



Jurassic tetrapod tracks from Italy: a training ground for generations of researchers

Fabio Massimo Petti ^{1,*}, Marco Avanzini ¹, Matteo Antonelli ², Massimo Bernardi ¹, Giuseppe Leonardi ³, Riccardo Manni ², Paolo Mietto ⁴, Johannes Pignatti ², Daniele Piubelli ⁵, Enrico Sacco ², Alexander Wagensommer ⁶

¹ MUSE, Museo delle Scienze, Trento, Italy

² Dipartimento di Scienze della Terra, SAPIENZA Università di Roma, Roma, Italy

³ Istituto Cavanis, Venezia, Italy

⁴ Dipartimento di Geoscienze, Università di Padova, Padova, Italy

⁵ Club Speleologico Proteo di Vicenza, Vicenza, Italy

⁶ GRID (Gruppo di Ricerca sulle Impronte di Dinosaurio), San Giovanni Rotondo, Foggia, Italy

* Corresponding author: fabio.petti@socgeol.it

ABSTRACT - This article reports the state of the art of research on the Jurassic tetrapod footprints from Italy. Most dinosaur ichnosites are located in the Southern Alps (Northeastern Italy, Veneto, Trentino Alto-Adige) with the exception of Mattinata (Southern Italy, Gargano Promontory, Apulia) and the Burano River ichnosite (Central Italy, Central Apennines), where a marine tetrapod reptile trackway was found. The Southern Alpine sites occur in four distinct stratigraphic levels of the Lower Jurassic Calcari Grigi Group whereas the Mattinata site is provisionally assigned to the Upper Jurassic Sannicandro Formation (Kimmeridgian-Tithonian).

In this review, we provide geographical and geological setting, age, ichnotaxonomy and the possible identity of trackmakers for each site. Additionally, we report on the history of discovery, the state of the art in ichnological knowledge and the evolution of methodological approaches and techniques adopted through time.

Keywords: dinosaur tracks; Early Jurassic; Calcari Grigi Group; Sannicandro Formation.

Submitted: 11 March 2020-Accepted: 29 May 2020

1. INTRODUCTION

In a chapter on Italian Mesozoic reptiles, written 36 years ago for the book 'Sulle orme dei dinosauri' (Bonaparte et al., 1984), one of the authors of the present study (GL) stated that a special chapter on Italian dinosaurs "cannot exist, because these reptiles had 'snubbed' Italy, or rather the whole of seas and islands that constituted the present Italian peninsula in the Mesozoic" (Leonardi, 1984a, p. 197). This statement reflects the state of knowledge about palaeontology, geology and Mesozoic palaeogeography of the peri-Mediterranean area at the beginning of the 1980's. Only a few years later the situation changed completely.

Actually, the chapter cited above included a picture of the Triassic dinosaur tracks of Mt. Pelmetto (Dolomites, northern Italy), not yet published at that time, that to the regret of the author (GL) was accompanied by a completely wrong caption, added by the publishing house. The trackways of the giant boulder from Mt.

Pelmetto were then soon studied (Mietto, 1988, 1990) and together with the discovery of many dinosaur trackways on the large landslide surface of the Lavini di Marco (Rovereto, Trento, northern Italy), only a few years after the publication of Leonardi (1984a, 1984b) the whole perspective on the Italian Mesozoic changed. At Lavini di Marco, Lanzinger and Leonardi (1991) and Leonardi and Lanzinger (1992) identified several track-bearing horizons in the Calcari Grigi Group, (Hettangian; Monte Zugna Formation). This discovery triggered great media interest and gave rise to a series of discoveries in various outcrops and different stratigraphic levels within the Calcari Grigi Group, both in the Trentino and the Veneto regions (Figs. 1, 2). The perspective widened, in both geographical and stratigraphical terms, when Late Jurassic dinosaur footprints from Apulia (southern Italy) were reported (Conti et al., 2005). In addition to the rich dinosaur-dominated tracksites from these marginal marine environments, unusual tracks referred to swimming marine reptiles have been reported from

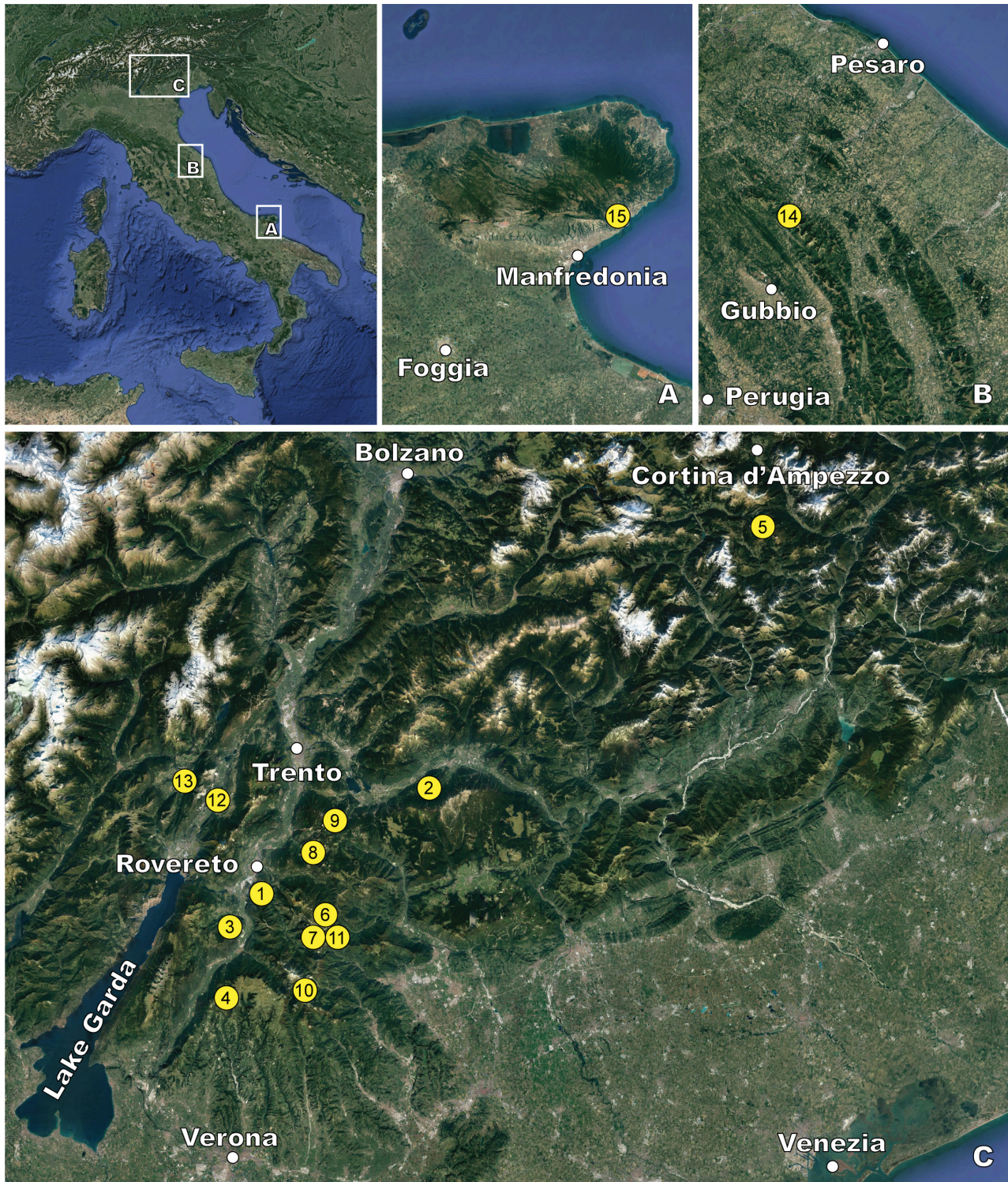


Fig. 1 - Synthetic maps with the location of the Early and Late Jurassic Italian tetrapod tracksites: A) Gargano Promontory. B) Umbria-Marche. C) north-eastern sector of the Southern Alps. Tracksites list: 1) Lavini di Marco; 2) Pizzo di Levico; 3) Chizzola; 4) Sega di Ala; 5) Monte Pelmo; 6) Malga Buse Bisorte; 7) Cima Palon; 8) Monte Finonchio; 9) Becco di Filadonna; 10) Bella Lasta; 11) Stol dei Campiluzzi; 12) Marocche di Dro; 13) Coste dell'Anglone; 14) Burano River; 15) Mattinata.

the Pliensbachian of central Italy (Marche Region; Manni et al., 2000).

Dinosaurs constitute the most conspicuous group of tetrapod trackmakers in the Jurassic of Italy. The Italian Jurassic dinosaur tracksites can be divided into two

groups: the diverse dinosaur ichnoassemblages from the Lower Jurassic Calcari Grigi Group of the Trento plateau (North-Eastern Italy) and the scattered dinosaur footprints from the Apulian platform, which are ex situ (?Late Jurassic or Early Cretaceous).

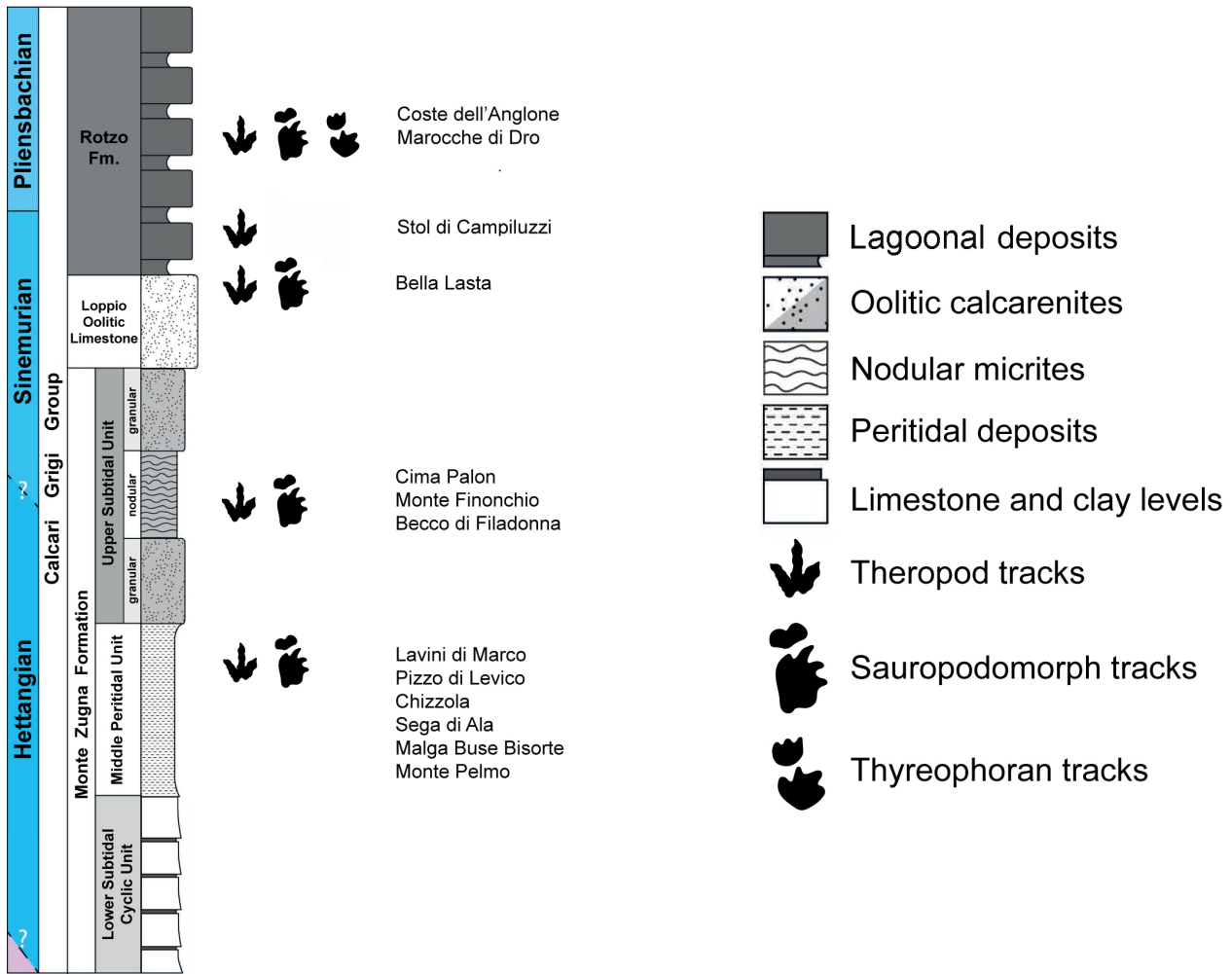


Fig. 2 - Lithostratigraphy of the Calcarei Grigi Group with the stratigraphic position of the track levels. Redrawn after Avanzini et al. (2006).

The Calcarei Grigi Group was deposited on the Trento carbonate platform (Fig. 3a), whose deposits crop out from Verona to Bolzano (NE Italy). This area, characterized by epicontinental deposits during the Triassic, was affected by the rifting phase of the Southern Alps since the Early Jurassic, linked to the opening of the central North Atlantic. Throughout the Early Jurassic, sedimentation was dominated by shallow-water carbonates that are represented by peritidal, subtidal and oolitic facies belts. The Trento carbonate platform was bounded by the Belluno pelagic basin to the east and the Lombardy pelagic basin to the west (Fig. 3A; Bosellini and Broglio Loriga, 1971; Winterer and Bosellini, 1981; Bertotti et al., 1993; Castellarin et al., 2005; Avanzini et al., 2006; Masetti et al., 2012).

The Apulian carbonate platform (Fig. 3B) is a large palaeogeographical unit which, during the Mesozoic, was part of the southern margin of the Tethys Ocean. It is considered one of the shallow-water domains within the Periadriatic sector ('Periadriatic carbonate platforms' *sensu* Zappaterra, 1990, 1994), quite similar in facies architecture, size and shape to the modern Bahama Banks (Bernoulli, 1972; D'Argenio, 1976).

During Middle-Late Jurassic and Cretaceous times, the Apulian carbonate platform has been interpreted as a small and isolated area, separated from other Periadriatic carbonate shelves (e.g. the Adriatic-Dinaric and Apenninic carbonate platforms) by pelagic basins (e.g. Lagonegro-Molise, Umbria-Marche-Sabina, Belluno, Imerese-Sicanian, and East-Gargano basins) and far from the continental margins of Eurasia and Gondwana (Zappaterra, 1990).

