Archosauriform footprints in the Lower Triassic of Western Alps and their role in understanding the effects of the Permian-Triassic hyperthermal (#51782)

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Archosauriform footprints in the Lower Triassic of Western Alps and their role in understanding the effects of the Permian-Triassic hyperthermal

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The most accepted killing model for the Permian-Triassic mass extinction (PTME) postulates that massive volcanic eruption (i.e. the Siberian Traps LIP) led to geologically rapid global warming, acid rain and ocean anoxia. On land, habitable zones were drastically reduced, due to the combined effects of heating, drought and acid rains. This hyperthermal had severe effects also on the paleobiogeography of several groups of organisms. Among those, the tetrapods, whose geographical distribution across the end-Permian mass extinction (EPME) was the subject of controversy of a number of recent papers. We here describe and interpret a new Early Triassic (?Olenekian) archosaur track assemblage from the Gardetta Plateau (Briançonnais, Western Alps, Italy) which, at the Permian-Triassic boundary, was placed at about 11° North. The tracks, both arranged in trackways and documented by single, well-preserved imprints, are assigned to *Isochirotherium gardettae* ichnosp. nov., and are here interpreted as produced by a non-archosaurian archosauriform (erytrosuchid?) trackmaker. This new discovery provides further evidence for the presence of archosauriformes at low latitudes during the Early Triassic epoch, supporting a model in which the PTME did not completely vacate low-latitude lands from tetrapods that therefore would have been able to cope with the extreme hot temperatures of Pangaea mainland.

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Key words: Isochirotherium gardettae n. ichnosp., climate warming, extinction, Lower Triassic, Italy.

ABSTRACT

The most accepted killing model for the Permian-Triassic mass extinction (PTME) postulates that massive volcanic eruption (i.e. the Siberian Traps LIP) led to geologically rapid global warming, acid rain and ocean anoxia. On land, habitable zones were drastically reduced, due to the combined effects of heating, drought and acid rains. This hyperthermal had severe effects also on the paleobiogeography of several groups of organisms. Among those, the tetrapods, whose geographical distribution across the end-Permian mass extinction (EPME) was the subject of controversy of a number of recent papers. We here describe and interpret a new Early Triassic (?Olenekian) archosaur track assemblage from the Gardetta Plateau (Briançonnais, Western Alps, Italy) which, at the Permian-Triassic boundary, was placed at about 11° North. The tracks, both arranged in trackways and documented by single, well-preserved imprints, are assigned to *Isochirotherium gardettae* ichnosp. nov., and are here interpreted as produced by a non-archosaurian archosauriform (erytrosuchid?) trackmaker. This new discovery provides further evidence for the presence of archosauriformes at low latitudes during the Early Triassic epoch, supporting a model in which the PTME did not completely vacate low-latitude lands from tetrapods that therefore would have been able to cope with the extreme hot temperatures of Pangaea mainland.

INTRODUCTION

The Permian-Triassic mass extinction (PTME) was the most severe biotic crisis of all times (Erwin, 1993), eliminating > 90% of marine and terrestrial species (Erwin, 1993; Song et al., 2013, 2015). After the mass extinction, totally new clades emerged, which include decapods and marine reptiles in the oceans and new tetrapods on land (Chen and Benton, 2012). In the last decade different physical environmental shocks have been identified as possible triggers for the huge crisis, which include increased atmospheric CO_2 concentrations, global warming, acid rain, ocean anoxia, ocean acidification and hypercapnia (Chen and Benton, 2012; Benton, 2018). The most accepted killing model (e.g. Benton & Twitchett, 2003; Chen & Benton, 2012; Benton & Newell, 2014; Shen et al., 2019) postulates an initial megascale eruption (more than 1,000 Gigatonnes of erupted lava, see Grasby et al., 2011), that released consistent amount of sulphate aerosols and methane from clathrate reservoirs (see Berner, 2002), which led to global warming and acid rain, causing a generalized plant die-offs and thus intensive erosion of the soil (Wignall, 2001; Benton, 2003, 2018; Benton & Twitchett, 2003; Sephton et al., 2005; Knoll et al., 2007). On land, habitable zones were drastically reduced, due to the combination of extreme heat, drought and acid rains, which caused progressive loss of soil and forests and had direct impact on lacustrine organisms and any land-dwelling animal (Benton & Newell, 2014).

According to several authors (Joachimski et al., 2012; Sun et al., 2012; Schobben et al., 2014; Song et al., 2015) the intense global warming started at the extinction horizon as testified in the Meishan section (South China), and then continued in the Early Triassic, very likely with the release of methane from deep ocean sediments and coals that triggered the process, and the release of additional greenhouse gasses by interactions of the Siberian traps with local permafrost soils, limestones, and other deposits rich in organic matter (e.g. Racki, 2003; Racki & Wignall, 2005; Retallack & Jahren, 2008; Grasby et al., 2011).

The hyperthermal had severe effects also on the paleobiogeographic patterns. In ~~the last~~ years the distribution of land tetrapods across the PTME was discussed ~~by~~ a number of studies which however suggested different scenarios. By compiling literature evidence on the main skeletal findings, Sun et al. (2012) suggested that, in the Early Triassic, terrestrial vertebrates totally vacated the equatorial belt, the so-called 'vertebrate equatorial-gap', as a consequence of the extreme hot temperatures. More recently, Bernardi et al. (2015, 2018) reviewed the Late Permian-Early Triassic terrestrial tetrapod record integrating skeletal and track data and concluded that tetrapod geographic distribution was much wider than previously suggested. In the Early Triassic it included also the low latitudes, though polarward dispersals were detected in the Early Triassic and possibly linked to the development of super-hot temperatures in the equatorial belt (Bernardi et al., 2018). Fossil track evidence, in particular, was key in denying the existence of an 'equatorial gap' (Bernardi et al., 2018).

Archosaur tracks and trackways are in fact well-known from Lower to Middle Triassic siliciclastic and carbonate sediments of the Upper Buntsandstein and Lower Muschelkalk (late Olenekian-early Anisian) of Germany (Haubold, 1971a, 1971b; Klein & Haubold, 2007), the Lower Triassic of the Holy Cross Mountains in Poland (Klein & Niedzwiedski, 2012), the Middle Triassic of Bourgogne (Gand, 1979), Massif Central (Demathieu, 1970) and Ardèche in France (Courel & Demathieu, 1976), the Iberian Range in Spain (Fortuny et al., 2011; Diaz-Martinez, et al., 2015) and Sardinia in Italy (Citton et al., 2020). Further sites, often with identical ichnotaxa and ichnoassemblages, are known from the Lower to Middle Triassic of Great Britain (King et al., 2005), North American southwest (Klein & Lucas, 2010), Argentina (Melchor & De Valais, 2006), Africa (Klein et al., 2011) and southern China (Xing et al., 2013). In the Alps, chirotherian footprints were described from the Lower to Middle Triassic of the

Dolomites, Piedmont and Ligurian Alps in Italy (Avanzini & Mietto, 2008; Petti et al., 2013; Santi et al., 2015), Aar Massif in eastern Switzerland (Feldmann et al., 2009; Klein et al., 2016) and the Aiguilles Rouges Massif (Western Alps), on the border between Switzerland and France (Demathieu & Weidmann, 1982; Avanzini & Cavin, 2009; Cavin et al., 2012; Klein et al., 2016).

We here describe and interpret a new archosaur track assemblage from the Gardetta Plateau (Western Alps, south-western Piedmont, Italy; Fig. 1) that was analyzed in two different field ~~works~~, during the summer 2009 and in the autumn 2017-2018.

Tracks are preserved on two distinct track surfaces, belonging to the same stratigraphic horizon. Some of them are badly preserved but distinct trackways, up to 3 m long, can be recognized together with other exceptionally preserved isolated tracks showing clear morphological details of the trackmaker's autopodium.

This discovery provides reliable evidence of the presence of archosauriforms in the Briançonnais domain during the Early Triassic, adding further support to the occurrence of terrestrial tetrapods at low latitudes soon after the PTME (Bernardi et al., 2015; 2018) and well-before a full land ecosystem recovery.

MATERIALS AND METHODS

All the specimens were identified in the same outcrop, located about 1 km SE of the Gardetta Plateau, close to Pianezza creek (44°24'5.75"N; 7° 1'45.29"E; Canosio Municipality, Cuneo Province, NW Italy; Fig. 1).

Most of the footprints are preserved as negative epichnia (concave epirelief) and were left *in situ* in the field. The footprints were discovered by EC and MP in summer 2008. A surface of about 10-15 m^2 was mapped ~~a~~ first time in 2009 by HF and then in 2017 by FP and HF. An exceptionally preserved trackway, consisting of three large pes and manus imprints, was then discovered during the 2017 and 2018 field ~~works~~ by EM and FP, about 10 m higher up on the same outcropping horizon. Tracks outlines were drawn on transparency acetate film and then digitized by a vector-based drawing software (Adobe Illustrator ©). Additional footprints were collected by the authors and hikers from loose sandstone slabs in the creek below the track surfaces. These isolated and usually fragmentary footprints are preserved both as concave epirelief and well-preserved convex epirelief, the latter being preserved in the basalmost level of the sandstone bed which overlies the track layer.

Close-range photogrammetry was used to document tracks and obtain three-dimensional model of the best-preserved ones (Petti et al., 2008; Remondino et al., 2010; Mallison & Wings, 2014). The data processing phase was performed using Agisoft PhotoScan ® Professional software, following the procedure indicated by Mallison & Wings (2014). In a second phase, the software Surfer®14 (GoldenSoftware, 2002), was used to convert elevation points to contour lines and to produce color coded maps of the studied material.

The obtained images are ideal for both ~~precisely measure~~ standard ichological parameters (Haubold, 1971b; Leonardi, 1987) and for recognizing anatomy related morphologies, therefore for the reconstruction of the trackmaker's autopodial osteology.

Trackmaker identification was carried out employing three different and integrated methodological approaches: i) Synapomorphy-based correlation (Olsen, 1995; Carrano & Wilson, 2001); ii) Phenetic correlation (Carrano & Wilson, 2001) and iii) Coincidence

correlation (Carrano & Wilson, 2001). The synapomorphy-based method focuses on the identification of osteologic-derived character states in the footprints that result from the impression of synapomorphic characters in the trackmaker autopodia (see Olsen et al., 1998; Carrano & Wilson, 2001; Wilson, 2005; Romano et al., 2015). The phenetic correlation is closely linked to ichnotaxonomy and derives from an accurate description of the footprint and the identification of the trackmaker through the recognition of an affinity between tracks and limbs osteology (Carrano & Wilson, 2001; Wilson, 2005). The coincidence correlation is usually adopted to refine trackmaker identification and is based on supplemental data including geological age, geographic provenance, local faunal composition and distributions, and abundances of skeletal taxa and ichnotaxa (Carrano & Wilson, 2001).

