



The Cisuralian tetrapod ichnoassociation from Italy: from historical findings to a standard reference status

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ABSTRACT - The Cisuralian tetrapod ichnoassociation from Italy is long known, in fact it is the first described from the Southern Alps. After some pioneering works in the 19th Century, several new research and discoveries were undertaken starting from the second half of the 20th Century until now. This ichnoassociation is characterised by abundant and diverse reptile tracks (*Dromopus*, *Erpetopus*, *Hyloidichnus*, *Merifontichnus* and *Varanopus*), uncommon anamniote tracks (*Amphisauropus*, *Batrachichnus* and *Limnopus*) and very rare synapsid tracks (cf. *Dimetropus*). The bulk of discoveries are located in the central Southern Alps, in the Orobic and Collio basins, and in minor part in the Athesian District. These basins include a well-preserved and diverse ichnoassociation that is central to tetrapod footprint biostratigraphy and in the definition of the late Cisuralian reptile radiation inferred from the footprint record, well-calibrated by several recent radiometric dates that constrain the ages of the footprint-bearing units. The new site from NW Sardinia includes few late Kungurian?-Roadian tetrapod footprints, that however deserve great attention because of the possible biostratigraphic implications and the unusual co-occurrence with tetrapod remains.

Keywords: Tetrapod ichnoassociation; Cisuralian; Southalpine; Sardinia.

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1. INTRODUCTION

The tetrapod footprints from the Cisuralian were the first ever described and illustrated from Italy (Curioni, 1870; Leonardi, 2008; Marchetti et al., 2018). After the first pioneering studies of the 19th Century on a specimen from the Collio Basin (Geinitz, 1869; Curioni, 1870; Gümbel, 1880), there was a long time interval with few new data on this topic (including the first record from the Orobic Basin: Dozy, 1935) until the end of the sixties, when new material from the Collio and Orobic basins was discovered and described (Casati and Gnaccolini, 1967; Berruti, 1970) and later revised (Haubold and Katzung, 1975; Ceoloni et al., 1987). New discoveries from the Collio Basin and the Athesian District were preliminarily published by Conti et al. (1991, 1997), and used in tetrapod footprint biostratigraphy to establish the Cisuralian Collio Ichnofaunal Unit (Conti et al., 1997; Avanzini et al., 2001; Marchetti et al., 2019a). New discoveries from the Orobic Basin were described in several works around the 20th-21st Centuries's transition (Cassinis et al., 1998; Santi and Krieger, 1999, 2001; Nicosia et al., 2000; Gianotti et al., 2001, 2002; Arduini

et al., 2003; Ronchi and Santi, 2003; Santi, 2003, 2005, 2007a, 2007b, 2008a, 2008b; Santi et al., 2008). Some new occurrences from the Athesian District were described as well (Avanzini et al., 2008). Nevertheless, although abundant by number of specimens, this ichnoassociation was still considered of low diversity (Avanzini et al., 2011a) until a new impulse for Cisuralian ichnology came in the last decade, represented by several new discoveries and a comprehensive revision of the collected material (e.g. Bernardi and Avanzini, 2011; Marchetti et al., 2013a, 2013b, 2014, 2015a, 2015b, 2015c, 2017a, 2017b, 2018; Marchetti, 2014, 2016; Petti et al., 2014; Citton et al., 2019). These studies highlighted a noteworthy abundance, diversity, and morphological preservation (*sensu* Marchetti et al., 2019b) of the tetrapod footprint material. This and the available radiometric ages enhanced the importance of the Cisuralian tetrapod ichnoassociation from Italy, which became key for the institution of the *Erpetopus* tetrapod footprint biochron (Voigt and Lucas, 2018; Schneider et al., 2020) and for the understanding of the Cisuralian reptile radiation observed in the tetrapod track record (Marchetti et al., 2019c). The goal of this contribution is a detailed review of the available literature

with particular focus on the most recent studies on the considered ichnoassociation.

2. ICHNOTAXA AND POSSIBLE TRACKMAKERS

Here we provide a list of the ichnogenera currently recognized in the Italian Cisuralian ichnoassociation and their possible trackmakers.

The ichnogenera *Batrachichnus* and *Limnopus* are considered small (*pes* length <2 cm) and relatively large (*pes* length 2-20 cm) tracks of temnospondyl anamniotes, respectively (e.g. Haubold, 1996; Voigt, 2005).

The ichnogenus *Amphisauropus* is considered a small to relatively large (*pes* length 2-7 cm) track of seymouriamorph anamniotes (e.g. Marchetti et al., 2017a).

The ichnogenus *Dimetropus* is considered a relatively large (*pes* length 5-20 cm) track of pelycosaur-grade synapsids, with the exception of varanopids (e.g. Voigt, 2005). Note that the varanopids may not be synapsids according to some recent interpretations (Ford and Benson, 2020).

The ichnogenera *Erpetopus* (*pes* length <4 cm) and *Varanopus* (*pes* length 2-7 cm) are considered tracks of parareptiles (e.g. Schneider et al., 2020). They have been considered also captorhinomorph tracks (e.g. Haubold and Lucas, 2001).

The ichnogenera *Hyloidichnus* (*pes* length 2-10 cm) and *Merifontichnus* (*pes* length 5-10 cm) are considered tracks of captorhinid eureptiles (e.g. Marchetti, 2016; Schneider et al., 2020). *Merifontichnus* has been considered also a therapsid track (e.g. Gand et al., 2000).

The ichnogenus *Dromopus* is considered a relatively small to large (0.5-7 cm) track of diapsid eureptiles or bolosaurid parareptiles (e.g. Voigt, 2005).

3. GEOLOGICAL SETTING AND STRATIGRAPHY OF THE OROBIC BASIN

The Orobic Basin, together with the Collio Basin (known also as Val Trompia or Triumplino Basin), is the widest in the Southern Alps. The Orobic Basin (Fig. 1) extends for about 45 km in length (E-W) and less than 10 km in width (N-S) and is represented from W to E, by three large anticlinoria, named: the Orobic, the Trabuchello-Cabianca and the Cedegolo Anticline (e.g. Casati and Gnaccolini, 1967; Cadel et al., 1996; Sciunnach, 2001a; Berra et al., 2016). This “multi-stage” basin shows an asymmetrical semi-graben structure with a thickness strongly increasing from the south to the north (Boriani et al., 2012). Some years ago, a revision of the lithostratigraphic nomenclature of the Orobic Basin (Cassinis, 2007) was proposed in the geological mapping project 1:50,000 of Italy (CARG): since then, the previously known “Collio vulcanico” and “Collio sedimentario” (Casati and Gnaccolini, 1967) are now informally named “vulcanite del Cabianca” and “Pizzo del Diavolo formation”, respectively. Also, the conglomeratic units interbedded with the “Collio sedimentario” (e.g. “conglomerato di Monte Aga”, “conglomerato della Val Sanguigno”, “conglomerato della Val Vedello”, Cadel et al., 1996; “Conglomerato del Ponteranica”, Casati and Gnaccolini, 1965) have been included in the “Pizzo del Diavolo formation”.

As a whole, the units from the “Basal Conglomerate” to the overlying “Monte Cabianca” and “Pizzo del Diavolo formations” now constitute the “Laghi Gemelli” group *sensu* Boriani et al. (2012). This succession is unconformably overlain by the “Verrucano Lombardo formation” red beds of Lopingian age. The main scope of this nomenclature revision was to differentiate the

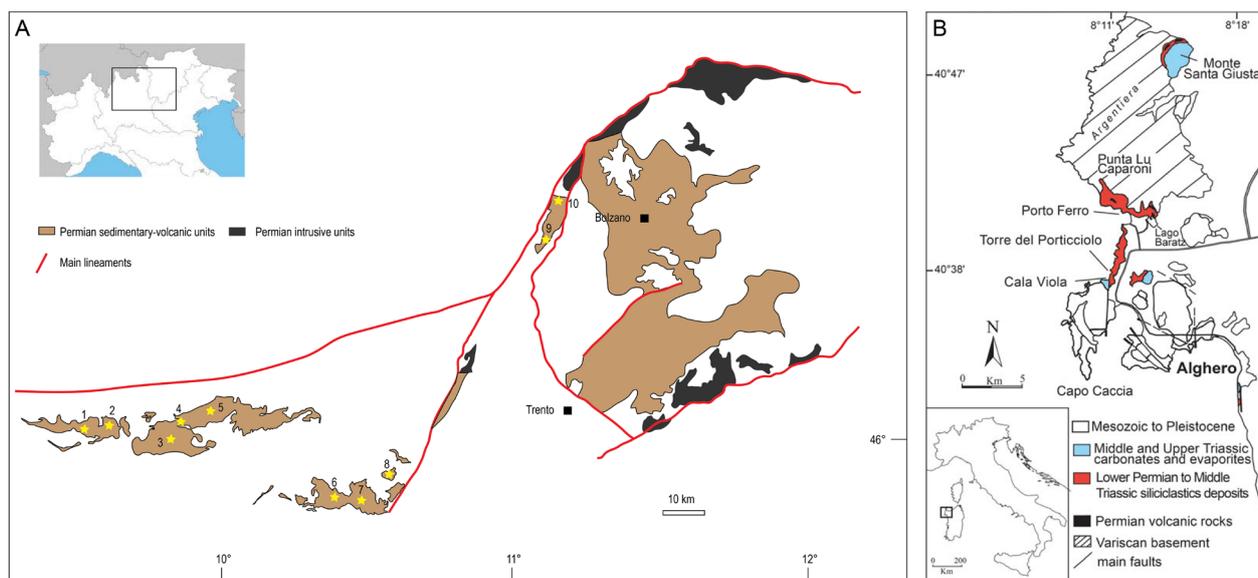


Fig. 1 - Geological setting and fossiliferous localities. A) Southern Alps. Stars represent the main fossiliferous localities: 1- Val Gerola, 2- Val di Scioc, 3- Pizzo Farno, 4- Upper Val Brembana, 5- Val Seriana, 6- Upper Val Trompia, 7- Val Caffaro, 8- Val Aperta, 9- Tregiovo, 10- Monte Luco. 1-5 Orobic Basin, 6-8 Collio Basin, 9-10 Athesian District. B) NW Sardinia (modified after Citton et al., 2019). The fossiliferous locality is Cala Viola.

sedimentary and volcanic units of the Orobic and Collio basins. The use of the formalised stratigraphic name Collio Formation in the Brescian Prealps (Cassinis, 1966a) for both basins was considered erroneous, since the Orobic and Collio basins developed in different palaeotectonic and chronostratigraphic settings (see Marchetti et al., 2015a; Marchetti, 2016), even if facies and palaeoenvironments are partly similar, but not strictly coeval.