2. EARLY JURASSIC TETRAPOD FOOTPRINTS FROM ITALY

2.1. LAVINI DI MARCO ICHNOSITE, ROVERETO (TRENTINO-ALTO ADIGE, NORTHERN ITALY), HETTANGIAN

Lanzinger and Leonardi (1991) and Leonardi and Lanzinger (1992) were the first to record the occurrence of several dinosaur tracks in the area of Lavini di Marco, located near Rovereto, some 25 kilometres SSW of Trento, on the western slope of Mt. Zugna (Trentino-Alto Adige) (Fig. 4). The tracksite is one of the most important European dinosaur track localities, and has been the

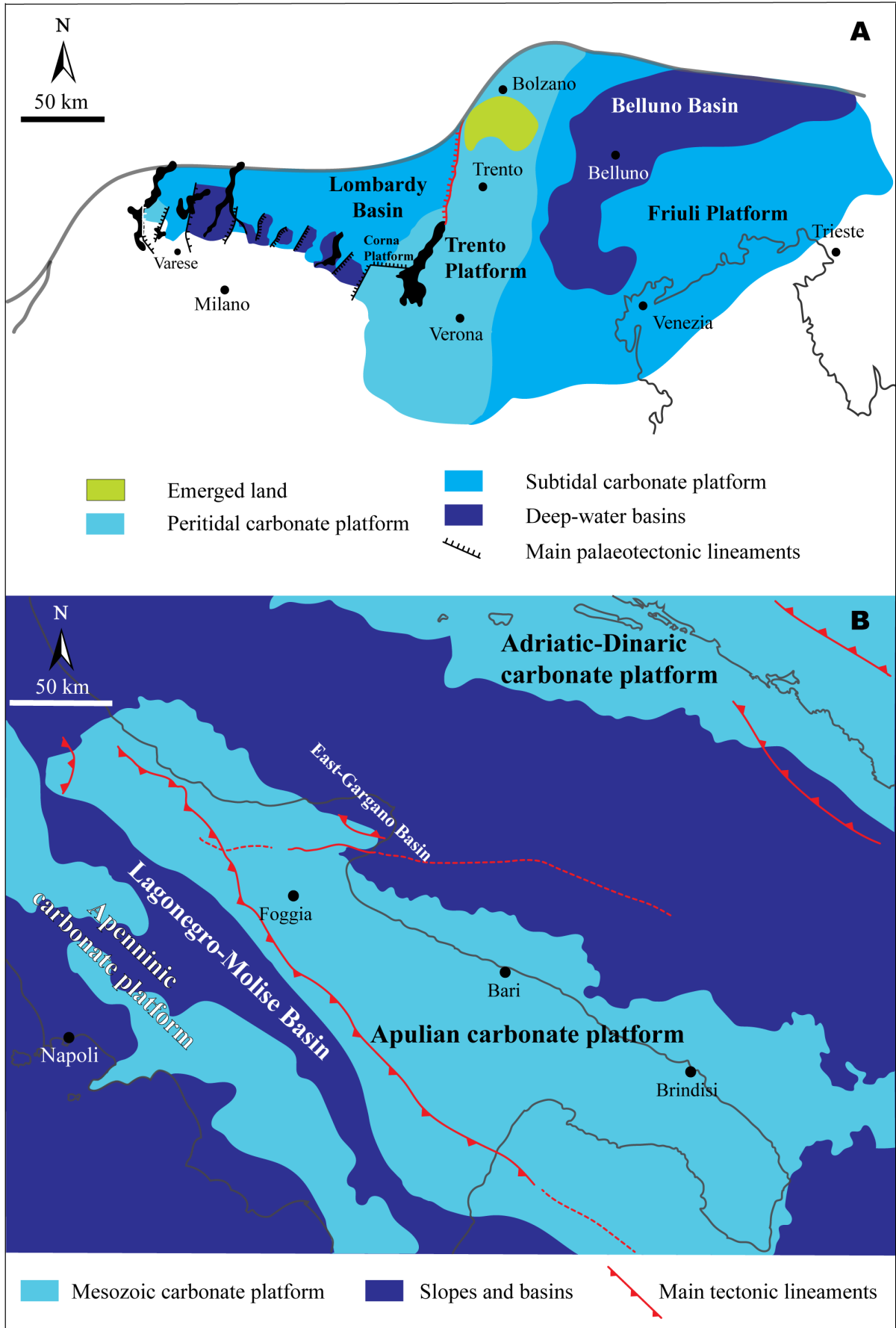


Fig. 3 - A) Palaeogeographic restoration of the central-eastern Southern Alps during the Early Jurassic. B) the Apulia carbonate platform and the adjacent Mesozoic palaeogeographic domains. Redrawn after Petti et al. (2011b) and Morsilli et al. (2017).

subject of several studies since its initial discovery in 1989 by the amateur naturalist Luciano Chemini (Lanzinger and Leonardi, 1991; Leonardi and Lanzinger, 1992; Avanzini and Leonardi, 1993, 1995, 1999; Leonardi and Avanzini, 1994; Avanzini et al., 1995, 1997, 2000 a,b,c, 2001a, 2003, 2006; Leonardi, 1996, 1997, 2000, 2008; Avanzini and Finotti, 1998; Leonardi and Mietto, 2000; Lockley and Meyer, 2000; Avanzini, 2002; Nicosia et al., 2005; Piubelli et al., 2005; Piubelli, 2006). The area is located on a wide monoclinial surface, produced by several landslide events of prehistorical and historical age between 21.200 ± 100 and 800 ± 200 years B.P. (Martin et al., 2014) that covers about $300,000 \text{ m}^2$ (Leonardi and Mietto, 2000; Piubelli et al., 2005).

The first systematic study of such a large and important ichnosite required several preliminary surveys and two major field campaigns (June 1992 and June 1993) directed by Giuseppe Leonardi and Paolo Mietto. Financial and logistical support came from the Museo Tridentino di Scienze Naturali di Trento (now MUSE, Science Museum of Trento), through its director Gino Tomasi and the then curator of the Geology and Palaeontology section Michele Lanzinger, presently director of MUSE. Additional support came from the Museo Civico di Rovereto, through its director Franco Finotti, who was a constant presence during the field campaigns and promoted the conservation, enhancement and musealisation of the Dinosaur Tracks Park of Rovereto (Arzarello et al., 2000). During these two campaigns the first 200 individual dinosaur tracks were numbered, photographed, classified,

and some of them were moulded. Trackways were marked with metal plates, each carrying the code and number of footprints, to provide a metric scale and to show the midline axis. Many other footprints were discovered and numbered later, currently reaching about 800 individual tracks in this locality (Avanzini et al., 2003, 2005, 2006; Piubelli et al., 2004, 2005; Piubelli, 2006; Antonelli, 2018; Sacco, 2018).

This site was the training ground for many Italian students and researchers to develop methods and techniques in modern ichnology. The first study of this tracksite led to the publication of a large collective volume, coordinated by the two above-mentioned museums and with the support of the National Research Council (CNR) and the Autonomous Province of Trento (Leonardi and Mietto, 2000).

The Lavini di Marco tracksite consists of alternating stromatolite and dolomite levels, light grey peloidal mudstones, dark grey bioclastic wackestones and reddish mudstones (Avanzini et al., 1997).

Seven track-bearing layers have been identified within a 7 meters thick section: they belong to the 'Middle Peritidal Unit' of the Monte Zugna Formation. Rare microfossils (e.g. the dasycladalean *Palaeodasycladus mediterraneus*) indicate a Hettangian age (Avanzini et al., 2006; Avanzini and Petti, 2008).

Several ichnological surveys led to the identification of hundreds of tracks, preserved as concave epirelief (*sensu* Leonardi, 1987) and assigned to both bipedal and quadrupedal dinosaurs (Figs. 5, 6; Leonardi and Mietto,



Fig. 4 - Field campaign at the Lavini di Marco tracksite in 1991; from left to right Michele Lanzinger, Franco Finotti, and Paolo Mietto.

2000).

Leonardi and Mietto (2000) described six functionally tridactyl morphotypes (Pl. 1, figs. a-f), attributed to small to medium-sized theropods, with footprint lengths rarely exceeding 20 cm. Depending on features such as size and divarication angle of the footprints, shape and relative proportions of the digits, presence/absence of a partial metatarsal impression (described as a wedge-shaped wide “heel”, often accounting for about half the area of the whole track) and hallux mark (reported from a single footprint only), the morphotypes were compared with the widespread Early Jurassic ichnotaxa *Grallator* and *Eubrontes*, the Triassic ichnogenus *Coelurosaurichnus* (junior synonym of *Grallator* according to Leonardi and Lockley, 1995) and the Cretaceous ichnogenera *Columbosauripus* and *Bueckeburgichnus*. The authors however explicitly stated that this comparison is meant to highlight morphological similarities and that they were not formally referring their morphotypes to any of these ichnotaxa.

Piubelli (2006) reassessed the morphotype subdivision and grouped all tridactyl tracks into four morphotypes only (named LA1, LA2, LA3, LA4), based on morphological and morphometrical analyses (Pl. 1, figs. g-j). A type specimen was designated for each



Fig. 5 - Aerial view of trackway ROLM 1 at the Colatoio Chemini taken in 1991.



Fig. 6 - The largest theropod footprints found at the Lavini di Marco ichnosite (ROLM 219). From left to right: Ilario Sirigu, Marco Avanzini, and Giuseppe Leonardi.

morphotype. LA1 is defined as a small-sized track, longer than wide, with low values of the total divarication and a highly extended digit III. LA2 is a medium to large-sized footprint, characterized by digits widening distally, high total divarication and triangular shape of the heel. LA3 is a small to large-sized tridactyl impression (FL between 10 cm and 27 cm), characterized by FL/FW ratio ranging between 1.2 and 1.5, narrow digit III, low mesaxony, total divarication about 55°. Tracks belonging to LA4 are large-sized (FL > 22 cm; FW > 15 cm), longer than wide ($1.3 < FL/FW < 1.5$), characterized by stubby and highly divaricated digits and marked extension of digit III ($te/FW \geq 0.5$).

The ichnotaxonomical analysis provided by Piubelli et al. (2005) and Piubelli (2006) led to the identification of a theropod ichnoassemblage composed by the ichnogenera *Grallator* and *Kayentapus* (type specimen ROLM 418; Pl. 1, fig. j). *Kayentapus* isp., an ichnogenus usually associated to a dilophosaur-like trackmaker and known from the Early Jurassic of North America (Welles, 1971) and Northern Europe (Gierliński, 1991; Gierliński and Alhberg, 1994), represents the main ichnotaxon of the Lavini di Marco ichnoassemblage (Piubelli et al., 2005;

Piubelli, 2006). The global distribution of this ichnotaxon led the authors to the conclusion that a wide connection, probably represented by the Southern Alps sector, between Laurasia and Gondwana existed during the Early Jurassic (Piubelli et al., 2005).

Avanzini et al. (2001a) reported the occurrence of a couple of tridactyl tracks representing the right and left foot of the same small individual, set side-by-side and sub-parallel with metatarsal impressions. This led them to the suggestion that they might represent a resting posture. The tracks were originally assigned to the ichnogenus *Anomoepus* and attributed to a small ornithischian. According to Avanzini et al. (2001a), these *Anomoepus* specimens show affinities with the forms documented from South Africa (Ellenberger, 1972; Olsen and Galton, 1984; Haubold, 1986), and differ from the specimens from Poland (Gierliński, 1991; Gierliński and Pieńkowski, 1999), thus suggesting a Gondwanan origin for the Lavini di Marco ichnoassemblage.

Recent investigations by FMP, MA and ES (Antonelli, 2018) have shown that the supposed 'metatarsal impressions' described by Avanzini et al. (2001a) are actually due to the overlap of distinct tridactyl footprints. The hypothesis of *Anomoepus* with metatarsal impressions is likely to be rejected.

Since the first studies, 15 trackways produced by herbivorous dinosaurs were identified. Leonardi and Mietto (2000) described two morphotypes, initially referred to sauropod and possible ornithopod trackmakers, respectively.

Undisputable sauropods (Fig. 7) are represented by about 15 short trackway segments, the longest being 7 meters long and constituted by 10 *manus-pes* couples. All trackways in this morphogroup are quadrupedal and narrow-gauge, with the *manus-pes* axis slightly outward oriented (32°) with respect to the trackway midline. The *pes* prints are pear-shaped and up to 52 cm long, often with evident raised rims, and sometimes four small digital impressions are identifiable. The *manus* prints are kidney-shaped, smaller than the associated pedal impressions and externally located with respect to the hindlimb tracks. In four trackways, the *manus* prints are not well-impressed or covered by the overlapping pedal track. Leonardi and Mietto (2000) compared the Lavini di Marco sauropod tracks to the ichnogenera *Parabrontopodus* and *Breviparopus* (Pl. 2, figs. d and f), attributing them to trackmakers belonging to the Eusauropoda group, such as the Vulcanodontidae or the Cetiosauridae.

Five trackways were assigned by Leonardi and Mietto (2000) to a bipedal or semi-bipedal trackmaker (Fig. 8; Pl. 2, fig. e), possibly an ornithopod (but see below for more recent discussion on this topic). The longest trackway in this morphogroup is fourteen meters long and composed of 24 tracks. It is characterized by alternating long and short oblique pace and sub-elliptical or pear-shaped tracks, in which three rounded large digits (II-III-IV) and, rarely, a short and small spur-shaped digit (I) are

recognizable. The remaining four trackways referred to this morphogroup are roughly similar, but partly differ in the stubbier shape of the ectaxonic *pes*, characterized by a triangular and elongated heel impression, given by the long impression of digit IV (Leonardi and Mietto, 2000).

After carefully reviewing these trackways and isolated footprints in the field, there is consensus among the authors of this study that they must be attributed to sauropods, which was given as a second alternative hypothesis by Leonardi and Mietto (2000, p. 209).

