Predator–prey interaction in the Permian of the Orobic Basin (North Italy). Behavioural consequences

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Abstract

Predator–prey interactions shown by ichnofossils are not very frequent and the interpretation of so–called 'terminated trackways' can represent a good opportunity of study. Especially the behavioural tendency of some vertebrates can be confirmed. In the Lower Permian of the Valtellina area (Orobic Basin, Southalpine, North Italy) a very peculiar development of arthropod walking–trails (*Dendroidichnites elegans* Demathieu, Gand & Toutin–Morin, 1992 and *cfr. Heteropodichnus variabilis* Walter, 1983) and the presence in suspicious position of *Dromopus* sp. footprints, should testify a possible predation attempt from the vertebrate maker on the formers. Thus, during the Lower Permian it should be also documented that the partial predator role in the Southalpine, was occupied just by the araeoscelid trackmaker of the *Dromopus*. Inside the trophic pyramid, probably with the *Varanopus* and *Camunipes* ones, *Dromopus*'s maker occupied the opportunist consumer role. *Amphisauropus latus* Haubold, 1971 and *A. imminutus* Haubold, 1971 makers played the primary consumer role, while a true carnivore is missing.

Contents

1. Introduction

In the last several years, the impulse carried out by the tetrapod ichnology in the palaeontologic and stratigraphic research of the Lower Permian in the Southalpine (North Italy) has allowed a better understanding of the systematic taxonomy, palaeogeographic and stratigraphic role of the trackmakers (Conti *et al.,*1997; Avanzini *et al.*, 2001). This was supported by the discoveries of new sites and with the detailed analyses of other historically known sites, especially inside the Orobic Basin (Lombardy Region, North Italy; for instance in the Brembana Valley to the Bocchetta di Poddavista, or 'Podavit', and in the neighbouring areas of the Camisana Valley [Dozy, 1935; Santi & Krieger, 2001; Santi, 2003], in the Gerola–Inferno Valleys, in the Pescegallo Valley–Valtellina–[Cassinis *et al.*, 2000; Nicosia *et al.*, 2001; Gianotti *et al.*, 2001, 2002; Ronchi & Santi, 2003]).

Vertebrate and invertebrate prints come from the Collio Formation only (Lower Permian); at present the overlapping formations, the Ponteranica Conglomerate and the Verrucano Lombardo, are not fossiliferous (figure 1). Though the ichnocoenosis should be poor in taxa (*Batrachichnus*, *Amphisauropus*, *Dromopus*, *Camunipes*, *Varanopus*), most of the ichnites referring to these ichnogenera are not considered to improve our understanding of the behaviour of the trackmakers. Referring to the Coconino Sandstone (North America) ichnites, Kramer *et al.* (1995: 245) underline a similar gap: "…behavioural aspects of extinct animals cannot be tested (Brand, 1978 p. 81)" Therefore, behavioural evidences of trackmakers can be discussed by studying the 'terminated trackways' *sensu* Kramer *et al.* (1995) or those that abruptly suddenly change direction. In the opinion of Kramer *et al.* (1995: 245), 'terminated trackways' are: "…one trackway…abruptly "terminated" upon intersection with another", therefore, the ones that suddenly change direction without a logical explanation could re–enter in this huge category. Just because the documented predator–prey combinations are rare, their analyses represent the only opportunity to study this aspect of behaviour (Lockley & Madsen, 1992; Hunt, 1993; Lockley & Hunt, 1995; Kramer *et al*., 1995).

