Early-Middle Triassic vertebrate tracksites from the Dolomites (Northern Italy)

by
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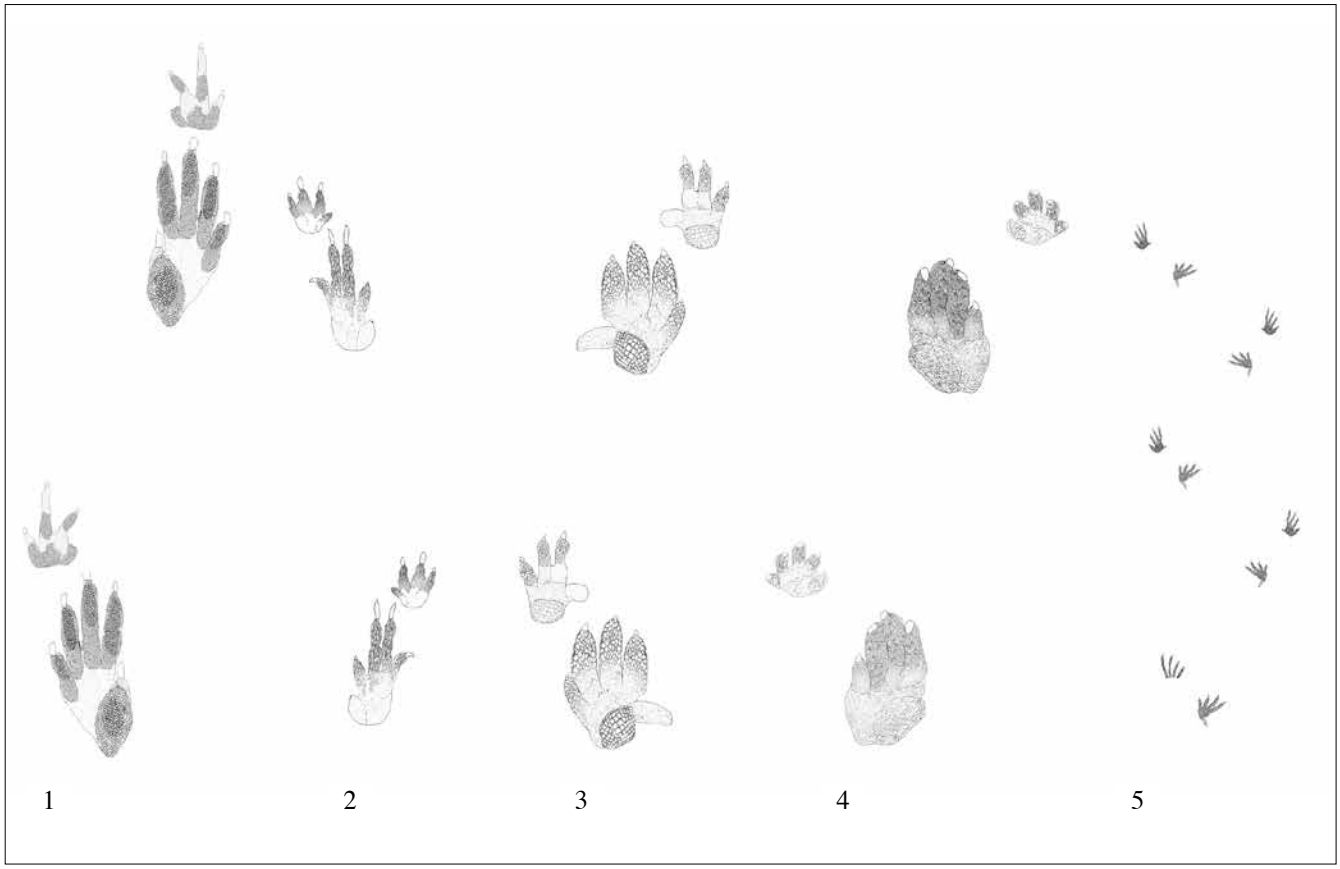
Abstract

The Dolomites are rich in Paleozoic-Mesozoic ichno-associations, which can be followed in the rock-sediments from the Early Permian till the Middle Triassic. Several well-preserved Anisian footprints were analysed and brought in the context to its paleoecosystem. In addition to the dominant *Rhynchosauroides tirolicus* imprints, the attention focuses especially on the larger-sized tracks from suggested archosaurs like *Isochirotherium delicatum, Chirotherium barthiii, Brachychirotherium parvum,* and especially on the only known ichno-species from the Dolomites – *Sphingopus ladinicus.* Mainly, all tracks evidence a clear tendency towards bipedalism with a functionally three-toed pes as is possible in the synapomorphies of basal dinosaurs.

Online: August 2018
Key words: *Rhyncosauroides*, *Chirotherium, Isochirotherium, Sphingopus,* archosaurs, Dolomites, Triassic



Different trackways from the Middle Triassic of the Dolomites: All are characterized by different skin-pattern: 1. *Sphingopus ladinicus* (ellipsoid pattern); 2. *Isochirotherium delicatum* (reticulate); *Chirotherium barthiii* (mosaic-shaped; 4. *Brachychirotherium parvum* (punctate to small rounded scales); *Rhyncosauroides tirolicus* (rectangular scales outlined in two parallel lines on the digits and rounded scales close to each palm).

Introduction

In the first decade of 1900, the Austrian geologist Julius von Pia, while working as a war field geologist in the Dolomites, recovered the first footprints of Triassic tetrapods from the Southern Alps in fine grained sediments near Lapadures (1850 m) over the hamlet of Olang. He handed the material to the scientist-colleague Othenio Abel, who on 25 September 1923, in occasion of the annual meeting of the Paleontological Society in Vienna (*Vorträge und Diskussionen auf der Wiener Tagung*), organized by himself, held a conference with the title '*Der erste Fund einer Tetrapodenfährte in der alpinen Trias*' (The first finding of a tetra-pod-imprint in the Alpine Trias).

Julius von Pia, Josef Felix Pompeckj, and Gustav Arthaber added, in the same discussion, a brief written comment: 'The discovery is also geologically interesting because the sediments are a red till dark-grey sediment holding many carbonised plant remains and ripple-marks.' The entire presentation was published in 1926 in the '*Palaeontologische Zeitschrift*' in Berlin. Therefore, more correctly, the publication date will be 1923. Abel described the tracks as 'Similar to those that Beasley defined as rhynchosauroid trackways from the Trias of England' and added '*It can be stated that the prints of the posterior foot are characterised by an increase in the size of the digits from one to the fourth like in todays Sphenodon.*

The young Othenio Abel (Vienna, 1875 – Mondsee, 1946), founder of the paleobiology, which studies the life and environment of fossilized organisms. The slab with Rhyncosauroides-tracks was handled him by the Austrian geologist Julius Pia, married with Dr. Marianne Möller, a women scientist with parental origins in the Puster-Valley. The first presentation of this discovery was given on 25. September 1923 in a meeting of the Paleontological Society (Courtesy GBA, Vienna).

TAGUNG IN WIEN

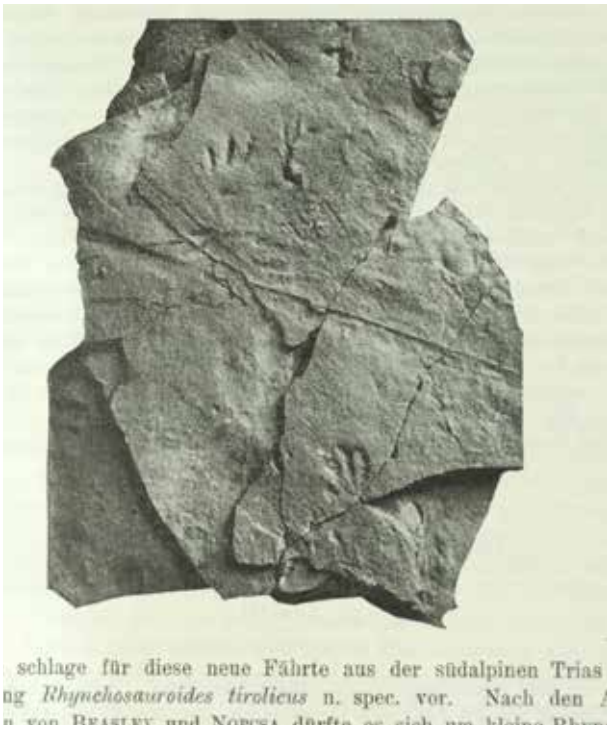
vom 24. bis 29. September 1923.

Montag, den 24. September.

3 Uhr: Sitzung des Vorstandes und Beirats im Palaeobiologischen Lehrapparat der Universität (Stiege IX, Hochparterre).
4 Uhr: Jahresversammlung im Hörsaale des geol., pal. u. palaeobiol. Instituts.
6 Uhr: Eröffnungssitzung im großen Festsaal der Universität:
a) Begrüßungs-Ansprachen.
b) J. F. Pompeckj-Berlin: Die Anfänge des Lebens.

Dienstag, den 25. September.

9—1 Uhr im Hörsaal des Instituts:
O. Abel-Wien: Der erste Fund einer Tetrapodenfährte in der alpinen Trias.



schlage für diese neue Fährte aus der südalpinen Trias
ng *Rhynchosauroides tirolicus* n. spec. vor. Nach den

Two sites of Anisian trackmakers, both first discovered by Michael Wachtler in 2007:

The Furkel-Pass-Piz da Peres. The terrigenous grey till red sediments hold rich ichnofaunas. The beautiful *Sphingopus*-imprints were found in the upper layers. The big *Rhyncosauorides* slabs came from the lower parts.