GEOLOGICAL FRAMEWORK

The Gardetta Plateau - Preit valley area is located in the southern part of the Western Alps (Fig. 1). It encompasses the Sautron, Rouchouze, Rocca Peroni tectonic units and the Gardetta deformation unit (*sensu* d'Atri et al., 2016) also known as "bande siliceuse de la Gardetta" (Gidon, 1972).These tectonic units pertain to the Briançonnais Domain (Gidon, 1958a, 1958b, 1972; Schmid et al., 2004, 2017) and in particular to the External Briançonnais Domain which is characterized by very low grade to anchizone metamorphism (d'Atri et al., 2016).

The upper Permian-Mesozoic sedimentary succession varies considerably within the Briançonnais Domain *s.l.* (Briançonnais Domain *s.s.* and Ligurian Briançonnais, Decarlis & Lualdi, 2009; Fig. 2) due to the slightly different paleogeographic positions of these sectors (see

Decarlis et al., 2013 for a review). The outcropping lithostratigraphic units, even ~~if~~ can be correlated across the distinct domains, display different thickness, vertical/lateral relationships and hiatuses. These differences led authors to adopt a multitude of official and unofficial names for the lithostratigraphic units. Despite these minor differences, the late Permian–Early Triassic sedimentation in the whole Briançonnais domain s.l. testifies to the evolution of a continental margin affected by extensional tectonics. The Briançonnais domain was positioned north of the westernmost sector of the Palaeotethys, in the western continental termination of the Meliata oceanic back-arc basin (Ziegler & Stampfli, 2001; Decarlis et al., 2013). Adopting the paleolatitude calculator developed by Van Hinsbergen et al. (2015) (model version 2.1) and using the Global Apparent Polar Wander Path of Torsvik et al. (2012) ~~as~~ paleomagnetic reference frame, the Early Triassic (250 Ma) palaeolatitude estimate for the Southern Briançonnais Domain is 11.8 N.

In the study area the volcano-sedimentary succession starts with upper Carboniferous - Permian volcanic rocks (andesitic lavas followed by rhyolites and rhyolitic ignimbrites) unconformably overlain by upper Permian-Lower Triassic siliciclastic continental-to-transitional deposits (the so called "*semelle silicieuse*" of French Authors). In particular these deposits are characterized by basal coarse grained conglomerates and quartz-conglomerates, named locally "Verrucano Brianzonese", (Carraro et al., 1970; Cassinis et al., 2018) that ~~evolve~~ upward into quartz-arenites and quartz-siltites of the "Werfenian quartzites" (Fig. 2; Gidon, 1958b; Malaroda, 1970; Megard-Galli & Baud, 1977; Costamagna et al., 2002; Costamagna, 2013). The siliciclastic sequence ~~indicate~~ deposition in an alluvial environment characterized by sandy braided fluvial system fed by the residual Variscan relieves (Costamagna, 2013). In the southernmost part of the Briançonnais domain (External Ligurian Briançonnais Domain,

Vanossi, 1974; 1991; Bertok et al., 2012) these latter lithostratigraphic units are known as "Scytian quartzites" or "Ponte di Nava Quarzites" (Fig. 2; Decarlis et al., 2013, 2015). Similar to the siliciclastic sequence of the Briançonnais Domain s.s., the "Ponte di Nava Quarzites" originated from the dismantling and reworking of the Paleozoic igneous and metamorphic basement.

The quartz-arenites can be topped either by greenish pelites (known as "Case Valmarenca Pelites" in the Ligurian Briançonnais, Vanossi 1974; 1991), that have been interpreted as mudflat deposits, or by a thin and discontinuous interval of cavernous dolostones called "*Cargneules Inférieures*" representing the sedimentation in an arid environment as an evaporitic sabkha (Fig. 2). According to Lualdi & Seno (1984), in the Ligurian Briançonnais Zone the "Case Valmarenca Pelites" could be laterally equivalent to the "*Cargneules inférieures*".

The continental succession and/or the evaporitic deposits are followed by Middle Triassic shallow water carbonates of the "*couverture carbonatée*" (Gidon, 1958b; Megard-Galli & Baud, 1977; Costamagna et al., 2002) comprising a lower calcareous complex (Costa Losera Fm, Lualdi and Bianchi, 1990, corresponding to the e St. Triphon Formation of the classic Briançonnais Domain) and an upper dolomitic complex (San Pietro dei Monti Fm, Vanossi, 1969). These carbonate deposits testify the sedimentation in a subsiding carbonate ramp.

The lower calcareous complex (Fig. 2) begins with a characteristic facies named "*Marbres Phylliteux*" by French Authors made of greyish and brownish fine-grained limestones, (lower to upper Anisian) with sericite, muscovite, chlorite laminated levels. Bedding can be locally masked by pervasive and intense bioturbation ("*Calcaires Vermiculés*" facies) assigned to the ichnogenus *Rhizocorallium*. The basal complex ends with varicolored pelites, interpreted as

cinerites (upper Anisian in age) by Caby & Galli (1964), recognizable throughout the whole Briançonnais Domain.

The upper dolomitic complex (Fig. 2) is ~~constituted by~~ massive to well-bedded dolostones followed by cyclically arranged carbonates ("C*alcaires rubanés*" – upper Anisian – upper Ladinian; Gidon, 1958b; Megard-Galli & Baud, 1977; Costamagna et al., 2002; Decarlis & Lualdi, 2009) characterized by subtidal crinoidal wackestones, intertidal oolitic limestones and supratidal dolomitic mudstones capped by reddish paleosols, that testify shallowing-upward cycles. The dolomitic succession includes dark limestones, dark fossiliferous and/or oolithic dolostones, meter-thick autoclastic breccias and gypsum–anhydrite pseudomorphs witnesses of major emersion events. These lithofacies, dated to the uppermost Ladinian, are known in the different Briançonnais domains as "*Dolomies blanches*" or "*Dolomies grises*" or "Couches a *C. goldfussi*" or "*Complexe schisto-dolomitique* basal".

THE PIANEZZA STRATIGRAPHIC SUCCESSION

In the framework of the abovementioned stratigraphic setting the footprint-bearing level is located in the Pianezza area along the track connecting Colle del Preit (2100 m a.s.l.) to Grange Isoardi (Pianezza area, 2275 m a.s.l.) (Fig. 2). The outcrop is located along the SW flank of a narrow antiformal anticline belonging to the Sautron Tectonic Unit which overthrusts the Rouchouze Tectonic Unit. Here the volcano-stratigraphic succession begins by meta-andesites and andesitic schists pertaining to the upper Carboniferous-Permian volcanic complex. The sedimentary succession continues upward with a thin and discontinuous (up to 1 meter) level of

graphitic schists, deriving from the weathering of the volcanic basement (Lorenzoni & Zanettin, 1958) and is then followed by up to 100 meters of quartz-conglomerates ("Verrucano Brianzonese") and by fine to very fine quartz-arenite and quartz-siltite with ripple marks and cross bedding ("Werfenian quartzites"). The track-bearing horizon occurs at the top of the latter clastic interval. The succession continues upward with 15 meters of gypsum/anhydrite deposits of the lower cargneule. In the Pianezza area the Middle Triassic *"couverture carbonatée"* is only represented in the north-eastern flank of Sautron Unit anticline.

CHRONOSTRATIGRAPHIC FRAMEWORK OF THE STUDY AREA

The sedimentary rocks belonging to the quartz-rich clastic succession does not allow precise dating because of the lack of biostratigraphic markers as commonly happen for these kind of deposits. They are here referred to the upper Permian-Lower Triassic ~~on~~ the base of their stratigraphic position in the Sautron Unit, similar to that of the ~~well~~ comparable quartz-conglomerate and quartzarenite rocks occurring not only in the Briançonnais Domain, but also in the Southern Alps, Sardinia and Provence. For this reason, in order to constrain the age of the track-bearing horizon, some considerations are required: i) the coarse quartz-conglomerates ("Verrucano Brianzonese") are commonly referred to the late Permian-earliest Triassic (Gidon, 1958b; Carraro et al., 1970; Megard-Galli & Baud, 1977; Decarlis & Lualdi, 2009); ii) the Lower Triassic age can be hypothesized considering the occurrence of *Estheria minuta* Alberti and *Myacites fassaensis* Bittner within the "Ponte di Nava Quarzites" (Decarlis & Lualdi, 2009); iii) the "lower cargneule" unit and its lateral equivalent "Case Val Marenca Pelites" are generally

attributed to the late Early Triassic (Gidon, 1958b; Carraro et al., 1970; Megard-Galli & Baud, 1977; Decarlis & Lualdi, 2009); iv) the lower ~~part~~ of "*Marbres Phylliteux*" are considered early Anisian in age, on the basis of the occurrence of *Rhizocorallium*, that is regarded ~~to be~~ an early Anisian marker all over the Tethyan realm (Baud, 1976); v) an early Anisian age for the base of the lower calcareous complex ("*Marbres Phylliteux*" and Costa Losera Fm.) is also suggested by the occurrence of Dasycladacean algae and crinoidal remains (*Dadocrinus* sp.; Carraro et al., 1970); vi) In the northern Briançonnais of southwestern Switzerland a find of the ammonoid *Beyrichites cadoricus* in the upper part of the St-Triphon Formation indicate a middle Anisian age (Baud et al., 2016).

Additionally, it is worth mentioning that both in the Geological Map of the Argentera Massif (Malaroda, 1970; Carraro et al., 1970) and in the Geological Map of France at the scale 1: 50.000 (Sheet 896, Larche; Gidon, 1978) the studied outcrop was attributed to Lower Triassic. All the above reported data thus point to a probable attribution of the trampled horizon to the late Early Triassic.

SYSTEMATIC ICHNOLOGY

Most footprints are preserved as natural molds (concave epirelief) on top of a 3-4 cm thick bed of fine sandstone. The tracks are shallow, less than 2 cm deep, but most of them are cut by small-scale tectonic cracks/fissures and strongly weathered. Two possible trackways with lengths of 4–5 m were identified on a track surface. Only one isolated track was visible on the underlying sandstone bed, also preserved as concave epirelief. Three solitary small footprints,

preserved as convex epirelief of the directly overlying sandstone bed, were collected from loose slabs. The upper surface of this 1–2 cm thick sandstone bed is marked by symmetric wave ripples, exposed on a spectacular bedding plane (Fig. 3).

An exceptionally preserved trackway, ~~made~~ of three consecutive manus-pes sets was found on another surface, belonging to the same stratigraphic horizon, upstream of the previously described ones (Fig. 4). The general features of the herein studied ichnoassemblage are typical for chirotherian tracks (Haubold & Klein, 2002).

Ichnogenus *Chirotherium* Kaup, 1835

Type ichnospecies: *Chirotherium barthii* Kaup, 1835

Chirotherium isp.