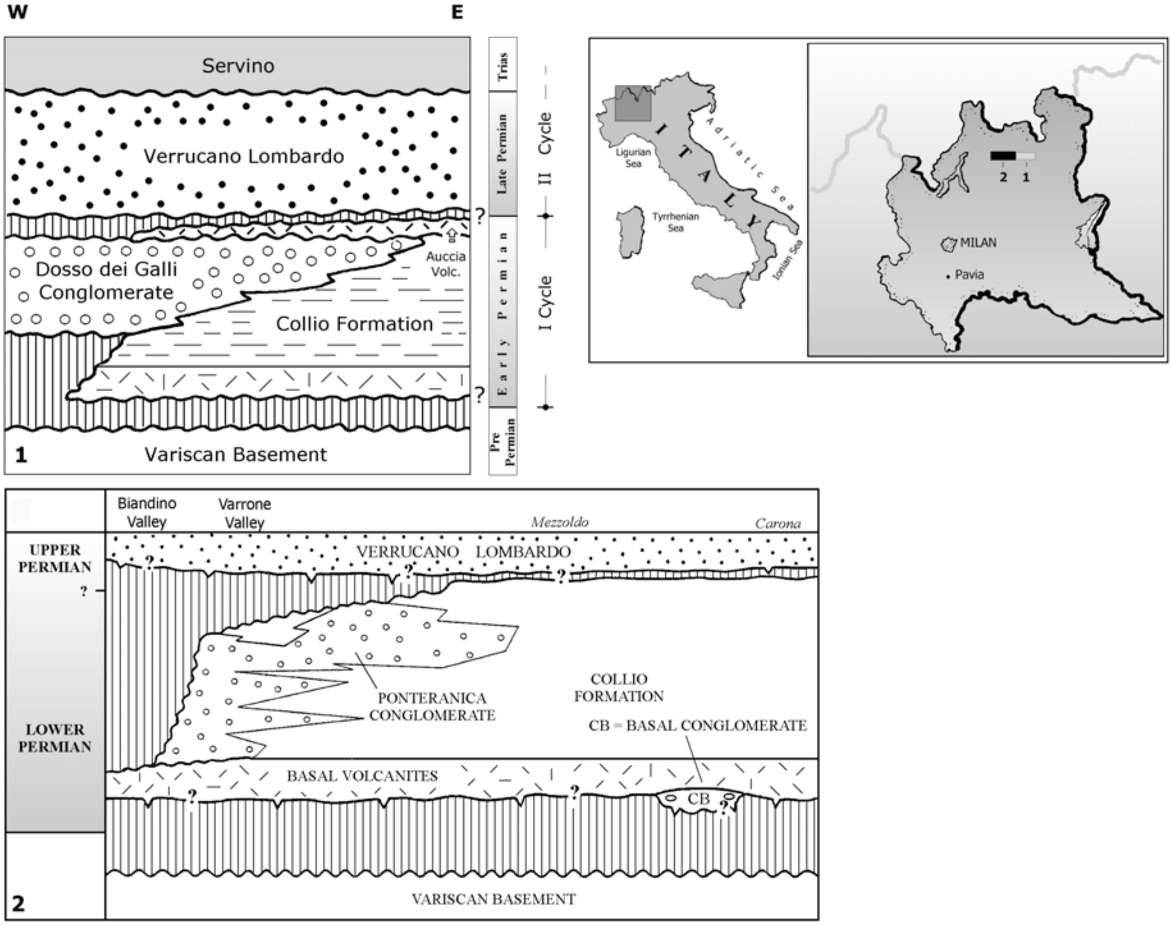

Figure 1. 1: Chronostratigraphic scheme of the Permian in Trompia Basin (modified after Cassinis et al.*, 1988); 2. Chronostratigraphic scheme of the Permian in the Orobic Basin (modified after Cassinis* et al.*, 2000).*

2. Regional setting and brief stratigraphic overview of the Orobic Basin

2.1. General setting

For a long time it has been known and analysed in several investigations (*e.g.* Cassinis *et al*., 2002; Cassinis & Ronchi, 2001 with references therein) that the aged Upper Carboniferous–early Middle Trias succession in the Southalpine is characterised by two tectono–sedimentary cycles separated by a regional angular unconformity (figure 1). The first of these referred to the ?Upper Carboniferous–Lower Permian, is composed by a continental sequence of volcanic deposits (from acid to intermediate nature) and alluvial–to–lacustrine sediments that formed the Basal Conglomerate, the Collio Formation, the Tregiovo Formation, the Ponteranica Conglomerate, the Dosso dei Galli Conglomerate and the Auccia Volcanites. The second cycle consists of reddish clastic deposits of the Verrucano Lombardo–Val Gardena Sandstone complex (figure 2). Based on the palaeontological records this second cycle is referred to the Upper Permian (Italian IGCP Group 203, 1988), but should continue inside the lower Anisian (Massari & Neri, 1997). An Upper Permian age is also confirmed by Menning (1995) that inserts it over the inversion magnetic event 'Illawarra event' (≤ 265 My). The length of the gap between the first and second cycle, a hiatus that could be put between the Lower and Upper Permian or at the base of this last (Cassinis *et al.,* 2000), is still a subject of discussion. According to the Harland *et al.* (1990), Odin & Odin (1990) and Menning (1995) chronological scale, the hiatus could be quantified as 5–10 My. Therefore, according to the recent data (Cassinis *et al*., 2002), the gap entity embraces a time–interval between 14 and 25 My; this could be in agreement with the faunistic change observable in the Southalpine, testified by the ichnoassociations substitution at the Lower–Upper Permian transition.

