prealps. A) Location of the study area in North Italy. B) Simplified geological map. 1= metamorphic basement, 2= Arenaria di Val Gardena Formation, 3=*Bellerophon* Formation, 4=Mesozoic sedimentary units, 5=Mesozoic volcanic units, 6=fossil sites. C) Synthetic stratigraphic log of the Permian of Venetian Prealps. 1=metamorphic rocks, 2=breccias and conglomerates, 3=sandstones, 4=laminated mudstones, 5=dolostones, 6=unconformity, 7-12=tetrapod tracks; a-c=facies associations. D) Location of Merendaore (1) and Ulbe (2) fossil sites. E) Location of Cortiana (3) fossil site. F) Linedrawing of a transition between red bed (Rb=laminated mudstone) and lagoon (Lg=dolostones) lithofacies in the Ulbe outcrop. Ps=incipient palaeosol with deep mud cracks. Hammer for scale. G) Linedrawing of the Ulbe outcrop. GAR=Arenaria di Val Gardena Formation, BEL=*Bellerophon* Formation.

5. THE RECOARO VERTEBRATE ICHNOASSOCIATION

5.1. HISTORICAL OVERVIEW

Tetrapod footprints found in the Recoaro area of the Venetian Prealps occur in the mudstone of the lower part of the Arenaria di Val Gardena Formation and in the mudstone and dolostone of the upper part of the same formation. The ichnological material, collected between 1972 and 1995 by P. Mietto and some collaborators of the Civic Museum "D. Dal Lago" of Valdagno (Vicenza), comes from three different localities (Fig. 6, Tab. 1). Merendaore and Ulbe are located near the village of Recoaro Terme (Vicenza), on the slopes of the Cima Campogrosso in the Agno valley, whereas Cortiana is located further north in the adjacent Leogra valley on the slopes of Monte Alba. The first indication of Permian footprints from this area is by Mietto (1975), who described and illustrated two samples from Merendaore, at the time attributed to *Eumechichnium gampsodactylum*.

Subsequently, Mietto (1981) described and illustrated a large footprint of pareiasaur coming from the locality of Ulbe, assigned to *Pachypes dolomiticus*. Some footprints from the same locality and generally referred to Procolophonomorpha were finally illustrated by Mietto (1995). The complete review of the Lopingian footprints of the Recoaro area, stored in the Civic Museum "D. Dal Lago" of Valdagno (MCV) and the Geological and Palaeontological Museum of Padua University (MGP-PD), is recent (Marchetti et al., 2015, 2017).

5.2. ICHNOASSOCIATION STRUCTURE

Based on Marchetti et al. (2017), in the Recoaro area the following tetrapod ichnotaxa are identified (Tab. 2):

- cf. *Capitosauroides* isp. (Fig. 7A). All tracks coming from Ulbe and Cortiana. This ichnotaxon has been referred to therocephalian therapsids (Marchetti et al., 2019c);

- undetermined track coming from Cortiana (Fig. 7B). Although it was not possible to classify the specimen because it was highly incomplete, the morphology of the footprint and the comparison with the known material led Marchetti et al. (2017) to refer it to therapsid synapsids. It can be compared with *Dolomitipes* (Marchetti et al., 2019a);

- *Pachypes* isp., left *manus*, preserved in convex hyporelief, coming from Ulbe (Fig. 7C). As noted by Leonardi et al. (1975), this taxon is referred to pareiasaur parareptiles;

- cf. *Merifontichnus* isp. (Fig. 7D), left *pes-manus* couple and right *pes* of a different step cycle, in convex hyporelief, coming from Ulbe. This ichnotaxon has been referred to captorhinid eureptiles. Citton et al. (2019b) questioned the occurrence of cf. *Merifontichnus* from the Arenaria di Val Gardena Formation and assigned this material to indeterminate tetrapod tracks; *Rhynchosauroides* isp., all tracks are coming from Merendaore (Fig. 7E). This ichnotaxon has been referred to lacertoid neodiapsid eureptiles;

- *Paradoxichnium* isp., all tracks are coming from Ulbe (Fig. 7F). This ichnotaxon, as noted by Marchetti et al. (2015, 2017) has been referred to archosauromorph eureptiles.

These are the first reports of cf. *Merifontichnus* isp. and *Capitosauroides* isp. in the Lopingian and one of the

Fig. 7 - Tetrapod tracks from the Venetian Prealps. A) MCV 7. cf. *Capitosauroides* isp., left *pes*, convex hyporelief. B) MCV 14/30. Therapsid track indet., partial right *manus*, concave epirelief. C) MCV 3. *Pachypes* isp., left *manus*, convex hyporelief. D) MCV 2. cf. *Merifontichnus* isp./tetrapod track indet., left *pes-manus* couple and right *pes*, convex hyporelief. E) MCV 65. *Rhynchosauroides* isp., two right *manus* imprints and a tail drag mark, convex hyporelief (plaster cast). F) MCV 9. *Paradoxichnium* isp., left *manus*, convex hyporelief. MCV - "Domenico Dal Lago" Civic Museum, Valdagno, Italy. Scale bars=2 cm.

few known occurrences of *Paradoxichnium* (Marchetti et al., 2015). Note that the occurrence of *Merifontichnus* is currently debated (Marchetti et al., 2017; Citton et al., 2019b).

