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LOWER PERMIAN ENVIRONMENTAL CHANGES PROVED BY ICHNOFAUNAL EVIDENCE IN THE COLLIO FORMATION TRANSITION OF THE SOUTH ALPINE REGION (NORTH ITALY)

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ABSTRACT

In the Collio Formation (Lower Permian) of the South Alpine region (Northern Italy), the biodiversity — composed of tetrapod footprints, invertebrate traces, and rare plants — is defined by a marked scarcity of taxa that becomes more well defined from the lower to the upper part of the formation. Regionally, the taxonomic compression appears to be the result of the combined effect of a tectonic and climatic change: continually humid environments became mainly dry. An examination of the ichnofossil distribution should support this hypothesis.

Key words: Ichnofauna, Lower Permian, North Italy, South Alpine region, variation

INTRODUCTION

Across the entire South Alpine, (Figs. 1, 2) the Lower Permian is characterized by typical continental formations that crop out with good continuity. The two most important closed troughs, the Orobic and Trompia Basins (Central Southern Alps), present the best exposures. In recent years, new ichnological discoveries have enhanced our knowledge on the biodiversity of the Permian faunas; however, at the same time, the large and widely dispersed data have prevented an accurate evaluation of the faunal picture. In addition, fresh views on ichnotaxonomy (particularly vertebrate) have prompted the revision of certain systematic interpretations by different researchers that heretofore seemed well established on morphological grounds (Haubold, 1996, 2000; Haubold and Stapf, 1998; Haubold and Lucas, 2001). Although Lower Permian vertebrate and invertebrate imprints from the Orobic Basin and, to a lesser extent, from the South Alpine region, though well known, have only recently been described in detail in a stratigraphic framework (Avanzini et al., 2001). Changes in the Permian South Alpine faunal record may reflect an interplay of tectonic and climatic events that affected the area before the break up of Pangea. This is particularly apparent in the Collio Formation (Lower Permian) of the entire South Alpine area in which the passage from the lower unit to the upper one mirrors an ichnofaunal depauperation linked to the environmental changes. The objective of this study is to prove that the changes in the faunal record have resulted from an interplay of tectonic and climatic events; this study uses only vertebrate and invertebrate traces because the acquisition of floral data (macroplants and pollens) is currently in progress.

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GEOLOGICAL AND STRATIGRAPHIC SETTING

This section mainly describes the features of the outcropping Permian lithofacies in the Orobic Basin because the records of the tectonic and climatic effects on the faunal changes are more evident in this area. The Permian stratigraphy of the Trompia Basin has been studied over a long period by Cassinis (1966a, b, 1999 and references therein for a historical review); and the stratigraphy described by him is similar to that of the Orobic Basin (Gianotti et al., 2001, 2002; Sciunnach, 2001).

Regional framework

The Central Alps are characterized by a series of Permian basins with a good continuity of outcrops, represented from West to East (Fig. 3). The Orobic and Trompia Valley basins are the most important (the latter is located to the east of the former in the Brescian Prealps); however, toward the east of the Adige River, the other basins of smaller dimensions are definitely significant for their particular ichnoassociations (Tione Basin, Tregiovo Basin) (Cassinis et al., 1988; Cassinis and Neri, 1990; Cassinis and Doubinger, 1991, 1992; Conti et al., 1997). Geological studies related to the Orobic trough were first carried out by Gümbel (1880) and Melzi (1891); however, the first noteworthy studies were conducted by Porro (1897, 1903, 1931, 1932). Subsequent to the detailed analysis of the crystalline rocks constituting the "Anticlinale Orobica," he analyzed the Permian–Triassic succession that outcrops in the Pizzo dei Tre Signori sector (Valtellina area). Further, De Sitter and De Sitter-Koomans (1949) published a geological map based on the surveys carried out by the students of Leida School (Jong, 1929; Cojin, 1928; Klompé, 1929; Wennekers, 1930; Dorsmann Crommelin, 1932; Dozy, 1935). Besides, important tectonostratigraphic studies were conducted by Casati (1967, 1969); on a 1:25,000 scale by Casati and Gnaccolini (1965, 1967), who also elaborated a geological map; on a 1:100,000 scale by Bonsignore et al. (1971) in the draft of Sheet no. 18, "Sondrio," of the C.G.I.; Casati and Forcella (1988), who introduced a more detailed geological map of the outcropping formations of the Orobic Basin; and Cadel et al. (1996). Further, Jadoul et al. (2000) published a geological map of the Bergamo Province at a 1:50,000 scale correlated by "*Note illustrative*" on the basis of recent detailed surveys, while Sciunnach (2001) analyzed the "Orobic Anticlinale" outcrops and also furnished a geological map at a 1:10,000 scale. In view of the future stratigraphic revision, Forcella et al. (2001) proposed a preliminary investigation of the Lower Permian deposits. Finally, detailed surveys of the Gerola-Inferno Valleys and the enclosed and eastern areas near the Ponteranica Mt. were carried out by Gianotti et al. (2001, 2002).

FIGURE 1. Area where the continental Permian lithologies crop out (Italy).

