

LOWER PERMIAN PALAEOICHOLOGY FROM THE OROBIC BASIN (NORTHERN ITALY)

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With 4 figures and 2 plates

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Abstract

The Lower Permian palaeoichnofauna of the South-Alpine region comes from the Collio Formation only, and mainly crops out in the Orobic and Trompia basins. It consists of traces of vertebrates (amphibians and reptiles) and invertebrates (insects, arthropods, burrowing, probable myriapods, gastropods, freshwater jellyfishes, conchostraceans and freshwater bivalves). It is poor in taxa and similar to the coeval ichnoassociation of Central Europe, N. America and Argentina. Inside the trophic pyramid relevant to the biodiversity of the lower unit of the Collio Fm., the top carnivore is absent. This role is partially occupied by reptiles (e.g. araeoscelids) having features similar to true lizards. Shifting from the sediments of the lower part of the Collio Formation to the upper part, impoverishment of the ichnocoenosis composition is linked either to a climatic shift (from more humid towards drier), or to tectonic activity that prevented the persistence of biotope formation. The Upper Permian uplift marks a strong ichnofaunistic change with the introduction of Triassic components.

Introduction

In the South-Alpine region the continental Lower Permian is characterized by vertebrate and invertebrate ichnofossils and by rare floral remains (macroplants, spores and pollen). They come almost exclusively from the Collio Fm. cropping out in the Orobic and Trompia (= Collio) basins, with the exception of rare fossiliferous remains from the Tregiovo Basin. The features, problems and hypotheses relating to the composition, distribution and behavioural features of the trackmakers and the ichnocoenosis variation are also different, moving from the lower "Collio" to the upper unit of the same formation, and from this to the Upper Permian when the faunistic change is profound. These aspects are very clear from analysing the fossil beds of the Collio Fm. in the Orobic Basin; this article will review the ichnofaunistic assemblages from this basin and discuss their significance and the problems inherent to them.

Brief stratigraphical framework

For a long time it has been known that the Palaeozoic of the Alps is very poor in vertebrate remains, with the only exception being the ichnites, which have recently become a great stratigraphical tool (Avanzini et al., 2001). Recent detailed research on the Permian of Europe (mainly in France and Germany) has enlarged our knowledge, particularly of the invertebrates, and of the stratigraphical-chronological role played by them (Gand et al., 2001 with references therein). The South-Alpine region is characterized by a series of basins created from W to E, as inherited Hercynian structures have produced structural highs of a metamorphic or igneous nature (Cassinis & Perotti, 1994; Cassinis et al., 1999 with references therein; Perotti, 1999). The main basins are the Orobic Basin and, to the east, the Trompia Basin (Fig. 1), but other smaller basins are important for their ichnofossil content (Tregiovo Basin, Tione Basin) (Conti et al., 1997).

