Rivista Italiana di Paleontologia e Stratigrafia | volume 108 | numero 1 | pagine 51-66 | Maggio 2002

A REVIEW OF RHYNCHOSAUROIDES TIROLICUS ABEL, 1926 ICHNOSPECIES (MIDDLE TRIASSIC: ANISIAN-LADINIAN) AND SOME INFERENCES ON RHYNCHOSAUROIDES TRACKMAKER

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Received August 2, 2001; accepted January 8, 2002

Key words: *Rhynchosauroides* ichnogenus, Anisian, Triassic, Trentino, Northern Italy, palaeontological attribution, Archosauromorpha, Reptilia.

Riassunto: *Rynhcosauroides tirolicus* (Abel, 1926) rappresenta la prima impronta di tetrapode documentata nel Triassico del Sudalpino orientale. La recente scoperta di nuove tracce, talvolta associate in piste ha permesso di documentare per la prima volta lo stile della pista, dimensioni e possibile dinamica funzionale dell'autore di questa icnite che appare peculiare dei depositi dell'Anisico superiore delle Alpi meridionali. Una attribuzione paleontologica tentativa di *Rhynchosauroides tirolicus* e di altri *Rhynchosauroides* medio-triassici, suggerisce che la morfologia proposta per il trackmaker corrisponde con rettili prolacertiformi simili a *Macrocnemus bassanii* Nopcsa, 1931, se quest'ultimo viene ricostruito con una mano non completamente plantigrada e con un piede digitigrado.

Abstract: *Rynhcosauroides tirolicus* (Abel, 1926) is the first ichnite of Triassic tetrapods known from the South-eastern Alps. The recent discovery of new tracks and trackways also permits, for the first time, the documentation of trackway pattern and to calculate the dimensions and possible functional dynamics of the author of this form which appears peculiar to the upper Anisian deposits of the Southern Alps. A tentative palaeontological attribution of *Rhynchosauroides tirolicus* and other Middle Triassic *Rhynchosauroides* trackmaker suggest with some confidence, that the morphology of the trackmakers matches the structure of prolacertiform reptiles like *Macrocnemus bassanii* Nopcsa, 1931 if this latter is reconstructed with a not fully plantigrade manus and pes, but rather with a semi-plantigrade manus and a digitigrade pes.

Introduction.

In the first decade of 1900, J. Pia found, in the sedimentary levels of the upper Anisian layer of the Braies Dolomites, the first footprints of Triassic tetrapods from the South-eastern Alps. The material were studied by Abel who established the new ichnospecies *Rynchosauroides tirolicus* (Abel, 1926). Abel described the tracks as follows: "*The tracks are very similar to those that Beasley described as rhynchosaur-like trackways from British Trias and the dimensions of the new tracks are about the same as the living reptile Sphenodon.... It can be seen that the prints of the posterior foot are characterised by an increase in the size of the digits from I to IV... digit V is turned backwards. The hands have the same dimensional characteristics as the feet and are situated very close to these latter... I propose to call these new tracks Rhynchosauroides tirolicus n. sp. In agreement with Beasley and Nopcsa these should be referable to a small Rhynchocephalian that left its tracks in the Triassic rocks of the Dolomites*" (Author's translation from German).

In 1973 Brandner described a group of tracks from the same area and the same formation (Bechstädt & Brandner 1970; Brandner 1973). Amongst these he identified several prints that could be attributed to *Rynchosauroides tirolicus*. In his observations Brandner substantially confirmed Abel's diagnosis and added a series of morphometric data based essentially on the observation of a pair of manus-pes tracks (PP1) (Fig. 1).

The same author noted that the tracks were very similar to *Rotodactylus mckeei* (recte *Rhynchosauroides*? *mckeey*) Peabody, 1948, especially for that regarding the dimensions of the manus and pes. However several differences were noted particularly with regards to the size of the manus and pes (24 mm in *Rynchosauroides tirolicus* and 40 mm in *Rotodactylus mckeei*) and to the backwards turned position of digit V of the *Rotodactylus mckeei* which are not comparable to *Rynchosauroides tirolicus*.

Rhynchosauroides tirolicus geographic and chronostratigraphic distribution

Recent research has led to the discovery of tracks of this type in other sites in the Dolomite region and an increase in documentation also from a statistical viewpoint. The discovery of associated tracks on trackways

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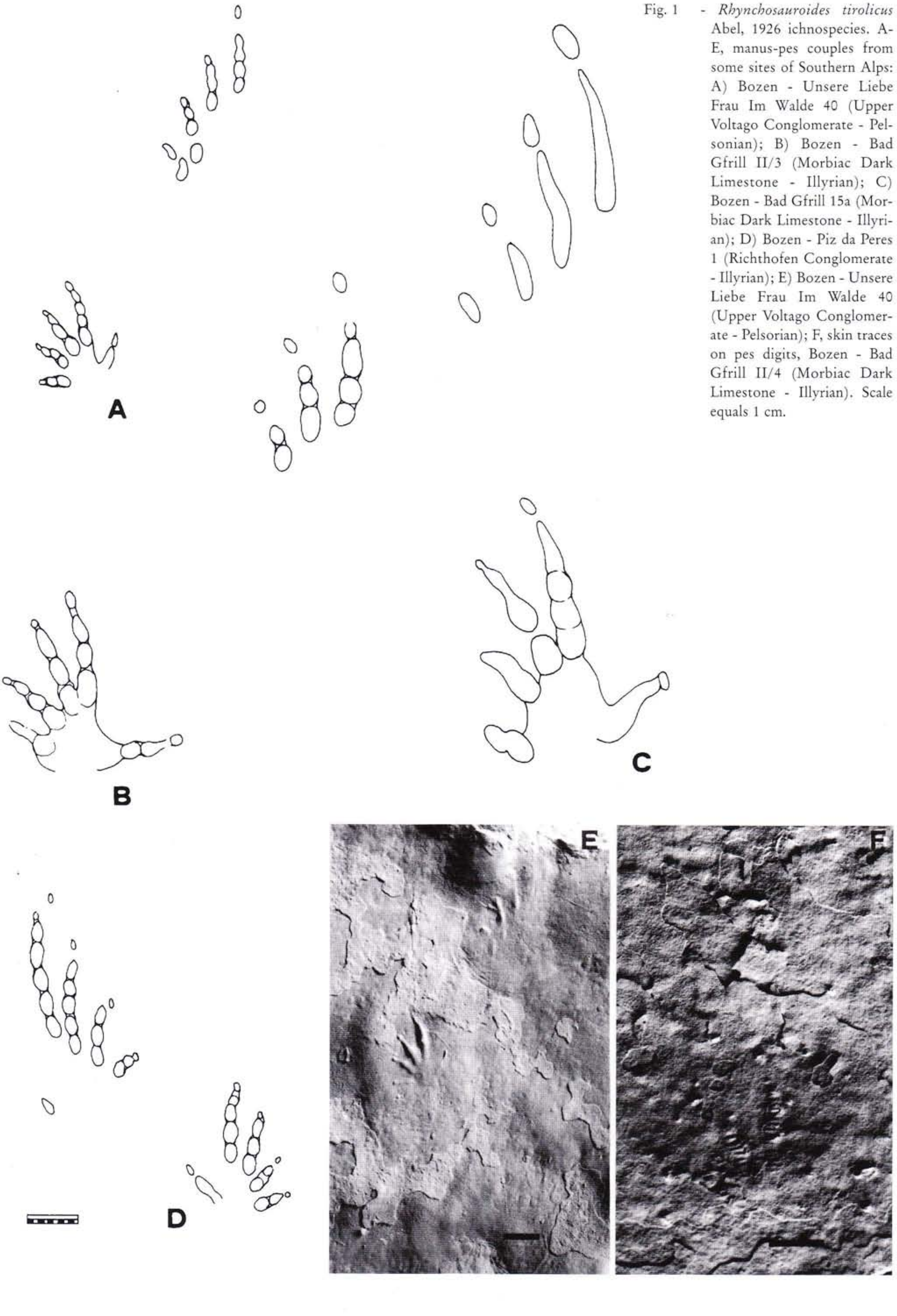

Fig. 1 - *Rhynchosauroides tirolicus* Abel, 1926 ichnospecies. A-E, manus-pes couples from some sites of Southern Alps: A) Bozen - Unsere Liebe Frau Im Walde 40 (Upper Voltago Conglomerate - Pelsonian); B) Bozen - Bad Gfrill II/3 (Morbiac Dark Limestone - Illyrian); C) Bozen - Bad Gfrill 15a (Morbiac Dark Limestone - Illyrian); D) Bozen - Piz da Peres 1 (Richthofen Conglomerate - Illyrian); E) Bozen - Unsere Liebe Frau Im Walde 40 (Upper Voltago Conglomerate - Pelsorian); F, skin traces on pes digits, Bozen - Bad Gfrill II/4 (Morbiac Dark Limestone - Illyrian). Scale equals 1 cm.

also permits, for the first time, the documentation of trackway pattern and to calculate the dimensions and possible functional dynamics of the author of this form which appears peculiar to the Anisian deposits of the Southern Alps (De Zanche et al., 1993). The investigated material come from the following formations and localities (Avanzini & Mietto in prep.):

Voltago Conglomerate (?Bithynian - earliest Pelsonian)

Gampenpass (BzNLF)(Valle di Non - Bozen)
Unsere Liebe Frau im Walde (BzULFIW)(Valle di Non - Bozen)

Grey centimetre/decimetre-thick strongly wavy to nodular silty lime grainstone beds bearing dasycladaceans, crinoids, gastropods and carbonate intraclasts, are interbedded with predominant red siltsontes and fine grained sandstones. Plants debris are abundant throughout the unit (this unit correspond with the "Voltzia beds" in the Recoaro area). Conglomerate beds, consisting of rounded centimetre-sized pebbles in a white and yellow sandy matrix, are subordinate. Normally they are a few decimetres, rarely more than 1 m, thick and erosional.