Synthetically, the “Laghi Gemelli” group is constituted, from the base to the top (Fig. 2), by the “Basal Conglomerate”, the “vulcanite del Cabianca” and the “Pizzo del Diavolo formation”. The “Basal Conglomerate”, interpreted as having been deposited in a proximal alluvial fan-braided setting, overlies discontinuously (0-100 m in thickness) the metamorphic basement and is constituted by poorly sorted conglomerates, breccias and coarse-grained sandstones, reddish or grey-green in colour. The “vulcanite del Cabianca” (500-1000 m in thickness) is represented by volcanoclastic rocks and less frequent sedimentary units. Within the formation, different effusive lava flows, pyroclastic flows and fall deposits can be recognised, together with stratified coarse-to-fine sedimentary clastics interpreted as having been deposited in braided river settings (Boriani et al., 2012). The “Pizzo del Diavolo formation” (more than 600 m in thickness) is made up of laminated pelites and

siltites, arenites, conglomerates and less frequent and thinner freshwater carbonatic and reworked pyroclastic intervals. The finer levels are alternating vertically and laterally with the coarser ones in a complex geometry, the result of an alluvial to lacustrine environment with alluvial fans on its sides (e.g. Cadel et al., 1996; Berra and Felletti, 2011; Berra et al., 2016). A possible type-section was described by Ronchi et al. (2005) in the “Val Camisana” and “Bocchetta Podavit” localities.

Five lithofacies have been distinguished in the formation (Boriani et al., 2012): lithofacies with prevailing pelites, lithofacies with prevailing arenites, conglomeratic lithofacies, carbonatic-evaporitic lithofacies, and interbedded volcanics. According to Berra et al. (2016), who proposed a partially different lithofacies subdivision, sedimentological features reflect a proximal fan system where mass-flow phenomena dominated, a distal fan-terminal setting with prevailing sandy sheet-flow processes and a silty floodplain environment, where sheet-flood events dominate. Laterally continuous siltstones and dark shales with carbonate nodules and layers of microbial and oncoidal carbonates occur in the most depocentral part of the basin indicate alternating conditions of shallow lake and desiccated floodplain (Berra et al., 2016, 2019).

The fossil content of the Orobic Basin is almost

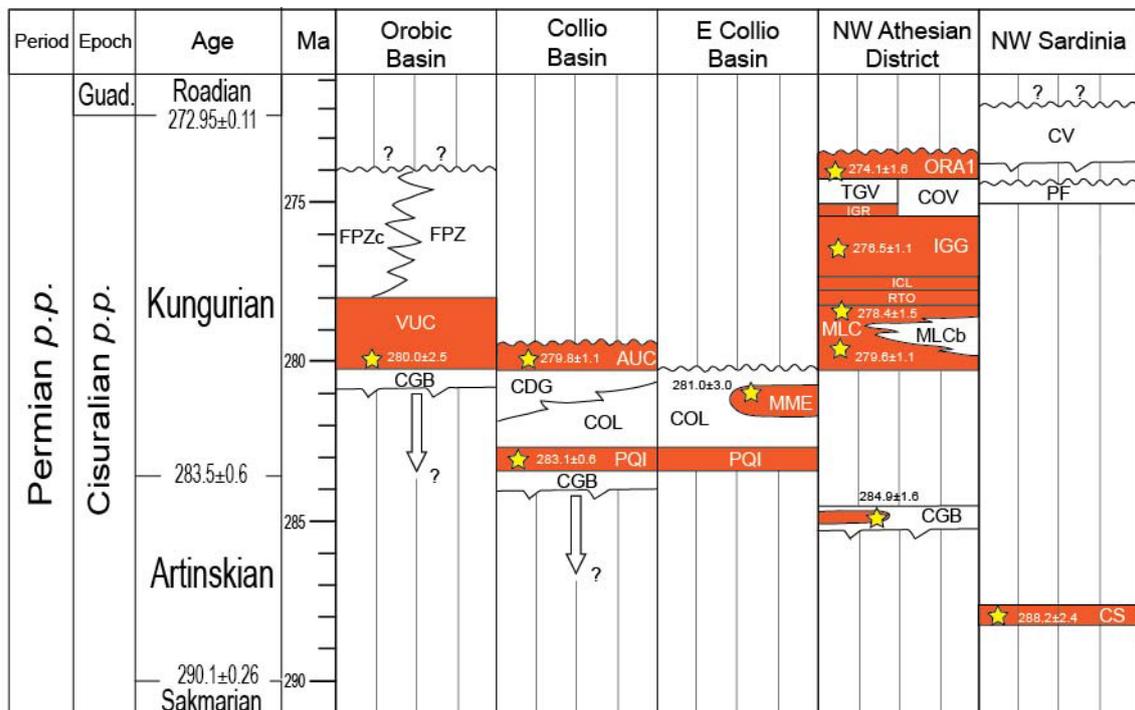


Fig. 2 - Stratigraphy of the fossiliferous units. Orobic and Collio basins acronyms: CGB = Basal Conglomerate, FPZ = Pizzo del Diavolo formation, FPZc = conglomeratic units of FPZ, VUC = Cabianca Volcanite. Collio Basin acronyms: AUC = Auccia Volcanite, CDG = Dosso dei Galli Conglomerate, CGB = Basal Conglomerate, COL = Collio Formation, MME = Monte Macaone formation, PQI = Lower Quartz Porphyries. Athesian District acronyms: CGB = Basal Conglomerate, COV = Verano formation, ICL = Castel Leone formation, IGG = Gargazzone formation, IGR = Gries formation, MCL = Monte Luco formation, MCLb = epiclastic units of MCL, ORA1 = Ora formation, Predonico member, RTO = Sarentino formation, TGV = Tregiovo formation. NW Sardinia acronyms: CS = Casa Satta formation, CV = Cala del Vino formation, PF = Porto Ferro formation. Volcanic units in red, stars represent radiometric ages, question mark mean uncertain age.

exclusively constituted by tetrapod and invertebrate traces, which are abundant and often well-preserved in the fine-grained facies deposits of the “Pizzo del Diavolo formation” (e.g. Nicosia et al., 2000; Santi and Krieger, 2001; Ronchi and Santi, 2003; Arduini et al., 2003; Marchetti et al., 2015a; Marchetti, 2016). Radiometric data from U-Pb methods on zircons in the ignimbrites of the “vulcanite del Cabianca” suggested a late Cisuralian age for this formation: 288 Ma in Cadel (1986), 287 Ma in Cadel et al. (1987), 280 Ma in Philippe et al. (1987) and 280 ± 2.5 Ma (Berra et al., 2015). Nevertheless, only the two latter dates are considered reliable (Kungurian; Marchetti, 2016). Also, a date by Berra et al. (2015), who suggested a Roadian age for the top of the “vulcanite del Cabianca” has been considered unreliable by Marchetti (2016) because of: 1) the occurrence of *Dimetropus* in the overlying Pizzo del Diavolo formation, 2) the too long deposition time inferred for the vulcanite del Cabianca, 3) the unbalanced selection of radioisotopic ages of the sample.

4. THE OROBIC BASIN VERTEBRATE ICHNOASSOCIATION

4.1. HISTORICAL OVERVIEW

Within the Cisuralian continental strata characterizing the Orobic Basin, a very rich record of amphibian and reptile tracks was discovered and represents a significant vertebrate ichnofauna. All these footprints occur in the “Pizzo del Diavolo formation”, known as Collio Formation of the Orobic Basin before Cassinis (2007).

The first pioneering research focusing on the Permian ichnites of Orobic Basin is due to Dozy (1935) from the Bocchetta di Poddavit locality or better known as “Podavit”, between Corno Stella and Pizzo del Diavolo di Tenda (Upper Val Brembana, central Orobic Basin, Trabuchello-Cabianca Anticline). He introduced the ichnotaxa *Anhomiiichnium orobicum* and *Onychichnium escheri*. These ichnotaxa were subsequently considered *nomina dubia* by Marchetti et al. (2015a). Notwithstanding, these ichnological discoveries represented a big novelty in this area of the Southern Alps, no other studies of this kind were put forth in the following decades until the sixties, when new field work led to the finding of further vertebrate tracks.

These were collected in the western Orobic Basin (Orobic Anticline) and mentioned by Casati and Gnaccolini (1967) and by Casati (1969), in Val di Scioc and around the Alpine-shelter FALC (Upper Val Gerola). About 20 years later, other footprints were reported by Casati and Forcella (1988) from the same area. These were occasional discoveries and these authors did not describe the material. The first detailed ichnotaxonomic study of the specimens collected by the above-cited authors in the Upper Val Gerola is by Ceoloni et al. (1987), who identified *Amphisauropus latus*, *A. imminutus*, *Dromopus lacertoides*, *?Laoporus dolloi* and lepidomorph tracks indet. They also assigned to *Camunipes cassinisi* some specimens coming from the nearby Val di Scioc and

previously classified as *Erpetopus* by Toniutti (1985).

In more recent times, straddling the 20th and 21st Centuries, the studies on the Orobic Basin vertebrate ichnofauna have shown an important acceleration. After a preliminary note by Cassinis et al. (1998), Santi and Krieger (1999) described a rich number of newly-found footprints in the fine sedimentary facies of the above-cited locality assigned to *Amphisauropus latus*, *A. imminutus*, *Varanopus curvidactylus* and *Dromopus lacertoides*. Nicosia et al. (2000) described and figured additional specimens from the same locality. They were the first to note the evident similarity of the Orobic ichnofauna of Upper Val Gerola with respect to that of the neighbouring Collio Basin (Brescian Prealps), historically much better known. The Orobic ichnoassemblage was considered comparable with the one found in the lower part of the Collio Formation, and with the coeval ones of central Europe and North America. The material from the Val di Scioc was described by Arduini et al. (2003), who identified *Amphisauropus latus*, *Camunipes cassinisi* and *Varanopus curvidactylus*.

The ichnoassemblage of the western Orobic Basin was then enlarged with the addition of new specimens of *Amphisauropus imminutus*, *Camunipes cassinisi*, *Dromopus* isp. and *Varanopus curvidactylus* found during some stratigraphic research around the Val di Pescegallo and Val Varrone (Gianotti et al., 2001) and between the Rocca di Pescegallo and the Valmora lake (Gianotti et al., 2002). Even though these works had the merit of better describing these ichnites as to define their ichnoassemblage, the biochronologic aspect was only mentioned.