The palaeoecology of the ichnoassociation highlights a relatively high diversity in the floodplain palaeoenvironment, a monospecific association of *Rhynchosauroides* isp. in distal floodplain/sabkha palaeoenvironments and the occurrence of *Paradoxichnium* isp. and cf. *Capitosauroides* isp. only in the lagoon palaeoenvironment, suggesting different habits of the trackmakers. The tetrapod ichnoassociation of the Recoaro area is characterised by tracks attributed to eureptiles, parareptiles and therapsids, and differs from the classic Lopingian tetrapod ichnoassociation of the Dolomites mainly because of the absence of chirotheriid tracks and small ichnotaxa attributed to parareptiles. Considering the small number of specimens, the Recoaro ichnofauna is likely affected by a sampling bias. A comparison of the Italian tetrapod ichnoassociation with other Lopingian non-eolian ichnofaunas suggested a possible preference for marginal marine settings by the archosauromorph and therapsid trackmakers at the low palaeolatitudes of Pangaea (Marchetti et al., 2017).

6. GEOLOGICAL SETTING AND STRATIGRAPHY - CARNIC ALPS

In the Carnic Alps, the Arenaria di Val Gardena Formation unconformably overlies the Permo-Carboniferous Pontebba Group, locally with the Sesto Conglomerate at its base. In this area, the Arenaria di Val Gardena Formation is about 40-240 m-thick and grades upwards in the *Bellerophon* Formation, which testifies multiple marine ingressions from South East (Massari et al., 1994). The facies of the Arenaria di Val Gardena Formation of this area are consistent with a meandering alluvial palaeoenvironment in a semi-arid and strongly seasonal climate, passing upwards to sabkha and shallow marine palaeoenvironments (e.g. Dalla Vecchia et al., 2012). Although the base of the formation may be diachronous, the inferred age should be consistent with the Arenaria di Val Gardena Formation of the Dolomites, i.e. Lopingian (late Wuchiapingian-Changhsingian). So, the palaeomagnetic reversal recognized in this area at about 20 m above the base of the formation (Dachroth, 1988) should be not consistent with the Guadalupian Illawarra Reversal but rather with a Lopingian reversal (e.g. Posenato, 2010). Tetrapod footprints come exclusively from two localities north the village of Ligosullo (Friuli-Venezia Giulia; Fig. 8A), where the Arenaria di Val Gardena Formation uncomformably overlies Carboniferous units.

7. THE CARNIC ALPS VERTEBRATE ICHNOASSOCIATION

7.1. HISTORICAL OVERVIEW

The first mention of tetrapod footprints from the Lopingian of the Carnic Alps is by Mietto and Muscio (1987), who described about 20 small footprints preserved in convex hyporelief and concave epirelief on the two sides of two slabs. The slabs were collected by Remo Englaro in the locality Valdajer, north of the Village of Ligosullo (Tab. 1). The footprints were assigned to *Prochirotherium permicum*. New footprints were found several years later, in 2011, by Mario Cuder in a nearby area. This new site is located north of Ligosullo, on the road between the Valdajer Castle and the Casera Valdajer locality, at about 1340 m of altitude (Tab. 1). These footprints are larger (*pes* length of about 20 cm), *in situ*, and arranged in an incomplete step cycle including five consecutive tracks belonging to three different *pes-manus* couples. They have been described by Dalla Vecchia et al. (2012) and assigned to *Pachypes* isp. Dalla Vecchia (2013) described and figured all the previously-studied material in a review of the tetrapod ichnology of the Carnic Alps.

7.2. ICHNOASSOCIATION STRUCTURE

The ichnoassociation from the Carnic Alps is currently small and includes the ichnogenus *Pachypes* and several small-sized tracks (Tab. 2).

The ichnogenus *Pachypes* is known from a step cycle including five relatively large (*pes* length of about 20 cm) consecutive footprints, which are a right *pes-manus* couple, a left *pes-manus* couple and a right *pes* imprint (Fig. 8 B,C). These tracks are preserved in concave epirelief *in situ*. Despite the relatively poor preservation, they have assigned to *Pachypes* isp. by Dalla Vecchia et al. (2012).

Several small tracks (*pes* length <2 cm) coming from two slabs have been assigned to *Prochirotherium permicum* by Mietto and Muscio (1987) (Fig. 8D). However, this ichnotaxon has been considered a *nomen dubium* by Marchetti et al. (2019a) and the type material was assigned to cf. *Procolophonichnium* isp. The lack of trackways and the relatively poor preservation of the material hampers a definitive re-assignment of this material. Dalla Vecchia (2013) suggested that the sample examined by Mietto and Muscio (1987) should be referred to the Lower Triassic Werfen Formation (Contrin Member), and not to the Arenaria di Val Gardena Formation. He also suggested that these footprints should not be referred to tetrapods but to the body of "sea stars", whose arms would have been mobilized by background currents and therefore oriented in the same direction. However, given the stratigraphic setting of the area, this hypothesis was not accepted by Marchetti et al. (2019b).