Tretto Conglomerate and Richthofen Conglomerate (Early Illyrian)

Val di Creme (OG/VC) (Recoaro - Vicenza)
Piz da Peres (BzPP)(Braies Dolomites - Bozen)
Val Fiorentina (Eastern Dolomites - Belluno)
Monte Ozol (MTSNTnMO)(Monte Ozol, Valle di Non - Trento)
Schwarzbach (Kaltern, Adige Valley - Bozen)
Eppan (Eppan, Adige Valley - Bozen)

This unit is dominated by red sandstones and siltstones which alternate with subordinate conglomerate beds, a few decimetre thick, erosionally based.

Morbiac dark Limestone (Illyrian)

Bad Gfrill (BzBG)(Tisens, Adige Valley - Bozen,

This unit prevalently consists of more or less silty, centimetre -thick grey or light brown lime wackestones and packstones bearing ostracods, foraminifers and porostromata. Stromatolite bindstones and thin grey or green siltstone layers are interbedded.

These units probably reflect a transitional continental to marine environment characterised by carbonate tidal flats and coastal delta mouth bars deposited under relatively arid conditions.

Systematic palaeontology.

Morphofamily: Rhynchosauroidae Haubold, 1966

Diagnosis: after Haubold (1966, p. 166). Wide quadruped trackway. Manus and pedes put side by side but sometime the pes oversteps the manus. The pace angle of the pes varies from 70° to 125°. The pes is slender and digitigrade, the manus is platigrade or semiplantigrade, stout and shorter. Digit length increases from I to IV, the digit V is shorther. The digit ends could be outward or inward rotated.

Distribution: Triassic of Europe and America.

Ichnogenus: *Rhynchosauroides* Maidwell, 1911

Generotypus: *R. rectipes* Maidwell, 1911, Sin. D_2 and D_4 Beasley 1905, A_9 Watson 1909, *R. membranipes* Maidwell, 1911, D_8 Maidwell 1914.

Distribution: Lower Triassic, Keuper Sandstone - Weston and Daresbury of Runcorn, Chesire and Shrewley, Warwichshire. Figg. 28 (1-4).

Ichnospecies: **Rhynchosauroides tirolicus**
Abel, 1926

1926, *Rhynchosauroides tirolicus* n. sp. Abel, fig. p. 23
1935, *Rhynchosauroides tirolicus* Abel, 1926, Abel, p. 124
1963, *Rhynchosauroides tirolicus* Abel, 1926, Kuhn, p. 62
1971, *Rhynchosauroides tirolicus* Abel, 1926, Haubold a, p. 437
1971, *Rhynchosauroides tirolicus* Abel, 1926, Haubold b, p. 46
1973, *Rhynchosauroides tirolicus* Abel, Brandner, fig. 3, tab.1.1
1984, *Rhynchosauroides tirolicus* Abel, Haubold, fig. 98
1998, *Rhynchosauroides tirolicus* Abel, Avanzini & Neri, fig. 5
1999, *Rhynchosauroides tirolicus* Abel, Avanzini, fig. 1
2000, *Rhynchosauroides tirolicus* Abel, Conti et al., fig. 11.20, 11.24

Holotype: slab with three incomplete trackways represented by a manus-pes pair University of Wien.

Type Locality: Lapadures, Flatschkofel-Col Valacia, Braies Dolomites (Bz)

Stratigraphical position: Upper Voltago Conglomerate, Richthofen Conglomerate and Morbiac Dark Limestone, Anisian (late Pelsonian - Illyrian).

Derivatio nominis: from Südtirol, the geographical region of origin.

Diagnosis: tracks attributable to a medium sized *Rhynchosauroides* (L pes 45-60 mm, L manus 25-50 mm). Digitigrade pes with characteristic relationships of lengths of slender digits IV>III>II>I. Digit I and V are rarely impressed.

Print of the very asymmetric and semiplantigrade manus (L/W=1.25) about half the length of that of the foot. The divergence of manus digits group I-IV varies from 34° at 90° with an average of about 60° Digit IV≅III>II>I>V.

Accentuated overstep with a pace angle of the pes of 85° with a positive rotation (outward) in respect to the midline (12°). Manus stride angle 125°. Negative divergence (inward rotation) in respect to the midline (25°). Traces of the tail are frequently preserved.

Description.

Manus: semiplantigrade and very asymmetric overall, with a length between 25 and 50 mm. The length to width ratio (L/W), in the examples studied, is constant and equal to about 1.25. The divergence of digits group I-IV varies from 34° at 90° with an average of about 60° (Tab. 1, Fig. 1). The morphology of the tracks however, varies depending on the substrate and the gait. In some cases a harder substrate and a faster gait has meant that

			PPI/1	BzPP1	BzULF40	BzULF37	BzULFIWI/1	BzBGII/1	BzBGII/2	BzBGII/3	BzBGII/4	BzBG15a	MTSNTnMO1/1	MTSNTnMO1/2	OG/VC 76
Manus	Lenght		26	24	23		35	25	29	36		50			25
	Width		20	20	22		30	19	23	30		36			21
	Digit lenght	I	7	7	7,3		10			10		10			5
		II	9	9	10		15	10	10	15		15			8
		III	12	12	13		20	14	17	21		30			16
		IV	15	15	16		20	15	18	22		32			18
		V	9	10	10		15	8		12		20			8
	divarication of digits	I-II	35°	30°	30°		25°	10°	10°	7°		12°			18°
		II-III	21°	27°	22°		40°	10°	25°	25°		20°			36°
		III-IV	20°	10°	30°		27°	16°	27°	16°		19°			26°
		IV-V	41°	50°	40°		61°	65°	75°°	85°		65°			65°
		I-IV	80°	65°	79°		90°	34°	67°	47°		52°			80°
		I-V	120°	117°	120°		127°	97°	141°	131°		116°			150°
	cross axis		58°	50°	64°		56°	55°	70°	60°		56°			66°
	palm lengt			10	10		16	13		17		20			
	palm width			9	11		15			15		18			
Pes	Lenght		43	43											45
	Width		21	21											24
	Digit lenght	I	4	5	10	8					12	7	10	10	5
		II	12	13	16	12				15	22	20	18	20	11
		III	23	20	15	18				20	30	30	24	22	16
		IV	29	26	22	25				30	35	38	23		25
		V		3											4
	divarication of digits	I-II	32°	38°	20°	10°					18°	20°	20°	10°	19°
		II-III	10°	10°	7°	10°				5°	12°	5°	7°	5°	18°
		III-IV	12°	7°	5°	12°				8°	7°	4°	5°		14°
		IV-V	50°	41°											105°
		I-IV	58°	52°	22°	32°					36°	26°	30°		50°
		I-V	95°	97°											154°
	cross axis		59°	55°	50°	80°						52°?	65°		50°
	palm lengt														
	palm width														

Tab. 1 - Data of the footprints. Measurements in mm and degrees.

