LOWER PERMIAN PALAEOICHNOLOGY 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).
Permian sediments occur in two tectono-sedi-
mentary 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 sub-
division for research in the South-Alpine area is
"Lower Permian" (from about the Asselian to
Kungurian) and "Upper Permian" (from the
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, together 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.
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 volcaniclastic 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 "berga-mask" 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-Westerholf 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 ichnoocoenoses 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 Gümbl (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.


Up to now, from these former data the composition of the invertebrate ichnocenosis 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.


A great affinity between the ichnocenoses of the two basins is evident, with the only exception being Ichnotherium cottae 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 l. cottae 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 ichnocenosis 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 "orobic" 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 (*Amphisauroopus, 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; Dickens, 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 Orobie 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. Ichnothorium 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 ichnoecosystems 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 ichnoecosystems 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 ichnoecosystems, 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.
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 Ichnotherium 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 cottae.

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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References


(Bassin de Saint-Affrique, Massif Central). Geobios, 29 (4): 370-400.


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Plate 1


Plate 2 (continued on next page)

plate 2