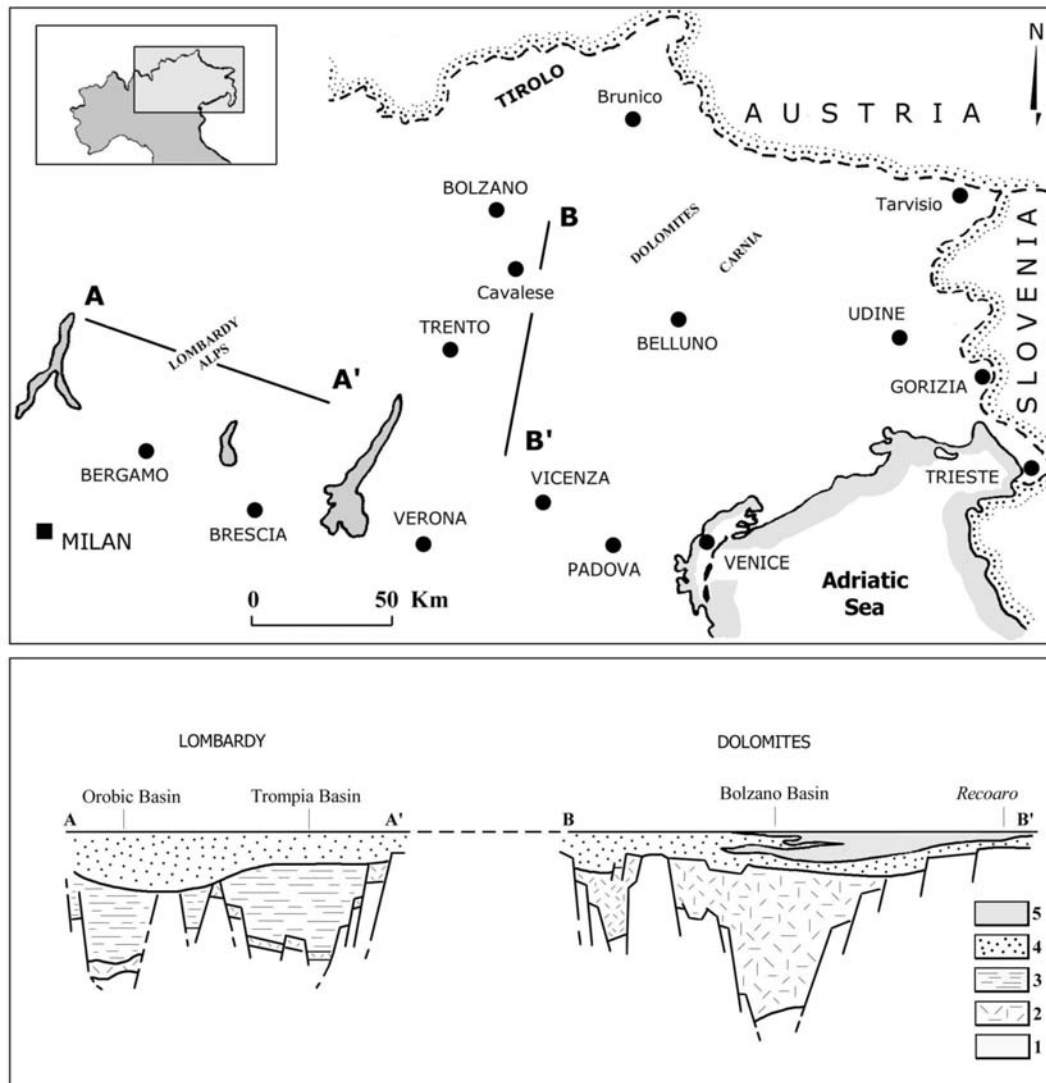


Fig. 1: Schematic non-palinspastic section of the main Permian basin distribution of the South-Alpine region (Conti et al., 1997, mod.). 1 – Pre-Permian basement, 2 – Volcanic deposits, 3 – Clastic units of the first cycle of sedimentation (Basal Conglomerate, Collio Fm, Ponteranica Conglomerate), 4 – Verrucano Lombardo-Val Gardena Sandstone complex, 5 – Bellerophon Fm.

Permian sediments occur in two tectono-sedimentary cycles separated by an uncertain age gap (between 14 and 25 My, according to the most recent data in Cassinis et al., 2002a). The first cycle, of ?Upper Carboniferous–Lower Permian age, is composed of a continental succession of volcanic deposits (from intermediate to acid chemistry) and by alluvial-to-lacustrine sediments that comprise the Basal Conglomerate, the Collio Fm, the Tregiovo Fm, the Ponteranica Conglomerate, the Dosso dei Galli Conglomerate and the Auccia Volcanics. The second cycle is assigned to the Upper Permian and is composed of the reddish clastic deposits of the Verrucano Lombardo-Val

Gardena Sandstone complex (Fig. 2). With their deposition the Palaeozoic ended.

The question of the use of a two- or three-fold subdivision of the Permian System for dating of continental successions has been debated for a long time. A detailed discussion relating to dating of the Permian continental beds in the South-Alpine region was recently carried out by Cassinis (2003), Cassinis and Ronchi (2001) and Cassinis et al. (2002b). The traditionally adopted Permian subdivision for research in the South-Alpine area is “Lower Permian” (from about the Asselian to Kungurian) and “Upper Permian” (from the

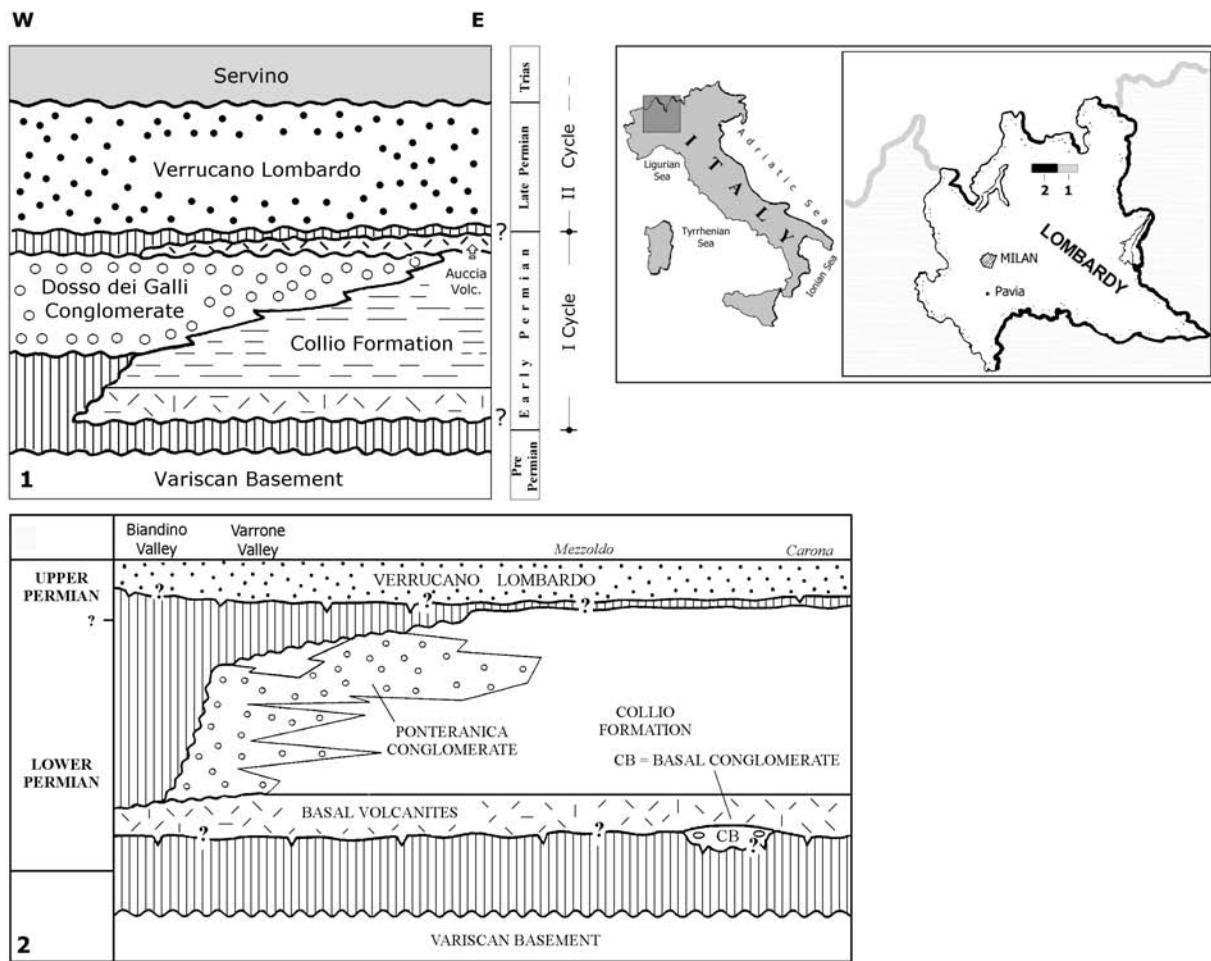


Fig. 2: 1 - Chronostratigraphical sketch of the Permian of the Orobic Basin. 2 - Chronostratigraphical sketch of the Permian of the Trompia Basin.

