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Lacertoid footprints from the Upper Triassic (Santa Maria Formation) of Southern Brazil

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ABSTRACT

The Triassic of Southern Brazil is well-known for its rich tetrapod body fossils. However, trace fossils such as tetrapod trackways and trails were discovered only recently from the Predebon outcrop (upper part of the Alemoa Member, Santa Maria Formation), providing new information on small-sized animals. The trackways can be identified as *Rhynchosauroides retroversipes* isp. nov., *Rhynchosauroides* isp., *Rhynchosauroides?* isp. and drag marks produced by swimming animals of lacertoid affinity. The preservation of the tracks and trackways was influenced by the water level whilst they were being made and subsequent subaerial exposure. The trackmaker of *R. retroversipes* isp. nov. corresponds to a lacertoid quadruped tetrapod with primitive autopodia, a sprawling gait and possibly a long tail, whilst the pes was directed postero-laterally. The trackmaker may have been a climbing animal, with adaptations that include curved claws and reversion of the pes. On the ground this animal would have had a slow, lumbering locomotion, although it could attain higher speeds over short distances using a bipedal gait. These trackways can be attributed to lacertoid reptiles, possibly sphenodontids, whose skeletons are encountered in the Caturrita Formation, which overlies the Santa Maria Formation.

1. Introduction

The Triassic strata of southern Brazil are widely known for their abundant tetrapod body fossils, represented by a large number of skeletons. However, fossil tracks and trackways were discovered only recently. In the Santa Maria Formation, preliminary track identifications have included lacertoid, theromorphoid and dinosauroid footprints (Silva et al., 2005a,b, 2007), although they were only recently described formally. This work deals with the description of the lacertoid trackways of the Santa Maria Formation (Late Triassic, Paraná Basin, Rio Grande do Sul State) and the analysis of conditions that permitted their preservation, as well as the description of morphological, biomechanical and behavioural characters of the trackmakers and their palaeoenvironmental relationships.

The tetrapod palaeofauna of the Triassic of southern Brazil is mainly represented by a variety of large animals including temnospondyls, rhynchosaurs, pseudosuchians, dinosaurs, cynodonts, dicynodonts, together with smaller animals such as procolophonids and sphenodonts (Bonaparte et al., 1999; Langer et al., 1999; Barberena and Dornelles, 2000; Dias and Dias-da-Silva, 2000; Kischlat, 2000; Langer and Lavina, 2000; Langer and Schultz, 2000; Schwanke and Araújo-Barberena, 2000; Ferigolo, 2000). Most of these animals are medium to large in size, except from a few cynodonts, procolophonids and sphenodonts. In contrast, the tracks and trackways described herein were produced by small-sized animals, and their study will therefore be an important contribution to expanding the current knowledge on Santa Maria tetrapod assemblages. The texture of the rock also allowed the preservation of morphological details in the tracks and trackways that are of great value for the identification of the trackmakers and a better understanding of the palaeoenvironmental conditions.

2. Materials and methods

The material consists of 16 rock samples containing tracks and trackways of tetrapods from the Santa Maria Formation. They were collected between 2002 and 2006 by J. Ferigolo and R.C. Silva and are housed in the palaeontological collection of the Museu de Ciências Naturais (MCN), Fundação Zoobotânica de Rio Grande do Sul, Porto Alegre, Rio Grande do Sul State, southern Brazil. This material originates from the lenticular sandstone layers at the Predebon Outcrop, located in the municipality of São João do Polêsine, Rio Grande do Sul (Fig. 1). Expeditions were conducted in collaboration with the CPRM (Companhia de Pesquisa de Recursos Minerais — Geological Survey of Brazil).

The specimens were prepared by mechanical processes under the stereomicroscope. The samples were impregnated with Paraloid solution in acetone to harden and waterproof the rock. Flexible casts

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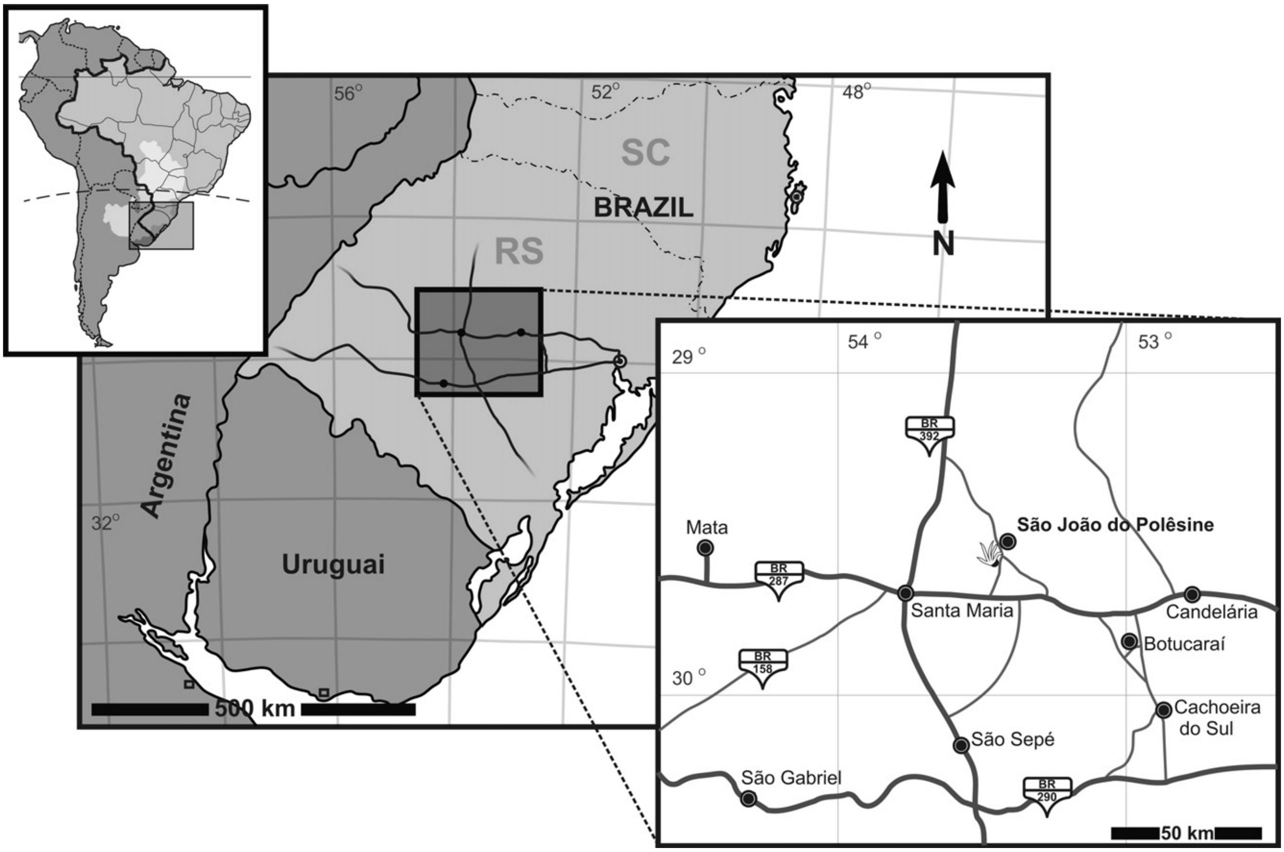

Fig. 1. Location of the Predebon outcrop, Santa Maria Formation (Triassic, Paraná Basin), municipality of São João do Polêsine, Rio Grande do Sul State, Brazil.

in silicone rubber and replicas in epoxy resin of several samples were manufactured following the techniques of Raup and Stanley (1971). The casts are housed in the palaeontological collection of the Instituto de Geociências, Departamento de Geologia, Universidade Federal do Rio de Janeiro. Interpretative drawings were made, using the computer program Corel Draw v. 12, following examination of original specimens, casts in silicone, replicas and photographs. The institutional acronym for the Museu de Ciências Naturais is MCN. PIC denotes the Palaeontology–Ichnology collection. These abbreviations prefix each sample and footprint number.

Trackway parameters were measured using the computer program ImageJ (Abramoff et al., 2004). Parameters of the footprints were not measured due to the presence of drag marks, which made it impossible to establish the true dimensions of the digits. Samples MCN-PIC.001, MCN-PIC.002, MCN-PIC.003 and MCN-PIC.004 were measured, whilst the other trackways were too irregular to yield adequate measurements.

3. Geological setting

The Paraná Basin is a large intracratonic basin and contains sedimentary and igneous rocks that formed between the Late Ordovician and the Early Cretaceous (Milani et al., 1994; Schneider et al., 1974). It is geographically distributed from the central-western region of Brazil southwards to Argentina and Uruguay and westwards to Paraguay, covering about 1,600,000 km^2. The basin overlies the crystalline basement and is one of the world's largest intracratonic basins. Fluvial–aeolian deposits associated with shallow and small lakes developed during the Triassic in the southern part of the basin. An important biocoenosis Triassic was present at this time, and its record is associated with rocks of the Rosário do Sul Group (e.g. Scherer et al., 2000). Following this, the fragmentation of Gondwana caused the elevation of parts of the basin, which produced an erosive stage that continued until the middle of the Jurassic (Milani et al., 1994). The Rosário do Sul Group is divided into the Sanga do Cabral, Santa Maria and Caturrita formations (sensu Andreis et al., 1980), all confined to Rio Grande do Sul State, Brazil (Fig. 2).