The tetrapod ichnoassociation from the Carnic Alps is currently small and thus not yet comparable with those from the Dolomites and the Venetian Prealps (Tab. 1, Fig. 9). The occurrence of *Pachypes* is anyway a trait in common, and the finding of a step cycle is of great importance because of the scarcity of *Pachypes* step cycles from the Dolomites. Further prospecting is recommended, in order to verify similarities and differences with the tetrapod ichnoassociations found

Fig. 8 - Tetrapod tracks from the Carnic Alps. A) Location of the Ligosullo ichnosites (star). B) *Pachypes* incomplete step cycle, concave epirelief. From Dalla Vecchia et al. (2012), modified. C) Enlargement of B, right *pes-manus* couple. From Dalla Vecchia (2013), modified. D) MFSN-NN 1. Small tetrapod tracks indet., concave epirelief. Slab B of Dalla Vecchia (2013), modified. MFSN -Museo Friulano di Storia Naturale, Udine, Italy. Scale bar=2 cm.

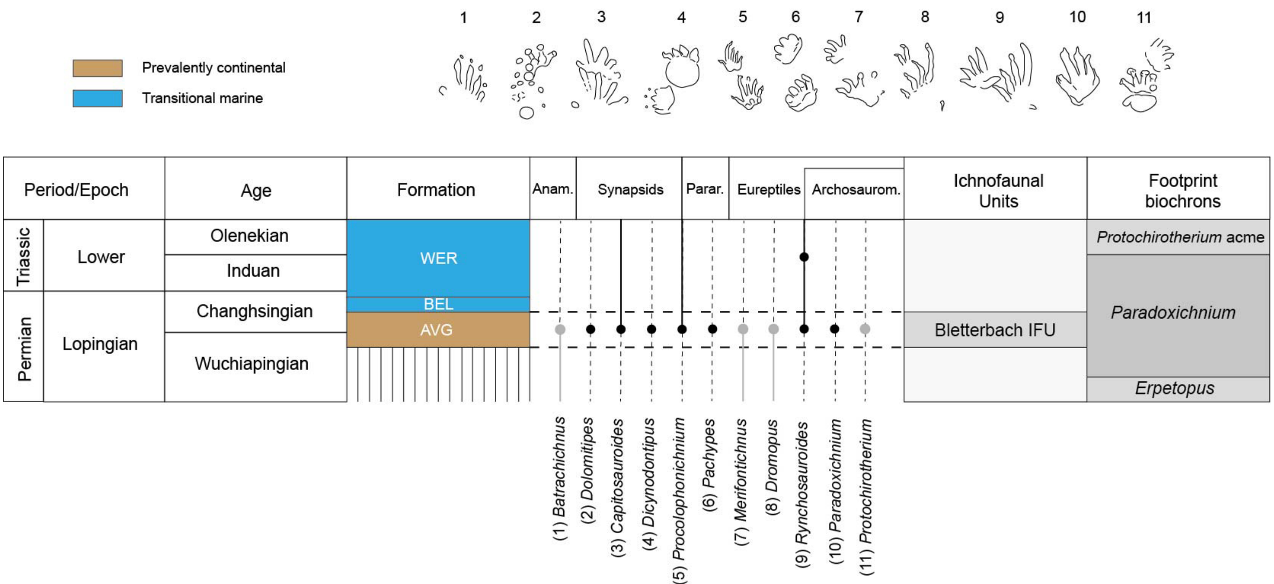

Fig. 9 - Stratigraphic distribution of tetrapod ichnogenera in the Lopingian of Italy. Grey dots mean uncertain occurrence, the ichnotaxa range includes only occurrences from Italy. Only ichnogenera known from more than a single site are considered. Note that the occurrence of *Merifontichnus* is currently debated. AVG = Arenaria di Val Gardena Formation, BEL = *Bellerophon* Formation, WER = Werfen Formation.

more westwards, which may have also a slightly different age and were subject to the marine ingressions later than in Carnia (e.g. Massari et al., 1988, 1994).

8. CONCLUSIONS AND PERSPECTIVES

After almost 130 years of study, the tetrapod ichnoassociation from the Lopingian of Italy is renown worldwide because of its exceptional preservation. Several studies on this ichnoassociation have been and are pivotal in the understanding of the Lopingian ichnofaunas and biotas, including ichnotaxonomy, track-trackmaker correlations, palaeobiogeography, biostratigraphy, palaeoecology and ichnotaphonomy. This ichnoassociation acquires an even bigger importance because of: i) the lack of tetrapod skeletons from this time interval in Italy and ii) the overall scarcity of tetrapod skeletons from the low palaeolatitudes of Pangaea during the Lopingian.