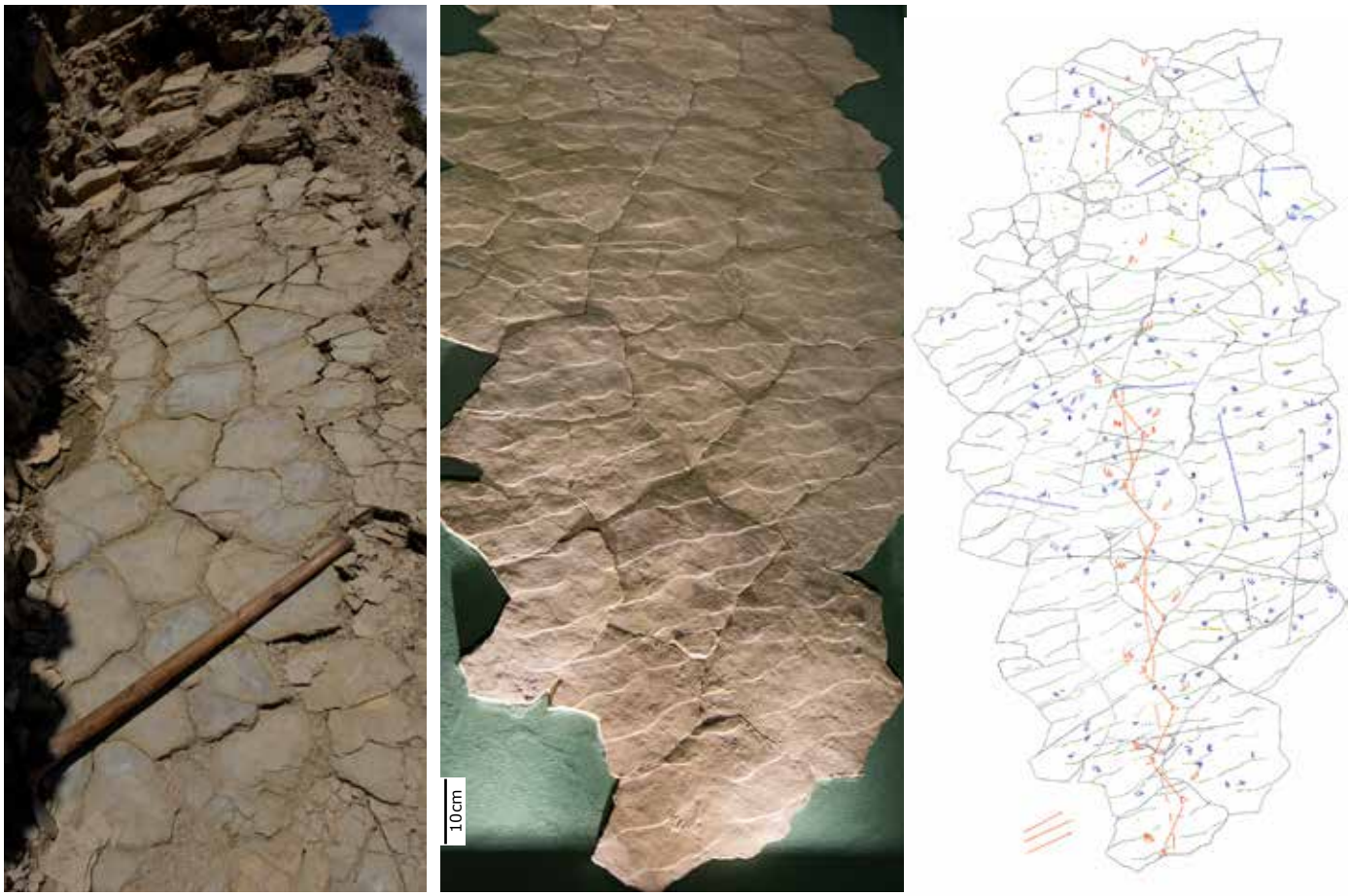
The locality Pozates in the Val Duron (Fassa-Valley), also discovered in 2007 by Michael Wachtler. There we encounter a fair amount of *Rhyncosauroides tirolicus* imprints together with *Chirotherium*, *Isochirotherium* and *Brachychirotherium.*

The hands have the same dimensional characteristics of the feet but are situated closer. I propose for these new tracks from the South-Alpine Trias the name Rhynchosauroides tirolicus. In agreement with Beasley and Nopcsa, these should be referable to a small Rhynchocephalian reptile that left its traces in the Triassic rocks.'

We had to wait until 1970 when Thilo Bechstädt and Rainer Brandner, in their PhD dissertation, recognized other footprints in the same area of Lapadures. Together with abundant *Rhynchosauroides tirolicus* imprints, Brandner (1973) described well-preserved chirotherian tracks defined as *Brachychirotherium parvum* (Hitchcock, 1889) and *Chirotherium rex.*

Then, in 2007, Wachtler discovered a new fossil site with interesting ichnospecies in a nearby area – the Furkel Pass in the direction to the Piz da Peres mountain (46°42'52.94"N, 11°58'38.13"E, 2202 m), holding an exhausting near-shore paleoecosystem with numerous tetrapod tracks (*Rhynchosauroides, Procolophonichnium, Chirotherium, Isochirotherium, Brachychirotherium, Sphingopus,* and *Rotodactylus*), marine biota (jellyfish, bivalves, etc.) and a rich flora, composed of conifers, ferns, horsetails, lycopods, and especially cycads (Todesco et al., 2008).

The strata belonged to the Obere Peresschichten sensu. Pia (1937) and Bechstädt & Brandner (1970) called it Richthofen Conglomerate and Morbiac Dark Limestone (Delfrati & Farabegoli, 2000) in the Italian stratigraphical nomenclature (both Illyrian in age). The Richthofen Conglomerate is dominated by red sandstones and siltstones and subordinate conglomerate beds. This unit has been interpreted as having been deposited in a relatively arid fluvial or in a tran-



A huge slab with R*hyncosauroides tirolicus* tracks. Right: In nature on the Furkel-Pass-Piz da Peres; middle: assembled (Coll. Michael Wachtler, Museum Dolomythos; right: drawing of the traces; green colour: ripple marks, red: continuous tracks and tail-drags, blue: other imprints, partly from juvenile animals. In the upper part invertebrate-traces, anellids, suggesting a small puddle.

sitional continental to marine environment (Todesco et al., 2008).

The depositional environment is referable to a marine marginal setting with lagoons and swamps contaminated by terrigenous input. In addition to the dominant *Rhynchosauroides tirolicus* imprints, other archosaurs like *Isochirotherium delicatum* (Courel & Demathieu 1976), *Chirotherium barthiii* (Kaup, 1845), and *Brachychirotherium aff. B. parvum* (Hitchcock 1858) are typical. Also a new and interesting ichnospecies was found there by Michael Wachtler and described as *Sphingopus ladinicus* (Avanzini & Wachtler, 2012).

Another relatively rich and new ichnosite was discovered also by Wachtler in 2007, near Pozates (Val Duron, Fassa-Valley). A fair amount of *Rhyncosauroides tirolicus* imprints together with *Chirotherium barthiii, Isochirotherium delicatum* and *Brachychirotherium* was recovered (Todesco et al., 2008). The trampled layers occur in the Illyrian Morbiac Formation consisting of decimetric-thick grey silty and silty-limestone layers becoming towards the top wack- and packstones. Isolated plant remains were common. For all the layers, the depositional environment is referable to a marine marginal setting as a terrigenous tidal flat (Todesco et al., 2008b). In the Triassic of the Dolomites, the tracks of *Rhynchosauroides* are the most abundant ichnogenus.

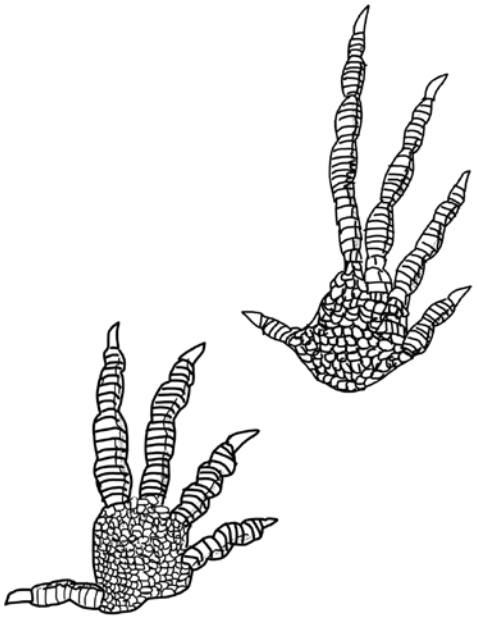
Larger imprints, like *Chirotherium, Isochirotherium, Sphingopus,* or *Brachychirotherium* are probably due to their greater size making it more difficult to recover entirely. Other Anisian tracks are recorded from the Early Triassic of the Gampenpass, the Richthofen Conglomerate of Val di Creme (Recoaro), Val Fiorentina (Belluno), and Val di Non over the Morbiac Limestone from Bad Gfrill near Tisens. Similar sites are distributed also in other parts of Europe.