The Santa Maria Formation was deposited in a continental fluvial–lacustrine system (Faccini, 1989; Zerfass et al., 2003; Da-Rosa, 2005) and is divided into the Passo das Tropas and Alemoa members (Andreis et al., 1980). The basal Passo das Tropas Member consists of conglomerates and coarse sandstones that were deposited in a braided fluvial system (Faccini, 1989; Zerfass et al., 2003). The upper Alemoa Member is characterized by massive or finely-laminated, reddish, calciferous nodule-rich mudstones, intercalated with siltstones and fine sandstones, levels of calcrete and palaeosols (Faccini, 1989; Zerfass et al., 2003; Da-Rosa, 2005). At the top of this member, the mudstones are intercalated with tabular and lenticular, fine to medium, whitish intraclast-rich sandstones with horizontal laminae and climbing ripples. These deposits are part of the Gondwana II Supersequence, which is temporally located between the Middle and the Late Triassic (Milani, 2002). The ages attributed to the Santa Maria and Caturrita formations are generally based on vertebrate biostratigraphy and are controversial, because the outcrops are discontinuous and few expose more than a few metres of section. According to Scherer et al. (2000) and Rubert and Schultz (2004), the Santa Maria Formation and the Caturrita Formation correspond to the Ladinian–Lower Norian Sequence (Fig. 2). However, Lucas (1998, 2001) and Lucas and Heckert (2002) have considered the upper part of the Alemoa Member and Caturrita Formation as Carnian. According to Langer (2005), the upper part of the Alemoa Member and the base of the Caturrita Formation can be tentatively correlated with the Ischigualasto Formation (Carnian) in Argentina, but some faunal associations of the Caturrita Formation appear to correspond to the

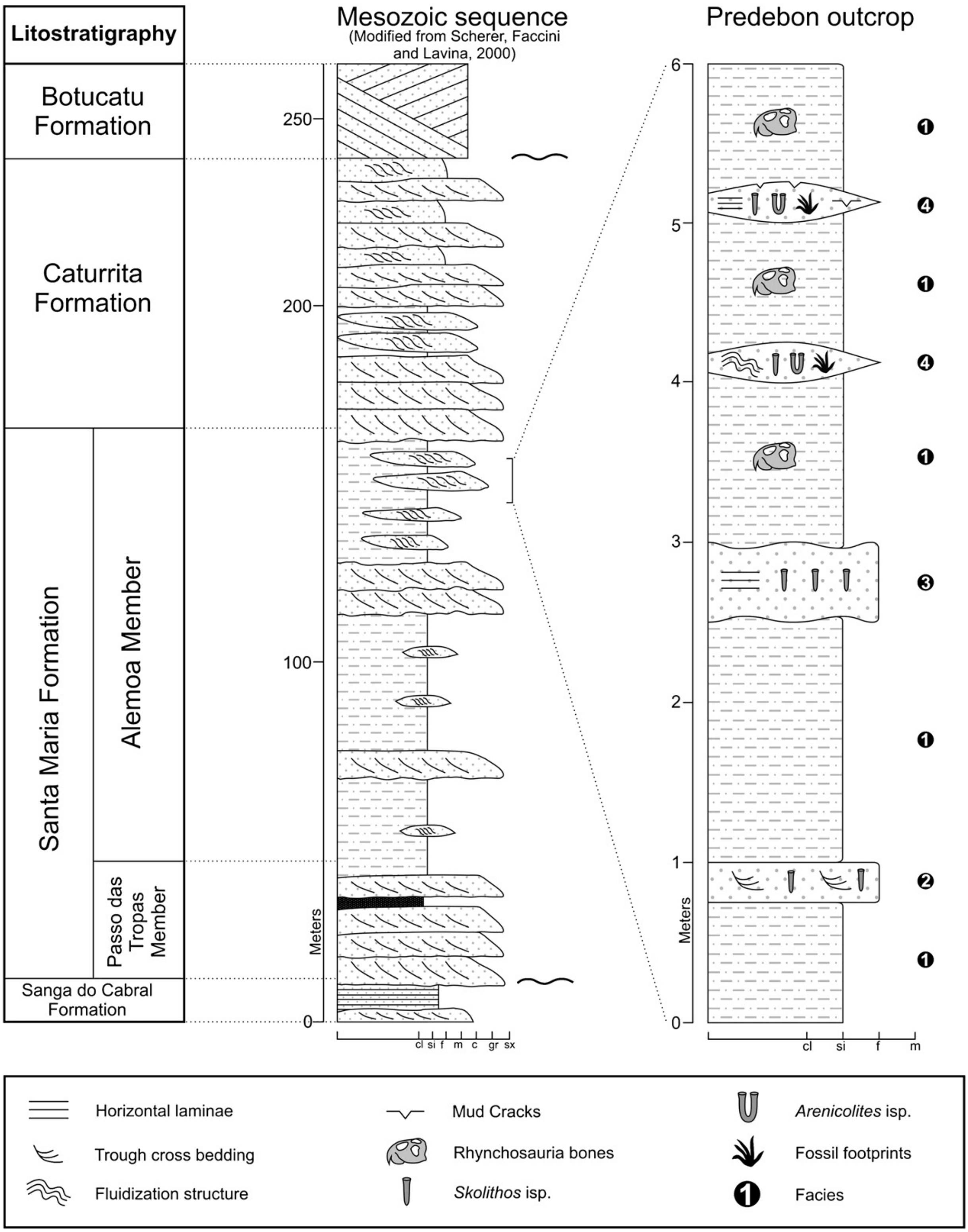

Fig. 2. Compound section of the Rosário do Sul Group (modified from Scherer et al., 2000) and detailed section of Predebon outcrop.

post-Ischigualastian, perhaps Norian. The general consensus is that the upper Alemoa Member corresponds to the Carnian.

3.1. Description of the Predebon outcrop

The Predebon outcrop is approximately 6 m thick and extends for around 100 m (Fig. 3A and B). The studied section corresponds to the upper part of the Alemoa Member of the Santa Maria Formation, and is close to the contact with the Caturrita Formation (Fig. 2). It can be divided into four distinct lithofacies: reddish massive mudstone containing calciferous nodules and fossils of Rhynchosauria (Facies 1); fine reddish or whitish tabular sandstone with small scale cross-bedding, calciferous nodules at the top of the layer and invertebrate trace fossils, mostly *Skolithos* isp. (Facies 2); fine, reddish, tabular, massive sandstone, with horizontal laminae in the upper parts and a high degree of bioturbation, mostly of *Skolithos* isp. (Facies 3); fine

Fig. 3. A) General view of the Predebon outcrop, upper portion of Santa Maria Formation; B) detailed view of the outcrop, showing the distribution of mudstone and sandstone facies.

reddish to orange sandstones with horizontal laminae on the scale of millimetres to centimetres, forming lenses a few metres in extent, with invertebrate trace fossils (*Skolithos* isp. and *Arenicolites* isp.) and vertebrates tracks and trackways, together with desiccation mud-cracks and deformation structures formed by fluidisation (Facies 4).

Facies 2 and 3 occur intercalated with Facies 1 in the lower half of the outcrop whilst Facies 4 is intercalated with Facies 1 in the upper half. The facies interpretations for the rocks from the upper part of the Santa Maria Formation have been controversial, and some different interpretations have been proposed. The mudstones are traditionally interpreted as representing deposition in a lacustrine water body (e.g. Faccini, 1989; Zerfass et al., 2003), whilst the lenticular layers represented by Facies 4 correspond to small channels that formed during events of subaerial exposure. A more recent interpretation suggests that this sequence was formed in a fluviatile system with stable to sinuous channels, where the mudstones correspond to floodplain deposits, whilst levels containing palaeosols also occur locally; the tabular sandstones correspond to the main channels, and the small sandstone lenses represent crevasse splay deposits (e.g. Fonseca and Scherer, 1998; Schultz et al., 2000). A fluvial setting is consistent with the ichnological evidence.

4. Systematic ichnology

Rhynchosauroides Maidwell, 1911

Diagnosis

Trackways with ectaxonic, asymmetrical tracks. Digit imprints are slender, frequently curved and increase in length from I to IV. There is a large angle between the digit imprints I and V. These general characters are common to the pes and manus, the latter being the smaller of the two tracks.

Type ichnospecies

Rhynchosauroides rectipes Maidwell, 1911.

Rhynchosauroides retroversipes isp. nov.

Material

MCN-PIC.001/1–11 (Fig. 4A), MCN-PIC.002/1–10 (Fig. 4B), MCN-PIC.003/1–15 (Fig. 5A), MCN-PIC.004/1–14 (Fig. 5B), MCN-PIC.005/1–5 (Fig. 6A), MCN-PIC.006/1–35 (Fig. 6B), MCN-PIC.025/1–7, tracks and trackways preserved in concave epirelief (upper surface).

Holotype

MCN-PIC.002/1–10, trackway in concave epirelief.

Paratypes

MCN-PIC.001/1–11, MCN-PIC.003/1–15, MCN-PIC.004/1–14, MCN. PIC-005/1–5, trackways in concave epirelief.

Etymology

Specific name *retroversipes*, from Latin, pes turned back.

Diagnosis

Rhynchosauroides retroversipes isp. nov. is distinguished from all the other species of *Rhynchosauroides* by the following combination of characters: trackways with pentadactyl tracks; pedal digit imprints increase in length from I to IV, but not in the manus; typical manus–pes sets are absent, with the pes and manus tracks on the same side of