The track-bearing unit is the alluvial and marginal marine Arenaria di Val Gardena Formation, deposited under a semi-arid climate during the late Wuchiapingian-early Changhsingian (Lopingian). These tracks come mostly from the Dolomites and especially from the famous Bletterbach gorge site. Because of the good outcrop exposure and abundance and diversity of trace fossils and plant remains, the Bletterbach gorge is an ideal reference for studies on palaeoecology and ichnotaphonomy. Fewer occurrences are known from the Venetian Prealps and the Carnic Alps, nevertheless they provide remarkable insights into palaeoecology and palaeobiogeography.

Future lines of research may include new prospecting in the less explored areas such as the smaller areas of the Dolomites region, such as Passo di S. Pellegrino, Pausa-Doladizza/Kalditsch and Pietralba/Weissenstein, the Venetian Prealps and the Carnic Alps and bed-by-bed sampling at the Bletterbach gorge site. As regards palaeoecology and ichnotaphonomy, the tetrapod ichnoassociation should be re-evaluated by diversity and relative abundance according to an updated ichnotaxonomy. The study of the invertebrate ichnoassociation may be added to the evaluation of the biota. Further work may be expected as regards tetrapod footprint ichnotaxonomy, biochronology, the comparison with contemporary high- and mid-palaeolatitude faunas and the remarkable abundance and diversity of neodiapsid tracks, which seems to differ from other Lopingian ichnoassociations.

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REFERENCES

Abel O., 1929. Eine Reptilfährte aus dem Oberen Perm (Grödener Sandstein) der Gegend von Bozen, Südtirol. Palaeobiology 2, 1-14.

Accordi B., 1958. Contributo alla conoscenza del Permiano medio-superiore della zona di Redagno (Bolzano). Annali dell'Università di Ferrara, Nuova Serie, Sezione IX, Scienze Geologiche e Mineralogia 3, 37-42.

Avanzini M., Bernardi M., Nicosia U., 2011. The Permo-Triassic tetrapod faunal diversity in the Italian Southern Alps. In: Dar I.A., Dar M.A. (Eds.), Earth and Environmental Sciences. InTech Rijek, 591-608.

Avanzini M., Ceoloni P., Conti M.A., Leonardi G., Manni R., Mariotti N., Mietto P., Nicosia U., Santi G., Spezzamonte M., 1999. Tetrapod footprints as key elements for the biochronology of the Permo-Triassic continental deposits. International Congress on "The continental Permian of the Southern Alps and Sardinia (Italy). Regional reports and general correlations". Brescia, Italy. Abstracts, 35.

Avanzini M., Ceoloni P., Conti M.A., Leonardi G., Manni R., Mariotti N., Mietto P., Muraro C., Nicosia U., Sacchi E., Santi G., Spezzamonte M., 2001. Permian and Triassic tetrapod ichnofaunal units of Northern Italy: their potential contribution to continental biochronology. In: Cassinis G. (Ed.), Permian Continental Deposits of Europe and Other Areas. Regional reports and correlations. Natura Bresciana, Annuario del Museo Civico di Scienze Naturali, Monografia 25, 89-107.

Avanzini M., Tomasoni R., 2004. Guida all'escursione: la gola del Bletterbach. Giornate di Paleontologia 2004, Bolzano. Studi Trentini di Scienze Naturali, Acta Geologica 79, 1-34.

Barbieri G., De Vecchi G.P., De Zanche V., Di Lallo E., Frizzo P., Mietto P., Sedea R., 1980. Note illustrative della Carta Geologica dell'area di Recoaro alla scala 1:20.000. Memorie di Scienze Geologiche 34, 23-52.

Bernardi M., Klein H., Petti F.M., Ezcurra M.D., 2015. The origin and early radiation of archosauriforms: integrating the skeletal and footprint record. PLoS One 10, e0128449.

Bernardi M., Petti F.M., Benton M.J., 2018. Tetrapod distribution and temperature rise during the Permian-Triassic mass extinction. Proceedings of the Royal Society B: Biological