Ufimian to Tatarian, according to the Cis-Uralian/Russian Standard Scale), and this last rarely includes the Middle Permian, corresponding approximately to the Guadalupian Series (Menning, 2001; Cassinis, 2003, Fig. 1). It is based on the palaeontological data from macroplants, palynomorphs, tetrapod footprints, and the radiometric and palaeomagnetic investigations. Therefore, the stratigraphical resolution is rather poor compared with the marine equivalents; so the absence of detailed data and of the wider correlations for the continental beds prevents the use of the three-fold subdivision of the Permian System into "Lower", "Middle" and "Upper". Only in those places where the lateral transition between the continental and marine deposits (*i.e.* in the Dolomite region between the Val Gardena Sandstone and the Bellerophon Formation, togeth-

er referred to the Upper Permian) is evident can the use of the marine stages be justified. For these reasons, and in agreement with Cassinis (2003), in this study the continental Permian "Lower" and "Upper" subdivisions are used.

Therefore, it is Lucas's opinion (*pers. comm.*) that in this study the term "Upper Permian" should include the "Middle Permian" (Ufimian and Kazanian), and only the Tatarian should really be "Upper Permian". As such, it may be better to utilize the marine timescale terms (Roadian, Wordian, Capitanian, Wuchiapingian, etc.) and not the old Russian terms. The utilized chronostratigraphy (Cisuralian and Russian stages) for the Early Permian represents the international subdivision of the Permian System, but in the dating of the continental beds, to leave out the post-Kungurian Russian terms that, in Lucas's opinion (*pers.*

		SCPS 2000	U.S.A. stages	RUSSIA stages My	TETHYS stages	CHINA stages	
P E R M I A N	UPPER	LOPPINGIAN CHANGXINGIAN		251	DORASHAMIAN	CHANGXINGIAN	
		WUCHIAPINGIAN	OCHOAN	?	DZHULFIAN	WUCHIAPINGIAN	
	MIDDLE	GUADALUPIAN CAPITANIAN	CAPITANIAN	TATARIAN		MIDIAN	MAOKOUIAN
		WORDIAN	WORDIAN	KAZANIAN	267	MURGHABIAN	
		ROADIAN	ROADIAN	UFIMIAN	272	KUBERGANDIAN	
	LOWER	CISURALIAN KUNGURIAN	LEONARDIAN CATHEDRALIAN	KUNGURIAN	274	BOLORIAN	CHHSIAN
		ARTINSKIAN	HESSIAN	ARTINSKIAN	277	YAKHTASHIAN	
		SAKMARIAN	LENOXIAN	SAKMARIAN	283	SAKMARIAN	MAPINGIAN
		ASSELIAN	NEALIAN	ASSELIAN	290	ASSELIAN	
				296			

Fig. 3: Permian stratigraphy (SCPS = Sub-Commission of Permian stratigraphy) (Vachard & Argyriadis, 2002. mod.)

comm.), are only the regional stages for the marine timescale, is more difficult for the reasons advanced above. Fig. 3 shows the different scales of the Permian stratigraphy.

In the classic succession of the Trompia Valley (Collio Basin) the COLLIO FORMATION was deposited on volcanoclastic rocks (ignimbrites) which do not crop out with continuity within the Orobic Basin, but are abundant in other areas (e.g. in the Acquaduro Valley -Introbio- and in the Cedrino Pass) (Sciunnach, 2001) and in the mainly "bergamask" sector of the same basin (Jadoul et al., 2000). Other subdivisions of lithofacies have been proposed on a petrographical basis by Cassinis et al. (1988), Cadel et al. (1996), Forcella et al. (2001) and Sciunnach (2001). The Collio Fm. can be informally subdivided into two units: the lower one is composed of grey-green and black sandstones and siltstones, while the upper unit is defined by mainly reddish sandstones and pelites of volcanic elements with quartz, plagioclase and muscovite. It is well stratified and locally contains some conglomeratic beds. The typical arenaceous zones frequently contain fragments of black clay (clay chips) and display planar lamination, while in the pelitic intervals there are different structures such as mud

cracks, raindrop imprints, ripple marks and fossil plant remains, as well as vertebrate and invertebrate ichnites.

This formation is interfingered with the Ponteranica Conglomerate (Casati & Gnaccolini, 1965, 1967). Utilising the fossils collected in the Trompia Basin, the Collio Fm. is referred to the Lower Permian based on chronological data provided by macroflora (Geinitz, 1869; Jongmans, 1960; Remy & Remy, 1978; Kozur, 1981; Visscher et al., 1999), pollen (Clement-Westerhoff et al., 1974; Cassinis & Doubinger, 1991, 1992) and tetrapod footprints (Ceoloni et al., 1987; Conti et al., 1991, 1997), and also for its position below the angular unconformity ascribed to the main post-Saalian phase (Palatine) of the Hercynian orogenesis.

Vertebrate and invertebrate ichnocoenoses of the Orobic Basin

In Italy, early knowledge of vertebrate footprints from the Collio Fm. in the Trompia Valley was advanced by Geinitz (1869) and Curioni (1870). Later, these fossils were studied by Gumbel (1880); the same ichnofauna from the Orobic Basin was analysed by Dozy (1935) and later re-exam-

ined by Haubold (1971). The studies of Berruti (1968), Haubold (1996, 2000), Haubold & Stapf (1998), Casati & Gnaccolini (1967), Ceoloni et al. (1987), Conti et al. (1991, 1997, 1999), Nicosia et al. (2000) and Santi & Krieger (2001) have advanced our knowledge of the vertebrate ichnofauna of the Lower Permian. Footprints from both the Orobic Basin and the Trompia Valley are of amphibians and reptiles, and they come from different parts of the volcano-sedimentary deposits of the Collio Formation (Conti et al., 1991; Santi, 2003) relating to main vegetated areas, to other alluvial zones, to more emergent humid areas, and others with shallow water.