A very detailed analysis of the Orobic Basin Permian ichnosystematics of the Upper Val Brembana and Val Seriana (central Orobic Basin) was authored by Santi and Krieger (2001), who described the footprints of *Amphisauropus latus*, *A. imminutus*, *Varanopus curvidactylus*, *Dromopus lacertoides*, *?Ichniotherium* isp. and *Camunipes cassinisi*, updating the list of ichnotaxa already known from the Orobic Basin.

Later on, different studies discussed the ichnoassemblage of the Orobic Basin (Conti et al., 2000; Confortini et al., 2002; Santi, 2003, 2005; Ronchi et al., 2005; Nicosia et al., 2005; Santi et al., 2008), although they did not update the overall ichnofaunal composition of the basin. Some further works focused on specific ichnotaxonomic topics, such as the dualism *Camunipes/Erpetopus* (Santi, 2007a), analysed the footprint extramorphologies (Santi, 2007b), and applied the ichnofacies and taphofacies concepts to the Orobic ichnoassemblage (Santi, 2008a, 2008b).

An updated and detailed biostratigraphic picture of the Cisuralian continental deposits, together with inferences on palaeoenvironments was provided by Ronchi and Santi (2003) and by Ronchi et al. (2005). In the same year and later on, other works on the utility of ichnostratigraphy for the Permian successions were also published by Cassinis and Santi (2005) and Cassinis et al. (2010).

More recently, a newly-discovered asymmetric

trackway with continuous tail/body and digit scratches, assigned to *Erpetopus* and from the Pizzo Farno locality (central Orobic Basin) was interpreted as locomotion of small reptiles on inclined planes (Bernardi and Avanzini, 2011). A new slab from the Upper Val Brembana was described by Petti et al. (2014). It included numerous and long trackways assigned to *Batrachichnus* and a trackway showing a possible locomotion-swim transition from muddy sediment to water by a small amphibian.

A preliminary ichnotaxonomic revision of the Orobic Basin ichnoassemblage was proposed by Marchetti et al. (2013a), who identified for the first time from this basin the ichnotaxa *Hyloidichnus bifurcatus* and *Limnopus heterodactylus*. Marchetti et al. (2014) described a new slab from the Upper Val Brembana with several trackways assigned to *Erpetopus cassinisi* and discussed the problem of the extramorphologies for small tracks. Marchetti et al. (2015a) comprehensively revised the ichnoassemblage from the Upper Val Gerola, with the addition of new material coming from three sites (including the historical FALC locality), showing a different ichnofaunal composition probably due to a different depositional environment. The ichnoassemblage includes the ichnogenera *Amphisauropus*, *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Limnopus* and *Varanopus*. For the first time, a comparison with contemporary low-latitude ichnosites all around the world suggested a higher relative abundance of reptile tracks compared to older ichnosites.

Marchetti et al. (2017a) described an *Amphisauropus* trackway from the FALC locality with the aid of digital photogrammetry. The continuous tail and digit marks were used to reconstruct the step cycle of the inferred trackmaker (seymouriamorph amphibian), after a synapomorphy-based track-trackmaker correlation.

Marchetti (2016) comprehensively revised the tetrapod ichnoassemblage of the central Orobic Basin, including new and already described material from the Pizzo Farno, the Upper Val Brembana and the Val Seriana. The following ichnogenera were identified: *Amphisauropus*, *Batrachichnus*, cf. *Dimetropus*, *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Limnopus*, cf. *Merifontichnus* and *Varanopus*. The ichnotaxa *Dimetropus* and *Merifontichnus* were described, although with a provisional assignment, for the first time from Italy. This ichnoassemblage suggests a late Kungurian age for the “Pizzo del Diavolo formation”, opposed to the hypotheses of Berra et al. (2015), who hypothesised a younger age for this formation based on a debated interpretation of radiometric ages from the top of the underlying “vulcanite del Cabianna”.

Lastly, Marchetti et al. (2017b) made a thorough study of the palaeoecology of tetrapod footprints, comparing the relative proportions of ichnogenera found in three different facies associations from the “Pizzo del Diavolo formation” of the central Orobic Basin (Berra et al., 2016). In order to do so, two new census methods for tracks were proposed and tested.

4.2. ICHNOASSOCIATION STRUCTURE

The tetrapod ichnoassemblage from the “Pizzo del Diavolo formation” of the Orobic Basin currently includes the following ichnogenera (Fig. 3, Tab. 1): *Amphisauropus*, *Batrachichnus*, cf. *Dimetropus*, *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Limnopus*, cf. *Merifontichnus* and *Varanopus*.

The ichnogenus *Batrachichnus* is relatively uncommon in the Orobic Basin. It has been identified by Petti et al. (2014) and Marchetti (2016). Marchetti (2016) described the ichnospecies *B. salamandroides*. The ichnogenus *Limnopus* is also relatively uncommon in the Orobic Basin. It has been identified as *L. heterodactylus* by Marchetti et al. (2013a, 2015a) and Marchetti (2016).

The ichnogenus *Amphisauropus* is locally abundant in the Orobic Basin. It has been identified by several authors (e.g. Ceoloni et al., 1987, Nicosia et al., 2000, Santi and Krieger, 2001, Marchetti et al., 2015a, 2017a; Marchetti, 2016). The ichnospecies currently considered valid (see Voigt, 2015) is *A. kablikae*. It has been described from the Orobic Basin by Marchetti et al. (2015a, 2017a) and Marchetti (2016).

The ichnogenus *Dimetropus* is rare in the orobic Basin. It has been identified as cf. *Dimetropus* isp. by Marchetti (2016).

The ichnogenus *Erpetopus* is very common in the Orobic Basin. It was first identified by Toniutti (1985). Subsequent work referred it instead to *Camunipes* (e.g. Ceoloni et al., 1987; Santi and Krieger, 2001; Gianotti et al., 2001, 2002; Arduini et al., 2003), until these two ichnogenera were synonymised (Santi, 2007a; Marchetti et al., 2014). Later on, this material was referred to *Erpetopus* (Bernardi and Avanzini, 2011; Marchetti et al., 2013a, 2014, 2015a, 2017b; Marchetti, 2016). Some works described the ichnospecies *E. cassinisi* from the Orobic Basin (Marchetti et al., 2014; Marchetti, 2016). The ichnogenus *Varanopus* is relatively common in the Orobic Basin. It has been described by some authors as *V. curvidactylus* (Santi and Krieger, 1999, 2001; Gianotti et al., 2001, 2002; Nicosia et al., 2001). After a revision, Marchetti et al. (2015a) and Marchetti (2016) assigned the same material to *Varanopus* isp., because they considered these specimens different from the type material of *V. curvidactylus*. Marchetti (2016) described also *V. microdactylus*.

The ichnogenus *Hyloidichnus* is a relatively common ichnotaxon in the Orobic Basin. It has been described as *H. bifurcatus* by Marchetti et al. (2013a, 2015a) and Marchetti (2016). The ichnogenus *Merifontichnus* is rare in the Orobic Basin. It has been described as cf. *Merifontichnus* by Marchetti (2016).

The ichnogenus *Dromopus* is a very common ichnotaxon in the Orobic Basin. It has been described by several authors, usually as *D. lacertoides* (Ceoloni et al., 1987; Santi and Krieger, 1999, 2001; Nicosia et al., 2000; Gianotti et al., 2001, 2002; Arduini et al., 2003; Marchetti et al., 2013a, 2015a, 2017b; Marchetti, 2016).

The tetrapod footprints from the “Pizzo del

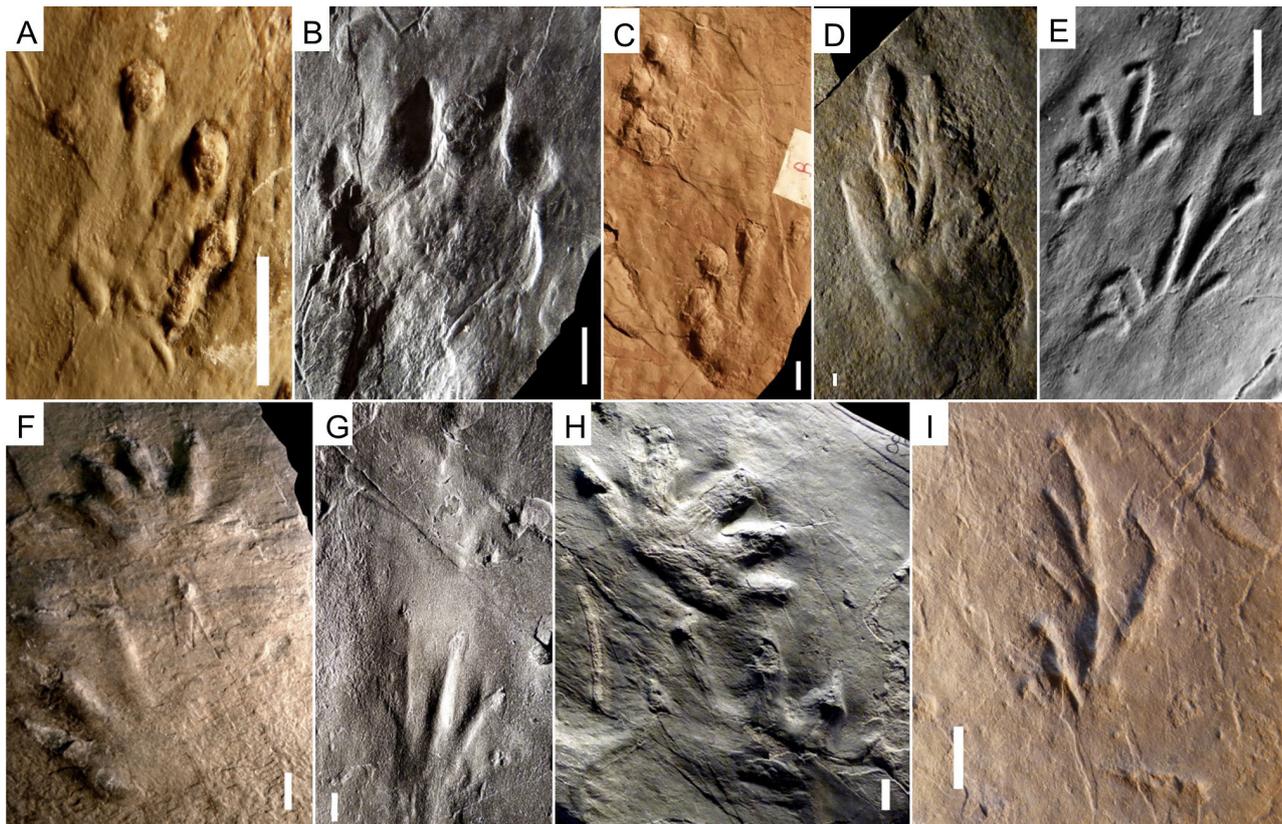


Fig. 3 - Tetrapod ichnogenera from the Pizzo del Diavolo formation of the Orobic Basin. A) MBG 13023. *Batrachichnus*, right manus, convex hyporelief. B) MBG 12527. *Limnopus*, left manus, concave epirelief, artificial cast. C) MSNM 32. *Amphisauropus*, right pes-manus couple, concave epirelief. D) MBG 8830. cf. *Dimetropus*, left pes, convex hyporelief. E) MBG 13045. *Erpetopus*, left pes-manus couple, convex hyporelief. F) MBG 13099. *Varanopus*, left pes-manus couple, convex hyporelief. G) MBG 12531. *Hyloidichnus*, left pes-manus couple, concave epirelief, artificial cast. H) MBG 8954. cf. *Merifontichnus*, right pes-manus couple, convex hyporelief. I) UPTF 13. *Dromopus*, right pes-manus couple, concave epirelief. MBG - Natural History Museum “Enrico Caffi”, Bergamo; MSNM - Natural History Museum of Morbegno; UPTF - Palaeontological Museum, University of Pavia. Scale bar 1 cm.