(Figs 3, 7)

Referred specimens: two trackways preserved as concave epirelief (GT-1 and GT-2). GT-1 consists of four clear and two weakly impressed imprints, arranged in a 2.10 m-long trackway in the lower part of the outcrop, just 2 meters above the creek level (Fig. 3). Its direction on the steep bedding plane points upwards to southeast. Trackway GT-2 is 2.40-m-long, is preserved in the lower part of the same bedding plane, about 2 meters above the creek level, running from northwest to southeast.

Description: pentadactyl and semi-digitigrade pes imprint. Pes is longer than wide, (Foot Length [FL] = 13 to 16 cm; Foot Width [FW] = 8-10 cm; FL/FW = 1.6 to 2.0) with digit group

296 II-IV roughly asymmetrical. Pedal digit impressions gradually increase from I to IV, with II sub-
297 equal or shorter than digit IV; digit III is the longest. In the best-preserved track (GT1-3; Figs 3,
298 7), digit I is pointed and placed posteriorly with respect to digit group II-IV. Digit V is oval and
299 tapers distally; it is positioned posteriorly and laterally to digit I-IV and directed antero-laterally.
300 No digital pad impressions can be observed on digit II-IV. Digit V shows a large rounded pad
301 impression and a possible sub-triangular shaped claw mark. Manus tracks are absent or faintly
302 preserved as small semi-circular imprints, placed in front of the pedal footprints. An isolated
303 tetradactyl imprints, measuring 4.5 cm in length and 7 cm in width, and another isolated circular
304 pentadactyl imprint 5.5 cm long are interpreted as possible manus imprints.
305 In the trackway the oblique pace varies between 26 and 41 cm, with a mean value of 36 cm.
306 The pes pace angulation varies between 145º and 165º, with a mean value of 157º.
307
308 **Discussion:** the ichnogenus *Chirotherium* with its holotype *Chirotherium barthii*, was
309 described by Kaup (1835) on trackways from the "Thüringischer Chirotheriensandstein" (Lower-
310 Middle Triassic) of the Thuringia region (Germany). The here described material, even if not
311 perfectly preserved, retains some diagnostic features of the ichnogenus *Chirotherium*, such as the
312 oval morphology and the position of digit V (slightly behind digit group II-IV), and the relative
313 digit length of group II-IV, with digit IV longer or sub-equal to digit II. Pes pace angulation is
314 also similar to the values to date reported for the ichnogenus (160°-170°). *Chirotherium barthii*
315 (Figs 7e, 7f) shows clear circular pads on digit group II-IV and digit impressions are broader
316 than in the studied specimens. In *C. barthii*, as well as in *C. rex*, *C. moquinense* and *C. vorbachi*
317 (Fig. 7h), digits I-IV are splayed whereas in the GT-1 and GT-2 trackways, pedal digits outlines
318 are closely arranged with only digit I medially spread. Digits II-IV seems to be almost parallel to

each other and the digit pattern resemble that of the ichnospecies *C. sickleri* Kaup, 1835 (Figs 7i, 7l, 7m) with digit I forming a narrow group with digits II, III and IV. Nevertheless, digit IV, though slightly shorter than III, is not much longer than II as observed in most of the specimens assigned to *C. sickleri*. Unfortunately, the bad preservation of pes imprints in GT-1 and GT-2 trackways preclude any accurate ichnospecific assignment.

Ichnogenus *Isochirotherium* Haubold, 1971a (Figs 4, 5, 8)

Type ichnospescies: *Isochirotherium soergeli* (Haubold, 1967).

***Isochirotherium gardettae* ichnosp. nov.**

Derivatio nominis: from the Gardetta plateau, type locality of the ichnospecies.

Type-level: "Werfenian quartzites", Lower Triassic.

Referred specimens: a trackway made of three well-preserved and consecutive manus-pes couples (GT-7; Fig. 4) not exceeding 2.20 m across. Another possible isolated track (GT-3) partially preserved in the lower track surface.

Diagnosis: chirotherian track with pentadactyl pes and small and tetradactyl manus imprint and pes digit IV noticeably shorter than II; pes digit group I-IV slightly longer than wide, pes digit V with large ovoid metatarsal pad and a reduced phalangeal portion. Pes length ranging

from 28 to 33 cm; cross axis equal to 90°. Trackway very narrow, pace angulation near 165°, and ratio of stride to pes length is 4.3.

Description: pentadactyl and semi-plantigrade pes imprint, longer than wide (FL = 33.4 cm; FW = 19.2 cm; FL/FW = 1.74). Digit III is the longest. It is slightly longer than II, whereas digit IV is shorter than II. Digit I is the shortest and is thinner than those of digit group II-IV. The total divarication I-IV is 22°; the angle between digit I and II is 8° and is equal to that between II and III but larger than II-IV (6°). Cross axis is nearly equal to 90°. Digit impressions are robust and pointed showing large sub-triangular claw marks. Two phalangeal pad impressions are present on each digit of group I-IV. The metatarsal-phalangeal portion is proximally arched and could be separated from digit V by a gap, or joined with it through a convex area, running from the basalmost portion of digit I to the medial digit V. Digit V shows a large oval impression joined to a rounded phalangeal-ungual portion, laterally spread out. In GT-7-2 and GT-7-3, pes digit V has a sub-triangular shape with a wider inner margin, almost aligned with the medial margin of digit I. Length of pes digits are: I) 118 mm; II) 173 mm; III) 186 mm; IV) 136 mm; V) 167 mm.

The manus is small, tetradactyl and digitigrade, wider than long (FL = 8.04 cm; FW = 13 cm; FL/FW = 0.62) and is placed in front of the pes. Digits are short and pointed. Digits II and III have nearly equal length and are longer than digits I and IV; the latter is moderately spread outward. Digit IV is possibly the shortest. Length of manus digits are: I) 49 mm; II) 74 mm; III) 68 mm; IV) 43 mm.

The trackway, made by three consecutive manus-pes sets, shows a clear narrow gait (pace angulation 164°). Oblique pace is 59 cm, whereas double pace is 119 cm across. Manus-pes couples turned slightly outward with respect to the midline (from 10° to 15° on average).

364

365 **Discussion:** the ichnogenus *Isochirotherium* was erected by Haubold (1971a); its type
366 ichnospecies *I. soergeli* (Haubold, 1967) comes, as for *Chirotherium barthii*, from the
367 "Thüringischer Chirotheriensandstein" (Lower-Middle Triassic) of the Thuringia region
368 (Germany). The ichnogenus is reported also from the Middle Triassic of Great Britain (Tresise &
369 Sarjeant, 1997; King et al., 2005), from the Lower–Middle Triassic of North American
370 Southwest (Peabody, 1948; Klein & Lucas, 2010), the Aiguilles Rouges Massif (Western Alps)
371 on the border between Switzerland and France (Avanzini & Cavin, 2009; Klein et al., 2016) and
372 from the Middle Triassic of North-East Italy (Avanzini & Leonardi, 2002).
373 The main diagnostic features of this ichnogenus, retained by our specimens are: i) the relative
374 digit length, with digit II longer than IV and shorter than III; ii) a marked heteropody; iii) the pes
375 pace angulation around 165°; iv) the weakly impressed distal portion of digit V and v) pes-
376 manus couples outward rotation of about 15°. However, the studied trackway shows clear
377 difference to most of the ichnospecies known to date. For example, the type ichnospecies *I.*
378 *soergeli* Haubold, 1967 (Fig. 8o), has smaller absolute dimensions, thinner pes digit marks and,
379 most importantly, display five clear digit impressions in the manus contrary to GT-7, where only
380 tetradactyl manus were observed.
381 *Isochirotherium hessbergense* Haubold, 1971a (Fig. 8m) has also a pentadactyl manus and is
382 clearly different from the material described in this paper for its digit group I-IV longer than
383 wider and for the relative pes digit length, notably digit I is longer than IV.
384 *Isochirotherium demathieui* Haubold, 1971a (Fig. 8n) can be excluded for its pentadactyl
385 manus and for the shorter distance between manus and pes.

386 *Isochirotherium coltoni* Peabody, 1948 (Fig. 8h) and *I. lomasi* Baird, 1954 (Fig. 8i) retain
387 much slenderer digit impressions, especially in the pes imprint and most notably have manus
388 tracks more internally placed than in the studied footprints. Interestingly *I. herculis* Egerton,
389 1839 (Fig. 8e) has similar dimensions (i.e. FL longer than 30 cm) but can also be excluded for i)
390 the tridactyl manus; ii) the digit group I-IV slightly wider than longer and iii) the manus imprint
391 position, very close to that of the pes.
392 *Isochirotherium marshalli* Peabody, 1948 (Fig. 8f) shows similar features such as: i) the pes
393 digit relative length; ii) the interdigital angles values; iii) the digit group I-IV as longer as wider;
394 iv) the arched metatarsal-phalangeal portion; v) the configuration of digit V whose phalangeal
395 portion is significantly smaller than the ovoidal and possibly tarsal-metatarsal pad. Nevertheless,
396 the assignment to this ichnospecies is precluded by its pentadactyl manus.
397 *Isochirotherium inferni* Avanzini & Leonardi, 2002 from the Illyrian (late Anisian, Middle
398 Triassic; Fig. 8g) of the Adige Valley (Bolzano, NE Italy) closely resembles the Gardetta
399 specimens for: i) the arched metatarsal-phalangeal portion; ii) the position of the base of pes digit
400 V, placed along the axis of digit III; iii) pes digit relative length; iv) cross axis equal to 90° v) pes
401 angulation of about 160°; vi) positive rotation of manus-pes couples respect to the midline (10°-
402 15°). However, pes digits are stouter and the manus is described as pentadactyl (even if in the
403 outline drawing only four digits are clearly appreciable). The tracks referred to *Isochirotherium*
404 *delicatum* Courel & Demathieu, 1976 and found in the Anisian-Ladinian deposits of Argentière
405 (Ardèche, France; Courel & Demathieu, 1976; Courel et al., 1979; Demathieu, 1984; Gand,
406 1978) and Gampempass (Southern Alps, Italy; Avanzini & Lockley, 2002) show less-thick digit
407 impressions and a markedly reduced digits IV and V; the latter is also much more backward
408 positioned if compared with the studied specimens.

We therefore erect the new ichnospecies *Isochirotherium gardettae* to describe a new and well-preserved *Isochirotherium* trackway that differs from all the other ichnospecies for all the features listed above.