Imprints of jelly-fishes, Furkel-Pass-Piz da Peres, Coll. Michael Wachtler

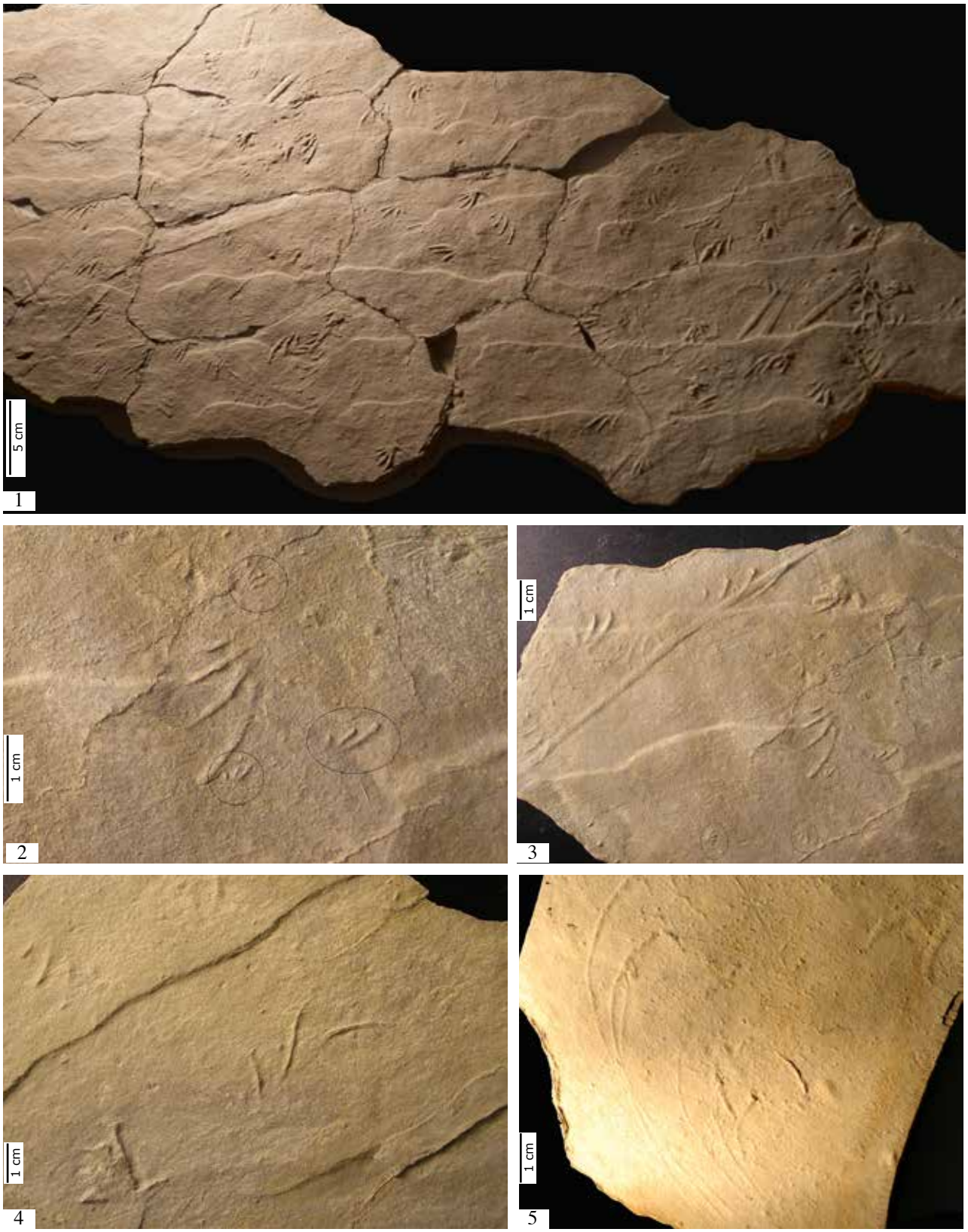
1. R*hyncosauroides tirolicus:* Two imprints, Val Duron, Coll. Michael Wachtler; 2. Detail of a manus showing well the skin-ripples (Piz da Peres, Coll. Michael Wachtler)

Rhynchosauroides tirolicus Abel 1926

The ichnogenus *Rhynchosauroides (rectipes)* was instituted by Maidwell (1911) on the basis of imprints found in association with skeletal remains of rhynchosaurs (Avanzini & Renesto, 2002). But contrary to the name given by Maidwell, *Rynchosauroides* can not be attributed to rhyncosaurs. Instead, it can be treated as the footprints of some lepidosauromorph or archosauromorph trackmakers. The long stratigraphic range from Early Permian of the Dolomites till the Late Jurassic (Spain) suggests that probably different ichnospecies attributed to *Rhynchosauroides* could have been made by different animals. They are characterized by relatively broad trackways of a small quadruped animal with low pace angulation. In most cases, the pes oversteps the manus laterally. The pentadactyl pes imprints are digitigrade and show long and slender digits that increase in length from I to IV, with digit IV being the longest. Its length varies from 45 till 60

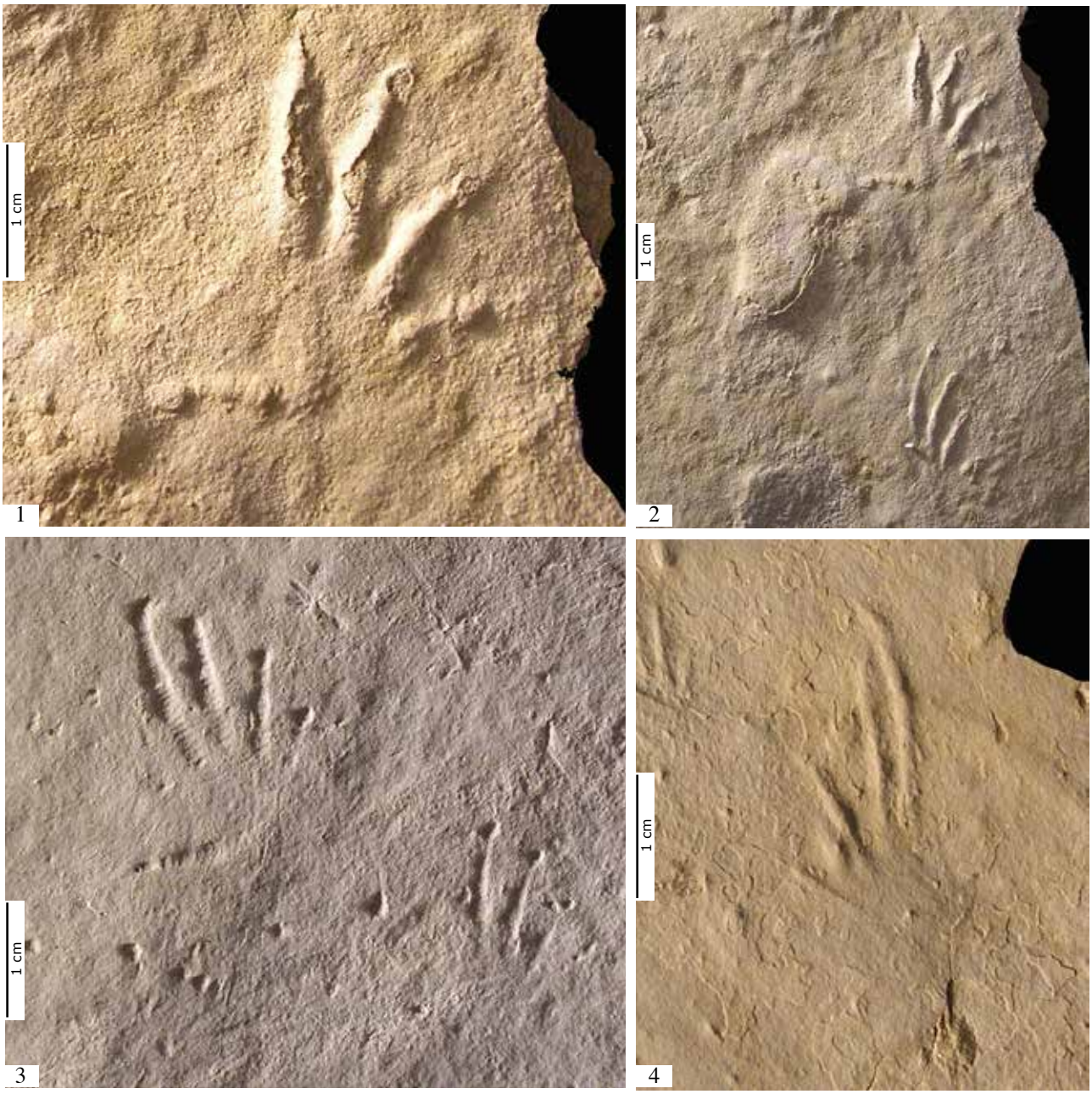


R*hyncosauroides tirolicus:* Manus-pes-sequence. Usually from the pes are preserved only the digits.



Rhyncosauroides tirolicus

1. A big slab with ripple marks, tracks and tail-drags (Coll. Michael Wachtler, Naturmuseum Südtirol, Bozen); 2. Juvenile and adult trackways; 3. Slender tracks with tail-drag; 4. Imprints with a broken digit; 5. Imprint with long slipping-trace (All Coll. Michael Wachtler, Naturmuseum Südtirol, Bozen).