Table 1. Tetrapod ichnogenera in the Cisuralian of Italy. Question marks mean uncertain occurrences.

	basin	Orobic Basin	Collio Basin	Collio Basin	Athesian District	Athesian District	NW Sardinia
	formation	Pizzo del Diavolo	Collio	Dosso dei Galli	Monte Luco	Tregiovo	Cala del Vino
	depositional environment	alluvial fan, floodplain, lacustrine	alluvial fan, floodplain, lacustrine	alluvial fan, lacustrine	alluvial fan, floodplain, lacustrine	alluvial fan, lacustrine	floodplain
anamniote tracks	<i>Amphisauropus</i>	X	X	X	X		
anamniote tracks	<i>Batrachichnus</i>	X	X?	X	X?	X	
anamniote tracks	<i>Limnopus</i>	X	X		X?		
synapsid tracks	<i>Dimetropus</i>	X?					
reptile tracks	<i>Dromopus</i>	X	X	X	X	X	
reptile tracks	<i>Erpetopus</i>	X	X			X?	
reptile tracks	<i>Hyloidichnus</i>	X	X			X?	
reptile tracks	<i>Merifontichnus</i>	X?	X				X
reptile tracks	<i>Varanopus</i>	X	X		X		

Diavolo formation” of the Orobic Basin show remarkable abundance, diversity and morphological preservation (*sensu* Marchetti et al., 2019b). The Orobic ichnoassemblage is characterised by a marked abundance and diversity of reptile tracks such as *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Merifontichnus* and *Varanopus*. The ichnotaxa *Dromopus* and *Erpetopus* are the most common, being predominant in specific lithofacies. The anamniote tracks such as *Amphisauropus*, *Batrachichnus* and *Limnopus* are less common and diverse. The synapsid tracks such as *Dimetropus* are very rare (e.g. Marchetti et al., 2015a, 2017b; Marchetti, 2016). The ichnoassemblages from the Orobic, Collio and Athesian District basins were central for the identification of the late Cisuralian reptile radiation observed in the tetrapod footprint record (Marchetti et al., 2019c). In all the European, North African and American tetrapod ichnoassociations during the late Artinskian and Kungurian show a high relative abundance of reptile tracks compared to older ichnoassociations. This abundance is not facies-related, because it was observed in lacustrine, alluvial fan, floodplain, eolian and tidal flat palaeoenvironments (e.g. Gand and Durand, 2006; Voigt et al., 2011; Marchetti et al., 2015a, 2015b, 2019a, 2019c, 2020; Mujal et al., 2016; Voigt and Lucas, 2017). Such reptile radiation is also observed in the skeletal record of the USA (e.g. Modesto et al., 2014; MacDougall et al., 2016). The low abundance of synapsid tracks in the Italian Cisuralian ichnoassociation is consistent with the contemporary tetrapod ichnoassociation in other parts of the World, and may mirror the progressive reduction of the synapsid diversity during the late Artinskian-Kungurian (e.g. Brocklehurst et al., 2017; Brocklehurst, 2018; Lucas, 2018).

5. GEOLOGICAL SETTING AND STRATIGRAPHY OF THE COLLIO BASIN

The most important and historically well-studied Cisuralian continental succession of Italy is located in the Upper Val Trompia (Brescia Province, Lombardy) and is commonly known as the Collio Basin (Fig. 1). At the end of the 19th Century and in the first half of the 20th Century, many geologists dealt with this important sedimentary and volcanic succession (see Marchetti et al., 2015b for a list of historical works). The first detailed study of the stratigraphic succession of the Collio Formation is from Cassinis (1966a, 1966b), along the Maniva - Croce Domini road (Upper Val Trompia), and this section was later used as a reference. Subsequently, the same author instituted both the “Dosso dei Galli Conglomerate” to distinguish the upper part of the Cisuralian section, characterised by coarse-grained sandstones and conglomerates (Cassinis, 1969a), and the “Auccia Volcanite” right above them (Cassinis, 1969b).

The Collio Basin developed in the late Cisuralian following a trans-tensional tectonics that generated pull-apart basins in the Southern Alps region (northern Italy) (Cassinis and Perotti, 1994, 1997, 2007; Cassinis et

al., 2000a). It extends for more than 20 km in a WSW-ENE direction, in a typical semi-graben structure, with a depocenter close to the eastern border (in the Val Caffaro; Cassinis and Perotti, 1997; Breitzkreuz et al., 2001; Cassinis et al., 2012).

Recently, the differentiation of the Collio Formation into two informal members has been proposed, into a “lower” Pian delle Baste member and an “upper” Val Dorizzo member, divided by the first of a series of volcanoclastic key beds (Cassinis, 2007).

The succession (Fig. 2) begins with the “Basal Conglomerate”, which unconformably lies on the metamorphic basement. It is overlain by the “Lower Quartz Porphyries” (or “Lower Rhyolitic Ignimbrites”), representing the first volcanic event. These are followed by deposits of the Collio Formation: it is a volcano-sedimentary succession that reaches about 700-800 m of thickness in the eastern part of the Basin (Ori et al., 1986). The “Pian delle Baste member” (Lower Collio *sensu* Cassinis, 1966a) is composed of conglomerates and coarse arenites representing a typical alluvial fan deposition, fine arenites of a sand-sheet deposit, and black laminated pelites. According to Ori et al. (1986) the recognised environments evolved in a fining-upwards sequence from distal fan to sandflat, and mudflat up to lacustrine settings.

The overlying “Val Dorizzo member” (Upper Collio *sensu* Cassinis, 1966a) begins after the deposits of a volcanoclastic key bed (“Mt. Dasdana bed I” *sensu* Cassinis and Perotti, 1997; Cassinis et al., 2000a, 2007, 2008; Breitzkreuz et al., 2001) and is composed of conglomerates, fine arenites and black laminated pelites in its lower part. In its upper part, fine to medium-coarse arenites are intercalated with the pelites, testifying a transition to the “Dosso dei Galli Conglomerate”. An overall fining upwards sequence is recognised by Ori et al. (1986) also in the “Val Dorizzo member”, from a distal fan to sandflat up to a lacustrine environment. The Collio Basin developed between 283.1 ± 0.6 Ma and 279.8 ± 1.1 Ma, from U-Pb age determinations on the “Lower Quartz Porphyries” and the “Auccia Volcanite” (Schaltegger and Brack, 1999, 2007), thus the age is constrained to the early Kungurian.

The Collio Formation has a rich fossil content (tetrapod and invertebrate trace fossils, plant fossils, sporomorphs, freshwater jellyfishes, bivalves, and conchostracans). Palynomorphs were also studied (Clement-Westerhof, 1974; Cassinis and Doubinger, 1991, 1992) and suggested a late Artinskian to ?early Ufimian (i.e. late Cisuralian to early Guadalupian age). This was subsequently refined by the isotopic data, that give an early Kungurian age (Schaltegger and Brack, 2007).

6. THE VERTEBRATE ICHNOASSOCIATION OF THE COLLIO BASIN

6.1. HISTORICAL OVERVIEW

The ichnological studies in Italy as a scientific discipline started historically with the discovery of vertebrate

footprints in the Cisuralian Collio Formation strata from the Collio or Val Trompia Basin (Brescian Prealps).

The first report of vertebrate tracks is by Geinitz (1869), who published a letter sent to him by Suess in 1868, where he had announced the discovery of a small slab with tetrapod tracks. These footprints were collected by Don Giovanni Bruni, a priest and naturalist, from an outcrop called by him “Pulpito” in the area of Cludona Pass and between the farmhouse Pofferatte Alta and the springs “Pisseri” of the Serimando creek (Upper Val Trompia). A more detailed stratigraphical location of the “Pulpito” is reported by Marchetti et al. (2018), who placed this fossiliferous outcrop in the upper part of the “Pian delle Baste member” (on the southern side of Monte Colombine). These footprints were first classified by Geinitz (1869) as *Chelychnis dunkani* (= *Chelichnus dunkani*) previously reported from the Permian of Dumfries (United Kingdom). He also noted some similarities with the material from the locality of Hohenhelbe (now Vrčlabí, Czech Republic), type locality of *Amphisauropus kablikae*. Curioni (1870) provided the first scientific description of this material

and its first illustration (Fig. 4). He reported the previous assignment of *C. dunkani* and identified also some smaller tracks, assigned to *Ornithichnites*. This constitutes the first scientific description of tetrapod footprints from Italy (Leonardi, 2008; Marchetti et al., 2018), although the date of discovery is unknown (but certainly not after 1868). Just some years later, Gümbel (1880) studied the same ichnofossils, ascribing them to *Chirotherium* on the basis of their comparison to those of *Saurichnites* from the Rotliegende of Germany.