Stratigraphy

The South Alpine Permian basins are pull-apart basins, which were created to tectonic activity at the end of the Hercynian orogeny (Cassinis and Perotti, 1994; Perotti, 1999). The resulting faults usually exhibit SSW–NNE and W–E directions and could represent the reactivation of older fault lines

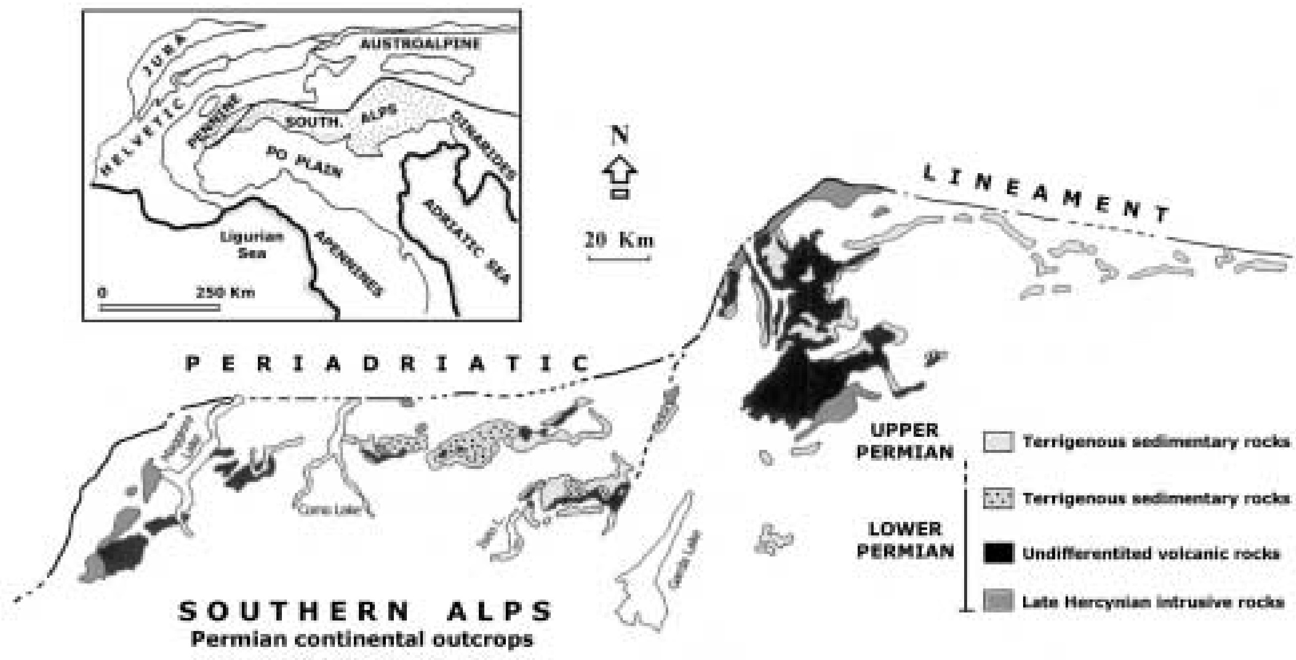

FIGURE 2. Permian continental outcrops in the Southern Alps. (from Cassinis and Neri, 1999, mod.)

(Trompia Valley Line, Giudicarie Line, Sugana Valley Line, etc). Studies of the Permian of the Southern Alps over the last ten years have resulted in the identification of two tectonosedimentary cycles separated by a clear, strong angular unconformity (Italian IGCP Group 203, 1986; Cassinis et al., 1988, 1999, 2000) that thus far was of indeterminate age (Fig. 4).

In the Orobic Basin, the first cycle of deposition (?Upper Carboniferous–Lower Permian) is characterized by volcanic and alluvio-lacustrine deposits (Basal Conglomerate, Collio Formation, Ponteranica Conglomerate), which, in better exposures, reach thickness of 1,500 m. Volcanics have a calcalkaline imprint and are composed of volcanoclastics and lava flows. In this basin, the first cycle either directly overlies the crystalline basement or is locally and unconformably atop a conglomeratic lithosome known as the Basal Conglomerate. The basement consists of micaschists and gneiss — the so-called "parametamorphic series" ("Gneiss di Morbegno" and "Gneiss Chiari") of De Sitter and De Sitter-Koomans's (1949), which crops out north of the Orobic Line. An unconformity marks the contact with the Basal Conglomerate and is observed only in some areas (e.g., in the Seriana Valley). Above this formation is the Collio Formation, whose base was laid down on the basal volcanics, particularly observable in the Aquaduro Valley (Introbio), Cedrino Pass (Sciunnach 2001), and the main "bergamasc" sector of the basin (Jadoul et al., 2000; Forcella et al., 2001).

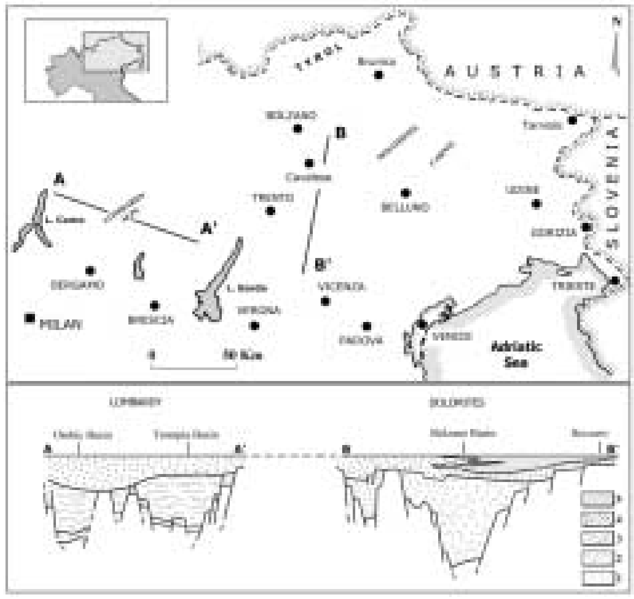

FIGURE 3. Main Permian basins across the Southalpine. **1**, Pre-Permian basement; **2**, volcanic deposits; **3**, clastic units of the first sedimentary cycle; **4**, Verrucano Lombardo-Val Gardena Sandstone; **5**, Bellerophon Formation.