Rhyncosauroides tirolicus

1. Excellent preserved manus; 2. Pes-manus trackway; 3. Pes-manus with skin impression; 4. Well preserved pes (All Coll. Michael Wachtler, Naturmuseum Südtirol, Bozen)

mm. Digit V even is short. Tiny sharp claws are present on all digits. Digit V is not always preserved, but in this case, it is positioned posterolateral to the other digits and is short.

The manus is similar in shape but shorter and rather semi-plantigrade or plantigrade. Well-preserved specimens show rounded pads and impressions of the scales. The manus length varies between 25 and 50 mm and in that it is something smaller than the pes. Occasionally, tail drag marks are preserved.

Rhyncosauroides footprints often occur on trampled surfaces in mass accumulations, together with scratch marks and tail gaits of the same trackmaker. Often, the trackways evidence an overstep of the manus by the pes. Therefore, the trackmaker belongs to a medium-sized lizard-like animal. Sometimes, the footprints, especially the manus, are so well preserved evidencing skin im-

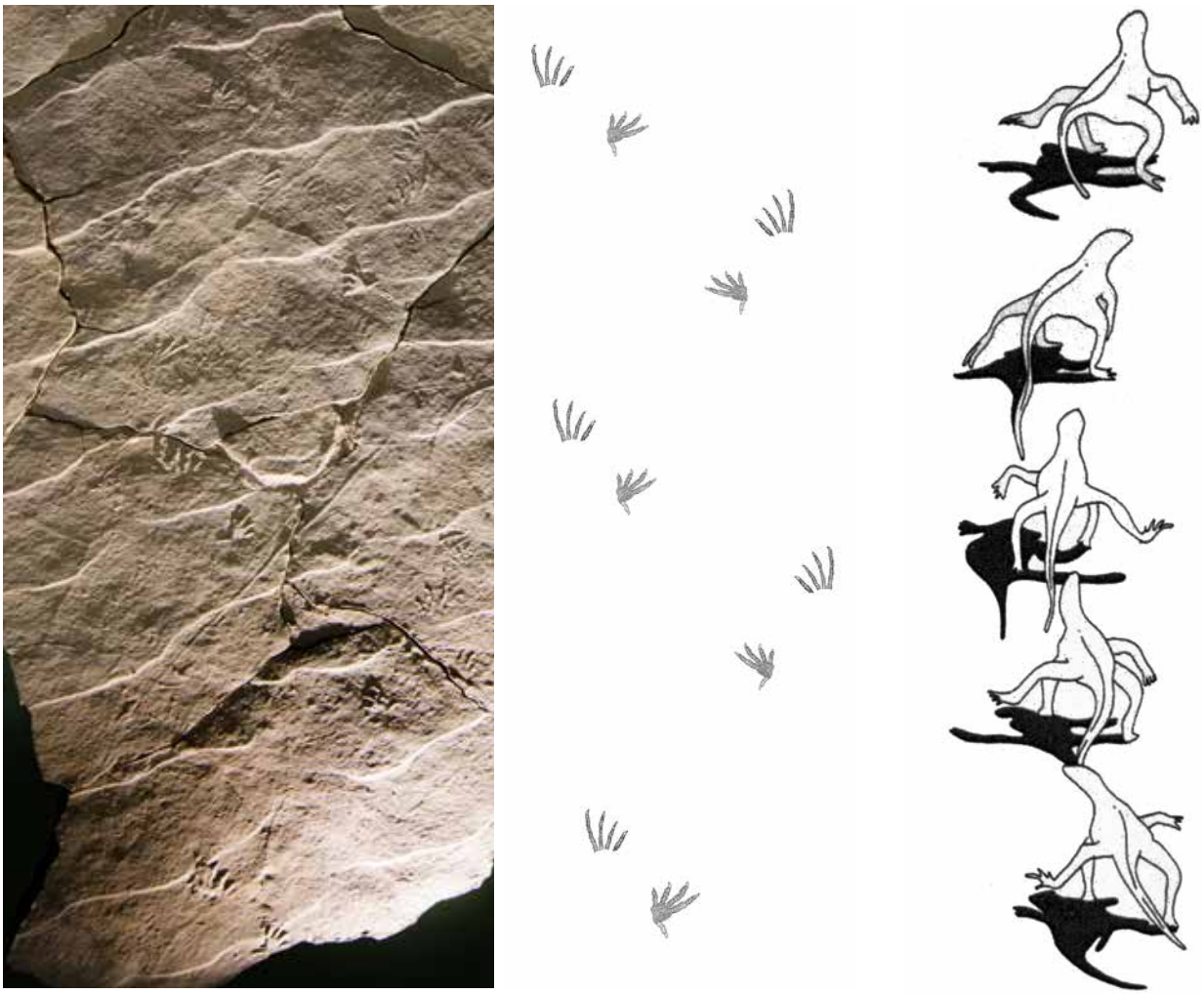
R*hyncosauroides tirolicus.* Well preserved slab with a pes-manus sequence. The pes imprints touch the soil only with the digits, but not with the heel (Coll. Michael Wachtler, Naturmuseum, Südtirol)

pressions with rectangular scales outlined in two parallel lines on the digits and a mosaic of rounded scales close to each other on the palm. Sometimes, especially from the Piz da Peres, the high preservation degree suggests that some of the footprints pertain to separate animals, but it can also be explained by a sexual dimorphism. Occasionally, the digits are thin and strongly arcuate inward. Other shows a pentadactyl pes with long and thin digits.

From all known Alpine skeletons of archosaurs, many can be excluded as trackmaker due to their different morphology. This is valid also for the enigmatic Rhyncosaurs. *Macrocnemus bassanii* (Nopcsa, 1930, 1931), a medium sized prolacertiform reptile recorded from lagoon deposits at the Anisian/Ladinian boundary in the Southern Alps (Avanzini & Renesto, 2002), especially from Monte San Giorgio is probably out of the question, because it seems to be a larger and more powerful terrestrial reptile.

Also, *Megachirella wachtleri* (Renesto & Posenato, 2003) discovered on the nearby Kühwiesenkopf/Pra della Vacca, belonging to the crown-group of squamates evidence different and more climbing-adapted manus digits and claws.

Another partly recovered skeleton from the Piz da Peres Furkel area, *Wachtlerosaurus ladinicus*, suggesting a classification in an early group of avian-line-archosaurs has more possibilities to be inserted as trackmaker from *Rhyncosauroides tirolicus* (Perner, 2018; Wachtler, 2018). The skeleton shows a well-preserved left hind limb and complete metatarsals from 1 till 5. The first metatarsal is stout and much shorter than the others (its length being about one-third of that of the second metatarsal and one-fourth of the third one), with a wide

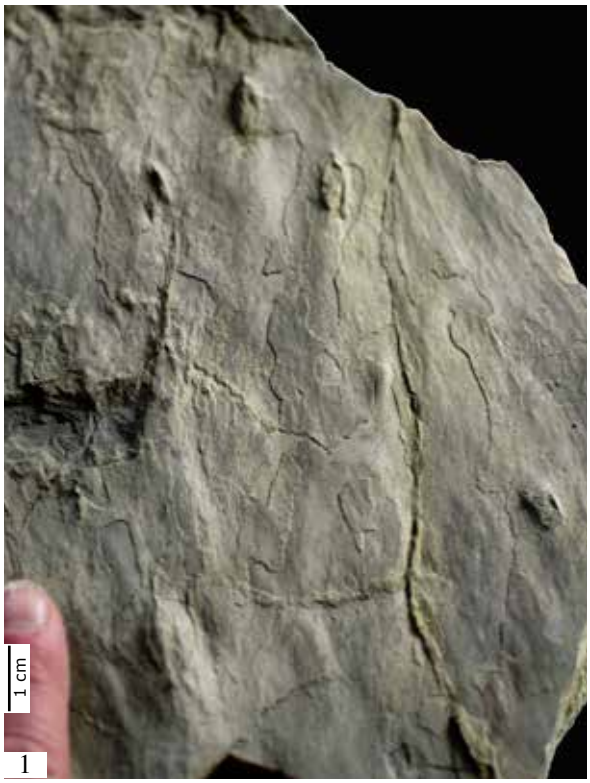


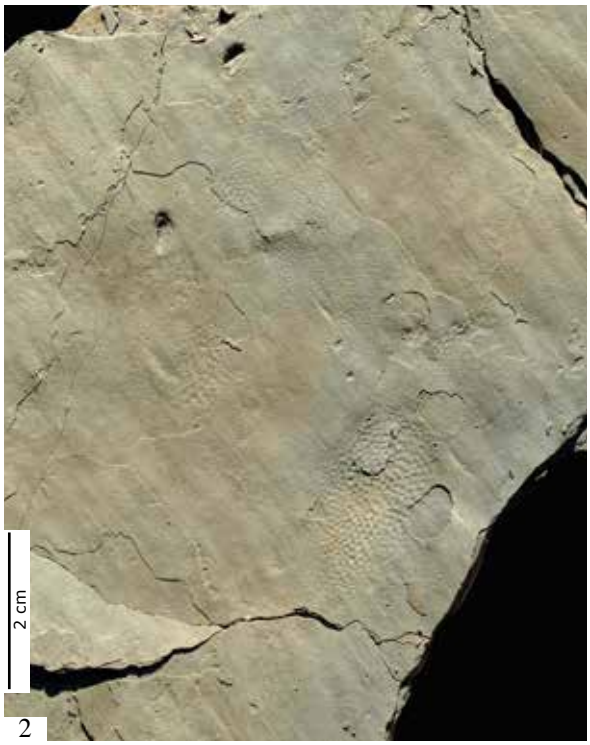
R*hyncosauroides tirolicus.* A detail of the big slab with a manus-pes trackway-sequence (Coll. Michael Wachtler, Dolomythos, Innichen). Movement of the animal after Avanzini & Renesto, 2002.

