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Sphingopus ladinicus isp. nov. from the Anisian of the Braies Dolomites (Southern Alps, Italy)

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KEY WORDS - Sphingopus ladinicus *isp. nov., Archosaur footprints, Middle Triassic, Anisian.*

ABSTRACT - A new ichnotaxon, Sphingopus ladinicus *isp. nov., is described from the Middle Triassic (Anisian-Illyrian) of Piz da Peres in the Braies Dolomites (Italy). The morphology of the footprints is related to the enigmatic group of Parachirotheriidae.* S. ladinicus *isp. nov. shows pentadactyl, narrow pedal tracks occasionally associated with small manus imprints (suggesting a possible facultative bipedal trackmaker). Pedal digit group II-IV shows little divarication (max 15°); the digit proportions are III>IV>II with the metatarsal-phalangeal articulation forming a compact group. Tracks show a clear tendency towards digitigrady with a functionally three-toed pes. These characters are interpreted as possible synapomorphies of basal dinosaurs.*

RIASSUNTO - [*Sphingopus ladinicus* isp. nov. dell'Anisico delle Dolomiti di Braies (Alpi meridionali, Italia)] - *È descritto un nuovo ichnotaxon,* Sphingopus ladinicus*, dal Triassico Medio (Anisico-Illirico) del Piz da Peres, Dolomiti di Braies (Italia). La morfologia delle impronte le collega al gruppo enigmatico dei Parachirotheriidae.* S. ladinicus *isp. nov. mostra orme del piede pentadattile associate con poche impronte della mano (suggerendo una bipedia facoltativa del trackmaker). Nel piede, il gruppo II-IV mostra divaricazione poco marcata (max 15°), dito III più lungo, dito IV>II con articolazioni metatarso-falangeali riunite in un unico gruppo. Le tracce mostrano una chiara tendenza digitigrada con piede funzionalmente tridattilo. Questi caratteri sono interpretati come possibili sinapomorfie con i dinosauri basali.*

INTRODUCTION

The first footprints and trackways in the Braies Dolomites were discovered during the First World War (1915-1917) by the Austrian Julius Pia while working as a war field-geologist in this area (Fig. 1). Near Bad Bergfall, well-known by its Roman bath, in a burrow called Lapedures, he collected the first Triassic reptile tracks of the Southern Alps. They were described and classified in 1926 by Othenio Abel, the founder of paleobiology, as *Rhynchosauroides tirolicus* (Abel, 1926).

We had to wait until 1970 when Thilo Bechstädt and Rainer Brandner in their PhD dissertation recognized other footprints from the same locality. Together with abundant *Rhynchosauroides tirolicus*, Brandner (1973) described well-preserved chirotherian tracks defined as *Brachychirotherium* aff. *B. parvum* (Hitchcock, 1889) and *Chirotherium* cfr. *Chirotherium rex*. De Zanche et al. (1992) and Zühlke (2000) studied the geology of Piz da Peres but did not tackle any ichnological aspects.

In 2007 one of the authors (Michael Wachtler) began an extensive survey around the massif of Piz da Peres, especially at the Furkel Pass (Fig. 1). In several places where the typical trampled layers emerge from the dense grass, forests and scrubland, he identified several fossil layers. They contained not only a rich spectrum of Anisian-Illyrian vertebrate ichnotaxa (*Rhynchosauroides*, *Procolophonichnium*, *Chirotherium*, *Isochirotherium*, *Brachychirotherium* and *Rotodactylus*), but also numerous land plants and invertebrates (worms, bivalves, jellyfishes). Later field researches (2007-2010) organized by the Museum of Nature South Tyrol (Bozen) (Todesco et al., 2008) led to the discovery of several ichnological and palaeobotanical specimens currently under study.

GEOLOGICAL SETTINGS

The geology of the Braies Dolomites is well known since the work of Pia (1937) in which he recognised several terrigenous and carbonate units of Anisian age, deposited in basinal, lagoonal, peritidal and continental environments.