Together with small- to medium-sized vertebrates, lived insects and arthropods (*Bifurculapes* Hitchcock, 1858, *Dendroidichnites elegans* Demathieu, Gand & Toutin-Morin, 1992, cfr. *Heteropodichnus variabilis* Walter, 1983, *Eisenachichnus* sp. (= *Secundumichnus*), *Tambia spiralis* Müller, 1956, *Permichnium* Guthörl, 1934, burrowing invertebrates (?*Scoyenia* White, 1929), gastropods (*Paleobullia* sp. vel. ?*Cochlea* sp.), probably myriapods and some unidentified trails, bivalves (Anthracosiididae), small crustaceans ("Estheria") and freshwater jellyfish (*Medusina limnica* Müller, 1978 and *Medusina atava* (Pohlig, 1892, Walcott, 1898) (Ronchi & Santi, 2003) (Pl. 1).

Up to now, from these former data the composition of the invertebrate ichnocoenosis shows: (a) imprints are typically of freshwater animals, (b) a dominance of surface traces and not infaunal burrows, (c) low biodiversity, (d) a lack of monospecificity, and (e) the ichnodiversity and the taxonomic composition suggest a terrestrial-freshwater origin.

The tetrapod ichnofauna of the Collio Basin consists of: *Batrachichnus* sp., *Camunipes cassinisi* Ceoloni et al., 1987, *Amphisauropus imminutus* Haubold, 1970, *Amphisauropus latus* Haubold, 1970, *Varanopus curvidactylus* Moodie, 1929, *Dromopus lacertoides* (Geinitz, 1861), *Dromopus didactylus* Moodie, 1930 and *Ichniotherium cottaie* (Pohlig, 1885). That of the Orobic Basin is composed of: "*Batrachichnus*" *salamandroides* (Geinitz, 1861), *Camunipes cassinisi* Ceoloni et al., 1987, *Amphisauropus imminutus* Haubold, 1970, *Amphisauropus latus* Haubold, 1970, *Varanopus curvidactylus* Moodie, 1929 and *Dromopus lacertoides* (Geinitz, 1861) (Pl. 2). The ichnocoenoses re-

enter in the so-called "red-bed ichnofacies" (defined as a variety of fluvial, deltaic, lacustrine and marginal marine environments; Haubold & Lucas, 1999), typically different from the "*Chelichnus* ichnofacies" related to the desert environment and aeolian facies (Lockley et al., 1994; Lockley & Meyer, 2000; Lucas, 2002).

A great affinity between the ichnocoenoses of the two basins is evident, with the only exception being *Ichniotherium cottaie* and *Dromopus didactylus* presenting together inside the Collio Basin, but lacking in the Orobic Basin. This last ichnospecies is present not only in the highest strata of the Collio Fm. in the Trompia Valley, but it is also a monotypic taxon of the Tregiovo Basin (Conti et al., 1997; Nicosia et al., 2000). At present *I. cottaie* should be a local taxon of the Trompia Basin. Besides, there is the problem linked to the validity of the ichnogenus *Camunipes*, namely if it effectively should be a true ichnogenus, or should be considered a synonym of *Erpetopus*. A discussion of this taxonomic problem is advanced by Haubold & Lucas (2001, 2003) and Santi (2004). On the whole, the Lower Permian ichnocoenosis actually consists of mostly reptiles and one amphibian (*Batrachichnus*); among the former we have a relevant "large" herbivore component, while the others are of smaller size.

The time interval into which the tetrapod ichnofauna is limited is between 286/283 Ma at the base and 278/273 Ma at the top (Avanzini et al., 2001). In agreement with the Permian subdivision effected by Menning (2001), this ichnoassociation may belong to the Artinskian and Kungurian, but other scales (i.e. Harland et al., 1990; Odin, 1994; Gradstein & Ogg, 1996) consider these values to be Sakmarian and upper Asselian. The South-Alpine ichnoassociation has a similarity to that of North America, with strong Wolfcampian affinities showing a great interaction between W-Central Europe and this continent.

It is a mostly homogeneous association, but also very poor in taxa, and even more reduced in the highest strata of the Collio Fm. In the Orobic Basin, the passage between the lower unit of this formation and the upper is marked among the tetrapod palaeoichnofauna by the absence of *Batrachichnus*, *Camunipes* (*Erpetopus*) and *A. imminutus*, and by the presence of only *A. latus*, *D. lacertoides* and *V. curvidactylus*, and among the

invertebrates, *Dendroidichnites* and *Medusina atava* are present. In agreement with the "Global Permian series of the marine Permian System", the above-mentioned ichnoassociation is considered coeval with the "Lower Permian Cisuralian" (Cassinis et al., 2002).

On the whole, factors producing the taxonomic compression of the Lower Permian palaeoichnofauna are different (Lucas, 1998), but regionally, the "deposition time compression" hypothesis (Nicosia et al., 2000) can be advanced on the basis of radiometric data presented by Schaltegger & Brack (1999) in the volcanic beds at the base and at the top of the Collio Fm. s.s. (= sedimentary "Collio") in the Trompia Valley. According to these authors, about 700 m of sediments were laid down in 4–5 My: a very high rate linked to strong tectonic activity. In my opinion this would prevent the establishment of useful biotopes for the survival of animals. A clear example is shown near to the Pizzo del Diavolo (Brembana Valley) neighbouring the Bocchetta di Poddavista ("Podavit") where the lower unit of the Collio Fm. (600 m up) is well exposed. In its lower portion abundant "signatures" of the tectonic activity are well evident. Repeated pyroclastic fall intercalations and the soft sediment deformations (seismites), sedimentary dykes, "ball & pillow" and slumping structures, were probably triggered by synsedimentary tectonics and frequent volcano-seismic activity. Only in the homogeneous silty-muddy part (last ten of metres) did the tectonic "peace" allow the development of more firm biotopes. Only in this position were the taxa of the "orobioic" ichnoassociation identified.