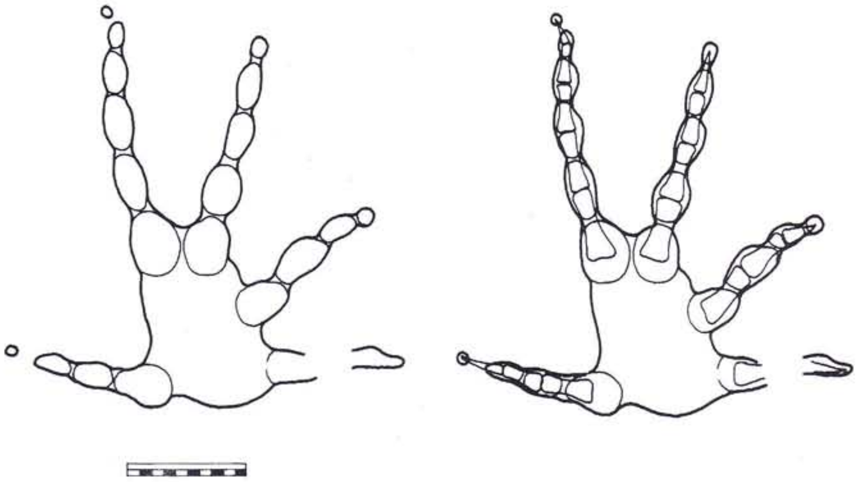

Fig. 2 - Manus print BzULFIWI/1 (Bozen - Unsere Liebe Frau Im Walde - Pelsonian) with phalangeal pads and skeletal phalanges restored. Scale equals 1 cm.

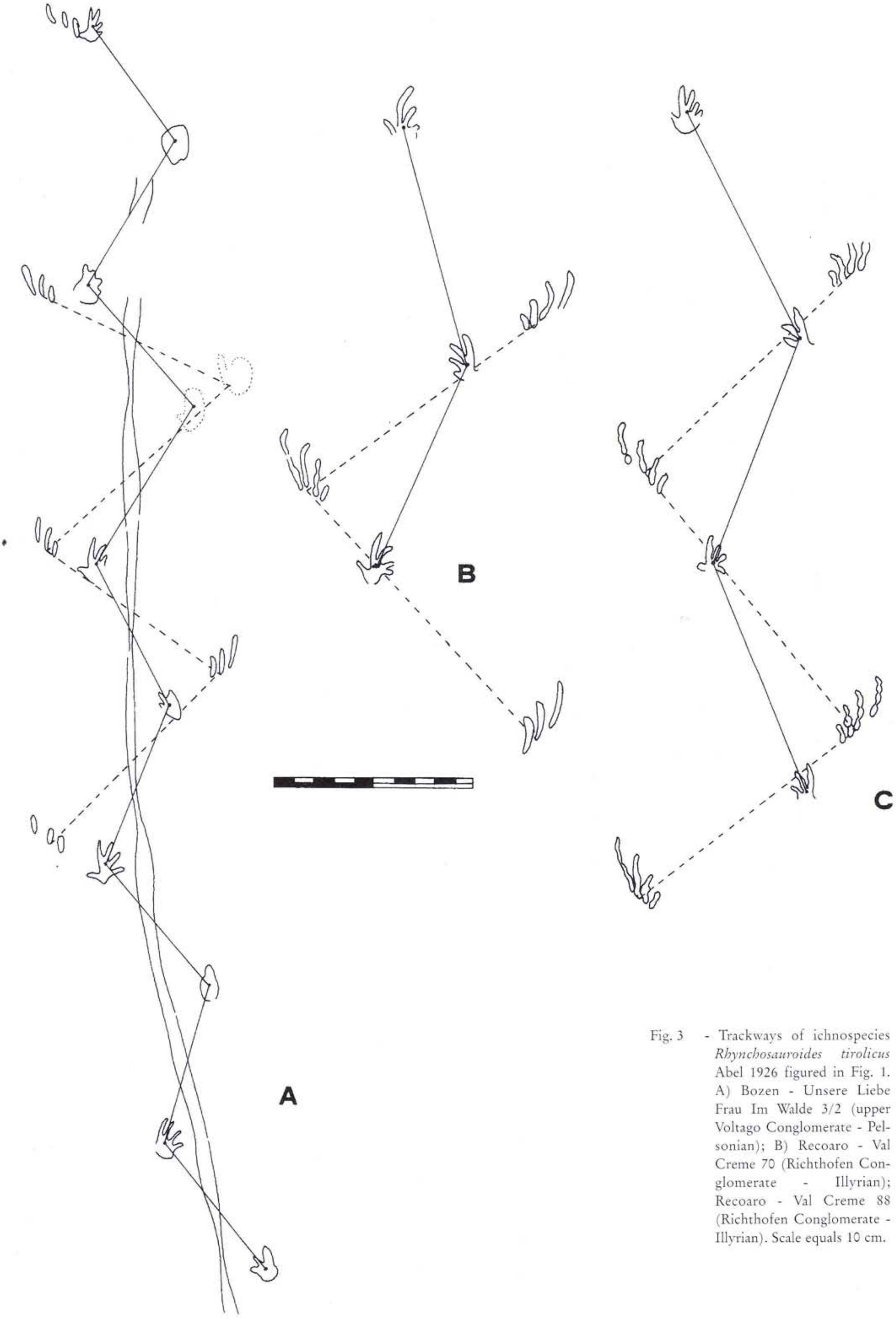

Fig. 3 - Trackways of ichnospecies *Rhynchosauroides tirolicus* Abel 1926 figured in Fig. 1. A) Bozen - Unsere Liebe Frau Im Walde 3/2 (upper Voltago Conglomerate - Pelsonian); B) Recoaro - Val Creme 70 (Richthofen Conglomerate - Illyrian); Recoaro - Val Creme 88 (Richthofen Conglomerate - Illyrian). Scale equals 10 cm.

digit V of the manus is rotated 65° outwards in respect to digit IV, demonstrating good mobility of the carpus. In the manus the greater and almost equal length of digits IV and III is evident, which shows metatarsus-phalangeal articulation that is almost aligned and more distal in respect to digits I-II.

The phalangeal formula, calculated by counting the phalangeal pads, is 2, 3, 4, 5, 3 (Fig. 2). The manus palm is covered by angular scales outlined by crossing rows oriented at 45° with respect to the axis of the manus. Similar scales also continue on the first phalanges of the digits, in irregular rows crossing obliquely, thus forming a checkerboard-like pattern.

Pes: shows a digitigrade tendency that is more marked in respect to the manus and generally only digits II, III, and IV are impressed, leaving traces of the last phalanges or even only the claws. The dimensions vary between 45 and ~70 mm (Tab. 1, Fig. 1). In contrast with the manus, the feet only show digit IV as much larger than III and the metatarsus-phalangeal articulation are aligned, showing metatarsus with decreasing lengths from IV to I.

The digits of the pes show a covering of wide rectangular scales with an axis of elongation perpendicular to the axis of the digit. To the side of these, two lines of small scales with raised margins are recognisable. This epidermal configuration closely resembles that found in the digits of the *Rotodactylus mckey Peabody*, 1948 (recte *Rhynchosauroides mckey*) and in many of today's lepidosauromorphs (Avanzini 2000).

			BzBGII/5	**BzULF3/2**	**OG/VC 88**	**OG/VC 70**	**OG/VC 72**
Stride		manus	290	156	253	250	273
		pes	280	156	255	236	
Pace (oblique)		manus	165	93	137	125	145
		pes	195	129	156	176	
distance manus-pes			30	14	37	37	
width of pace		manus	76	40	57	46	60
		pes	140	98	125	125	
trackway width		internal	55	29	40	22	35
		external	165	127	148	158	
intermanus distance			55	29	40	22	35
interpedes distance			120	77	98	101	
pace angulation		manus	122°	123°	125°	136°	
		pes	87°	80°	88°	83°	
divarication from midline		manus	-25°	-28°	-26°	-24°	
		pes	+10°	+10°	+13°	+15°	
gleno-acetabular distance			115	82	85	95	
Manus	Lenght		30	25	23	28	31
	Width		24	20	18	22	22
	Digit lenght	I	8	7	6	7	9
		II	13	9	8	10	13
		III	16	11	11	15	16
		IV	17	12	15	20	18
		V		8		10	7
	divarication of digits	I-II	24°	26°	27°	12°	20°
		II-III	9°	22°	38°	27°	20°
		III-IV	12°	28°	17°	28°	16°
		IV-V		66°	50°	47°	65°
		I-IV	45°	75°	85°	67°	55°
		I-V		142°	133°	112°	120°
	cross axis		63°	70°	60°	54°	65°
	palm lengt			13	13	12	13
	palm width			10	12	10	10
Pes	Lenght						
	Width						
	Digit lenght	I	4		10	9	
		II	15	10	15	21	
		III	24	14	24	26	
		IV	25	20	32	35	
		V				5	
	divarication of digits	I-II	? 38°		18°	12°	
		II-III	12°	4°	18°°	20°	
		III-IV	7°	13°	12°	8°	
		IV-V	41°			105°	
		I-IV	52°		48°	40°	
		I-V				145°	
	cross axis		55°	50°	45°	50°	
	palm lengt						
	palm width						

Tab. 2 - Data of the trackways. Measurements in mm and in degrees.