The Anisian succession, cropping out along the Braies Dolomites, shows a mixed carbonate and terrigenous succession that overlies the top of the Early Anisian (Aegean) carbonates (Lower Serla dolomite) and is overlain by the lower beds of the Late Anisian (Illyrian) carbonates (Contrin Formation) (Bechstädt & Brandner, 1970; De Zanche et al., 1992; Fig. 1).

All the trampled layers are attributed to the Obere Peresschichten *sensu* Pia (1937) and Bechstädt & Brandner (1970), now officially called Richthofen Conglomerate (Avanzini et al., 2007) and Morbiac Dark Limestone (Delfrati & Farabegoli, 2000) (both Illyrian in age).

The Richthofen Conglomerate is dominated by red sandstones and siltstones and subordinate conglomerate beds. This unit has been interpreted as being deposited in a relatively arid fluvial or in a transitional continental to marine environment (De Zanche et al., 1992, 1993; Avanzini et al., 2007).

The Morbiac Dark Limestone prevalently consists of silty, decimetre-thick, grey or light brown lime wackestones and packstones with foraminifers and ostracods. Stromatolite bindstones and thin grey or green siltstones layers are interbedded. Plant debris is common. The depositional environment is referable to a marine marginal setting with lagoons and swamps contaminated by terrigenous inputs (Delfrati & Farabegoli, 2000).

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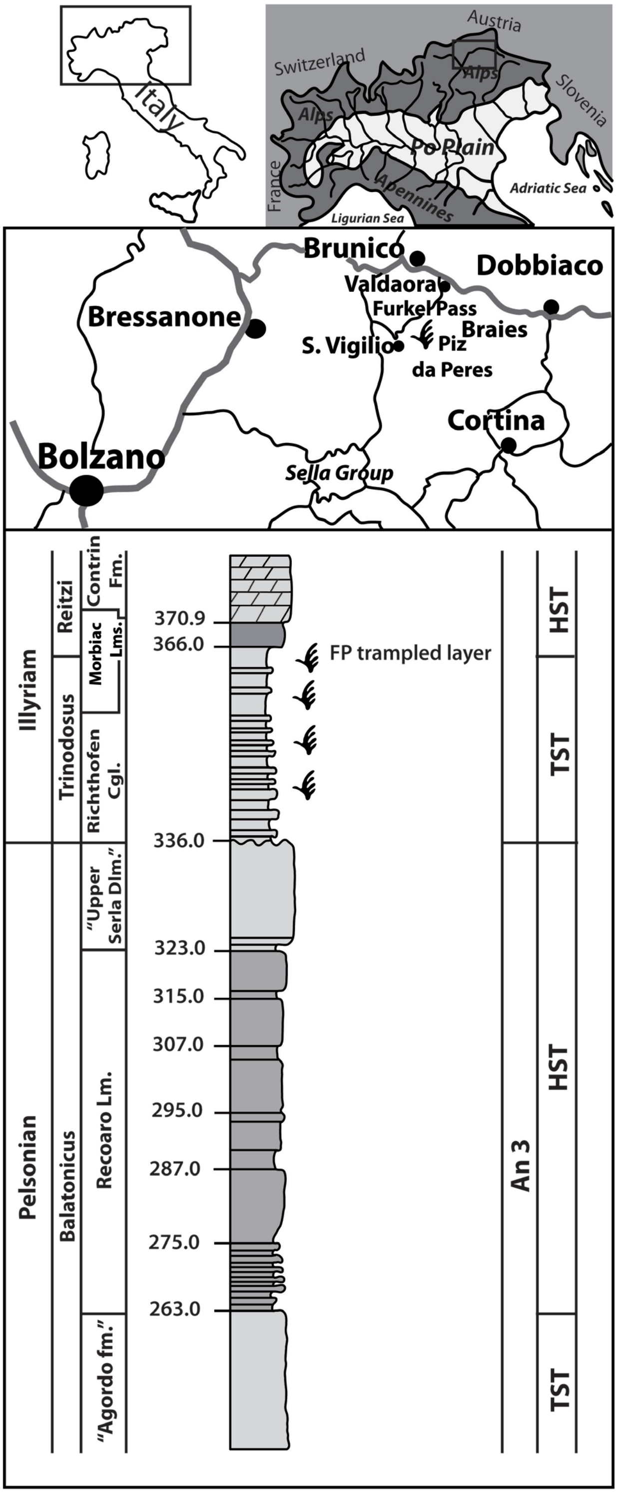

Fig. 1 - Geographic and stratigraphic position of the described material (from Todesco et al., 2008 and Zühlke, 2000 mod.).