Avanzini et al. (2003) described the new ichnotaxon *Lavinipes cheminii* from the Lavini di Marco tracksite, referred to a quadrupedal dinosaur (Pl. 2, figs. a-c). The holotype trackway is narrow-gauge, with a tetradactyl *pes* longer than wide (FL=43 cm; FW=31 cm) and a pentadactyl, U-shaped *manus*, wider than long (FL=19 cm; FW=25 cm). Beside the holotype, Avanzini et al. (2003) refer a second trackway to this new ichnotaxon. This quadrupedal form shares some affinities with the ichnotaxa *Otozoum* and *Pseudotetrasauropus*, generally referred to sauropodomorph dinosaurs, but it clearly differs for other characters such as gait (quadruped), digit morphology and numbers.

As a result, the ichnotaxonomical analysis justifies the establishment of the new ichnotaxon *Lavinipes*

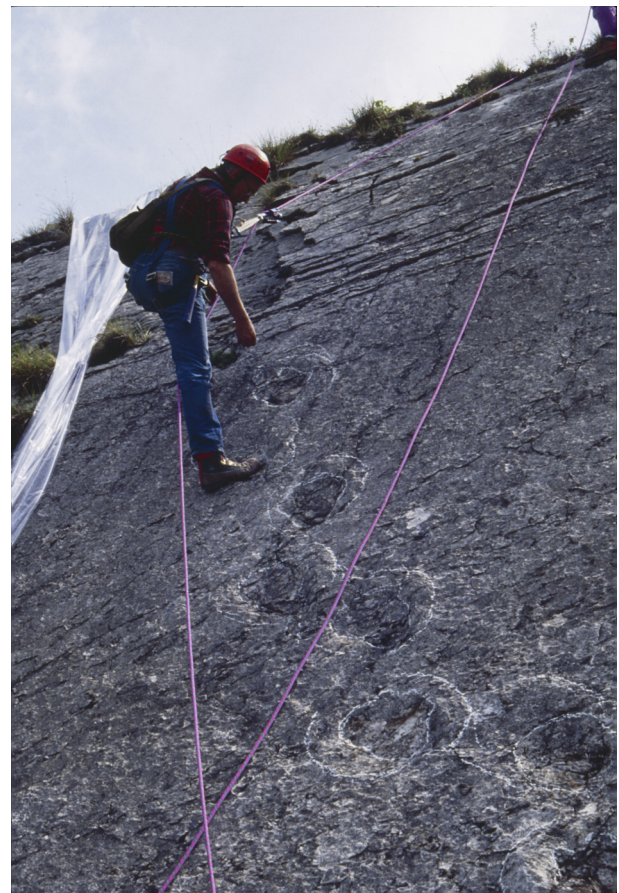


Fig. 7 - Giuseppe Leonardi on the rope analysing one of the quadrupedal trackways (ROLM 26) of the Lavini di Marco tracksite during the field campaign of 1992.



Fig. 8 - The bipedal trackway ROLM 9 at the Colatoio Chemini taken in 2019 (Giuseppe Leonardi for scale).

cheminii Avanzini, Leonardi and Mietto, 2003. Avanzini et al. (2003) attributed *Lavinipes cheminii* to a primitive sauropod trackmaker, related to the basal Eusauropoda group.

In summer 2010 new ichnological surveys were performed by a team composed by researchers from the Geology Section of the Museo Tridentino di Scienze Naturali (now the MUSE, Science Museum of Trento) and the Geological Survey of the Autonomous Province of Trento. During this period the various track-bearing surfaces were carefully analysed and each footprint was georeferenced (Fig. 9).

In 2018, an ichnological review of the Lavini di Marco tracksite was carried out by FMP, MB, MA and ES, within a joint project between MUSE, Sapienza University of Rome and the Autonomous Province of Trento. The results were preliminarily published in two master's degree theses (Antonelli, 2018; Sacco, 2018). The analysis started with a new ichnological survey that led to the identification of more than 700 tridactyl footprints and several quadrupedal trackways. The field work was carried out with combining close-range and aerial photogrammetry to study the tracksite both at the meso- and macroscale. Different types of Unmanned Aerial Vehicles (UAVs; i.e. drones) were used to produce the first detailed map of the large and complex dinosaur track-bearing surface. Close-range photogrammetry

models provided extremely detailed information, permitting careful analysis of morphological characters and more reliable ichnotaxonomical assignments and ichnosystematic attributions. Morphological and morphometrical analyses led to assign the tridactyl tracks to the ichnogenera *Anchisauripus*, *Grallator*, *Eubrontes*, and *Kayentapus* (Antonelli, 2018). The ichnotaxonomical review of quadrupedal trackways led to an emended diagnosis of *Lavinipes cheminii* and to assign several other isolated tracks and trackways to *L. cheminii* (Sacco, 2018). *Panguraptor*-like and *Sinosaurus*-like theropods have been identified as most likely trackmakers for the tridactyl footprints (Antonelli, 2018), whereas the sauropodomorph *Gongxianosaurus* has been identified as the most likely trackmaker of *Lavinipes cheminii* (Sacco, 2018). The ichnoassemblage reveals a clear Laurasian affinity allowing to hypothesize that during the Early Jurassic the Trento carbonate platform was probably connected to Laurasia through the northern and western sectors of the Southern Alps. These issues will be dealt with in a forthcoming publication.

It should be noted that also a synapsid track assigned to the ichnogenus *Brasilichnium* Leonardi, 1981, has been discovered at the Lavini di Marco ichnosite (Piubelli et al., 2004).

From 2001, the Lavini di Marco ichnosite has been under the supervision of the Civic Museum of Rovereto



Fig. 9 - Georeferencing footprints at the Colatoio Chemini in summer 2010.

and the Museo Tridentino di Scienze Naturali (now MUSE), with the creation of educational trails, walkways and illustrative panels.

2.2. PIZZO DI LEVICO ICHNOSITE, CALDONAZZO LAKE (TRENTINO-ALTO ADIGE, NORTHERN ITALY), HETTANGIAN

Avanzini and Tomasoni (2002) described an isolated tridactyl dinosaur track from the carbonate deposits of Pizzo di Levico. The ichnite was discovered by the authors during the geological survey of the Cima Vezzena area for the CARG Project (Geological CARTography). The locality is about 6 kilometres south-east of the Caldonazzo Lake (Valsugana, Trentino-Alto Adige).

The outcrop belongs to the 'Middle Peritidal Unit' (*sensu* Avanzini et al., 2006) of the Monte Zugna Formation (Hettangian). The track (Fig. 10) is preserved at the top of a reddish oolitic grainstone with intraclasts and black pebbles, but it is most likely an underprint of a tridactyl track left in the overlying stromatolitic horizon (Avanzini and Tomasoni, 2002). The specimen, referred to a medium-sized theropod, shows two clear phalangeal pads on digits II and IV, with digit III better preserved and not exceeding the length of the other digits. It was originally assigned to the ichnogenus *Eubrontes* (Avanzini and Tomasoni, 2002); later, Avanzini and Petti (2008) referred it to the ichnogenus *Kayentapus*.

2.3. CHIZZOLA ICHNOSITE, ALA (TRENTINO-ALTO ADIGE, NORTHERN ITALY), HETTANGIAN

Leonardi and Mietto (2000) described three dinosaur tracks along the provincial road SP 22 leading from Mori to Ala (TN), 3 km south of the Lavini di Marco tracksite. These tracks are no longer visible, having been destroyed during road work.

The track layer forms part of the 'Middle Peritidal Unit' (Fig. 2) of the Monte Zugna Formation and it is therefore Hettangian in age (Leonardi and Mietto, 2000; Avanzini and Petti, 2008). The tracks are preserved as convex hyporelief (*sensu* Leonardi, 1987) on the lower surface of a light-grey stromatolitic interval, dolomitized at the top (Avanzini et al., 1997; Leonardi and Mietto, 2000). The best-preserved track was a left tridactyl footprint, 33 cm long (Pl. 3, fig. a); it showed stubby digits, in which several phalangeal pads were recognizable, with sharp claw marks (Leonardi and Mietto, 2000). Although originally attributed to the ichnogenus *Eubrontes* (Leonardi and Mietto, 2000), the morphology of this track shows close affinities with *Kayentapus* *isp.* (Avanzini and Petti, 2008). This large footprint was referred to a large ceratosaur-like trackmaker (Leonardi and Mietto, 2000). The remaining two tracks were poorly preserved: the first was originally referred to an herbivorous dinosaur, while the second was attributed to a small-sized theropod (Leonardi and Mietto, 2000).

2.4. SEGA DI ALA ICHNOSITE, LESSINI MOUNTAINS (TRENTINO-ALTO ADIGE, NORTHERN ITALY), HETTANGIAN

Avanzini (2001) described an isolated dinosaur track from a section along the Ala-Passo Fittanze road, south-east of Ala (Lessini Mountains, Trentino-Alto Adige).

The track layer is Hettangian in age, belonging to the 'Middle Peritidal Unit' (Fig. 2) of the Monte Zugna Formation. The footprint is preserved in a natural vertical section (Avanzini, 2001). Three depressions are clearly visible, suggesting the occurrence of a tridactyl track. The central depression, interpreted as that of digit III, is the deepest (i.e. 3 cm in depth), while the lateral depressions, interpreted as digits II and IV, reach 2 cm in depth. The track was referred to a medium-sized theropod (Avanzini and Petti, 2008).

2.5. MONTE PELMO ICHNOSITE, DOLOMITES (VENETO, NORTHERN ITALY), HETTANGIAN

Mietto et al. (2012) first recorded the occurrence of possible dinosaur tracks from Monte Pelmo (Dolomiti di Zoldo, Belluno, Veneto), 3037 m above sea level. Belvedere et al. (2017) described the tracksite, located in the lower part of the Calcarei Grigi succession, which is characterized by shallowing upward peritidal cycles (Fig. 11). The track-bearing level lies within the 'Middle Peritidal Unit' (Fig. 2) of the Monte Zugna Formation, indicating a Hettangian age (Belvedere et al., 2017).

Twenty tracks have been recognized, forming three or four trackways: they are very poorly preserved but can be



Fig. 10 - The medium-sized theropod footprint from the Pizzo di Levico ichnosite.

attributed to three different morphotypes.

The first one is represented by a shallow tridactyl footprint (PELM. A1), referred to a theropod trackmaker and morphologically similar to *Kayentapus* isp., although the lack of anatomical details prevents a reliable ichnotaxonomical assignment (Belvedere et al., 2017).

The second morphotype is represented by five or six irregular tracks arranged in a bipedal trackway (PELM. B), in which anatomical details are not preserved. Only PELM. B5 displays a slender tridactyl morphology: the elongated digit III and the narrow interdigital angles show some morphological affinity with the ichnogenus *Grallator* (Belvedere et al., 2017).

The third morphotype is represented by six large tracks (PELM. D), longer than wide, in which only one (PELM. D1) shows a smaller impression, interpreted as the forelimb track of a quadrupedal trackmaker with a marked heteropody. The poor preservation of the tracks prevents a reliable ichnotaxonomical assignment, although they share some affinity with *Parabrontopodus* isp., usually referred to a sauropodomorph trackmaker (Belvedere et al., 2017).

The ichnosite of Monte Pelmo is illustrated in the Vittorino Cazzetta Museum in Selva di Cadore (Belluno) together with a 3D reproduction of theropod footprint derived from a photogrammetric model.

2.6. MALGA BUSE BISORTE AND CIMA PALON ICHNOSITE, MONTE PASUBIO (TRENTINO-ALTO ADIGE, NORTHERN ITALY), LATE HETTANGIAN - EARLY SINEMURIAN

Avanzini (2001) recorded the discovery of two track-bearing outcrops from the Monte Pasubio area, about 10 kilometres south-east of Rovereto (Trentino-Alto Adige). The first track horizon is situated near Malga Buse Bisorte, 1885 m above sea level.

The dinosaur tracks occur at the top of the lower stromatolitic layers of the 'Middle Peritidal Unit' (Fig. 2) of the Monte Zugna Formation, so their age can be referred to the Hettangian (Avanzini and Petti, 2008).

The second track-bearing surface is located west of Cima Palon (Dente Italiano), 2187 m above sea level. It crops out within a stratigraphic interval characterized by nodular brown and dark grey, bioturbated mudstones to wackestones, and marked by the occurrence of two different stromatolitic layers (Fig. 12). The deposits belong to the 'Upper Subtidal Unit' (*sensu* Avanzini et al., 2006) of the Monte Zugna Formation, suggesting a Hettangian to Sinemurian age (Avanzini and Petti, 2008). Tracks from Monte Pasubio are isolated and show a sub-circular morphology, with an average diameter of 30 cm (Avanzini and Petti, 2008). They are surrounded by clear raised rims, whereas the deepest part of the depression occasionally shows collapse structures. The ichnoassemblage of the Monte Pasubio has been attributed to medium-sized sauropodomorph trackmakers, whereas an ichnotaxonomical assignment remains difficult, due to the poor preservation of the anatomical features of the analysed tracks (Avanzini and Petti, 2008).

2.7. MONTE FINONCHIO ICHNOSITE, ROVERETO (TRENTINO-ALTO ADIGE, NORTHERN ITALY), LATE HETTANGIAN - EARLY SINEMURIAN

Avanzini et al. (2008) described five *manus-pes* sets from the western flank of the Monte Finonchio, close to S. Corrado, within the deposits of the 'Upper Subtidal Unit' (Fig. 2) of the Monte Zugna Formation (late Hettangian-early Sinemurian). The stratigraphic interval is characterized by a basal grainy deposit covered by brown and dark grey mudstone-wackestone, within which nodular beds show tractive sedimentary structures (Avanzini et al., 2008).