Sciences 285(1870), 20172331.
Bernardi M., Petti, F.M., Kustatscher E., Franz M., Hartkopf-Fröder C., Labandeira C.C., Wappler T., van Konijnenburg-van Cittert J.H.A., Peecook B.R., Angielczyk K.D., 2017a. Late Permian (Lopingian) terrestrial ecosystems: a global comparison with new data from the low-latitude Bletterbach Biota. Earth-Science Reviews 175, 18-43.
Bernardi M., Petti F.M., Citton P., Romano M., 2017b. L'icnoassociazione a tetrapodi del Bletterbach (Trentino Alto-Adige) e le sue relazioni con gli ecosistemi terrestri di fine Permiano/The tetrapod ichnoassociation of the Bletterbach (Trentino Alto-Adige) and its place among Late Permian terrestrial ecosystems. Geo Alp 14, 63-83.
Bosellini A., Hardie A.L., 1973. Depositional theme of a marginal evaporite. Sedimentology 20, 5-27.
Cassinis G., Cortesogno L., Gaggero L., Massari F., Neri C., Nicosia U., Pittau P., 1999. Stratigraphy and facies of the Permian deposits between Eastern Lombardy and the Western Dolomites. Field Trip Guidebook, International Field Conference of "The Continental Permian of the Southern Alps and Sardinia (Italy). Regional Reports and General Correlations", pp. 157.
Cassinis G., Nicosia U., Pittau P., Ronchi A., 2002. Palaeontological and radiometric data from the Permian continental deposits of the Central-Eastern Southern Alps (Italy), and their stratigraphic implications. Mémoires de la Association des Géologues du Permien 2, 53-74.
Ceoloni P., Conti M.A., Mariotti N., Nicosia U., 1988a. New Late Permian Tetrapod Footprints from the Southern Alps. Memorie della Società Geologica Italiana 34, 45-65.
Ceoloni P., Conti M.A., Mariotti N., Mietto P., Nicosia U., 1988b. Tetrapod footprint Faunas from Southern and Central Europe. Zeitschrift fur geologische Wissenschaften 16, 895-906.
Citton P., Carluccio R., Nicolosi I., Nicosia U., 2019a. Re-evaluation of *Chelichnus tazelwürmi*, a non mammalian therapsid-grade track from the Upper Permian Arenaria di Val Gardena. Historical Biology 31, 322-340.
Citton P., Ronchi A., Maganuco S., Caratelli M., Nicosia U., Sacchi E., Romano M., 2019b. First tetrapod footprints from the Permian of Sardinia and their palaeontological and stratigraphical significance. Geological Journal 54, 2084-2098.
Citton P., Nicolosi I., Carluccio R., Nicosia U., 2016. Unveiling trampling history through trackway interferences and track preservational features: a case study from the Bletterbach gorge (Redagno, Western Dolomites, Italy). Palaeontologia Electronica 19, 1-20.
Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1975. Tetrapod footprints, fishes and molluscs from the Middle Permian of the Dolomites (N. Italy). Memorie Geopaleontologiche dell'Università di Ferrara 3, 139-150.
Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1977. Tetrapod footprints of the "Val Gardena Sandstone" (North Italy). Their paleontological, stratigraphic and paleoenvironmental meaning. Palaeontographia Italica 70, 1-91.
Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1979. Nuovo contributo alla stratigrafia delle "Arenarie di Val Gardena". Memorie della Società Geologica Italiana 20, 357-363.
Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1980. Tetrapodi e pesci della Val Gardena. In: I tetrapodi fossili italiani - Catalogo della Mostra, Verona, Sine Editore, 51-60.
Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1981. A review of a group of Permian tetrapod footprints from Northern Italy. Memorie di Scienze Geologiche 34, 143-152.
Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1987. Sobre uma nova localidade com icnofauna de répteis do Permiano Superior na formação Arenarie di Val Gardena nos arredores de Redagno (Bolzano, Itàlia). Anais do X Congresso Brasileiro de Paleontologia, Rio de Janeiro, Sociedade Brasileira de Paleontologia 2, 319-331.
Conti M.A., Leonardi G., Mietto P., Nicosia U., 2000. Orme di tetrapodi non dinosauriani del Paleozoico e Mesozoico in Italia. In: Leonardi G., Mietto P. (Eds.), Dinosauri in Italia. Le Orme Giurassiche dei Lavini di Marco (Trentino) e gli Altri Resti Fossili Italiani. Accademia Editoriale, Pisa-Roma, 297-320.
Conti M.A., Mariotti N., Nicosia U., Pittau P., 1997. Selected bioevents succession in the continental Permian of the Southern Alps (Italy): improvements of intrabasinal and interregional correlations. In: Dickins J.M., Zunyi Y., Yhongfu Y., Lucas S.G., Acharyya S.J. (Eds.), Late Palaeozoic and Early Mesozoic Circum-Pacific Events and Their Global Correlation. Cambridge University Press, Cambridge, New York, Melbourne, 51-65.
Dachroth W., 1988. Gesteinsmagnetischer Vergleich Permischer Schichtenfolgen in Mitteleuropa. Zeitschrift für Geologische Wissenschaften 16, 959-968.
Dalla Vecchia F.M., 2013. Sulle tracce del passato. Piste e impronte fossili di vertebrati in Carnia e nelle aree contermini./Auf den Spuren der Vergangenheit. Fossilien-Spuren und Abdrücke von Wirbeltieren in Karnien und den benachbarten Gebieten. Lithostampa, Passian di Prato, pp. 176.
Dalla Vecchia F.M., Ponton M., Muscio G., 2012. Two new ichnosites from the Permo-Triassic of Carnic Alps (Friuli Venezia Giulia, NE Italy). Gortania 34, 41-50.
Ezcurra M.D., 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. PeerJ 4, e1778.
Ezcurra M.D., Scheyer T.M., Butler R.J., 2014. The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS ONE 9, e89165.
Gubin Y.M., Golubev V.K., Bulanov V.V., Petuchov S.V., 2003. Pareiasaurian tracks from the Upper Permian of Eastern Europe. Paleontological Journal 37, 514-523.
Haubold H., 1966. Therapsiden- und Rhynchocephalen-Fährten aus dem Buntsandstein Südthüringens. Hercynia 3, 147-183.
Haubold H., 1971. Ichnia amphibiorum et reptiliorum fossilium. In: Kuhn O. (Ed.). Handbuch der Paläoherpetologie. Gustav Fischer Verlag, Stuttgart, 18, pp. 124.
Hminna A., Voigt S., Saber H., Schneider J.W., Hmich D., 2012. On a moderately diverse continental ichnofauna from the Permian Ikakern Formation (Argana Basin, Western High