Trackways.

In the examples documented, the prints of the feet always overstep those of the manus and generally the overstep is accentuated. The ratio between the oblique step of the pes and manus is about 1.2. The pes pace angulation varies between 83° e 87° (on average it is 85°), the manus pace angulation varies between 122° e 136° (on average 125°). The divarication angle from midline is relatively constant on the trackways, positive rotation (12°) for the pes, negative rotation (25°) for the manus. The external trackway width varies between 127 and 165 mm. (Tab. 2). The gleno-acetabular distances calculated from the parameters of the trackways (Leonardi 1984) varies between 82 and 115 mm. The gleno-acetabular distances estimated on the basis of the size of single tracks or manus-pes pairs gives acceptable results (even if it is a little less reliable than that measured on trackways), and varies between 75 and 163 mm (Fig. 3).

Impression of the tail.

Traces of the tail are frequently conserved on the trackways in the form of an irregular furrow that widens and narrows at regular intervals.

Evidently the different widths are in relation to the different distances from the surface of the body of the author which caused the tail to touch the substrate in a more or less passive fashion. An attempt at making a correlation between stride and tail track was applied to trackway BzULF3/2. The findings established a close relationship between the geometry of the trackway and the entity of the dragging with an apparent complete cycle of lowering-rising of the body every four steps, that is each double stride. This would seem to be related to a gait with brief regular spurts (Sukanov 1968) that involves a complete undulation of the body both in respect to the axial plane, left-right-left (or viceversa) and the vertical plane (high-low-high) followed by a longer stride (and a consequent rise relative to the tail) which introduces a successive symmetric cycle.

This behaviour would seem to be limited to trackways with low stride angles (slow trackways). These are trackways where the impression of tail furrow is more marked. The fact that the traces left by the tail are less evident in trackways with higher stride angles, suggests that with an increase in speed the tail is raised (Fig. 4).

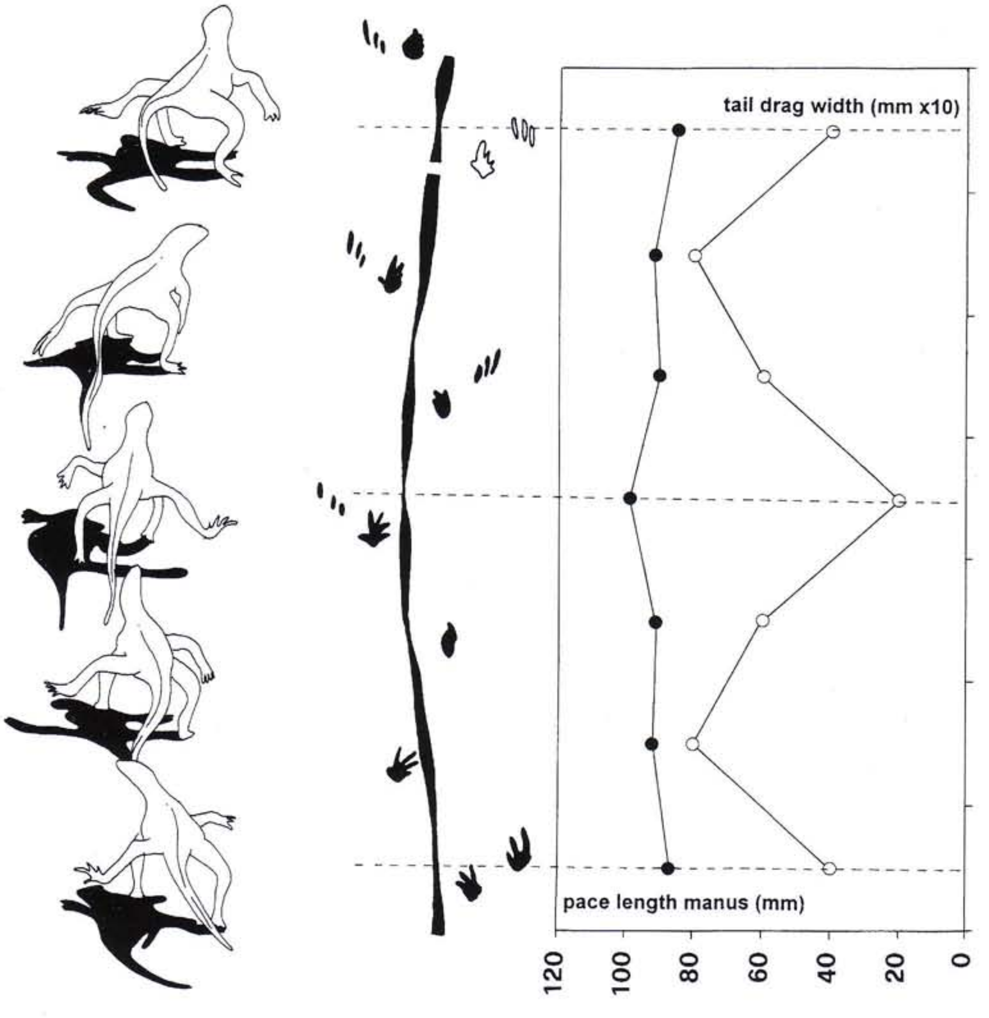

Fig. 4 - Relationships between traces of the tail width and pace length in *Rhynchosauroides tirolicus* BzULF3/2 trackway. The variation of the width of tail drag is function of the distances of the body of the trackmaker from the surface. This seems related to a gait with brief regular spurts.

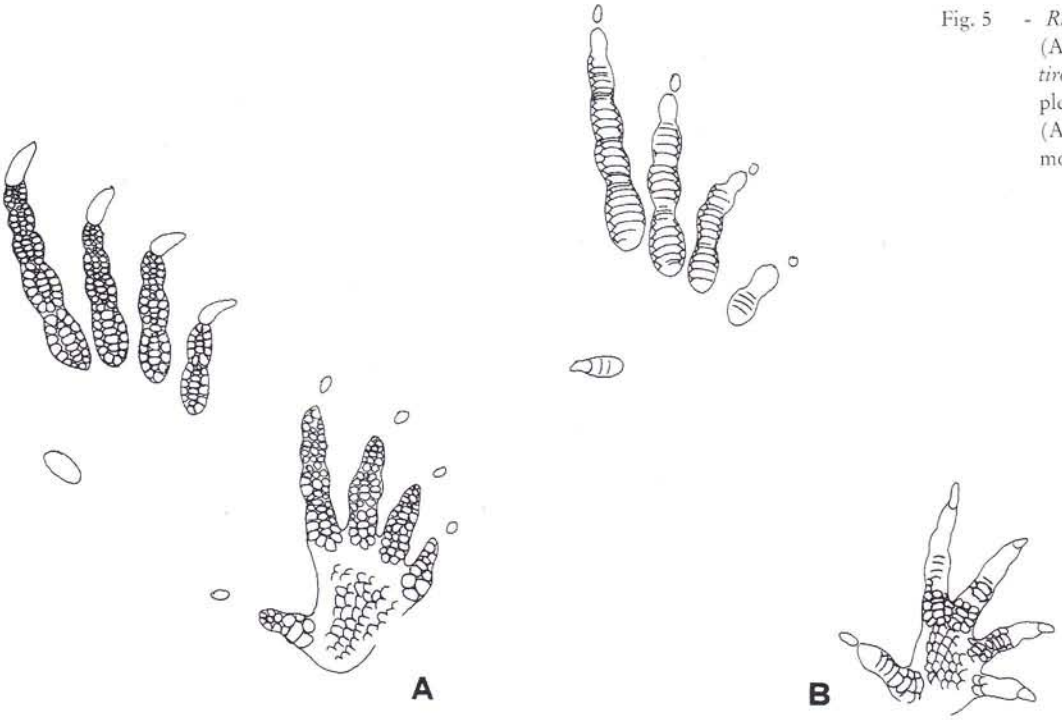

Fig. 5 - *Rhynchosauroides peabodyi* (A) and *Rhynchosauroides tirolicus* (B) manus-pes couple with traces of skin cover (A: from Diedrich, 2000 modified).

Discussion

R. tirolicus may be compared with such large Triassic *Rhynchosauroides* representatives as *R. rectipes* Maidwell, 1911, *R. schocardthi* Rühle von Lilienstern, 1939, *R. peabody*, Faber, 1958, R. hyperbates Baird, 1957, *R. moenkopiensis* Haubold, 1971a, and *R. rdzaneki* Ptaszynski, 2000.

R. tirolicus differ distinctly from *R. hyperbates* Baird, 1957 (from Late Triassic Milford Fm.- New Jersey) in wider divarication of manus and pes digits I-IV and I-V and for outward rotation angle of the manus in respect to the midline of the trackways.