MATERIAL AND METHODS

All specimens described here come from the same trampled layer located at the top of the Richthofen Conglomerate and very near to the uppermost Morbiac Dark Limestone boundary in the same locality described by De Zanche et al. (1992) and Zühlke (2000) (46°42'52.94"N, 11°58'38.13"E, 2202 m).

Two of the specimens are preserved on isolated slabs (print and counterprint) (FP001 and FP002). Other three are associated in a short trackway (FP003/A, FP003/B, FP003/C). All the prints are moderately well preserved. In two of these (FP002, FP003/C) skin traces can be observed.

The terms concerning vertebrate palaeoichnology mainly follow Leonardi (1987). To avoid repetition in the systematics, authors and years of publication of ichnotaxa will only be listed at the first mention.

SYSTEMATIC ICHNOLOGY

Morpho-family Parachirotheriidae Haubold, 1969
Ichnogenus *Sphingopus* Demathieu, 1966

Sphingopus ladinicus ichnosp. nov.
(Fig. 2)

Etymology - From Ladinia, the area of the discovery.

Holotype - Print and counterprint of a manus-pes set (FP003/C) (Figs 2A, E).

Paratypes - Counterprints FP001, FP002 (Figs 2C-D).

Type horizon and locality - Late Anisian (Illyrian) Richthofen Conglomerate at Passo Furcia/Furkel Pass, Piz da Peres-Northern side (Pustertal, Bozen), Italy (46°42'52.94"N, 11°58'38.13"E, 2202 m).

Referred material - Trackway containing the holotype, consisting of three footprints, one with an associated manus imprint (FP003/A, FP003/B, FP003/C) (Fig. 2E).

Repository - Naturmuseum Südtirol, Bindergasse 1, 39100 Bozen, Italy.

Diagnosis - Pes long and slender, pentadactyl (III>IV>II>I>V) with anteriorly directed, subparallel digits II-IV, a small and proximally positioned digit I and a marked proximal pad V.

Manus tracks are tridactyl and rounded (pronounced heteropody - manus/pes ratio 0.4) and placed in front of the hind foot.

Narrow trackway, with a slightly outward rotation of the manus impressions from the midline.

Description (based on the holotype) - Narrow trackway of a quadrupedal chirotheriid with footprint length and width of about 28 cm and 11 cm, respectively, and without space between trackway midline and inner margin of pes tracks. Pes pentadactyl (III>IV>II>I>V) with anteriorly directed digits II-IV, a small and proximally positioned digit I and a marked proximal pad V. Manus tracks are tridactyl and rounded (pronounced heteropody - manus/pes ratio 0.4) and placed in front of the hind foot.

Pes - Pentadactyl, longer than wide (L= 28 cm, W= 12 cm). Digit III is the longest, II and IV are subequal in length and digit I is the shortest (Tab. 1). All digits are slender