Furthermore, the orogenic activity is not **the** cause, but **one** cause of the taxonomic paucity, together with climatic change (Santi, 2004).

Partially in agree with the opinion of Lucas (pers. comm.) that the global paucity in Permian ichnotaxa reflects the conservative nature of the footprint structure (Santi, 2004), the ichnoassociation of the South-Alpine region is very similar to the other European and extra-European countries (see later): then *a priori* it is not possible to exclude the hypothesis that it could accurately reflect the original vertebrate biodiversity. Overall, local geological events could have played a crucial role for the original biodiversity composition in this sector of Palaeoeurope ("deposition time compression" hypothesis).

Paucity in taxa could depend on internal properties and external conditions:

- a) linked to niche dimensions for vertebrates and invertebrates. In fact, the species with the narrowest niches have high probabilities of speciation either because species are unstable and have patchy populations, or because there are potential new niches to invade through evolutionary divergences. The "Collio" area was undoubtedly large and less ecologically diversified, and this should favour extinction rather than speciation.
- b) Species with small and patchy populations tend to isolate frequently; consequently this pattern of species has a greater probability of extinction (Stanley, 2001). The orogenic forces and climatic changes probably operated above a very brittle biodiversity with low numbers, and determined their extinction. Only the ability of some taxa to disperse and to colonize different biotopes might have allowed them to survive (*Amphisauropus*, *Dromopus*, *Varanopus*), but probably the attempt did not occur completely within an unstable framework (coeval orogenesis + climatic changes).

In the palaeo-European domain, documented examples of terrestrial environments with fossiliferous assemblages have been described (e.g. Debriette & Gand, 1990; Schneider, 1994; Gand et al., 1997 a, b, c; Eberth et al., 2000). It is noteworthy that in many European Lower Permian basins, which can represent excellent analogues to those of the central Southern Alps, the facies distributions and environmental settings record, from base to top, an evolution from grey-black alluvial-to-lacustrine deposits to reddish flood-plain and playa sediments. Over a large part of Western Europe, Early Permian times were characterised by a climatic shift from warm, with alternating wet and dry seasons, to semi-arid, up to the very warm and hot conditions of the Late Permian (Ori, 1988; Dickins, 1993; Parrish, 1993; Golonka & Ford, 2000). Thus, during the mid to late Early Permian (Artinskian–Kungurian?), a regional and geologically rapid decrease in the rate of precipitation and the onset of oxidising climatic conditions were suggested by both lithofacies and biofacies changes. In the Orobio Basin (at least in its western sectors), the dominant alluvial-to-lacustrine dark-coloured facies pass quite abruptly, towards the

stratigraphic top of the succession, to reddish fine sediments. The former dark deposits suggest that a higher groundwater level produced reducing conditions, while the red fines indicate muddy playa conditions with high evaporation rates and an oxic environment. A similar environmental-climatic transition could also be envisaged in the western Val Trompia Basin, where the Collio Fm. fluvial and lacustrine scenario evolves from the proximal to distal alluvial-fan facies (Dosso dei Galli Conglomerate) and up-section to the lateral and bioturbated, purple-red, fine sandstones and siltstones (Pietra Simona Mb.). The consequences were, at the beginning of the Upper Permian, a clear change in fauna with more modern features (Conti et al., 1999); its origin is contained in the regional temporal gap which divides the first cycle from the second.

Behavioural features of the Early Permian tetrapods

It seems opportune to talk about the problem of the behavioural features of the trackmakers. The rarity of fossil remains of vertebrates in the continental deposits of the Permian of Central and South Europe makes a discussion about their behavioural features rather difficult, but the ichnoassociation can be considered as a good starting point for this goal. The Lower Permian ichnoassociation of the South-Alpine zone reflects the vertebrate association living in this area of Palaeoeurope at the time, like those of France, Germany and also North America and Argentina, with only rare exceptions of elements considered as "local form" (*i.e. Ichniotherium* for the South-Alpine region) (Conti et al., 1999). Within the ichnoassociation of the South-Alpine region (Orobic and Trompia Basins), until now typical prints attributed to a top carnivore are absent; either the trackmaker belonged to a population effectively reduced in number compared with the herbivores, or it was totally absent. Maybe during the Lower Permian of southern Europe, its specific role was partially occupied by other vertebrates. The low number of taxa (common also in the Lower Permian ichnoassociations from other countries) suggests that the ichnodiversity could be, if not real, then the almost complete composition of the vertebrate biodiversity. Then the prints can be, if not an exact mirror, then at least a

significant indicator of the original vertebrate and invertebrate biodiversity. This would not explain why the trophic pyramid should effectively be that here carried out, but until now the ichnocoenosis composition and the frequency with which some footprints are discovered (*i.e. Batrachichnus* is very rare compared with the reptiles, and among these *Amphisauropus latus* and *Dromopus lacertoides* are clearly much frequent in comparison with *Varanopus*) allows us to propose the hypotheses advanced here. This is rather different to Lucas's opinion (pers. comm.) referring to the Moenkopi ichnoassociation from the Triassic of the USA: "...The tracks are almost all of archosaurs (*chirotheres*), but the bones from the same formation are almost all of amphibians...".