The dinosaur tracks are preserved as underprints at the top of a mudstone level overlain by a stromatolitic horizon. The track-bearing surface is represented by a steep wall and extremely difficult to access (Fig. 13). For this reason, the ichnological documentation was carried out using a terrestrial laser scanner (TLS), with the aim to obtain a 3D model of the whole surface. The acquisition was performed with a Leica ScanStation 2 laser scanner from a distance of 90 m, setting a mean point to point spacing of 0.005 m (Avanzini et al., 2008). The poorly preserved quadrupedal tracks occur on three superimposed carbonate layers and were interpreted as undertracks, due to their shallow depth (Avanzini et al.,

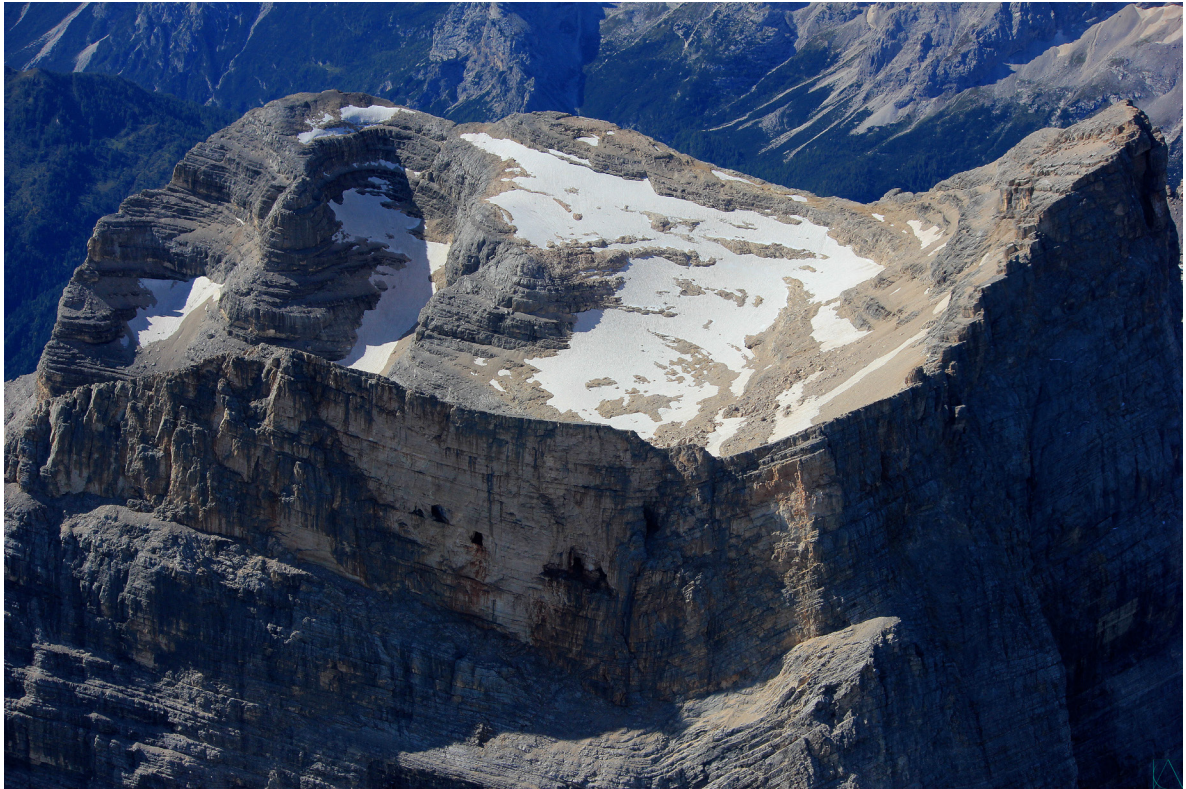


Fig. 11 - The Mount Pelmo in the Eastern Dolomites; in the foreground, the narrow surface where dinosaur footprints are preserved (Photo by M. Belvedere).



Fig. 12 - Medium-sized saurpodomorph tracks preserved in vertical cross section at Cima Palon (Monte Pasubio, Rovereto; Hettangian-Sinemurian).

2008). The pes tracks show an elliptical shape and are larger than the associated *manus* tracks (sub-circular or sub-elliptical), showing a marked heteropody. The *manus-pes* distance is generally about 50 cm, even if sometimes the tracks overlap. The forelimb prints are outward rotated with respect to pes-long axis, with an angle ranging from 20° to 25° (Avanzini et al., 2008). In the best-preserved set, the *manus* is 15.5 cm long and 14 cm wide, whereas the *pes* is 64 cm long and 57 cm wide, showing an asymmetric morphology, narrower and deeper in the proximal area (Avanzini et al., 2008). After comparison with some narrow-gauge sauropod trackways from the Early Jurassic of Poland (Gierliński, 1997; Gierliński and Pieńkowski, 1999) and other large sauropod footprints from the Calcari Grigi (Avanzini et al., 2006), Avanzini et al. (2008) referred the Monte Finonchio tracks to the ichnogenus *Parabrontopodus*.

2.8. BECCO DI FILADONNA ICHNOSITE, VAL GOLA (TRENTINO-ALTO ADIGE, NORTHERN ITALY), LATE HETTANGIAN - EARLY SINEMURIAN

Avanzini (1997) described two distinct dinosaur track-bearing horizons, recognized on the slope of the Val Gola, a wide valley west of the Becco di Filadonna massif in the Province of Trento.

The track-bearing horizons are found in the Monte

Zugna Formation. The first layer is represented by a dolomitized stromatolitic bindstone of the 'Middle Peritidal Unit'. The second horizon is located at the top of two stromatolitic levels, overlying bioturbated brown and dark grey wackestones to packstones: these deposits belong to the 'Upper Subtidal Unit' of Hettangian-early Sinemurian age (Avanzini, 1997; Avanzini et al., 2006; Avanzini and Petti, 2008).

The ichnoassemblage from Becco di Filadonna consists of isolated tridactyl tracks, assigned to medium-sized theropods, and large quadrupedal trackways, referred to medium-sized sauropods (Fig. 14) (Avanzini, 1997; Leonardi and Mietto, 2000; Avanzini and Petti, 2008).

The tridactyl tracks are not well preserved, but stout and deep digit impressions are clearly recognizable, suggesting a tentative ichnotaxonomic assignment to *Eubrontes* isp. (Avanzini, 1997; Leonardi and Mietto, 2000).

Likewise, the *manus-pes* couples, arranged in narrow-gauge trackways, show a poor preservation, without anatomical details (Avanzini and Petti, 2008). In the best-preserved tracks, the *manus* print is wider (FW=44 cm) than long (FL=32 cm) and shows an irregular outline, with three shallow impressions, interpreted as possible digit prints. The associated *pes* print, emphasized by large raised rims, is sub-elliptical, deeper in its proximal portion and longer (FL=75 cm) than wide (FW=50 cm) (Avanzini, 1997; Leonardi and Mietto, 2000). The



Fig. 13 - The steep surface of the Monte Finonchio ichnosite where faintly visible quadrupedal footprints are preserved.

narrow-gauge arrangement of the trackways suggests an assignment of these quadrupedal footprints to the ichnogenus *Parabrontopodus* (Avanzini, 1997; Avanzini and Petti, 2008).

2.9. BELLA LASTA ICHNOSITE, LESSINI MOUNTAINS (VENETO, NORTHERN ITALY), LATE SINEMURIAN

Mietto et al. (2000) analysed several dinosaur tracks from the 'Bella Lasta' site (Province of Verona), located on the western slope of the Revolto Valley, between Passo Malera and Cima Trappola (Lessini Mountains).

Five track layers have been recognized in a 8.5 m thick stratigraphic succession, near the boundary between the Loppio Oolitic Limestone and the Rotzo Formation (Mietto and Roghi, 1993; Roghi, 1994; Mietto et al., 2000; Avanzini and Petti, 2008).

The lower track-bearing interval (layers VRBL 20, 25, 1 and 5) is 70 cm thick. It is characterized by oolitic grainstone (oolitic bars), produced by tidal currents in shallow marine environments and early cemented by endolithic algae, while the upper interval (layers VRBL 2, 3 and 4) is a wackestone with pyrite nodules, suggesting a lagoonal palaeoenvironment (Mietto et al., 2000).

These deposits are covered by a 10 cm thick slightly



Fig. 14 - Sauropodomorph tracks of the Becco di Filadonna ichnosite (Val Gola, Trento; scale bar 30 cm).

terrigenous limestone, with abundant bivalves and gastropods (Mietto et al., 2000; Avanzini and Petti, 2008). The age of the track-bearing interval is late Sinemurian (Avanzini and Petti, 2008).

So far as the ichnological record reported by Mietto et al. (2000) is concerned, only two morphotypes have been identified. The first, comprising only two well-preserved successive footprints, is tridactyl, with tracks about 31.5 cm long and 28 cm wide (Fig. 15; Pl. 3, fig. b). The high total divarication angle between digits II and IV suggested to Mietto et al. (2000) to assign these tridactyl tracks to the ichnogenus *Kayentapus*. The second morphotype is represented by irregular *manus-pes* sets left by a quadrupedal trackmaker. The *pes* print is sub-circular and wider than long (FL=21 cm; FW=30 cm). The associated *manus* is sub-circular, 17 cm long and 14 cm wide. Mietto et al. (2000) noticed an affinity of the Bella Lasta quadrupedal specimen with some tracks from the Lavini di Marco site referred to sauropods. Nevertheless, due to the significantly different shape of the *manus* print of the Bella Lasta quadrupedal track, with respect to sauropod forelimb tracks, the analysed specimen was just tentatively referred to a sauropod or prosauropod trackmaker (Mietto et al., 2000).

By order of the Soprintendenza Archeologica del Veneto, in 2001 the two tridactyl footprints were removed by the staff of the Civic Museum of Natural History of Verona. These ichnites are currently on exhibit at the Geopaleontological Museum of Camposilvano (Velo Veronese, Verona).

2.10. STOL DEI CAMPILUZZI ICHNOSITE, MONTE PASUBIO (TRENTINO-ALTO ADIGE, NORTHERN ITALY), LATE SINEMURIAN

Petti et al. (2011a) reported the occurrence of three dinosaur tracks in the Stol dei Campiluzzi tunnel, dug by the Austro-Hungarian and Italian armies during the First World War. The tunnel is located below the Campiluzzi saddle, west of Monte Buso, in the Monte Pasubio massif (Trentino-Alto Adige); it is about 250 m long, 2.5 m wide and 2 m high (Petti et al., 2011a).

The stratigraphic section of the Stol dei Campiluzzi has a thickness of 19 m. At the base it is composed of massive oolitic grainstone, 80 cm thick, marked by low-angle cross laminations: these deposits belong to the Loppio Oolitic Limestone, and are overlain by a reddish surface, interpreted as evidence of subaerial exposure. The overlying Rotzo Formation starts with a 13 m thick interval composed of well-stratified, grey to yellow limestone-marl alternations. The deposits are characterized by the occurrence, in various layers, of: i) wackestone to packstone with intraclasts and bioclasts; ii) four black shale levels with bivalves (*Eomiodon* sp. and *Lithioperma* sp.). The dinosaur track-bearing horizons are located between the second and the third level rich in organic matter. Thin-bedded and nodular limestones (5 m thick), showing invertebrate burrows (*Thalassinoides* isp.), are found at the top of the section. The age of the



Fig. 15 - A theropod track from Bella Lasta ichnosite (Lessini Mountains, Verona; scale bar 10 cm).

dinosaur tracks is considered as late Sinemurian (Petti et al., 2011a).

The vertebrate track record is composed of three mesaxononic and functionally tridactyl tracks preserved on the roof of the tunnel (Fig. 16; Pl. 3, fig. c) as convex hyporeliefs *sensu* Leonardi (1987), and likely produced by medium-sized theropods. Footprint length is in the range 25-26 cm, by a width of about 22-24 cm. Mesaxonony is weak (te about 8 cm), while total divarication angle is relatively high at values in the range 57°-64°.

Following Thulborn (1990) and Weems (2006), Petti et al. (2011a) estimated for the trackmaker a hip height of 1.25 m, a body length of 5 m and a body mass of 206 kg. The morphological analogies and the statistical affinities (FL/te ratio, according to Weems, 1992) with the coeval tridactyl tracks from Poland (Gierliński et al., 2004), allowed the authors to assign the Stol dei Campiluzzi tracks to *Kayentapus* isp.

2.11. MAROCHE DI DRO ICHNOSITE, SARCA VALLEY (TRENTINO-ALTO ADIGE, NORTHERN ITALY), LATE SINEMURIAN - PLIENSCHACHIAN

Avanzini et al. (2001b) analysed some track-bearing limestone blocks in the Marocche di Dro landslides, about 2 km north of Drena in the Sarca Valley (Trentino-Alto Adige).

The boulders are composed of light-grey to yellowish grey packstone, characterised by the occurrence of oolites, bioclasts, algal lumps, pellets, dasycladacean algae, and litiolid and miliolinid foraminifera (Avanzini et al., 2001b; Avanzini and Petti, 2008). A subtidal palaeoenvironment was suggested, with mud banks and sand deposits, constituted by oolitic bars, occurring close together. The dinosaur tracks are filled with the same sediment as the substrate, separated from the track-bearing surface by laminae of red clay. The blocks were assigned to the upper part of the Calcarei Grigi Group (Tovel Member of the Rotzo Formation *sensu* Castellarin et al., 2005), deposited during the late Sinemurian to Pliensbachian (Avanzini et al., 2001b; Avanzini and Petti, 2008).

Within the ichnoassemblage, several tracks were identified, some of which were grouped into three trackways (Fig. 17; Pl. 2, fig. g). Among these, two display sub-elliptical *pes* prints about 25 cm in diameter associated to ellipsoidal *manus* prints wider than long (FL=16 cm and FW=20 cm on average). A low heteropody is clearly recognizable: the quadrupedal trackmaker had a stout forelimb, with a *manus* slightly smaller than the *pes* (Avanzini et al., 2001b). Four stubby digits are recognizable in at least one of the footprints. The morphological features of these trackways rule out sauropods and prosauropods as possible trackmakers. The tracks share some morphological affinity with those referred to the Ankylosauridae, such as the ichnogenera *Metatetrapodus* and *Tetrapodosaurus* (McCrea et al., 2001; Hornung and Reich, 2014). A small-sized basal thyreophoran, such as *Scelidosaurus* from the Early Jurassic of England, was assumed as the most likely trackmaker (Avanzini et al., 2001b; Avanzini and Petti, 2008).

The third trackway, preserved on the surface of another quadrangular block, is characterised by four *manus-pes* couples. The *pes* prints are elliptical, elongated and asymmetrical with respect to the axis (FL=30 cm; FW=20.7 cm, on average). The forelimb prints are sub-circular and smaller than the associated hindlimb print (FL=14.2 cm; FW=13.5 cm, on average). This trackway strongly differs from the two discussed above: the morphological and morphometrical analysis suggests a best fit with a prosauropod trackmaker (Avanzini et al., 2001b; Avanzini and Petti, 2008).