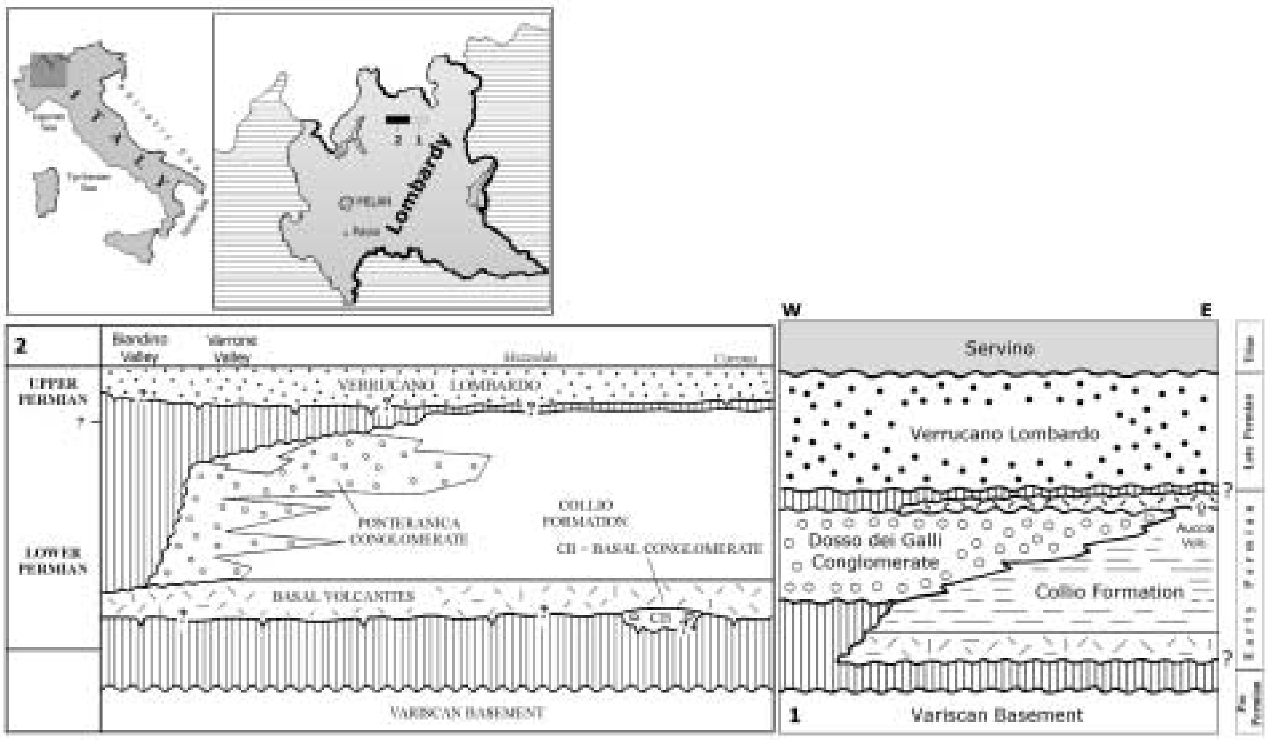

FIGURE 4. **1**, Chronostratigraphic scheme of the Permian in the Trompia Basin; **2**, Chronostratigraphic scheme of the Permian in the Orobic Basin.

Within the type-area in the Trompia Valley (Brescian Prealps), the Collio Formation is composed of a series of volcanic and volcaniclastic products as well as sedimentary deposits; the latter are indicative of fluvio-lacustrine environments (Fig. 5). Cassinis (1966b) described the successive members of this formation in detail. The following is a brief description of the formation, starting from the base.

Member A, around 100 m thick, consists of a rhyolitic ignimbrite directly overlying the crystalline basement; the subsequent Member B — around 80 m thick — is defined by volcaniclastic deposits with intercalations of accretionary lapilli layers and conglomeratic beds. These two members comprise the so-called "Volcanic Member Auct." Member C, around 200 m thick, is mainly composed of variegated pelites that, from the base, are indicated as "green strata," "red strata," and "black strata". This unit is also known as "Scisti di Collio" or "Collioschichten" (sensu Gümbel, 1880). Member D is around 10 m thick and comprises rhyolitic sodic lavas with several xenoliths, while member E, around 80 m thick, comprises volcanogenic sandstones intercalated with pelitic layers. At its base, the subsequent member, Member F (around 80 m thick), is defined by sandstones followed by very fine, silty and grey-green and black pelites rich in ichnofossils. Similar pelitic facies are often intercalated with graded clastic fluvial deposits. Cassinis (1966b) designated this interval (150 m thick) as Member G. This complex of members (from C to G) is known as the "Sedimentary Member Auct." A characteristic bed of a few meters in thickness composed of bioturbated red sandstones (Pietra Simona) is present between the upper limit of the final Member G and the base of the following Dosso dei Galli Conglomerate Formation.

The Collio Formation in the Orobic Basin is not different from that which crops out in the Trompia Valley; however, the red sandstone facies is thicker and more exposed.

The Collio Formation can be informally subdivided into two parts: a lower one consisting of sandstones and grey-green and black pelites and an upper one characterized by sandstones and mostly reddish pelites composed of volcanic materials rich in quartz, plagioclase, and muscovite. It is well stratified and locally exhibits some conglomeratic intercalations. The upper unit is more fossiliferous and is known as "Scisti di Carona" (De Sitter and De Sitter-Koomans, 1949). The "lower and upper Collio" strata clearly record the prelude to the faunal change that becomes more distinct in the Verrucano Lombardo Formation (Western and Central Alps) and the Val Gardena Sandstone (Dolomites) complex.

The Collio Formation interfingers with an alluvial-fan deposit, known as the Ponteranica Conglomerate, that consists of volcanic pebbles with micaschists and quartzite fragments. According to Cassinis et al. (2002), this first cycle is probably Sakmarian to Artinskian in age.