After the first pioneering phase of tetrapod footprint collection in the Collio Basin and the related above-cited works in the last part of the 19th Century, many decades followed with no other findings nor reports of ichnofossils. A renewed interest on this topic arose thanks to the indication of possible new ichnites in the Collio Formation informal “member F” (now part of the “Val Dorizzo member”) by Cassinis (1966a), close to the locality Malga Dasdana Busa in the Upper Val Trompia. On these bases, after a palaeontological field-work between this locality and the nearby Monte Dasdana between 1966-67, new tetrapod footprints were first



Fig. 4 - The first tetrapod footprints described from Italy, Collio Basin, Collio Formation, Upper Val Trompia. A) ISPRa specimen n. 4426. Original plate by Curioni (1870). B) Photograph of the slab, including *Amphisauropus* (larger tracks) and *Dromopus* (small and shallow tracks) preserved in concave epirelief. ISPRa - Italian National Institute for Environmental Protection and Research, Rome. Scale bar 1 cm.

reported (Berruti, 1967) and then ichnotaxonomically described and figured by Berruti (1970). Within this latter work, he described and figured also two slabs collected by Don Bruni (in 1873, according to Ceoloni et al., 1987) in the informal “member C” of the same formation (now part of the Pian delle Baste member) between Malga Cuta or Malga Stabul Maggiore in Upper Val Trompia. The ichnoassemblage comprised: *Eumechichnium gamspodactylum*, *Thecodontichnus* isp., *Prochirotherium permicum*, *Ichnium acrodactylum tambacense* and *I. sphaerodactylum tambacense*. This ichnoassemblage was later revised by Haubold and Katzung (1975) who re-assigned this material to ?*Anthichnium salamandroides*, *Amphisauropus imminutus*, *A. latus*, *Dromopus lacertoides* and cf. *Gilmoreichnus brachydactylus*. The material originally reported by Curioni (1870) and Berruti (1970) and some additional specimens were then studied by Ceoloni et al. (1987), who introduced the ichnotaxa *Gracilichnium berrutii* and *Camunipes cassinisi* based on footprints from the Malga Dasdana Busa locality. They identified also *Amphisauropus latus* and *Dromopus lacertoides*. Ceoloni et al. (1987) assigned the specimen figured by Curioni (1870) to *Amphisauropus latus*, notwithstanding they could not get access to the original material.

Thanks to the large number of ichnofossils collected (about 600 specimens) in the Collio Formation during the successful field-campaigns in 1987-1989 led by La Sapienza University (Rome), in the Val Trompia and Val Caffaro, this ichnoassemblage represented the basis of several subsequent ichnotaxonomic and biostratigraphic studies (Conti et al., 1991, 1997, 2000; Santi, 2007a; Marchetti et al., 2013a, 2014; Marchetti et al., 2015b). Conti et al. (1991) published a first report on these new discoveries regarding 15 localities in the Upper Val Trompia. They listed: *Amphisauropus imminutus*, *A. latus*, *Camunipes cassinisi*, *Dromopus lacertoides*, *Gracilichnium berrutii*, *Laoporus* isp. and *Varanopus* isp. from the Collio Formation and *Dromopus lacertoides* from the Pietra Simona Member of the overlying “Dosso dei Galli Conglomerate”. Conti et al. (1997) reported also *Ichniotherium cottae* and *Dromopus didactylus* from the Collio Formation and *D. didactylus* from the Pietra Simona Member. This material led to a “new era” for the “Collio Triumplino” ichnoassemblage, which was used as paradigm for the concept of “Ichnofaunal Unit” in tetrapod footprint biostratigraphy (Conti et al., 1997; Avanzini et al., 2001; Cassinis et al., 2010; Marchetti et al., 2019a). The ichnoassemblage from the Collio Basin was the main reference for the establishment of the Collio Ichnofaunal Unit, divided into the Pulpito and Tregiovo subunits (Conti et al., 1997).

The possible synonymy of *Camunipes* and *Erpetopus*, first discussed by Haubold and Lucas (2001) and Santi (2007a), was re-analysed by Marchetti et al. (2014), who proposed the combination *Erpetopus cassinisi* for the material from the Southern Alps. In a preliminary revision of the Collio Basin tetrapod ichnoassemblage,

Marchetti et al. (2013a) identified for the first time from this basin the ichnotaxa *Hyloidichnus bifurcatus* and *Limnopus heterodactylus*. The material from the Collio Formation of the Upper Val Trompia and the Val Caffaro, including a large number of unpublished specimens, was comprehensively studied by Marchetti et al. (2015b). The following ichnotaxa were recognised: *Amphisauropus kablikae*, cf. *Batrachichnus* isp., *Dromopus lacertoides*, *Erpetopus cassinisi*, *Hyloidichnus bifurcatus*, *Limnopus heterodactylus* and *Varanopus* isp. These authors identified a typical late Cisuralian tetrapod ichnoassemblage and the possible first appearance (FAD) of the ichnotaxon *Erpetopus*. Marchetti et al. (2018) restudied the original specimen described by Curioni (1870) with the aid of digital photogrammetry. These footprints have been re-assigned to *Amphisauropus kablikae* and *Dromopus* isp. Marchetti et al. (2013b) described new material from the “Val Dorizzo member” of Collio Formation of Val Aperta. They identified *Amphisauropus kablikae* and *Erpetopus willistoni* and proposed a reconstruction of the sequence of events that occurred on the trampled surface. Later on, the trackway assigned to *A. kablikae* was re-assigned to *Merifontichnus* (Marchetti, 2016).

6.2. ICHNOASSOCIATION STRUCTURE

The tetrapod ichnoassemblage from the Collio Formation of the Collio Basin (Fig. 5, Tab. 1) currently includes the following ichnogenera: *Amphisauropus*, cf. *Batrachichnus*, *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Limnopus*, *Merifontichnus* and *Varanopus*.

Batrachichnus is a relatively rare ichnotaxon in the Collio Formation. It has been recognized by Marchetti et al. (2015b) as cf. *Batrachichnus* isp. This material includes the footprints previously assigned to *Gracilichnium berrutii* by Ceoloni et al. (1987) and Conti et al. (1991). *Limnopus* is a relatively uncommon ichnotaxon in the Collio Formation. It has been described as *L. heterodactylus* by Marchetti et al. (2013a, 2015b). This material includes also a specimen previously classified as *Batrachichnus* by Marchetti et al. (2013a).

The ichnogenus *Amphisauropus* is locally abundant in the Collio Formation. It has been recognised by several authors (e.g. Haubold and Katzung, 1975; Ceoloni et al., 1987; Conti et al., 1991; Marchetti et al., 2013a, 2015b, 2018). The first specimen described from Italy (Curioni, 1870) includes tracks assignable to this ichnotaxon (Marchetti et al., 2018). The only ichnospecies currently considered valid (see Voigt, 2015) is *A. kablikae* and it has been described from the Collio Formation by Marchetti et al. (2015b).

The ichnogenus *Erpetopus* is a very common ichnotaxon in the Collio Formation. The material assignable to this ichnogenus has been originally described as *Camunipes* (e.g. Ceoloni et al., 1987; Conti et al., 1991). Later on, the two ichnogenera were synonymised under the first erected, which is *Erpetopus* (Haubold and Lucas, 2001; Santi, 2007a; Marchetti et al., 2014). The ichnospecies *E. cassinisi* was described by Marchetti et al. (2014, 2015b).

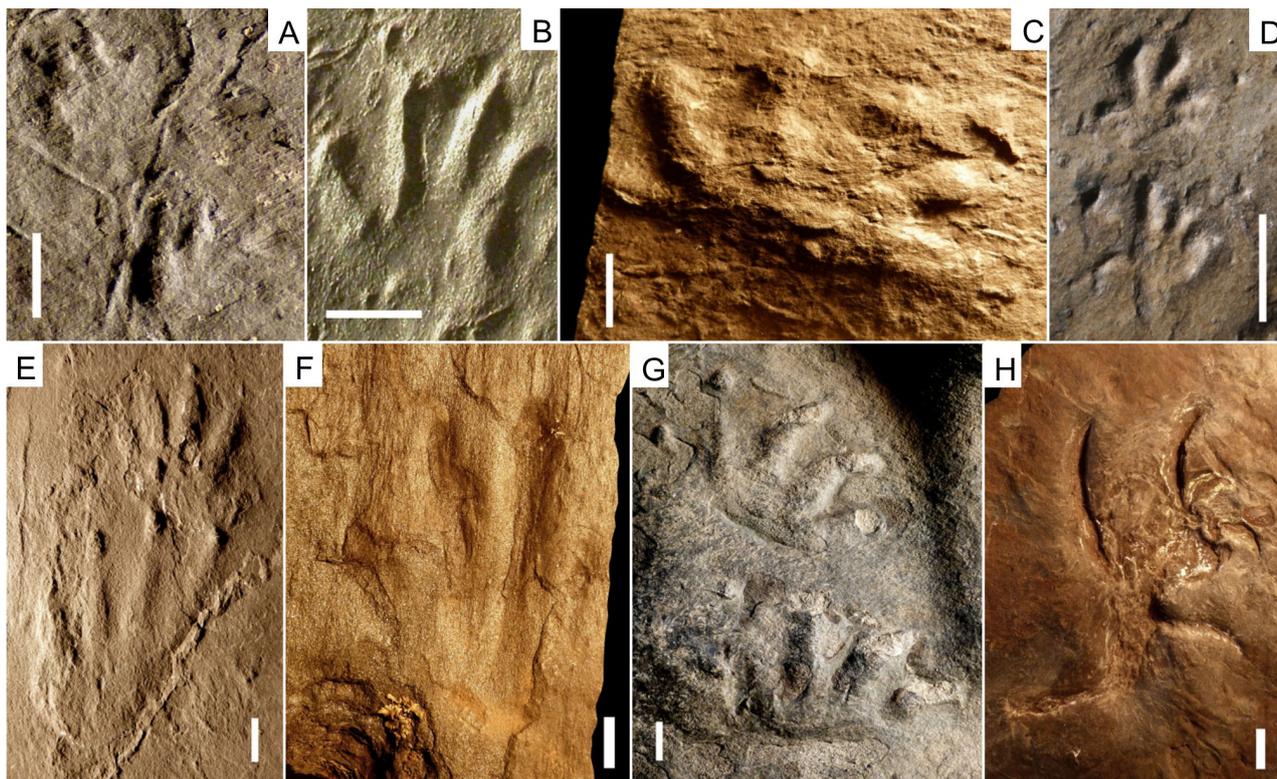


Fig. 5 - Tetrapod ichnogenera from the Collio Formation of the Collio Basin. A) MCSNBS 268-269. cf. *Batrachichnus*, left pes-manus couple, convex hyporelief. B) MCSNBS 277. *Limnopus*, left manus, concave epirelief. C) UR-NN 1. *Amphisauropus*, right manus, convex hyporelief. D) MCSNBS 319. *Erpetopus*, left pes-manus couple, concave epirelief. E) UR-NN 2. *Varanopus*, left pes-manus couple, convex hyporelief. F) MCSNBS 10973. *Hyloidichnus*, left pes, concave epirelief. G) MUSE 7086. *Merifontichnus*, right pes-manus couple, convex hyporelief. H) UR NS 43-111. *Dromopus*, left pes-manus couple, concave epirelief. MCSNBS - Natural History Museum of Brescia; MUSE- Museo delle Scienze, Trento; UR - Palaeontological Museum, SAPIENZA Università di Roma. Scale bar 1 cm.