TRACKMAKER IDENTIFICATION

Grounding on previous studies and new observations Bernardi et al. (2015) showed that chirotherian footprints, such as *Protochirotherium*, *Chirotherium*, *Brachychirotherium* and *Isochirotherium*, can be confidently attributed to archosauriforms, based on the presence of a digit IV shorter or as long as digit III. Being metatarsal length directly proportionate to digit length, this assumes that metatarsal IV is shorter than or as long as metatarsal III, a synapomorphy of the archosauriforms (Nesbitt, 2011). Other characters useful to identify archosauriforms traces are: i) the presence of a compact digit group I-IV; ii) a posterolateral positioned and strongly reduced digit V; iii) a massive metatarsal-phalangeal region, shorter than or as long as digit I. However, the first character occurs in archosauriforms and non archosauromorphs diapsids (Haubold, 1971a, 1971b; Smith & Evans, 1996) whereas the second is present in archosauriforms, lepidosaurs and basal archosauromorphs (Haubold, 1971a, 1971b; Evans & Wang, 2005; Gottman-Quesada & Sander, 2009).Other features suggesting an archosaur affinity for chirotherian footprints (observed also in the here described traces), are narrow trackways linked to the disposition of limbs under the body, and the presence of small manus relative to the pes, which indicate a possible early tendency toward bipedal posture and gate (see Haubold, 1971a, 1971b, 1984, 2006; Klein et al., 2010).

To reconstruct the hind- and fore-limb autopodial bones, we assumed an arthral position for the joint articulations within digital pad impressions (Fig. 9a).

In our opinion, the sub-elliptical to pyriform impression behind group I-IV in *Isochirotherium* could be the result of the coalescence of the impression of the phalangeal-metatarsal portion of digit V and of a thick fleshy pad beneath the astragalus, the calcaneus and some of the tarsal bones. Overall, the trackmaker's pes may have had a semi-plantigrade posture, as evidenced by the gap between digit group I-IV and digit V, corresponding to the part of the foot held up during locomotion. The manus has a marked digitigrade posture and its tetradactyly might result by the fact that manual digit V likely held off the ground during the touch-down and weight bearing phases (*sensu* Manning, 2004).

The reconstructions thus obtained shows the following pes and manus phalangeal formulas: pes 2-3-4-4-1 and manus 1-2-3-3. They are compared with the anterior and posterior limbs of the main groups of archosauriforms known in the Triassic period (Huene, 1902; Broom, 1903; 1905; Romer, 1971; Welles, 1947; Young, 1964; Zhang, 1975; Peyer et al*.,* 2008; Ezcurra et al*.*, 2013; Sookias & Butler, 2013; Trotteyn et al*.*, 2013).

The first considered non-archosaurian archosauriforms groups are Proterosuchidae (Ezcurra et al*.*, 2013), Proterochampsidae (Trotteyn et al*.*, 2013) and Euparkeriidae (Sookias & Butler, 2013). In all the three representatives *Proterosuchus fergusi* Broom, 1903 (South Africa, Induan–?early Olenekian; Fig. 9e), *Chanaresuchus bonapartei* Romer, 1971 (Argentina, Ladinian; Fig. 9i) and *Euparkeria capensis* Broom, 1913 (South Africa, Anisian; Fig. 9h), the IV metarsal has a length similar or greater than that of the III but the digit II is much shorter than digit III and nearly equal to digit IV, in contrast to what we observe in specimens GT-7-1, GT-7-

2 and GT-3. No fore- or hind limb bones are known for the Doswelliidae, another clade of non-archosaurian archosauriforms (Middle-Late Triassic; Sues et al., 2013).

Diedrich (2015) recently attributed the *Isochirotherium* tracks to *Arizonasaurus* Welles, 1947, a member of Poposauroidea (archosaurian archosauriforms) found in the Moenkopi Formation (Arizona, USA, Anisian,), from the same levels as *Isochirotherium* tracks. Unfortunately, no bones of the fore- and hind-limbs are known from *Arizonasaurus*, as well as from *Ctenosauriscus koeneni* (Huene, 1902) (Germany, latest Olenekian), the Lower Triassic poposauroid archosaur, and additionally findings are needed to test Diedrich's hypothesis.

The hind-limb bones are known in *Lotosaurus adentus* Zhang, 1975 (China, Ladinian; Fig. 9d), another member of Poposauroidea with semi-plantigrade posture. If compared with the restored autopodium, it is characterized by larger fore-limbs, V digit positioned further forward, longer metatarsals of digit group I-IV and different digit proportions.

The pedal phalangeal relative length of the rauisuchid archosaur *Postosuchus alisonae* Peyer et al., 2008 (USA, Norian; Fig. 9c), is similar but all the five metatarsals are much longer, implying a digitigrade posture, as in the reconstruction proposed by Peyer et al. (2008).

Postosuchus kirkpatricki Chatterjee, 1985 (USA, Norian; Fig. 9b), is also characterized by very long metatarsals and thus excluded as a possible trackmaker. The smaller but complete skeleton of *Ticinosuchus ferox* Krebs, 1965 (see Lautenschlager & Desojo, 2011 for a review of the species) from the uppermost Anisian of Monte San Giorgio (southern Switzerland), shows long metatarsals and a digit IV longer than digit II and is commonly considered as the producer of *Chirotherium* trackway (Haubold, 1984, 1986).

By contrast, the hind limbs of the non-archosaurian archosauriform clade of Erythrosuchidae (Ezcurra et al., 2013) are characterized by relative digit length very similar to that outlined for

476 *Isochirotherium gardettae* and a pedal phalangeal formula that is approximately 2-3-4-5-3
477 (Young, 1964; Cruickshank, 1978; Gower, 1996).
478 Metatarsals II and III are sub-equal and slightly longer than IV in *Erythrosuchus africanus*
479 Broom, 1905 (South Africa, lower Anisian; Fig. 9f. See also Cruickshank, 1978; Gower, 1996).
480 Metatarsals II and III are the longest in *Shansisuchus shansisuchus* Young, 1964 (Fig. 9g),
481 another member of Erythrosuchidae found in upper Anisian deposits of China; *S. shansisuchus*
482 also possesses a hook-shaped proximal end of metatarsal V and its relative digit proportion
483 closely fits that of our individual, but as for *E. africanus* digit V seems to be too forwardly
484 positioned. However, digit V impression in *I. gardettae* likely records only the distal metatarsal
485 and phalangeal (ungual) portions. During locomotion the former was held off the ground
486 whereas the latter was likely being retracted due to the presence of a thick fleshy pad beneath
487 calcaneum and astragalus.
488 The morphology of the acetabulum and proximal end of the femur in erythrosuchids suggests
489 a distinctly sprawling gait (Gower, 2003; Ezcurra et al., 2013), that clashes with the narrow
490 trackway seen in *I. gardettae*. Nevertheless, the prominence of metatarsal II and III is evidenced
491 only in non-archosaurian archosauriforms (Gower, 1996) and thus an individual belonging to this
492 group, possibly a yet unknown taxon and with a more erect stance and characterized by a marked
493 heteropody, is the most suitable producer (Fig. 10).
494
495 **BIOCHRONOLOGY AND BIOGEOGRAPHY**
496 The Gardetta ichnoassemblage represented by *Chirotherium* and *Isochirotherium* is typical
497 for terrestrial deposits of the late Olenekian and early Anisian (Klein & Haubold, 2007) and the
498 Gardetta chirotheriid tracks correlate with the international *Chirotherium barthii* Assemblage

Zone of Klein & Lucas (2010a). This biochron is characterized by the occurrence of *Chirotherium* and *Isochirotherium*, but also by two other ichnogenera not present at Gardetta, *Rotodactylus*, and *Synaptychium*. The *Chirotherium barthii* Assemblage Zone ranges from the late Early to early Middle Triassic (late Olenekian – early Anisian), and independently confirms the Early Triassic (?Olenekian) age, derived by stratigraphic correlation with other sections in the Briançonnais of the Western Alps.

The Gardetta outcrop enlarges also the knowledge on biogeography of archosaurs in the Lower Triassic of Europe, so far based on archosaur ichnosites discovered in Italy (Val Marenca, Santi et al., 2015; Sardinia, Citton et al., 2020), Spain (Moncayo and Tagamanent, Díaz-Martínez & Pérez-García, 2012), Switzerland (Cascade d'Emaney and Vieux Emosson; Cavin et al., 2012), Austria (Drau Range; Krainer et al., 2012), Germany (Bundsandstein; Klein & Haubold, 2007) and Poland (Wióry, Holy Cross Mountains, Klein & Niedźwiedzki, 2012).

Early Triassic erythrosuchid skeletal fossils are known from the late Olenekian of Russia, South Africa, China and India (see Gower, 2003; Ezcurra et al., 2013, 2019, 2020; Gower et al., 2014; Ezcurra, 2016). The Gardetta ichnosite testifies the presence of erythrosuchids and more generally of Archosauriformes at low latitudes (11.8° N) also during the Early Triassic (Fig. 11). This supports the conclusions of Bernardi et al. (2015, 2018) that Early Triassic ichnosites are mainly distributed ~~along~~, the tropics, ~~contrasting~~, the pattern ~~described~~ by skeletal findings and the hypothesis of a low-latitude vacancy of continental tetrapods during or soon after the PTME (Sun et al., 2012).

Discussion and conclusions

The Gardetta ichnosite is characterized by archosaur footprints assigned to *Chirotherium* isp. and to the new ichnospecies *Isochirotherium gardettae* ichnosp. nov. They represent the first record of terrestrial tetrapods in the Briançonnais domain of the Western Alps and expand the record of archosaur footprints in the Lower Triassic of Central Europe.

The morphological characters of the tracks assigned to *Isochirotherium gardettae* ichnosp. nov. suggest a non-archosaurian archosauriform (Erythrosuchidae?) as possible trackmaker candidate (even though the presence of crown-archosaurs cannot be excluded), thus providing crucial information about continental tetrapod occurrence in Europe in the Early Triassic. Based on a phylogenetic dataset made by 108 middle Permian–early Late Triassic species, Ezcurra & Butler (2015) investigate principal patterns of early archosauromorph biodiversity change across the Permo-Triassic mass extinction. The study, performed using phylogenetic diversity, morphological disparity, number of species and rates of phenotypic evolution across 35 million years of early archosauromorph evolution, indicates consistent phylogenetic diversification of the clade in the Olenekian. In particular, the basal diversification of main taxa, which include erythrosuchids, rhynchosaurs and tanystropheids, resulted in significantly high evolutionary rates, with a diversification interpreted by the authors as a radiative response to vacant ecological space, made available by the EPME (Ezcurra & Butler, 2015). If the trackmakers' attribution for the ~~here described~~ ~~footprints~~ is correct, the material from Gardetta could represent an evidence from Europe of such radiation, with an archosauromorph fauna composed at least by ?erythrosuchids (*Isochirotherium gardettae*) and pseudosuchids (*Chirotherium* isp.). Such clades as putative trackmaker for the Gardetta traces are ~~well-compatible~~ with an Early Triassic (likely late Early Triassic) age, considering that the early history of Archosauriformes is represented essentially by members of Proterosuchidae and Erythrosuchidae (Charig & Reig, 1970;

Cruickshank, 1972; Charig & Sues, 1976; Gower & Sennikov, 2000; Gower, 2003; Ezcurra et al., 2013).