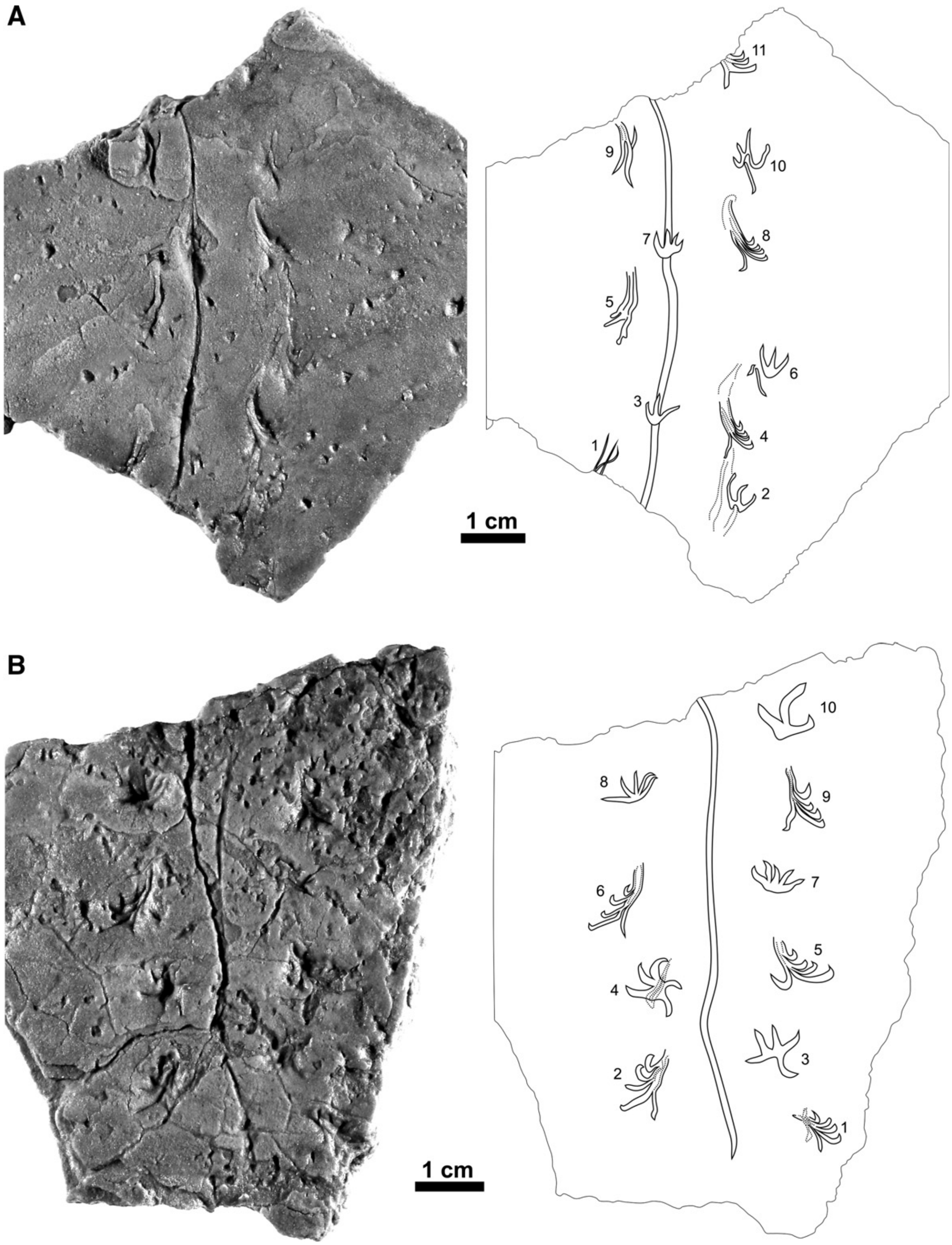

Fig. 4. *Rhynchosauroides retroversipes* isp. nov., from the Santa Maria Formation: A) Sample MCN-PIC.001; B) sample MCN-PIC.002.

the trackway being similarly spaced; the axis of the pes tracks is turned latero-posteriorly; the pes tracks occur laterally to the concave segments of the curved tail drag marks, whilst the manus tracks occur laterally to the convex segments of the curved tail drag marks.

Rhynchosauroides retroversipes isp. nov. differs from *R. tirolicus* Abel, 1926 in the anterior position of the manus in the manus–pes set (Avanzini and Renesto, 2002). It also differs from *R. peabodyi* Faber, 1958, *R. moenkopiensis* Haubold, 1971 and *R. schochardti* Rühle von Liliestern, 1939, which have a greatly lengthened palm or sole imprint. *R. retroversipes* isp. nov. further differs from *R. tirolicus* Abel, 1926, as well as *R. articeps* (Owen, 1842), *R. franconicus* Heller, 1956, *R. hyperbates* Baird, 1957, *R. petri* Demathieu, 1966, *R. bornemanni* Haubold, 1966, *R. pusillus* Haubold, 1966, *R. sphaerodactylus* Demathieu, 1971 and *R. virgiliae* Demathieu, Ramos and Sopeña, 1978, in minor dimensions and the position of the manus and pes in the set. In *R. santanderensis* Demathieu and Omeñaca, 1976, *R. brunswickii* (Ryan and Willard, 1947) and *R. pallinii* Conti, Leonardi, Mariotti and Nicosia, 1977, digit imprint V is oriented latero-posteriorly or at a right angle with relative to digit imprint IV, and thus differ from *R. retroversipes* isp. nov.

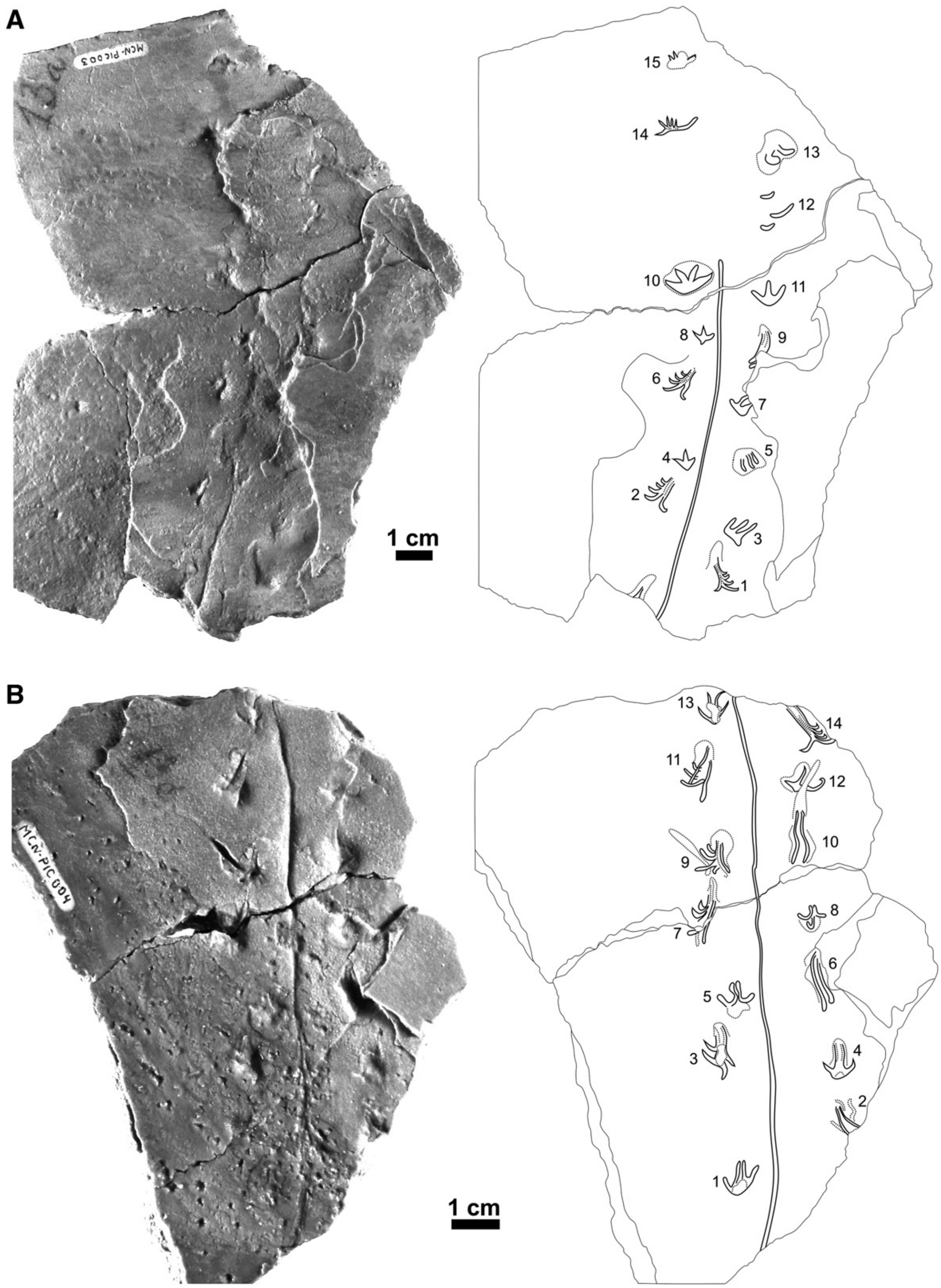

Fig. 5. *Rhynchosauroides retroversipes* isp. nov., from the Santa Maria Formation: A) Sample MCN-PIC.003; B) sample MCN-PIC.004.

Description

The tracks are preserved in concave epirelief and form indicating and alternating walking gait in which the left manus is opposite the right pes and vice-versa (Fig. 7). The trackways are associated with a strongly marked, continuous sinuous medial impression, consisting of a central furrow and elevated lateral edges. The pes tracks are pentadactyl, ectaxonic, digitigrade to semiplantigrade, and the digit imprints increase progressively in length from I to IV. Digit imprint V is smaller than digit imprint IV and they are separated by a large degree of interdigital divergence. The hypicies are acute. The axis of the track is oriented latero-posteriorly, being oblique to the metapodium-phalangeal axis, which is oriented parallel to the axis of the trackway. The tracks frequently preserve a broad, proximal drag mark, directed antero-medially, and preserved in concave epirelief,