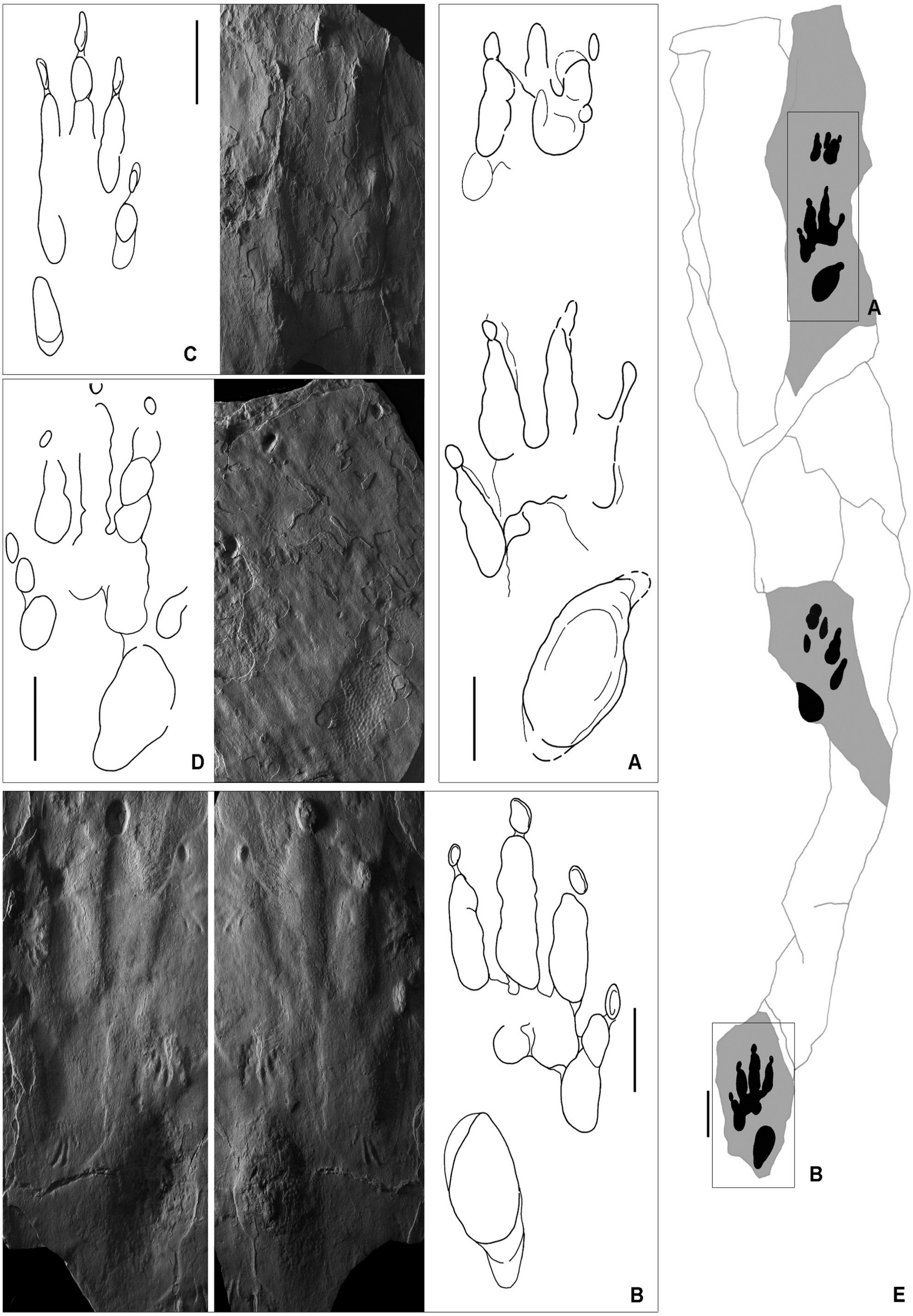

Fig. 2 - *Sphingopus ladinicus* ichnosp. nov. Trackway FP003 (E) with footprints FP003/A (B) and FP003/C (A, Holotype) evidenced. The shaded slabs are housed in the Naturmuseum Südtirol, Bozen (Italy). Isolated footprints FP001 (C) and FP002 (D). Scale bar corresponds to 5 cm (A-D) and 10 cm (E).

with sub-elliptical pads clearly evident in digit group I-IV. Elliptical claw marks are well visible on all digits of group I-IV, and are about 1-2 cm in length. Digits II-IV are almost parallel. Digit I is slightly inward oriented. Digit V is preserved only as an elliptical pad placed laterally and behind the digit group I-IV, and slightly outward rotated

		L	W	L/W	I-II	II-III	III-IV	IV-V	II-IV	I-IV	I-V
FP001		18	6	**3**	5°	6°	5°	10°	12°	15°	24°
FP002		20.5	10	**2.05**	10°	7°	5°	16°	15°	20°	36°
trackway FP003	A	27	12	**2.25**	8°	10°	10°	15°	15°	23°	40°
	B	28	13	**2.16**	13°	13°	10°	15°	15°	36°	52°
	C	28	12	**2.3**	15°	10°	10°	15°	15°	35°	50°

Tab. 1- Measurements (in cm and degrees) of the described footprints.

with respect to digit IV. Digit V is separated from the digit I-IV and tapers distally apparently without a phalangeal portion (only in FP003/C - Fig. 2A - a possible short phalangeal portion seems to be preserved). Sometimes (FP001, FP002, FP003C) an outward directed claw trace is recognizable at the digit tip I, II and III. The pes is outward oriented with respect to the trackway midline.