2.12. COSTE DELL'ANGLONE ICHNOSITE, MONTE BRENTO (TRENTINO-ALTO ADIGE, NORTHERN ITALY), LATE SINEMURIAN - PLIENSCHACHIAN

Petti et al. (2011b) described hundreds of dinosaur tracks, originally reported by Avanzini et al. (2007), from the wide monoclinical surface of Coste dell'Anglone, located on the eastern slope of the Mt. Biaina-Mt. Brento ridge (Dro, Trentino-Alto Adige), a few kilometres north of the Garda Lake.

The track-bearing horizon belongs to a stratigraphic succession characterised by shallowing-upward cycles. Each cycle is characterised by the transition from a low energy subtidal unit (intensely bioturbated



Fig. 16 - Theropod tracks preserved as natural casts on the roof of Stol dei Campiluzzi tunnel, dug during the First World War; scale bar 10 cm.



Fig. 17 - Basal thyreophoran trackway at Marocche di Dro tracksite (Trento, Sinemurian-Pliensbachian); scale bar 1 m.

nodular limestone), with associated invertebrate traces (*Thalassinoides* isp., *Chondrites* isp.), to high energy subtidal deposits (oolitic grainstone with intraclasts and bioclasts) up into inter- and supra-tidal deposits (Petti et al., 2011b).

In the upper part of the sequence, the track layer consists of poorly fossiliferous dark grey stromatolitic and peloidal mudstone (Avanzini and Petti, 2008; Petti et al., 2011b). The section belongs to the lowermost portion of the Rotzo Formation (formerly Tovel Member *sensu* Castellarin et al., 2005) and the microfossil assemblages indicate a late Sinemurian to Pliensbachian age (Avanzini and Petti, 2008; Petti et al., 2011b).

The Coste dell'Anglone tracksite probably represents the last dinosaur occurrence on the Trento Platform. The ichnological record is represented by 544 tridactyl footprints arranged in 20 trackways (Fig. 18), left by bipedal trackmakers and mainly oriented between ESE and SSE (Petti et al., 2011b). The tracksite was investigated using both traditional study methods and modern techniques, such as close-range photogrammetry and laser scanner, to gain more objective morphological details for the ichnotaxonomical analysis (Petti et al., 2008a; Pl. 3, fig. d).

The dinosaur footprints, preserved as concave epirelief (*sensu* Leonardi, 1987), are mesaxonitic, functionally tridactyl and asymmetric. The best-preserved tracks are small to medium-sized, slightly longer than wide ($14.5 \text{ cm} \leq \text{FL} \leq 26 \text{ cm}$; $12.7 \text{ cm} \leq \text{FW} \leq 20 \text{ cm}$); *te* is moderate (Pl. 3, figs. d,e). The digits appear similar and slender, with sharp claw marks at the end. The total divarication between digits II and IV ranges between 48° and 70° . The footprints form a typical narrow-gauge trackway, with pace angulation ranging between 170° and 180° . The high morphological variation that can be observed among the tracks mainly results from local changes in the physical properties of the substrate covered by a microbial mat. Nevertheless, all tracks were probably produced by individuals with the same functional anatomy of the hind foot (Petti et al., 2011b). The tracks show morphologies similar to some specimens assigned to the ichnogenera *Kayentapus* and *Anchisauripus* and mainly distributed in North America (Irby, 1995) and Northern Europe (Gierliński et al., 2004; Gierliński and Niedźwiedzki, 2005). Analysis of the morphometrical parameters suggests assigning the Coste dell'Anglone footprints and trackways to *Kayentapus* isp. (Petti et al., 2011b) and attributing them to small to medium-sized theropods.

3. PALAEOECOLOGY OF THE EARLY JURASSIC DINOSAUR MEGATRACKSITES FROM THE SOUTHERN ALPS

All the described ichnosites from the Trento Platform can be grouped into four main dinosaur megatracksites (Leonardi and Mietto, 2000; Avanzini et al., 2006). Their track fossils occur in carbonate units once thought to be totally marine in origin and constitute the most extensive

Early Jurassic dinosaur tracksites among those currently known in Europe (Lockley and Meyer, 2000). The older megatracksite spans multiple horizons in the middle part of the lower Hettangian Monte Zugna Formation of the Calcarei Grigi Group. The second megatracksite occurs near the top of the Monte Zugna Fm. and is of early Sinemurian age. The third one is preserved at the top of the Oolite di Loppio Formation which is Sinemurian in age. The youngest megatracksite occurs at the base of Rotzo Formation, late Sinemurian-early Pliensbachian in age.

The first level corresponds to several important supratidal intervals of exposure of a wide tidal flat. The second is represented by two intertidal, stromatolitic levels recognizable across the whole Trento Platform. The third level is located at the top of the Loppio Oolite and corresponds to an important regional unconformity. The fourth level corresponds to a marked sea level fall and is related to a complex regional palaeogeographic scenario, with brackish ponds and subtidal channels recognizable across the whole Trento Platform.

Avanzini et al. (2006) carried out a quantitative palynological analysis of samples from the footprint-bearing horizons, in order to reconstruct the plant assemblages of the ecosystem in which the dinosaurs lived. The predominant palynomorphs are *Azonotriletes* spores belonging to pteridophytes, bisaccate and circumpolles grains belonging to conifers, *Chasmatosporites* pertaining



Fig. 18 - Theropod trackways of the Coste dell'Anglone ichnosite (Trento, late Sinemurian-Pliensbachian; F.M. Petti for scale).

to the Cycadales, and *Eucommiidites* of uncertain affinity. In the lower samples, circumpolles dominates the flora (80%) and indicate a subtropical, warm, and rather arid climate. Upsection, an increment of spores (*Azonotriletes* group) typical of humid environments indicates a climate change as well as freshwater influence. Palynomorphs suggest therefore the constant presence of conifers belonging to the Cheirolepidiaceae (circumpolles), arborescent plants living in coastal environments (Avanzini et al., 2006).

The vertebrate ichnofauna of the studied track levels is a typical, dinosaur-dominated (and saurischian-dominated), Early Jurassic tetrapod assemblage characterized by the presence of theropod footprints such as *Eubrontes*, *Kayentapus*, *Anchisauripus* and *Grallator*. This typical track assemblage includes sauropodomorph (*Parabrontopodus* and *Otozoum*-like tracks such as *Lavinipes*), crocodylomorph, and synapsid (*Brasilichnium* Leonardi, 1981) footprints.

Theropods dominate in the Hettangian megatracksite level 1, whereas megatracksite levels 2 and 3, both Sinemurian, are dominated by sauropodomorph tracks. Theropods dominate in megatracksite level 4, late Sinemurian to early Pliensbachian in age. The inversion in predominance between theropod and sauropodomorph tracks between levels 1 and 2-3 coincides both with a change in regional floras, as corroborated by palynomorphs, and sedimentological data indicating an environmental shift from arid to humid conditions between megatracksites 1 and 2-3. From these data, it follows that the Early Jurassic dinosaur faunas of the Southern Alps were controlled by the environmental and climatic variations of this palaeogeographic region across the Hettangian-Sinemurian boundary. Large Sinemurian sauropodomorphs that preferred humid tidal flats replaced the small sauropodomorphs of arid Hettangian tidal flats. Theropods that were dominant in the arid Hettangian tidal flats became subordinate to sauropods in this region during the Sinemurian. In the late Sinemurian the complex local palaeogeography reduces the presence of sauropods and despite the ever more humid conditions theropods become again the most widely represented group. *Kayentapus* is the most widespread ichnotaxon among the above-described ichnosites. Its tentative attribution to ceratosaurian dinosaurs, such as *Dilophosaurus* from the Early Jurassic of Arizona (USA), suggests a possible geographical connection between the Southern Alps sector and the southern margin of the Laurasian mainland (North America and Europe) up to the Sinemurian (Petti et al., 2011b).

4. EARLY JURASSIC MARINE REPTILE TRACKS

4.1. BURANO RIVER ICHNOSITE (MARCHE, CENTRAL ITALY), LATE PLIENSCHACHIAN

Manni et al. (2000) described an unusual tetrapod trackway from the Upper Pliensbachian pelagic deposits of the Corniola Formation. The track-bearing surface was

found by the late B. Accordi in the early 1980's along the Burano River, between the villages of Cantiano and Cagli (Marche, Central Italy); it was later removed and is now deposited in the collections of the Museo Universitario di Scienze della Terra (MUST) of SAPIENZA University. In order to constrain its stratigraphic position, Manni et al. (2000) performed a bed-by-bed sampling collecting several ammonite specimens that indicate the upper *A. algovianum* Zone or the basal *E. emaciatum* Zone (late Pliensbachian). The trackway, named *Accordiichnus natans*, is 3.13 m long and about 50 cm wide and is composed of two rows of pear-shaped impressions (22 imprints) and by a sinuous central row made by 21 groups of centimetre-sized oval impressions. Each group is composed of five impressions connecting two consecutive pear-shaped imprints. Manni et al. (2000) attributed this trackway to an unknown marine reptile swimming near the sea-bottom. They interpreted the pear-shaped imprints as the *manus* impression, whereas the five separate imprints would represent the *pes*. This interpretation has been questioned by Seilacher (1997, 2007), who proposed other hypotheses, such as “burrow system or large plants with regular branching” or a giant “asterosomid burrow system”. It is noteworthy that in 1994 some poorly-preserved tracks, closely matching those described by Manni et al. (2000), were found on a track-bearing surface at Palareto, near Cantiano (Arduini, 1996). Also this horizon belongs to the Corniola Formation and can be ascribed to the early Pliensbachian (Manni et al., 2000). The tracks were interpreted by Arduini (1996) as undertracks of sauropodomorphs, but, being the Corniola Formation a pelagic unit, this hypothesis must be discarded. As reported by Manni et al. (2000) an attribution to a marine reptile is more likely.

5. SUPPOSED LATE JURASSIC FOOTPRINTS FROM ITALY

5.1. MATTINATA ICHNOSITE, GARGANO (PUGLIA, SOUTHERN ITALY)

Conti et al. (2005) reported the find of three closely associated dolomitized limestone blocks with dinosaur footprints on a small pier near the town of Mattinata on the Gargano Promontory, Province of Foggia. The pier was constructed during the 1960s with material derived from the western Gargano quarrying district, where Upper Jurassic to Upper Cretaceous carbonates crop out. Although today all active quarries are set within the Upper Cretaceous San Giovanni Rotondo Limestone, there has been quarrying in the underlying Sannicandro Formation in the mid-20th century, so both formations can be considered as possible sources of the Mattinata blocks. According to Bosellini et al. (1999, 2001), the Sannicandro Formation was deposited in a time interval from at least the Callovian to the early Valanginian, whereas the Calcare di Bari Formation (formerly San Giovanni Rotondo Limestone) was formed in the late Valanginian-early Aptian interval. Based mainly on

their lithological features, the blocks were referred to the peritidal facies of the Sannicandro Formation and assigned a Kimmeridgian-Tithonian age. Although some uncertainty remains about this age assignment (L. Spalluto, pers. comm.), the Mattinata footprints are, at present, the only dinosaur ichnological record in non-Alpine Italy tentatively referred to the Jurassic, and as yet the only possibly Late Jurassic tracks recorded from Italy.

The sedimentological study of the blocks revealed a complex texture ranging from brecciated intervals to well-laminated beds probably produced by microbial mats; the dinosaur footprints themselves are impressed on a surface that shows evidence of such a microbial mat. The footprints are preserved as concave epirelief on two of the blocks (named MPA and MPC) and as convex hyporelief on the third one (MPB). Together, the three blocks preserve 37 dinosaur footprints. All are tridactyl and mesaxonic, in a size range around 30 cm (footprint length without metatarsal impression). Conti et al. (2005) discuss only the best-preserved footprints (17 out of 37) and divide the assemblage into three morphotypes. Morphotype 1 tracks (Fig. 19A) are the most abundant (12 out of 17) and are characterized by displaying a short hallux impression, sometimes associated with a partial imprint of the metatarsus; digits II-IV are slender with sharply pointed tips. Morphotype 2 tracks (Fig. 19B), represented by three specimens, are characterised by stout digits, no hallux or metatarsal impression, and rather low divarication angles if compared with type 1. Morphotype 3 tracks (two specimens only) resemble morphotype 1 in having a wider divarication angle but are similar to morphotype 2 in having stout digits and lacking hallux and metatarsus impression. The choice of dividing the ichnoassemblage into morphotypes instead of applying ichnotaxonomic names leaves the possibility open that

the observed differences may be related to preservational factors, rather than to different trackmakers. In any case, mid-sized theropod trackmakers are inferred for all the footprints, and the possibility is discussed that morphotype 1 tracks may be assigned to the ichnogenus *Theroplantigrada*, an ichnotaxon based on Aptian dinosaur tracks from La Rioja.

At the time of their discovery, the Mattinata footprints were one of only three finds of dinosaur footprints on the Apulian carbonate platform, the other two being the Early Cretaceous site of Borgo Celano (Gianolla et al., 2000; Petti et al., 2008b) and the Late Cretaceous site of Altamura (Nicosia et al., 2000). Since then, a number of new tracksites, all Early Cretaceous in age, have been discovered from this palaeogeographic domain (see Petti et al., 2020, for an updated review in this issue). The occurrence of abundant dinosaur tracks at different stratigraphical levels within the Apulian carbonate platform triggered a rediscussion of established palaeogeographical models, which is still continuing (Bosellini, 2002; Conti et al., 2005; Petti, 2006; Nicosia et al., 2007; Zarcone et al., 2010; Citton et al., 2015). The Jurassic tracksites of Italy thus become part of a wider context; they have proved to be useful sources of information that give us a glimpse into the biodiversity, ecology and palaeogeography of a long-lost world.