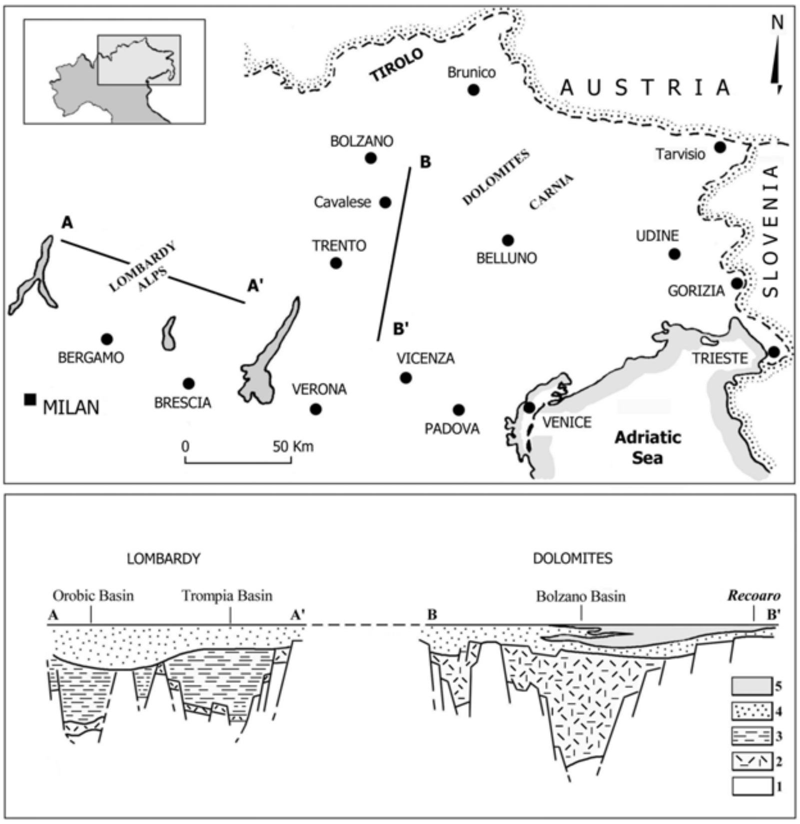

Figure 2. Main Permian basins across the Southalpine. 1: Pre–Permian basement; 2: volcanic deposits; 3: clastic units of the first sedimentary cycle; 4: Verrucano Lombardo–Val Gardena Sandstone; 5: Bellerophon Formation (modified after Conti et al.*, 1997).*

2.2. Stratigraphy

In the Lower Permian of the Southalpine the Collio Formation represents the only fossiliferous deposits. It lies over the Basal Conglomerate, a conglomeratic lithosome about ten meters thick that discontinuously crops out in the Orobic Basin (*e.g.* Seriana Valley, Lombardy). In the classic succession of the Brescian Region (eastern to the Orobic Basin), the Collio Formation is laid down over a volcaniclastic bed (ignimbrites) that does not crop with continuity inside the Orobic Basin, *i.e.* Acquaduro Valley (Introbio) and to the Cedrino Pass (Sciunnach, 2001), or in the mainly 'bergamsc' sector of the same basin (Jadoul *et al.,* 2000). Based on the petrographic analyses, other different lithofacies subdivisions have been proposed by Cassinis *et al.* (1988), Cadel *et al.* (1996), Forcella *et al.* (2001) and Sciunnach (2001). Informally the Collio Formation can be subdivided in two units: the lower consists of grey–green and black sandstones and siltstones, while the upper one merely by wine–reddish sandstones and pelites composed by volcanic elements mainly with quartz, feldspar and muscovite. It is well–stratified and locally presents some conglomeratic intercalations. The typically arenaceous component frequently contains clay chips and has a planar lamination, while in the pelitic intervals, mud cracks, rain drops, ripple marks, vertebrate, invertebrate imprints and plant remains are shown.

This formation is eteropic with the Ponteranica Conglomerate (Casati & Gnaccolini, 1965, 1967). The age of the Collio Formation is referred to the Lower Permian utilising fossils gathered in the Trompia Basin, (macrofloras: Geinitz, 1869; Jongmans, 1960; Remy & Remy, 1978; Kozur, 1981; Visscher *et al.,* 1999; palynomorphs: Clement–Westerholf *et al*., 1974; Cassinis & Doubinger, 1991, 1992; tetrapod footprints: Ceoloni *et al*., 1987; Conti *et al*., 1991, 1997) and for its position below to the angular unconformity linked to the main post–Saalian (Palatine) phase of the Hercynian orogenesis also.

3. The Collio Formation ichnocoenosis

Footprints either from the Orobic Basin or from the Trompia Valley are of Amphibians and Reptiles. They come from different zones inside the sedimentary layers of the Collio Formation ('Collio *s.s.*') (Ronchi & Santi, 2003 with references therein) representing very well–vegetated areas, alluvial ones, others humid and repetitively rising out too. Together with small–medium size vertebrates, several kind of insects, arthropods (*Bifurculapes* Hitchcock, 1858; *Dendroidichnites elegans* Demathieu, Gand & Toutin–Morin, 1992; *Tambia spiralis* Müller, 1956; *Permichnium* Guthörl, 1934 and ?*Scoyenia* White, 1929; *Eisenachichnus* sp. [synonym of *Secundumichnus*]; *Paleobullia* Götzinger & Becker, 1932; vel. ?*Cochlea* Hitchcock, 1858), bivalves (*Anthracosiidae*), small crustaceans ("*Estheria"*) and fresh–water jellyfish (*Medusina limnica* Müller, 1978; *Medusina atava* (Pohlig, 1892), Walcott, 1898) were present. Table 1 shows the tetrapod ichnocoenoses of the Orobic and Trompia Basins; a heavy affinity between the two is evident, with the only exception of *Ichniotherium cottae* and *Dromopus didactylus* found in Trompia Basin and missing in the Orobic one. This last ichnospecies is not only present in the uppermost layers of the Collio Formation in the Trompia Valley, but is also a monotypic taxon of the Tregiovo Basin (Conti *et al*., 1997; Nicosia *et al*., 2000). At present *I. cottae* should be a local taxon of the Trompia Basin. Globally, this ichnocoenosis is referred to the Sakmarian–Artinskian times and to the *red–bed ichnofacies* (Lockley *et al*., 1994; Lockley & Meyer, 2000). Considering the recent subdivision in faunistic units and faunistic ages created by Conti *et al*. (1997) for the 'Collio' in Trompia Basin, the ichnoassociation of the Orobic Basin can be inserted in the lower subunit *Pulpito Subunit* (Conti *et al*., 1999) of the Collio Faunal Unit. In the biochronological scheme of figure 3 is the interval corresponding to the Rabejac Subage of the Collio Faunal Age. Besides, the same authors define a scale of bioevents for the Italian continental Permian successions and advance some correlations with those of France, Great Britain and Germany. The most important of them are, according to Conti *et al*. (1997: 54): "… The first two intervals are characterised, from the evolutionary point of view, by a single evolving lineage (*Dromopus lacertoides–D. didactylus*), whereas, the third features an absence of evolutionary change. Additional data include the presence of a characteristic impoverished fauna at the top of the first cycle sediments, whereas the faunal assemblage of the second cycle is the most diversified of all Permian tetrapod faunal assemblage".