Following the huge Permo-Triassic biotic crisis, unfavorable environmental conditions characterized much of the Early Triassic, testifying ~~one~~ of the slowest recoveries for ecosystems after an extinction in Earth history. A period between five and nine million years for a full recovery has been proposed in several ~~contributions~~ (Hallam, 1991; Erwin, 1992, 2001; Payne et al., 2004, 2011; Algeo et al., 2011; Whiteside & Ward, 2011), inferring a fully restored complex ecosystems only at the beginning of the Middle Triassic (see Chen & Benton, 2012). Such long recovery time led to a revolution ~~on~~ both marine and terrestrial ecosystems (Chen & Benton, 2012), with a major influence in the evolution of crucial vertebrates clades ~~in~~ the rest of Mesozoic and Cenozoic eras (Sepkoski, 1984; Benton, 2010). The recovery period led to the emergence of totally new groups, with a rapid diversification of several lineages of sauropsid both on sea and land (Nesbitt et al., 2010; Butler et al., 2011; Gower et al., 2014; Scheyer et al., 2014; Motani et al., 2015a, 2015b; Peecook et al.,2018). Avemetatarsalians (which include dinosaurs and pterosaurs) originated in this period (Brusatte et al., 2010; Nesbitt et al., 2010; Chen & Benton, 2012; Benton et al., 2014), along with the evolution of crucial modern group ancestors, including crocodiles, lizards, turtles, frogs and mammals. All these aspects highlight the crucial importance of the Early Triassic in the ecosystems restructuring after the Permo-Triassic mass extinction.

Retallack et al. (2011) ~~propose~~ that the long recovery from the mass extinction was strongly influenced by repeated greenhouse crises during the Early Triassic, with consistent negative excursions in carbon isotope ratios indicating at least five greenhouse crises in the 5 Myr following the EPME (Induan-Anisian) (see Kidder & Worsley, 2004; Retallack, 2005, 2009,

2013; Graisby et al., 2011; Retallack et al., 2011; Sun et al., 2012; Chen & Benton, 2012). In this regard, according to Sun et al. (2012) the entire Early Triassic was characterized by temperatures consistently in excess ~~with respect to~~ the modern equatorial annual sea surface temperatures (SSTs), thus exceeding a tolerable threshold for life in both oceans and ~~land.~~ Inferring SSTs approaching 40°C, according to Sun et al. (2012) the temperature on land very likely fluctuated to even higher levels, with terrestrial tetrapods generally absent between 30°N and 40°S in the Early Triassic.

In this framework, and although some uncertainties on the chronological attribution persists, the Gardetta ichnosite provides important evidence to the low latitude distribution of archosaurus during the Early Triassic period, soon after the PTME, confirming the pattern described by Bernardi et al. (2018). In particular, the new discovery provides further evidence for an early recovery terrestrial ecosystems and the presence at low latitudes of archosauriformes during the Early Triassic. Such evidences support a model in which the EPME did not completely vacate low-latitude lands from tetrapods that, therefore would, have been able to cope with the extreme hot temperatures of Pangaea mainland.

According to Botha and Smith (2006), Archosauromorpha (along with Procolophonomorpha) could be pre-adapted to extremely arid and hot environment conditions, considering that extant reptiles rarely drink water, excrete quite dry fecal pellets, and are characterized by solute-linked water reabsorption mechanisms, water-resistant integument and low ventilation rates (Withers, 1992; Pough et al., 1996). Such physiological aspects and water conserving mechanisms, probably suggest that the archosaurus response to the extreme hot condition of the Early Triassic (Benton, 2018) have probably been much more efficient and ~~plastic~~ than previously thought, and

589 did not necessarily imply massive dispersal towards higher latitudes as previously suggested
590 (Sun et al., 2012).

591 Different anatomical features described above indicate ~~a possible~~ ?Erythrosuchids as the most
592 probable ~~trackmaker~~ for the new described ichnospecies *Isochirotherium gardettae*. This
593 attribution can also be supported by track parameters such a narrow trackway and high pace
594 angulation, which indicate a more upright posture with respect to a classic plesiomorphic
595 sprawling gait (see Kubo & Benton, 2007). In particular, according to Ezcurra et al. (2013),
596 erythrosuchids were heavily built and characterized by a probably less sprawling gait, when
597 compared to the condition observed in proterosuchids. The narrow trackway, along with
598 consistently high pace angulation in the Gardetta material, also confirm the statement by Kubo &
599 Benton (2009) that, even if proterosuchids and erythrosuchids are traditionally considered as
600 sprawlers, ichnological evidences indicate that more derived erect-limbed ~~archosaurian~~ already
601 evolved in the Early Triassic; the latter conclusion is also supported ~~on the base of~~ ghost ranges
602 from cladograms (Sereno, 1991; Benton, 1999), and fragmentary materials from Russia (Gower
603 & Sennikov, 2000).

604 To date, Erythrosuchids are totally unknown from North America and Europe, being
605 described only from Russia, South Africa, China and India (see Gower, 2003; Ezcurra et al.,
606 2013, 2019, 2020; Gower et al., 2014; Ezcurra, 2016). ~~The~~ material from the Lower Triassic
607 deposits of Gardetta ~~thus~~ could represent the first occurrence of the clade in Europe, although, as
608 already pointed out, the attribution is for the moment only tentative, and new studies are
609 underway to better constrain the identity of the zoological trackmaker.

610 The planned future excavations in the Gardetta ichnosite will hopefully provide additional
611 data to improve our knowledge of the evolutionary history of Archosauriformes in the aftermath
612 of the EPME.
613
614 **ELECTRONIC SUPPLEMENTARY MATERIAL**
615 This article contains electronic supplementary material.
616
617 ACKNOWLEDGMENTS
618 We warmly thank the Associazione Escarton that generously supported by this research during
619 the field campaigns held in 2009, 2017 and 2018. A special thanks to Giovanni Raggi for his
620 valuable and constant support during the field works and the project organisation. We
621 acknowledge insightful discussions with A. d'Atri (University of Torino). The authors wish also
622 to thank Dr. Debora Rocchietti (Soprintendenza Archeologia Belle Arti e Paesaggio per le
623 province di Alessandria, Asti e Cuneo) and Dr. Attilio Dalmasso (Museo dei fossili in San Rocco
624 di Bernezzo) and Fabio Manucci for video production and artwork. Finally, a special thank is
625 also due to Hanna Luginbühl for her help in mapping 2009 and to Cecilia Gomiero, Jacopo
626 Valori and Nicolò Amoruso for their precious help during 2018 fieldwork.
627 This paper is part of the project 'The end-Permian mass extinction in the Southern and Eastern
628 Alps: extinction rates versus taphonomic biases in different depositional environments' financed
629 by the Euregio Science Fund (call 2014, IPN16) of the Europaregion Euregio.
630
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Figure captions

Fig. 1 - Geologic map of the Pianezza area. In the upper row the location of Maira Valley and Gardetta-Pianezza area. For the geologic map: 1= volcanic complex and graphitic schist (upper Carboniferous - Permian); 2= conglomerate, 3= quartz-conglomerate, and 4= quartz-arenite and quartz-siltite of the quartzitic complex (upper Permian - early Lower Triassic); 5= lower carniole complex (late Lower Triassic); 6= lower calcareous complex (lower Anisian - early upper Ladinian); 7= upper dolomitic complex (upper Ladinian); 8= lakes and peat bog; 9= faults; 10= location of the footprint site; in white the detritic cover and moraines.

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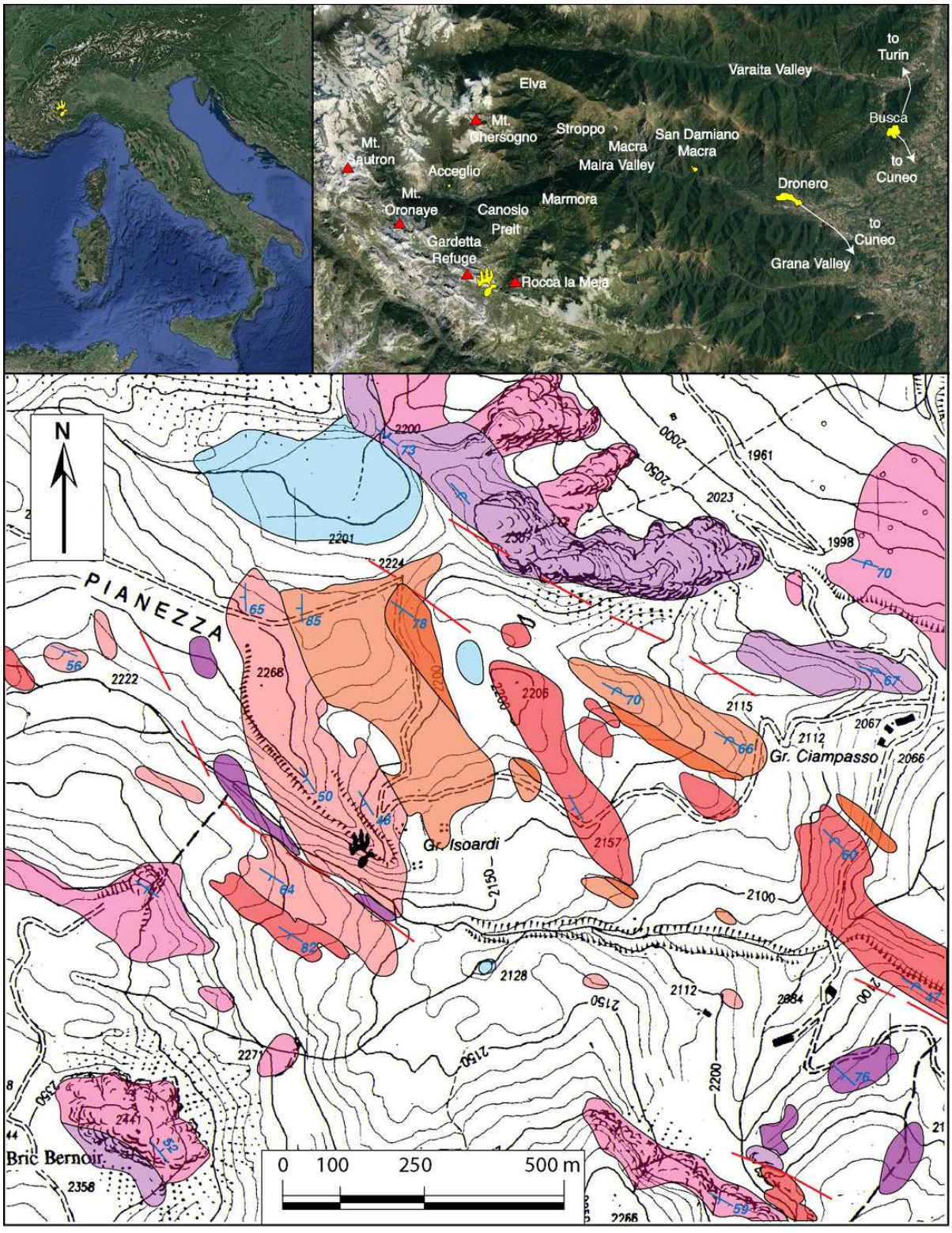
Elva
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San Damiano Macra
Varaita Valley
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Busca
to Cuneo
Dronero
Mt. Oronaye
Canosio
Marmora
Prelt
Gardetta Refuge
Rocca la Meja
to Cuneo
Grana Valley
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PIANEZZA
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Gr. Isoardi
Bric Bernoir
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Figure 2

Correlation scheme among the Briançonnais s.s., the Ligurian Briançonnais

Fig. 2 - Correlation scheme among the Briançonnais s.s., the Ligurian Briançonnais, from De Carlis & Lualdi, 1990 redrawn and modified. (PNQ) “Ponte di Nava Quartzites”. (CVP) Case Val Marenca Pelites. The footprint silohuette marks the position of the track-bearing horizon.