6. CONCLUDING REMARKS

The discovery of several dinosaur tracksites in Trentino Alto-Adige and Veneto has triggered a review of the palaeobiological, palaeoclimatic and palaeogeographic framework of the Southern Alps sector during the Jurassic. The dinosaur tracks occur in four distinct and laterally continuous horizons (“megatracksites”) within the Calcarei Grigi Group. The analysis of the faunal

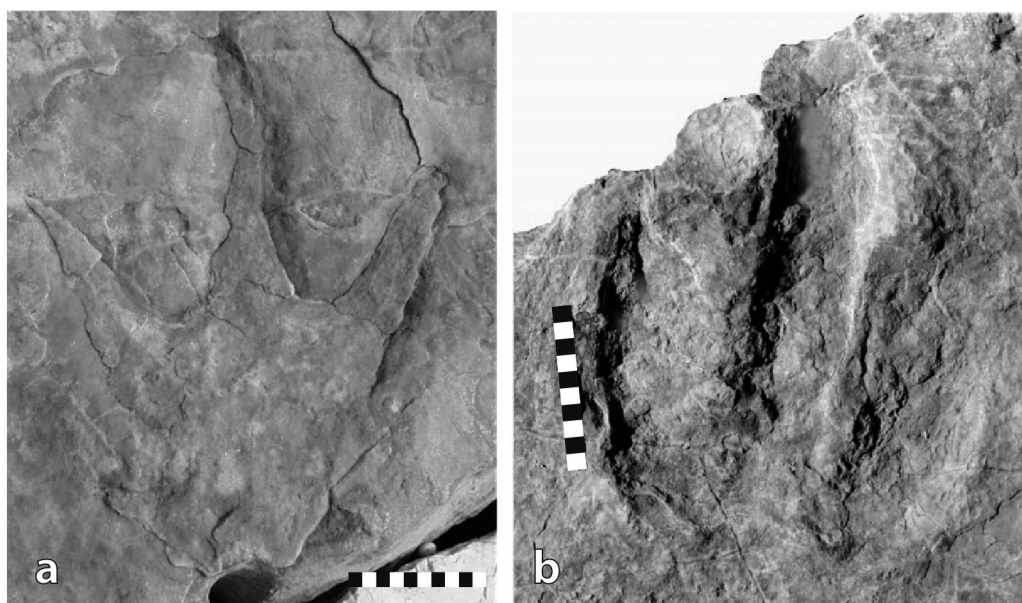


Fig. 19 - Tetradactyl (a) and tridactyl theropod tracks (b) of the Mattinata ichnosite (Gargano Promontory, Kimmeridgian-Tithonian, scale bar 10 cm).

composition indicates significant differences among them, suggesting an environmental shift from arid to humid conditions between the Hettangian and the Sinemurian.

Additionally, the dinosaur ichnological record of the Trento carbonate platform provides clues on the palaeogeography of the South Alpine sector during the Jurassic. The palaeobiological constraints provided by the dinosaur ichnoassemblages suggest a connection between the Laurasian mainland and the Southern Alps during the Early Jurassic.

The Mesozoic tectonic evolution of the Southern Alps sector thus explains the lack of dinosaur tracks in Northern Italy since the Toarcian.

The occurrence of possibly Late Jurassic dinosaur tracks in Apulia (Mattinata tracksite) stresses the need for a review of the palaeogeographic evolution of the Periadriatic sector during the Mesozoic, based on the palaeontological constraints provided by the abundance of dinosaur ichnosites in this region.

ACKNOWLEDGEMENTS - First of all, we would like to express our gratitude to several people that greatly helped the authors during the field work in many of the cited ichnosites: P. Ferretti (MUSE), R. Tomasoni (MUSE), M.C. Deflorian (MUSE), R. Todesco (formerly at MUSE), M. De Gasperi (Geological Survey of the Autonomous Province of Trento), M. Belvedere (University of Florence), F. Remondino (FBK-ICT), S. Girardi (formerly at FBK-ITVAPP), F. Finotti (Civic Museum of Rovereto) and F. Zandonai (Civic Museum of Rovereto). We thank L. Spalluto for his useful suggestions. The authors are indebted to the reviewers C. Meyer (University of Basel) and D. Castanera (Institut Català de Paleontologia) for their helpful comments and suggestions that greatly improved the paper.

REFERENCES

- Antonelli M., 2018. Le orme dinosauriane del sito dei Lavini di Marco (Hettangiano-Trento): icnotassonomia, icnosistemica e paleobiogeografia. MSc thesis, SAPIENZA Università di Roma, pp. 286.
- Arduini P., 1996. Early Jurassic tracks from Monte Acuto (Apennino Marchigiano), central Italy. *Ichnos* 4, 239-240.
- Arzarello P., Finotti F., Galeazzo G., Lanzinger M., Mezzanotte M., Veronese L., 2000. Il parco delle piste dei dinosauri di Rovereto: conservazione, valorizzazione e musealizzazione. In: Leonardi G., Mietto P. (Eds.), *Dinosauri in Italia, le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani*. Accademia Editoriale, Pisa-Roma, 377-390.
- Avanzini M., 1997. Impronte di sauropodi nel Giurassico inferiore del Becco di Filadonna (Piattaforma di Trento-Italia settentrionale). *Studi Trentini di Scienze Naturali, Acta Geologica* 72, 117-122.
- Avanzini M., 2001. Possibili impronte di dinosauro nel Giurassico inferiore del Monte Pasubio e dei Monti Lessini settentrionali (Italia nord-orientale). *Studi Trentini di Scienze Naturali, Acta Geologica* 76, 183-191.
- Avanzini M., 2002. The dinosaur site at the Lavini di Marco and the Lower Jurassic Calcari Grigi Megatracksite. In: Santantonio M. (Ed.), *General Field Trip Guidebook, 6th International Symposium on the Jurassic System, 12-22 September 2002, Palermo, Italy*, 279-281.
- Avanzini M., Finotti F., 1998. Sulle orme dei dinosauri italiani. *Le Scienze* 60, 80-81.
- Avanzini M., Leonardi G., 1993. Dinosauri nel Trentino: il giacimento dei Lavini di Marco. *UCT, Trento* 18, 35-41.
- Avanzini M., Leonardi G., 1995. I dinosauri dei Lavini di Marco ed i grandi vertebrati fossili del Trentino Alto-Adige. *Natura Alpina* 44, 1-14.
- Avanzini M., Leonardi G., 1999. Prima segnalazione di orme di un dinosauro accucciato (*Anomoepus*) nel Giurassico inferiore europeo - Italia. *Geoitalia 1999, 2° Forum Italiano di Scienze della Terra. Riassunti* 1, 63-65.
- Avanzini M., Petti F.M., 2008. Updating the dinosaur tracksites from the Lower Jurassic Calcari Grigi Group (Southern Alps, Northern Italy). *Italian Ichnology. Proceedings of the Ichnology Session of Geoitalia 2007. Studi Trentini di Scienze Naturali, Acta Geologica* 83, 289-301.
- Avanzini M., Tomasoni R., 2002. I Calcari Grigi di Cima Vezzana - Pizzo di Levico. *Studi Trentini di Scienze Naturali, Acta Geologica* 77, 245-267.
- Avanzini M., Leonardi G., Masetti D., Mietto P., 2000a. Conclusioni. In: Leonardi G., Mietto P. (Eds.), *Dinosauri in Italia, le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani*. Accademia Editoriale, Pisa-Roma, 393-398.
- Avanzini M., Leonardi G., Mietto P., Roghi G., 2000b. Ichnofaune dinosauriane nel Giurassico inferiore della Piattaforma di Trento: aspetti stratigrafici, paleoambientali e paleogeografici. In: Carulli G.B., Longo Salvador G. (Eds.), *Riassunti delle comunicazioni orali e dei poster 80ª Riunione estiva Società Geologica Italiana, Trieste*, 42-44.
- Avanzini M., Frisia S., Rinaldo M., 2000c. I Lavini di Marco nel Giurassico inferiore: la ricostruzione di un antico ambiente di vita. In: Leonardi G., Mietto P. (Eds.), *Dinosauri in Italia, le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani*. Accademia Editoriale, Pisa-Roma, 247-272.
- Avanzini M., Gierliński G., Leonardi G., 2001a. First report of sitting *Anomoepus* tracks in European Lower Jurassic (Lavini di Marco site - northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 107, 131-136.
- Avanzini M., Campolongo M., Leonardi G., Tomasoni R., 2001b. Tracce di dinosauri nel Giurassico inferiore della Valle del Sarca. *Studi Trentini di Scienze Naturali, Acta Geologica* 76, 167-182.
- Avanzini M., Leonardi G., Mietto P., 2003. *Lavinipes cheminii* ichnogen., ichnosp. nov., a possible sauropodomorph track from the Lower Jurassic of the Italian Alps. *Ichnos* 10, 179-193.
- Avanzini M., Petti F.M., Tomasoni R., 2007. A new Lower Jurassic (Sinemurian - Pliensbachian) dinosaur tracksites in the Central-Eastern Southern Alps (Dro, Trento - Italy): a preliminary report. *Geoitalia 2007, VI Forum Italiano di Scienze della Terra, Rimini 12-14 settembre 2007, Epitome* 2, 305.

- Avanzini M., Frisia S., Van den Driessche K., Keppens E., 1997. A dinosaur tracksite in an Early Liassic tidal flat in Northern Italy: paleoenvironmental reconstruction from sedimentology and geochemistry. *Palaios* 12, 538-551.
- Avanzini M., Leonardi G., Mietto P., Piubelli D., 2005. The dinosaur ichnosite at the Lavini di Marco (Calcarei Grigi Group, Lower Jurassic). *Studi Trentini di Scienze Naturali, Acta Geologica* 80, 31-36.
- Avanzini M., Franceschi M., Petti F.M., Girardi S., Ferretti P., Tomasoni R., 2008. New Early Jurassic (Hettangian-Sinemurian) sauropodomorph tracks from the Trento carbonate Platform (Southern Alps, Northern Italy). *Studi Trentini di Scienze Naturali, Acta Geologica* 83, 317-322.
- Avanzini M., Frisia S., Keppens E., Leonardi G., Rinaldo M., Van den Driessche K., 1995. Sedimentology and diagenesis of a dinosaur tracksite: new perspectives on Early Jurassic palaeogeography of the Southalpine. Abstract volume for Talks and Posters, 10th Bathurst Meeting of Carbonate Sedimentologists. Royal Holloway University of London, Egham, Surrey, 10-11.
- Avanzini M., Piubelli D., Mietto P., Roghi G., Romano R., Masetti D., 2006. Lower Jurassic (Hettangian-Sinemurian) dinosaur track megasites, Southern Alps, Northern Italy. In: Harris J.D., Lucas S.G., Spielmann J.A., Lockley M.G., Milner A.R.C., Kirkland J.I. (Eds.), *The Triassic-Jurassic Terrestrial Transition*. New Mexico Museum of Natural History and Science Bulletin 37, 207-216.
- Belvedere M., Franceschi M., Sauro F., Mietto P., 2017. Dinosaur footprints from the top of Monte Pelmo: new data for Early Jurassic palaeogeography of the Dolomites (NE Italy). *Bollettino della Società Paleontologica Italiana* 56, 199-206.
- Bernoulli D., 1972. North Atlantic and Mediterranean Mesozoic facies, a comparison. In: Hollister, C.D., Ewing, J.I. (Eds.), *Initial Reports of the Deep-Sea Drilling Project* 11, 801-807.
- Bertotti G., Picotti V., Bernoulli D., Castellarin A., 1993. From rifting to drifting: tectonic evolution of the South-Alpine upper crust from the Triassic to the Early Cretaceous. *Sedimentary Geology* 86, 53-76.
- Bonaparte J.F., Colbert E.H., Currie P.J., de Ricqlès A., Kielan-Jaworowska Z., Leonardi G., Morello N., Taquet P., 1984. *Sulle orme dei dinosauri*. Erizzo Editrice, Venezia, pp. 334.
- Bosellini A., 2002. Dinosaur "re-write" the geodynamics of the eastern Mediterranean and the paleogeography of the Apulia Platform. *Earth Science Reviews* 59, 211-234.
- Bosellini A., Broglio Loriga C., 1971. I "Calcarei Grigi" di Rotzo (Giurassico inferiore, Altopiano di Asiago) e loro inquadramento nella paleogeografia e nella evoluzione tettono-sedimentaria delle Prealpi Venete. *Annali dell'Università di Ferrara* 5, 1-61.
- Bosellini A., Morsilli M., Neri C., 1999. Long-term event stratigraphy of the Apulia Platform margin: Upper Jurassic to Eocene, Gargano, Southern Italy. *Journal of Sedimentary Research* 69, 1241-1252.
- Bosellini A., Morsilli M., Neri C., 2001. The Eastern Margin of the Apulia Platform: The Gargano Transect. Guide Book of SEPM (Society for Sedimentary Geology) Cretaceous Resources Events and Rhythms Working Group 4th Conference, Vieste-Gargano, Italy, 25-28 September 2000, 48.
- Castellarin A., Picotti V., Cantelli L., Claps M., Trombetta L., Selli L., Carton A., Borsato A., Daminato F., Nardin M., Santuliana E., Veronese L., Bollettinari G., 2005. Note Illustrative della Carta Geologica d'Italia alla scala 1:50.000, Foglio 080 Riva del Garda. APAT, Dipartimento Difesa del Suolo, Servizio Geologico d'Italia, pp. 145.
- Citton P., Nicosia U., Sacchi E., 2015. Updating and reinterpreting the dinosaur track record of Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 439, 117-125.
- Conti M.A., Morsilli M., Nicosia U., Sacchi E., Savino V., Wagensommer A., Di Maggio L., Gianolla P., 2005. Jurassic dinosaur footprints from Southern Italy: footprints as indicators of constraints in paleogeographic interpretation. *Palaios* 20, 534-550.
- D'Argenio B., 1976. Le piattaforme periadriatiche: una rassegna di problemi nel quadro geodinamico mesozoico dell'area mediterranea. *Memorie della Società Geologica Italiana* 13, 137-159.
- Ellenberger P., 1972. Contribution à la classification des pistes de vertébrés du Trias: les types du Stromberg d'Afrique du Sud (I): Paleovertebrata. *Mémoire Extraordinaire, Montpellier*, pp. 117.
- Gianolla P., Morsilli M.D., Bosellini A., 2000. First discovery of Early Cretaceous dinosaur footprints in the Gargano Promontory (Apulia carbonate platform, southern Italy): quantitative models on Cretaceous carbonates and the eastern margin of the Apulia Platform. SEPM (Society for Sedimentary Geology) Cretaceous Resource Events and Rhythms Working Group 4th Conference, Vieste-Gargano, Italy, 25th-28th September 2000, Abstracts, 9.
- Gierliński G., 1991. New dinosaur ichnotaxa from the early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85, 137-148.
- Gierliński G., 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 42, 533-538.
- Gierliński G., Ahlberg A., 1994. Late Triassic and Early Jurassic dinosaur footprints in the Höganäs Formation of southern Sweden. *Ichnos* 3, 99-105.
- Gierliński G., Niedźwiedzki G., 2005. New saurischian dinosaur footprints from the Lower Jurassic of Poland. *Geological Quarterly* 49, 99-104.
- Gierliński G., Pieńkowski G., 1999. Dinosaur track assemblages from the Hettangian of Poland. *Geological Quarterly* 43, 329-346.
- Gierliński G., Pieńkowski G., Niedźwiedzki G., 2004. Tetrapod track assemblage in the Hettangian of Sołtyków, Poland, and its paleoenvironmental background. *Ichnos* 11, 195-213.
- Haubold H., 1986. Archosaur footprints at the terrestrial Triassic-Jurassic transition. In: Padian K. (Ed.), *The beginning of the Age of Dinosaurs: faunal change across the Triassic-Jurassic boundary*. Cambridge University Press, Cambridge, 189-201.
- Hornung J.J., Reich M., 2014. *Metatetrapous valdensis* Nopcsa, 1923 and the presence of ankylosaur tracks (Dinosauria: Thyreophora) in the Berriasian (Early Cretaceous) of Northwestern Germany. *Ichnos* 21, 1-18.