R. schochhardti Rühle von Liliestern, 1939 is a large *Rhynchosauroides* ichnospecies with a pes larger than 60 mm. The species type comes from the Upper Buntsandstein, Turingischer Chirotheriensandstein (Lower Triassic). It is a form that, while it is similar for the dimensional range, would appear to be more robust with a wider I-IV digit group. The divarication of manus and pes digits I-IV and I-V of manus and pes are wider than *R. tirolicus*. Moreover, all four robust digits of the pes end in distinct sharp claws outward rotated, that differs from those of *R. tirolicus*.

R. rdzaneki Ptaszynski, 2000 from the Lower Triassic Labyrinthodontidae Beds (Middle Buntsandstein) of Poland shows a characteristic position of digit V of the pes that is less posterior and more lateral in relation to I-IV group than in *R. peabody, R. hyperbates* and *R. tirolicus.* The other pes digits, slender and with a comparable divarication angle (40°), ends in curved claws. The manus I-IV angle is smaller than in *R. tirolicus* and digit IV is the longest while in *R. tirolicus* manus the digits IV and III are almost equal in length.

R. tirolicus, is relatively comparable with *R. moenkopiensis* Haubold, 1971 and *R. peabody* Faber, 1958, with regards the parameters relative to digits angle I-IV (manus and pes). Although it is known that the inter-digital angle may vary depending on the substrate, the presence in both forms of a similar manus morphology, a similar divarication (I-IV) angle and an accentuated divergence of digits IV-V appears peculiar. *R. moenkopiensis* Haubold, 1970 from the Middle Triassic (Anisian) Upper Moenkopi Formation, has a plantigrade manus inward rotated (25°) similar to *R. tirolicus*, but the pes is shorter with digits I-IV similar those of *R. schochardti.* The only form which there exists strictly resemblance is *R. peabodyi* Faber, 1958, of Central Europe recently attributed to the Middle and Upper Anisian (Bythinian-Illyrian) (Diedrich, 2000). *R. peabodyi* has a more robust but analogous structure, with manus and pes very similar to *R. tirolicus.* The manus is plantigrade or semiplantigrade with a divergence of the I-IV digits group of 60°. The pes is digitigrade, the V digit when visible, is placed posterior of digit group I-IV and the divarication of digits I-IV is 30°. In both ichnospecies the digits of the manus and pes are relatively long and thin, with a manus inward oriented and a pes outward oriented in respect to the trackways midline. The similarity is so marked that *R. tirolicus* could maybe the older synonym of *R. peabodyi.* Only the excellent state of conservation of the skin cover on several specimens of *R. tirolicus* and *R. peabodyi*, evidences the possible diversity of the two ichnospecies (Demathieu & Oosterink 1983; 1988; Diedrich 1998a; 1998b). In *R. tirolicus* pedal print, the digits are covered by rectangular scales that are laterally bordered by two small quadrangular scales (fringe scales), while in *R. peabodyi*, the digits are covered entirely by a mosaic of small scales that are close together (Demathieu & Oosterink 1983 fig. 23 and 29; Diedrich 2000 fig. 3) (Fig. 5). Comparison with other ichnospecies of this group do not give rise to any substantial morphological conformity (Haubold 1971a, 1971b, 1984).

Functional behaviour of *Rhynchosauroides tirolicus* trackmaker.

In the most complete trackways found to date in various areas of the Southern Alps, the pace angulation is relatively constant. In general terms, within the same ichnospecies, higher pace angulation (or longer stride) correspond to faster gaits, while lower pace angulation (or shorter stride) correspond to slower gaits. The variability found in the pes stride and pace angulation in our sample is very low (5° between the maximum and minimum) and it can be stated that all the specimens examined move with very little speed differences between them. However, even with such a low variability several small modifications in the characteristics of the trackways are visible. The outward rotation angle of the manus and pes in respect to the mid-line of the trackway (often evidenced by the furrow left by the dragging tail), increases slightly with the increase in the stride angle (and therefore the speed).

The trackways, also when they are incomplete or partial, with low pace angles (slow gait), show well impressed manus and very digitgrade pes.

Trackways with slightly higher angles (faster gait) still have digitigrade pes but with more clearly impressed digits, with digit V being recognisable amongst them, which is always represented only by the claws ending. In these trackways the manus seem to be less impressed and tend to be semiplantigrade (something that is also common in isolated tracks).

Another variable element is represented by the entity of the overstep. The higher is the angle of the pace (speed) the higher appears the overstep.

These features seem to suggest several implications on the deambulation modality of the trackmakers:

- Passage from a sprawling attitude to a less sprawling attitude with the increase in velocity (the pace angle increases and the trackway narrows)
- Increasing of outward rotation of the manus and pes with the increase in velocity (even if the manus always remain turned towards the inside of the trackway and the pes towards the outside).
- During slow walking more of the body weight is carried on the front limbs, which are plantigrade or semiplantigrade. The rear limbs are digitigrade with digit V being rarely impressed and less angled in respect to IV (≅ 50°).
- During fast walking body weight is equally balanced between the front and rear limbs. Therefore there is a movement of the load onto the rear limbs in respect to previous point. The pes are still digitigrade but more marked. Digit V, when present, is much more angled in respect to IV and almost turned backwards towards group I-IV (>100°).
- Pes overstep is higher with the increase in gait.

These observations would seem to indicate that with the increase in speed the stride of the rear limbs progressively lengthens in respect to that of the manus (overstep) and that the body weight of the trackmaker is progressively removed from these latter.

A tentative palaeontological attribution of Middle Triassic Rhynchosauroides trackmaker.

The ichnogenus *Rhynchosauroides* was erected by Maidwell (1911) on the basis of ichnites found in association with skeletal remains of rhynchosaurs. Presently, however, there is no consensus regarding the attribution of these tracks to rhynchosaurs and the possibility that the trackmaker may have been a lepidosauromorph reptile has been suggested by Lockley & Hunt (1995).

The structure of rhynchosaurs pes (e. g. *Noteosuchus* Watson 1912) is rather primitive and therefore not too different from that of some lepidosauromorphs or of other basal archosauromorphs (Benton 1985; Carroll 1988). In all cases the pes is functionally pentadactyl and plantigrade, the length of the toes gradually increases till the fourth which is the longest one, while the fifth toe is somewhat longer than the first one and divergent with respect to the other toes.

The rhynchosaur manus is less known and it is sometimes reconstructed with a fourth digit that is longer than the third (Woodward 1907, Benton 1990). There is some variability however, since in *Rhynchosaurus articeps* the fourth digit is longer than the third one (Benton 1990), but in *Hyperodapedon* (Benton 1983) even if the phalangeal formula is 2, 3, 4, 5, 3, the fourth digit is shorter than the third one and the manus appears more symmetrical (Parrish 1986). On the basis of the more symmetrical outline of the *Hyperodapedon* manus, Parrish (1986) suggests that this genus is a better candidate as a trackmaker for *Apatopus lineatus*.

It has to be pointed out, however, that the ichnogenus *Rhyncosauroides* shows wide chronological occurrence that extends for most of the Permian and Mesozoic. This may suggest that probably the different ichnospecies attributed to *Rhynchosauroides* could have been made by different trackmakers.

The good preservation of the materials described here permits the affirmation, with some confidence, that the morphology of *Rhynchosauroides tirolicus* and other Middle Triassic *Rhynchosauroides* (i.e. *R. peabody*) better matches the structure of prolacertiform reptiles like *Macrocnemus bassanii* Nopcsa, 1931.

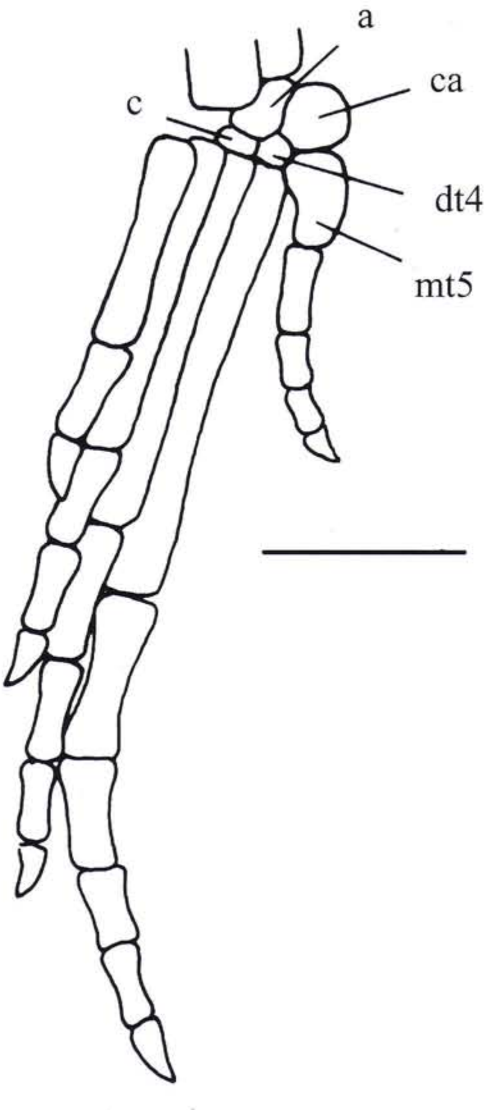

Fig. 6 - Right tarsus and pes of *Macrocnemus bassanii*, specimen BES SC 11 (Renesto & Avanzini in press). Abbreviations: a) astragalus; c) centrale; ca) calcaneum; dt 4) distal tarsal four; mt5) fifth metatarsal. Scale bar equals 0.5 cm.