The ichnospecies *E. willistoni* was instead identified by Marchetti et al. (2013b). The ichnogenus *Varanopus* is relatively common in the Collio Formation. It has been described by Conti et al. (1991) and Marchetti et al. (2013a, 2015b).

The ichnogenus *Hyloidichnus* is a relatively uncommon ichnotaxon in the Collio Formation. It has been described as *H. bifurcatus* by Marchetti et al. (2013a) and Marchetti et al. (2015b). The ichnogenus *Merifontichnus* is a rare ichnotaxon in the Collio Formation. It has been described by Marchetti (2016), who re-assigned a trackway originally described as *Amphisauropus kablikae* by Marchetti et al. (2013b).

The ichnogenus *Dromopus* is a very common ichnotaxon in the Collio Formation. It has been described by numerous authors (e.g. Haubold and Katzung, 1975; Ceoloni et al., 1987; Conti et al., 1991; Marchetti et al., 2013a, 2015b). The only ichnospecies occurring is *D. lacertoides*. The material originally assigned to *D. didactylus* by Conti et al. (1997) has been subsequently reassigned to *D. lacertoides* by Marchetti et al. (2015b).

The tetrapod ichnoassemblage from the Pietra Simona Member of the “Dosso dei Galli Conglomerate” of the Collio Basin (Tab. 1) currently includes the ichnogenera: *Amphisauropus*, *Batrachichnus* and *Dromopus*. The

ichnogenera *Batrachichnus* and *Amphisauropus* are relatively rare in the “Dosso dei Galli Conglomerate” (Marchetti, 2014). The ichnogenus *Dromopus* is very abundant in the “Dosso dei Galli Conglomerate” (Conti et al., 1991, 1997; Marchetti, 2014). The occurrence of the ichnospecies *D. didactylus* supposed by Conti et al. (1997) was not confirmed by Marchetti (2014).

The tetrapod footprints from the Collio Basin show remarkable abundance, diversity and morphological preservation (*sensu* Marchetti et al., 2019b). As for the Orobic Basin the ichnoassemblage is characterised by a marked abundance and diversity of reptile tracks such as *Dromopus*, *Erpetopus*, *Hyloidichnus*, *Merifontichnus* and *Varanopus*. The ichnotaxa *Dromopus* and *Erpetopus* are the most common, being predominant in specific lithofacies. The anamniote tracks such as *Amphisauropus*, *Batrachichnus* and *Limnopus* are less common and diverse. Differently from the Orobic Basin, the synapsid tracks have not been recorded so far.

Because of the calibration with radiometric data (Schaltegger and Brack, 1999, 2007) and the abundance, preservation and diversity, the Collio tetrapod ichnoassemblage is considered to be the main reference in the Kungurian for the definition of the *Erpetopus* footprint biochron (Voigt and Lucas, 2018; Schneider et

al., 2020) and of the Collio Ichnofaunal Unit (Conti et al., 1997; Marchetti et al., 2019a).

7. GEOLOGICAL SETTING AND STRATIGRAPHY OF THE ATHESIAN DISTRICT

The Athesian District is a volcano-sedimentary succession cropping out in an area extending between the towns of Trento and Merano/Meran in the Trentino-Alto Adige region for about 70x70 km (Fig. 1). The maximum thickness of the succession is about 2000 m (Avanzini et al., 2007; Marocchi et al., 2008). The lower limit of the Athesian District is an unconformity with the crystalline basement, and the upper limit is an unconformity with the Lopingian red beds of Val Gardena/Gröden formation. The prevailing units are constituted by deposits of pyroclastic flows, less common domes and lava flows, whereas deposits of pyroclastic surges are rare (Avanzini et al., 2007). Siliciclastic and freshwater carbonate successions occur at different levels in the succession (Avanzini et al., 2007), representing short-lived interruptions in the protracted volcanic activity, often yielding tetrapod and invertebrate trace fossils, plant remains, fossil wood, conchostracans, palynomorphs and rare vertebrate remains (Avanzini et al., 2007). The stratigraphic position of some key fossiliferous intervals of the Athesian District (Leonardi, 1959; Krainer and Spötl, 1998; Hartkopf-Fröder et al., 2001; Fritz and Krainer, 2006) follows the recent chronostratigraphic and petrographic revision of the Athesian District (Avanzini et al., 2007; Morelli et al., 2007, 2012; Marocchi et al., 2008; Willcock et al., 2013, 2015).

In the NW area of the Athesian District (Fig. 2), after the deposition of the “Basal Conglomerate”, the oldest sedimentary intercalation is constituted by the epiclastic units of “Monte Luco formation”, mostly constituted by rhyodacitic lavas and domes for a maximum thickness of 1300 m. The sedimentary intercalations are thin (20-90 m in thickness) and discontinuous, and include coarse to fine-grained sandstones, laminated mudstones and carbonate layers. These were interpreted as floodplain to lacustrine environments (Avanzini et al., 2007). The two most important outcrops are the northern flank of Luco Piccolo (Avanzini et al., 2008, 2011b) that yields tetrapod/invertebrate traces and Sinigo/Sinnich (Krainer and Spötl, 1998; Fritz and Krainer, 2006), which yields plant remains and silicified trunks. U-Pb radiometric dates of the volcanic units of the Monte Luco formation indicate an age between 279.6±1.1 Ma and 278.4±1.5 Ma (Marocchi et al., 2008).

The deposition of this sector of the basin continues with the rhyodacitic lavas and ignimbrites of the “Castel Leone” and “Gargazzone” formations, with an overall maximum thickness of about 1000 m, which are locally covered by the conglomerates and sandstones of the “Verano formation”. The “Gargazzone formation” is overlain also by the “Gries formation”, formed by rhyolitic ignimbrites and volcanoclastic breccias and cropping out discontinuously for a maximum thickness of about 150

m. In turn, the “Gries formation” is overlain by the most important epiclastic unit of the Athesian District, the “Tregiovo formation”. This unit crops out continuously in the NW area of the Athesian District (Tregiovo, Pescarill, Lauregno, Monte Dian) for a maximum thickness of about 250 m. It includes a basal conglomeratic unit, a middle fine-grained unit with mudstone and carbonate-chert and an upper unit composed of sandstones. It has been interpreted as an alluvial fan environment passing upward to ephemeral lacustrine and alluvial settings (Marchetti et al., 2015c). This is the most known fossiliferous formation of the Athesian District yielding abundant, diverse and well-preserved plant remains and poorly-preserved but abundant tetrapod/invertebrate traces, conchostracans and sporomorphs. Plant-damage interactions were also observed (Remy and Remy, 1978; Neri et al., 2000; Visscher et al., 2001; Avanzini et al., 2007; Marchetti et al., 2015c). U-Pb radiometric dates of underlying and overlying formations in the type area suggest an age between 276.5±1.1 Ma (“Gargazzone formation”) and 274.1±1.6 Ma (“Ora formation”, “Predonico member”), respectively, and between 274.6±2.1 (“Andriano formation”) and 274.2±2.9 (“Ora formation”, “Predonico member”) in the Adige Valley.

8. THE ATHESIAN DISTRICT VERTEBRATE ICHNOASSOCIATION

8.1. HISTORICAL OVERVIEW

Tetrapod footprints from the Athesian District were first reported at the end of the 20th Century, by Conti et al. (1997) and Neri et al. (2000). These authors identified the ichnotaxon *Dromopus didactylus* in great abundance in the laminated mudstones of the “Tregiovo formation”, near the village of Tregiovo. This find was used to establish the upper part of the Collio Ichnofaunal Unit, the Tregiovo sub-unit (Conti et al., 1997). Nevertheless, this material has not been figured nor described. Marchetti et al. (2015c) did the first ichnotaxonomic study on material from the Tregiovo Formation, including about 100 specimens from two different stratigraphic intervals in the locality “Le Fraine” nearby the village of Tregiovo. These authors identified: *Batrachichnus* isp., *Dromopus* isp., cf. *Erpetopus* isp. and *Hyloidichnus* isp. A palaeoenvironmental reconstruction highlighted a different footprint palaeoecology between the two stratigraphic intervals. Avanzini et al. (2007) first reported the occurrence of tetrapod tracks from the epiclastic units of the “Monte Luco formation”, in the locality Luco Piccolo. The first ichnotaxonomic description of this material was by Avanzini et al. (2008), who identified: cf. *Amphisauropus*, cf. *Batrachichnus*, *Dromopus lacertoides* and *D. cf. didactylus*. Marchetti (2014) described also cf. *Limnopus* and *Varanopus* from this locality.

8.2. ICHNOASSOCIATION STRUCTURE

The ichnoassemblage from the “Monte Luco formation” of the Athesian District (Fig. 6, Tab. 1) currently