Manus - Small and apparently functionally tridactyl (II-IV), slightly longer than wide (L= 12 cm, W= 9 cm) (Fig. 2A). The manus axis is rotated outward by about 10° with respect to the foot axis and 30° on average with respect to the trackway midline. Digit impressions are splayed and taper distally. Digit II-IV are almost equal in length, but digit II is slightly shorter than the others. Digit traces are pointed with distinct claw marks.

Trackway - Narrow, with a slightly outward rotation of the manus impressions from the midline. The manus is placed in front of the pes and divergent from the long axis through pedal digit III by about 10°. The oblique pace of the pes varies from 95 cm to 98 cm. The oblique pace of the manus is about 100 cm (estimated). The stride length of the pes is 190 cm. The pace angulation of the pes and manus is 190°.

DISCUSSION

Despite the apparent difference in size and morphology, all the described footprints can be linked to the same morphotype. The L/W ratio shows an alignment according to a logarithmic regression curve (Fig. 3), comparable with the growth curves of extant and fossil reptiles (see Avanzini & Lockley, 2002). Dimensional and morphological differences thus can be explained as an increased size of the same kind of trackmaker (different age classes or sexual dimorphism).

The described footprints can be compared with the so-called "slender forms" that immediately precede the appearance of *Sphingopus* footprints, worldwide documented in the Late Anisian - Ladinian (Klein & Lucas, 2010). They are part of what Haubold & Klein (2002) consider a functional-evolutionary succession from *Chirotherium barthii* to *Parachirotherium postchirotheroides* and further on to the tridactyl "grallatorids" in the Late Triassic. The dominance of the digit-group II-IV, with digit III being the longest, is a striking feature, as is the posteriorly-shifted digit I, in all very similar to the "trend" established by *C. barthii* (Haubold & Klein, 2005). However, *C. barthii* is more robust and pedal digit I is less posterior shifted compared to here described footprints. Similar, but smaller and slender forms from the Anisian of Germany and Poland are assigned to *Sphingopus* or cf. *Sphingopus* by Haubold & Klein (2002) and Brusatte et al. (2010).

The type species, *Spingopus ferox*, was first described by Demathieu (1966) from the Middle Triassic (Late Anisian to Ladinian) of the eastern margin of the Massif Central (France). Subsequently, *S. ferox* has been documented in strata of similar age from the western margin of the Bohemian Massif in northern Bavaria (Haubold & Klein, 2002). The French specimens are similar to ours; the differences are basically the broadness