These beds exhibit dips ranging from 15° – 20° to nearly horizontal, forming an angular unconformity with the overlying

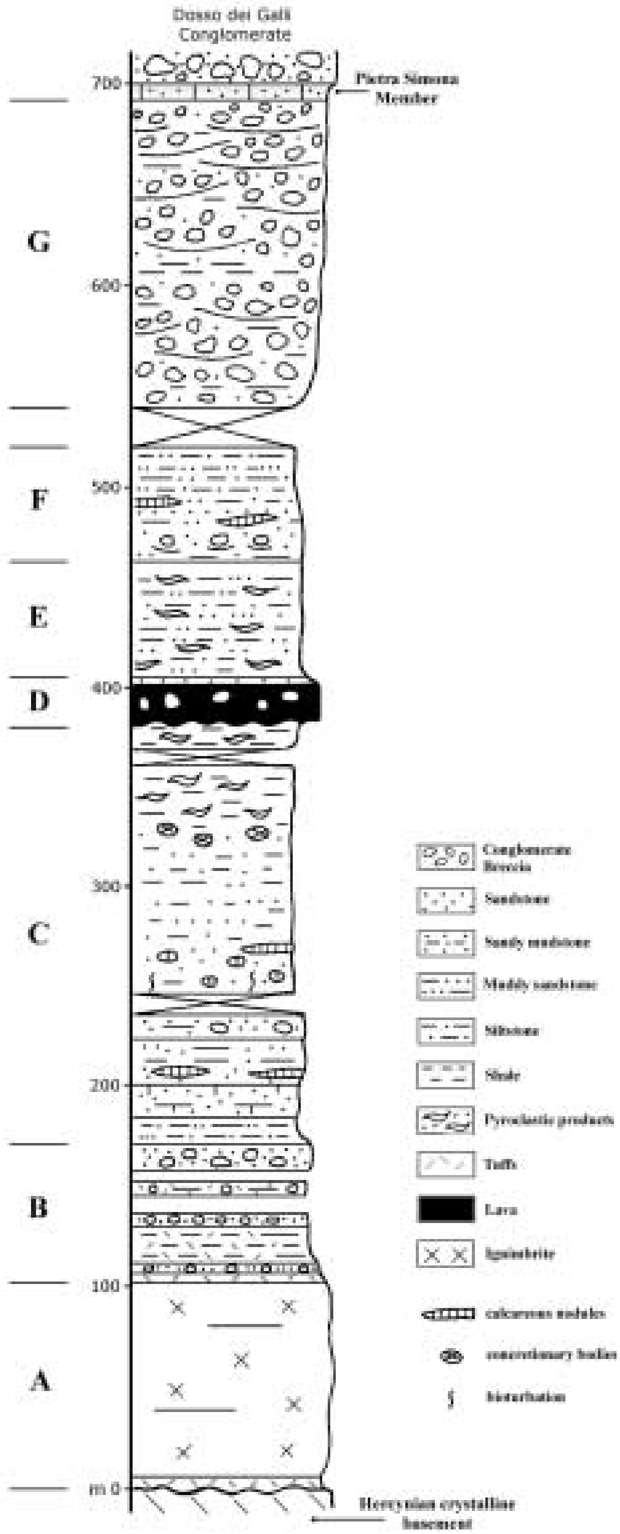

FIGURE 5. Type-section of the Collio Formation in the upper Trompia Valley. (adopted from Cassinis, 1966a, b, mod.)

second cycle, which is represented by the Verrucano Lombardo Formation, a mostly conglomeratic lithosome, reddish in color, with quartzitic, volcanic quartz, "porphyritic" pebbles, and rare fragments of basement rocks. It also comprises red and light green subordinate sandstones. The deposition of the Verrucano Lombardo Formation marks the end of the Permian.

Based on paleontological evidence, the second cycle is considered to be of Upper Permian age (Broglio Loriga et al., 1988; Massari et al., 1988, 1994; Kozur, 1989), although Massari and Neri (1994) extended its age to the Lower Anisian. The duration of the gap between the first and second cycles was subsequently discussed; the hiatus was placed between the Lower and Upper Permian boundaries (Cassinis et al., 2000), while Harland et al. (1990), Odin and Odin (1990), and Menning (1995) opined that it was in the 5–10 myr range. However, according to the more recent data (Cassinis and Neri, 1999), the duration of the gap could be approximated as 14–27 myr or, according to Cassinis et al. (2002), restricted to 24–25 myr. This estimate might be correct if it refers to the faunal change observed as the substitution of ichnoassociations at the Lower–Upper Permian transition in the South Alpine area (Conti et al., 1999; Cassinis et al., 2002).

ICHNOLOGY

Previous work on vertebrate ichnology of the Orobic Basin

This treatment is limited to vertebrate ichnology because studies on invertebrate traces thus far are very rare (Alessandrello et al., 1988; Santi and Krieger, 2001, 2003; Ronchi and Santi, 2003).

It has been known for some time that the continental layers of the Alpine Permian are poor in vertebrate remains (Blieck et al., 1995, 1997). Further, tetrapod footprints are the most important fossils used for palaeogeographic reconstructions and/or as stratigraphic tools (Avanzini et al., 2001). A majority of the studies are concerned with ichnites of the Trompia Basin — the first to be discovered (see Cassinis and Santi, 2001 and references therein for a historical review). The Orobic Basin has only recently received scientific attention, long after tetrapod footprints were first discovered by Dozy (1935) at the Bocchetta di Poddavista or "Podavit" and in the Pizzo di Tenda area (Brembana Valley). He identified two species *Anhomoiichnium orobicum* and *Onychichnium escheri* (Dozy, 1935). A revision by Haubold (1971) recognized the first ichnospecies as valid but regarded the second as *incertae sedis* (?*Actibates*). A later revision by Haubold (1996) that took extramorphological variation and the ghost track phenomenon into account identified the *Anhomoiichnium orobicum* of Dozy (1935) as an underprint of *Batrachichnus salamandroides* (Geinitz, 1861). Research in vertebrate ichnology was given new impetus by the discovery of imprints in the Scioc Valley, NE of Ornica (Bergamo, Lombardy), and in the Varrone Valley near Shelter Falc, NE of the Pizzo Varrone; however, these finds were not systematically studied (Casati and Gnaccolini, 1967). In addition, Casati (1969), Casati and Forcella (1988), and Cita and Forcella (1998) documented vertebrate trace fossils near Pizzo di Trona, while Forcella et al. (2001) did so in the Collio Formation of the Cedegolo Anticline. The first, most important list of the "Orobic" ichnoassociation was compiled by Ceoloni et al. (1987). The ichnocoenosis consists of *Camunipes cassinisi*, Ceoloni et al., 1987; *Amphisauropus latus*, Haubold, 1970; *A*. *imminutus*, Haubold, 1970; ?*Laoporus dolloi*, Schmidtgen, 1928, and Lepidosauria ind. In the last few years, several ichnoassociation studies have been conducted in the Orobic Basin by Conti et al. (1999), Cassinis et al. (2000), Nicosia et al. (2000), Santi and Krieger (1999, 2001), Confortini et al. (2002), Santi (2001, 2003), Arduini et al. (2003), and by Gianotti et al. (2001, 2002).