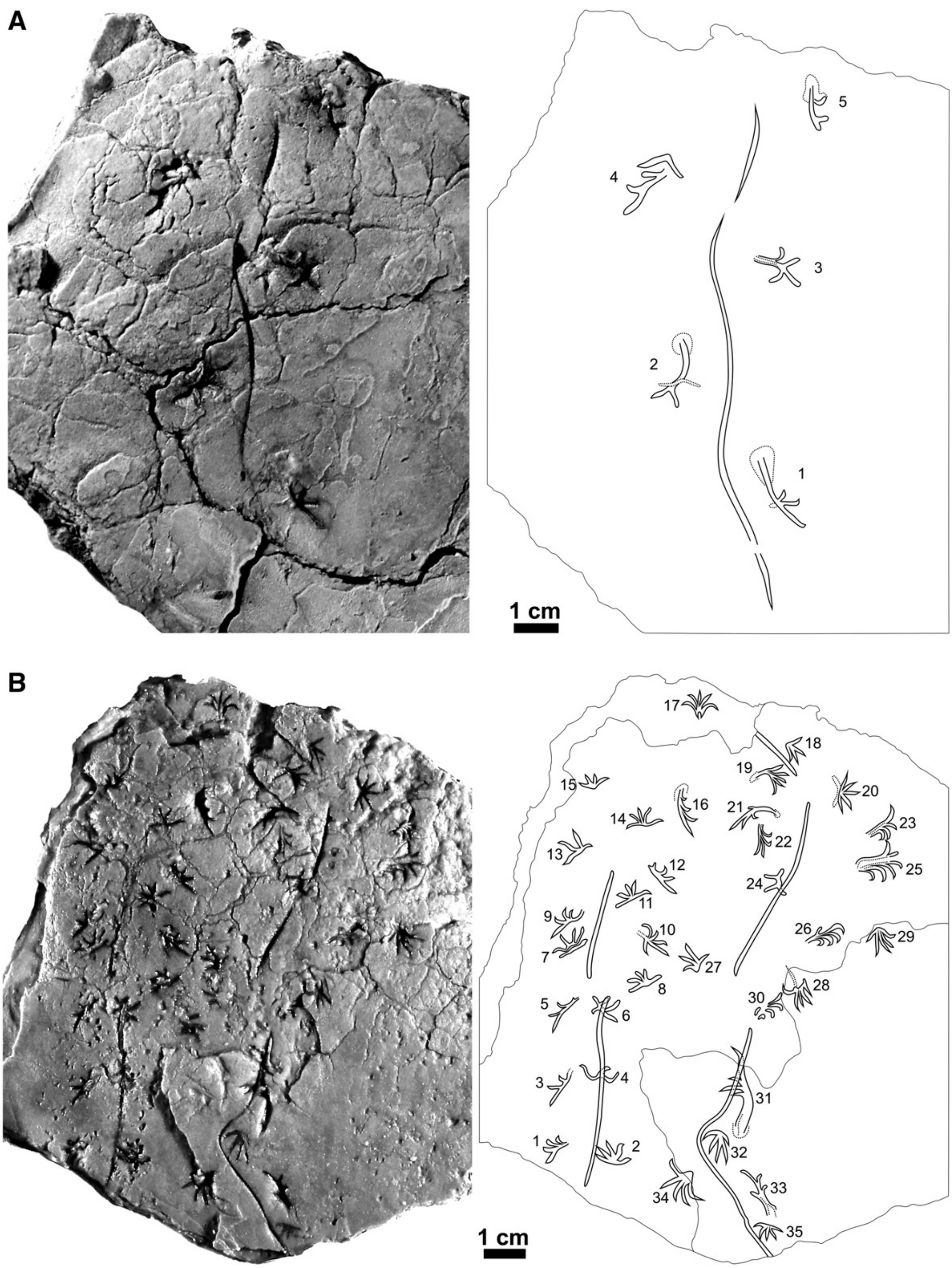

Fig. 6. *Rhynchosauroides retroversipes* isp. nov., from the Santa Maria Formation: A) Sample MCN-PIC.005; B) sample MCN-PIC.006.

whilst an elongated anterior projection produced by the crawling action of the autopodia is preserved in convex epirelief. The distal extremities of digit imprints I to IV are curved latero-anteriorly. These tracks occur laterally to the concave parts of the curved tail trace. The manus tracks are pentadactyl, but generally only the three central digit imprints are preserved. These tracks demonstrate a pronounced variation in preservation, varying from semipalmigrade to digitigrade, mesaxonic to ectaxonic and occur laterally to the convex curved tail trace. The digit imprints are long, slender, similar in length and the hypices are acute. The axis of these tracks is oriented approximately parallel to the axis of the trackway. The angle between the digit imprints IV and V is quite variable and in some cases (MCN-PIC.002/3–4, MCN-PIC.001/10) digit imprint V is oriented posteriorly. Both the pes and the manus tracks have long, pointed digit imprints and frequently curved distal extremities. It is not possible to distinguish imprints of the phalangeal and plantar (or palmar) sole pads. The measured parameters of the trackways are presented in Table 1.

Fig. 7. Reconstruction of the trackway of *Rhynchosauroides retroversipes* isp. nov. based on the mean of the measured parameters (artwork of the specimen by Renata Cunha).

Discussion

Several ichnogenera attributed to lacertoid reptiles are known in the fossil record, mostly from the Permian–Triassic interval. The most representative is *Rhynchosauroides* Maidwell, 1911, due to the large number of constituent ichnospecies and their wide geographic and temporal distribution. Amongst the several known ichnogenera attributed to lacertoid reptiles, the studied footprints can be identified as *Rhynchosauroides* due to the presence of tracks with digit imprints that progressively increase in length from I to IV, have a smaller digit imprint V that is oriented antero-laterally and separated from the others by a larger interdigital angle, whilst the manus and pes tracks are different sizes. A further ichnogenus attributed to lacertoid reptiles, *Varanopus* (Moodie, 1929), has large interdigital angles, particularly between digit imprints IV and V, which distinguishes it from the analysed material. This material also differs in a similar fashion from the ichnogenus *Dromopus* Marsh, 1894, which has long and sinuous digit imprints with a strong increase in their length and a narrow and lengthened sole imprint, and ichnogenus *Phalangichnus* Schmidt, 1959, which has manus tracks where digit imprint V is opposed to III, whilst the manus track is anterior and medial to the pes track and the digit imprints show a strong increase in length. They differ also from *Procolophonichnium* Nopcsa, 1923, which exhibits broader and shorter digit imprints, a proportionally larger sole imprint and an evident increase of digit imprint length, with digit imprint III approximately equal in length to digit imprint IV (e.g. Holst et al., 1970; Diedrich, 2000; Diedrich, 2002). *Rhynchosauroides retroversipes* isp. nov. also shows some similarities with the specimen of *Lunichnium rotteroidium* Walter, 1983 described by Minter and Braddy (2006, pp. 1137–1138), such as the presence of a slightly sinuous medial impression and drag marks produced during the movement of the autopodia, but it differs in the presence of clearly defined manus and pes tracks with well-preserved digit imprints. *Lunichnium* is considered a swimming trace produced by a temnospondyl amphibian, and this particular specimen corresponds to a part walking, part swimming trackway produced in shallow water (Minter and Braddy, 2006).

Rhynchosauroides isp.

Material

MCN-PIC.015/1–8 (Fig. 10B), trackway preserved in concave epirelief.

Description

The trackways have alternate symmetry and the tracks are preserved in concave epirelief with two to five digit imprints. The tracks were originally pentadactyl, asymmetrical, ectaxonic and digitigrade with a progressive increase in the length of digit imprints from I to IV, which are slightly curved medially. Digit imprint IV is prevalent, whilst digit imprint V is smaller, is separated from the others by a larger interdigital angle, and is laterally curved. Digit imprint I is only preserved in track MCN-PIC.015/4. All digit imprints have acute extremities. There is no clear morphological distinction between the manus and pes tracks, except for the size, the pes track being larger than that of the manus. The axis of the tracks is oriented parallel to the axis of the trackway. Two of the tracks (MCN-PIC.015/5 and 7) show a small proximal, posterior elevation in the shape of a half moon. Tracks MCN-PIC.015/2, 5, 7 and 8 preserve a divergent interdigital angle. Medial impressions and imprints of the phalangeal and plantar (or palmar) sole pads are absent. In the manus–pes sets the manus track is situated anteriorly to the pes track, with a slight overlap, and the longitudinal axes of the two tracks are approximately parallel. The trackway shows an alternating pattern with preferential preservation of the pes track.

Discussion

These trackways can be identified as *Rhynchosauroides*, mainly due to the presence of digit imprints that progressively increase in length from I to IV, a smaller digit imprint V that is oriented antero-laterally, and manus and pes tracks of different sizes. *Rhynchosauroides* isp. is larger than *Rhynchosauroides retroversipes* isp. nov. and also differs in

Table 1
Rhynchosauroides retroversipes isp. nov. Parameters of the trackways: ID = intermanus/interpedes distance; PA = pace angulation; OP = oblique pace; LP = length of pace; LS = length of stride; DMP = distance between manus and pes

		Manus					Pes					DMP
		ID	PA	OP	LP	LS	ID	PA	OP	LP	LS	
		(cm)	(°)	(cm)	(cm)	(cm)	(cm)	(°)	(cm)	(cm)	(cm)	(cm)
MCN-PIC.001	Mean	1.74	80.00	2.65	1.45	3.01	1.95	75.12	2.52	1.59	3.03	1.78
	Median	1.75	72.59	1.12	1.26	2.94	1.95	77.32	2.46	1.54	3.08	1.73
	Standard deviation	0.19	15.77	0.33	0.58	0.62	0.03	6.23	0.17	0.27	0.33	0.38
	Coefficient of variability (%)	10.91	19.71	12.45	40.00	20.60	1.54	8.29	6.75	16.98	10.89	21.35
MCN-PIC.002	Mean	1.90	67.05	2.26	1.14	2.52	2.21	58.29	2.56	1.21	2.48	1.26
	Median	1.88	69.58	2.34	1.15	2.44	2.18	57.93	2.51	1.24	2.42	1.23
	Standard deviation	0.19	8.70	0.21	0.16	0.27	0.09	5.18	0.16	0.32	0.15	0.15
	Coefficient of variability (%)	10.00	12.97	9.29	14.03	10.71	4.07	8.89	6.25	26.45	6.05	11.90
MCN-PIC.003	Mean	1.44	99.13	2.22	1.68	3.37	2.04	73.85	2.57	1.55	3.12	1.31
	Median	1.46	99.91	2.19	1.67	3.48	2.05	73.99	2.57	1.58	3.11	1.29
	Standard deviation	0.09	6.71	0.12	0.17	0.20	0.02	6.75	0.29	0.48	0.39	0.23
	Coefficient of variability (%)	6.25	6.77	5.40	10.12	5.93	0.98	9.14	11.28	2.58	12.50	17.56
MCN-PIC.004	Mean	1.90	79.19	2.52	1.66	3.15	2.23	64.45	2.70	1.48	2.85	1.28
	Median	1.88	81.17	2.40	1.57	3.07	2.23	64.28	2.55	1.33	2.93	1.27
	Standard deviation	0.12	3.75	0.30	0.33	0.34	0.12	6.60	0.28	0.41	0.33	0.14
	Coefficient of variability (%)	6.31	4.73	11.9	19.88	10.79	5.38	10.24	10.37	27.70	11.58	10.94
Total	Mean	1.76	81.03	2.34	1.50	3.03	2.13	67.43	2.60	1.47	2.87	1.40
	Median	1.80	80.05	2.33	1.49	3.04	2.10	67.57	2.53	1.43	2.91	1.30
	Standard deviation	0.23	13.54	0.27	0.39	0.45	0.15	8.74	0.23	0.38	0.36	0.31
	Coefficient of variability (%)	13.07	16.71	11.54	26.00	14.85	7.04	12.96	8.85	25.85	12.54	22.14

the absence of the characteristic rotation of the pes track, with the axis of the tracks oriented parallel to the axis of the trackway. The distances between the digit imprints are also greater and the manus and pes tracks in a manus–pes set are closer together. These tracks also preserve characters indicative of both subaqueous and terrestrial production, which precludes their identification to an ichnospecific level. Other records of *Rhynchosauroides* in South America occur in the Permian of southern Brazil (Leonardi et al., 2002) and in the Triassic of Argentina (Melchor and Valais, 2006).