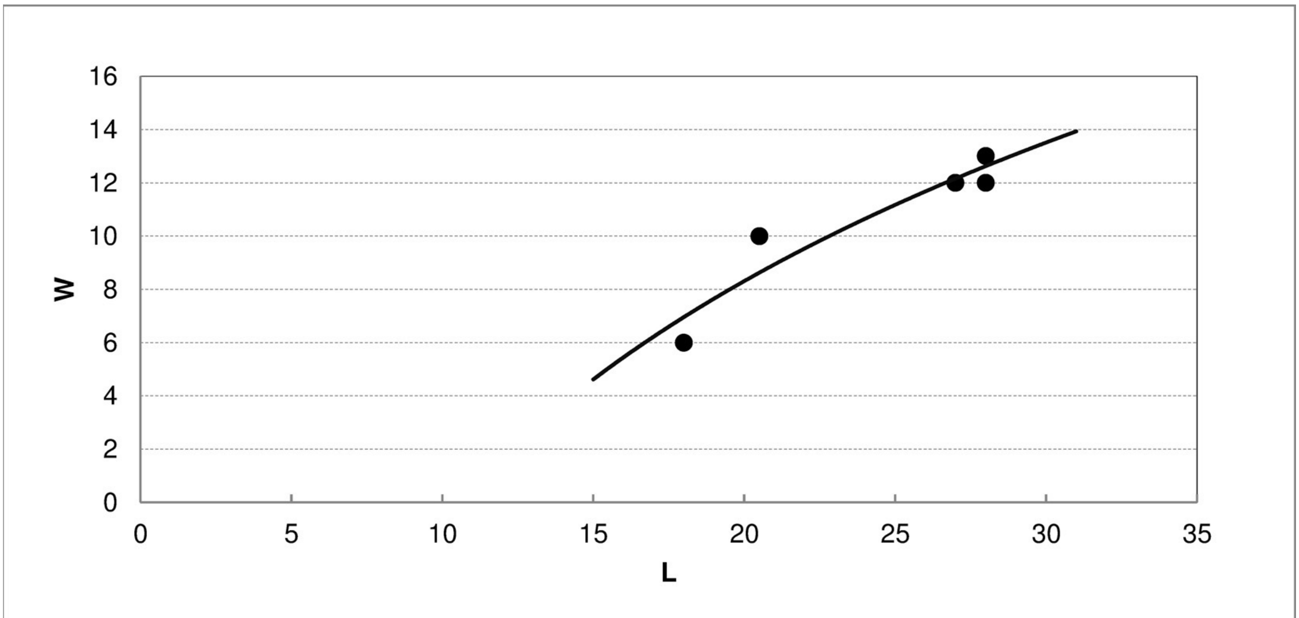

Fig. 3 - W/L ratio of several *S. ladinicus* footprints evidences a possible growth trend of the same form.

of the digits, pedal digit I impressed with the claw tip only, and the smaller dimensions of the former.

So, the new ichnotaxon can be assigned to the ichnogenus *Sphingopus* by the dominance of the nearly parallel digits II-IV, with digit III being the longest, a well-developed metatarsal-phalangeal pad V and a posteriorly shifted digit I positioned very close to the digit group II-IV. *Sphingopus ladinicus* can be distinguished from *S. ferox* by its greater size (L ~ triple), the more slender digits, the completely impressed digit I (claw tip only in *S. ferox*) and the more posteriorly positioned digit V.

Another form was only poorly known for a long time. It was first described by Rehnelt (1950) as *Dinosaurichnium postchirotherioides* (Haubold, 1969) and later assigned to *Parachirotherium postchirotherioides* by Kuhn (1958). Haubold (1969) included this ichnotaxon in a new morpho-family, the Parachirotheriidae. The type species of the ichnogenus *Parachirotherium* is *P. postchirotherioides* (Rehnelt, 1950), from the Middle Triassic (latest Ladinian) of Germany (Gipskeuper) (Haubold, 1971a, b, 1984). Recently, Haubold & Klein (2000) described new material from the Gipskeuper cropping out southeast of Bayreuth, in Bavaria. The layers with footprints form part of the Benker Sandstein which is Ladinian to Early Carnian in age. The pes is usually no longer than 14 cm; the manus is small and pentadactyl. The transition from a pentadactyl/quadruped to a tridactyl/biped pattern is occasionally documented in the same trackway (Haubold & Klein, 2000).

S. ladinicus differs from *Parachirotherium* by its double length of the pes (25-30 cm). The manus - pes ratio is 0.4 (0.3 in *Parachirotherium*) and the divarication of digit group I-IV is 35° (40° in *Parachirotherium*). 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.

CONCLUSIONS

Sphingopus ladinicus, Sphingopus ferox and *Parachirotherium* represent ichnites that are currently not well known and whose systematic position is still debated (Fig. 4). In the last years, the anatomical interpretations of *Chirotherium*, *Rotodactylus*, *Eubrontes*, *Grallator*, and other classical Triassic ichnotaxa were shown to parallel the evolutionary sequence of Triassic archosaurs (Haubold & Klein, 2000, 2002; Klein & Haubold, 2007). Klein & Haubold (2003) defined an "exceptional position" for *Chirotherium barthii* and *Chirotherium sickleri* within chirotherians, regarding them as "modern" footprints in the early evolution of archosaurs.