Paleontological record

Tetrapod footprints: Tetrapod footprints represent the most important fossils from the Lower Permian of the Orobic and Trompia basins as well as the entire South Alpine region. The Collio Formation can be subdivided in two informal units of conformable lithology (mainly sandstones and pelites) that differ in color: the lower unit is grey-green to black, while the upper one is red-wine in color. In the Collio Formation beds of the Orobic and the Trompia Basins, the ichnocoenosis is characterized by very similar species, with the exception of *Dromopus didactylus* (Moodie, 1930) and *Ichniotherium* sp., which are clearly present only in the brescian "Collio." Two explanations can be proposed for the presence of these ichnotaxa: *D*. *didactylus* has thus far been considered to be a monotypic taxon of the uppermost strata of the brescian "Collio" and the Tregiovo Basin, while, in contrast, *Ichniotherium* is a local form of the Trompia Basin. Table 1 shows a comparison of the ichnoassociations of the Orobic and Trompia Basins (Santi and Krieger, 2001).

The transition to the Upper Permian (Verrucano Lombardo Formation in the Western and Central Alps and Val Gardena Sandstone Formation in the Dolomites) is marked by a sharp faunal change, with the ichnotaxa exhibiting Triassic affinity (Conti et al., 1999). However, an ichnocoenosis change from the lower to the upper units of the Collio Formation is also present. The lower unit has a fair diversity of ichnospecies, but the upper unit is comparatively poor, lacking in certain forms like *Batrachichnus* and *Camunipes*. The absence of *Batrachichnus*, whose trackmaker is interpreted as a non-amniote tetrapod, may reflect a scarcity of such tetrapods in the Permian, which is also seen in the osteological record.

Lockley et al. (1994) defined the ichnofacies concept as the repeated occurrence of key vertebrate tracks in particular sedimentary facies. The following ichnofacies are recognized from the Early Permian:

TABLE 1. Comparison of the ichnocoenosis of the tetrapod footprints from the Orobic and Trompia basins (Santi and Krieger, 2001).

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

a) the *Chelichnus* ichnofacies and
b) the subdivided red-bed ichnofacies (Lockley et al., 1994; Lockley and Meyer, 2000).

These ichnofacies were defined to describe the tetrapod footprint records of the Permian of North America and are now utilized as a tool to recognize paleoenvironment-track relationships worldwide. The *Chelichnus* ichnofacies is an association of a restricted desert fauna within an eolian lithofacies (McKeever and Haubold, 1996), while the red-bed ichnofacies is characteristic of a variety of fluvial, deltaic, lacustrine, and marginal marine environments (Haubold and Lucas, 1999). The latter ichnofacies consists of the following ichnogenera: *Dromopus*, *Gilmoreichnus*, *Batrachichnus*, *Hyloidichnus*, *Dimetropus*, *Amphisauropus*, *Ichniotherium*, *Limnopus*, and possibly two or three additional ones (Haubold et al., 1995; Swanson and Carlson, 2002).

The "Collio" ichnocoenosis readily matches the red-bed ichnofacies of the Rabejac sub-age (sensu Conti et al., 1997); *Camunipes* can be considered as a local form of the Lower Permian of the South Alpine region.

The time interval in which this tetrapod fauna was widespread is limited to between 286/283 myr at the base and 278/273 myr at the top (Avanzini et al., 2001). Following Menning's (2001) Permian timescale this ichnoassociation can be extended up to the Artinskian and Kungurian. However, other scales (e.g., Harland et al., 1990; Odin, 1994; Gradstein and Ogg, 1996) relate these geochronological values to the Sakmarian and latest Asselian. The South Alpine ichnoassociation is very similar to that of the Wolfcampian of North America, indicating a close connection between Central Western Europe and this continent. According to the global correlation of the marine Permian System, the above tetrapod footprint association can be considered to be coeval with the Lower Permian Cisuralian (Cassinis et al., 2002).

Invertebrate traces: Invertebrate taxa of both the Orobic and Trompia basins are rarer than those of vertebrates; they are mainly freshwater jellyfish, bivalves, arthropods, and small crustaceans.

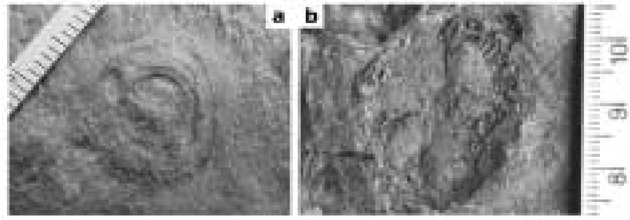

FIGURE 6. **a**, *Medusina limnica* Müller, 1978 — Malga Pofferatte "il Pulpito" — Trompia Basin; **b**, *Medusina atava* (Pohlig, 1892) Walcott, 1898. Gerola-Inferno valleys — Orobic Basin.