Orobic Basin	Trompia Basin
"Batrachichnus"salamandroides	*Batrachichnus* sp.
cfr. *"Batrachichnus"salamandroides*	*Camunipes cassinisi*
Camunipes cassinisi	*Amphisauropus latus*
Amphisauropus imminutus	*Varanopus* sp.
Amphisauropus latus	*Dromopus lacertoides*
cfr. *Amphisauropus imminutus*	*Dromopus didactylus*
Varanopus curvidactylus	*Ichniotherium* sp.
Dromopus lacertoides	
?*Ichniotherium cottae*	

Table 1. Comparison between the tetrapod footprints ichnocoenoses from the Orobic and Trompia Basins (from Santi & Krieger, 2001).

In reality the footprint distribution in the Collio Formation is not homogenous; all ichnogenera cited above indicated are individuated in the 'lower Collio' with an high abundance of *A. latus* and *D. lacertoides*, but the 'upper Collio' transition is marked by a reduction of taxa arriving in the highest strata to the sole presence of *D. didactylus*.

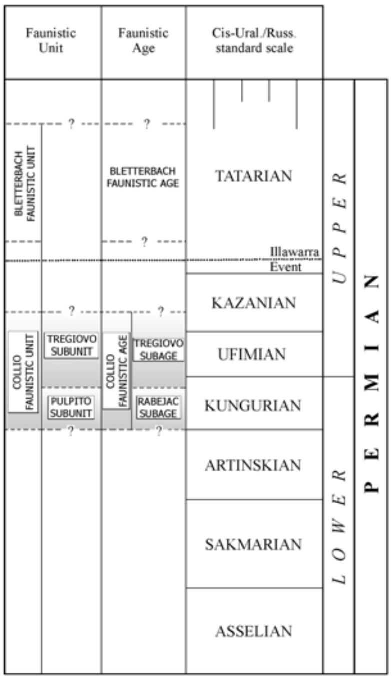

Figure 3. Correlation scheme between the Permian succession of the Southalpine (Collio, Tregiovo, Bletterbach) and of the Lodève Basin (Rabejac) south of the French Central Massif (modified after Conti et al., *1997)*