Notwithstanding the paucity of taxa of the tetrapod ichnofauna, the ichnocoenoses have not been utilised to examine the behavioural features of the trackmakers. A similar gap is also underlined by Kramer et al. (1995) referring to the ichnites from the Coconino Sandstone (North America): "...behavioural aspects of extinct animals cannot be tested" (Brand, 1978 p. 81) (Kramer et al., 1995 p. 245). Furthermore, behavioural evidence from trackmakers can be discussed when studying "terminated trackways" *sensu* Kramer et al. (1995), or those that suddenly change direction. From the "orobic" Lower Permian beds come some data on the reptilian diet. Among the components of the ichnocoenosis, the *Dromopus* trackmaker is commonly ascribed to the araeoscelid, considered a consumer of small invertebrates with exoskeletons. Figure 4A suggests the following event sequence, pointing to a lack of superimposition of walking-trail and footprints. A trackmaker arthropod (*Dendroidichnites elegans*) is moving on a firm silty bed (point A). On its left side a probable adult araeoscelid reptile, trackmaker of *Dromopus*, is approaching. At point B the arthropod abruptly deviates towards its right side, probably trying an evasive manoeuvre; by this point the trail impression is not very clear, probably because the trackmaker was alarmed and progress was disordered. The final trackway-tract was not preserved by the sediments, but we realise that the araeoscelid preyed upon the arthropod without pursuing it. Figure 4B shows a clear "terminated trackway" *sensu* Kramer et al. (1995) of an arthropod (*Heteropodichnus* trackmaker) pursued by a *Dromopus* one; traces of its trail abruptly disappear.

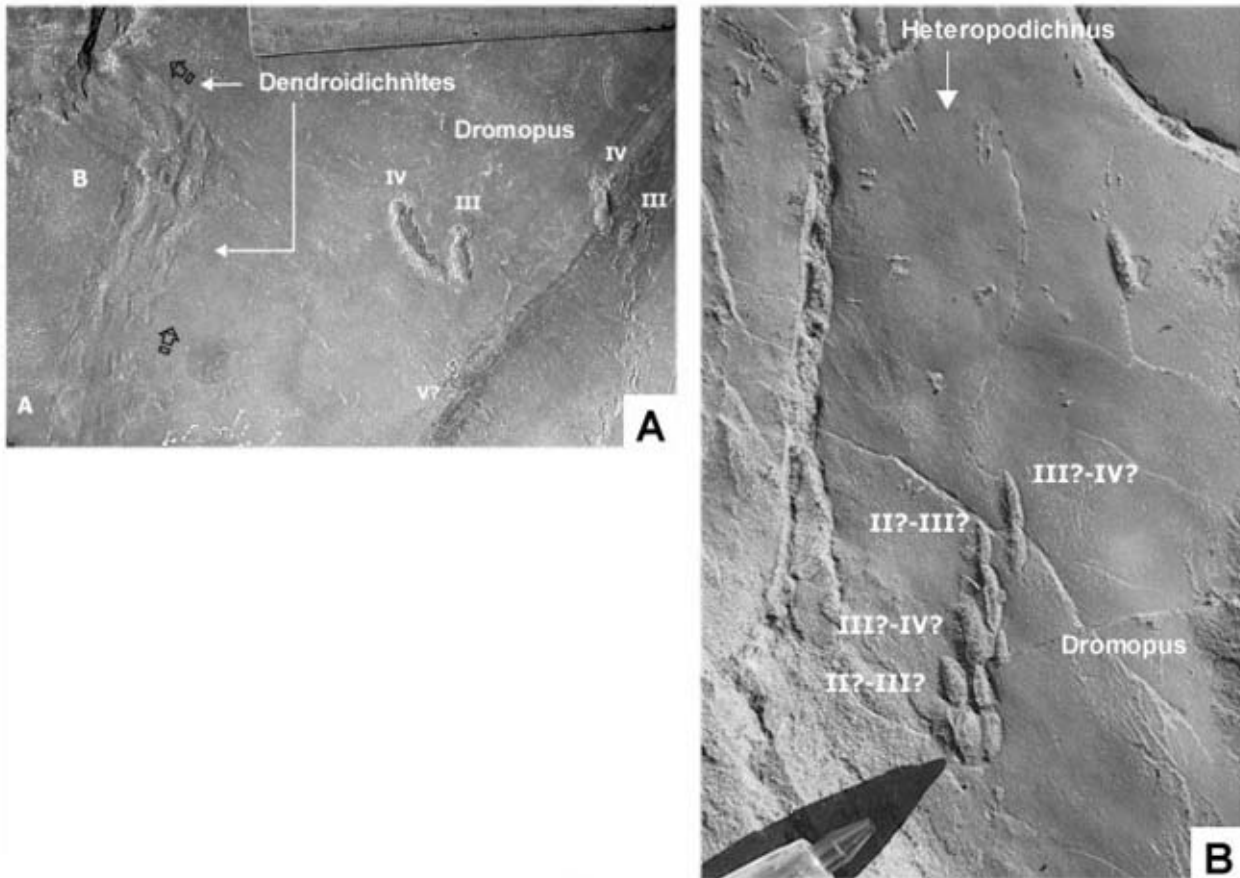


Fig. 4: A - Interaction between the *Dendroidichnites elegans* Demathieu, Gand and Toutin-Morin, 1992 trail and *Dromopus* sp. footprints. Black arrows indicate the arthropod trail directions. B - "Terminated trackway" of cfr. *Heteropodichnus variabilis* Walter, 1983 with *Dromopus* sp

As witnessed by the prints upon the slabs in Fig. 4, it is possible that the predator role in the Lower Permian of the South-Alpine region was played partially by these reptiles. Rare amphibians and mainly reptiles compose the tetrapod ichnocoenosis; it is an association with a paucity in taxa and comprises herbivores from small size (*Amphisauropus imminutus*) to medium-large size (*Amphisauropus latus*). At present, large footprints referred to large vertebrates (*i.e.* such as the Middle Permian pareiasaur *Pachypes*) have not been found. A top carnivore seems lacking. Thus, in the Lower Permian of the South-Alpine region the trophic pyramid was probably like this:

Primary consumer. Medium-sized herbivore: cotylosaurs identified as the trackmaker *Amphisauropus latus*, a tetrapod of relatively large dimensions (the true "giant" of the association in comparison with the sizes of other trackmakers), with short and stumpy legs, probably strong and

adapted to support a relatively great weight. The frequency with which the *A. latus* footprints are found is highest, so it represented the dominant animal of "Collio" lands. Similar in size or possibly larger was the *Ichniotherium* trackmaker (an edaphosaur pelycosaur), but as seen above, its presence is very rare, and thus its role inside the trophic pyramid is much diminished.