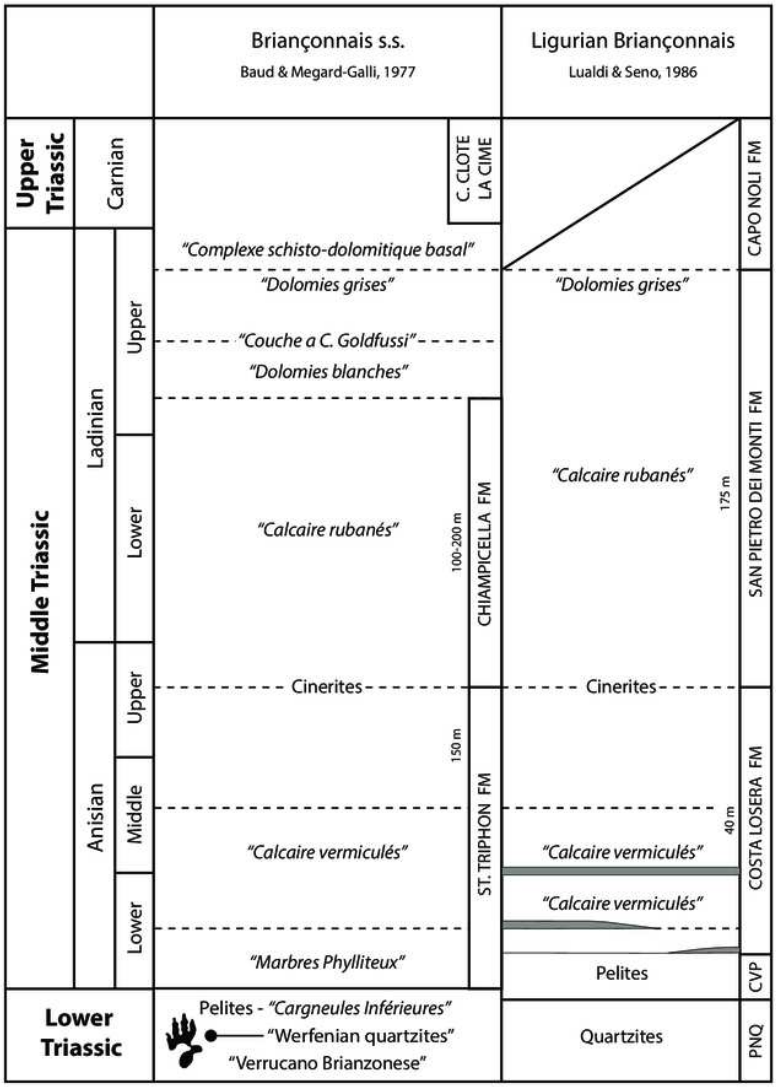
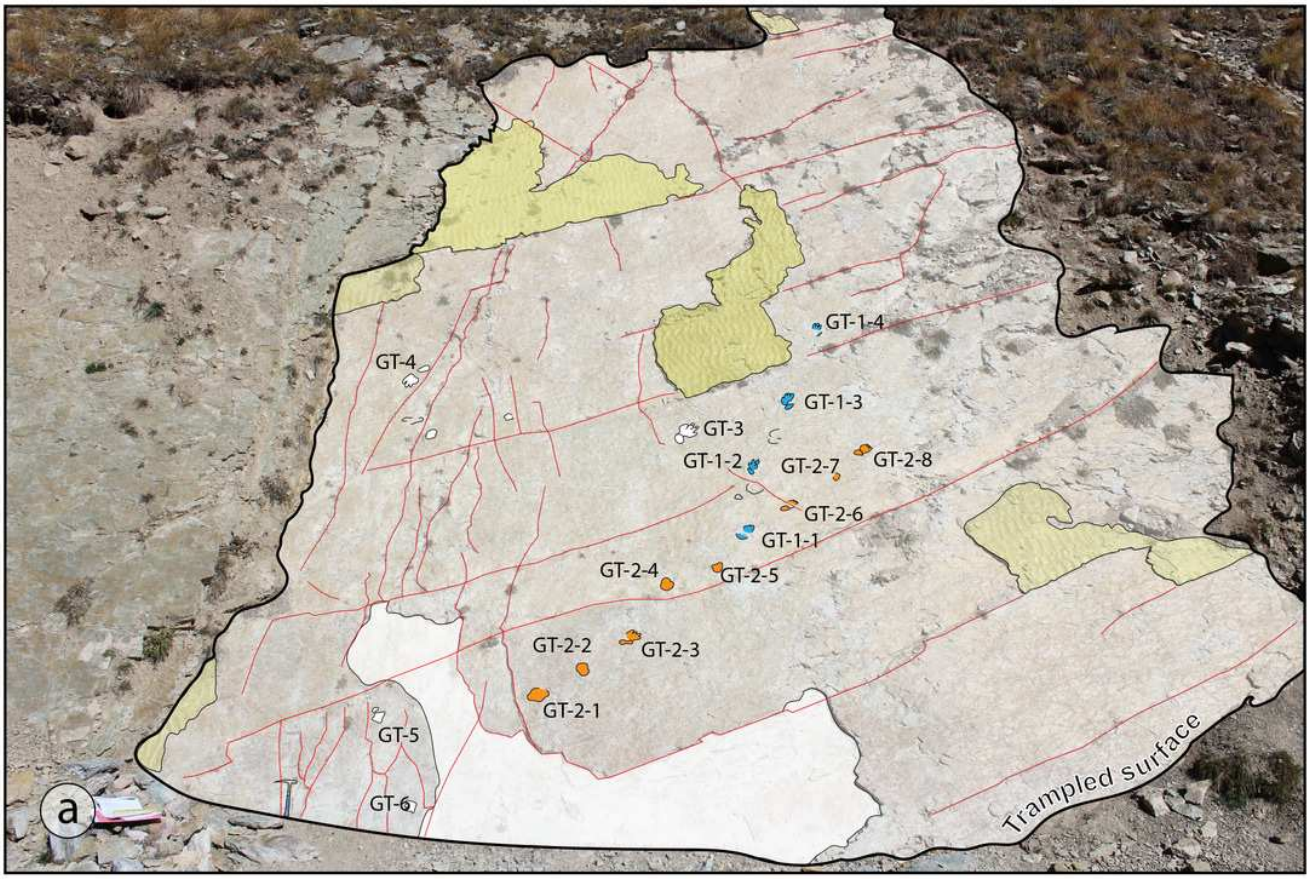

Briançonnais s.s.
Baud & Megard-Galli, 1977
Ligurian Briançonnais
Lualdi & Seno, 1986
Upper Triassic
Carnian
Middle Triassic
Ladinian
Upper
Lower
Anisian
Upper
Middle
Lower
C. CLOTE LA CIME
"Complexe schisto-dolomitique basal"
"Dolomies grises"
"Couche a C. Goldfussi"
"Dolomies blanches"
"Calcaire rubanés"
100-200 m
CHIAMPICELLA FM
Cinerites
150 m
ST. TRIPHON FM
"Calcaire vermiculés"
"Marbres Phylliteux"
Pelites - "Cargneules Inférieures"
"Werfenian quartzites"
"Verrucano Brianzonese"
Lower Triassic
"Dolomies grises"
"Calcaire rubanés"
175 m
Cinerites
40 m
"Calcaire vermiculés"
"Calcaire vermiculés"
Pelites
Quartzites
CAPO NOLI FM
SAN PIETRO DEI MONTI FM
COSTA LOSERA FM
CVP
PNQ

Figure 3

Panoramic view of the track surface with the line-drawing of the chirotherian trackways

Fig. 3 – (a) Panoramic view of the track surface with the line-drawing of the chirotherian trackways. In pale yellow the above-lying bed characterized by symmetric wave ripples. (b) Detailed view of the GT-1 and GT-2 trackways, highlighted with the black colour.


GT-1-4
GT-4
GT-1-3
GT-3
GT-1-2
GT-2-7
GT-2-8
GT-2-6
GT-1-1
GT-2-4
GT-2-5
GT-2-2
GT-2-3
GT-2-1
GT-5
GT-6
Trampled surface
a