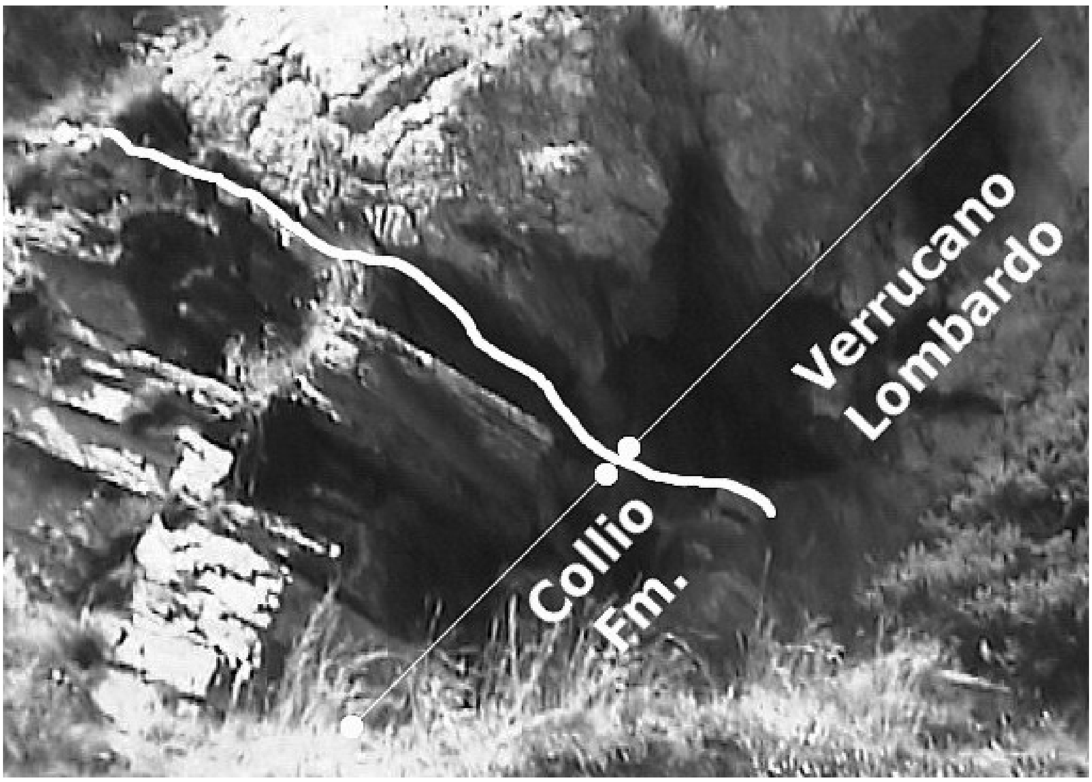

Figure 4. Collio Formation–Verrucano Lombardo Formation. Boundary in the Pescegallo zone near Mount Mincucco. The slab was recovered from the 'Collio' strata. Photograph by G. Santi.

4. Description of the materials

4.1. Premise

This examination is concerns two pelitic slabs found by one of us (G.S.) and Dr. Morini S. in the summer 2003, coming from Collio Formation cropping out in the easternmost sector of the Pescegallo Valley, near to the Mount Mincucco. In this Valtellina zone across an angular unconformity the 'Collio' is in direct contact direct contact with the Verrucano Lombardo Formation (Upper Permian) (figure 4). The former slab (spec. DrDe1) measures 43 x 29 cm and shows a prevailing greenish colouring; vertebrate and invertebrate ichnites and trackways are impressed. This specimen is deposited in the Dipartimento di Scienze della Terra of the Pavia University. The second (spec. Het1) crops out in the same level of the Collio Formation from which the first slab comes and it shares similar granulometric and colour features with the former.

4.2. Systematic palaeoichnology (figures 5–6)

Tetrapod footprints

Ichnogenus *Dromopus* Marsh, 1894

Dromopus sp.

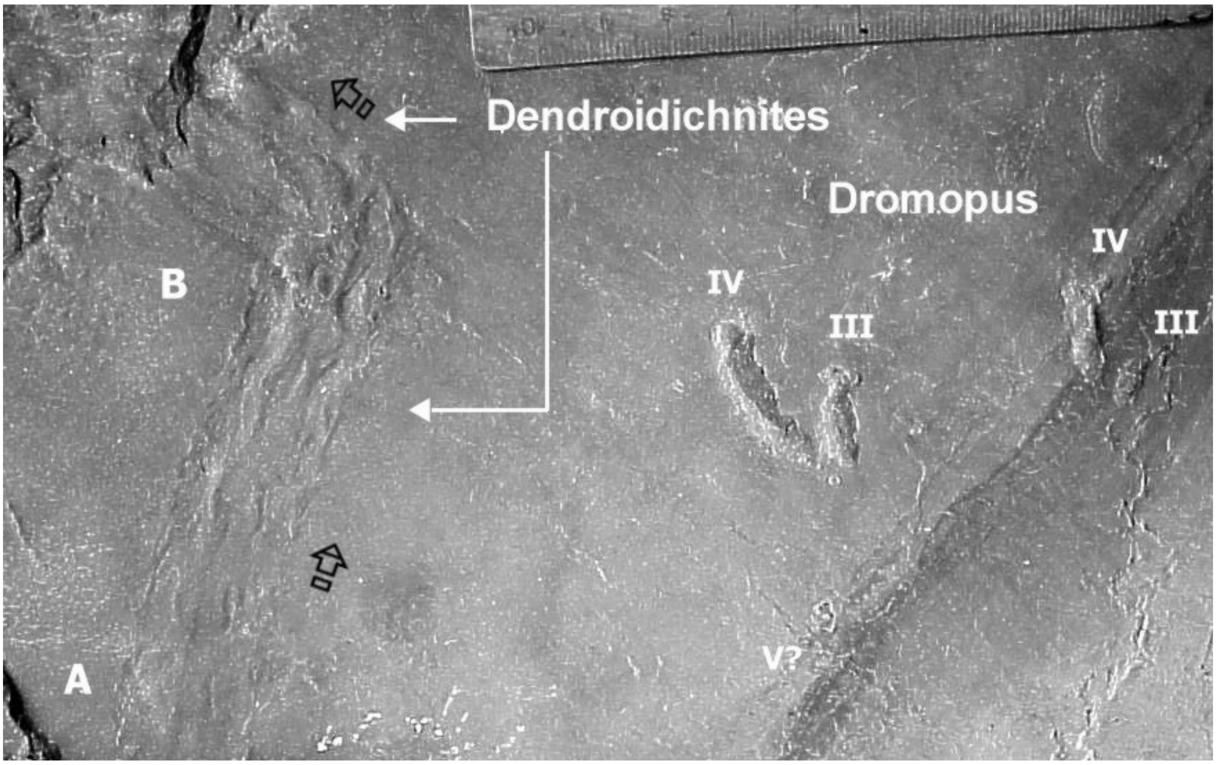

Figure 5. Dendroidichnites elegans *trail and* Dromopus *sp. footprints (spec. DrDe 1). Mount Mincucco, Orobic Basin. Photograph by G. Santi.*