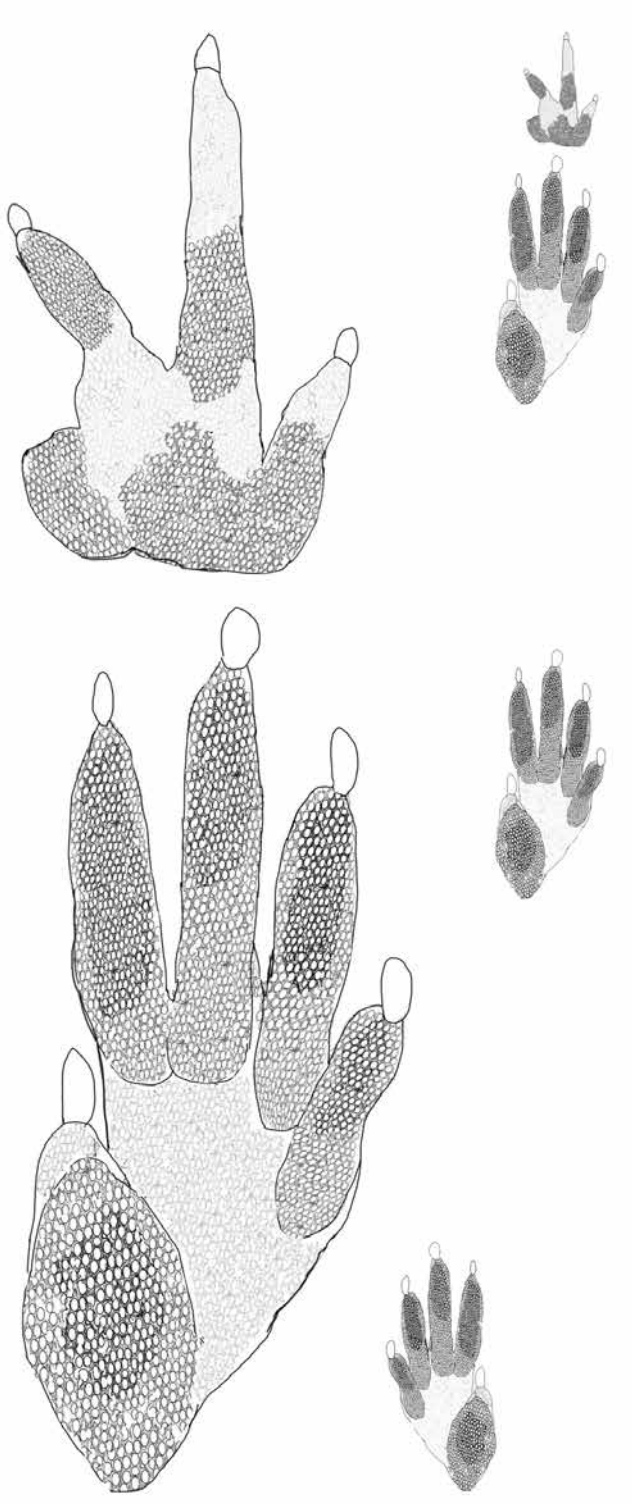
proximal head, the second and third metatarsals show a straight shaft with slightly expanded heads. The proximal articular sur- face is deeply concave as it appears in hatch- lings or very immature specimens of extant reptiles where metatarsals are not yet fully ossified. The fourth metatarsal has approximately the same size or is slightly larger than the proximal head of the third metatarsal, suggesting that it was possibly as long as, or somewhat longer, than the third metarsal; the fifth metatarsal has an expanded proximal head which is medially bent, with an articular
area for the lateral surface of the fourth distal tarsal. The phalanges are short, the ungual phalanges form laterally compressed and dorsoventrally high claws. There are good possibilities that *Rhyncosauroides tirolicus* tracks pertain therefore to some Avemetatarsalian archosaurs.

Sphingopus ladinicus (Avanzini & Wachtler, 2012

Another interesting ichno-species is represented by *Sphingopus ladinicus* (Avanzini & Wachtler, 2012), with almost 30 cm length the biggest tracks recorded in the Triassic Dolomites and having some affinities with the Parachirotheriidae. The Late Anisian (Illyrian) succession, cropping out on the Piz da Peres, shows in the upper layers – in vicinity to the Contrin Formation – a mixed carbonate and terrigenous succession with bigger footprints, although also the characteristic *Rhyncosauroides tirolicus* imprints are common (Avanzini & Wachtler, 2012; Todesco et al., 2008). The mud deposits were made in a marine marginal lagoon, plant debris is common, but entire or bigger plant remains are missing. All specimens from *Sphingopus ladinicus* came from the same

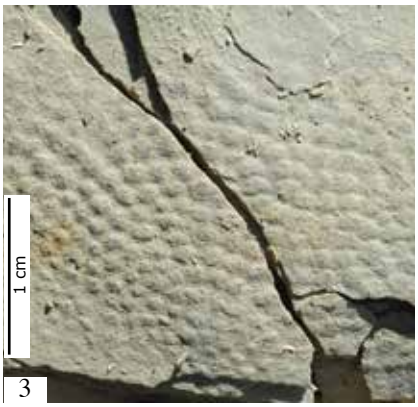


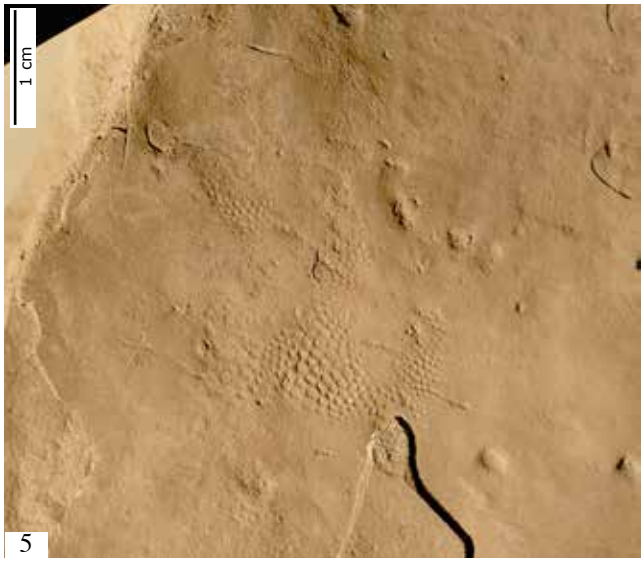




Sphingopus ladinicus (Avanzini & Wachtler, 2012). Manus-pes

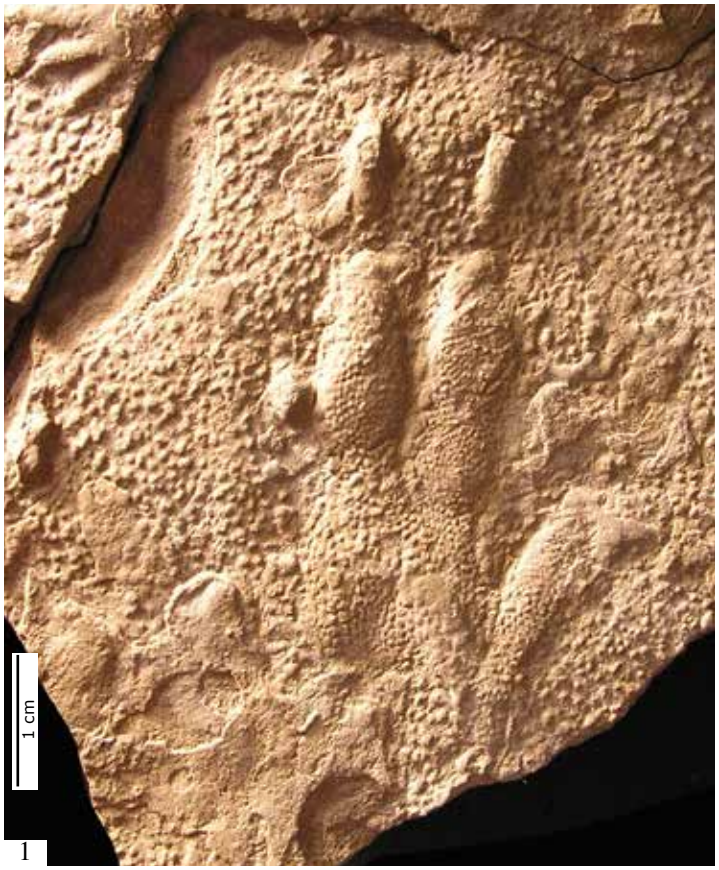
The slabs photographed immediately after the recovery. 1. The holotype FP003. Print and counterprint of a manus-pes set. The pes is long and slender, pentadactyl with anteriorly directed, subparallel digits II-IV, a small and proximally positioned digit I and a marked proximal pad V. The manus track is small and tridactyl, rounded with a pronounced heteropody - and placed in front of the hind foot. It is slightly longer than wide (12cm long,9 cm wide. The manus is placed in front of the pes and divergent from the long axis (Coll. Michael Wachtler, Naturmuseum Südtirol)