Following Haubold & Klein (2000, 2002), the tracks of *Parachirotherium* document the transition from basal archosaurs to bipedal and tridactyl dinosauroids. Haubold (1971a), tentatively referred this ichnogenus to the suborder Theropoda on the basis of the tendency toward a tridactyl digit group II-IV. Recently, Haubold & Klein (2000) proposed that bipedal trackways attributable to the ichnogenus *Grallator* can be derived from quadrupedal trackways of the *Parachirotherium* type, suggesting that *Parachirotherium*-*Atreipus*-*Grallator* could represent an evolutionary sequence of trackmakers interpreted as dinosauromorph archosaurs.

If the attribution to Dinosauromorpha is true, the Illyrian age of our form is unique with respect to what has been found in Europe to date. This, however, is not an isolated case. Scattered tracks that can be referred to archosaurs with a functionally tridactyl pes come from the same stratigraphic levels (Avanzini, 2002) and from the Bithynian - Pelsonian boundary. These types of tracks have been interpreted as dinosauroid, not dinosaurian, but given our current state of knowledge, they could as well be crurotarsan in origin. More realistic would be to indicate them as "ancestors" of dinosaurs or more exactly an affiliated evolutionary-line.

The worldwide Middle Triassic track record is archosaur-dominated and includes the oldest dinosauromorph tracks (Klein & Lucas, 2010). These archosaur- (chirotheroid) dominated assemblages persist during most of the Middle Triassic. They are best known from deposits of Early to early Middle Triassic (Olenekian-Anisian) age and have an Euramerican distribution. They comprise a diversity of archosaur ichnogenera, including *Chirotherium*, *Isochirotherium*, *Synaptichnium*, *Brachychirotherium* and *Rotodactylus*. Equivalent ichnofaunas were found also in Germany, France, Poland and North America (Moenkopi Formation in Arizona and New Mexico) (Lucas, 2007; Klein & Lucas, 2010). In these sequences dinosauromorph footprints (e.g., *Rotodactylus*) are documented in the Lower Triassic (Olenekian) and continue (e.g., *Sphingopus* and *Parachirotherium*) throughout the Anisian and Ladinian (Haubold & Klein, 2000, 2002; Klein & Lucas, 2010). The first fully dinosaurian ichnoassociations are Ladinian in age and are represented by tridactyl tracks (Marsicano et al., 2007). In the Carnian ichnoassociations, tetradactyl footprints (as *Evazoum*) are often associated with small to medium-sized three-toed footprints (*Atreipus, Grallator*) (Haubold, 1986; Silvestri & Szajna, 1993; Lucas & Hancox, 2001; Lucas, 2003; Lucas & Huber, 2003; Klein et al., 2006; Lockley et al., 2006; D'Orazi Porchetti et al., 2008; Brusatte et al., 2010).

Early forms of this "dinosauriform trend" were usually even smaller (less than 15 cm in length), but unlike what is documented worldwide, in the Anisian of the Southern Alps (Pelsonian and Illyrian), large dinosauriform footprints such as *Sphingopus ladinicus* were found. They are functionally three-toed, narrow tracks and are associated with a few forelimb traces. The digit group II-IV has a low divarication (max 15°) with a compact metatarsal-phalangeal articulation and a distinct tendency toward digitigrady. 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.

Crurotarsans (Nesbitt, 2011) have 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 as *Sphingopus ferox* and *Sphingopus ladinicus* could also reflect a split within Avemetatarsalia and according to recent interpretations (Sookias et al., 2012), this seems to suggest an early phyletic split for dinosaurians in the Early Anisian.