b
1 m

Figure 4

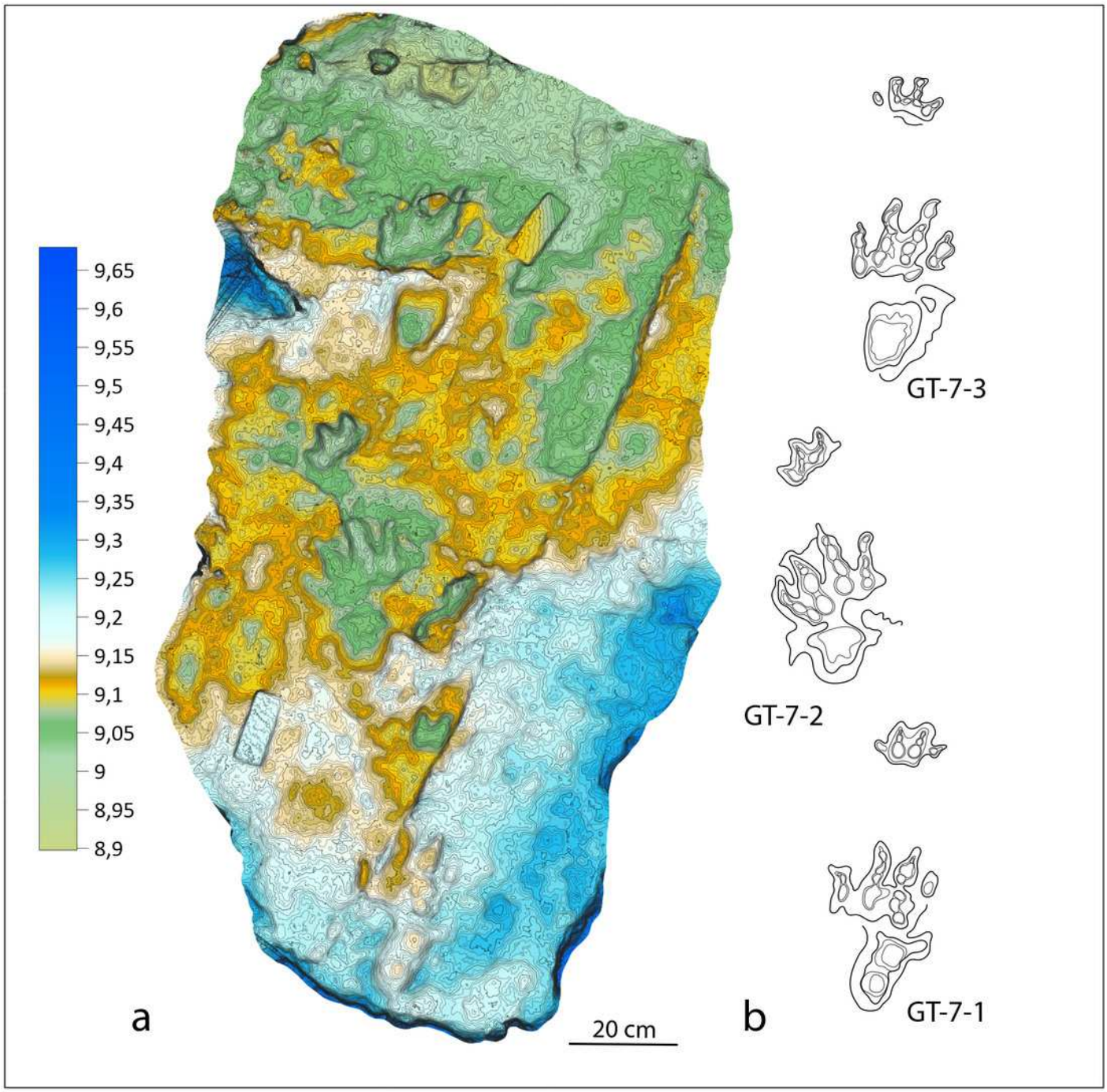
Isochirotherium gardettae ichnosp. nov

Fig. 4 – *Isochirotherium gardettae* ichnosp. nov. The GT-7 trackway, made of three consecutive manus-pes couples, is here highlighted by the red chalk and preserved in the upper track-bearing surface. Scale bar: 13 cm.

Figure 5

Isochirotherium gardettae ichnosp. nov. Colour-coded and contour line image of the GT-7 trackway

Fig. 5 – a) *Isochirotherium gardettae* ichnosp. nov. Colour-coded and contour line image of the GT-7 trackway; b) Interpretative drawing of the GT-7 trackway.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9
8,95
8,9
a
20 cm
b
GT-7-3
GT-7-2
GT-7-1

Figure 6

Reconstruction of the trackmaker’s fore- and hind limbs, based on the 3D model and its interpretative drawing

Fig. 6 – Reconstruction of the trackmaker’s fore- and hind limbs, based on the 3D model and its interpretative drawing. Dashed lines define the metatarsal of digit V held lifted off the ground during locomotion.

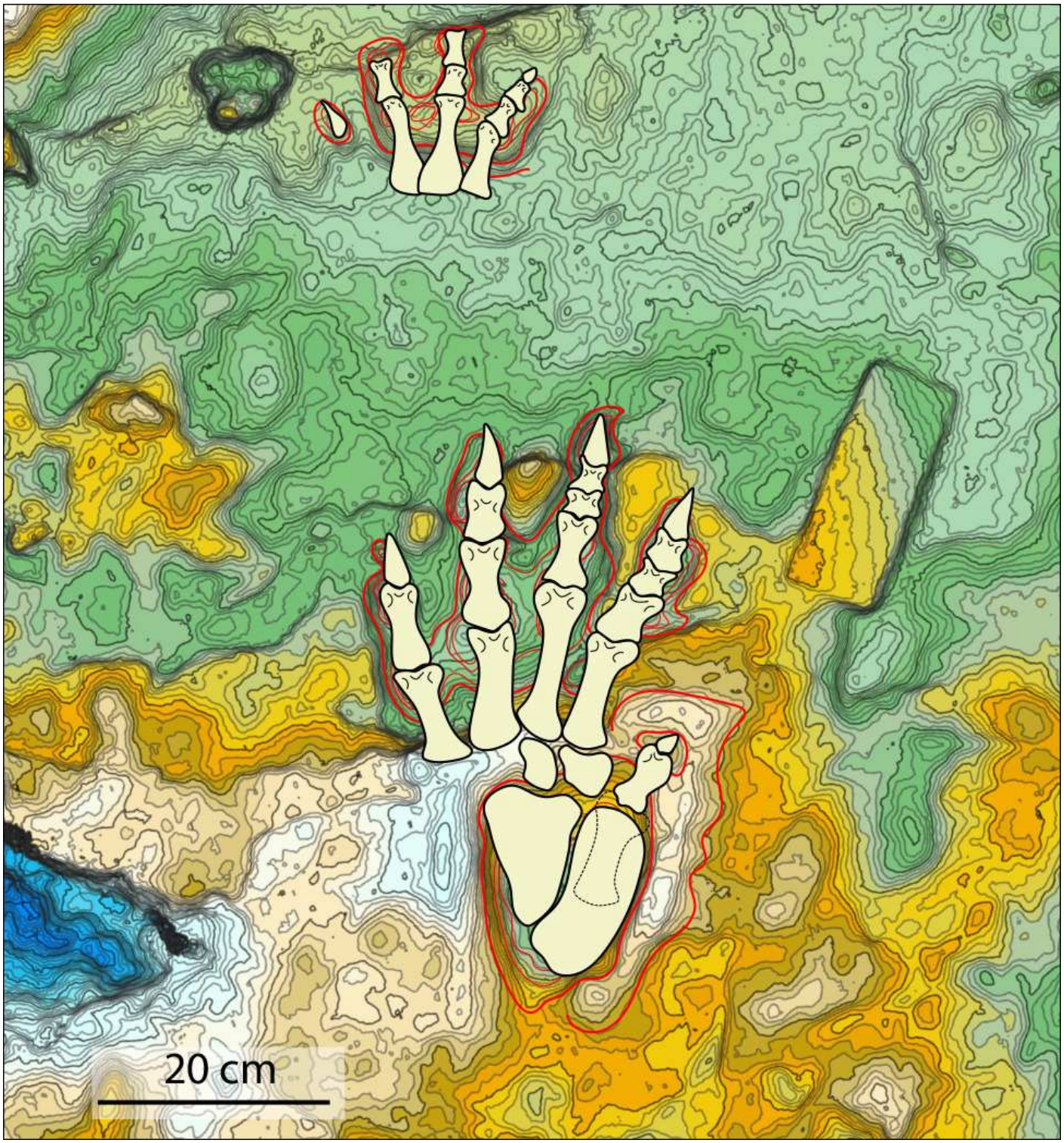
20 cm

Figure 7

Pentadactyl tracks from the Lower and Middle Triassic, assigned to the ichnogenus *Chirotherium* and their comparison with the studied tracks of the Gardetta ichnosite

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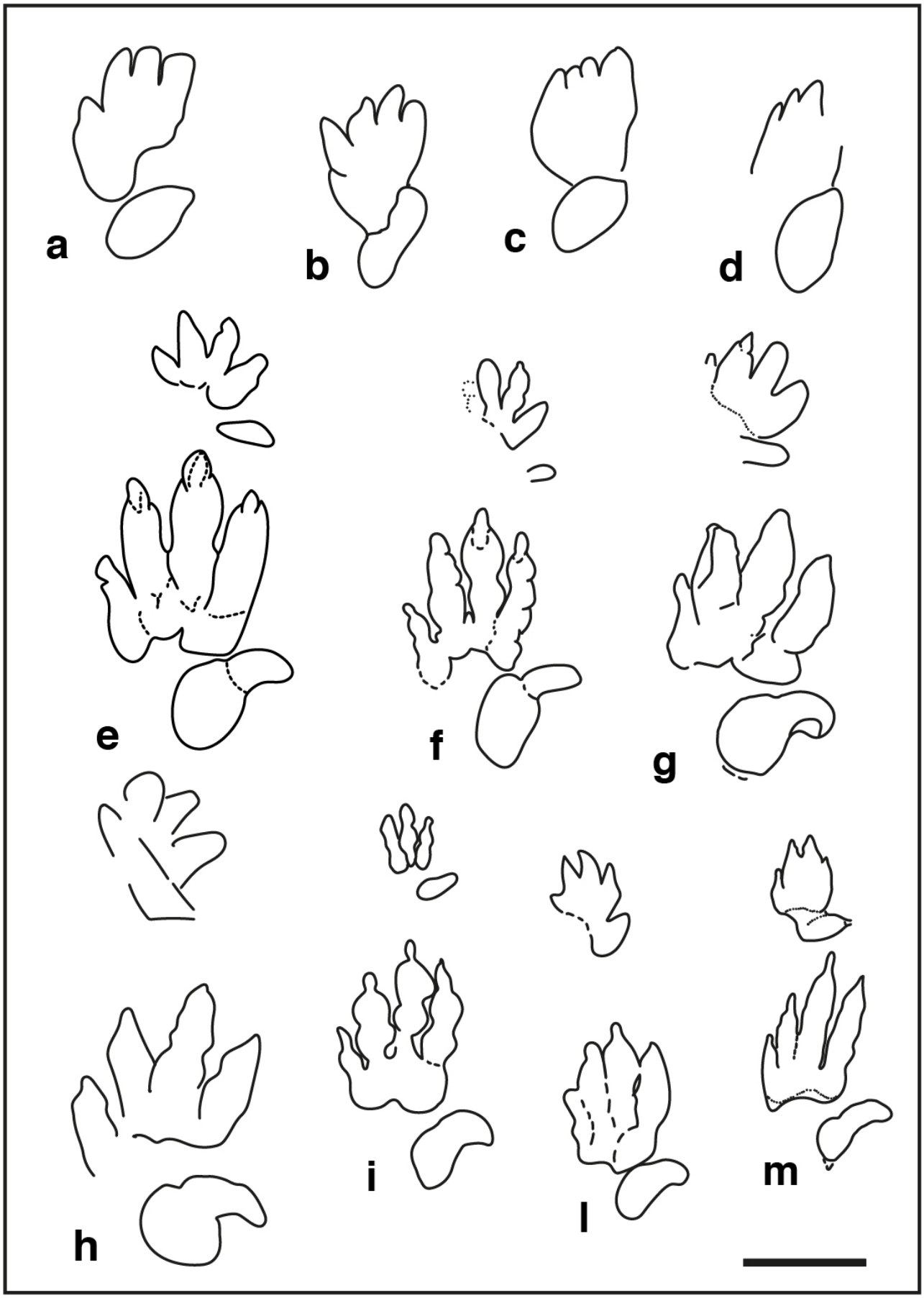
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Figure 8