- Irby G.V., 1995. Posterolateral markings on dinosaur tracks, Cameron dinosaur tracksite, Lower Jurassic Moenave Formation, northeastern Arizona. *Journal of Paleontology* 69, 779-784.
- Lanzinger M., Leonardi G., 1991. Piste di dinosauri del Giurassico Inferiore ai Lavini di Marco (Trento). In: Muscio G. (Ed.), *Dinosaurs, il mondo dei dinosauri*. Kaleidos, Trento, 89-94.
- Leonardi G., 1981. *Brasilichnium elusivum* gen. n., sp. n.: pistas de tetrapóde mesozóico guardadas nas coleções do Museu Nacional do Rio de Janeiro. *Anais da Academia Brasileira de Ciências* 53, 793-805.
- Leonardi G., 1984a. I rettili mesozoici italiani. In: Bonaparte J.F., Colbert E.H., Currie P.J., de Ricqlès A., Kielan-Jaworowska Z., Leonardi G., Morello N., Taquet P. (Eds.), *Sulle orme dei dinosauri*. Erizzo Editrice, Venezia, 195-204.
- Leonardi G., 1984b. Le impronte fossili di dinosauri. In: Bonaparte J.F., Colbert E.H., Currie P.J., de Ricqlès A., Kielan-Jaworowska Z., Leonardi G., Morello N., Taquet P. (Eds.), *Sulle orme dei dinosauri*. Erizzo Editrice, Venezia, 161-186.
- Leonardi G., 1987. Glossary and manual of tetrapod footprint palaeoichnology. Ministério das Minas e Energia, Departamento Nacional da Produção Mineral, Brasília, pp. 75.
- Leonardi G., 1996. Le piste di dinosauri dei Lavini di Marco (Rovereto, TN, Italia) e alcune questioni generali sull'icnologia dei Tetrapodi. *Atti della Accademia Roveretana degli Agiati* 6, 65-104.
- Leonardi G., 1997. Problemática actual de las icnitas de dinosaurios. *Revista de la Sociedad Geológica de España* 10, 341-353.
- Leonardi G., 2000. The dinosaurs of Italy and neighbour countries. In: Leonardi G., Mietto P. (Eds.), *Dinosauri in Italia: le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani*, Accademia Editoriale, Pisa-Roma, Parte sesta - Abstracts Dalla Vecchia F.M. (Ed.), *Italian dinosaurs: the Jurassic tracks of the Lavini di Marco site (Trento Province) and the other italian fossil remains*, 475-476.
- Leonardi G., 2008. Vertebrate ichnology in Italy. *Studi Trentini di Scienze Naturali. Acta Geologica* 83, 213-221.
- Leonardi G., Avanzini M., 1994. *Dinosauri in Italia*. Le Scienze, Quaderni 76, 69-81.
- Leonardi G., Lanzinger M., 1992. *Dinosauri nel Trentino: venticinque piste fossili nel Liassico di Rovereto (Trento, Italia)*. *Paleocronache* 1, 13-24.
- Leonardi G., Lockley M.G., 1995. A proposal to abandon the ichnogenus *Coelurosaurichnus* Huene, 1941 - A junior synonym of *Grallator* E. Hitchcock, 1858. *Journal of Vertebrate Paleontology* 15, 40.
- Leonardi G., Mietto P. (Eds.), 2000. *Dinosauri in Italia. Le orme giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani*. Accademia Editoriale, Pisa, pp. 497.
- Lockley M., Meyer C., 2000. *Dinosaur tracks and other footprints of Europe*. Columbia University Press, New York, pp. 323.
- Manni R., Nicosia U., Nobili G., 2000. An unusual tetrapod trackway from Lower Jurassic marine sediments of central Italy: *Accordiichnus natans* n. ichnogen., n. ichnosp. *Geologica Romana* 35, 167-187.
- Martin S., Campedel P., Ivy-Ochs S., Viganò A., Alifimov V., Vockenhuber E., Andreotti E., Carugati G., Pasqual D., Rigo M., 2014. Lavini di Marco (Trentino, Italy): ³⁶Cl exposure dating of a polyphase rock avalanche. *Quaternary Geochronology* 19, 106-116.
- Masetti D., Fantoni R., Romano R., Sartorio D., Trevisani E., 2012. Tectonostratigraphic evolution of the Jurassic extensional basins of the eastern southern Alps and Adriatic foreland based on an integrated study of surface and subsurface data. *American Association of Petroleum Geologists Bulletin* 96, 2065-2089.
- McCrea R., Lockley M.G., Meyer C.A., 2001. Global distribution of purported ankylosaur track occurrences. In: Carpenter K. (Ed.), *The Armored Dinosaurs*. Indiana University Press, Bloomington, 413-454.
- Mietto P., 1988. Piste di dinosauri nella Dolomia Principale (Triassico Superiore) del Monte Pelmetto (Cadore). *Memorie della Società Geologica Italiana* 30, 307-310.
- Mietto P., 1990. Le piste di dinosauri sulle rocce triassiche del Pelmetto. *Associazione Culturale Amici Museo Selva di Cadore, Feltre*, pp. 32.
- Mietto P., Roghi G., 1993. Nuova segnalazione di impronte di dinosauri nel Giurassico Inferiore del Sudalpino: le Piste della Valle del Revolto. *Paleocronache* 2, 39-43.
- Mietto P., Belvedere M., Barbuni M., Manucci F., 2012. *Dinosauri nelle Dolomiti - Recenti scoperte sulle impronte di dinosauro nelle Dolomiti*. Fondazione Giovanni Angelini, Belluno, pp. 110.
- Mietto P., Roghi G., Zorzini R., 2000. Le impronte di dinosauri liassici dei Monti Lessini Veronesi. *Bollettino del Museo Civico di Storia Naturale di Verona* 24, 55-72.
- Morsilli M., Hairabian A., Borgomano J., Nardon S., Adams E., Bracco Gartner G., 2017. The Apulia Carbonate Platform-Gargano Promontory Italy (Upper Jurassic-Eocene). *American Association of Petroleum Geologists Bulletin* 101, 523-531.
- Nicosia U., Avanzini M., Barbera C., Conti M.A., Dalla Vecchia F., Dal Sasso C., Gianolla P., Leonardi G., Loi M., Mariotti N., Mietto P., Morsilli M., Paganoni A., Petti F.M., Piubelli D., Raia P., Renesto S., Sacchi E., Santi G., Signore M., 2005. I vertebrati continentali del Paleozoico e Mesozoico. In: Bonfiglio L. (Ed.), *Paleontologia dei vertebrati in Italia. Evoluzione biologica, significato ambientale e paleogeografia*. Memorie del Museo Civico di Storia Naturale di Verona, 2 serie, sezione Scienze della Terra 6, 41-66.
- Nicosia U., Marino M., Mariotti N., Muraro C., Panigutti S., Petti F.M., Sacchi E., 2000. The Late Cretaceous dinosaur tracksite near Altamura (Bari, Southern Italy). I - Geological framework. *Geologica Romana* 35, 231-236.
- Nicosia U., Petti F.M., Perugini G., D'Orazi Porchetti S., Sacchi E., Conti M.A., Mariotti N., Zarattini A., 2007. Dinosaur tracks as paleogeographic constraints: new scenarios for the Cretaceous geography of the periadriatic Region. *Ichnos* 14, 69-90.

- Olsen P.E., Galton P.M., 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia africana* 25, 87-110.
- Petti F.M., 2006. Orme dinosauriane nelle piattaforme carbonatiche mesozoiche italiane: sistematica e paleobiogeografia. PhD Thesis, Università di Modena e Reggio Emilia, pp. 221.
- Petti F.M., Bernardi M., Todesco R., Avanzini M., 2011a. Dinosaur footprints as ultimate evidence for a terrestrial environment in the late Sinemurian Trento carbonate platform. *Palaios* 26, 601-606.
- Petti F.M., Bernardi M., Ferretti P., Tomasoni R., Avanzini M., 2011b. Dinosaur tracks in a marginal marine environment: the Coste dell'Anglone ichnosite (Early Jurassic, Trento Platform, NE Italy). *Italian Journal of Geosciences* 130, 27-41.
- Petti F.M., Avanzini M., Belvedere M., De Gasperi M., Ferretti P., Girardi S., Remondino F., Tomasoni R., 2008a. Digital 3D modelling of dinosaur footprints by photogrammetry and laser scanning techniques: integrated approach at the Coste dell'Anglone tracksite (Lower Jurassic, Southern Alps, Northern Italy). *Studi Trentini di Scienze Naturali, Acta Geologica* 83, 303-315.
- Petti F.M., Conti M.A., D'Orazi Porchetti S., Morsilli M., Nicosia U., Gianolla P., 2008b. A theropod dominated ichnocoenosis from late Hauterivian-early Barremian of Borgo Celano (Gargano Promontory, Apulia, Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 114, 3-17.
- Petti F.M., Antonelli M., Citton P., Mariotti N., Petruzzelli M., Pignatti J., D'Orazi Porchetti S., Romano M., Sacchi E., Sacco E., Wagensommer A., 2020. Cretaceous tetrapod tracks from Italy: a treasure trove of exceptional biodiversity. In: Romano M., Citton P. (Eds.), *Tetrapod ichnology in Italy: the state of the art*. *Journal of Mediterranean Earth Sciences* 12, 167-191. doi: 10.3304/jmes.2020.16873.
- Piubelli D., 2006. Icnologia delle impronte tridattile dinosauriane dei Lavini di Marco (Rovereto-Trento). PhD thesis, Università di Padova, pp. 140.
- Piubelli D., Avanzini M., Mietto P., 2004. The Lavini di Marco ichnosite (NE Italy): two different approaches to the study of tridactyl dinosaur tracks. 32nd International Geological Congress - Florence. Abstract Volume 128-20, 600.
- Piubelli D., Avanzini M., Mietto P., 2005. The Early Jurassic ichnogenus *Kayentapus* at Lavini di Marco (NE Italy). Global distribution and palaeogeographic implications. *Bollettino della Società Geologica Italiana* 124, 259-267.
- Roghi G., 1994. Segnalazione di impronte di Dinosauri nei Monti Lessini Veronesi. *La Lessinia-Ieri Oggi Domani* 17, 73-78.
- Sacco E., 2018. Le orme dinosauriane del sito dei Lavini di Marco (Giurassico inferiore, Hettangiano - Trentino Alto-Adige): nuove metodologie di studio, icnotassonomia ed icnosistematica. MSc thesis, SAPIENZA Università di Roma, pp. 194.
- Seilacher A., 1997. Fossil Art: an exhibition of the Geologisches Institut, Tuebingen University. Royal Tyrrell Museum of Palaeontology, Drumheller, pp. 64.
- Seilacher A., 2007. Trace Fossil Analysis. Springer-Verlag, Berlin-Heidelberg, pp. 226.
- Thulborn T., 1990. Dinosaur Tracks. Chapman & Hall, London-New York, pp. 410.
- Welles S.P., 1971. Dinosaur footprint from the Kayenta Formation of Northern Arizona. *Plateau* 44, 27-38.
- Weems R.E., 1992. A re-evaluation of the taxonomy of Newark Supergroup saurischian dinosaur tracks, using extensive statistical data from a recently exposed tracksite near Culpeper, Virginia. In: Sweet P.C. (Ed.), *Proceedings 26th Forum on the Geology of Industrial Minerals*, May 14-18, 1990. Virginia Division of Mineral Resources Publication 119, 113-127.
- Weems R.E., 2006. The manus print of *Kayentapus minor*: Its bearing on the biomechanics and ichnotaxonomy of early Mesozoic saurischian dinosaurs. In: Harris J.D., Lucas S.G., Spielmann J.A., Lockley M.G., Milner A.R.C., Kirkland J.I. (Eds.), *The Triassic-Jurassic Terrestrial Transition*. New Mexico Museum of Natural History and Science Bulletin 37, 369-378.
- Winterer E.L., Bosellini A., 1981. Subsidence and sedimentation on Jurassic passive continental margin, Southern Alps, Italy. *American Association of Petroleum Geologists Bulletin* 65, 394-421.
- Zappaterra E., 1990. Carbonate paleogeographic sequences of the Periadriatic region. *Bollettino della Società Geologica Italiana* 109, 5-20.
- Zappaterra E., 1994. Source-rock distribution model of the Periadriatic region. *AAPG bulletin* 78, 333-354.
- Zarcone G., Petti F.M., Cillari A., Di Stefano P., Guzzetta D., Nicosia U., 2010. A possible bridge between Adria and Africa: new palaeobiogeographic and stratigraphic constraints on the Mesozoic palaeogeography of the Central Mediterranean area. *Earth Science Reviews* 103, 154-162.