Rhynchosauroides? isp.

Material

MCN-PIC.007/1–16 (Fig. 8A), MCN-PIC.012/1–7 (Fig. 8B), MCN-PIC.013/1–6 (Fig. 8C), MCN-PIC.024/1–6, trackways preserved in concave epirelief with mudcracks.

Description

The tracks are pentadactyl, ectaxonic, semiplantigrade to digitigrade, with claw imprints and acute hypices. The digit imprints are frequently curved medially and their length increases progressively from I to IV. Digit imprint V is smaller than digit imprint IV and is separated from it by a larger degree of interdigital divergence. Imprints of the sole are half moon-shaped and are preserved in convex epirelief with a posterior concavity, and may preserve imprints of tubercles and striations that are directed antero-posteriorly. Sample MCN-PIC.007 preserves sixteen chaotically distributed tracks (although they seem to have a preferential orientation) associated with mudcracks that occur preferentially around the tracks, and cross cut them in some cases (MCN-PIC.007/5, 8, 10, 12 and 13). The tracks MCN-PIC.007/1–16 preserve four to five curved digit imprints and are associated with a small medial impression. The tracks MCN-PIC.007/5, 14, 15 and 16 preserve portions of the sole in convex epirelief, whilst MCN-PIC.007/4 preserves portions of the sole and the inner part of the digits in convex epirelief. Specimen MCN-PIC.012 preserves seven tracks with narrow and lightly elongated digit imprints, probably constituting two trackways with a disordered pattern. The imprints of the palm/sole are half moon-shaped and are preserved in convex epirelief with a posterior concavity. The tracks MCN-PIC.012/2, 3, 4 and 6 preserve imprints of tubercles and striations that are directed antero-posteriorly. It is not possible to determine the pattern of gait with certainty. These tracks are associated with a possible lightly sinuous medial impression and mudcracks are absent. The sample MCN-PIC.013 consists of six tracks associated with mudcracks. The preservation of these tracks is poor and few characteristics are observable. The tracks preserve three to five digit imprints. Tracks MCN-PIC.013/1, 2 and 3 preserve a small posterior elevation. The tracks MCN-PIC.013/1, 3 and 5 preserve a slight increase in the length of digit imprints from I or II to IV, whilst the digit imprint V is separated from the others. In the other tracks of the sample, the digit imprints are similar in length. It is not possible to distinguish the pattern of the gait. MCN-PIC.024 consists of six tracks with acute claw imprints and hypices, constituting a probable quadruped track. Tracks MCN-PIC.024/2 and 6 preserve only digit imprints II to V, with a slight increase in the digital imprint length from II to IV, whilst digit imprint V is separated from the others by a higher interdigital angle. MCN-PIC.024/4–5 consist of tracks with four digits imprints preserved that are symmetrical in form without evident increase in length. The tracks MCN-PIC.024/1 and 3 consist of only portions of digit imprints.

Discussion

The presence of mudcracks cross cutting some tracks in sample MCN-PIC.007 demonstrates that desiccation occurred after their production. The track MCN-PIC.013/2 preserves drag marks of the claws produced by the tractive movement of the autopodia during the locomotion of the animal. The tubercle imprints and striations found in tracks MCN-PIC.012/2, 3, 4 and 6 are oriented antero-posteriorly and resemble the pattern of striations described by Gatesy (2001) in dinosaur footprints from Late Triassic that have been interpreted as skin impressions and drags marks of scales. These striations occur in the direction of the movement of autopodia. In tracks, impressions of the skin are more commonly preserved in the form of rugose textures (Avanzini, 2000). The tracks analysed in this study are small in size, and are unlikely to preserve impressions of the skin, but the striations and tubercle imprints may represent drag marks of the scales, or more probably the cushions of the palm or sole, produced during the locomotion of the animal. The absence of a characteristic pattern of tracks makes identification difficult. The presence of some tracks with digit imprints that increase in length, claw imprints and acute hypices suggests that they are similar to the ichnogenus *Rhynchosauroides*, although these tracks are smaller than *Rhynchosauroides* isp. and do not demonstrate the typical reversion of the pes track as in *Rhynchosauroides*

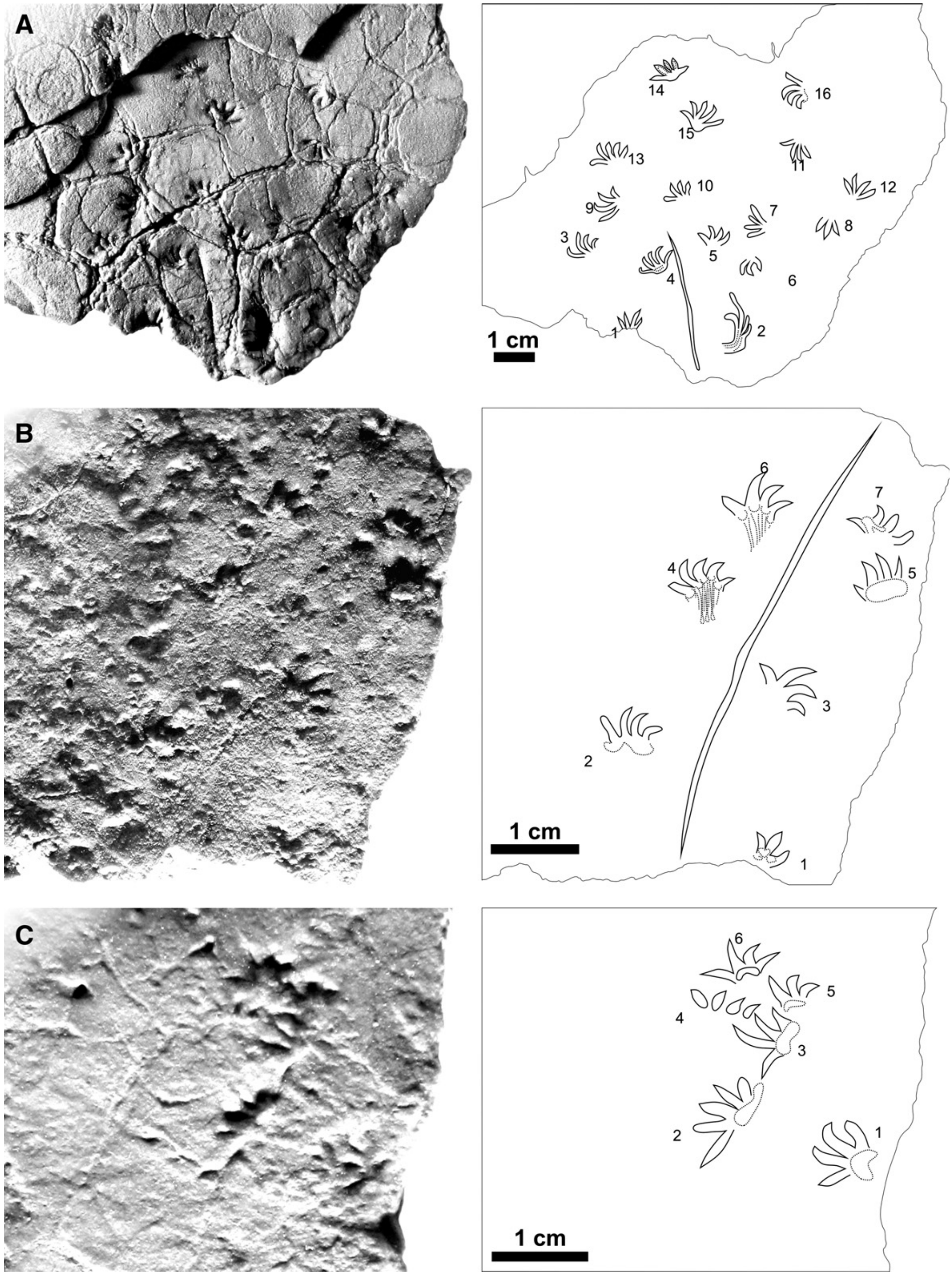

Fig. 8. *Rhynchosauroides?* isp., from the Santa Maria Formation: A) Sample MCN-PIC.007; B) sample MCN-PIC.012; C) sample MCN-PIC.013.

retroversipes isp. nov. The absence of this character in other tracks may be product of the preservational variation.

Drag marks of autopodia

Material

MCN-PIC.008/1–7 (Fig. 9A), MCN-PIC.010 (Fig. 9C), MCN-PIC.011 (Fig. 10A), traces preserved in concave epirelief; MCN-PIC.009/1–9 (Fig. 9B), traces preserved in convex hyporelief.

Description

These traces may be isolated or occur in groups of two to four, that are parallel. They may be sinuous and elongate (MCN-PIC.009). They are V-shaped in transverse section. Some groups of traces may describe a curve resembling an arch, with the traces on the inside of the curve being more strongly curved (MCN-PIC.008/2, MCN-PIC.011). Several traces are quite thin and short, consist of two or three imprints (MCN-PIC.008/3, 4, 5, 6). Several parallel and anastomosed traces occur in sample MCN-PIC.010; three of which are elongated,