Secondary consumer. Carnivores: the ichnological association seems to lack typical footprints attributed to this consumer.

Mixed diet. Opportunistic consumers: on the whole these are small reptiles, morphologically and in their general structure similar to small lizards, also with autopodia features and with more or less sharp teeth (*Camunipes* trackmakers). Their diet could be similar to that of true lizards of small dimensions, swallowing and biting anything either living or dead. In this category should re-enter the *Dromopus* trackmaker which, together with the

Amphisauropus, is a common form, and less frequently that of *Varanopus*. A novel feature of an araeoscelid trackmaker (*Araeoscelis*) is the lateral temporal opening, which could have been closed in relation to the skull extension as the consequence of a more massive dentition (Carroll, 1988). Such araeoscelids could prey upon protein-bearing organisms and consume some strong parts such as their exoskeleton (arthropods), or small vertebrates (amphibians?) also.

Thus, it does not seem that the Lower Permian association of the South-Alpine area needs to be balanced. It is possible that the araeoscelids and the *Dromopus* trackmaker could have partially occupied the small predator role.

Conclusions

Lower Permian palaeoichnoassociations of the Orobic Basin (the Collio Fm, the only fossiliferous unit), although poor in ichnotaxa, perfectly reflect the ichnofaunistic panorama of Central Europe, North America and Argentina. On the basis of actual knowledge, different conclusions can be advanced.

- 1) The ichnocoenosis has a similarity to those from Central Europe, North America and South America (Argentina; Melchor & Sarjeant, 2004) (Lucas et al., 2004 and references therein).
- 2) An impoverishment of the ichnofaunistic composition, shifting from the lower unit to the upper unit of the Collio Fm., is recognized and probably linked to the mutual action of tectonic activity and climatic change (from more humid to drier). It is also probable that the originally low number of ichnotaxa might be due to both internal properties of the biodiversity and external conditions.
- 3) The presence of *Camunipes* in the lower "Collio" may have created some problems, either evolutive or systematic, for its similarity to *Varanopus* and mainly with *Erpetopus* (Haubold & Lucas, 2003). If it should be considered a separate ichnogenus, its presence in the South-Alpine region could be interpreted as a local form (more frequent in the Orobic Basin, less so in Trompia Valley) as is *Ichniotherium cotta*.

- 4) The trophic pyramid relevant to the Lower Permian of the South-Alpine region does not seem balanced because of the lack of a top carnivore. This role might have been occupied by reptiles, some araeoscelids having features similar to true lizards.