Sphingopus ladinicus (Avanzini & Wachtler, 2012). Pes

The slabs photographed immediately after the recovery. 1-2. Paratype FP001 - Print and counterprint of a single pes. The pes is (28 cm long and 12 cm wide. All digits are slender, the claws are elliptical. R*hyncosauroides tirolicus* tracks are also visible. 3. Impression of skin traces. 4. Impression of a digit. 5. Isolated Manus. (All Coll. Michael Wachtler, Naturmuseum Südtirol)



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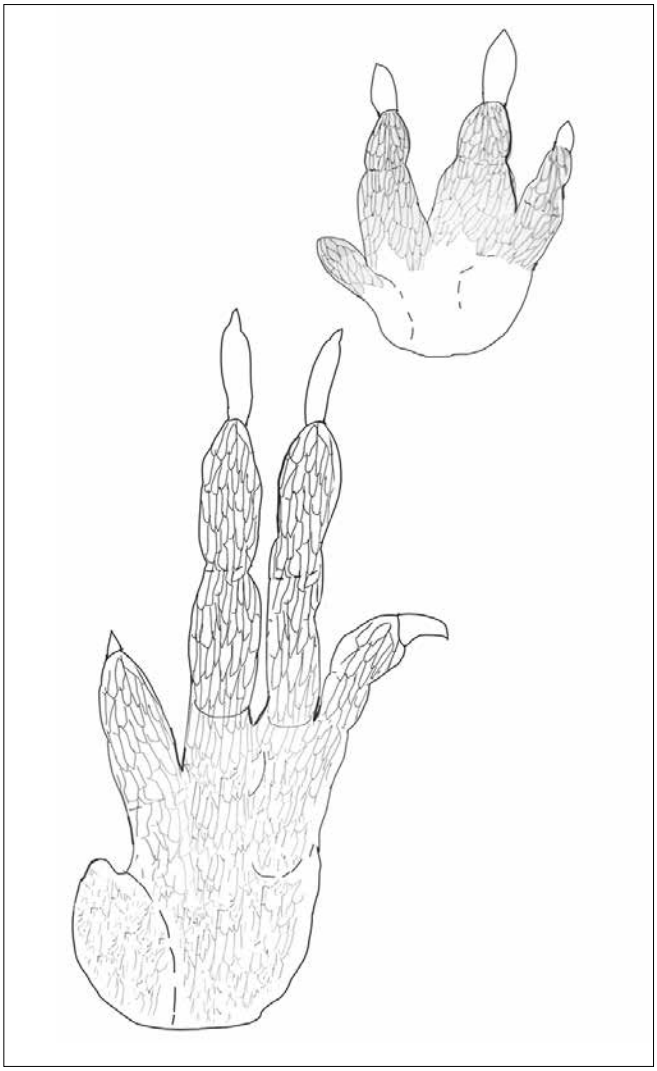
***Isochirotherium delicatum*, Courel & Demathieu 1976**

1. Well-preserved pes with phalanges and claw impressions of digits, 2. Pes; 3. Perfect impressed manus with skin traces. 4. Manus (All Piz da Peres, Furkel, Coll. Michael Wachtler, Naturmuseum Südtirol, Bozen)



Isochirotherium delicatum. Tracks. Pes. Manus. Succession. Isochirotherium was close to a bipedal movement. The pes was huge in comparison to the manus.

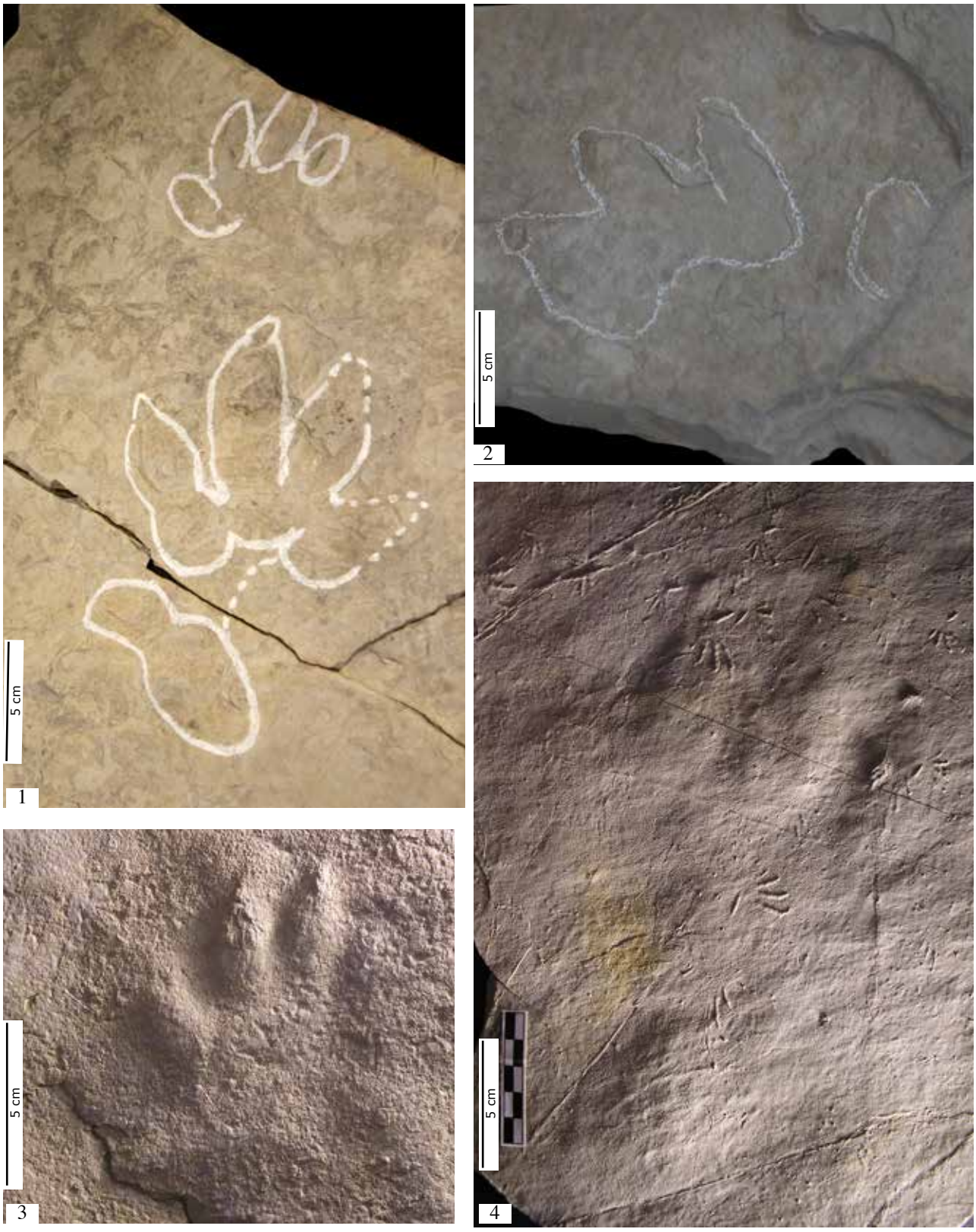
layers located at the top of the Richthofen Conglomerate and very near to the uppermost Morbiac Dark Limestone boundary (46°42'52.94"N, 11°58'38.13"E, 2202 m).

The transition from Early to Middle Triassic is marked by a relatively faster metamorphosis of archosaurs to dinosauromorpha and finally to fully dinosaurian (and also birdlike) animals. Having a Euramerican distribution, first, we encounter archosaur-(chirotheroid) dominated assemblages persisting during most of the Middle Triassic. They are known from deposits of Early to Early Middle Triassic (Olenekian-Anisian) age from Poland over Germany, France, till North America (Arizona and New Mexico) (Klein & Lucas, 2010). They comprise suggested archosaur ichnogenera like *Chirotherium, Isochirotherium, Synaptichnium, Brachychirotherium* and *Rotodactylus* (Avanzini & Wachtler, 2012). Simultaneously, we encounter just a gradual evolving to dinosauromorph tracks (*Sphingopus* and *Parachirotherium*) between the Anisian and Ladinian (Haubold & Klein, 2000, 2002). Only beginning from the Ladinian stage do we have fully evolved dinosaurian tridactyl ichnoassociations, which gradually became more common in the Carnian (small to medium-sized three-toed footprints from *Atreipus* or *Grallator)*.

Anisian *Sphingopus ladinicus*-trackways from Piz da Peres are interesting because they show pentadactyl narrow pedal tracks occasionally associated with small manus imprints (suggesting a possible facultative bipedal trackmaker). The imprints suggest a clear tendency towards digitigrady with a functionally three-toed pes. These characters are interpreted as possible synapomorphies of basal dinosaurs. The heel evidence elliptic skin-impression and the digits have the same pattern. From there, the impressions can be distinguished well from the other chirotherian tracks.