On the specimen DrDe1 partial reverse–prints of manus and pes are impressed. Manus: the central digits are preserved only, apex of both are curved toward to internal of the trackway. Pes: also for this autopodium the central digits are preserved; besides two other traces well–separated by the digits, are impressed, one near to the IIIrd and the second is disposed more back to the IVth digit. Both could indicate the impression of the apical part of one digit, but that on the back disposed, could be belong to digit V. In the specimen Het1 that comes from the lower unit of the Collio Formation near to the Mount Mincucco (Valtellina area), an incomplete right couplet of digitigrade *manus–pes* is observable. The *Manus* is characterised by the impression of the II–III and IV digits, and for the *pes* by digit II–III, the last is hardly overlapped to the hand. There is no doubt about *Dromopus* as the ichnogenus of appurtenance of these ichnites, being very characteristic and common in the continental Permian not only in Italy, but in Europe and in the North America also (Haubold, 1996; Haubold & Lucas, 2001). In this ichnogenus, the ichnospecies *D. lacertoides* and *D. didactylus* are separated by the position of digit V with respect to digit IV (nearest in *D. lacertoides*, separated and turned in back in *D. didactylus*). In the DrDe1 slab the digit impression has a rounded aspect, turned in backward and well–separated by digit IV is a part of digit V, attributing it to *D. didactylus*. In this case, for the first time its presence is established in the Orobic Basin with important regional geographic and stratigraphic consequences. At present, *D. didactylus* is discovered in the highest strata of the Collio Formation in Trompia Basin only, and considered a monotypic taxon of the Tregiovo Basin located easternmost to this. Therefore, the lack of well–impressed ichnites and trackways hampers a clear identification of these footprints to *D. didactylus*, thus we choose to identify them as *Dromopus* sp.

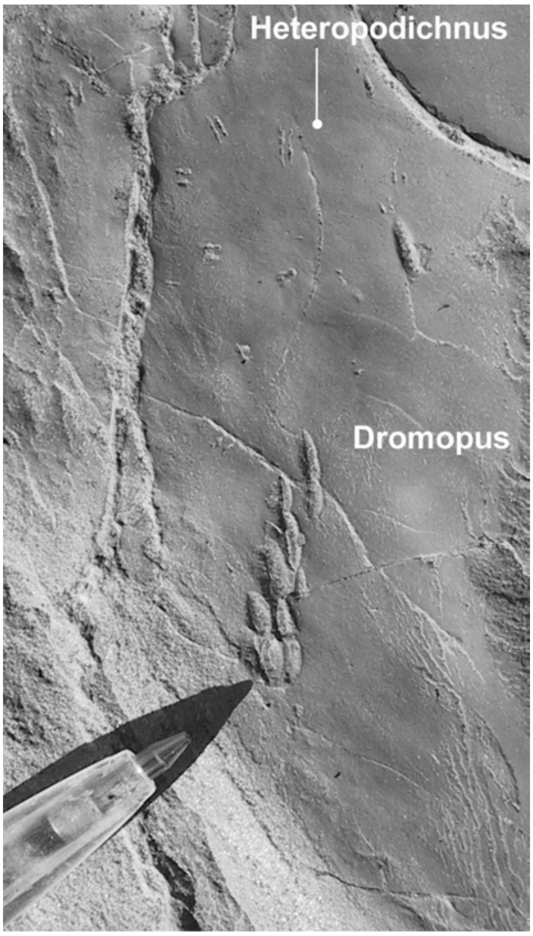

Figure 6. Cfr. Heteropodichnus variabilis *and* Dromopus *sp. Mount Mincucco, Orobic Basin. Photograph by S. Morini.*

Invertebrate traces

Ichnogenus *Dendroidichnites* Demathieu, Gand & Toutin–Morin, 1992

Dendroidichnites elegans Demathieu, Gand and Toutin–Morin, 1992

Material: DrDe 1

A trackway 20 mm large of an arthropod developed in two orthogonal directions. The former part is 72 mm long and better impressed, characterised by a wider central area in which some discontinuous marks are formed by segments longitudinally disposed about 1/3 of the total width and of about 7 mm in length continuously, are defined. The lateral part consists of comma–like traces, some of which are clear, with the apex turned in backwards, although they are often blurred. The second part of the trackway is mainly blurred; only in one side the small autopodia traces of the arthropod are impressed and the walking–trail, in its final portion, seems to become more obscure and faint. This second segment of the trackway compared to the *Dromopus* ones is less clear because of an incomplete support of the arthropod autopodia. This may have been due to a sudden quick movement that disturbed the trackmaker during its locomotion. Although the walking–trail is blurred, it shows some taxonomical features that are reminiscent of the ichnospecies *Dendroidichnites elegans* (Demathieu *et al*., 1992, Fig. 7 n.8) known either in Europe (France and Italy) or in North America (Demathieu *et al*., 1992; Braddy, 1995; Santi & Krieger, 2001; Ronchi & Santi, 2003).