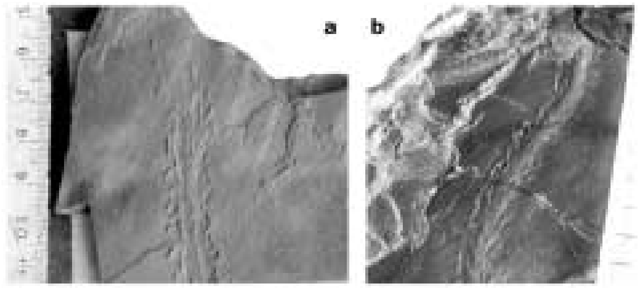

FIGURE 7. *Dendroidichnites elegans* Demathieu, Gand, and Toutin-Morin, 1992 — Orobic Basin. **a**, upper portion of the Collio Formation crops out in the Pescegallo Valley; **b**, lower portion of the Collio Formation crops out in the Brembana Valley.

In the Collio Formation, jellyfish prints corresponding to two ichnospecies have been found in the different units. From the lower unit of the Collio Formation in the Trompia Basin, only *Medusina limnica* Müller, 1978 prints have been collected (Conti et al., 1991), while in the upper part that crops out in the Orobic Basin, only the rare *Medusina atava* (Pohlig, 1892) Walcott, 1898 imprints have been found (Fig. 6). Thus far, they have never been discovered in assemblages from the "lower Collio" or the upper one. In the entire Collio Formation (both lower and upper units), the arthropod ichnotaxon (Ronchi and Santi, 2003) *Dendroidichnites elegans* Demathieu, Gand, and Toutin-Morin, 1992 has been identified (Santi and Krieger 2001, 2003) (Fig. 7). As with the jellyfish, bivalves (Anthracosiidae) are exclusively found in the layers of the lower part of the brescian "Collio," particularly in the Trompia Valley, which is also the case with small crustaceans belonging to the genus *Estheria* (Conti et al., 1991).

Problems associated with *Camunipes — Varanopus* ichnogenera: The absence of *Camunipes* in the upper portion of the Collio Formation ("red Collio") may have a different implication from the absence of *Batrachichnus* (see above). In fact *Camunipes* shows strong similarities to the *Varanopus* ichnogenus, which

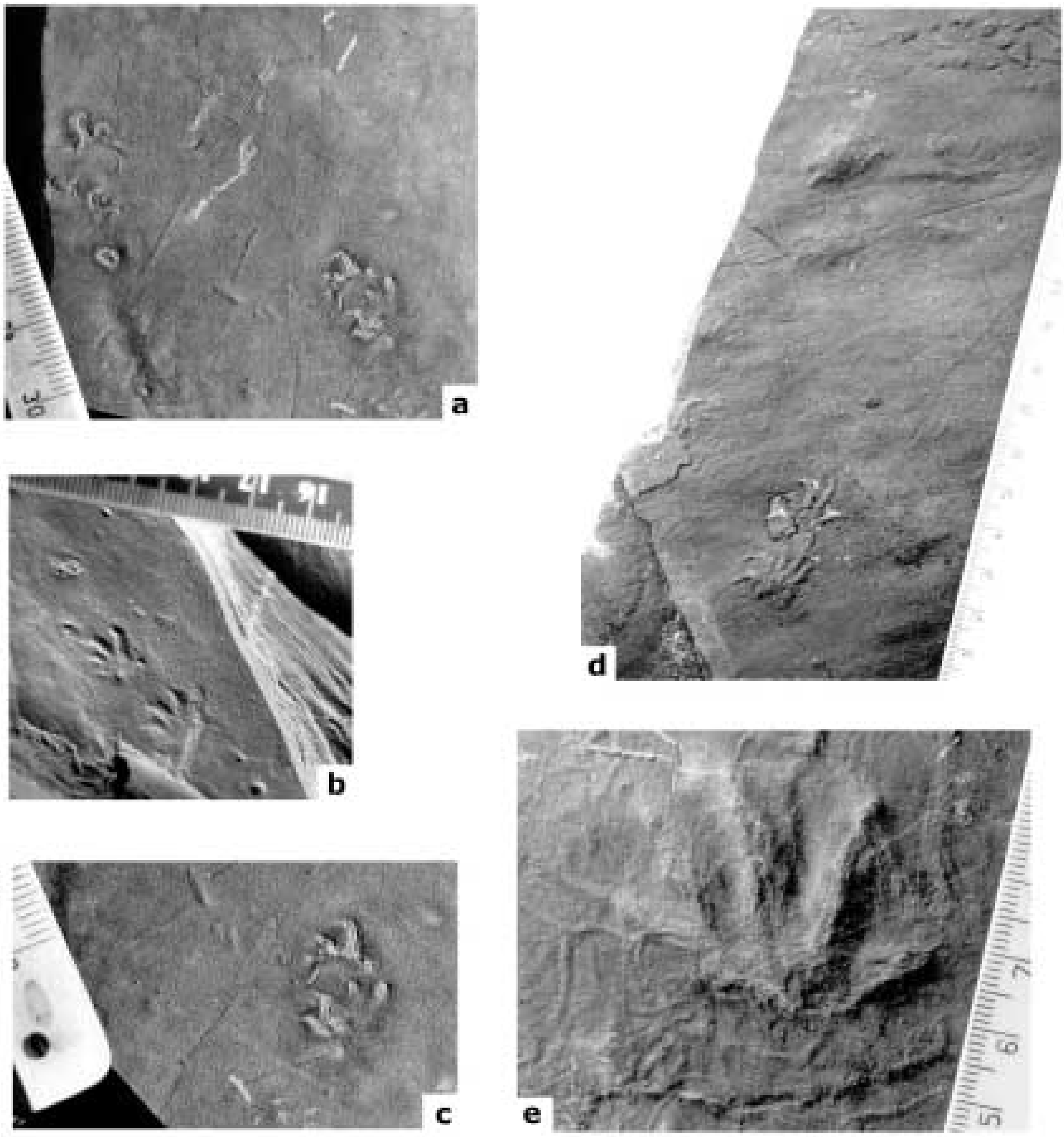

FIGURE 8. **a**, *Camunipes cassinisi* Ceoloni, Conti, Mariotti, Mietto, and Nicosia, 1987. Scioc Valley — Orobic Basin; **b**, *Camunipes cassinisi* Ceoloni, Conti, Mariotti, Mietto, and Nicosia, 1987. Brembana Valley — Orobic Basin; **c**, *Camunipes cassinisi* Ceoloni, Conti, Mariotti, Mietto, and Nicosia, 1987. Scioc Valley — Orobic Basin; **d**, *Varanopus curvidactylus* (Moodie, 1929). Gerola-Inferno valleys — Orobic Basin; **e**, *Varanopus curvidactylus* (Moodie, 1929). Gerola-Inferno valleys — Orobic Basin.

is well represented in the "upper Collio."