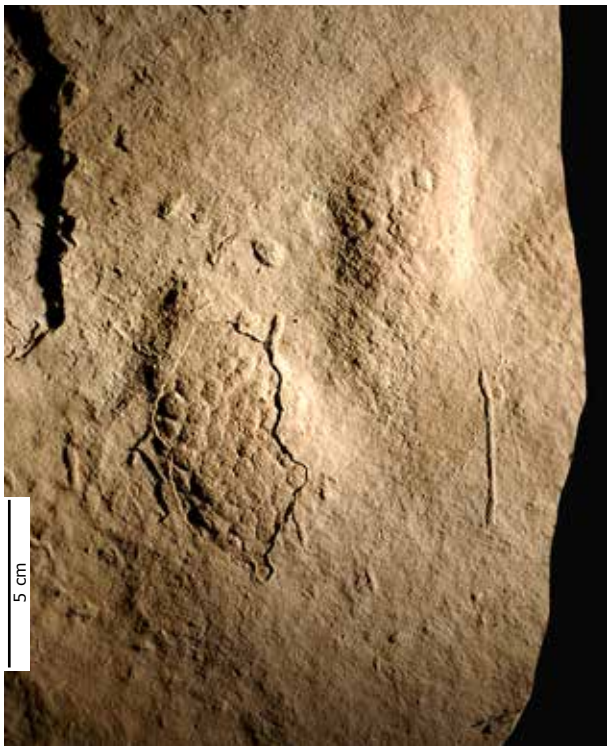
Otherwise, early forms of this 'dinosauriform trend' were usually even smaller (less than 15 cm in length). Also the type species, *Spingopus ferox*, first described by Demathieu (1966) from the Middle Triassic (Late Anisian to Ladinian) of the eastern margin of the Massif Central (France) and then documented in the strata of similar age from the western margin of the Bohemian Massif in northern Bavaria (Haubold & Klein, 2002) has smaller dimensions.

Another similar form, first described by Rehnelt (1950) as *Dinosaurichnium postchirotherioides* (Haubold, 1969), from the Middle Triassic (latest Ladinian) of Germany (Gipskeuper), was later assigned to *Parachirotherium postchirotherioides* by Kuhn (1958). Haubold (1969) included this ichnotaxon in a new morpho-family, the Parachirotheriidae. *Sphingopus ladinicus* differs from *Parachirotherium* by its double length of the pes (25–30 cm). In *Sphingopus ladinicus*, the basal pad of digit V is in a more proximal position than it usually occurs in *Parachirotherium* or other *Sphingopus* ichnospecies. The trackways are functionally three-toed, with a slightly outward rotation of the manus impressions from the midline. The manus is

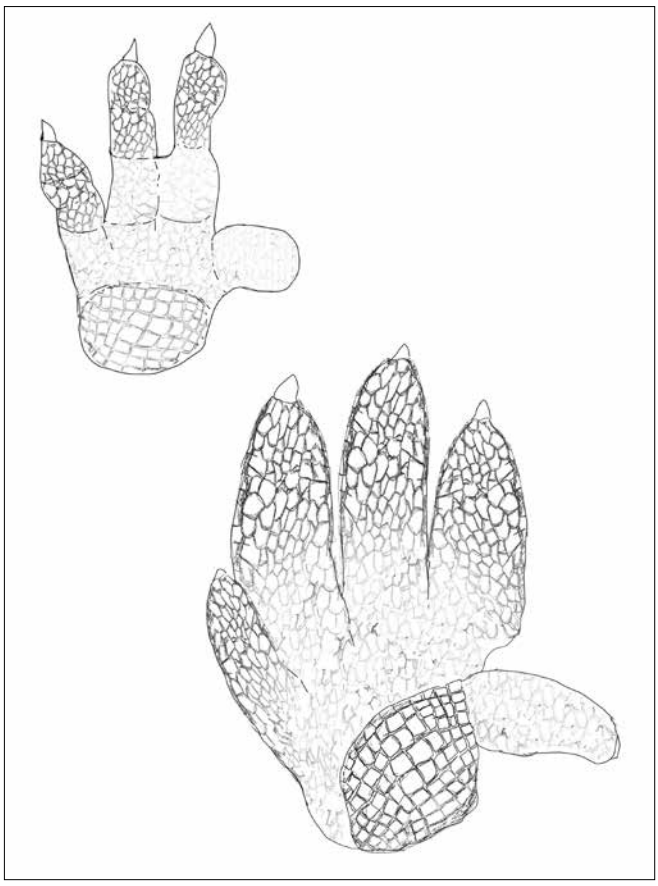


Chirotherium barthii Kaup, 1835

1. Well preserved manus-pes, Val Duron, Museo Scienze Naturali MUSE, Trento, 2. Pes; 3. Perfect manus with skin traces. 4. Rhyncosauroides tirolicus imprints overlie a Chirotherium track (All Piz da Peres, Furkel, Coll. Michael Wachtler, Naturmuseum Südtirol, Bozen)



Chirotherium barthii, pes with skin traces. Piz da Peres, Furkel, Coll. Michael Wachtler, Dolomythos Museum



Chirotherium barthiii. Manus-pes-trackway. The imprints are slightly different as known from German Buntsandstein

placed in front of the pes diverging a little from the long axis through the pedal digit. Furthermore, the narrow symmetrical digit group II–IV and the strong reduction and isolated posteriorly shifted position of digit I could be interpreted as synapomorphies with basal dinosaurs.

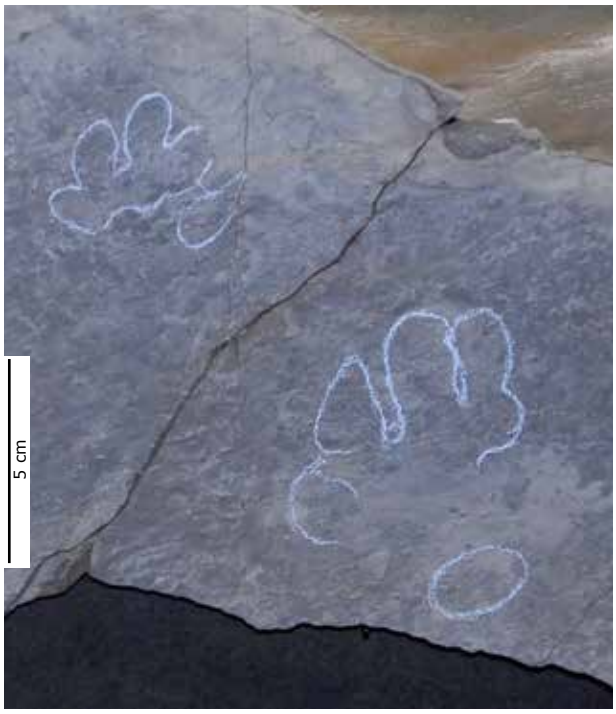
Sphingopus ladinicus imprints can be compared with the so-called 'slender forms' that immediately precede the appearance of the other *Sphingopus* footprints, globally documented in the Late Anisian-Ladinian (Klein & Lucas, 2010). They are part of what Haubold and Klein (2002) consider a functional evolutionary succession from *Chirotherium barthiii* to *Parachirotherium postchirotheroides* and further on to the tridactyl 'grallatorids' in the Late Triassic. However, *Chirotherium barthiii* is more robust and the pedal digit I is less posterior shifted compared to the footprints described here.

The anatomical interpretations of *Chirotherium, Rotodactylus, Eubrontes, Grallator,* and other classical Triassic ichnotaxa were shown to be parallel to the evolutionary sequence of Triassic archosaurs (Avanzini & Wachtler, 2012). The tracks of the Parachirotheriidae document the transition from basal archosaurs to bipedal and tridactyl dinosauroids. The Crurotarsi in direction to the Crocodylomorpha has a broader metatarsal portion while the avemetatarsalian pes is indicated in *Sphingopus* and *Parachirotherium* by the narrow and posteriorly concave metatarsal phalangeal axis reflecting long and slender bunched metatarsals with strong overlap. These slender forms like *Sphingopus ferox* and *Sphingopus ladinicus* could also reflect early phyletic split within Avemetatarsalia between real dinosaurians and bird-like ancestors in the Early Anisian (Wachtler, 2018).

Therefore, the tracks of *Sphingopus ladinicus* can be interpreted as dinosauroid and not dinosaurian. More realistic would be to indicate them as 'ancestors' of dinosaurs or more exactly an affiliated evolutionary-line.

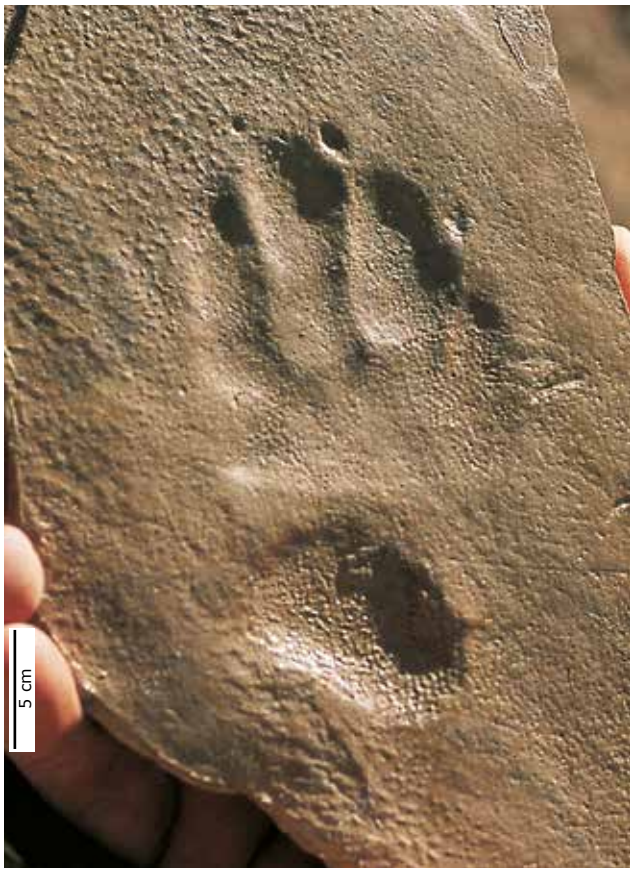
Isochirotherium delicatum Courel & Demathieu 1976