Atlas, Morocco). Journal of African Earth Sciences 68, 15-32.

Kittl E., 1891. Saurier Färthe von Bozen. Mittheilungen Osterreichischer Touristenclub, Wien 3, 7.

Kustatscher E., Bernardi M., Petti F.M., Franz M., van Konijnenburg-van Cittert J.H.A, Kerp H., 2017. Sea-level changes in the Lopingian (late Permian) of the northwestern Tethys and their effects on the terrestrial palaeoenvironments, biota and fossil preservation. Global and Planetary Change 148, 166-180.

Kustatscher E., van Konijnenburg-van Cittert J.H.A., Bauer K., Butzmann R., Meller B., Fischer T.C., 2012. A new flora from the Upper Permian of Bletterbach (Dolomites, N-Italy). Review of Palaeobotany and Palynology 182, 1-13.

Leonardi G., 1974. Sobre una série de rastos de tetrápodes do Permiano das Dolomitas (Itália). Anais XXVIII Congresso Sociedade Brasileira Geologia 2, 205-220.

Leonardi G., 1979. A review of a group of Permian tetrapod footprints (*Prochirotherium permicum, Ornithoidipus perwangeri, Nanopus grimmi, Eumeckichnium gampsodactylum*). Dusenia 11, 151-159.

Leonardi G., 2008. Vertebrate ichnology in Italy. Studi Trentini di Scienze Naturali, Acta Geologica 83, 213-221.

Leonardi G., Nicosia U., 1973. Stegocephaloid footprint in the Middle Permian Sandstone ("Grödener Sandsteine") of the western Dolomites. Annali dell'Università di Ferrara IX 5, 116-124.

Leonardi P., 1951. Orme di tetrapodi nelle Arenarie di Val Gardena (Permiano medio-inferiore) dell'Alto Adige Sud Orientale. Memorie dell´ Istituto di Geologia e Mineralogia dell'Università di Padova 17, 1-23.

Leonardi P., 1952. Ricerche sulla Geologia e Paleontologia della regione dolomitica. La ricerca Scientifica 22(9), 1-7.

Leonardi P., 1953. Ricerche geo-palontologiche nella regione dolomitica. La Ricerca Scientifica 25(8), 1-10.

Leonardi P., 1955. Quarta campagna geo-paleontologica nelle Dolomiti. La Ricerca Scientifica 25(3), 1-9.

Leonardi P., 1957. Campagne geo-paleontologiche 1954-1956 dell'Istituto geologico di Ferrara nelle Dolomiti. La Ricerca Scientifica 27(12), 1-19.

Leonardi P., 1960. Campagne geo-paleontologiche 1957-1959 nella regione Dolomitica e nei Colli Berici. La Ricerca Scientifica 30(12), 1-32.

Leonardi P., 1967. Le Dolomiti-Geologia dei monti tra Isarco e Piave. Manfrini, Rovereto, pp. 519.

Leonardi P., Conti M.A., Leonardi G., Mariotti N., Nicosia U., 1975. *Pachypes dolomiticus* n. gen. n. sp.; Pareiasaur footprint from the "Val Gardena Sandstone" (Middle Permian) in the Western Dolomites (N. Italy). Atti Accademia Nazionale dei Lincei 57, 221-232.

Lucas S.G., 2019. An ichnological perspective on some major events of Paleozoic tetrapod evolution. Bollettino della Società Paleontologica Italiana 58, 223-266.

Marchetti L., Belvedere M., Mietto P., 2015. Late Permian footprints from the Venetian Prealps (northeast Italy): new discoveries in a largely incomplete panorama. 13th Annual Meeting of the European Association of Vertebrate Palaeontologists, Opole, Poland, 8-12 July 2015. Abstracts, 109.

Marchetti L., Belvedere M., Mietto P., 2017. Lopingian tetrapod footprints in the Venetian Prealps (Italy): new discoveries in a largely incomplete panorama. Acta Palaeontologica Polonica 62, 801-817.

Marchetti L., Voigt S., Klein H., 2019a. Revision of Late Permian tetrapod tracks from the Dolomites (Trentino-Alto Adige, Italy). Historical Biology 31, 748-783.