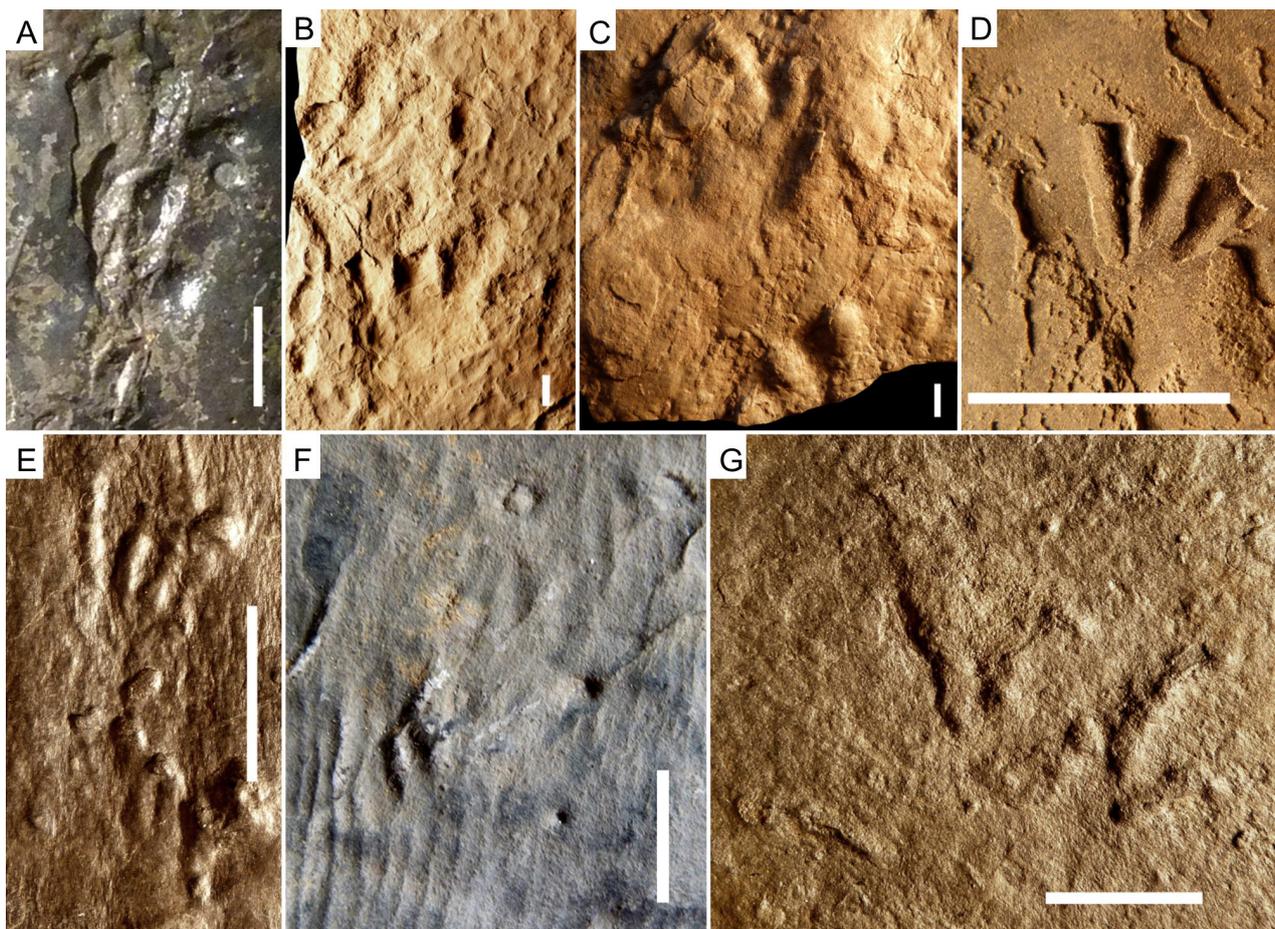


Fig. 6 - Tetrapod ichnogenera from the Athesian District. A) *Batrachichnus*, right pes-manus couple, convex hyporelief. B) MSNBZ LU 1.17. cf. *Limnopus*, left pes-manus, concave epirelief. C) MSNBZ LUDT 8. *Amphisauropus*, left pes-manus couple, convex hyporelief. D) MUSE PAI 162. cf. *Erpetopus*, left manus, concave epirelief. E) MSNBZ ML2.8. *Varanopus*, left pes-manus couple, concave epirelief. F) MUSE PAI 161. *Hyloidichnus*, left pes, concave epirelief. G) MSNBZ ML 5.6. *Dromopus*, right pes-manus couple, convex hyporelief. MUSE- Museo delle Scienze, Trento; MSNBZ-Museum of Nature South Tyrol, Bolzano. A, D, F from Tregiovo Formation. B, C, E, G from Monte Luco Formation. Scale bar 1 cm.

includes the following ichnogenera: *Amphisauropus*, cf. *Batrachichnus*, *Dromopus*, cf. *Limnopus* and *Varanopus*. The ichnogenus *Batrachichnus* is a rare ichnotaxon from the Monte Luco formation. It has been described as cf. *Batrachichnus* isp. by Avanzini et al. (2008). *Limnopus* is a rare ichnotaxon from the “Monte Luco formation”. It has been described as cf. *Limnopus* isp. by Marchetti (2014).

Amphisauropus is a relatively uncommon ichnotaxon from the “Monte Luco formation”. It has been described by Avanzini et al. (2008) and Marchetti (2014).

Dromopus is a very common ichnotaxon in the “Monte Luco formation”. It has been described by Avanzini et al. (2008) and Marchetti (2014). The only ichnospecies occurring is *D. lacertoides*, after the revision by Marchetti (2014).

Varanopus is a rare ichnotaxon from the Monte Luco formation. It has been described by Marchetti (2014).

The ichnoassemblage from the “Tregiovo formation” of the Athesian District (Fig. 6, Tab. 1) currently includes the following ichnogenera: *Batrachichnus*, *Dromopus*, cf. *Erpetopus* and cf. *Hyloidichnus*. The ichnogenus

Batrachichnus is a rare ichnotaxon in the “Tregiovo formation”. It has been described by Marchetti et al. (2015c). The ichnogenus *Erpetopus* is a rare ichnotaxon in the “Tregiovo formation”. It has been described as cf. *Erpetopus* by Marchetti et al. (2015c).

The ichnogenus *Hyloidichnus* is a rare ichnotaxon in the “Tregiovo formation”. It has been described by Marchetti et al. (2015c).

Dromopus is a very common ichnotaxon in the “Tregiovo formation”, often occurring in heavily-trampled surfaces (Marchetti et al., 2015c). It has been reported by Conti et al. (1997) and Neri et al. (2000) and described by Marchetti et al. (2015c). The occurrence of *D. didactylus* supposed by Conti et al. (1997) was not confirmed by Marchetti et al. (2015c).

The tetrapod footprints from the Athesian District show remarkable abundance, but compared with the Collio and Orobic basins, the diversity and morphological preservation (*sensu* Marchetti et al., 2019b) are relatively low. As in the Orobic and Collio basins, the ichnoassociation shows a remarkable abundance of

reptile tracks (*Dromopus*, *Erpetopus*, *Hyloidichnus*) and relatively uncommon anamniote tracks (*Amphisauropus*, *Batrachichnus*, *Limnopus*). Nevertheless, the described ichnotaxa represent all the main trackmaker groups found in the Cisuralian of Italy, with the only exception of synapsid tracks that are generally very rare because only one specimen is known (Marchetti, 2016). So, all the main Cisuralian basins of the Southern Alps (Orobic, Collio and Athesian District) show an overall analogue ichnofaunal composition, which is only little modified by lithofacies and age (e.g. Marchetti et al., 2015c, 2017b). Further findings in the Athesian District would be important because the age of the footprint-bearing formations is well-constrained by radiometric dates in this sector (e.g. Marocchi et al., 2008).

9. GEOLOGICAL SETTING AND STRATIGRAPHY OF NW SARDINIA

The continental succession of the Nurra region (northwestern Sardinia) (Fig. 1) was deposited unconformably on Cambro-Ordovician Variscan crystalline basement during the Cisuralian to Middle Triassic, and is represented by a succession of continental sediments evolving into continental-to shallow marine Triassic deposits with the classic Germanic facies (Buntsandstein, Muschelkalk and Keuper *Auct.*). The studied succession, represented by alluvial deposits intercalated with volcanoclastic products, has been investigated in the last decades by several authors (Pecorini, 1962; Vardabasso, 1966; Gasperi and Gelmini, 1980; Cassinis et al., 1996, 2000b; Fontana et al., 2001; Sciunnach, 2001b; Costamagna and Barca, 2002) and was recently correlated with the Toulon succession in SW France (Cassinis et al., 2002, 2003; Durand 2006, 2008; Ronchi et al., 2011a). On the basis of the latest stratigraphic framework (Cassinis et al., 2002, 2003; Ronchi, 2001; Ronchi et al., 2008, 2011a; Romano et al., 2019), the whole succession has been subdivided into three cycles or unconformity-bounded units (or sequences *sensu* Sloss et al., 1949).

The first sequence (0-40 m thick) consists of the “Basal Conglomerate” and the overlying “Punta Lu Caparoni formation”. The very thin “Basal Conglomerate” is made of breccias sourced from the metamorphic bedrock, and rapidly evolves into the “Punta Lu Caparoni formation” (Gasperi and Gelmini, 1980), which in turn consists of dark shales, sandstone sheets and conglomerate bodies deposited in a lacustrine-to alluvial environment. This formation is rich in “late” Autunian macro- and microfloras (Pecorini, 1962; Broutin et al., 1996; Cassinis et al., 2000b). Acidic volcanic rocks of presumed calc-alkaline affinity discontinuously occur in the upper part of the “Punta Lu Caparoni formation” and were recently dated by radiometric methods to the Asselian (Gaggero et al., 2017).

The second sequence (about 600 m in thickness) is widely exposed in the Nurra region (Fig. 2) and consists

of three stacked formations separated by minor erosional surfaces and named, from the bottom to the top, “Pedru Siligu formation”, “Porto Ferro formation” and “Cala del Vino formation”. The “Pedru Siligu formation” (ca. 50 m in thickness) consists of quartz-conglomerates and arenites deposited in a braided stream setting, and at the top it hosts a 20 m thick volcanic interval (Casa Satta volcanic rocks: Cassinis et al., 1996; Cortesogno et al., 1998), recently dated to the early Artinskian (Gaggero et al., 2017). The “Porto Ferro formation” (about 150-200 m in thickness) is made of fossil-barren conglomerates rich in porphyritic clasts and formed in a low-sinuosity river setting. This formation is correlated to the “Les Salettes formation” in Provence where a “post-Kungurian to pre-Tatarian” (i.e. the current late Kungurian macro- and microflora was found (Broutin and Durand, 1995). The “Cala del Vino formation” (ca. 350-400 m in thickness) is made of reddish sandstone and siltstone formed in a meandering river setting. Recent vertebrate and ichnological finds in this last formation provided gross age constraints for this unit to the late Kungurian?-Roadian (e.g. Citton et al., 2019; Romano et al., 2019).

The third sequence (ca. 50 m in thickness) consists of two formations, named “Conglomerato del Porticciolo” and “Arenarie di Cala Viola”, respectively, which are separated by a minor erosional surface. The “Conglomerato del Porticciolo” accumulated in a gravelly braided river setting under conditions of persisting aridity, as suggested by the common occurrence of wind-worn clasts. The “Arenarie di Cala Viola” are made of reddish arenites and subordinate siltstones laid down in relatively sinuous channels. The age of the “Arenarie di Cala Viola” is provided by two distinctive palynomorph assemblages documented in red clastics from the subsurface. Specifically, these suggest Olenekian?-early Anisian and late Anisian ages, respectively (Pittau and Flaviani, 1982; Pittau in Cassinis et al., 2000b; Pittau and Del Rio, 2002).