PLATES

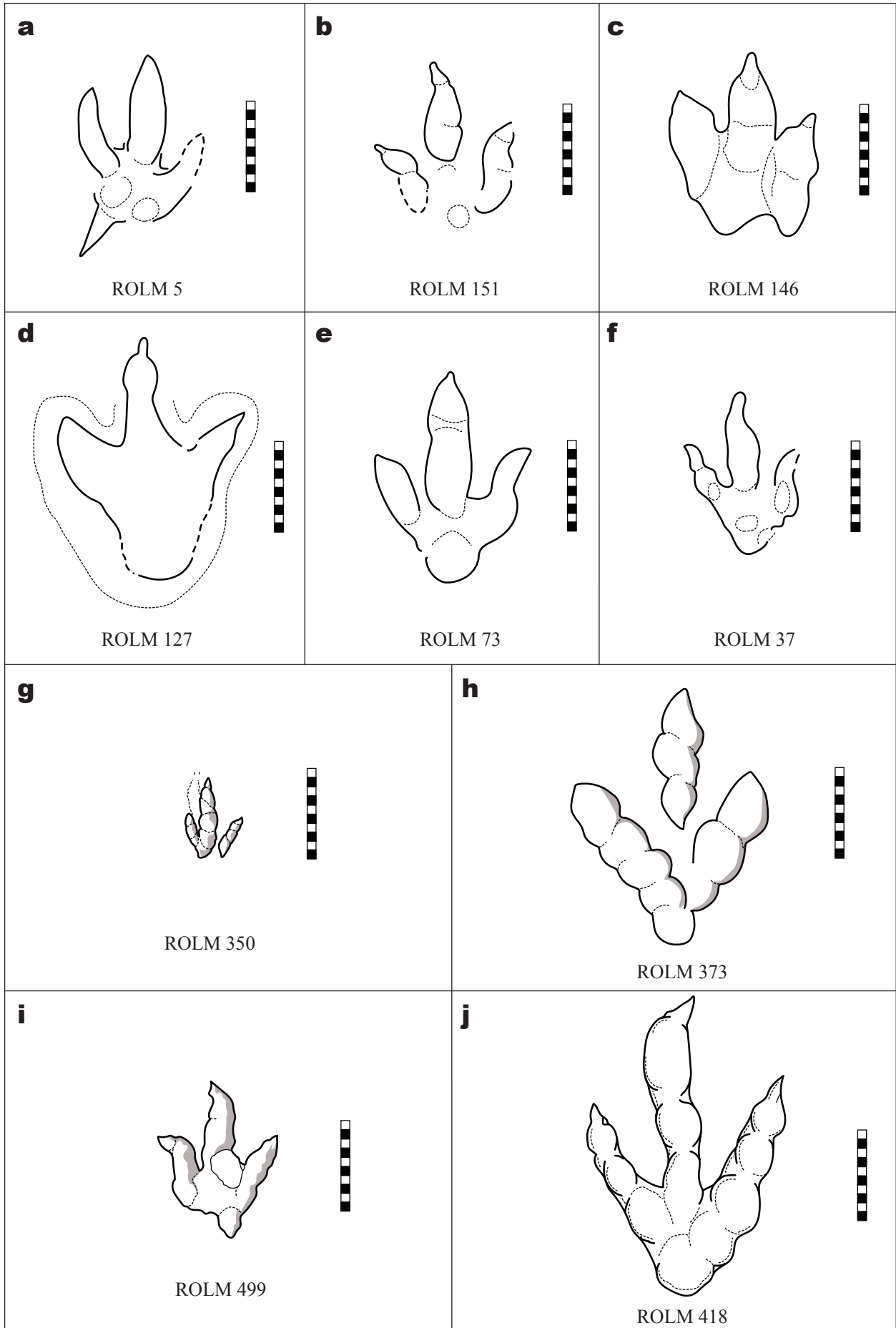


Plate 1 - Theropod tracks from the Lavini di Marco tracksite (Hettangian - Trentino-Alto Adige, Northern Italy). a) specimen ROLM 5, representative of the first morphotype of Leonardi and Mietto (2000). b) specimen ROLM 151, representative of the second morphotype of Leonardi and Mietto (2000). c) specimen ROLM 146 representative of the third morphotype of Leonardi and Mietto (2000). d) specimen ROLM 127, representative of the fourth morphotype of Leonardi and Mietto (2000). e) specimen ROLM 73, representative of the fifth morphotype of Leonardi and Mietto (2000). f) specimen ROLM 37, representative of the sixth morphotype of Leonardi and Mietto (2000). g) specimen ROLM 350, representative of the morphotype LA1 of Piubelli (2006). h) specimen ROLM 373, representative of the morphotype LA2 of Piubelli (2006). i) specimen ROLM 499, representing the morphotype LA3 of Piubelli (2006). j) specimen ROLM 418, representative of the morphotype LA4 of Piubelli (2006). Scale bars = 10 cm. Specimens are redrawn from Leonardi and Mietto (2000) and Piubelli (2006).

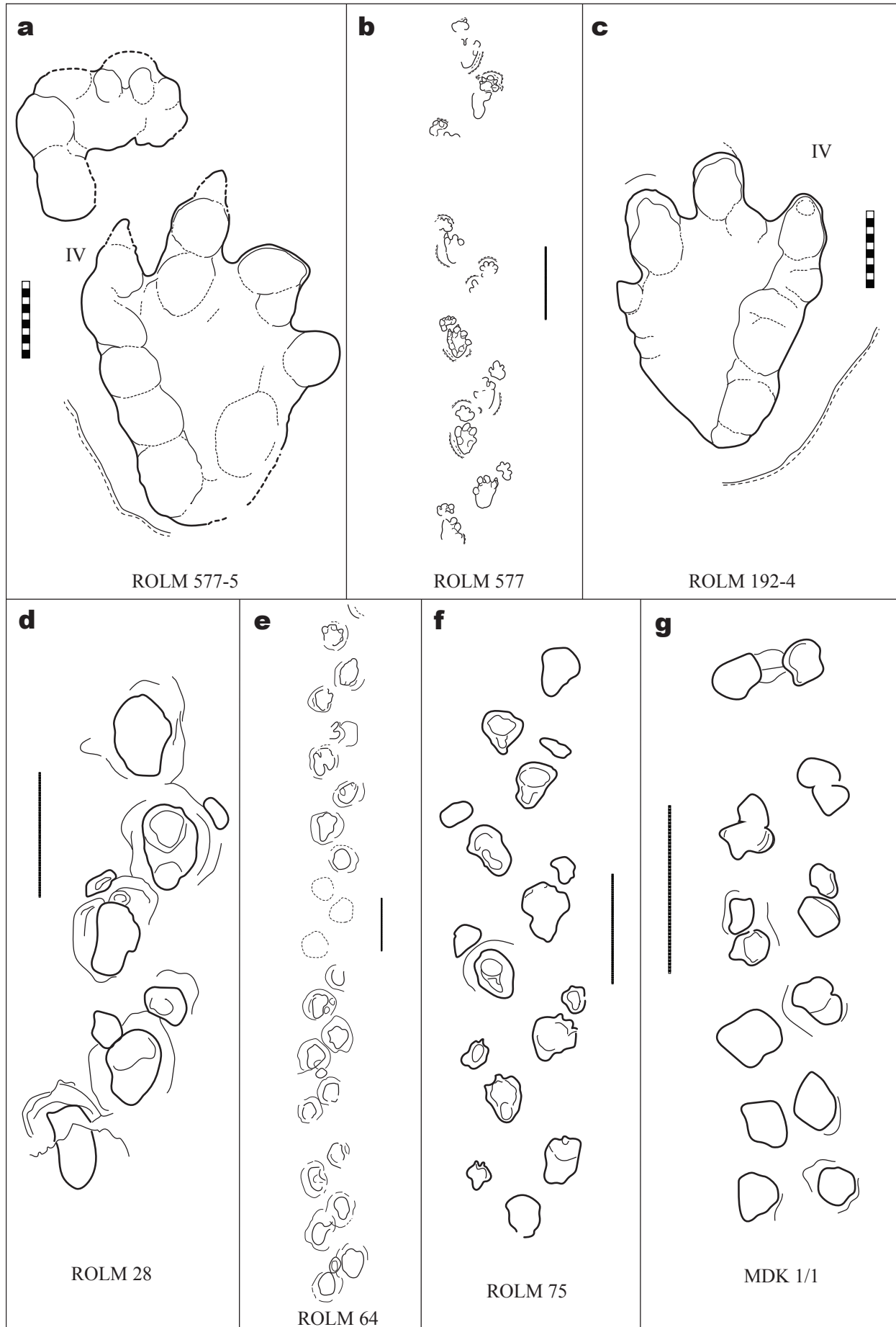


Plate 2 - Tracks and trackways attributed to herbivorous dinosaurs from the Lavini di Marco (a-f; Hettangian - Trentino-Alto Adige, Northern Italy) and Marocche di Dro tracksites (g; late Sinemurian - Pliensbachian; Trentino-Alto Adige, Northern Italy). a) ROLM 577-5 *manus-pes* set, holotype of *Lavinipes cheminii*; scale bar = 10 cm. b) ROLM 577 trackway; scale bar = 1 m. c) ROLM 192-4 *manus-pes* set, paratype of *Lavinipes cheminii*; scale bar = 10 cm. d) ROLM 28 trackway (*Parabrontopodus* isp.); scale bar = 1 m. e) ROLM 64 trackway, formerly referred to a possible ornithopod trackmaker; scale bar = 1 m. f) ROLM 75 trackway (*Parabrontopodus* isp.); scale bar = 1 m. g) MDK 1/1 trackway, morphologically similar to ichnogenera *Metatetrapodus* and *Tetrapodosaurus* and referred to basal thyreophoran; scale bar = 1 m. Specimens are redrawn from Leonardi and Mietto (2000), Avanzini et al. (2003) and Avanzini and Petti (2008).

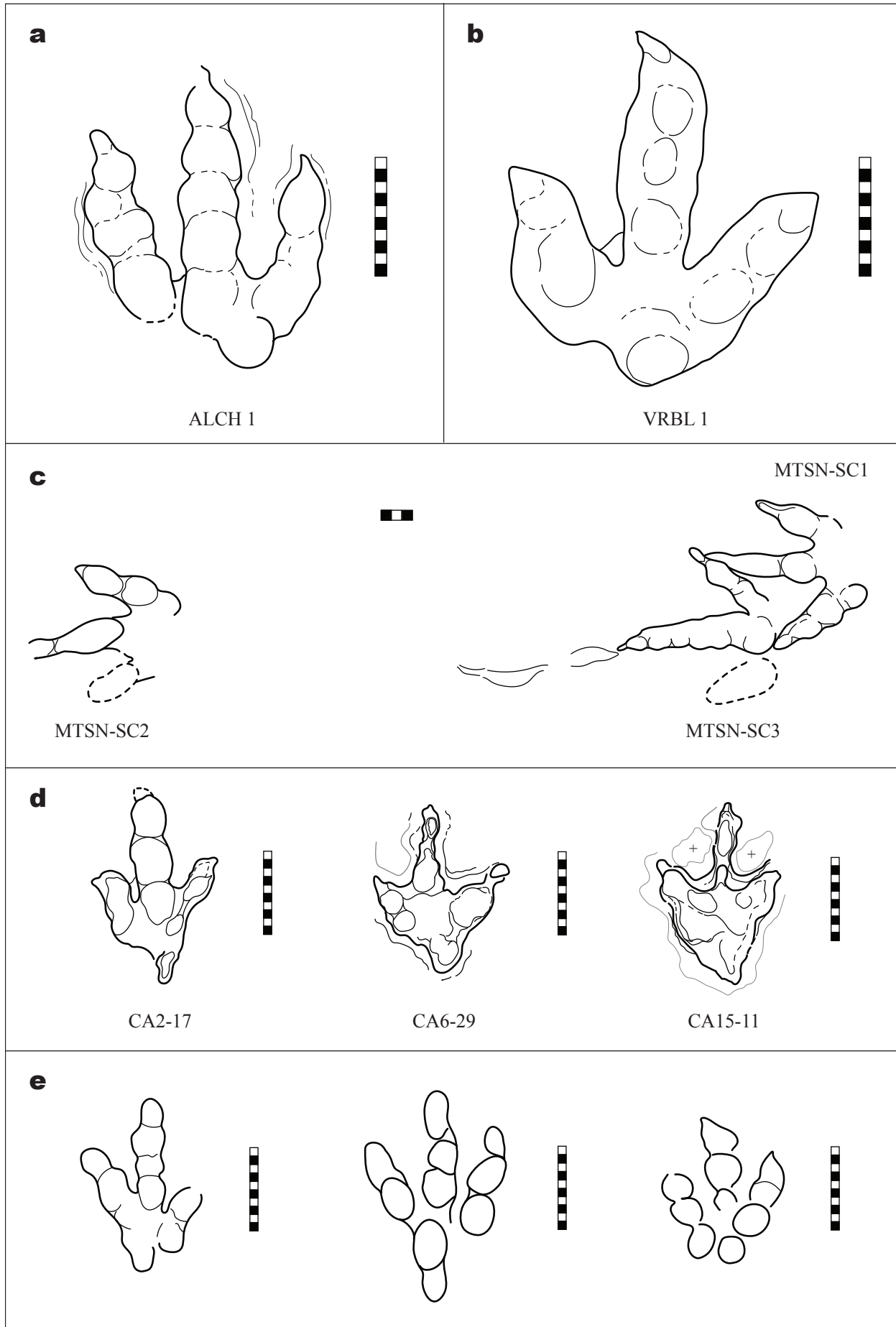


Plate 3 - Theropod tracks from other ichnosites belonging to the Calcarei Grigi Group (Lower Jurassic, Southern Alps). a) specimen ALCH 1 (*Kayentapus* isp.) from the Chizzola tracksite. b) specimen VRBL 1 (*Kayentapus* isp.) from the Bella Lasta tracksite. c) medium-sized tridactyl tracks (*Kayentapus* isp.) from the Stol dei Campiluzzi tracksite. d) medium-sized tridactyl tracks from the Coste dell'Anglone tracksite (specimens CA2-17, CA6-29 and CA15-11). e) unnamed medium-sized tridactyl tracks from the Coste dell'Anglone tracksite. Scale bars = 10 cm. Interpretative sketches are redrawn from Avanzini and Petti (2008), Petti et al. (2011a, 2011b).