Ichnogenus *Heteropodichnus* Walter, 1983

cfr. *Heteropodichnus variabilis* Walter, 1983

Material: Het1

On the slab an incomplete hyporelief trail of an arthropod is defined by an external and internal part, the first is a series of disposed–ray 'commas', while the second is only a light couple of commas, linked by a lightly impressed circular 'structure'. External commas are longer and asymmetrical than to the internal ones. The heteropody was found in this disposition. The externally streaking pairs present a positive rotation evident to the internal one. Trail development is short; nevertheless it shows features similar to the *Heteropodichnus variabilis* Walter, 1983 ichnospecies (Walter, 1983: tafel II, figs 8–9) gathered in the Upper Palaeozoic in Germany (Hornburger Schichten, Blättertonhorizonte rHr2't). Nevertheless some morphological features are reminiscent of the holoichnotype (*e.g.* the two folds disposition of the external and internal commas, the light presence of the circular structure, and the traces disposition closed to holoichnotype). The general morphology of the walking–trail is characteristic of *H. variabilis*, though the incompleteness of the features prevents a confident classification; hence, we think that this trail should be classified as cf. *Heteropodichnus variabilis*.

5. Behavioural interpretation

Figure 7 suggests the succeeding events sequence pointing the lack of superimposition between walking–trails and footprints. A trackmaker arthropod (*Dendroidichnites elegans*) is moving on a silty–firm bed (point A). On its left side a probable adult araeoscelid reptile, trackmaker of *Dromopus*, is approaching. At the point B the arthropod abruptly deviates towards its right side probably trying an evasive manoeuvre; by this moment the trail impression is less clear, probably because the trackmaker was frightened and tried a disordered fugue. The final trackway–tract stops in the sediments, and we suggest that the araeoscelid preyed upon the arthropod without pursuing it. Figure 8 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.

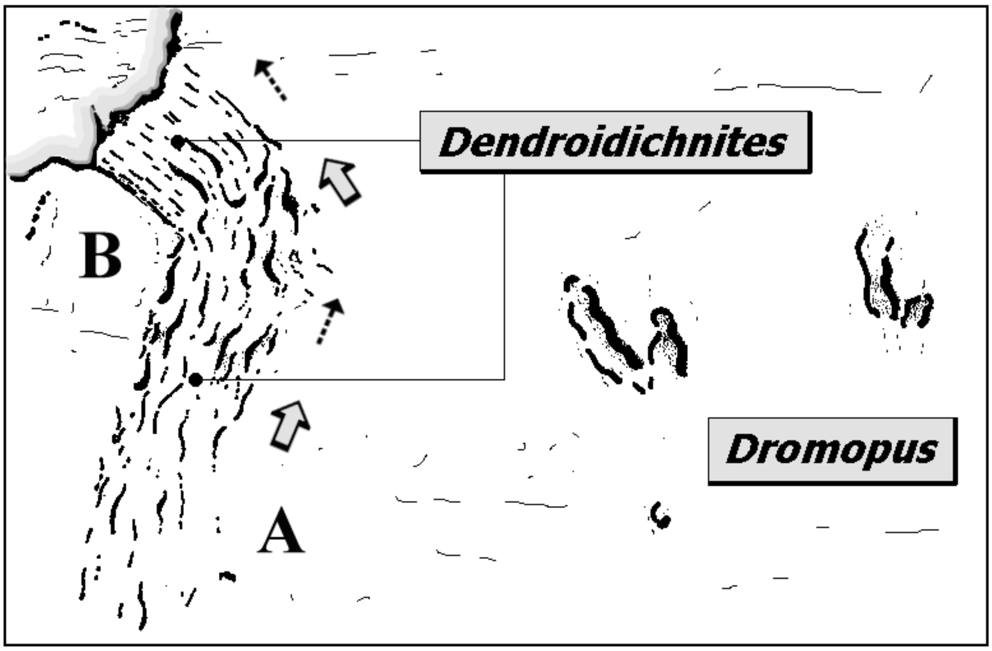

Figure 7. Interaction between the Dendroidichnites elegans *trail and* Dromopus *sp. footprints (spec. DrDe 1). Grey arrows indicate the arthropod trail directions and the black ones the their supposed continuation. Explanations in the text. Drawing by G. Santi.*