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Plate 1

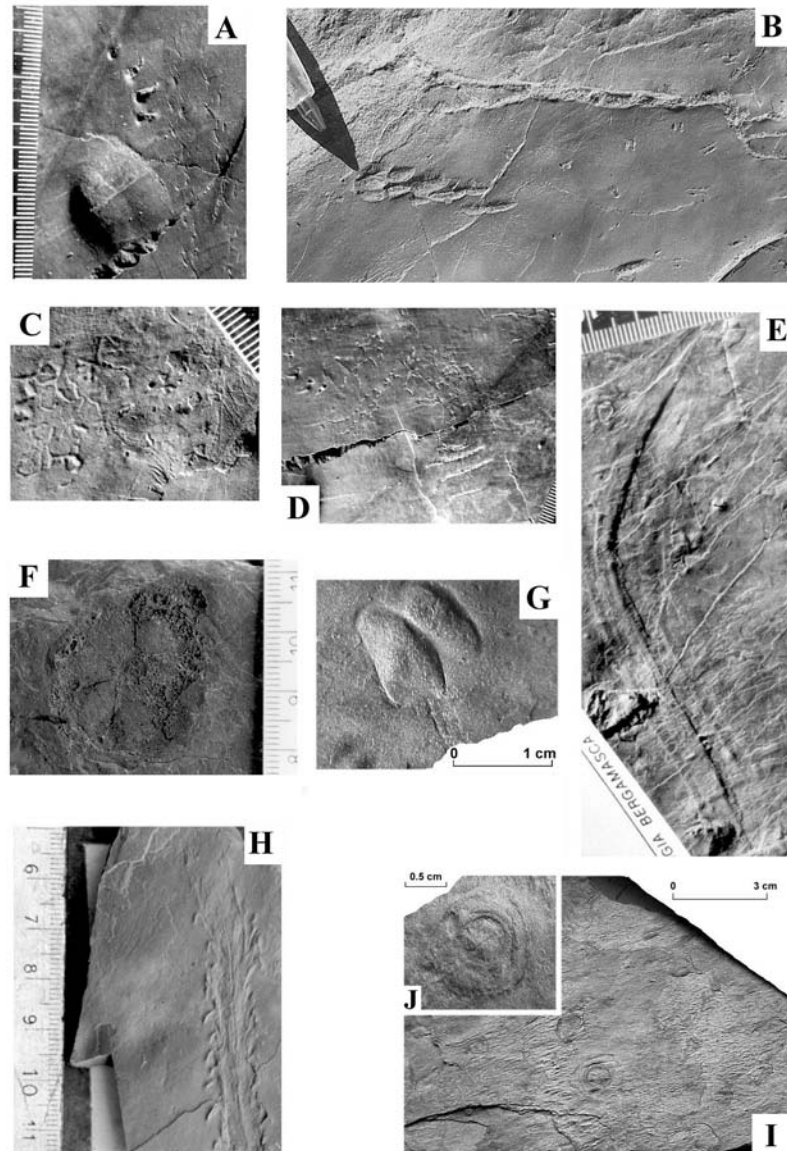


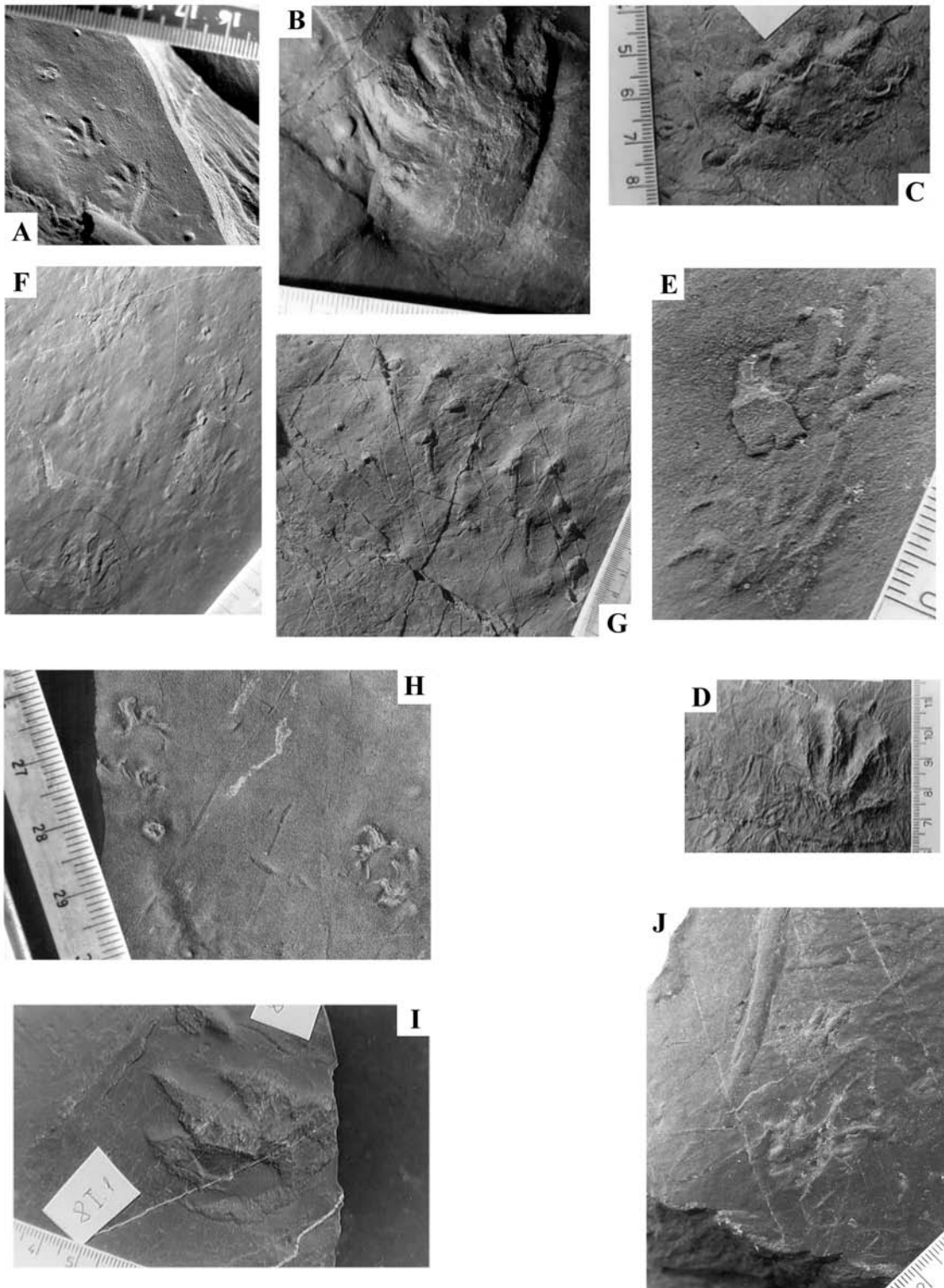
Plate 1

A – *Bifurculapes* sp. Bocchetta di Poddavista, Orobic Basin. **B** – cfr. *Heteropodichnus variabilis* Walter, 1983. Mincucco Mt. Orobic Basin. **C** – *Paleobullia* Göttinger & Becker, 1932 vel. ?*Cochlea* Hitchcock, 1858. Brembana Valley, Orobic Basin. **D** – *Secundumichnus* sp. Brembana Valley, Orobic Basin. **E** – Undetermined traces. Brembana Valley, Orobic Basin. **F** – *Medusina atava* (Pohlig, 1982) Walcott, 1898. Inferno Valley, Orobic Basin. **G** – *Anthracosiidae* Trompia Valley Basin. **H** – *Dendroidichnites elegans* Demathieu, Gand & Toutin-Morin, 1992, Mincucco Mt. Orobic Basin. **I, J** – *Medusina limnica* Müller, 1978. Trompia Valley Basin .

Plate 2 (continued on next page)

A– *Camunipes cassinisi* Ceoloni *et al.*, 1987, reverse print left couple manus-pes. Brembana Valley, Orobic Basin. **B** – *Amphisauropus latus* Haubold, 1971, reverse print right pes. Inferno Valley, Orobic Basin. **C** – *Amphisauropus latus* Haubold, 1971, reverse print left manus. Inferno Valley, Orobic Basin. **D** – *Varanopus curvidactylus* Moodie, 1929, reverse print left pes. Inferno Valley, Orobic Basin. **E** – *Varanopus curvidactylus* Moodie, 1929, reverse print left couple

Plate 2



manus-pes. Inferno Valley, Orobic Basin. **F** – *Dromopus lacertoides* (Geinitz, 1861), trackway. Brembana Valley, Orobic Basin. **G** – *Amphisauropus latus* Haubold, 1971, set reverse print manus-pes. Inferno Valley, Orobic Basin. **H** – *Camunipes cassinisi* Ceoloni *et al.*, 1987, set reverse print manus-pes. Scioc Valley, Orobic Basin. **I** – *Amphisauropus latus* Haubold, 1971, reverse print manus?-pes?. Inferno Valley, Orobic Basin. **J** – *Varanopus curvidactylus* Moodie, 1929, trackway. Inferno Valley, Orobic Basin.