Macrocnemus bassanii Nopcsa, 1931

Macrocnemus is a small to medium sized prolacertiform reptile known from lagoon deposits at the Anisian/Ladinian boundary in the Southern Alps. In *Macrocnemus*, the phalangeal formula is also primitive (2, 3, 4, 5, 3) and the length of the metacarpals increases gradually from the first to the third one, while in the

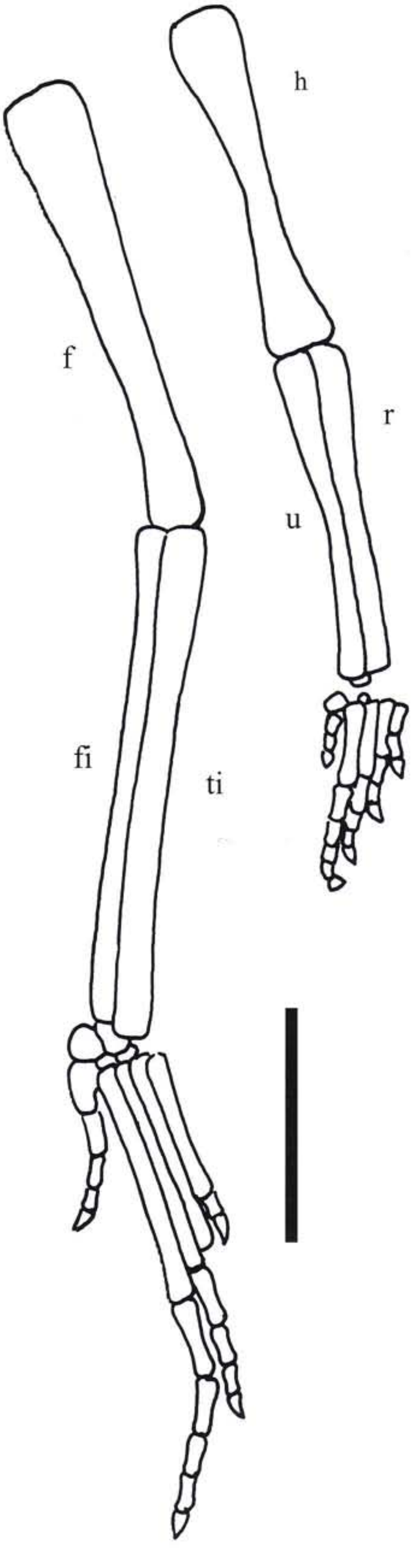

Fig. 7 - Comparison between anterior and posterior limbs in *Macrocnemus bassanii* specimen BES SC 11. Abbreviations f) femur; fi) fibula; h) humerus; r) radius; ti) tibia, u) ulna. Scale bar equals 1 cm.

fourth the increase is more pronounced, the bone being approximately three times longer than the first, while the fifth metacarpal is much shorter (Peyer 1937, Kuhn-Schnyder 1962; Rieppel 1989, Renesto & Avanzini, in press).

It must be noted, however, that the increase of the length from the first to the third metacarpals approximately follows the same ratio, while the difference in length between the third and fourth metacarpals is approximately an half that ratio (Fig. 6). As a consequence there is a variation of the hinge line linking the metacarpal-phalangeal articulation, in correspondence to the third and fourth digits.

The posterior limbs of *Macrocnem*us were held in a sprawling posture as testified by the shape of the pelvis and of the proximal end of the femur (Peyer 1937; Rieppel 1989; Renesto & Avanzini in press). The distal articular surface of the femur is a distinctly trochlea, with well developed articular surface, suggesting good possibilities of flexion between the femur and the tibia (Fig. 7). The number of tarsal elements varies in relation to growth and ranges from four to six (Rieppel 1989). However, the tarsal elements are always closely associated forming a compact functional unit (Rieppel 1989). The first four metatarsals are very elongated and tightly compacted, while the fifth metatarsal is short and hooked (fig. 6). The phalangeal formula for the pes is (2, 3, 4, 5, 4). Peyer (1937) gave an overall estimate length of 35-86 cm implying the existence of specimens of larger size. According to Rieppel (1989) larger specimens of *Macrocnemus* might have reached 1 m in (overall) length. The hypothetical size of the *R. tirolicus* trackmaker should range within 34.5 - 75 cm overall length if extrapolated from *Macrocnemus* overall morphology. Thus the *R. tirolicus* trackmaker size matches only that of smaller and medium sized *Macrocnemus*. This does not contradict our hypothesis, however, since large specimens are much rarer and their true size is also an estimation, because no large complete specimens are known.

Macrocnemus has been considered a terrestrial reptile (Peyer, 1937, Rieppel, 1989, Renesto & Avanzini, in press) and the great length disparity between the anterior and posterior limbs (Fig. 7-8), along with the morphology of the tarsus, has been considered as indicative of a bipedal gait for *Macrocnemus* during running (Rieppel 1989), like the modern lizards *Chlamydosaurus* (Shine & Lambeck 1989), *Basiliscus* (e. g. Snyder, 1962) and *Tupinambis* (Leonardi, 1975). During slow walking *Macrocnems* should have assumed an obligatory quadrupedal gait.

A comparison between *Macrocnemus* and *Rhynchosauroides* has already been considered (Demathieu, 1970; Demathieu & Haubold 1974) without however leading to a definite conclusion. This may be explained by the fact that *Rhynchosauroides petri* was taken as the

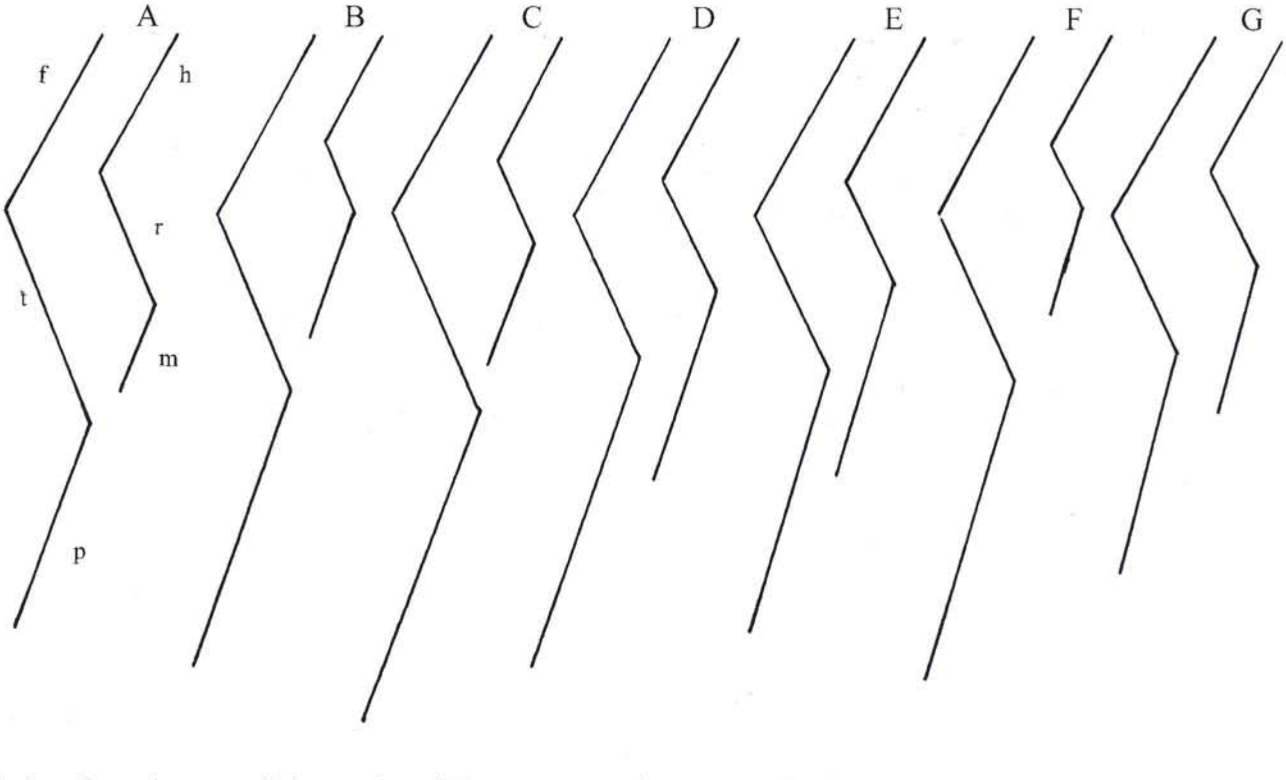

Fig. 8 - Comparison among limb proportions of *Macrocnemus* (A) and representative bipedal (B, C, F) and quadrupedal (D, E, G) lizards. B= *Basiliscus*; C= *Crotaphytus*; D=*Iguana*; E= *Scelophorus* F= *Amphibolurus*, G= *Agama* (B-G redrawn from Snyder 1962). Femora have been reported to same length. Other abbreviations are f) femur; h) humerus; t) lower leg; r) antebrachium; p)tarsus and pes; m) carpus and manus.