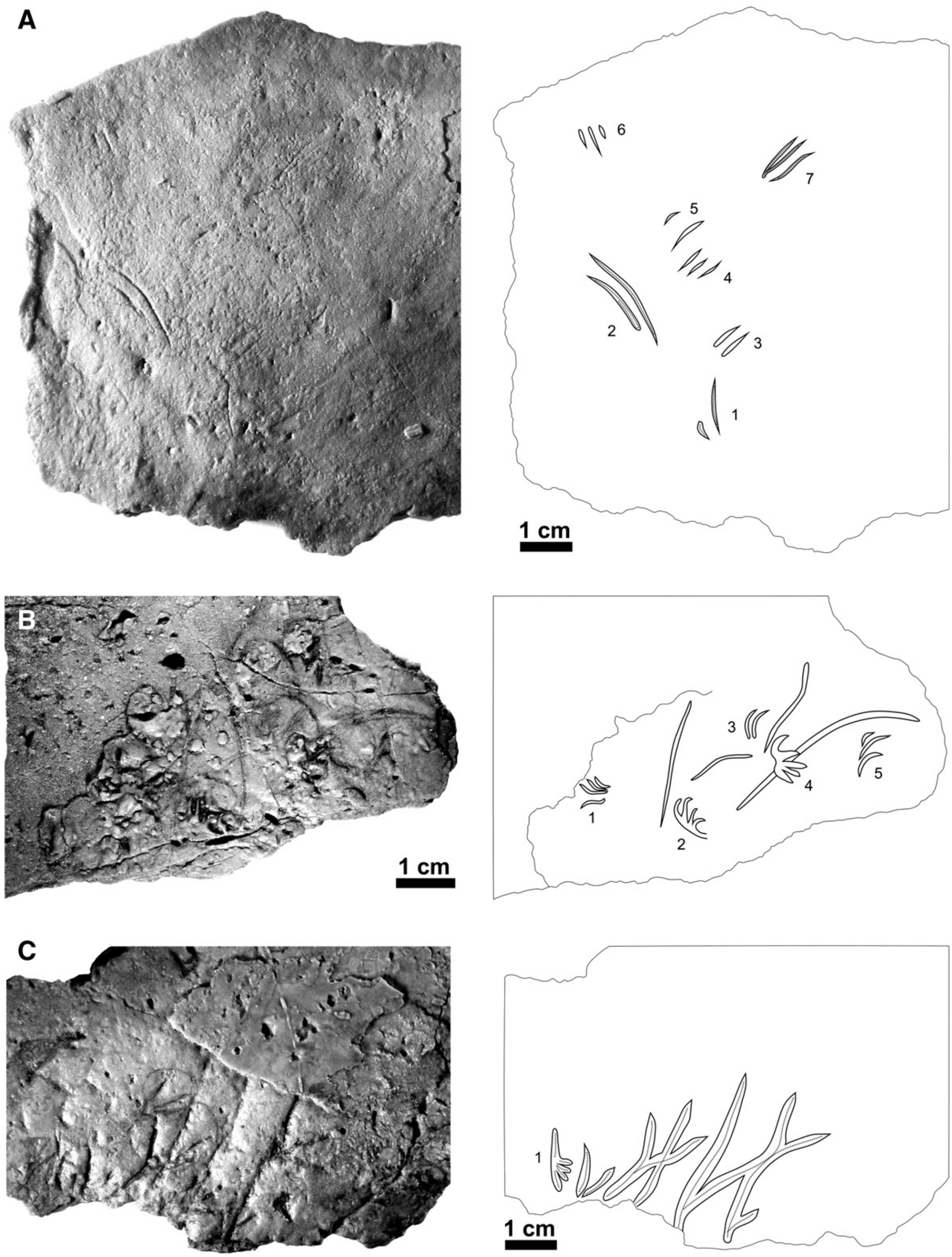

Fig. 9. Swimming traces from Santa Maria Formation: A) Sample MCN-PIC.008; B) sample MCN-PIC.009; C) sample MCN-PIC.010.

rectilinear and parallel, with Y-shaped bifurcation in two of them and also in a fourth, smaller, trace. MCN-PIC.011 preserves two elongated, curved and approximately parallel traces, together with a third trace that is shorter but also parallel to the others. The central of these traces has a small rounded mark with an elevated posterior margin and there is a further rounded mark between the central trace and the shorter trace. The three traces have elevated posterior margins and deepen from the anterior part to the posterior of the trace. Isolated tracks that resemble those of the pes (MCN-PIC.009/2, MCN-PIC.010/1) and manus (MCN-PIC.009/4) of *Rhynchosauroides retroversipes* isp. nov. are also present.

Discussion

The presence of isolated tracks of *Rhynchosauroides retroversipes* isp. nov. suggests that the drag marks of autopodia correspond to behavioural or preservational variations of this ichnotaxon, produced by the paddling action of autopodia. The subaqueous traces and tracks studied by McAllister (1989) and McAllister and Kirby (1998)

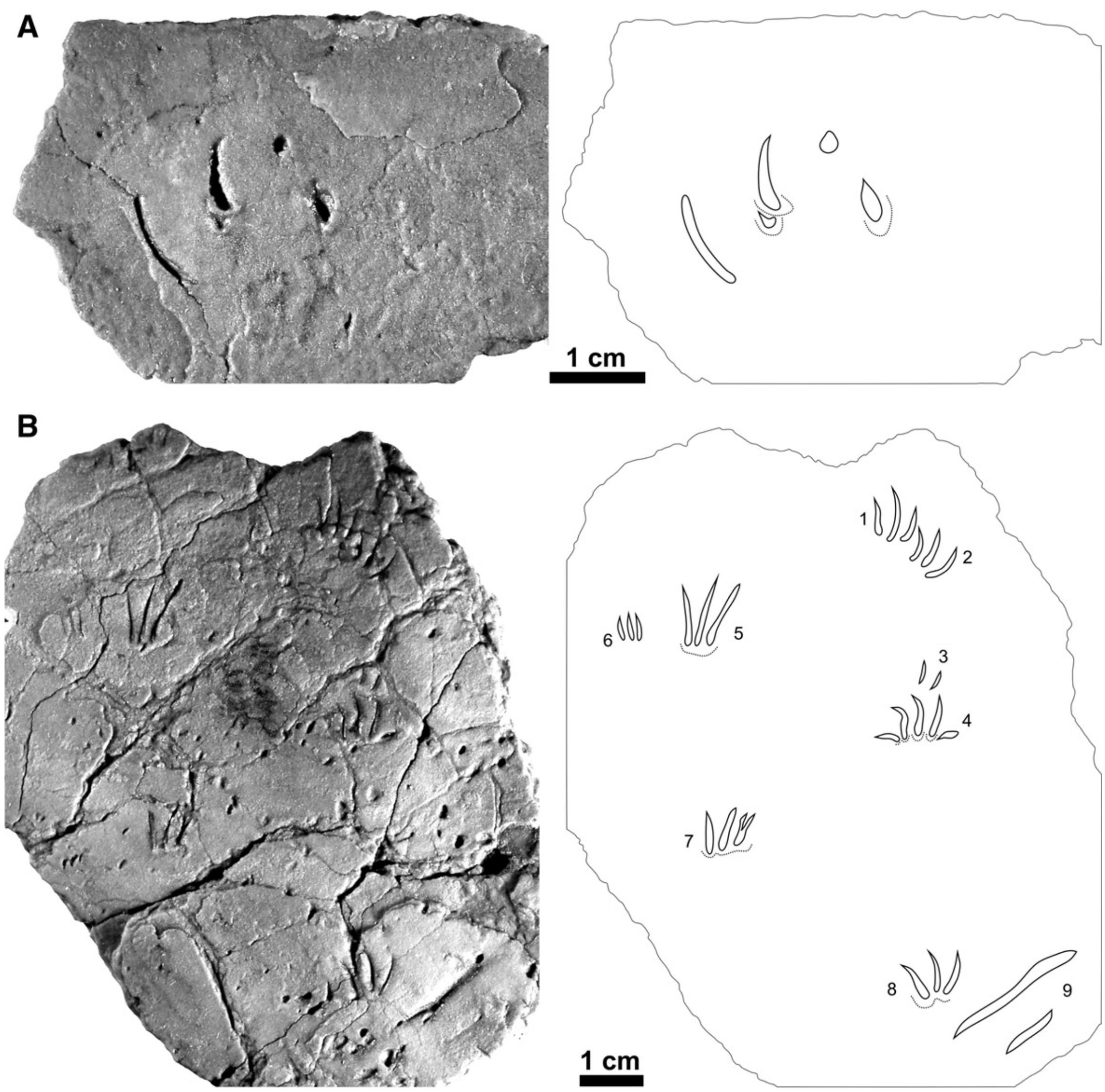

Fig. 10. Footprints from Santa Maria Formation: A) Swimming trace, sample MCN-PIC.011; B) *Rhynchosauroides* isp., sample MCN-PIC.015.

demonstrate similar variations and characteristics such as excessively variable trace lengths compared to the widths of the traces and traces with unusual configurations. The parallel oriented and anastomosed traces in sample MCN-PIC.010 show some similarities with the ichnogenus *Undichna* Anderson, 1976 (e.g. Minter and Braddy, 2006), but the sample is too small to make this identification possible with certainty. The studied material also resembles the ichnogenus *Lunichnium* Walter, 1983 in the presence of discontinuous and paired curvilinear imprints, but differs because there is no regular pattern or bifurcated imprints. Swimming traces, which were attributed to crocodiles, were also described by Foster and Lockley (1997) as *Hatcherichnus* and consist of irregular toe scratch marks and tail traces, but they are much larger than the material described herein.

5. Discussion

5.1. Preservation of the tracks

Several features associated with the tracks allow us to deduce the plasticity of the sediment and the water depth in which they were produced, together with factors that permitted their preservation. Some of these features, such as a reduction in the number of preserved digit imprints and digitigrady, are typical of undertracks. However, many of the studied tracks (MCN-PIC.001, MCN-PIC.003, MCN-PIC.004, MCN-PIC.005, MCN-PIC.006, MCN-PIC.009, MCN-PIC.011 and MCN-PIC.015) have displacement rims preserved in convex epirelief, and these were produced during the movement of the autopodia over the substrate. These structures are not preserved in undertracks because they are not produced by weight or disruption of the substrate, and consequently do not affect sediment levels below the surface. These tracks therefore do not represent undertracks. The presence of sinuous medial impressions, produced by dragging of the tail, provides further evidence that the surfaces with tracks correspond to the original surface of track production (Swanson and Carlson, 2002; Milàn and Bromley, 2006). Samples MCN-PIC.008 and MCN-PIC.010 do not show such evidence and consequently may represent undertracks produced by disruption of the surface during swimming.

The pes tracks of *Rhynchosauroides retroversipes* isp. nov. also preserve a proximal, anterior progression mark produced during the withdrawal movement and typical latero-posterior rotation of the pes. The presence of drag marks associated with displacement rims (MCN-PIC.001, MCN-PIC.003, MCN-PIC.004, MCN-PIC.005, MCN-PIC.006) may indicate a greater degree of plasticity and water content of the sediment at the time of track production compared to those samples without these features (MCN-PIC.002, MCN-PIC.024). The preservation of the manus tracks is also related to the plasticity of the sediment and those with the largest number of preserved characters occur in sample MCN-PIC.002. The other samples demonstrate a greater degree of morphological variation in the manus tracks, exceeding drag marks and plastic deformation features associated with the tracks. A similar kind of preservation occurs in samples MCN-PIC.012, MCN-PIC.013 and MCN-PIC.024.