Footprints whose trackmaker is identified as *Camunipes* exhibit the following distinctive morphological features: "*ectaxonic and semiplantigrad footprint. Slightly falcate digits increase in length from I to IV*; *V digit directed backward…V digit is as long as I and slightly turned backwards*. *All the digits have claws*" (Ceoloni et al., 1987: 220–221) (Fig. 8a, b, c).

According to Moodie (1929), the digit V disposition should distinguish *Camunipes* from *Varanopus curvidactylus*, where, in contrast, digit V is very close to IV and not turned away from it (Fig. 8d, e) ; this is indicative of the mobility of digit V in early amniotes, which is related to the different pedal skeleton construction. (Based on the assumption that the trackmakers were pelycosaurs, which are no longer considered as reptiles in cladistic classification).

It is noteworthy that the highest stratigraphic occurrence of *Camunipes* is in the Orobic Basin "lower Collio", which is less abundant in the Trompia Basin (lower Collio). *Camunipes* is absent in the "upper Collio" of both basins. These observations prompt the following questions:

a) Could *Camunipes* be considered as an endemic form?

b) Does its morphological similarity to *Varanopus* permit it to be considered as the possible ancestor of the latter, or should they rather be considered to have had a common ancestor?

c) Could the rapid sedimentation of the "Collio" (Schaltegger and Brack, 1999; Nicosia et al., 2000) have influenced outward migration of the trackmaker?

In the Scioc Valley (Lombardy Region, Orobic Basin) several *C. cassinisi* trackways have recently been discovered. *Camunipes* is abundantly represented in the "lower Collio" and consistently shows morphological differences from *Varanopus*. In my opinion, such morphologic differences should be accorded great importance in distinguishing between the ichnospecies. The abundance of footprints and trackways in the "Collio" outcrops of the Brembana Valley provides evidence to support the hypothesis that *Camunipes* and *Varanopus* are different genera. Footprints in these strata consistently show an outward- and backward-turned digit V, which is never close and parallel to IV. Ceoloni et al. (1987) established the ichnogenus *Camunipes* based on the characteristic position of the V digit and considered it to be different from *Erpetopus* and *Varanopus.* I do not believe that all the *Camunipes* prints should be regarded as extramorphological prints of *Erpetopus* and *Varanopus*; further, I maintain that different genera should be considered.

In contrast, Haubold (2000) and Haubold and Lucas (2001) do not recognize the three ichnogenera as distinct, but rather consider them as "subjective synonyms" of *Erpetopus* on the basis of ichnomorphologies from the Choza Formation and Castle Peak (Texas). Furthermore, Haubold (2000) affirms that "*Much rarer is the record from the high Lower to the Upper Permian*, *and the status of the known ichnotaxa is less well established*;" therefore, the status of *Camunipes* in the "upper Collio" is not clear. With regard to the contrary position advocated here, two precedents may be cited: ichnotaxonomic distinctions between *Amphisauropus latus*–*Amphisauropus imminutus* and *Dromopus lacertoides*–*Dromopus didactylus*, considering the footprint morphology, should be regarded as the fundamental elements of the definition of ichnospecies. The former two species were established by Haubold (1970) by considering the different morphologies of footprints observed in Nierstein and Saar Nahe-Gebeit (Germany) and Lodève area (France) (see also Haubold, 1996). In the latter pair, *D. didactylus* differs from *D. lacertoides* in exhibiting a farther backward position of digit V with a large divarication from IV. If in these two cases, the species that constitute the pair are regarded as distinct, *Camunipes*, which differs from *Varanopus* both in terms of dimensions as well as morphology, should be retained as a different ichnogenus from the latter and *A. latus* and *A. imminutus* should be treated in a similar manner as *D. lacertoides* and *D. didactylus* — a hypothesis supported by Gand (1987), Haubold (2000), and Haubold and Lucas (2001). The question concerning the synonymy of *Camunipes* and *Erpetopus* ichnogenera by using different tools for making comparisons between the holotypes, skeleton structure, and extramorphological prints, is also debated in detail by Santi (in press). This study suggests that the ichnogenus should be composed of two ichnospecies, namely, "*Erpetopus*" *willistoni* and "*Erpetopus*" *cassinisi*. This interpretation appears to provide a better explanation for the taxonomical features of the two ichnogenera.

In view of the present taxonomy, I consider it best to regard *Camunipes* as a different ichnogenus from *Varanopus*.

The ichnogenus *Camunipes*, or in other words, footprints morphologically similar to those of *Camunipes*, are absent in the "upper Collio." Likewise, *Batrachichnus* is lacking, and the ichnospecies present in the "upper Collio" are limited to *A. latus*, *A. imminutus*, *V. curvidactylus*, and *D. lacertoides*.