Pentadactyl tracks from the Lower and Middle Triassic, assigned to the ichnogenus *Isochirotherium* and their comparison with the studied tracks of the Gardetta ichnosite

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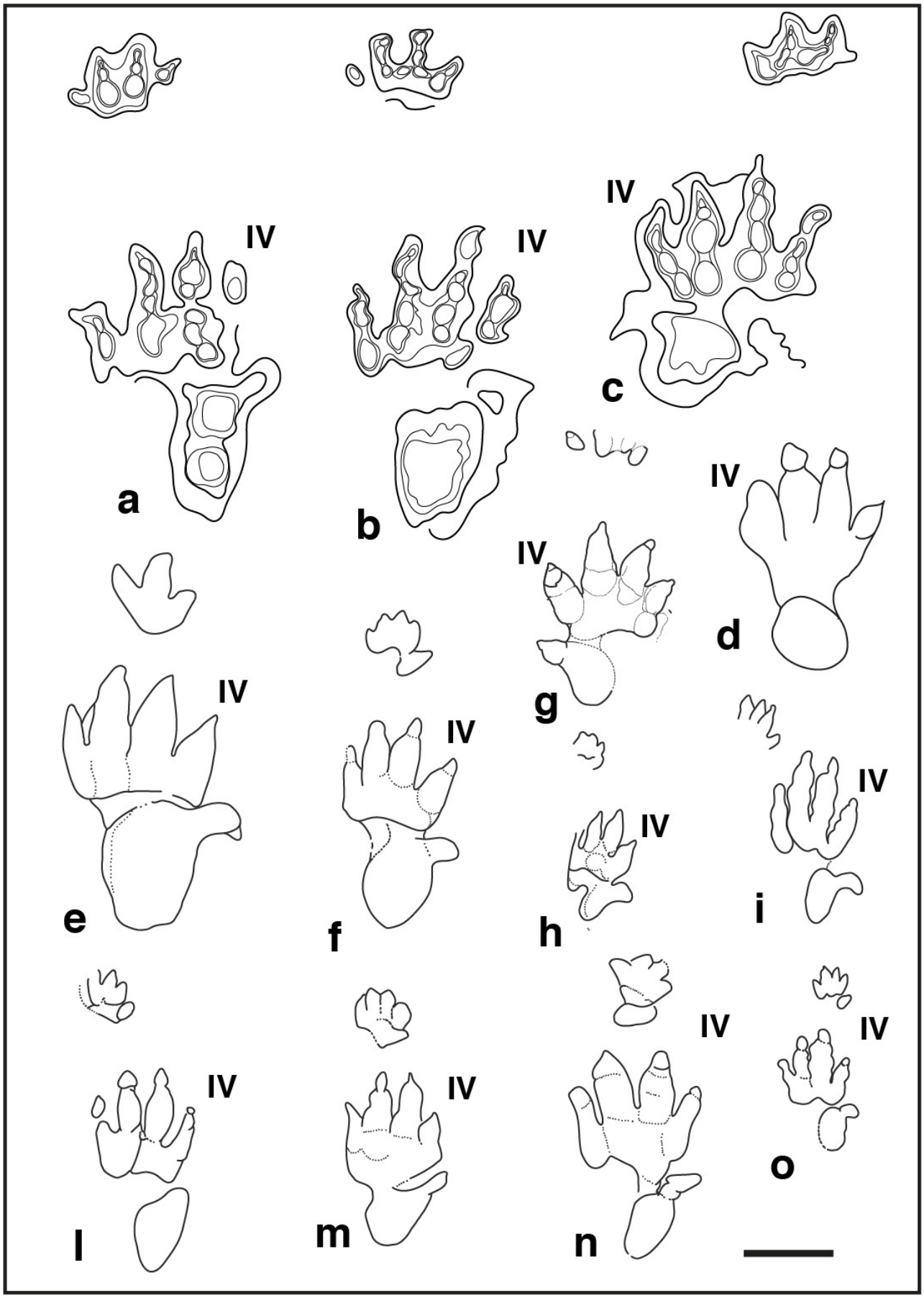
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Figure 9

Fore- and hind-limb skeletons of Triassic archosauriforms and of the *Isochirotherium gardettae* trackmaker

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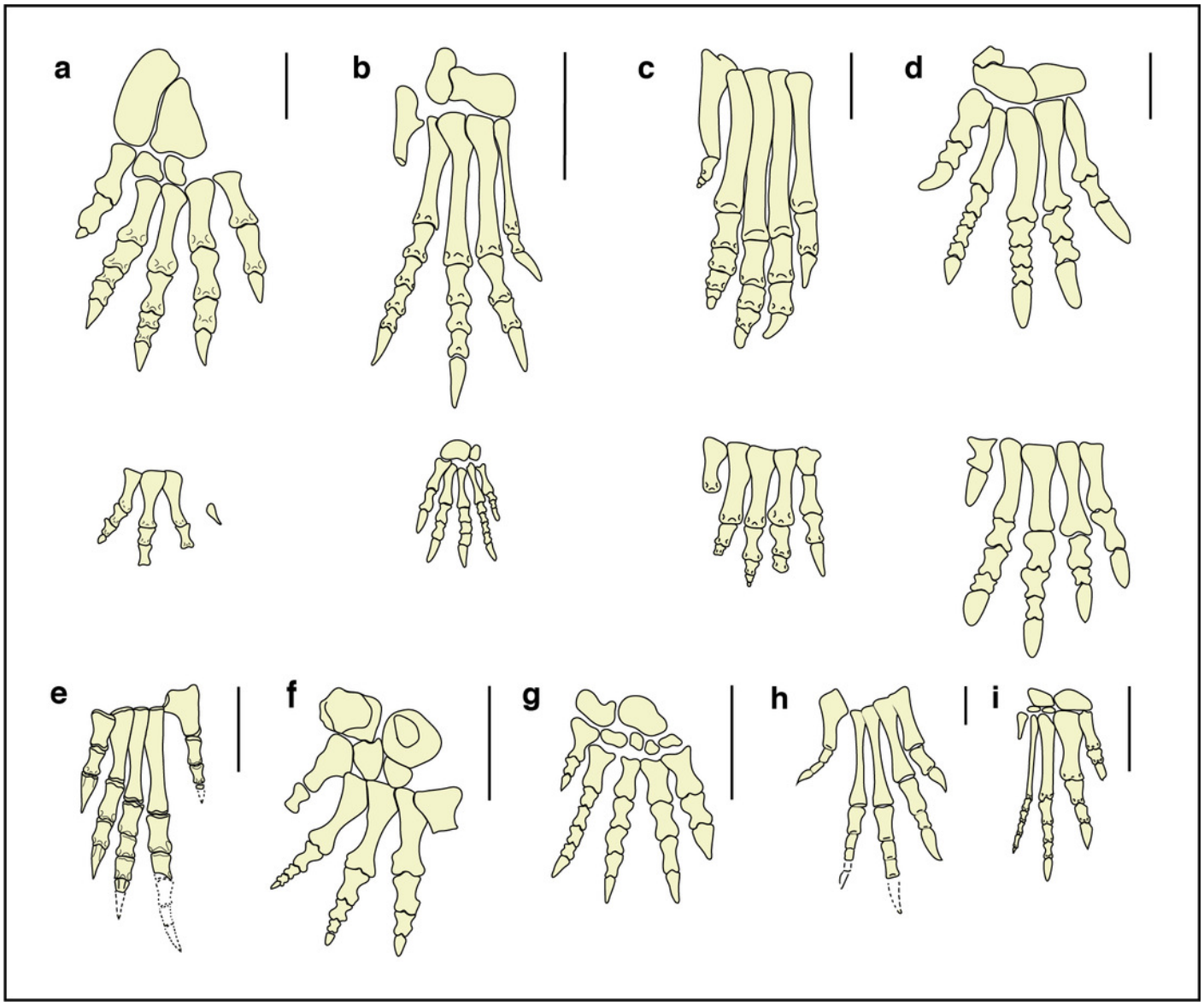
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Figure 10

Life appearance of the non-archosaurian archosauriform (?Erythrosuchid) the most suitable producer of *Isochirotherium gardettae*

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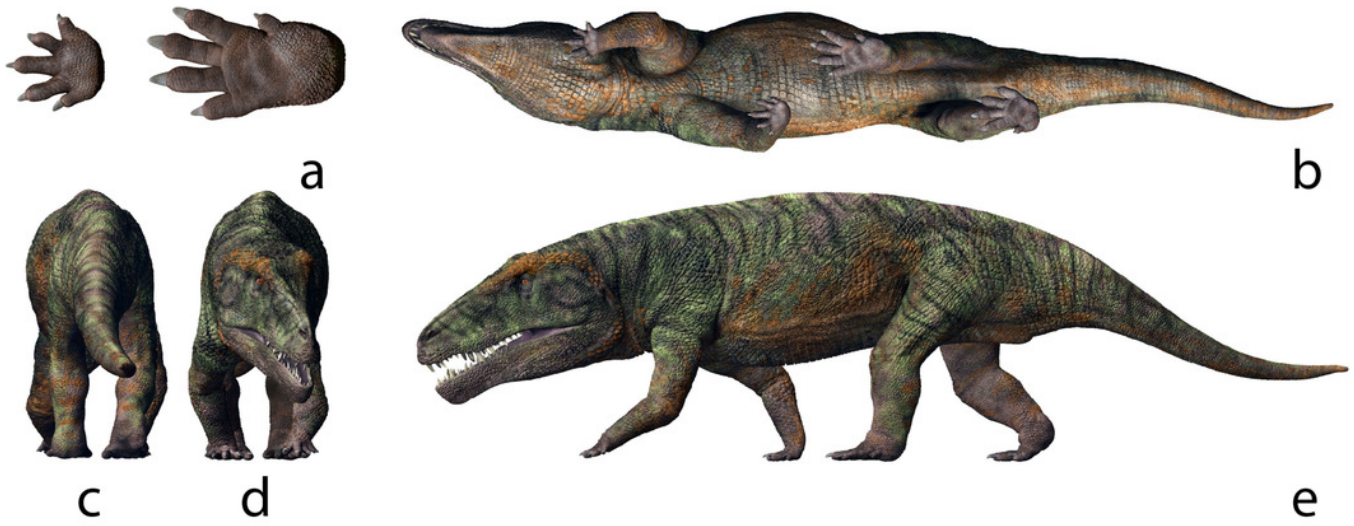

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Paleogeographic distribution of Early Triassic archosauriform footprints and body fossil localities across Pangea

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