Isochirotherium delicatum represents a characteristic ichnospecies of the French Central Massif, identified there by Courel and Demathieu in 1976 at the Anisian-Ladin-



Brachychirotherium parvum. Manus-pes trackway-sequence. Val Duron, MUSE, Museo delle Scienze, Trento

ian boundary in the area of Largentière (Ardèche, France). It is also common in the Anisian beds of the Southern Alps. A relatively well-preserved ichnoassociation of the Pelsonian age was recognised along the Adige Valley (Avanzini & Lockley, 2002) and in the Val Duron (Todesco et al., 2008) but, especially in the Piz da Peres, they can be encountered in fair and well-preserved amounts.
On the Piz da Peres Furkel mountain range, sometimes they crop out as well preserved archosaurian ichnocoenosis. They are characterized by their narrow, quadrupedal trackways with footprints characteristically longer than wide, with relatively long digits II and III. The digits II and III are almost equal in length and definitely the longest. The digit I impressions are usually very small and thin and parallel to digit II from which it is almost indistinguishable. Digit V is characterised by the presence of a large metatarsal-phalangeal pad impression. The skin-impressions leave a reticulate pattern.
The claw impressions of digits II and III are robust and triangular; those of fingers I and IV are thinner and arched. The manus imprints are small (about 1/5 of the length of the footprints) with short, small and variable digit traces. A small pentadactyl manus impression occurs regularly in front of a much

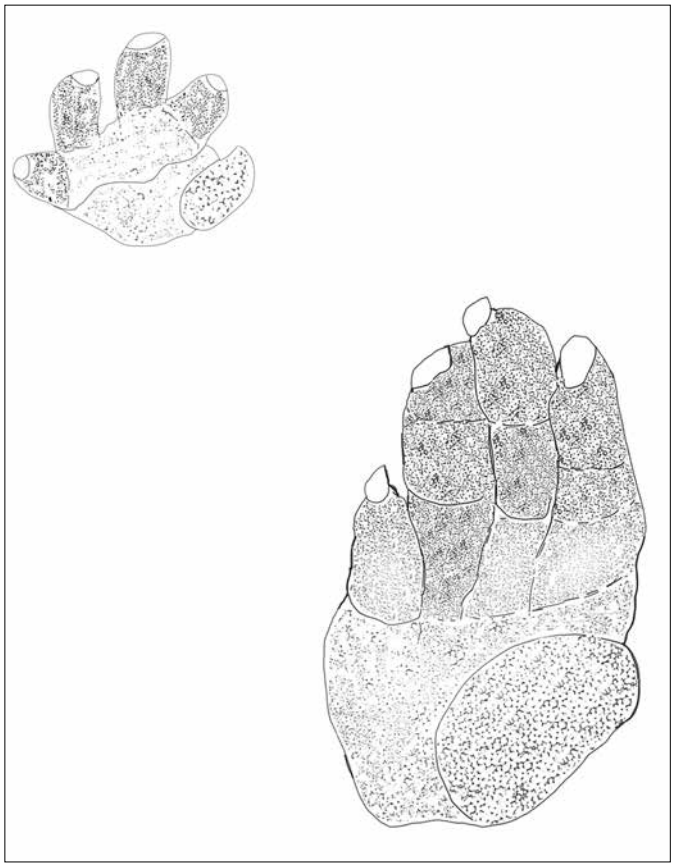


Brachychirotherium parvum. Excellent preserved footprint. Piz da Peres, Lapadures. Coll. Brandner, Universität Innsbruck

larger pentadactyl pes, which resembles a reversed human hand. Manus and pes are digitigrade (Todesco et al., 2008).

Chirotherium barthii Kaup 1835

The first discovery of *Chirotherium* footprints was made about 150 years ago in Germany referring to the Buntsandstein (Early Triassic). Over the course of time, similar ichnogenera like *Brachychirotherium, Isochirotherium,* and *Parachirotherium* – most of them with several different species – were introduced. *Chirotherium barthii* footprints are one of the best documented Triassic archosaur tracks in Europe and include specimens from the classic Buntsandstein locality (Olenekian-Anisian) of Hildburghausen, England, North America (Moenkopi Formation in New Mexico and Arizona), France, Southern Alps, Spain, and China. As the trackmaker were identified archosaurs, pseudosuchians (*Euparkeria, Ctenosauriscus*) thecodonts or rauisuchids.
The evolutive trend of most of the terrestrial archosaurs during the Triassic was orien-



Brachychirotherium parvum. Manus-pes trackway-sequence.

tated to the complex development of erect walk and the bipedalism in connection with a digitigrade and tridactyl pes. This originated from former animals having a quadruped sprawling gait and lacertoid pes with five functional digits. It can be shown that in the Lower Triassic archosaur, footprints exhibit tendencies towards bipedalism, more erect gait, tridactylism, and a mesotarsal foot joint (Haubold, 1983).

Several interesting features occurred between the Early and Middle Triassic, which can be observed especially in the trackways: A reduction of the manus as the function of bipedalism, a stride length in relation to the width of trackway and pace angulation (small track-way pattern) as a function of semi-erect to erect gait, a reduction of pes digits I and V as a function of tridactylism, the cross axis of the pes (ankle between digit III and metatarsal joint of front digits I – IV), and the outward orientation of the pes axis (digit III) to the direction of movement.

The gradual acquisition of these characters in the archosaur locomotion can be seen well in chirotherian impressions (Haubold, 1983) The pes of *Chirotherium barthiii* is much more complete and clearly impressed than the manus. Tridactylism of the pes is present in the closed digit group II – IV, of which III is the longest. Digit I is somewhat separated from the group of II-IV but all are rather equal in length. Digit V is placed behind digits I – IV. The manus is three or more times smaller than the pes. Additional reduction of the manus is suggested by light impressions and the occasional absence of manus tracks; this points to partial bipedalism. The nearly rectangular cross axis and tridactylism indicate an advanced thecodont of dinosaurian-like habit. The skin-impressions of the underside of the legs are mosaic-like. If the *Chirotherium barthii* tracks belong effectively to this Olenekian-Buntsandstein species or have to be inserted in a new species, further studies are required.

Brachychirotherium parvum Hitchcock 1889

The ichnogenus *Brachychirotherium* was introduced by Beurlen in 1950 based on the material from the Upper Triassic (Carnian) Coburger Sandstein in Germany. It is characterized by a broad sole surface and short, clumsy digits. *Brachychirotherium* is distributed in many Middle Triassic localities of Europe and was subdivided in several ichnospecies like *Brachychirotherium hassfurtense, B. eyermani, B. thuringiacum*, and especially *Brachychirotherium parvum*.

There were some suggestions to restrict *Brachychirotherium* only to Upper Triassic deposits (Klein & Haubold, 2004) and to include stratigraphically older material from the Early and Middle Triassic in the ichnogenera *Synaptichnium* (Tanner et al., 2018). The trackways were pentadactyl, which evidence a broad pes imprint with short clumsy digits and thin, short claws. Usually, the pes in an adult specimen is more than 10 cm long and about 8 – 9 cm wide. Digit I is the shortest and is placed behind the digits group II – IV. The longest digit is III, but it is quite equal with IV. Digits group I – IV are well impressed, while the V is represented usually only by a small elliptic metatarsal pad placed behind along the IV digit axis. Digits are short and blunt with robust, rounded pads. The manus is much smaller but of similar shape and exhibit rounded digits splayed like a fan and rotated outwards. Digit V is placed behind IV and nearly parallel to it.

Skin impressions are recognizable on pedal and manual prints with small rounded scales of different sizes on different areas of the tracks (Todesco et al., 2008). The manus-pes distance is about 9 – 10 cm. The manus is placed in front of the pes and more internally with respect to the trackway axis.
Brachychirotherium footprints have most probably been left by rauisuchians, aetosaurs, or crocodylomorph archosaurs (Tanner et al., 2018). The pes of this stem is distinguished from that of the dinosaur birdline archosaurs (Avemetatarsalia sensu, Benton, 1999) by the broader configuration of the metatarsals. This feature is reflected in the typically broad pes imprints of *Brachychirotherium*. Especially aetosaurs like *Typothorax* or rauisuchians such as *Postosuchus* are till now regarded as the trackmakers of this ichnogenus.
Brachychirotherium trackways are common in the Dolomites, found in spectacular specimen on the Piz da Peres area from Lapadures (Brandner, 1973) and Furkel (Wachtler, 2007) to the Val Duron (Todesco et al., 2008).

Conclusion

The ichnofaunas of the Dolomites are rich, and, in some localities like the Piz da Peres, well preserved. Difficulties arose about the identity of the trackmakers. The imprints suggest that many of the already available classifications are doubtful. The high amount of small manus imprints in comparison with sometimes huge pes-tracks are an indication that we experience a broad and fasten radiation of semi-erect to erect and bipedal walk, which include many reptile genera from small to medium-sized archosaurs in direction to the dinosaurs in the Middle Triassic.

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