A moderate degree of sediment plasticity (and possibly a thin sheet of water) appears to have been present during the production of the tracks in sample MCN-PIC.006, many of which are deformed and have a displacement rim, whilst the tail drag marks are discontinuous and the trackways quite irregular. The surface is partially affected by mudcracks, which demonstrates that there was limited subaerial exposure before the burial.

Sample MCN-PIC.005 is attributable to *Rhynchosauroides retroversipes* isp. nov., although only the pes tracks, associated to an intermittent medial impression produced by the tail, are preserved. This trackway appears to be an artefact produced by a swimming animal, with the legs driving the body, and the tail accidentally touching the bottom. Alternatively it could be the result of undertracking, with the pes and the tail penetrating the substrate to a greater depth than the manus. However, the tail would probably not penetrate a plastic sediment more than the manus which suggests that they are not undertracks. Swanson and Carlson (2002) described swimming tracks produced in shallow water, but they do not preserve drag marks of the tail. Another hypothesis is that the trackway indicates a bipedal gait representing a higher velocity than during quadrupedal progression with the tail touching the ground. A number of lines of evidence support this hypothesis. The tracks in this sample are more deeply impressed than in the other samples and the relative values of the trackway parameters are greater than the mean relative values of the other trackways. For example, the stride is almost the double (ID = 2.88 cm; PA = 77.15 cm; OP = 3.76 cm; LP = 2.20 cm; LS = 4.59 cm, abbreviations from Table 1), which implies a greater speed (see for instance Irschick and Jayne, 1999). The tracks are also digitigrade, without a large crawling mark corresponding to the sole, and Irschick and Jayne (1999) observed that lizards running at high speed with a bipedal gait have a tendency to show digitigrady. The presence of mudcracks covering the sample surface suggests moderate subaerial exposure and consequently only a very thin water sheet would be inferred at the time of imprint.

Samples MCN-PIC.015, MCN-PIC.009, MCN-PIC.010, MCN-PIC.008 and MCN-PIC.011 all demonstrate characteristics that McAllister (1989) and McAllister and Kirby (1998) used in other instances for the recognition of tracks produced subaqueously, such as: reflexion of the digit imprints, the depth of the track corresponding to arc of digit imprints, elongation of tracks, posterior overhang, imprints of distal digits, track lengths excessively variable compared to widths, and trackways with unexpected configurations. The digit drag marks present in these samples can therefore be interpreted as traces produced by a swimming animal in deeper water in such a way that the autopodia touch the sediment surface whilst the body and the tail floated in the water. The presence of *Rhynchosauroides retroversipes* isp. nov. tracks in the samples MCN-PIC.009/2, MCN-PIC.010/1 and MCN-PIC.009/4 suggests that the drag marks were produced by the same trackmaker and represent a variation of that track type produced in a deeper water column. Drag marks similar to these, which were attributed to Mesosauridae (Sauropsida), are recorded by Sedor and Silva (2004) in Permian rocks of Brazil. Brand (1979, 1996) observed similar configurations of drag marks and tracks in experiments with modern salamanders.

The preservation of tracks in sample MCN-PIC.015 suggests the possibility of production in a greater water depth than in the former samples. The reduction of the number of digit imprints in some tracks, which is typical for tracks produced subaqueously, supports this hypothesis (Brand, 1996). The tracks in sample MCN.PIC-015/1–8 preserve characteristics suggesting production by traction, such as a posterior displacement rim produced by the movement of the animal (Brand, 1979) and well-preserved tracks reflecting the morphology of the autopodia. However, there are also features suggesting that the animal was swimming, such as distal elongation of the digit imprints due to dragging of the digits, particularly in track MCN-PIC.015/5. A medial impression produced by the tail is absent and the tail would be expected to float in deeper water, as has been observed by McAllister and Kirby (1998). Track MCN-PIC.015/9 represents a swimming trace. The largest imprint is medial with reference to the smallest, which can be inferred from the angle of inclination of the walls and the slight curvature of the imprints. The occurrence of two types of tracks (traction and swimming) on the same surface indicates that they were produced at different times and under at least three different conditions, which were, in temporal order: deep water (swimming), shallow water (traction), and subaerially exposed (mudcracks). A similar preservation occurs in samples MCN-PIC.009 and MCN-PIC.010, where tracks produced by traction (MCN-PIC.009/2,4; MCN-PIC.010/1) occur associated with drag marks produced by swimming (MCN-PIC.009/1, 3, 5) and longer traces, possibly tail drag marks, which are all distributed chaotically and are characteristic of subaqueous track production (Peabody, 1956; Brand, 1979).

Samples MCN-PIC.008 and MCN-PIC.011 consist of chaotically distributed digit drag marks, which indicate that the water only allowed the trackmaking animals to touch the bottom with the claws when swimming (Brand, 1996; McAllister and Kirby, 1998). The track MCN-PIC.008/2 comprises a longer external digit imprint compared to the internal digit imprint, which may be evidence of a lacertoid origin consistent with the typical increase of digit imprint length in this type of tracks. Mudcracks do not occur in these two samples, which suggests minimal, or a lack of, subaerial exposure. Generally, the tracks produced in deep water were subjected to minimal or no subaerial exposure.

The tracks and trackways from the Predebon outcrop were classified by Silva et al. (2007) into five different categories with reference to the water content of the substrate or water depth at the time of production prior to subaerial exposure (Fig. 11): (1) underwater tracks — only swimming traces with no mudcracks (MCN-PIC.008, MCN-PIC.011); (2) semi-aquatic tracks — prevalence of swimming traces but also show traction footprints without mud cracks (MCN-PIC.009, MCN-PIC.010); (3) semi-terrestrial tracks — prevalence of traction tracks, but also associated with swimming traces and drag marks, whilst mudcracks may be present (MCN-PIC.015); (4) wet substrate tracks — tracks forming irregular trackways, with intermittent tail drag marks and mudcracks partially covering the surface (MCN-PIC.001, MCN-PIC.003, MCN-PIC.004, MCN-PIC.005, MCN-PIC.006, MCN-PIC.012, MCN-PIC.013, MCN-PIC.024, MCN-PIC.025); (5) damp substrate tracks — tracks forming regular trackways, with continuous tail drag marks and mudcracks (MCN-PIC.002, MCN-PIC.007). Similar forms of preservation were described by Diedrich (2000, 2002).

In general, according to Silva et al. (2007), the underwater and semi-aquatic tracks could have been produced in the central parts of channels with greater water depths, whilst the other forms of track preservation may have formed closer to the margins and were subject to greater degrees of subaerial exposure (Fig. 12). Avanzini et al. (2005) described a similar pattern in trackways produced by turtles, but on a larger scale.

5.2. Considerations about the trackmakers

The statistical analysis of *Rhynchosauroides retroversipes* isp. nov. (Table 1) revealed that the mean and median values are very close and therefore constitute good representations of the studied populations. The angular measurements (PA) of the trackways have greater

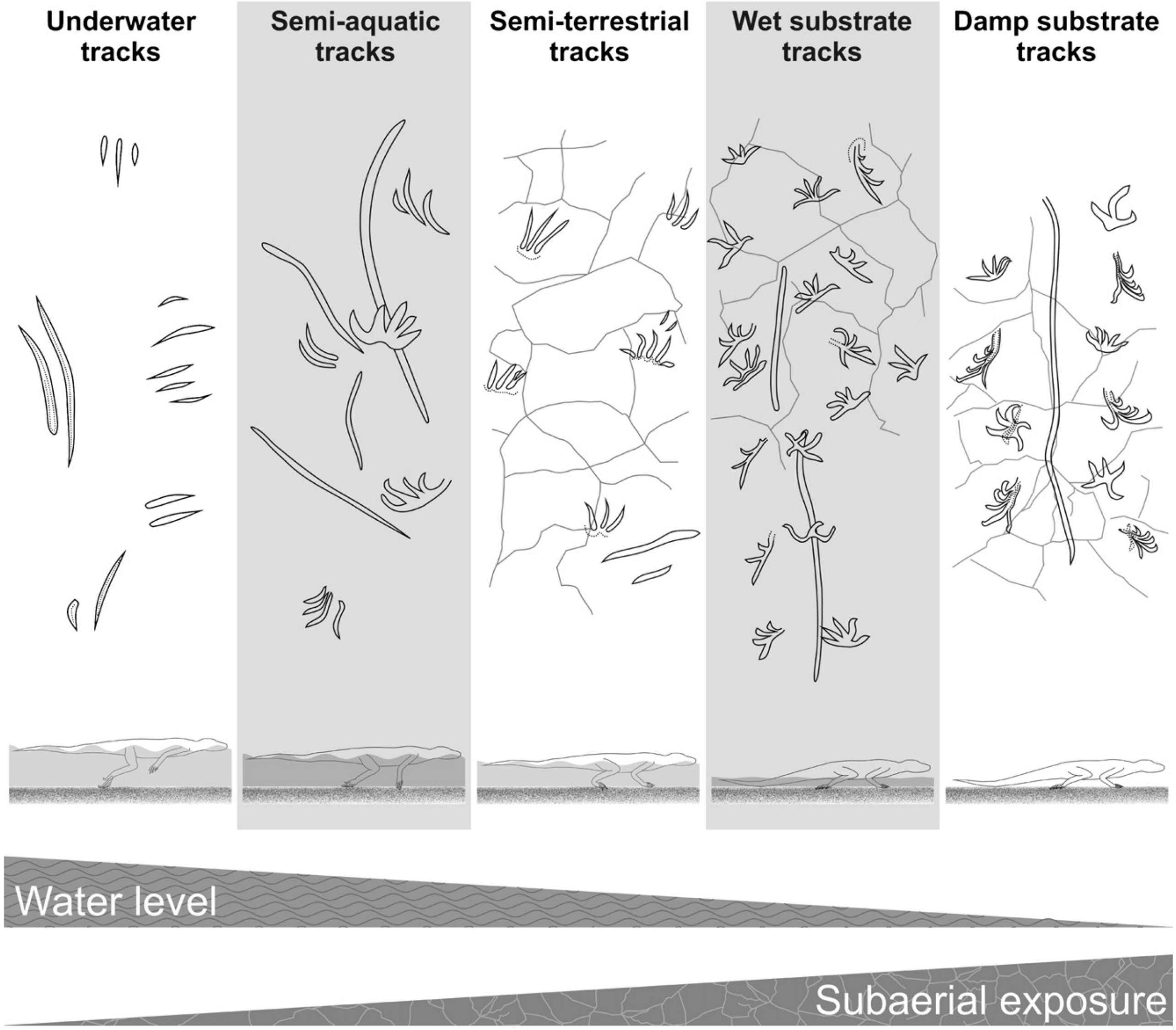

Fig. 11. Relationship between the preservation of the tracks from the Santa Maria Formation, the water content of the substrate when the tracks were produced and subsequent subaerial exposure (modified from Silva et al., 2007).

coefficients of variability compared to the linear measurements (ID = intermanus/interpedes distance, OP = oblique pace, LS = length of stride). The pace (LP) and distance between the manus and pes (DMP) were exceptions and showed the greatest range of variation. The measurements regarding the pes tracks have a lower range of variation than those of the manus tracks. The large degree of preservational variation encountered in the samples that were not measured is characteristic of subaqueously produced tracks (Brand, 1979).