Marchetti L., Ronchi A., Preto N., Gianolla P., Mietto P., Santi G., Avanzini M., 2019b. Update of ichnofaunal units and link with footprint biochrons in the late Palaeozoic to early Mesozoic of the Southern Alps: towards a better correlation with the marine realm. 3rd International Conference on Continental Ichnology, Halle (Saale), Germany, 23-29/09/19. Hallesches Jahrbuch für Geowissenschaften, Beiheft 46, 55.

Marchetti L., Klein H., Buchwitz M., Ronchi A., Smith R.M., De Klerk W.J., Sciscio L., Groenewald G.H., 2019c. Permian-Triassic vertebrate footprints from South Africa: ichnotaxonomy, producers and biostratigraphy through two major faunal crises. Gondwana Research 72, 139-168.

Marchetti L., Belvedere M., Voigt S., Klein H., Castanera D., Díaz-Martínez I., Marty D., Xing L., Feola S., Melchor R.N., Farlow J.O., 2019d. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. Earth-Science Reviews 193, 109-145.

Marchetti L., Voigt S., Lucas S.G., 2019e. An anatomy-based study of the Lopingian eolian tracks of Germany and Scotland reveals the first evidence of the end-Guadalupian mass extinction at low paleolatitudes of Pangea. Gondwana Research 73, 32-53.

Marocchi M., Morelli C., Mair V., Klötzli U., Bargossi G.M., 2008. Evolution of large silicic magma systems: new U-Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). The Journal of Geology 116, 480-498.

Massari F., Conti M.A., Fontana D., Helmod K., Mariotti N., Neri C., Nicosia U., Ori G.G., Pasini M., Pittau D., 1988. The Val Gardena Sandstone and *Bellerophon* Formation in the Bletterbach Gorge (Alto Adige, Italy): biostratigraphy and sedimentology. Memorie di Scienze Geologiche 40, 229-273.

Massari F., Neri C., Fontana D., Manni R., Mariotti N., Nicosia U., Pittau P., Spezzamonte M., Stefani C., 1999. Excursion 3: the Bletterbach section (Val Gardena Sandstone and *Bellerophon* Formation). The Continental Permian. International Congress, Brescia, Italy. Stratigraphy and facies of the Permian deposits between eastern Lombardy and the western Dolomites. Field Trip Guidebook, 111-134.

Massari F., Neri C., Pittau P., Fontana D., Stefani C., 1994. Sedimentology, palynostratigraphy and sequence stratigraphy of a continental to shallow-marine rift-related succession: Upper Permian of the eastern Southern Alps (Italy). Memorie di Scienze Geologiche, Università di Padova 46, 119-243.

Mauritsch H., Becke M., 1983. A magnetostratigraphic profile in the Permian (Gröden beds, Val Gardena Fm.) of the Southern Alps near Paularo (Carnic Alps, Friuli, Italy). Newsletter IGCP Project 5, 80-86.

Mietto P., 1975. Orme di tetrapodi nelle arenarie permiche di

Recoaro (Vicenza). Studi Trentini di Scienze Naturali, Acta Geologica 52, 57-67.

Mietto P., 1981. Una grande impronta di pareiasauro nel Permiano di Recoaro (Vicenza). Rendiconti della Società Geologica Italiana 4, 363-364.

Mietto P., 1995. Museo Paleontologico "Dott. Domenico Dal Lago". Guida illustrativa. Centro Culturale Comunale "G. Marzotto", Valdagno, pp. 70.

Mietto P., Muscio G., 1987. *Prochirotherium permicum* Leonardi, 1951 (Reptilia: ?Chiroteriidae) nelle Arenarie di Val Gardena della Carnia. Atti del Museo Friulano di Storia Naturale 8, 81-94.

Morelli C., Bargossi G.M., Mair V., Marocchi M., Moretti A., 2007. The Lower Permian volcanics along the Etsch Valley from Meran to Auer (Bozen). Mitteilungen der Österreichischen Mineralogischen Gesellschaft 153, 195-218.

Nicosia U., Avanzini M., Barbera C., Conti M.A., Dalla Vecchia F.M., Dal Sasso C., Gianolla P., Leonardi G., Loi M., Mariotti N., Mietto P., Morsilli M., Paganoni A., Petti F.M., Piubelli D., Rasa P., Renesto S., Sacchi E., Santi G., Signore M., 2005. I vertebrati continentali del Paleozoico e Mesozoico. In: Bonfiglio L. (Ed.), Paleontologia dei vertebrati in Italia. Evoluzione Biologica, Significato Ambientale e Paleoecologia. Memorie del Museo Civico di Storia Naturale di Verona, Sezione Scienze della Terra 6, 41-66.

Nicosia U., Sacchi E., Spezzamonte M., 2001. New paleontological data for the Val Gardena Sandstone. Natura Bresciana, Annuario del Museo Civico di Scienze Naturali di Brescia 25, 83-88.

Nopcsa F., 1923. Die Familien der Reptilien. Fortschritte der Geologie und Paläontologie 2, 1-210.