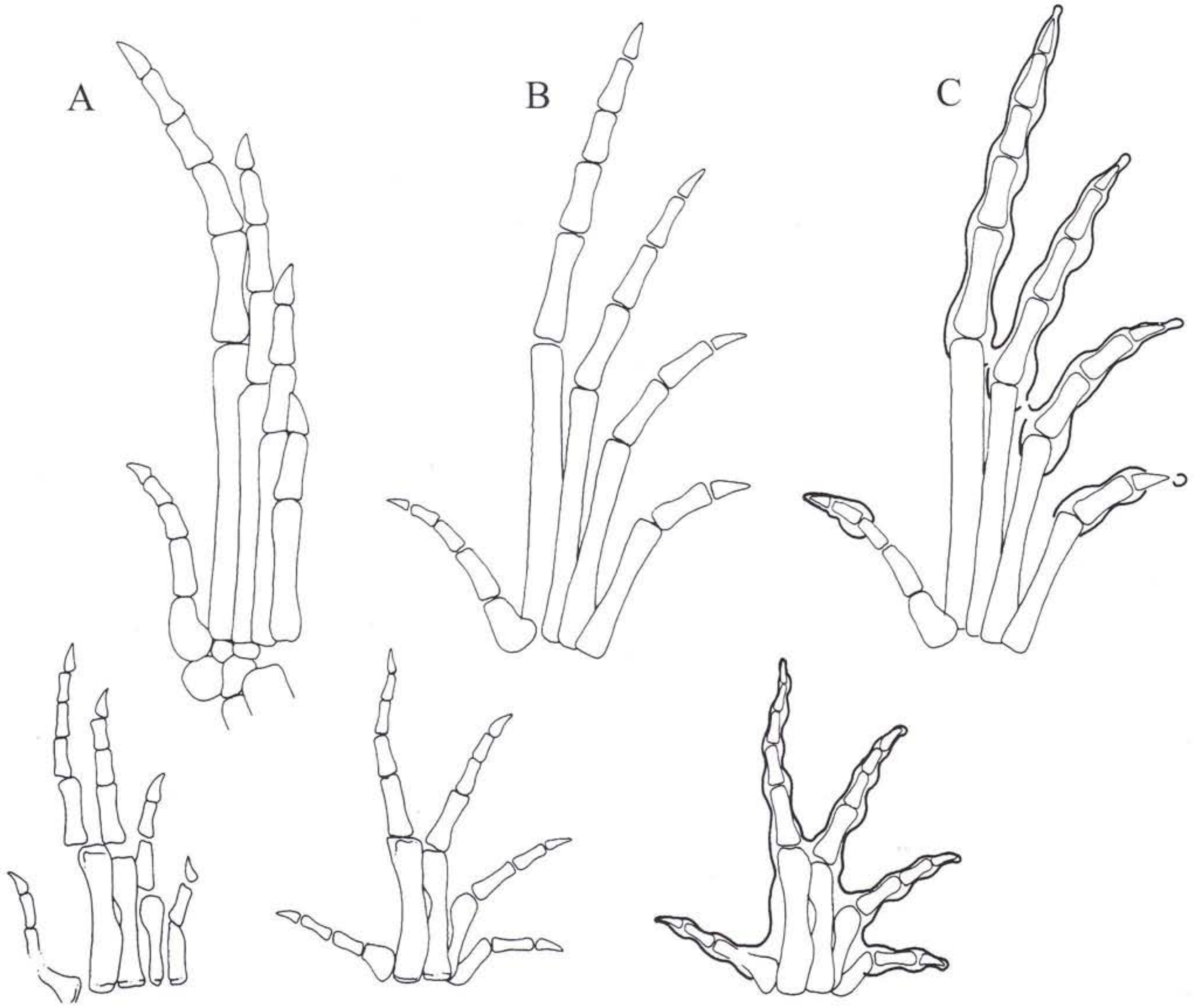

Fig. 9 - Manus and pes of *Macrocnemus bassanii* specimen BES SC 11 as preserved (A), recostructed in flat view as semiplantigrade (manus) and digitigrade (pes) configuration (B) and the same reconstructions superimposed to *Rhychosauroides tirolicus* ichnites (C)

most suitable ichnospecies for the comparison, despite the existence of several elements of incompatibility, the most important one being the different size and outline of the manus. Other Middle Triassic *Rhynchosauroides* tracks show a different manus and pes morphology. In a recent discovery of *R. hyperbates* specimens at the Newark basin, walking and swimming trackways as well as resting belly impressions are present, all with remarkably detailed skin impressions (Silvestri & Olsen 1988). Cladistic analysis of the reconstruction shows that the trackmaker had feet of the primitive diapsid pattern. Consideration of the range of diapsids known from the Triassic suggests that a sphenodontid was the most likely trackmaker.

The manus of *Rhynchosauroides tirolicus* shows instead a substantial affinity with the skeletal structure of *Macrocnemus* while the pes, being digitigrade, renders the comparison somewhat more difficult, even if the size ratios match very well. The main difference between *Macrocnemus* and *Rhyncosauroides tirolicus* trackmakers seem to be the different freedom of movement and degree of divergence between the digits and between the toes, while the metacarpals and metatarsals of *Macronemus* have been always preserved closely associated. This difference is present however only if the manus and the pes are reconstructed as fully plantigrade. If the manus of *Macrocnemus* is reconstructed as semiplantigrade, it matches perfectly the manus of *Rhynchosauroides tirolicus* and can be, for instance, fully superimposed with print BzULFIWI/1 (Fig. 9). Also the pes of *Macrocnemus* when reconstructed as functionally digitigrade reveals great similarity with the traces of the pedes ascribed to *R. tirolicus* (Fig. 9-10). In addition these reconstructions match the continuity of the interphalangeal hinge lines (Peters 2000a and following section) which are interrupted if the pes is reconstructed follow-

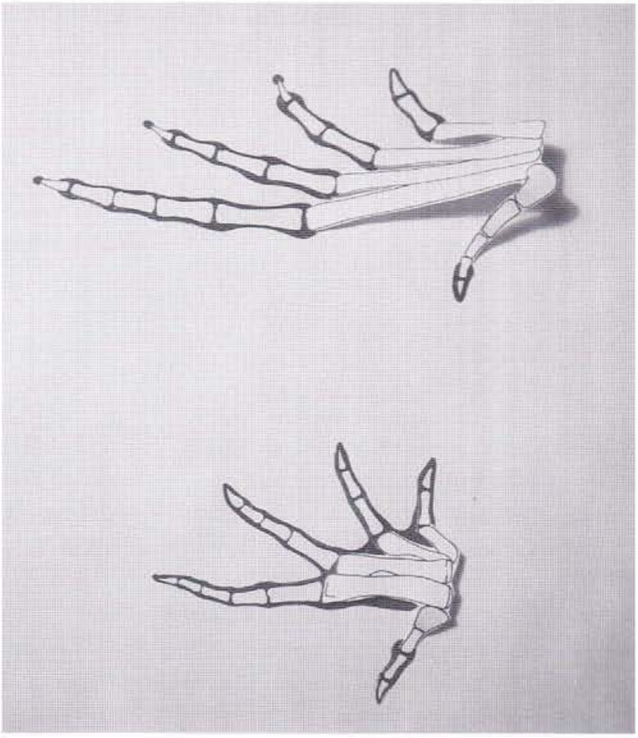

Fig. 10 - Models of *Macrocnemus* manus (below) and pes (above) reconstructed as semiplandigrade and digitigrade in three dimensional view matching well the traces ascribed to *Rhynchosauroides tirolicus*.

ing Rieppel (1989). A similar configuration is also consistent with *Rhynchosauroides peabody*, Faber 1958.