The vertebrate footprint and body fossil-bearing “Cala del Vino formation” consists of alternating dark red, poorly cemented, mudstone-siltstone deposit and grey-greenish sandstone bodies characterised by different geometries and thickness. The alluvial plain fine sediments appear homogeneous and deeply bioturbated, while the sandstones often have lenticular shape and erosive bases and, where not amalgamated, show internal trough cross-to plane parallel-stratification. Laminations occur also in the medium-to-fine ripple, cross-laminated sandstone. Many of these sandstone bodies show lateral accretion and are thought to represent pointbars. The lenticular sandstone at the top of these bars could represent the infill of small chute-channels cut at the bar top during the main floods. Such lithologies and fluvial architecture are typical of a meandering-channel alluvial system (Fontana et al., 2001; Ghinassi et al., 2009; Ronchi et al., 2011b; Citton et al., 2019). These deposits were laid down by medium-scale, bed-load streams, under a relatively mild semi-arid climate (Ghinassi et al., 2009).

10. THE NW SARDINIA VERTEBRATE ICHNOASSOCIATION

10.1. HISTORICAL OVERVIEW

Recently, tetrapod tracks were found near Cala Viola (Nurra, NW Sardinia) and this find represents the first ichnological record from the Permian of Sardinia (Citton et al., 2019). The ichnological analysis allowed the recognition of tetrapods presently not recognised, from the skeletal remains. This new evidence sheds more light on the faunal diversity within the late Kungurian?-Roadian “Cala del Vino formation”, which is one of the few examples in the Permian of Europe of a combined ichno- and body- fossil record (Ronchi et al., 2011b; Romano and Nicosia, 2014; Romano et al., 2019, Citton et al., 2019). The tracks have been referred by Citton et al. (2019) to *Merifontichnus*, an ichnotaxon established from the uppermost portion of the Permian succession of the Lodève Basin, in southern France (Gand et al., 2000). According to Citton et al. (2019), the new material would be the first reliable occurrence of this ichnotaxon from Italy (see Marchetti, 2016; Marchetti et al., 2017c for other possible occurrences) and may also represent, to date, the oldest occurrence of the ichnogenus.

10.2. ICHNOASSOCIATION STRUCTURE

The tetrapod ichnoassociation from the “Cala del Vino formation” of NW Sardinia (Fig. 7, Tab. 1) currently includes the ichnogenus *Merifontichnus*. Citton et al. (2019) described a left pes of relatively large size (pes

length 9,6 cm) and two consecutive pes-manus couples of smaller size (pes length about 5 cm), belonging to an incomplete step cycle. This occurrence is consistent with a Kungurian or slightly younger age for this tracksite (Schneider et al., 2020), in agreement with the discovery of sphenacodonts and large caseids at the same site (Romano et al., 2019), which is suggestive of a late Kungurian-Roadian age (possibly time-equivalent with the “San Angelo formation” of Texas or slightly younger; Lucas, 2018). The tetrapod footprints from NW Sardinia show a relatively good morphological preservation (*sensu* Marchetti et al., 2019b). The NW Sardinia ichnoassociation is characterized by the only occurrence of possible reptile tracks (*Merifontichnus*) so far. Additional tetrapod footprint material from this site is currently under study.

11. CONCLUSIONS AND PERSPECTIVES

The Cisuralian tetrapod footprints from Italy are generally abundant, well-preserved (*sensu* Marchetti et al., 2019b) and diverse. The ichnoassociation (Tab. 1) is characterised by abundant and diverse reptile tracks (*Dromopus*, *Erpetopus*, *Hyloidichnus*, *Merifontichnus* and *Varanopus*), uncommon anamniote tracks (*Amphisauropus*, *Batrachichnus* and *Limnopus*) and very rare synapsid tracks (cf. *Dimetropus*). The most abundant and diverse ichnoassemblage come from the “Pizzo Del Diavolo formation” of Orobic Basin (e.g. Dozy, 1935; Ceoloni et al., 1987; Nicosia et al., 2001; Santi and

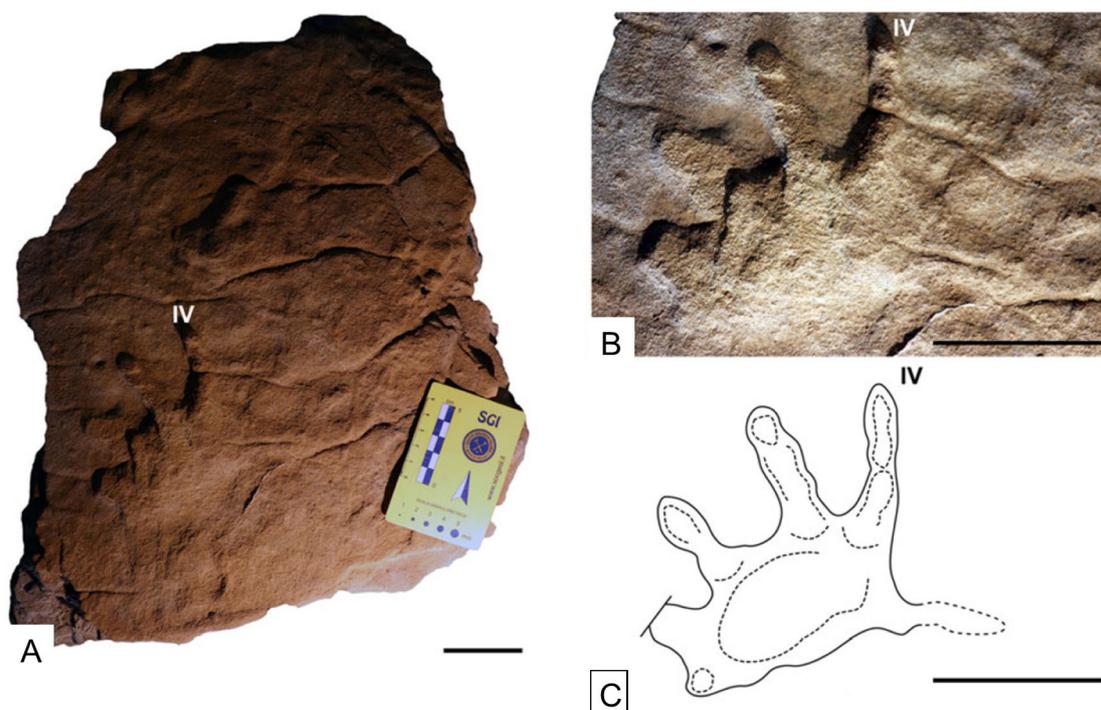


Fig. 7 - Tetrapod ichnogenera from NW Sardinia, Cala del Vino formation. A) UR-NS 170/2. *Merifontichnus*, left pes, convex hyporelief. B) Enlargement of A. C) Interpretive drawing of A. UR- Palaeontological Museum, SAPIENZA Università di Roma. Scale bar 5 cm. (modified after Citton et al., 2019).

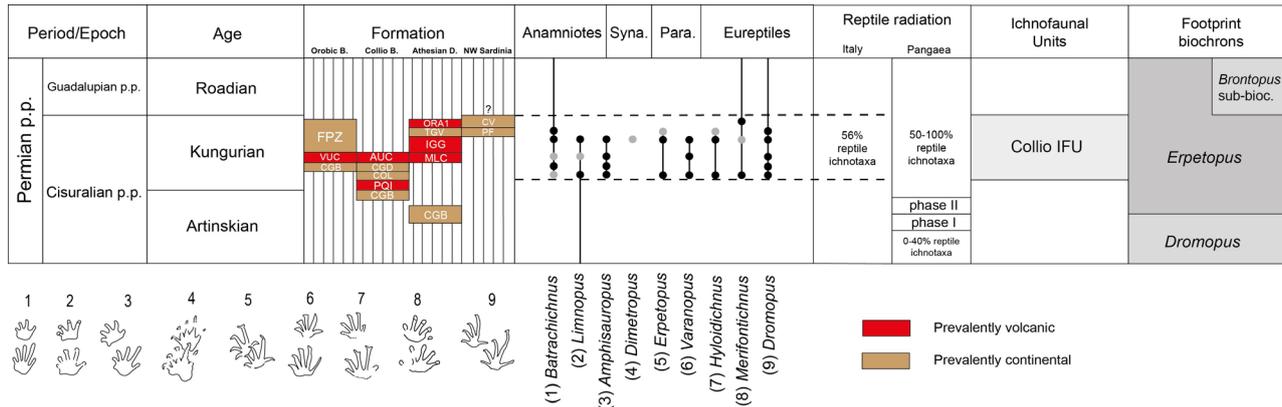


Fig. 8 - Stratigraphic distribution of tetrapod ichnogenera in the Cisuralian of Italy. Grey dots mean uncertain occurrence, the ichnotaxa range includes only occurrences from Italy. See figure 2 for the formation acronyms.

Krieger, 2001; Bernardi and Avanzini, 2011; Marchetti et al., 2013a, 2015a, 2017a, 2017b; Marchetti, 2016; Petti et al., 2014) and the Collio Formation of Collio Basin (e.g. Curioni et al., 1870; Berruti, 1970; Ceoloni et al., 1987; Conti et al., 1991, 1997; Santi, 2007a; Marchetti et al., 2013a, 2013b, 2014, 2015b). Less abundant and diverse occurrences are known from the “Dosso dei Galli Conglomerate” of Collio Basin and the “Monte Luco” and “Tregiovo” formations of the Athesian District (e.g. Conti et al., 1997; Avanzini et al., 2008; Marchetti, 2014; Marchetti et al., 2015c). All these assemblage are central in tetrapod footprint biostratigraphy (Fig. 8), especially because of the availability of several associated radiometric dates (Schaltegger and Brack, 2007; Marocchi et al., 2008; Berra et al., 2016) and sporomorphs (e.g. Cassinis and Doubinger, 1991, 1992; Neri et al., 2000) that constrain the age of the footprint-bearing units to the Kungurian. Thus, these formations are important at the global scale in the definition of the Collio Ichnofaunal Unit (Conti et al., 1997; Avanzini et al., 2001; Marchetti et al., 2019a) and in the definition of the *Erpetopus* tetrapod footprint biochron (Voigt and Lucas, 2018; Schneider et al., 2020). Moreover, the abundance and diversity of reptile tracks compared to anamniote tracks and the rarity of synapsid tracks help to understand the reptile radiation and the decline of anamniotes and pelycosaur-synapsids that started by the mid Cisuralian (Marchetti et al., 2019c; Lucas, 2019) (Fig. 8). The new site from NW Sardinia (Citton et al., 2019) includes few footprints, but the quality of preservation and the association with body fossils are remarkable.

In all, the tetrapod ichnoassociation from the Cisuralian of Italy is central in the studies of ichnotaxonomy, trackmaker attribution, evolution, palaeoecology and biostratigraphy of this time interval. Therefore, further prospecting is strongly recommended especially in the most recently discovered footprint-bearing units.

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