DISCUSSION AND CONCLUSIONS

The stratigraphic distribution of fossils in the Collio Formation of the South Alpine area together with the color variations of otherwise similar sediments between the lower and the upper units support the hypothesis of a climatic shift during the deposition of "Collio" sediments in this area. The "red Collio," an expression of climatic change, is particularly observable in the Orobic Basin, much less so in the Trompia Basin where it is possibly represented by the thinner sediments of the "Pietra Simona Member." Fan conglomerates of the Dosso dei Galli Conglomerate may have "covered" the arenaceous-pelitic succession that, in contrast, continued to be deposited in the Orobic Basin. Based on this view, it can be stated that the "red Collio" of the Orobic Basin is the equivalent of the Dosso dei Galli Conglomerate in the Trompia Valley. Preliminary indications of the approaching climatic change are observed in the sediments of Member C of the brescian Collio Formation, which shows red beds in addition to green to black layers (Conti et al., 1991). *M. limnica* has been discovered in these beds; it has a very large stratigraphic range that covers practically the entire sedimentary Collio Formation — around 700m in thickness.

The indication of a climatic change is based on the following points:

a) the missing assemblages of *M. limnica* and *M. atava*,

b) the absence of Anthracosiidae and *Estheria* in the upper unit of the Collio Formation, and

c) the scarcity of vertebrate ichnoassociations in the upper unit of the Collio Formation.

Conti et al. (1991) and Gand et al. (1996) considered *M. limnica* to be a fossil that gives a clear picture of the environmental and climatic conditions, being indicative of continually humid environments (ponds and swamps). Nevertheless, the presence of *M. limnica* in the Collio

Formation of the Trompia Valley requires an explanation. This hydromedusa has also been found in the red strata of the brescian "lower Collio." Consequently, these beds probably represent fluctuations between humid conditions of relatively long durations and short-term dry spells. The presence of this jellyfish may not indicate a consistently humid climate. After the deposition of the "red Collio," which occurred in progressively drier climatic conditions, *M. limnica* is no longer found. It was replaced instead by *M. atava*, which was resistant to the dry climate. This variation in the Orobic Basin is evident by the transition from pond and alluvial – lacustrine environments to muddy plains crossed by ephemeral streams (Ronchi and Santi, 2003).

From a general environmental-climatic viewpoint, even if local discrepancies are considered, the following can be supposed:

(a) In the sedimentary member of the middle-upper stratigraphic section of the "Orobic" Collio Formation, a facies analysis indicates water-rich lacustrine to alluvial environments. The rainfall appears to become increasingly seasonal and, within this semi-arid or tropical context, periods of aridization are evidenced by the deposition of evaporites in saline lakes as well as repeated dessication structures and caliche soil horizons,

(b) Toward the topmost part of the basin fill, the gradual but deep reddening of the Collio Formation immediately below the unconformity with the Verrucano Lombardo Upper Permian red beds as well as the decreasing fossil content indicate the shift toward a long period of repeated subaerial exposure and oxidization under considerably more arid conditions, which can be regionally correlated to a similar occurrence in wide areas during the mid Early Permian interval.

The habitat conditions of the "upper Collio" also prevented the migration of the Anthracosiidae and *Estheria* that, contrary to *M. limnica*, are found only in member F of the brescian Collio Formation (Conti et al., 1991). On the basis of the rare finds, it can be additionally suggested that if *M. limnica* is indeed abundant in the "lower Collio" biodiversity, the fresh water bivalves should be significantly lesser in number than the small crustaceans.

The occurrence of *Dendroidichnites elegans*, an arthropod trackway, has a unique and different implication. It is found in the lower and upper parts of the Collio Formation of the South Alpine region. This indicates that the trackmaker may have been resistant to the climatic changes.

Finally, the tetrapod footprint contribution presents yet another interpretation. The ichnotaxonomic association is considerably low in diversity in the "lower Collio;" however, it reduces even further in the upper part. A similar decline in ichnodiversity is observable in the Lower Permian of Central Europe and North America. The reasons for this decline in ichnodiversity vary globally (Nicosia et al., 2000); however, for the South Alpine it could possibly be a consequence of combined tectonic and climatic influence.

In a large part of Western Europe, the Early Permian was characterized by a climatic shift from warm, alternating wet and dry seasons to semi-arid, which evolved into the very warm and hot conditions of the Late Permian (Ori, 1988; Dickins, 1993; Parrish, 1993; Golonka and Ford, 2000). Thus, during the mid-late Early Permian (?Artinskian, ?Kungurian), a regional and geologically rapid decrease in the amount of precipitation and the onset of oxidizing climatic conditions are suggested by changes in both lithofacies and biofacies.

In the more recent past, radiometric data obtained for the volcanic layers at the base and top of the Collio Formation in the Trompia Valley have indicated a sedimentation rate of approximately 1000 m over 4 – 5 myr for this formation (Schaltegger and Brack, 1999). On this basis, the "deposition time compression" hypothesis was invoked by Nicosia et al. (2000) to explain the high rate of sedimentation that prevented the natural development of the habitat, which is essential for the survival of the vertebrate trackmakers. This explanation was extended to the entire Collio Formation in order to account for both its development of habitat over time and faunal composition. The disappearance and appearance of new species in moving from the lower to upper units of the Collio Formation, however, seems related to other factors. Though commonly regarded as a background factor, strong tectonic activity is more likely the main factor responsible for the taxonomic compression. The tectonic effect in combination with the climatic variation that was associated with the "lower-upper Collio" transition resulted in an increased potential for depletion of the faunal population. Thus, tectonic activity prevented the regular and lasting development of the habitat, and the climatic variation prevented the adjustment of some species to the new and variable conditions. The consequence of this combination of events was an additional taxonomic compression in the biodiversity components of the invertebrates and vertebrates of the Lower Permian. These events persisted through the creation of the angular unconformity with the Verrucano Lombardo (Western and Central Alps) and Val Gardena Sandstone (Dolomites) (Upper Permian); they involved a sharper change in the fauna, which was manifested in a strong Triassic affinity (Conti et al., 1999; Cassinis et al. 2002). It is correct to suppose that the temporal gap in the Upper Permian transition, whose age may vary from 7 – 14 myr (Cassinis et al., 2000) or 24 – 25 myr (Cassinis et al., 2002), might record the final moments of an association that was destined for extinction and successively replaced by another with distinctively modern features.

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