6. Discussion and conclusions

The Collio Formation laid down inside the mainly swamps–ponds environments in a high tectonic activity climax. In fact, radiometric data effected on the volcanic beds at the its base and at the its top in Trompia Valley (Schaltegger & Brack, 1999) indicate a deposition of about 700m of sediments in 4–5 My. Usually the *Dromopus* trackmaker is considered as an araeoscelid and a consumer of small invertebrates. Witness provided by the prints left on the slabs here analysed show that the partially predatory role in the Lower Permian of the Southalpine was played by these reptiles. Rare amphibians and mainly reptiles compose the tetrapod ichnocoenosis; it is an association with a paucity in taxa and composed small (*Amphisauropus imminutus*) to medium–large size herbivores (*Amphisauropus latus*). At present, large footprints referring to large vertebrates (*e.g.* comparable to a pareiasaur, *Pachypes,* of the Upper Permian) have not been found. A true carnivore seems lacking. Thus, the trophic pyramid in the Lower Permian of the Southalpine is probably as follows:

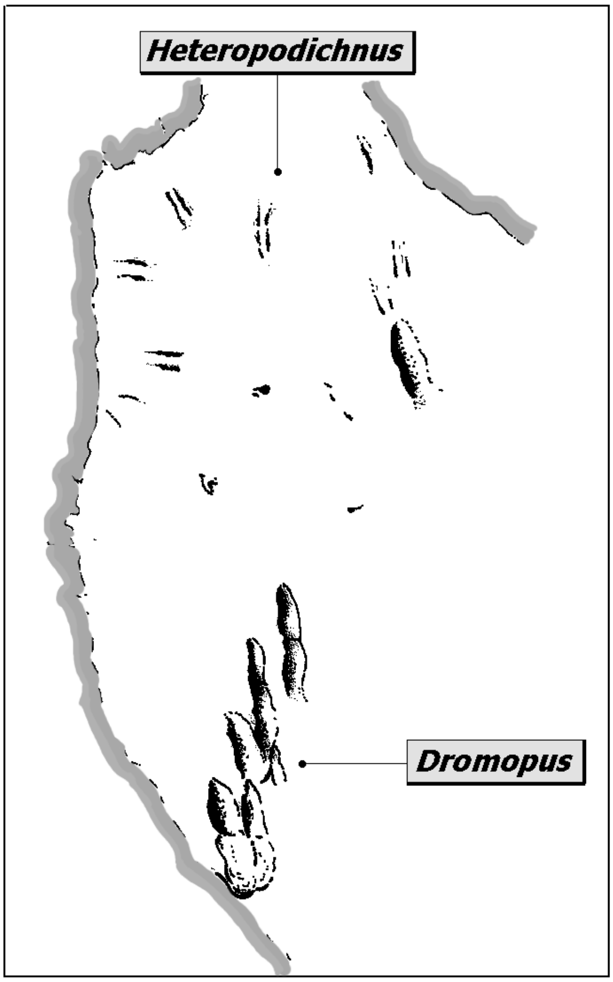

Figure 8. 'Terminated trackway' (spec. Het1) of cfr. Heteropodichnus variabilis *with* Dromopus *sp. Explanations in the text. Drawing by G. Santi.*

Primary consumer: Medium size herbivore. cotylosaurs identified by the *Amphisauropus latus'*s maker, tetrapod of relevant big dimensions (the true 'giant' of the association in comparison to the sizes of other ichnotaxa trackmakers), with short and stumpy legs probably strong and adapted to support a relevant great weight. The frequency with which the *A. latus* footprints are found is high, so that it represented the true dominator of "Collio" lands.

Secondary consumer: Carnivore. In the ichnological association, some typical footprints associated to this consumer seem to be lacking.

Mixed diet: Opportunist consumers. Normally are generalised small reptiles, morphologically and structurally similar to the small size lizards, similar also in the autopodia features and with more or less sharp teeth (*Camunipes*'s trackmakers). Their diet could be similar to that of several actual lizards of small dimensions, swallowing up and biting whatever living, or dead organisms. This category should include the *Dromopus*'s trackmaker (that together the *Amphisauropus*, is a common form) and *Varanopus* (less frequent). The novelty advanced by the araeoscelids (*Araeoscelis*), is the lateral temporal opening that subsequently could have been closed for the skull extension as consequence of a more massive dentition (Carroll, 1988). Such araeoscelids could prey upon (?) protein–bearing organisms with some strong portions of their exoskeleton (arthropods), or small vertebrates (?) (amphibians).

The interpretation of the footprints–trackways interaction of these slabs could confirm that the arthropods were at least one component of the araeoscelid diet. Thus, it would not seem that the Southalpine Lower Permian association is balanced (in the modern sense). It is possible that the araeoscelids and the *Dromopus*'s maker could partially fill the small predator role as well. A possible regional explanation could be linked to the 'deposition time compression' hypothesis (Nicosia *et al.,* 2000) that explains the lack of large diversification with high geological instability that hampered the formation of a stable habitat.

In conclusion, 'terminated trackways' are often rare, thus their study gives new knowledge about the organism's behaviour "…adding colour to an otherwise black and white picture." (Kramer *et al*., 1995: 249).

7. Acknowledgements

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