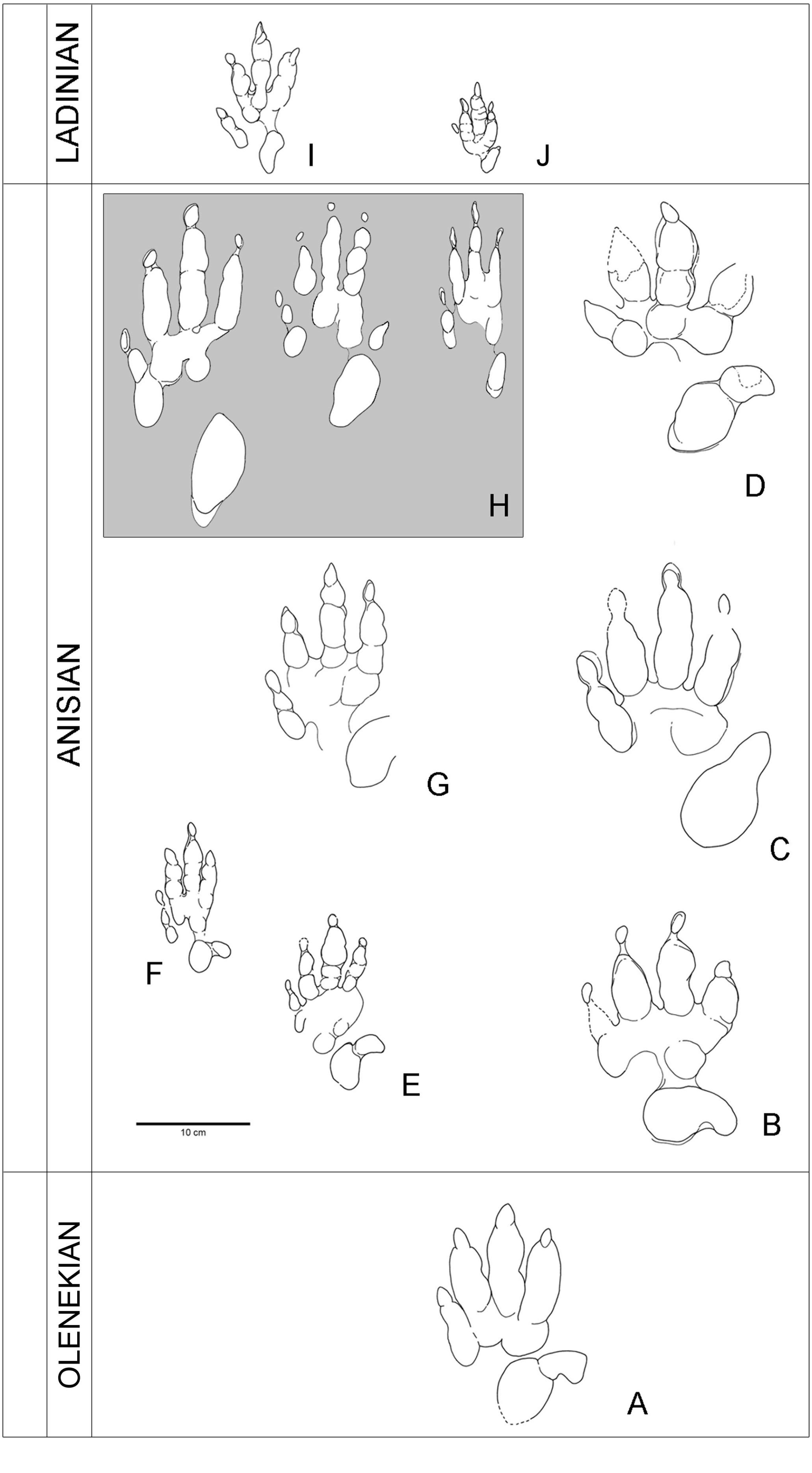

Fig. 4 - Anisian footprints from the Southern Alps compared to the classical *Chirotherium barthii* (A), *Parachirotherium postchirotheroides* (I) and *Sphingopus ferox* (J) footprints. B) *Chirotherium barthii* from Bad Gfrill - Tisens (BZ), early Pelsonian; C) *Chirotherium barthii* from Bad Gfrill - Tisens (BZ), late Pelsonian; D) *Chirotherium barthii* from Val Duron (TN), early Illyrian; E) cfr. *Sphingopus* sp. from Rio Urban (TN), early Pelsonian; F) cfr. *Sphingopus* sp. from Bavaria, Anisian (? Pelsonian) - redrawn from Klein & Haubold, 2007 (fig. 7); G) Unnamed footprint from Bad Gfrill - Tisens (BZ), late Pelsonian; H) *Sphingopus ladinicus* from the Furkel Pass, Illyrian. Scale: 10 cm for all footprints.

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