The morphological and statistical analysis of the trackways enables some morphological aspects of the trackmaker to be determined. *Rhynchosauroides retroversipes* isp. nov. can be attributed to a lacertoid reptile with autopodia resembling the primitive condition of the amniotes, as is demonstrated by the increase of digit imprint lengths (I–IV) in the tracks, and pes tracks that are oriented postero-laterally. The morphology of the trackways indicate that the producer was a pentadactyl, semiplantigrade and semipalmigrade to digitigrade, quadruped, with a sprawling gait and a long tail that touched the ground during locomotion. The trackway evidence also indicates that the producer could attain high speeds over short distances using a bipedal gait. The gleno-acetabular distance (GAD), calculated using the formula GAD = LS / 2 + DMP (Leonardi, 1987; LS = length of stride, DMP = distance between manus and pes), is 2.8 cm. The total length of the body, is generally estimated to be twice the gleno-acetabular distance (McKeever, 1994), giving a value of 5.6 cm, although it may have been slightly longer considering the difficulty of locomotion in a plastic sediment. According to Irschick and Jayne (1999), high speed locomotion using a bipedal gait is frequent in living lizards, particularly in those species that have a long tail, granting an equilibrium point near the pelvic girdle, although the tail generally remains raised during locomotion, thus avoiding interference with the posterior locomotory appendages. In contrast, the trackway evidence indicates that the producer of *Rhynchosauroides retroversipes* isp. nov. evidently dragged the tail over the ground when using a bipedal gait and was therefore less adapted to this kind of locomotion. These characteristics indicate that *R. retroversipes* isp. nov. can be attributed to a lacertoid reptile. The producer of *Rhynchosauroides* isp. was larger than that of *R. retroversipes* isp. nov., but was also likely to be a lacertoid reptile with a quadrupedal sprawling gait, and pentadactyl, semiplantigrade and semipalmigrade to digitigrade autopodia. The ichnogenus *Rhynchosauroides* is traditionally attributed to the Rhynchocephalia (e.g. Peabody, 1948), although some authors consider that Prolacertiformes were more likely producers (Avanzini and Renesto, 2002). The only

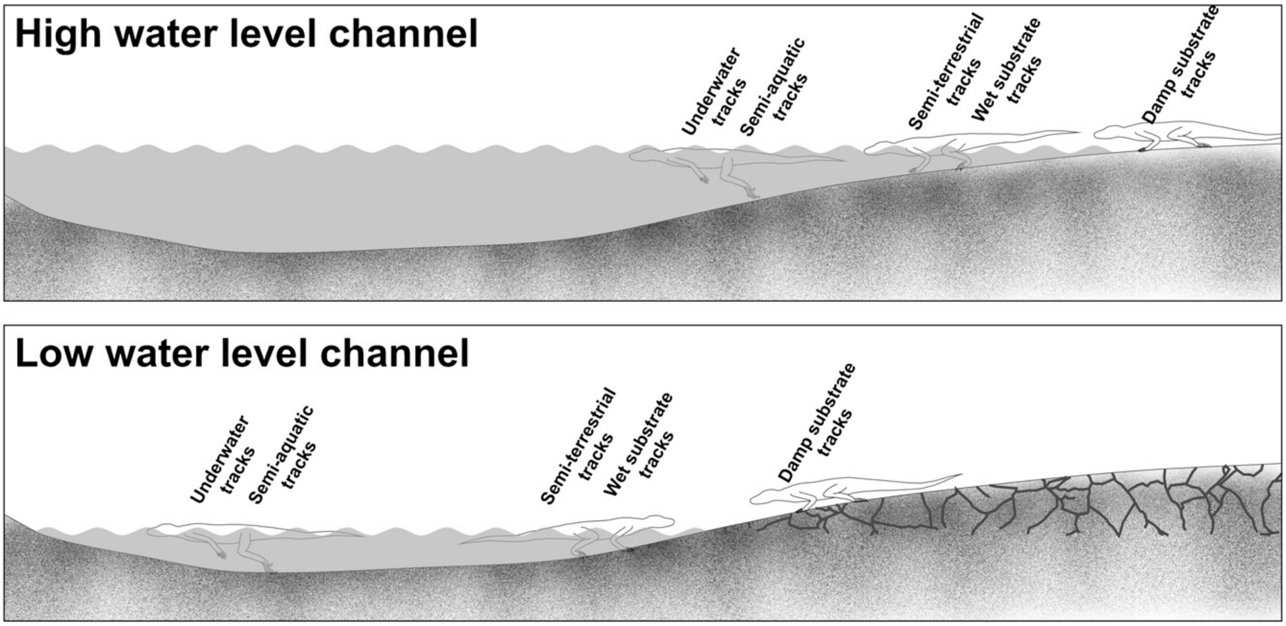

Fig. 12. Influence of water depth on the production of tracks in the Santa Maria Formation.

animals known from the Late Triassic of Brazil that would be able to produce tracks such as these are the Sphenodontia (Rhynchocephalia) (Ferigolo, 2000; Bonaparte and Sues, 2006).

Other notable characteristics in *Rhynchosauroides retroversipes* isp. nov. are the very long, slender and curved digit imprints that end in curved claw imprints, thus indicating that the autopodia were not well-adapted for efficient quadrupedal walking on the ground, which is evident from the low values of pace and stride (McKeever, 1994; Irschick and Jayne, 1999; Spezzano Jr. and Jayne, 2004). Such characteristics occur in some living, poorly-specialized, climbing lizards (Hildebrand, 1995; Higham, Davenport and Jayne, 2001; Higham and Jayne, 2004). A long tail is also characteristic of climbing animals and contributes to maintaining balance (Hildebrand, 1995). The producer of *R. retroversipes* isp. nov. may therefore have had a climbing habit. According to Hildebrand (1995) most climbing animals that do not possess adhesive or prehensile structures utilize strong and curved claws, similar to those inferred for the producer of *R. retroversipes* isp. nov., to grip the substrate. In plant stems or trunks of large diameter, this type of adaptation is more efficient than prehensile fingers. The reversion of the pes also represents an adaptation for maintaining a firm anchoring on vertical surfaces, such that the posterior claws can be pulled against the anterior claws (Hildebrand, 1995). A number of lines of evidence therefore indicate a climbing habit for the trackmaker, and these characteristics are unlikely to be present in an entirely terrestrial trackmaker. Reversion of the pes is known in several groups of mammals and lizards, and the inferred occurrence in the producer of *R. retroversipes* isp. nov. could constitute one of the oldest records of this kind of adaptation for a climbing habit.

It is more difficult to establish the producer of the swimming traces, although there is some evidence that they may have been the same as those that produced *Rhynchosauroides retroversipes* isp. nov. and *Rhynchosauroides* isp. The measurements of the swimming traces are consistent with those of the tracks produced by traction. Samples MCN-PIC.009 and MCN-PIC.010 also preserve a combination of swimming traces and tracks produced by traction, the latter corresponding to the manus (MCN.PIC.009/1,4) and pes (MCN-PIC.009/2; MCN-PIC.010/1) of *R. retroversipes* isp. nov. Swimming traces MCN-PIC.008/2 and MCN-PIC.015/9 also show lateral drag marks that are longer than the medial ones, indicating an increase in the length of the digits as found in lacertoid reptiles.

The succession consisting of the Alemoa Member (Santa Maria Formation) and Caturrita Formation can be divided into three temporal successive assemblages through time: the Cenozone of Therapsida, the Cenozone of Rhynchosauria, and the *Jachaleria* Level (Schultz et al., 2000). The Predebon outcrop occurs in the Cenozone of Rhynchosauria, where rhynchosaurs occur in large proportion, along with cynodonts and dinosaurs. Sphenodonts are not present in the Santa Maria Formation, although they do occur in the overlying Caturrita Formation (Ferigolo, 2000). Some recorded specimens coincide approximately in size with the estimates for *Rhynchosauroides* isp. Considering the Alemoa–Caturrita sequence to be concordant and continuous, then the difference in age would be relatively small, possibly within the limits of the Carnian (Schultz et al., 2000), and therefore attribution of the trackways from the Predebon outcrop to sphenodonts is not problematic.

6. Conclusions

1) Trackways from the Santa Maria Formation can be identified as *Rhynchosauroides retroversipes* isp. nov., *Rhynchosauroides* isp., *Rhynchosauroides?* isp. and drag marks interpreted as swimming traces of reptiles with lacertoid affinity;
2) The preservation of the tracks was influenced by the presence and depth of a water sheet during their production and by the subsequent subaerial exposure. The tracks produced in wet or damp substrates were the best-preserved;
3) The trackmaker of *Rhynchosauroides retroversipes* isp. nov. corresponds to quadrupedal lacertoid reptile with primitive autopodia, a sprawling gait, long tail, and a postero-laterally oriented pes. It most likely correspond to a climbing animal, with indications of adaptations for climbing that include curved claws and reversion of the pes. On the ground this animal would have a rather inefficient locomotion, although it could attain higher speeds over short distances using a bipedal gait;
4) All of the documented trackways, including *Rhynchosauroides retroversipes* isp. nov., *Rhynchosauroides* isp., *Rhynchosauroides?* isp. and swimming traces, can be attributed to lacertoid reptiles, possibly sphenodonts, whose skeletons are found in the Caturrita Formation, which overlies the Santa Maria Formation.

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