Perwanger L., 1946. Geologisch Beobachtenswertes auf der Hochfläche von Radein. Der Schlern 20, 362-370.

Petti F.M., Bernardi M., Klein H., 2015. Towards a redefinition of the lower boundary of the *Protochirotherium* biochron. Permophiles 61, 22-24.

Pittau P., 2001. Correlation of the upper Permian sporomorph complexes of the Southern Italian Alps with the Tatarian complexes of the stratotype region. In: Cassinis, G. (Ed.), Permian Continental Deposits of Europe and Other Areas. Regional Reports and Correlations. Natura Bresciana, Annuario del Museo Civico di Scienze Naturali di Brescia 25, 109-116.

Posenato R., 2010. Marine biotic events in the Lopingian succession and latest Permian extinction in the Southern Alps (Italy). Geological Journal 45, 195-215.

Posenato R., 2019. The end-Permian mass extinction (EPME) and the Early Triassic biotic recovery in the western Dolomites (Italy): state of the art. Bollettino della Società Paleontologica Italiana 58, 11-34.

Ronchi A., Santi G., Marchetti L., Bernardi M., Gianolla P., 2018. First report on swimming trace fossils of fish from the Upper Permian and Lower Triassic of the Dolomites (Italy). Annales Societatis Geologorum Poloniae 88, 111-125.

Schneider J.W., Lucas S.G., Scholze F., Voigt S., Marchetti L., Klein H., Opluštil S., Werneburg R., Golubev V.K., Barrick J.E., Nemyrovska T., Ronchi A., Day M.O., Silantiev V.V., Rößler R., Saber H., Linnemann U., Zharinova V., Shen S., 2020. Late Paleozoic-early Mesozoic continental biostratigraphy - links to the Standard Global Chronostratigraphic Scale. Palaeoworld 29, 186-238.

Sennikov A.G., Golubev V.K., 2017. Sequence of Permian tetrapod faunas of Eastern Europe and the Permian-Triassic ecological crisis. Paleontological Journal 51, 600-611.

Smith R.M.H., Sidor C.A., Tabor N.J., Steyer, J.S., 2015. Sedimentology and vertebrate taphonomy of the Moradi Formation of northern Niger: a Permian wet desert in the tropics of Pangaea. Palaeogeography, Palaeoclimatology, Palaeoecology 440, 128-141.

Surkov M.V., Benton M.J., Twitchett R.J., Tverdokhlebov V.P., Newell A.J., 2007. First occurrence of footprints of large therapsids from the Upper Permian of European Russia. Palaeontology 50, 641-652.

Valentini M., Conti M.A., Mariotti N., 2007. Lacertoid footprints of the Upper Permian Arenaria di Val Gardena formation (Northern Italy). Ichnos 14, 193-218.

Valentini M., Conti M.A., Nicosia U., 2008. Linking tetrapod tracks to the biodynamics, paleobiogeography, and paleobiology of their trackmakers: *Pachypes dolomiticus* Leonardi et al., 1975, a case study. Studi Trentini di Scienze Naturali, Acta Geologica 83, 237-246.

Valentini M., Nicosia U., Conti M.A., 2009. A re-evaluation of *Pachypes*, a pareiasaurian track from the Late Permian. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 251, 71-94.

Voigt S., 2005. Die Tetrapodenichnofauna des kontinentalen Oberkarbon und Perm im Thüringer Wald - Ichnotaxonomie, Paläoökologie und Biostratigraphie. Cuvillier, Göttingen, pp. 179.

Voigt S., Klein H., Bernardi M., Kustatscher E., Schneider J.W., Saber H., Marchetti L., Mietto P., Scholze F., Faath V., 2015. *Paradoxicnium problematicum* Müller, 1939 - a principal morph of Late Permian tetrapod tracks and its paleoecological significance. 13th Annual Meeting of the European Association of Vertebrate Palaeontologists, Opole, Poland, 8-12 July 2015. Abstract volume, 44.

Voigt S., Lucas S.G., 2018. Outline of a Permian tetrapod footprint ichnostratigraphy. In: Lucas S.G., Shen S.Z. (Eds.), The Permian Timescale. Geological Society of London, Special Publications 450, 387-404.

Walsh S.L., 1998. Fossil datum and paleobiological event terms, paleontostratigraphy, chronostratigraphy, and the definition of land mammal "age" boundaries. Journal of Vertebrate Paleontology 18, 150-179.

Wopfner H., 1999. Über Tetrapoden-Fährten, Kohlen und versteinerte Hölzer aus dem Grödner Sandstein (Perm) bei Deutschnofen. Der Schlern 73, 23-32.

Wopfner H., Farrokh F., 1988. Palaeosols and heavy mineral distribution in the Groeden Sandstone of the Dolomites. In: Cassinis G. (Ed.), Permian and Permian-Triassic Boundary in the South-Alpine segment of the Western Tethys and Additional Regional Reports. Memorie della Società Geologica Italiana 34, 161-173.