Skeletal correlates supporting a digitigrade configuration in the pes of Macrocnemus.

In 1930 Nopcsa reconstructed the Middle Triassic prolacertiform *Macrocnemus* as a biped, with a parasagittal gait and digitigrade stance. Rieppel (1989) criticized Nopcsa's reconstruction because *Macrocnemus* does not show any modification in the pelvis and posterior limbs which is shared by vertebrates that adopt a fully parasagittal gait, e. g., a femur with an in turned proximal head and a symmetrical metatarsus. Rieppel (1989) suggested that *Macrocnemus* was a facultative biped as many extant lizards in which only minor modifications are present.

In the previous section it was suggested that *Rhyncosauroides tirolicus* may match the skeletal configuration of a *Macrocnemus*-like prolacertiform, if this latter is reconstructed with a not fully plantigrade manus and pes, but rather with a semi-plantigrade manus and a digitigrade pes.

The low number of ossified carpal elements in *Macrocnemus* (Peyer 1937, Rieppel 1989) along with the general structure previously described suggest that little weight was placed on the forelimb and probably a fully plantigrade stance for the manus was not required.

In order to understand how a digitigrade configuration in the pes of *Macrocnemus* is more than plausible, the entire structure of the posterior limb must be taken into consideration.

Macrocnemus shares many features with extant facultative bipedal lizards like the presence of an anterior process of the ilium (Snyder 1954) and size related characteristics, mainly great disproportion between the short anterior limbs and the much longer posterior ones. Fieler and Jayne (1998). Irschick and Jayne (1999) note that a bipedal gait during high speed running is achieved in certain lizards simply because the elongate posterior limbs outrun the shorter anterior ones even at sustained quadrupedal locomotion. Such a model may be applied to *Macrocnemus* (Rieppel 1989).

The long, narrow, and hollow femur has a slightly expanded proximal head and a distal trochlea. The twin condyles of the tibia and the fibula are well developed and lie on the same axis, as they do in birds and pterosaurs. The crus is slightly longer than the femur. The straight and slender tibia and fibula are separated only by a very small spatium interosseum. The small and compact tarsus consists of four to six elements depending on the growth stage (Rieppel 1989): a large rounded calcaneum contacts medially a much smaller L shaped astragalus; this latter meets laterodistally a wide centrale and distally a fourth distal tarsal. A number of much smaller distal tarsal are present distal to the astragalus, the centrale and lateral to the fourth distal tarsal. The first four metatarsals are very long and narrow rods, slightly more expanded at their proximal end than at their distal one. Their length increases laterally. In all specimens the metatarsals are closely associated and their proximal heads are slightly superimposed on each other. The fifth metatarsal is much shorter and it is hooked. The phalangeal formula is 2, 3, 4, 5, 3. The length of the phalanges decreases distally and the ungual is small and triangular. Among extant reptiles each segment of the posterior limb of *Macrocnemus* is comparable to those of extant bipedal iguanids tabulated by Snyder (1954) (Fig. 8). Longer distal segments, such as the elongate metatarsus of *Macrocnemus*, serve to increase hip height, stride length and speed (Irschick & Jayne 1999). It has to be pointed out that, as for these lizards, the elongation of the pes in *Macrocnemus* is useful only if it is digitigrade, in fact, the mass of the distal part of the limb has a great influence in locomotor performances, because a heavier foot implies that a greater force is required for recovery during a stride if the animal is plantigrade and the limb does not operate in a fore and aft footfall. In a digitigrade configuration however, a further segment is added to the limb, enhancing speed and thrust.

The proximal head of the femur in *Macrocnemus* strongly suggests that the femora were sprawling in this

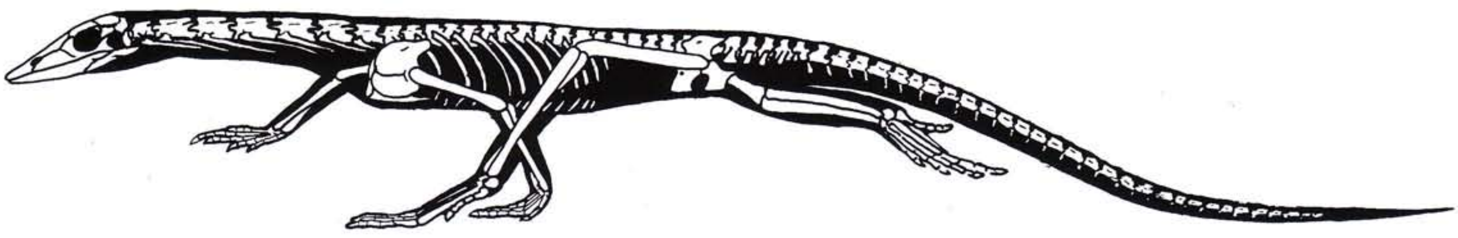

Fig. 11 - Walking *Macrocnemus*, a possible trackmaker for *Rhynchosauroides tirolicus*?

taxon. However, the distal articular area is hinge-like with well developed symmetrical condyles for the tibia and the fibula in contrast with typical sprawlers.

In *Macrocnemus* like most other prolacertiforms (Peters 2000b) interphalangeal hinge lines appear *only* during a *digitigrade* configuration. Interpahalangeal line analysis (Peters, 2000a) indicates that in *Macrocnemus* the strongest set of lines is the medial set that parallels the metatarsophalangeal articulations. Extension (= dorsoflexion) of the toes would be perpendicular to these lines as they are in lizards during slow locomotion and the third and fourth (also the third - only the second would be parallel to the direction of travel) toe would remain obliquely (outward) oriented to the direction of locomotion. A second set of interphalangeal lines, the transverse set, involves just digits III and IV distally. A shift in these lines would occur during rapid locomotion, as it does in extant lizards (Irschick & Jayne 1999), when the axial rotation of the pelvis changes the orientation of the footfall to one in which digit IV is reoriented to the direction of locomotion.

Interpretation of stepping cycle of *Rhynchosauroides tirolicus* and comparison with *Macrocnemus*-like prolacertiform

The different configuration of manus and pes tracks depending on speed, as proposed in the previous section, is consistent with the morphology of a *Macrocnemus*-like prolacertiform.

At a slow walk the body was held parallel to the ground and the outrun by the posterior limb was moderate and the prints of the hands were deeper, this was due also to the presence of the long and stiff neck that probably shifted anteriorly to the centre of mass, placing more weight on the forelimbs than during faster locomotion (Fig. 11). Conversely the digitigrade configuration of the pedes kept the fifth toe off the substrate. In some extant lizards, such as *Dypsosaurus dorsalis*, with increased speed the erectness of the femur increases (Fieler & Jayne 1998), but the width of the strides increases as well and the trunk becomes angled with respect to the substrate leading to clearance of the forelimb from the contact with the ground when the bipedal running phase is reached. Changing the angle of the trunk with respect to the substrate also shifts the centre of gravity backwards toward the hips. The tail is also raised to an appropriate angle to help balance the body, to avoid interference with the posterior limbs and it also stretches the caudifemoralis muscle, enhancing its effectiveness (Fieler & Jayne 1998). The longer strides and heavier impressions of the second kind of tracks may reflect a slight increase in speed when the trunk and the tail begin to be slightly raised, the weight is shifted back and the fore limbs looses in part their contact with the ground, while the posterior limbs supported more weight and the fifth toe makes contact wit the ground. A further increase in speed may have led to a bipedal stance with the trunk more raised, the fore limbs off the substrate and a different orientation of the pes at foot fall. This latter locomotory pattern, while feasible, however, has not been documented.

Conclusion

The recent finds of a large number of ichnological documentation referable to *Rhynchosauroides* in the upper Anisian of the Southern Alps permitted to better describe the characteristics of the ichnospecies *Rhynchosauroides tirolicus* Abel, 1926.

The comparison between the appendicular skeleton of the prolacertiform *Macrocnemus bassanii* and *Rhynchosauroides* tracks, has pointed out the substantial similarity between the tracks and potential trackmaker suggesting that prolacertiform archosauromorphs similar to *Macrocnemus* could be the trackmaker of ichnites similar to *Rhynchosauroides tirolicus* in the European Middle Triassic lagoons and tidal flats.

*Acknowledgements.*We are grateful to H. Haubold (Halle) and G. Leonardi (Naples) for reviewing the manuscript. Their comments greatly improved the paper. Thanks are due also to P. Mietto (Padova University) for the access to unpublished data on the Recoaro and Braies Dolomites *Rhynchosauroides* footprints and for the useful discussions.

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